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 S
ECHINODERMATA 1

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TREATISE ON INVERTEBRATE PALEONTOLOGY

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Part S. Echinodermata 1 (Echinodermata General Features, Homalozoa, Crinozoa, exclusive of Crinoidea), xxx+650 p., 2868 fig., 1967.

VOLUMES IN PREPARATION (1967)

Part A. Introduction.
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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.

A generous grant of $35,000 has been made by the Geological Society of America for the purpose of preparing *Treatise* illustrations. Administration of expenditures has been in charge of the Editor and most of the work by photographers and artists has been done under his direction at the University of Kansas, but sizable parts of this program have also been carried forward in Washington and London.

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. An additional grant (No. GB 4544) of $102,000 was made by the National Science Foundation in January, 1966, for the two-year period 1966-67. 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 with 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.).*

Additional to the groups differentiated above, the *Code* (Art. 17) specifies that a zoological name is not prevented from availability a) by becoming a junior synonym, for under various conditions this may be re-employed, b) for a species-group name by finding that original description of the taxon relates to more than a single taxonomic entity or to parts of animals belonging to two or more such entities, c) for species-group names by determining that it first was combined with an invalid or unavailable genus-group name, d) by being based only on part of an animal, sex of a species, ontogenetic stage, or one form of a polymorphic species, e) by being originally proposed for an organism not considered to be an animal but now so regarded, f) by incorrect original spelling which is correctable under the *Code*, g) by anonymous publication before 1951, h) by conditional proposal before 1961, i) by designation as a variety or form before 1961, j) by concluding that a name is inappropriate (Art. 18), or k) for a specific name by observing that it is tautonymous (Art. 18).

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 names, *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.

Subclass ENDOCERATOIDEA Teichert, 1933

[*nom. transl.* Teichert, 1964 (*ex* superorder Endoceratoidea Shimanskiy & Zhuravleva, 1961, *nom. transl. ex* order Endoceroidea Teichert, 1933)]

Order ENDOCERIDA Teichert, 1933

[*nom. correct.* TEICHERT, 1964 (*pro* order Endoceroidea TEICHERT, 1933)]

Suborder ENDOCERINA Teichert, 1933

[*nom. correct.* TEICHERT, 1964 (*pro* suborder Endoceracea SCHINDEWOLF, 1935, *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 or 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 the type species of a genus or subgenus in an original publication is stipulated by the *Code* (Art. 68) in order of precedence as 1) *original designation* (in the *Treatise* indicated as OD) when the type species is explicitly stated or (before 1931) indicated by "n. gen., n. sp." (or its equivalent) applied to a single species included in a new genus, 2) defined by use of *typus* or *typicus* for one of the species included in a new genus (adequately indicated in the *Treatise* by the specific name), 3) established by *monotypy* if a new genus or subgenus includes only one originally included species which is neither OD nor TYP (in the *Treatise* indicated as M), and 4) fixed by *tautonymy* if the genus-group name is identical to an included species name not indicated as type belonging to one of the three preceding categories (indicated in the *Treatise* as T).

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 two or more species as belonging to the genus but did not designate a type species, then a later "SD" designation is necessary. Examples of the use of "SD" 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 DE LAUBENFELS, *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.

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 two or more synonyms of differing date are recognized, these are arranged in chronological order. Objective synonyms are indicated by accompanying designation "(obj.)," others being understood to constitute subjective synonyms. 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)
Abt., Abteilung(en)
adj., adjective
aff., *affinis* (related to)
Afr., Africa(an)
Ala., Alabama
Alg., Algeria
Alta., Alberta
Am., America(n)
Ann., Anñaes, Annales, Annual
ant., anterior
approx., approximately
Arenig., Arenigian
Ariz., Arizona
Ark, Arkansas
art., article
Ashgill., Ashgillian
auctt., *auctorum* (of authors)

B.C., British Columbia
Bd., Band
Beil., Beilage
Belg., Belgium, Belgique
Blackriv., Blackriveran
Boh., Bohemia
Brit., Britain, British
Bull., Bulletin

Calif., California
Cam., Cambrian
Can., Canada
Caradoc., Caradocian
Carb., Carboniferous
cf., *confer* (compare)
chapt., chapter
Chazy., Chazyan
Chester., Chesterian
Cincinnati., Cincinnatian
cm., centimeter
Co., County
Coll., Collections
Cong., Congress
Contrib., Contribution(s)
Czech., Czechoslovakia

dec., decade
Dev., Devonian
diagram., diagrammatic
diam., diameter
Dol., Dolomite

E., East
ed., editor
edit., edition
e.g., *exempli gratia* (for example)
emend., *emendatus(-a)*
Eng., England
enl., enlarged
Est., Estonia
etc., *et cetera* (and others, objects)
Eu., Europe
ext., exterior

F., Formation
fig., figure(s)
Förhandl., Förhandlingar
Fr., France, French, Français(e)

gen., genus
gen. hypoth., genus hypothetical
Geol., Geology, Geological, Geologische, etc.
Ger., Germany, German
Gotl., Gotland
Gr., Group, Great

Handl., Handlingar
hypoth., hypothetical

I., Isle(s)
ICZN, International Commission of Zoological Nomenclature
Ill., Illinois
illus., illustrations
incl., including, inclined
Ind., Indiana
indet., indetermined
int., interior
Internatl., International
Ire., Ireland
Is., Island(s)

Jaarb., Jaarboek
Jaarg., Jaargang
Jahrb., Jahrbuch
Jahresv., Jahresversammlung
Jahrg., Jahrgang
Jour., Journal

Ky., Kentucky

L., **Low.**, Lower
lat., lateral
Lief., Lieferung(en)
loc., locality
long., longitudinal
low., lower
Ls., Limestone

M., **Mid.**, Middle
M, monotypy

Md., Maryland
Medd., Meddelanden, Meddelelser
Mem., Memoir(s), Memoria, Memorie
Mém., Mémoire(s)
Meramec., Meramecian
Mex., Mexico
Mich., Michigan
Minn., Minnesota
Miss., Mississippi, Mississippian
mm., millimeter(s)
Mo., Missouri
mod., modified
Mon., Monograph, Monographia
Monatsber., Monatsberichte
Monatsh., Monatshefte
Mont., Montana

n, new
N., North
N.Am., North America(n)
Nev., Nevada
N.Mex., New Mexico
no., number
nom. conserv., *nomen conservatum* (conserved name)
nom. correct., *nomen correctum* (corrected or intentionally altered name)
nom. dub., *nomen dubium* (doubtful 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)
NW., Northwest
N.Y., New York
N.Z., New Zealand

OD, original designation
Okla., Oklahoma
Ont., Ontario
Ord., Ordovician
Osag., Osagian

p., page(s)
Pa., Pennsylvania
Penn., Pennsylvanian
Perm., Permian
Philos., Philosophical
photogr., photographed
pl., plate(s), plural
Pol., Poland
Port., Portugal
post., posterior
Proc., Proceedings
Prof., Professional
Prog., Progress
pt., part(s)
publ., publication, published

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

Rec., Recent, Record(s)
reconstr., reconstructed (-ion)
Rept., Report
Richmond., Richmondian

S., South, Sea
S.Am., South America
Scand., Scandinavia
Sci., Science
Scot., Scotland
SD, subsequent designation
sec., section(s)
ser., series, serial, etc.
Sh., Shale
Sib., Siberia
Sil., Silurian
sing., singular
Sitzungsber., Sitzungsberichte
sp., species (spp., plural)
spec., special, specimen
s.s., *sensu stricto* (in the strict sense, narrowly defined)
suppl., supplement
syn., synonym

T, tautonymy
tang., tangential
Tenn., Tennessee
Tournais., Tournaisian
Trans., Transactions
transv., transverse
Tremadoc., Tremadocian
Trenton., Trentonian

U., Up., Upper
up., upper
USA, United States (America)
USSR, Union of Soviet Socialist Republics

v., volume(s)
Va., Virginia
Verhandl., Verhandlung(en)
vert., vertical
viz., *videlicet,* namely

W., West
W.Va., West Virginia
Wis., Wisconsin

Yorks., Yorkshire

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.).

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Academy of Natural Sciences of Philadelphia, Journals; Proceedings.
Academy of Science of St. Louis, Bulletins; Memoirs; Transactions.
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Akademie der Wissenschaft zu München, mathematische-physikalische Klass, Denkschriften; Sitzungsberichte.
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[K.] Akademie der Wissenschaften zu Wien, mathematische-naturwissenschaftliche Klasse, Denkschriften; Sitzungsberichte.
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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
Namurian Stage	**Tennesseean Series (Upper Mississippian)**
	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)
	Richmondian Stage
Ashgill Series	Maysvillian Stage
	Edenian Stage
Caradoc Series	**Champlainian Series (Middle Ordovician)**
	Mohawkian Stage
	Trentonian Substage
	Blackriveran Substage
Llandeilo Series	Chazyan Stage
Llanvirn Series	
Arenig Series	**Canadian Series (Lower Ordovician)**
Tremadoc Series[9]	
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 S

ECHINODERMATA 1

GENERAL CHARACTERS

HOMALOZOA—CRINOZOA (EXCEPT CRINOIDEA)

By H. H. BEAVER, K. E. CASTER, J. W. DURHAM, R. O. FAY, H. B. FELL,
R. V. KESLING, D. B. MACURDA, JR., R. C. MOORE, GEORGES UBAGHS, and
†JOHANNES WANNER

VOLUME 1

CONTENTS

[Volume 1, p. i-xxx, 1-296; Volume 2, p. 297-650]

INTRODUCTION

By RAYMOND C. MOORE

The unit of the *Treatise* designated as Part S (Echinodermata 1) has been very long in preparation, for initial agreements of contributing authors selected to produce some of the sections date back to the late 1940's. By 1952 typescript and illustrations (or directions for making them) had been completed by at least one author, Professor JOHANNES WANNER, whose death occurred in July, 1956. Others who promised to care for important sections found that they could not produce them and thus after several years new assignments had to be arranged. *Treatise* authors receive no financial compensation for their work and consequently only such persuasion as I can muster eventually leads to desired accomplishments.

We are especially indebted to collaborators who completed work on tasks accepted at relatively late dates: 1) GEORGES UBAGHS in 1959 for a chapter on general characters of Echinodermata (completed March, 1961, revised 1962, 1963, 1964, 1965); 2) K. E. CASTER in 1959 for "carpoid" classes (Homoiostelea completed December, 1966); 3) H. B. FELL in 1960 for chapter on echinoderm ontogeny (completed October, 1961, revised 1962); 4) R. O. FAY and H. H. BEAVER in 1960 for morphology and systematic descriptions of blastoids (nearly completed July, 1961, revised 1962, 1963, 1964, 1965); 5) R. V. KESLING in 1962 for chapters on cystoids and paracrinoids (completed December, 1962, and January, 1963); 6) GEORGES UBAGHS in 1963-64 for chapters on Homostelea, Stylophora, and Eocrinoidea (completed July, November, December, 1965); and 7) D. B. MACURDA, JR., in 1966 for discussion of the development and hydrodynamics of blastoids (completed February, 1966).

It is appropriate to draw attention to the very large amount of basic research which is demanded from authors of *Treatise* volumes, for work by them is far from merely compilative in nature. Of course, the vast sum of information recorded in zoological and paleontological literature needs to be surveyed, digested, and organized, but additional to this are challenges to conduct important new studies. What are the most significant morphological features of each discriminated animal group and how do these bear on improvements in taxonomy? Do advancements in techniques of fossil preparation and discoveries based on new materials or critical new investigations of old contribute to better understanding of relationships that bear on classification and interpretation of phylogeny and evolution? Readers of chapters published in *Treatise* Part S assuredly will find that the various authors have responded to such challenges.

In many ways the echinoderms included in Part S are "difficult" groups in that all are extinct, some having vanished from the earth not less than 500 million years ago and the latest near the end of Permian time, approximately 200 million years before the present. None are closely related to surviving echinoderms. Accordingly, we should not be surprised to find that paleontologists have differed in interpreting and classifying them. Described genera have been shifted back and forth among different recognized classes and orders. They include some forms now considered to be crinoids and cyclocystoids.

Treatise Part S distinguishes many more taxa of homalozoans and crinozoans (exclusive of crinoids) than have been recognized previously. This is indicated by the following tabulation of genera and families in echinoderm groups equivalent to the 11 classes (not including crinoids) given in the present volumes.

Genera and Families Recognized in Treatise Part S Compared to Those in Some Earlier Publications

Source	Genera	Families
Zittel, 1896	63	15
Bather, 1900	94	27
Jaekel, 1918	99	36
Springer, 1913	109	23
Cuénot and Bergounioux, 1953	139	38
Bassler & Moodey, 1943	159	35
Gekker, 1964 (1965)[1]	106	34
Treatise Part S, 1967	273	71

[1] Incomplete listing because consideration mostly confined to Soviet Union.

Data of this sort are inadequate as a measure of expanding knowledge but they reflect it partly.

In my opinion, the most valuable contribution of *Echinodermata 1* is its survey of general characters and ontogeny observed in the phylum and delineations of morphological attributes of the crinozoan and homalozoan classes treated.

The introductory chapters by UBAGHS and FELL serve excellently for cross-tying the divergent outlooks of neozoologists and paleozoologists in studies of echinoderms, providing readily comprehensible information that each of these groups should have. It may be noted that UBAGHS (p. *S*8, Fig. 2,5,6) rejects interpretation of echinoids advanced by MOORE and FELL (*Treatise* p. *U*120-125, Fig. 100, 106). The disagreement is allowed to stand.

I commend to all readers the exceptional body of new information, including new illustrations, contained in the chapters on cystoids, blastoids, eocrinoids, and "carpoid" classes. The many kinds of advancement in knowledge speak for themselves. Although short and added at last moments, interesting new classes named Lepidocystoidea and Camptostromoidea are contributed by DURHAM. In overall view, the fossils considered in Part S demonstrate the present incompleteness in comprehension of early echinoderms and they emphasize both the need and the opportunities of future investigations in this field.

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GENERAL CHARACTERS OF ECHINODERMATA

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[Université de Liège, Belgium] [I am much indebted to RAYMOND C. MOORE for translating my manuscript and for valuable criticism. Also I acknowledge helpful suggestions received from H. BARRACLOUGH FELL and J. WYATT DURHAM, together with the loan of some unpublished manuscripts prepared by them. My sincerest thanks are expressed for this assistance.]

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INTRODUCTION

The echinoderms comprise one of the most important and best-characterized of all invertebrate phyla. They are marine, benthonic (or exceptionally pelagic) Metazoa, living in an attached position or free, but never colonial. Also, they may be defined as enterocoelic, nonsegmented coelomates, without differentiated head or brain, bilaterally symmetrical fundamentally, but modified by asymmetry introduced by atrophy of some organs of the right anterior side of the body and corresponding overdevelopment of organs of the left side. Three characters serve to distinguish them easily: (1) radial symmetry (typically pentamerous), secondarily imposed on larval asymmetry; (2) an endoskeleton formed of plates or distinct ossicles, composed of crystalline calcite deposited in an organic mesenchymatous network displaying a reticulate microstructure and distinctive crystallographic properties; (3) a water-vascular system of sacs and canals of coelomic nature opening outward in a pore and giving rise to numerous small projections on the surface of the body. Finally, they lack any sort of differentiated excretory apparatus.

Several of the characters just enumerated are not constant or, at least, invariably observable. Thus, the presence of a water-vascular system, though probable, has not been recognized certainly among all fossil echinoderms. The endoskeleton may be much reduced or even completely absent among some rare holothuroids. Radial symmetry does not affect the endoskeleton of certain archaic forms (?machaeridians, "carpoids"), or it may be that this radial symmetry is lost or obscured by secondary developments of adaptive character which have affected the organism; one may recognize examples of this in most classes. Despite these variations, the definition above given suffices to constitute a diagnosis for the phylum.

Echinoderms have a structure very unlike that of other zoological groups. Nevertheless, they are by no means an isolated assemblage in the animal kingdom. The **tornaria** larva of Enteropneusta so strikingly resembles the auricularia stage of starfishes and of holothurians that MÜLLER (1850) accepted it as a larval echinoderm. Various workers have suggested that echinoderms are related to the Stomochorda and in lesser degree to the Pogonophora and Chordata. Most modern classifications express such relationships. However, metamorphoses that echinoderms undergo in the course of their ontogenetic development, as well as their general organization, prove that they stand considerably apart from any other phylum. The existence from earliest Cambrian time of types that appear to possess all essential attributes of the group and to represent at least three different classes indicate strongly that their origin belongs to the extremely remote past. One cannot doubt that the echinoderms comprise one of the most ancient and best-individualized invertebrate phyla.

The echinoderms are also one of the most highly diversified phyla, since they include five classes of present-day groups (Crinoidea, Holothuroidea, Echinoidea, Asteroidea, and Ophiuroidea—the last two often combined with Somasteroidea, as a single class, Stelleroidea — and other extinct classes (according to chosen mode of classification), which are restricted to Paleozoic rocks (?Machaeridia, Homostelea, Stylophora, Homoiostelea, Eocrinoidea, Paracrinoidea, Cystoidea, Parablastoidea, Blastoidea, Edrioblastoidea, Edrioasteroidea, Cyclocystoidea, Helicoplacoidea, Ophiocistioidea, Lepidocystoidea, and Camptostromatoidea). All these forms are so different in appearance that, as Bather has remarked, no commonly used vernacular name is available to indicate them collectively. The term Echinodermata, introduced by J. T. Klein in 1734 for application to the test of sea urchins, is a scientific word constructed from two Greek words, *echinos,* hedgehog or urchin, and *derma,* integument or skin; this name is based on the spiny nature of the covering of many of these animals. It was not until 1789, however, that Bruguière established the order of the *"Vers èchinodermes"* for the two genera *Echinus* and *Asterias* recognized by Linné, still placing the third genus recognized by Linné, *Holothuria,* under *"Vers mollusques."*[1]

The existence of a generally well-developed calcareous endoskeleton explains the richness of echinoderm remains in all geological systems from the Ordovician onward. Indeed, certain rock formations are largely composed of their remains. Besides this, the close relationship of the echinoderm endoskeleton, which faithfully forms a framework for the body, with other systems of organs provides very special interest for studies of the paleontological records concerning this phylum. Reconstruction of the endoskeleton of a fossil echinoderm commonly serves to give reliable indication of its original form and by appropriate analyses permits recognition in certain measure of its mode of life and biologic relationships.

In the natural world of today, echinoderms are numerous and varied. Exclusively marine and usually stenohaline, they are unknown as primary fossils in fresh-water deposits. Some species occur in such large numbers that they are among the most characteristic organisms of diverse animal populations. Echinoderms are found in all seas, in all latitudes, on all types of sea bottoms, and at all depths from the littoral zone to oceanic abysses. Oceanic expeditions have collected representatives of the phylum, chiefly Holothuroidea, at depths ranging to more than 10,000 meters (Philippines Trench). Almost exclusively, the echinoderms belong to the vagile or sessile benthos; only a few forms—both living and fossil—have become pelagic or pseudoplanktonic. Finally, they enjoy generally an important role in the economy of the ocean, both as consumers of great quantities of other animals and organic detritus and in themselves serving as food sources of various animals, including man.

Inasmuch as outstanding comprehensive reviews of our knowledge of echinoderms have been given recently by Cuénot (1948) and Hyman (1955), the present chapter is confined to subjects that are judged to be particularly significant for understanding of the paleontology of echinoderms.

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[1] The echinoderms have received many names. The following list, without pretending to be complete, probably contains the main ones: Centroniae Pallas, 1766; Vers échinodermes Bruguière, 1789; Radiaires échinodermes Lamarck, 1801; Cératodermaires de Blainville, 1822; Echinoderma Latreille, 1825; Echinodermata Fleming, 1828; Cyclozoa echinoderma *(partim)* Eichwald, 1829; Echinodermaires de Blainville, 1830; Cirrhodermaires de Blainville, 1833; Enteractinozoa Bronn, 1860; Annuloida *(partim)* Huxley, 1869.

MORPHOLOGY

SIZE, SHAPE, LIFE POSTURE, AND MAIN DIVISIONS OF BODY

The echinoderms are animals of small to large size, but never microscopic. The smallest and the largest of their representatives belong probably to the crinoids: fossil species of crinoids are reported to have possessed stalks longer than 20 meters, whereas others had their visceral mass enclosed in a tiny cup of a few millimeters in diameter.

The body of echinoderms may show a great diversity of shapes. It is spheroidal, discoid, ovoid, or cordiform in echinoids; it is flattened, pentagonal, or more generally star-shaped in stelleroids, with a central disc which either passes progressively into five projections called arms or rays (Asteroidea) or is sharply set off from long, slender flexible arms, simple or branched (Ophiuroidea); it is cucumber-shaped or vermiform and generally capable of considerable changes of shape in holothuroids; it is usually prolonged by a peduncle or stem, and provided with more or less branched arms in crinoids; it resembles a flower bud in blastoids; it is ovoid or spheroidal in most cystoids, discoid in edrioasteroids; it is depressed in "carpoids," with simple contour or, on the contrary, strange, complicated, and very asymmetrical outlines.

Crinoids and most extinct classes are typically attached directly or by a stalk with the face carrying the mouth, termed **oral face**, directed upward and the opposite or **aboral face** turned downward. "Carpoids" were free; most of them rested horizontally on the substratum, with probably their food-catching apparatus and anal opening directed upward. Holothuroids generally lie upon one side that consists of a flattened creeping surface; their mouth is at one end of the body and the anus at the other. Asteroids, ophiuroids, and echinoids move about on their oral surface, which is strongly differentiated from the aboral surface.

Typically, the body of echinoderms is divided into five rays, arms, grooves, or zones that diverge radially or meridionally from the mouth and carry rows of **tentacles** or podia (sing., podion, from Greek, signifying foot) belonging to the water-vascular apparatus. Since the series of podia or **tube feet** are ordinarily arranged like trees along an avenue, sectors of the body bearing these organs have been named **ambulacra** (Latin, sing., **ambulacrum,** signifying promenade bordered by trees). The mid-line of each ambulacrum is termed **radius** (pl., **radii**); it corresponds to the trace of a plane passing through the oral-aboral axis of the body and dividing the ambulacra into two equal parts. Each structure **(ray)** bisected by this plane is indicated as **radial,** or more exactly as **perradial.** In similar manner, the five sectors **(interrays)** comprised between the five ambulacra are termed **interambulacra** and their mid-lines are designated as **interradii**; organs and structures located between two adjacent radii are **interradial.** In all regularly pentamerous echinoderms, an interradius invariably lies opposite to a radius.

SYMMETRY

The subject of symmetry among echinoderms involves much complexity, and study of it calls for consideration of development of this charatcer in the course of ontogeny. The early larval stage of the classes Asteroidea, Ophiuroidea, Echinoidea, and Holothuroidea outwardly exhibits a bilateral symmetry that may be considered fundamental and primitive—that is to say, derived from the common hypothetical ancestor of the phylum. However this symmetry is by no means perfect, for unequal development of the right and left coeloms gives a structural asymmetry to the larva from its beginning, defining one of the dominant traits in morphology of the echinoderms. But this asymmetry, in spite of its early appearance and great morphological importance, is secondary. Reasons for this conclusion will be presented subsequently.

On this asymmetry of the larva, the pentamerously radial symmetry, so characteristic of the phylum, comes to be imposed. Genetically, the latter is therefore secondary. Moreover, it is neither perfect nor complete,

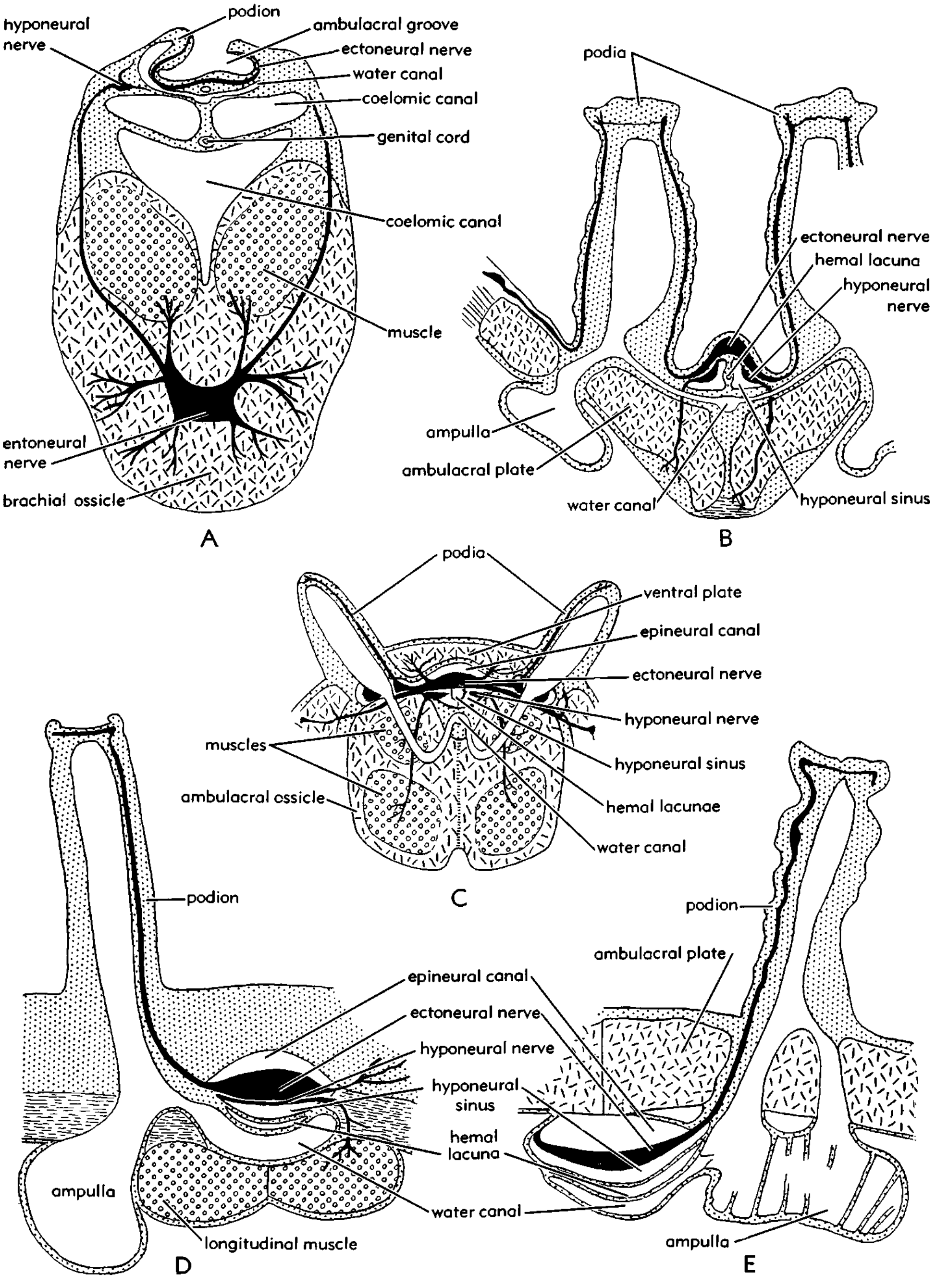

FIG. 1. Comparison of radial structures (sections of ambulacrum) in different echinoderm groups.——*A*. Crinoid.——*B*. Asteroid.——*C*. Ophiuroid.——*D*. Holothuroid.——*E*. Echinoid (Ubaghs, n).

since all echinoderms have organs or structures entirely escaping from any pentaradial arrangement. No trace of radial symmetry is ever found in the endoskeleton of archaic echinoderms such as the "carpoids." Variations of diverse sorts—mutations, atrophies, reduplications of radii—may disturb pentamerism and secondarily produce tetramerous, hexamerous or polymerous forms, as well as others that lack any discernible radial symmetry. Finally, not to be overlooked is the fact that in certain lines a radial symmetry of another order may have been acquired independently.

These alterations, however, do not hinder pentaradial symmetry from comprising one of the most striking traits in the structure of most echinoderms. In the adult, this symmetry is responsible for the remarkably uniform plan manifested in the general disposition of the food grooves, the ectoneural nervous system, the hyponeural coelomic system, the circulatory or hemal (blood) system, the water-vascular system, and the axial endoskeleton of the rays. The parallelism of these structures (Fig. 1), so extremely different in their nature and origin, comprises one of the very prominent features of echinoderm architecture.

Pentaradial symmetry, as we have said, is by no means perfect. It is disturbed by a more or less evident bilateral symmetry, which should be recognized at once as having no relationship to the fundamental bilaterality of the early larval stage. The larva, which undergoes metamorphoses or follows a more or less direct development to the adult stage, tends to acquire a new median plane which does not coincide with that identified previously. Therefore, the definitive bilateral symmetry of the organism is secondary in relation to that of the larva from which it was derived.

Comparison of different types of echinoderms reveals in addition that the bilaterality of adult individuals, when sharply defined, is of adaptive nature and that the plane of symmetry is not always the same in different groups. In certain classes several planes of symmetry may be distinguished, which are unrelated to others; many examples may be observed. We will see also that, within the limits of a single class, a same structure—for instance, the anal opening—may allow recognition of several distinct planes by its diverse positions. It is even true that the organs or parts of the body of certain echinoderms present differently oriented symmetries.

These remarks suffice to show that we may not attribute to bilaterality of echinoderms, such as appears in the adults, any far-reaching morphologic significance. In some respects, choice of a plane for orientation and comparison of classes in the phylum is arbitrary and does not postulate real homologies between the parts that receive the same orientation. For instance, the interambulacrum containing the anus or the **madreporite** (a skeletal perforated plate connecting the water-vascular system with the sea water) is not necessarily homologous throughout the phylum. Yet it is convenient to have some system of reference allowing comparison between the classes. The plane passing through the oral-aboral axis and the madreporite (or better the **hydropore** in very young echinoderms, i.e., the primary pore connecting the water-vascular system with sea water through the medium of the most anterior coelomic pouches on the left side) may furnish such a reference. This plane is designated as the **madreporite plane** or **M plane** of BATHER (Fig. 2,*2-6*). According to the nomenclature proposed by P. H. CARPENTER (1884) (Fig. 2,*1*), the ray opposite to the interray containing the hydropore is designated by the letter *A*, the other rays being then indicated by *B, C, D, E,* in clockwise direction when the animal is placed with its mouth upward. The interrays are designated by the letters of rays that bound them *(AB, BC, CD, DE, EA)*. The hydropore in the postlarval growth stages occurs in interray *CD*, as generally does also the madreporite in the adult.[1]

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[1] Other systems of nomenclature for rays and interrays have been proposed. Echinoid specialists commonly use a numeration proposed by LOVÉN (1874), based on the antero-posterior plane of irregular echinoids. Starting from the interambulcrum containing the anus and going in clockwise direction in oral view, they designate the ambulacra by roman numerals *I* to *V* and the interambulacra by arabic numerals *1* to *5* or by listing the adjoining ambulacra (Fig. 2,*6*). Thus the interambulacrum following ambulacrum I in clockwise direction is designated as *1* or *I-II*. Generally it is admitted that ambulacrum *I* in echinoids corresponds to ambulacrum *B* of CARPENTER's system, but FELL & MOORE (1965) correlate *I* with *D* for reasons which are given in Part U of the *Treatise*. The same symbols have been employed by JAEKEL (1895) and some other specialists for attached echinoderms, but taking as a reference the interambulacrum containing the hydropore and gonopore. As a consequence, ambulacrum *I* of JAEKEL's system becomes

ambulacrum *D* in CARPENTER's system. Finally, BATHER (1900) proposed directional terms that have been commonly adopted by workers on fossil crinoids and other attached forms. The organism is placed in its natural position with mouth upwards and is viewed from the anal side; the anal interambulacrum is called **posterior** and the opposite ambulacrum **anterior**; right and left corresponds with the right and left of the observer; the other rays (or interrays) are then termed **right anterior**, **right posterior**, **left anterior** and **left posterior**; compared with CARPENTER's system, anterior ray corresponds to *A* ray and posterior interray to *CD* interray.

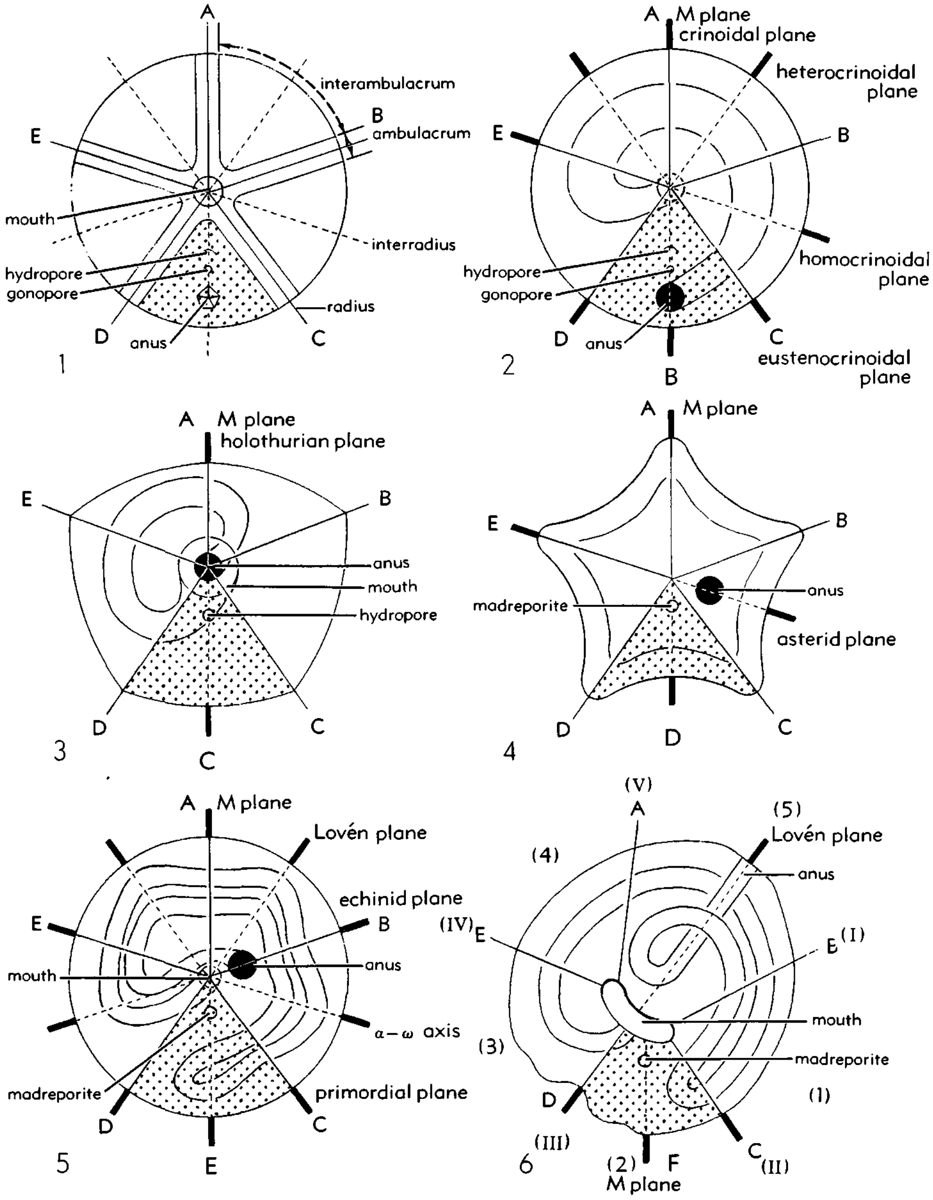

FIG. 2. Disposition of rays in relation to other structure in different echinoderm groups, all viewed from oral side (Ubaghs, n).——*1*. Orientation of generalized echinoderm according to nomenclature of rays proposed by P. H. CARPENTER. ——*2-6*. Various planes of symmetry observed in *(2)* crinoids and other attached radiate forms, *(3)* holothuroids, *(4)* asteroids, *(5)* regular echinoids, and *(6)* irregular echinoids (with LOVÉN's numerical designations in parentheses). [Explanation: Dotted area shows interambulacrum containing hydropore or madreporite.]

Among most crinoids and many other attached echinoderms a prominent plane of bilateral symmetry is typically determined by the mouth, anus, hydropore (if present) and the apical pole. This is the plane, called **crinoidal plane** (Cuénot, 1948) (Fig. 2,*2*), which in modern crinoids contains the first pore for passage of water and the first embryonic indication of the gonad. It is also in this plane, or immediately adjacent to it that among many cystoids, edrioasteroids, and archaic crinoids, one or two supplementary pores open; these are respectively interpreted as hydropore or gonopore, or a combination of both. The crinoidal plane thus coincides with the madreporite plane as defined above.

Other more or less evident planes of bilateral symmetry may exist among attached echinoderms. Thus the crown of some disparid crinoids tends to become more or less symmetrical in relation to a plane passing through the *E* ray and *BC* interray **(homocrinoidal plane)** or through the *D* ray and *AB* interray **(heterocrinoidal plane)** or through *C* ray and *AE* interray **(eustenocrinoidal plane)** (Fig. 2,*2*). The mouth of certain comasteroid crinoids is displaced toward the *AB* interray, accompanied by modification of the opposite *D* ray. Among cystoids and eocrinoids, the anus may be shifted so as to open in an interray (*AB* or *BC*) other than that characterized by the occurrence of a hydropore; this then determines an anal plane distinct from that of the crinoidal plane. Finally, the basal circlet of the theca commonly presents a local bilateral symmetry in which the plane may not coincide with the bilaterality of the remainder of the body.

In holothuroids, the body, elongated along the oral-aboral axis, is generally differentiated into a "ventral" flattened surface, on which the animal creeps, and an opposite arched "dorsal" surface (Fig. 2,*3*). The *A, B,* and *E* rays, forming the trivium, occupy the "ventral" surface; the *C* and *D* rays comprise the bivium on the "dorsal" surface. The median ambulacrum *(A)* of the trivium and the opposed mid-dorsal line clearly define a plane of symmetry known as the **holothurian plane** (Cuénot, 1891). This plane passes through the external orifice (gonopore) of the single genital gland, the "dorsal" mesentery in which the gonad is included and among forms retaining it in the adult stage, through the hydropore or madreporite. It is therefore considered as probably equivalent to the crinoidal plane and madreporite plane.

Several planes of bilateral symmetry have been recognized in echinoids. The madreporite plane seems generally to be identifiable by the eccentric position of the madreporite which mostly occurs in the *CD* interray (in irregular echinoids, it may migrate during early development into the *AB* interray, but this is of course a secondary feature). On the other hand, in most echinoids, the anus does not open exactly at the aboral pole; rather, it is found in the *B* ray or *AB* interray. These two positions permit determination of two anal planes. The first, known among some Regularia *(Salenia, Heterosalenia),* defines a **salenian plane** (Cuénot, 1948), also known as the **echinid plane** (Cuénot, 1891), passing through the *B* ray and *DE* interray so as to make an angle of 72 degrees with the madreporite plane (Fig. 2,*5*). The second determines the appearance of another anal plane oriented in the *D* ray and *AB* interray; the angle made by this plane with the madreporite plane is then 36 degrees. Cuénot (1891) has designated this as the **Lovén plane** (Fig. 2,*5,6*). It is recognized as having chief importance for orientation of echinoids. In particular, the bilateral symmetry so clearly manifested exteriorly and interiorly in numerous irregular echinoids (clypeasteroids, spatangoids) is developed in relation to this plane; their body tends to show differentiated functional anterior and posterior extremities and their ambulacra are divided into a trivium *(C, D, E)* and a bivium *(A, B),* which, according to adopted premises, are different from the trivium and bivium of holothuroids. As applied to sea urchins, the Lovén plane takes precedence over all others in its relation to organization of these echinoderms.

During ontogeny, however, in both regular and irregular echinoids, the newly metamorphosed urchin shows a bilateral arrangement of the plates of the apical system according to a plane corresponding neither with the madreporite plane nor the Lovén plane. Similarly, on the oral side, the skeletal and water-vascular systems appear more symmetrical with respect to this plane than to all others. Called **primordial plane** by von Übisch (1913), it makes an angle of 90° with the plane of symmetry of the larva and passes through the *C* ray and *EA* interray (Fig. 2,5). During further growth, all morphological trace of this symmetry is lost, except nearly always in the crystallographic orientation of the genital plates that encircle the aboral pole (Raup, 1965).

Lovén (1874) in discussing the morphology of echinoids has pointed out the existence of a distinctive axis (designated α-ω) passing through the *E* ray and *BC* interray (Fig. 2,5).

Among Asteroidea, the madreporite, located on the aboral side of the body in the adult, defines the *CD* interray, but the anus in all species possessing this vent opens more or less excentrically in the *BC* interray on the aboral side. One then may define an anal plane (**asterid plane** of Cuénot, 1891) which is distinct from the madreporite plane, making an angle of 72 degrees with it. But, as Asteroidea are almost perfectly radiate animals, these two planes have practically no morphological significance.

Among ophiuroids, one of the interradially situated plates (buccal or oral shield) covering the jaws acts as a madreporite, being pierced usually by a single pore. As this pore, however, cannot generally be recognized on the outer side, orientation is hardly determinable externally.

Finally, the presence in an interray of certain ophiocistioids of a madreporite or a pore interpreted as a hydropore and gonopore, or a combination of these two, allows orientation of these echinoderms according to the madreporite plane. An anal vent occurs in the same interray on the aboral side of at least one genus.

The preceding discussion leads to the following conclusions: 1) fundamental bilateral symmetry of the larva, disturbed by asymmetric development of the anterior right and left halves of the body, cannot be identified in adults; 2) pentamerously radial symmetry is secondary and superposed on the larval asymmetry; 3) bilaterality determined in young postmetamorphic individuals (and *a fortiori* in adults) by the hydropore, madreporite, anus, or any other structure is secondary with respect to fundamental larval symmetry; 4) the selection of any one plane as a plane of reference for orientation of all the classes is more or less arbitrary, and homologies based on such comparisons are judged as not being proven; 5) varied influences may produce bilateral symmetries of a third order, which in some species acquire a great importance and even may obscure other symmetries.

BODY WALL

The body wall of all echinoderms comprises three layers; an **external epithelium** or **epidermis,** a thick **median layer (conjunctive, muscular,** or **calcareous)** and an **internal epithelium (endothelium** or **peritoneum)** lining the coelomic cavities.

The external epithelium, generally covered by a very thin superficial cuticle, exhibits a rather variable organization with respect to its place of occurrence and the form considered. It may be relatively thick, formed of long, narrow, nearly threadlike cells, among which commonly neurosensory cells and glandular mucus cells are intermixed. On the other hand, it may be extremely thin, showing no definite cellular organization, and it may even disappear in adults of certain forms and in certain parts of the body. Locally, or over its entire surface, it may possess a covering of cilia producing vibratile currents capable of carrying particles toward the mouth or food grooves, or, on the other hand, toward the exterior; these currents play an important role in nutrition and in cleaning the test, as well as in respiration probably. At the base of the epithelium and more or less clearly differentiated from it, is a nervous stratum of variable thickness that forms part of the ectoneural nervous system. The external epithelium continues into the median layer, or more rarely it is found separated from it by a delicate basal membrane.

The median layer, as we have noted, consists of muscular tissues, conjunctive noncalcified **(mesenchyme)** tissues, and calcareous tissues.

(1) **Muscle fiber,** produced by differentiation of a single mesodermic cell, displays

the same characters in all classes. It is smooth, straight, or faintly wavy, sharply terminated at its extremities, and provided with a lateral nucleus. Striated muscle fibers have been distinguished among a certain number of echinoids. In the body wall, the musculature occurs under the dermis; it is well developed among holothuroids, which have a readily deformable body, but hardly perceptible among echinoids, enclosed by a rigid endoskeleton. Crinoids possess a special tissue designated as ligamentary, between the skeletal plates. It has a connective function and is shown to be formed of parallel hyaline nucleated fibers that intermingle at their two extremities with the organic network of skeletal ossicles; this tissue, probably elastic, seems to have some contractile ability.

(2) **Noncalcified mesenchyme** is composed of a fundamentally noncellular substance, amorphous or fibrillar, gelatinous or more or less firm, with disseminated, rounded or star-shaped connective cells and enclosing numerous nucleated fibers.

(3) **Calcareous tissue,** found in all echinoderms, except a few holothurians, is one of the most important features of the phylum. Its histologic constitution and crystallographic properties serve to establish the unity of the group and allow identification under the microscope of the smallest skeletal fragment.

Universally, where mesoderm exists in the body, but especially in the body wall itself, certain of its cells have the ability to secrete calcium carbonate. As a result, a skeleton is produced and this consequently is an endoskeleton. The endoskeleton, generally well developed, is composed of plates, ossicles, spicules, microscopic pieces, and integumentary appendages such as spines. It is to be understood that in life the external appendages, like the main skeleton, are clothed with epidermis and a thin layer of dermis, although this covering may rub off from prominently projecting parts.

The plates and ossicles of the main skeleton generally bear spines, knobs, granules or other projections. Particularly important are the spines to which the name of the phylum refers. Among the extant forms they occur in asteroids, ophiuroids, and echinoids, but they were also present in at least some species of most extinct groups. They are of various shapes and structures, and they have many functions, such as protection, locomotion, digging, burrow-building, production of currents, and brooding the young. Detailed descriptions will be found in chapters devoted to the different classes.

Worthy of special mention are the **pedicellariae,** which are tiny, grasping organs of various sorts, found only in starfishes and sea urchins. Typically they consist of two or several jaws, articulated proximally, and mounted on a movable stalk of varied length; the jaws and at least in part the stalk are supported by internal calcareous pieces. According to their types, they act as defense weapons or cleansing organs and they assist in capturing small prey.

Throughout its entire thickness the calcareous tissue consists of a spongy or reticulated mass. Exceptions to this fundamental rule include nonreticulate spicules, described from most extant classes, and the teeth of echinoids, formed by fusion of a series of nested cones. During life, all of the pores and small canals of the mineralized parts are filled up with mesodermic tissue. This is easily demonstrated by decalcifying a skeletal piece of a living echinoderm; the decalcification produces an organic residue pierced by holes that correspond to the calcareous elements removed by the acid. Thus the skeleton of echinoderms is composed of two interlocked networks, one composed of mineral substance **(stereom)** and the other of organic matter **(stroma).** While the stroma is continuous throughout the body wall, the stereom, comprising distinct skeletal pieces, is discontinuous.

The stroma may occupy as much as 60 percent of the volume of a particular skeletal element. It generally consists of an essentially amorphous material, less commonly fibrillar, with numerous interspersed mesodermic cells and in some instances black pigments and excreted granules. Permeable to nutritive fluids, it serves for nutrition of the calcareous network, repairing it when damaged and restoring it when a skeletal part has been lost. This intimate relation between stroma and stereom explains how the skeletal pieces enlarge during development of individuals and how the parts remain alive throughout the animal's

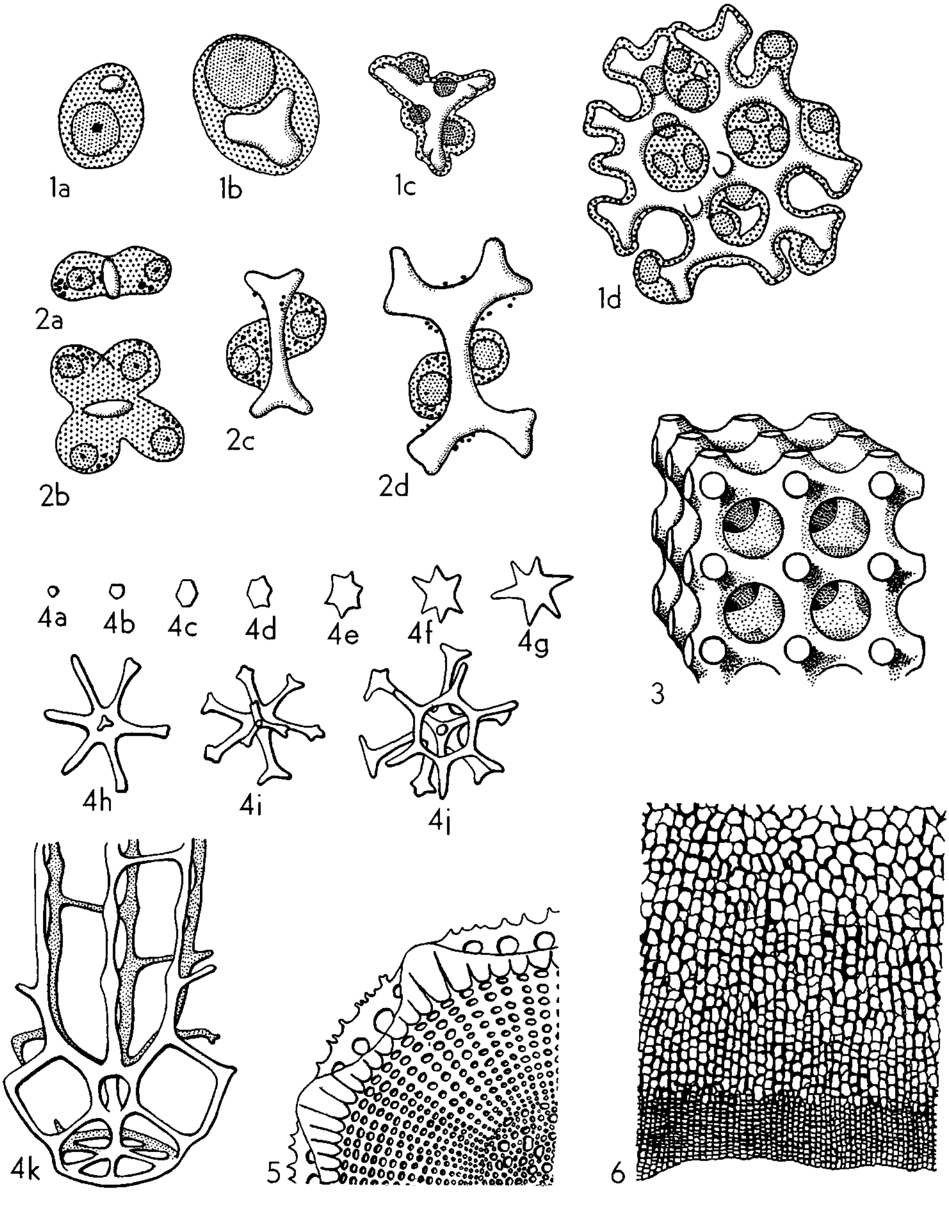

Fig. 3. Formation and biologic structure of echinoderm endoskeleton.——*1a-d.* Stages in development of plate of young ophiuroid, *Amphipholis squamata* (Chiaje); *1a,b,* ×1,280; *1c,d,* ×640 (Woodland).——*2a-d.* Stages in development of ossicles of *Cucumaria* sp. (holothuroid), ×750 (Woodland).——*3.* Regular stereom in cup plate of *Holopus rangi* d'Orbigny (crinoid), ×55 (P. H. Carpenter).——*4a-k.* Formation of typical echinoid spine, ×800 (Gordon).——*5.* Part of cross section of spine of *Stereocidaris japonica* (Döderlein) (echinoid), ×40 (Mortensen).——*6.* Closely set and less compact stereom in cidaroid spine, ×30 (Bather).

existence. Commonly they show growth lines which may demonstrate peripheral excretion of calcium carbonate without requiring, as wrongly supposed by some, an internal resorption. On the other hand, in some echinoderms, the lime-producing cells also have the power of resorbing and redepositing calcium carbonate so that the form and structure of the skeletal changes with growth of the animal. Finally, stereom and stroma are adapted to functions of particular skeletal elements; their network structure varies in different parts of an individual (Fig. 3,*5,6*), as well as from one species to another. These variations are related to the dimensions, form, and mode of grouping of meshes in the network. In addition, the existence of isostatic lines of stress may simulate conditions seen in the spongy bones of mammals.

The endoskeleton is secreted by lime-secreting cells of the mesenchyme (Fig. 3, *1a-d*). Each reticulate element is initiated by forming a calcareous granule on the inside of a single cell, the granule becoming transformed rapidly into a trifid spicule. This spicule enlarges and bifurcates at its extremities, while other lime-depositing cells join in making the secretion. The bifurcations fuse at their points of contact so as to form a fenestrated small plate. This increases along all of its periphery by the production and fusion of numerous branches, developed in all special directions. Thus, from repeated branchings and fusions is developed a three-dimensional network of more or less regular nature (Fig. 3,*3*) in which the meshes include calcite-producing cells joined in a syncytium.

In most holothuroids, the main endoskeleton consists of microscopic calcareous spicules scattered in the connective tissues, chiefly in the superficial layers of the dermis. A compact skeleton, with stereom and stroma, as in other echinoderms, is to be found only in a ring of plates encircling the pharynx, in the madreporite and in five small "teeth" occurring in some genera around the anus or within its rim. The spicules occur in a great variety of shapes (rods, crosses, plates, anchors, wheels) and are useful in identifying species. Generally an holothurian spicule begins as a minute rod between two or more secreting cells. The rod takes an X-shape by forking of its extremities, and repeated forkings and fusion of the branches result in production of a fenestrated plate, which subsequently is variously transformed into definite ossicles (Fig. 3,*2a-d*). The primordial rod of an anchor forks at one end only and the wheel-like spicules start as minute discs on which the spokes differentiate by notching of the margins. The lime-secreting cells that have produced a spicule then migrate and the spicule remains isolated in the soft tissues.

Spines are formed (Fig. 3,*4a-k*) somewhat differently from plates and spicules. In a typical echinoid spine, for instance, the primordial granule develops into a six-rayed star, the branches of which divide at their extremity, meet those of neighboring rays and thus form a complete ring that constitutes the base of the spine. A process grows vertically from the center of the star and gives rise to three branches which grow outward and upward, divide at their free end, and fuse to form a hexagonal ring more or less parallel to the base. From this ring vertical prongs are sent out which are joined by cross bars at more or less regular intervals and the whole structure elaborates to form the spine shaft. Spines in asteroids originate in about the same way.

The chemical composition of the endoskeleton of living echinoderms, as determined by studies of CLARKE & WHEELER (1922), is that of a limestone (71 to 95 percent calcium carbonate) having a moderate content of magnesium carbonate in ionic substitution. The proportion of magnesium carbonate (3 to 15 percent) seems mainly to be determined as a function of the temperature, individuals of warm seas being more magnesian than those of cold seas. Generally present, in addition, are small quantities of phosphate and calcium sulfate, salts of alumina, and iron, as well as traces of strontium, barium, copper, zinc, manganese, cobalt, nickel, cadmium, and some other elements.

Each unit part of the skeleton of every echinoderm comprises a single crystal of calcite. This rule seems to have only a few isolated exceptions and is supported by all optical evidence. However, X-ray data suggest that each skeletal element is actually a composite of tiny crystal units, which are nearly parallel in the *c* direction. In that case, the optical measurements would represent orientations of large crystal aggregates (Garrido & Blanco, 1947; Nissen, 1963; Raup, 1965).

In the living organism, the stereom does not show the characteristic cleavages of the calcite, because of its latticed structure and the presence, in the meshes of the calcareous network, of the organic stroma. But, after fossilization, the stroma generally is replaced by secondary calcite, which invariably is oriented crystallographically with the calcite of the skeleton and thus makes evident its cleavages. Fossilization does not modify the original orientation of the calcite unless the mineral was completely dissolved and reprecipitated.

The crystallography of echinoderm calcite has been mainly studied by Kirchner (1929) on crinoids, Schmidt (1925) and Panning (1933) on holothuroids, Merker (1916), Schultz (1935), and Raup (1959, 1960, 1962) on echinoids. The crystallographic orienttaion seems to be more varied than was formerly supposed. For instance in echinoids, recent studies by Raup have revealed that most species conform to one or two types, according to orientation of the *c* axes of the coronal plates, the *c* axes being either uniformly perpendicular to the plate surface or tangential to the plate surface and aligned longitudinally (aboro-adorally) on the test. Exceptions are found in some cidaroid genera in which ambulacral plates have perpendicular *c* axes and interambulacral plates have tangential *c* axes, whereas in other forms the orientation is modified as a function of growth of the individual, since it may pass, for instance, from perpendicular in the first-formed ambulacral plates (located near the oral pole in the adult) to tangential in the youngest ambulacral plates (near the aboral pole) within the limits of a single column of an adult individual. According to present knowledge, such *c*-axes orientation patterns are constant at the species and genus levels, mostly also at the family and even order levels.

Also, in the apical system of sea urchins, distribution of crystal orientations shows a strong bilateral symmetry, which nearly always is identical with the primordial plane of von Übisch (Lucas, 1953; Jesionek-Syzmanska, 1959; Raup, 1965).

The functional significance of these crystallographic data is not understood. It has been suggested that crystal orientation of the coronal plates of echinoids may be useful in building curved plates (Raup, 1962) or in controlling the amount of light that can pass through the test (Raup, 1959, 1962). In the echinoid apical system, the arrangement of *c* axes may serve the organism as a navigational aid (Raup, 1965).

The skeletal tissue of echinoderms often has been compared with the bones of vertebrates. Assuredly there are analogies between them, but only analogies, for the stereom of echinoderms differs from bone in three essential characters, (1) its typically calcareous, nonphosphatic chemical composition, (2) the intracellular, rather than extracellular, formation of spicules, and (3) its very characteristic crystalline properties.

NERVOUS SYSTEM

The five classes of living echinoderms show a common pattern in the gross morphology of their nervous system. This is somewhat artificially described as composed of three related systems, namely the **ectoneural, hyponeural,** and **entoneural** systems, located at different levels within the body; all three are affected by radiate symmetry.

ECTONEURAL SYSTEM

The **ectoneural** or **oral system** consists of a subepithelial nerve plexus, and five radial cords united around the esophagus by a nerve ring. The subepithelial, mainly sensory, nerve plexus lies just beneath the epidermis of almost the whole body. It may thicken locally, where special activity is required, as, for instance, at the tip of some tube feet or at the base of echinoid spines. Among crinoids (Fig. 1,*A*) and asteroids (Fig. 1,*B*) the five radial cords and the ring around the esophagus have a superficial place immediately under the epidermis and they are in direct continuity with the general subepithelial plexus. Among ophiuroids (Fig. 1,*C*), holothuroids (Fig. 1, *D*), and echinoids (Fig. 1,*E*), they underlie a tubular noncoelomic cavity **(epineural**

canal). As in crinoids and asteroids, the radial nerves of ophiuroids, holothuroids, and echinoids are still joined to the subepithelial plexus of the body wall by connecting branches. In all living representatives, the nerve ring around the esophagus gives off nerves into the digestive system and into buccal podia (ophiuroids) or tentacles (holothuroids) where such structures exist.

HYPONEURAL SYSTEM

The **hyponeural** or **deep oral system,** primarily motor in function, lies aborally to the preceding. It is found among all extant echinoderms except echinoids that lack a masticatory apparatus. In crinoids, it consists of a ring round the esophagus and two longitudinal nerves, lying laterally, in each arm (Fig. 1,*A*); these branches supply the musculature of the water vessels, pinnules, etc. In holothuroids (Fig. 1,*D*) each radial nerve cord is divided by a longitudinal partition into an outer (ectoneural) and an inner (hyponeural) part, the latter supplying muscle fibers of the body wall; there is no hyponeural nervous ring. Among asteroids (Fig. 1,*B*), the hyponeural system is represented by paired nerves **(Lange's nerves)** lying internal to the ectoneural radial cord, and by five interradial thickenings in the floor of the ring sinus that lies aboral to the main nerve ring; the Lange's nerves supply the lower transverse muscles between the ambulacral ossicles. Among ophiuroids (Fig. 1,*C*), a thin membrane separates an outer thick ectoneural and an inner thin hyponeural system in the nerve ring and in radial nerves; it is from the hyponeural system that the nerves to the muscles that extend between the ambulacral ossicles are given off. Finally, the hyponeural system is represented in echinoids having a masticatory apparatus by five centers radially located on the aboral surface of the main ring; these centers send nerves to the muscles activating the masticatory apparatus.

ENTONEURAL SYSTEM

The **entoneural** or **aboral system** is the main motor system in crinoids. It is joined to an apical ganglionic nervous mass surrounding a coelomic cavity divided into five chambers (chambered organ); this nervous mass presents the characters and functions of a nerve center; from it a nervous sheath proceeds into the axial canal of the stem and axial nerve cords are given off to the arms; these cords are connected with each other by ring commissures within the theca that envelopes the viscera. Except for holothuroids, an entoneural system exists also in the other classes, but it is not known whether this is exactly equivalent to that of the crinoids. Moreover, it is more or less continuous with the hyponeural nervous system.

The echinoderms possess few sharply defined sensory organs. However, they are known to be sensitive to touch, to light, to odors, to quality of the water, and to orientation. Tactile sensibility is furnished by the podia, radioles, pedicellaria (or microscopic claws of echinoids and asteroids) and by the integuments themselves, often rich in cells considered as touch or chemical receptors. Light-sensitive receptors exist in holothuroids, asteroids, and echinoids. Certain holothuroids have statocysts and the sphaeridia of echinoids possibly serve for orientation of these organisms.

DIGESTIVE SYSTEM

Mouth and anus of nonradiate echinoderms are located at or near opposite extremities of the body in Stylophora and Homoiostelea, but they are near each other at the same end in Homostelea.

In radiate echinoderms, the mouth invariably is found in the oral surface and generally at its center, at the point of convergence and ending of the ambulacra. It is secondarily displaced from the center along the *A* radius or toward the *AB* interray in certain crinoids and forward along the *D* radius in spatangoid echinoids. It opens directly to the exterior, but in numerous Paleozoic fixed echinoderms it may become secondarily internal by development of a tegumentary ceiling.

The anus has a much more variable position. It is never located at the aboral pole in fixed forms, but generally is found in the upper or adoral half in the *CD* interrays, typically located laterally in cystoids, blastoids, eocrinoids, and paracrinoids, and on the oral face in crinoids and edrioasteroids; among crinoids it may occur secondarily at the center of the oral face, whereas it migrates toward the *BC* interray or *AB* interray among a few cystoids and eocrinoids. It opens at or near the aboral pole in holothuroids and some regu-

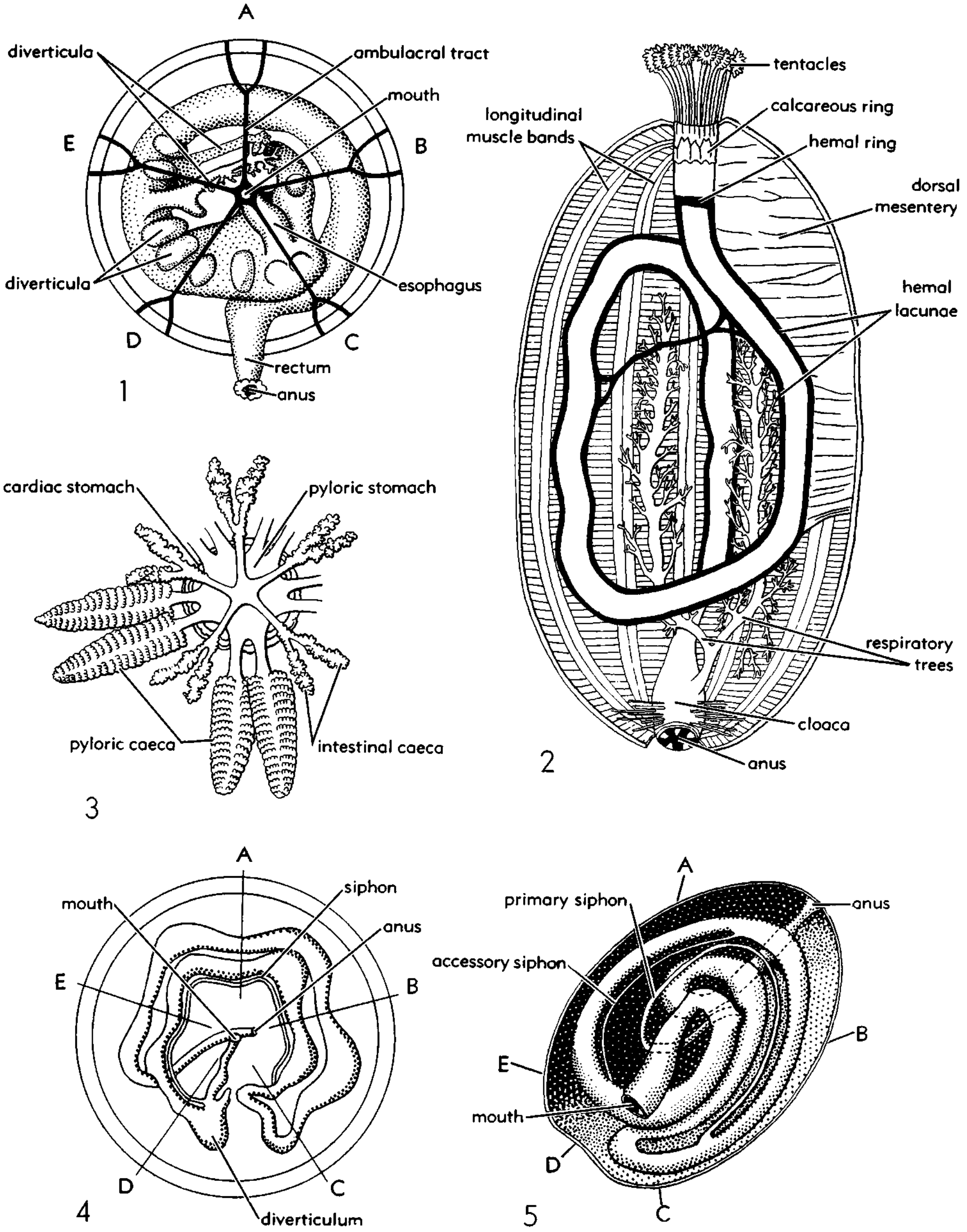

Fig. 4. Digestive systems of echinoderms.——*1.* Crinoid *(Antedon),* showing many diverticula (Chadwick).——*2.* Holothuroid, with respiratory trees and hemal system (main lacunae, solid black) (Ludwig).——*3.* Asteroid *(Culcita)* (Hamann & Ludwig).——*4.* Regular echinoid *(Echinus)* (Cuénot).——*5.* Irregular echinoid *(Brissus)* (Cuénot). [Orientation according to P. H. Carpenter's nomenclature, except *2* and *3*.]

lar echinoids. It is aboral but somewhat excentric in other regular echinoids (*E* ray or *AB* interray) and most asteroids (*BC* interray). In a few ophiocistioids where it is known, it is aboral, located near the margin or at mid-distance between center and margin. It is lateral or on the oral side in irregular echinoids and invariably in the *AB* interray. It is lacking in somasteroids, ophiuroids, and certain asteroids which discharge excrements through the mouth.

The digestive tract consists of a more or less elongate tube, spirally enrolled in a clockwise direction (the organism presenting its oral face to the observer) in attached echinoderms, holothuroids, and very young echinoids. In adult echinoids, it is extended and this extension more or less masks the preceding arrangement. The stelleroids have a short straight digestive tube with a pronounced stomach enlargement, subdivided in asteroids by a horizontal constriction into two portions.

The digestive tube is differentiated more or less clearly into an esophagus, stomach, intestine, and rectum. It is modified by adjoined appendices that perform particular functions or simply augment secreting surfaces: diverticula of crinoids (Fig. 4,*1*); gastric brachial caeca of asteroids, somasteroids, and the ophiuroid *Ophiocanops* (Fig. 4,*3*); diverticulum and siphons in many echinoids (Fig. 4,*4*,*5*); and respiratory trees of holothuroids (Fig. 4,*2*). In general, cords or mesenterial bands composed of two peritoneal layers attach the digestive tube to the body wall; but, although present in the embryo, they are generally more or less lacking in adults.

COELOM

The general cavity of echinoderms of coelomic origin forms a large free space, except in crinoids, where it is secondarily filled by strands and membranes of connective tissue.

This cavity, carpeted by peritoneum, encloses the principal organs of the body, especially the digestive tube and the gonads (except in living crinoids where the gonads have migrated to the arms, or more generally their appendages, the pinnules). It extends broadly into the arms of asteroids, narrowly into those of ophiuroids, and by four canals into those of crinoids. It is traversed by mesenteries or strings diversely placed between the viscera and walls. Partitioning may serve partly or completely to isolate small compartments, such, for example, as the **perivisceral spaces** and cavities of the chambered organ in crinoids, the **peripharyngeal sinus** of echinoids and holothuroids, the **periesophageal sinus** of asteroids and ophiuroids, the **periproctal sinus** of echinoids, the **perianal sinus** of echinoids and holothuroids, and the **aboral** or **genital sinus** in the form of a pentagon ring in asteroids, ophiuroids, and echinoids, which furnishes for each gonad a genital branch.

The general cavity is by no means the only one that may be of coelomic origin. Likewise derived from the coelom, as proved from their development and the fact that they are lined by peritoneum, are the **axial sinus**, the **hyponeural sinuses**, the **madreporic vesicle**, and the **water-vascular system.** Because of its importance, this last will be discussed in a special section.

The **axial sinus** of crinoids comprises a vertical space enclosed by the ring of the digestive tube and surrounding the esophagus orally. Also, it contains a characteristic elongated organ, the **axial gland**, to be described presently. Some authors report that in holothuroids the axial sinus disappears during ontogeny, whereas in echinoids it is lacking entirely. Among asteroids (Fig. 5,*1*,*2*) and ophiuroids, it contains, in addition to the axial gland, an essential component of the water-vascular system known as the **stone canal**; thus in stelleroids it comprises a complex of cavities and organs, the **axial complex,** enclosed in an interbrachial septum of the *CD* interray or intimately joined to it. At its aboral extremity the axial sinus communicates with the ampulla of the stone canal, located on the internal face of the madreporite, and it ends in the genital or aboral sinus already mentioned. At its oral extremity, it opens into a large **circumoral ringlike sinus** that lies on the aboral side of the nerve ring surrounding the mouth. In asteroids this sinus is divided by an oblique partition into internal and external rings. The axial sinus opens into the internal ring, which thus appears as an extension of the axial coelom.

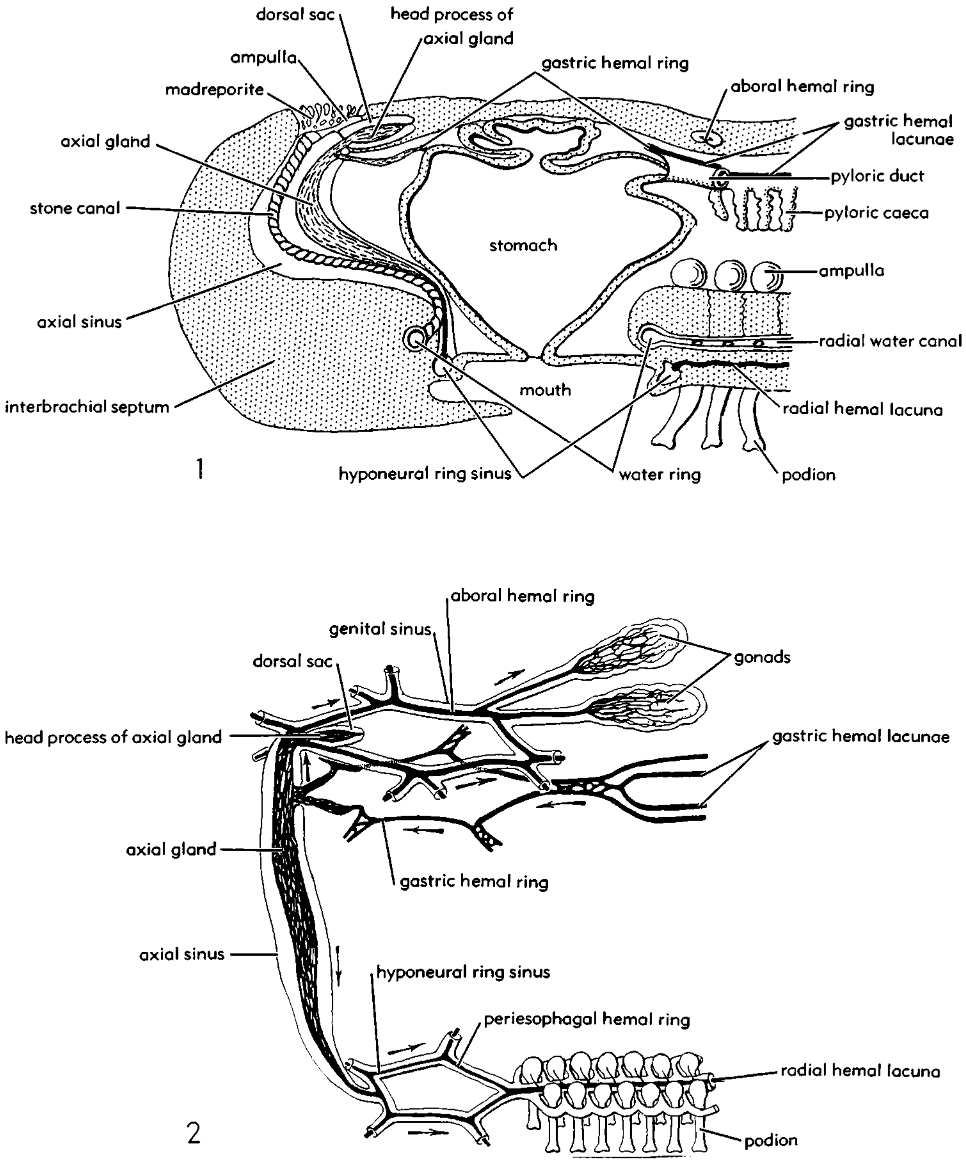

FIG. 5. Axial complex, hyponeural, and hemal systems in asteroid (Ubaghs, n).——*1.* Sagittal section through *CD* (left) interray and *A* ray (mod. from Cuénot).——*2.* Scheme of axial complex, hyponeural and hemal systems.

The **hyponeural sinuses (hyponeural sinus system)** consist of a group of tubular cavities forming typically and essentially, a **circumoral sinus,** from which lead five **radial sinuses** located on the aboral face of the five radial nerve cords (ectoneural) (Fig. 5). These radial sinuses may give off transverse branches that penetrate the podia. The ensemble of tubes has often been considered as constituting a second circulatory system designated **perihemal** (also **pseudohemal** or **perilacunar**), because tubules of this sinus system encloses distributional lacunae of the hemal system or are closely

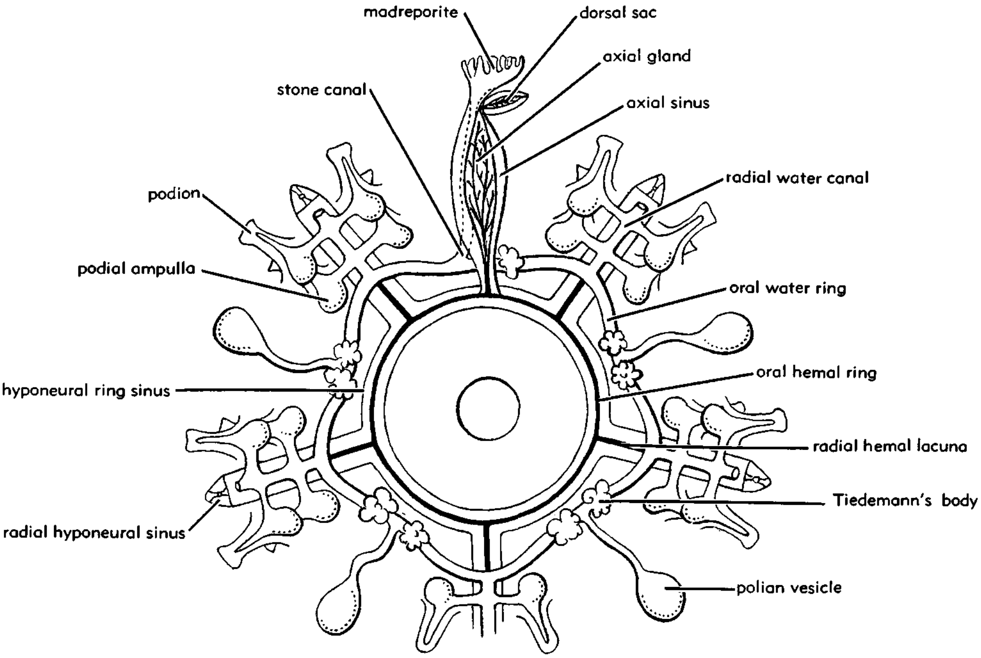

FIG. 6. Organization of water-vascular, hemal, and hyponeural-sinus systems in asteroid (diagram.) (Ubaghs, n).

associated with them. In reality, between the entire hyponeural sinus system, which is of coelomic nature, and the hemal (blood) circulatory system, formed of spaces developed in the mesenchyme, there exists only a simple physiologic analogy resulting from the fact that the hyponeural sinuses, like all coelomic cavities, contribute somewhat to the functions of nutrition, respiration, and excretion of the tissues.

The **madreporic vesicle** or **dorsal sac** of echinoids, asteroids (Fig. 6), and ophiuroids envelops the aboral part of the axial organ already mentioned. We shall refer to it again in later discussion.

The coelomic cavities are carpeted by an endothelium which ordinarily is ciliated. In the liquid contained by the cavities are numerous free cells or **coelomocytes,** classifiable according to morphologic types and varied functions; they are amoebocytes, capable of wandering through all the tissues and acting as carriers of food, as calcigenous cells, as phagocytes, and as bearers of waste products. Hemocytes (red nucleated globules with hemoglobin) exist in holothuroids.

WATER-VASCULAR SYSTEM

The **water-vascular** or **ambulacral system** is one of the most characteristic features of echinoderms. It essentially represents a hydraulic mechanism and consists of an assemblage of canals, which we have seen are part of the coelom. The system includes the following structures: 1) **oral water ring** with the **polian vesicles** and other accessory organs; 2) **radial water canals** from which arise lateral branches leading to special evaginations of the body wall comprising the **tube feet** or **podia**; and 3) **stone canal** with the **hydropore** or **madreporite.**

The oral water ring may be considered as the central part of the system. It surrounds the esophagus (Figs. 6, 7). Among echinoids it is slightly displaced inward by development of the masticatory apparatus and in holothuroids by that of the pharyngean bulb. As a rule, it bears the large pedicellate vesicles known as **polian vesicles,** located interradially and probably serving to maintain the turgescence in the apparatus. These vesicles are lacking in crinoids and echinoids; among ophiuroids four

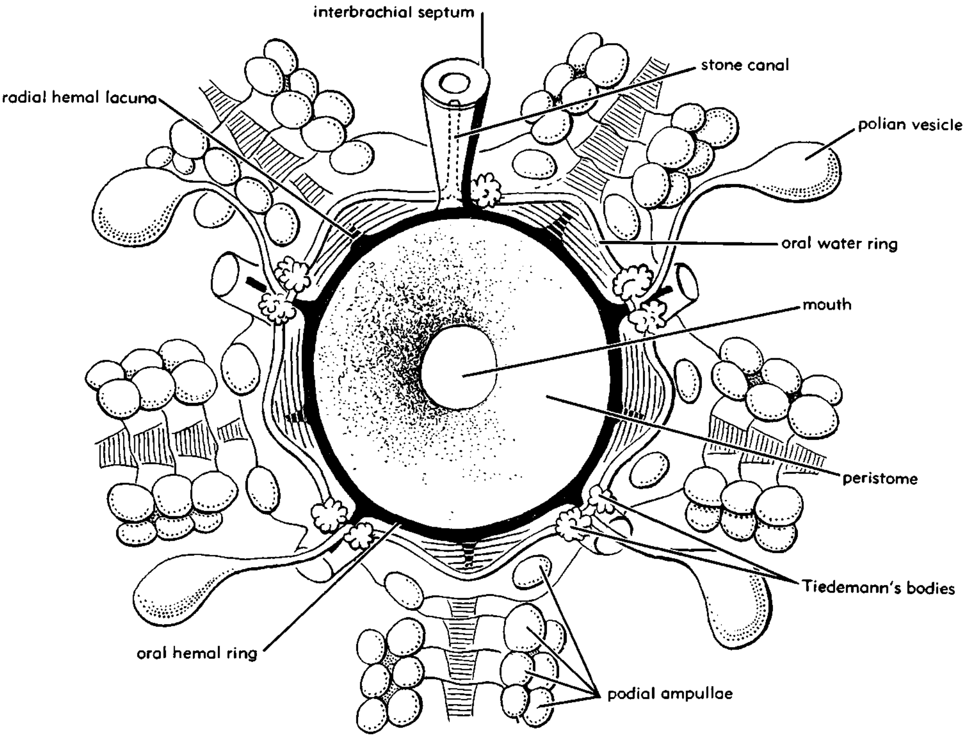

FIG. 7. Internal view of peristomial region of *Asterina gibbosa* (PENNANT) (asteroid), showing water-vascular and hemal systems, ×10 (Cuénot).

such vesicles normally occur, and in asteroids there are generally five, but in holothuroids the number is highly variable (one to more than 50). Connected with the oral ring or related to it, some lymphoid organs are found in echinoids forming the so-called **spongy body** or **spongy ring,** that is penetrated by caecal diverticula given off by the oral ring; in asteroids, the interradial **Tiedemann's bodies,** of unknown function, enclose tubules that terminate blindly but open into the oral ring.

The oral water ring gives off five radial water canals (Fig. 6) located aborally with respect to the hyponeural coelomic sinus and hemal lacuna (Fig. 1). Among holothuroids and echinoids, the canals and accompanying radial structures lie in the inner part of the body wall (holothuroids) or on the inner surface of certain plates of the endoskeleton (ambulacral plates) which are closely associated with the water-vascular apparatus. Among crinoids and stelleroids, on the other hand, they are external to the brachial (crinoids) or to the ambulacral endoskeleton (stelleroids), resting in a ventral groove (ambulacral groove) open to the exterior, except in ophiuroids where it is secondarily closed by soft integument or by ventral arm plates and transformed into an epineural canal. (In living and probably fossil somasteroids, there is no permanent ambulacral groove, but a muscular mechanism permits temporary erection of the ambulacral plates to form an open furrow, homologous with the ambulacral furrow of asteroids).

Throughout their course the radial water canals give off (to right and left) branches that end in the ambulacral tube feet or podia. In crinoids, each branch divides into three smaller branches that give rise to three podia or tentacles. The podia are found in all living classes, and probably were present in most, if not all, of the extinct groups. They exhibit a truly remark-

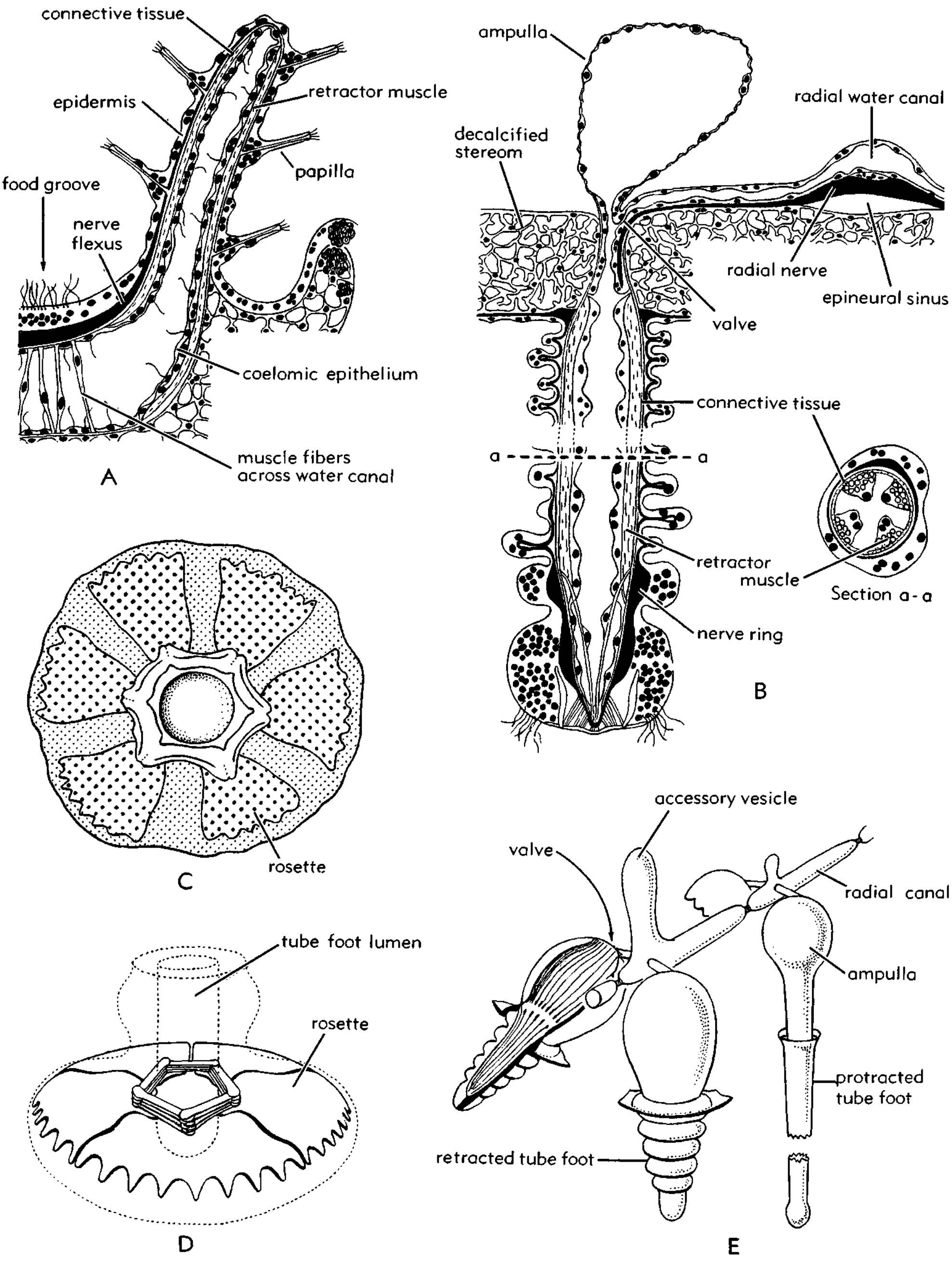

FIG. 8. Structure of tube feet.——*A*. Longitudinal section of tube foot of *Antedon bifida* (crinoid) (Nichols).——*B*. Longitudinal section of suckered tube foot and radial water canal of *Echinocyamus pusillus* (echinoid) (Nichols).——*C, D*. Structure and arrangement of skeletal elements in disc of suckered tube foot of *Echinus esculentus* (echinoid) (Cuénot, Nichols).——*E*. Diagram of part of radial water-vascular system of *Amphiura filiformis* (ophiuroid) (Buchanan & Woodley).

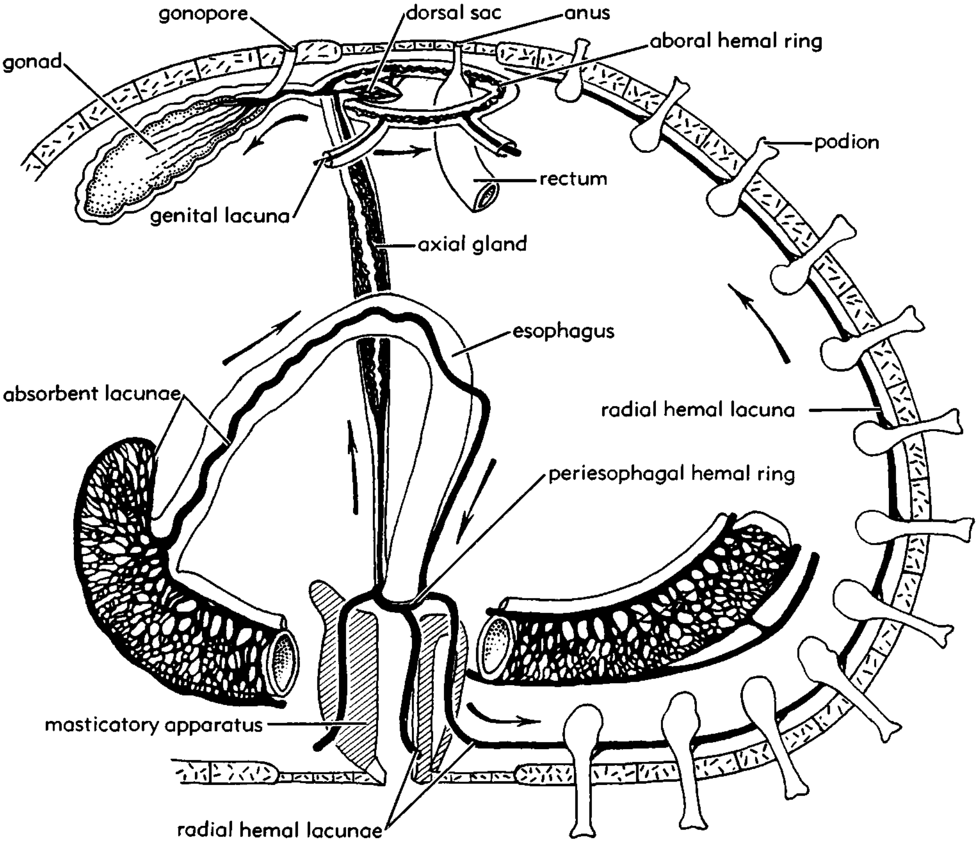

FIG. 9. Scheme of hemal system in regular echinoid (mod. from Cuénot).

able polymorphism that corresponds to their varied functions as feeding, respiratory, locomotory, burrow-building, or sensorial organs. Yet they are constructed according to the same basic plan. Each tube foot comprises (from outside to inside) an epidermis, which is continuous with that of the rest of the body, a nervous plexus, a conjunctive layer, a layer of longitudinal muscle fibers, and a flat vibratile endothelium that covers the internal cavity or lumen (Fig. 8,*A,B*). The nervous plexus is thickened on one side to form the longitudinal tube foot nerve, and generally at the distal and proximal ends to form nerve rings. The conjunctive layer may contain a spicular endoskeleton of its own; the collagen connective tissue of which it is made up constitutes the framework of the tube foot. The longitudinal muscular fibers are retractor muscles, apparently serving also for bending the tube foot. The cilia of the endothelium lining the lumen in many forms are arranged in two longitudinal bands which, as they are beating in opposite directions, determine a circulation of coelomic fluids in the internal cavity.

In crinoids and ophiuroids, the epidermis of the tube feet is raised at intervals into papillae which contain mucous cells and sensory elements (Fig. 8,*A*). Secretion of mucus is brought about in the crinoid papilla by the contraction of a single longitudinal muscle fiber, and in the ophiuroid papilla probably by a flattening of the epidermis resulting from normal protraction of the tube foot (NICHOLS, 1963).

In many holothuroids, echinoids, and asteroids, the free end of the podia is expanded into a disc having the properties of a sucker, serving for locomotion and feeding. In asteroids, the main framework of the sucker consists of connective tissue; in echinoids, it comprises a complicated calcite skeleton, consisting of a terminal rosette of five or more ossicles, and a series of much smaller ossicles arranged around the tube-foot lumen (Fig. 8,*C,D*); in ophiuroids, the skeleton supporting the disc is generally made up of a single ossicle. Adhesion in holothuroids is obtained by the stickiness of mucus secretions from cells belonging to the epidermis of the disc. In asteroids and echinoids, the sucker is operated by special muscles which create a suction when they contract. As the functioning and structure of the suctorial tube feet are different in the three classes just mentioned, one may conclude that they have evolved independently.

The podia of holothuroids, echinoids, asteroids and of the only known surviving member of the somasteroids *(Platasterias)* are each provided with an internal contractile vesicle, the **ampulla** (Fig. 6, 7). The wall of the ampulla consists of an inner coelomic epithelium, a sheath of muscles (antagonistic in action to the retractor muscles of the tube foot), commonly a thin layer of connective tissue, and a flat covering peritoneal endothelium. When the ampulla contracts, the tube foot is protracted by hydraulic pressure. A valve at the point where the branch from the radial water canal ends into the tube foot prevents ambulacral fluids from flowing back into the rest of the system (Fig. 8,*B,E*).

Since the ampulla is internal and the tube foot external, their union is effected by a canal extending through the body wall (holothuroids) or passing through a pore (generally doubled in echinoids) that lies between the ambulacral plates or perforates them (Fig. 9). The existence of similar pores in fossil forms suggests the former presence of ampullae.

In groups lacking ampullae, such as crinoids and ophiuroids, other devices may be functional equivalents of the ampullae (Fig. 8,*A,E*). In crinoids, muscle fibers stretch across the cavity of the radial water canal, except along its axis; when the muscle fibers contract, they first divide the canal into a series of compartments; then they reduce the volume of each compartment and force out the ambulacral fluid to the tube feet (NICHOLS, 1960). In ophiuroids, the radial water canal may be also constricted at intervals, but this is done by muscular sphincters; as no muscle fibers traverse the canal, it is elasticity of its walls that forces fluid back to the tube feet. Moreover, the musculature of each tube foot is differentiated into two systems, one in the long distal part of the tube foot and the other in the proximal part of it, which is more or less swollen; these systems seem to be antagonistic and the proximal part acts as an ampulla; a valve cuts off the ampulla and its tube foot from the water radial canal. In species with considerable power of podial protraction, the radial canal bears nonmuscular vesicles which are housed in special cavities in the ambulacral ossicles and probably takes excess fluid when the tube feet retract (BUCHANAN & WOODLEY, 1963; NICHOLS, 1963).

Now, to return to the oral ring, we find that into this opens (in the *CD* interray) a canal, secondarily multiplied in some echinoderms, called the **stone canal,** because calcareous spicules generally encrust its conjunctive wall. This canal opens outward in a vibratile funnel, the **hydropore,** or it connects with the internal face of a perforated calcareous plate, the **madreporite,** generally through the medium of a rather large collecting space, called the **ampulla** (Fig. 5,*1*). This ampulla maintains definite connections with the axial sinus, as already indicated. The presence of a hydropore or madreporite is the only indication that permits conclusion as to the existence of the water-vascular system in several extinct classes such as the cystoids or the eocrinoids. In most holothuroids the madreporite is internal, its pores opening into the coelom. This condition is secondary, for in the larva the water tube opens externally. In some forms, the hydropore of the madreporite may be secondarily multiplied.

HEMAL SYSTEM

The elements of the mesenchyme are throughout the body separated from one another by interstitial spaces that form a plexus of interconnected lacunae known as the **hemal** or **lacunar system.** At some points these lacunae are enlarged as canaliform passageways organized in a complicated network of channels and sinuses. The absence of an internal endothelial lining and the fact that their wall is composed essentially of connective tissue prove that they are neither part of the coelom nor true vessels but simple cylindroid spaces. The latter form a system particularly evident in holothuroids and echinoids but less clearly defined, perhaps, in other classes (Fig. 9). In such echinoderms, one may recognize, at least typically, the following principal parts: 1) a **periesophagal hemal ring** or an oral annular plexus closely associated with the nervous, hyponeural, and water-vascular oral rings; 2) five **radial hemal lacunae,** leading from the hemal ring and accompanying (beneath each of the ambulacra) the hyponeural radial sinuses and the radial hydrovascular canals with branches given off by the radial lacunae in the direction of the podia; 3) **absorbent lacunae** of the digestive tube, opening also into the hemal ring, developed as a network on the surface of the digestive tube; 4) springing from the hemal ring in the *CD* interray, another lacuna that penetrates the **axial gland** considered by some authors as a center of the entire lacunar system; 5) at the outlet of this organ, the just-mentioned lacuna reformed into a channel that centers an **aboral hemal ring**; and 6) the **genital lacunae** developed from this aboral ring but lost by branching in the conjunctive wall of the gonads. Finally, to the hemal lacunae one or several lymphoid organs may be joined, filling perhaps a purifying function.

AXIAL GLAND

The axial gland or organ (termed also ovoid gland, brown gland, heart) occurs in all modern echinoderms except holothuroids, which are said to have none or at most a poorly developed one. It is an organ closely related morphologically and functionally to the hemal system.

The axial gland is a vertically elongated mass, covered by peritoneum and formed of lacunar connective tissue. As FEDOTOV (1924) has shown, it is composed in echinoids and stelleroids of an oral and aboral portion. Among asteroids and ophiuroids, the oral part is enclosed in the axial sinus (Fig. 5, 6), placed in a longitudinal fold of the wall in contact with the stone canal in the *CD* interray; it represents one of the components of the **axial complex** of these organisms. Among echinoids (Fig. 9), it is also in close contact with the stone canal but not enclosed in a coelomic cavity; on the other hand it contains an irregular cavity, lined by endothelium, and therefore of coelomic origin. The aboral portion of the axial gland is well developed only among ophiuroids; in the two other classes mentioned it is reduced to a digitiform appendage (Fig. 5, 6, 9); in all it is enclosed in another coelomic cavity, the **dorsal sac or madreporic vesicle,** reported to have a contractile wall.

The axial gland of crinoids is an elongated body consisting of tubules of glandular epithelium set in conjunctive tissue and covered exteriorly by peritoneum; it occurs inside the axial sinus. The gland is prolonged at its aboral extremity by a conjunctive cord located in the axis of the chambered organ (portion of the general coelom surrounded by the aboral nerve center) and it continues inside of the stem; at its adoral extremity it enters into close relation with the oral plexus of the hemal system. According to CUÉNOT, the axial gland of crinoids is not homologous to that of other echinoderms, but this view is not generally accepted.

REPRODUCTIVE SYSTEM

The genital organs originate in the wall of one of the compartments of the general cavity. The facts that in ontogeny of living echinoderms the first indication of the genital apparatus makes appearance in the same interray as that containing the anus and hydropore, and further, that among numerous ancient echinoderms, one finds in the same place a single orifice interpreted as a gonopore, lead to the conclusion that originally echinoderms possessed a single gonad, opening in the *CD* interray. This primitive condition is retained by the holothuroids. Among all other classes the genital organs are multiplied and have been affected by pentameral radial symmetry. They are primarily interradial structures, though they are located in the arms of adult asteroids and of some ophiuroids, and in the arms or, more generally, in the genital pinnules (appendages of the arms) of crinoids.

In asteroids and ophiuroids, they are connected by an annular stolon enclosed by a hemal lacuna surrounded by a coelomic sinus; the same arrangement is seen in crinoids, where the genital cords, similarly sheathed, traverse the arms and penetrate into the central visceral mass, where they are lost. The genital cords uniting the gonads disappear in adult echinoids.

The sexes of echinoderms ordinarily are separate, although certain species of holothuroids and ophiuroids are hermaphroditic. The sexes cannot be distinguished on external characters except in species (known in all classes) that show anatomical features designed for care of the young and in cases, quite rare, of sexual dimorphism observed in echinoids, asteroids, and ophiuroids.

An asexual mode of reproduction by spontaneous fission of the body has been observed in a few holothuroids, asteroids, and ophiuroids. This may have relation to the great power of regeneration manifested in all echinoderms following accidental injuries, spontaneous eviscerations (holothuroids) and autotomies (Crinoidea, Asteroidea, Ophiuroidea), observed among many.

ONTOGENY

SEGMENTATION AND GASTRULATION

The eggs of echinoderms are small and poor in deutoplasm (Fig. 10,*A*), although a rather large number of species, particularly those that incubate their young or attach their eggs to foreign bodies, produce large eggs filled with yolk (vitellus).

As a general rule, cleavage is complete, almost equal, and of the radial type (Fig. 10,*B*,*C*). It results in the formation of a coeloblastula, ordinarily covered by long flagella (Fig. 10,*D*,*E*), and later this is transformed by invagination (emboly) into a gastrula (Fig. 10,*F*). At this stage, or even in the blastula stage, the embryo throws off its ovular envelope and becomes a free-moving pelagic larva.

From the beginning of gastrulation, some isolated cells become detached from the wall of the gastrular invagination (archenteron) and invade the blastocoel. They are mesodermal elements which have the aspect and serve the function of a mesenchyme. This indicates that the mesenchyme of echinoderms is of entodermal origin and thus is an entomesoderm. Not uncommonly, however, blastoderm cells migrate into the blastocoel before gastrulation and form a localized or diffused basis of an ectomesoderm, within cells of which occur calcareous granules destined to form the larval skeleton. A **primary mesenchyme** (Fig. 11) derived from the blastoderm, or true mesenchyme, appears then to exist in echinoderms, as well as a **secondary mesenchyme** derived from the archenteric wall (Fig. 11,*C*). Since these two mesenchymes shortly lose their identity, however, it is not possible to delineate their respective roles in morphogenesis.

FORMATION AND FIRST DEVELOPMENT OF COELOMS

An evagination from the upper surface of the archenteron soon becomes separated into the form of a closed sac (doubled in some forms) (Fig. 11,*D*; 12), the cavity of which is the **coelom,** thus produced by enterocoely.[1] This sac, when unpaired, becomes divided into two vesicles which are symmetrically placed on each side of the part of the archenteron that persists (Fig. 12,*B*). Theoretically at least, each of these two vesicles becomes divided into three successive compartments, that in anterior position being termed the **axocoel,** that in the middle known as the **hydrocoel,** and the posterior compartment known as the **somatocoel** (HEIDER, 1912) (Fig. 12,*C*,*D*). As a rule, however, the division is incomplete except in the left half of the body, only the posterior coeloms being invariably

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[1] In species with large, yolk-rich eggs, the archenteron may remain rudimentary. The coelom then may open through slitlike gaps in the mesenchyme (schizocoely). Development of this sort in echinoderms is almost universally regarded as secondary. [See, however, *Direct Development* in the chapter by FELL, p. S77.]

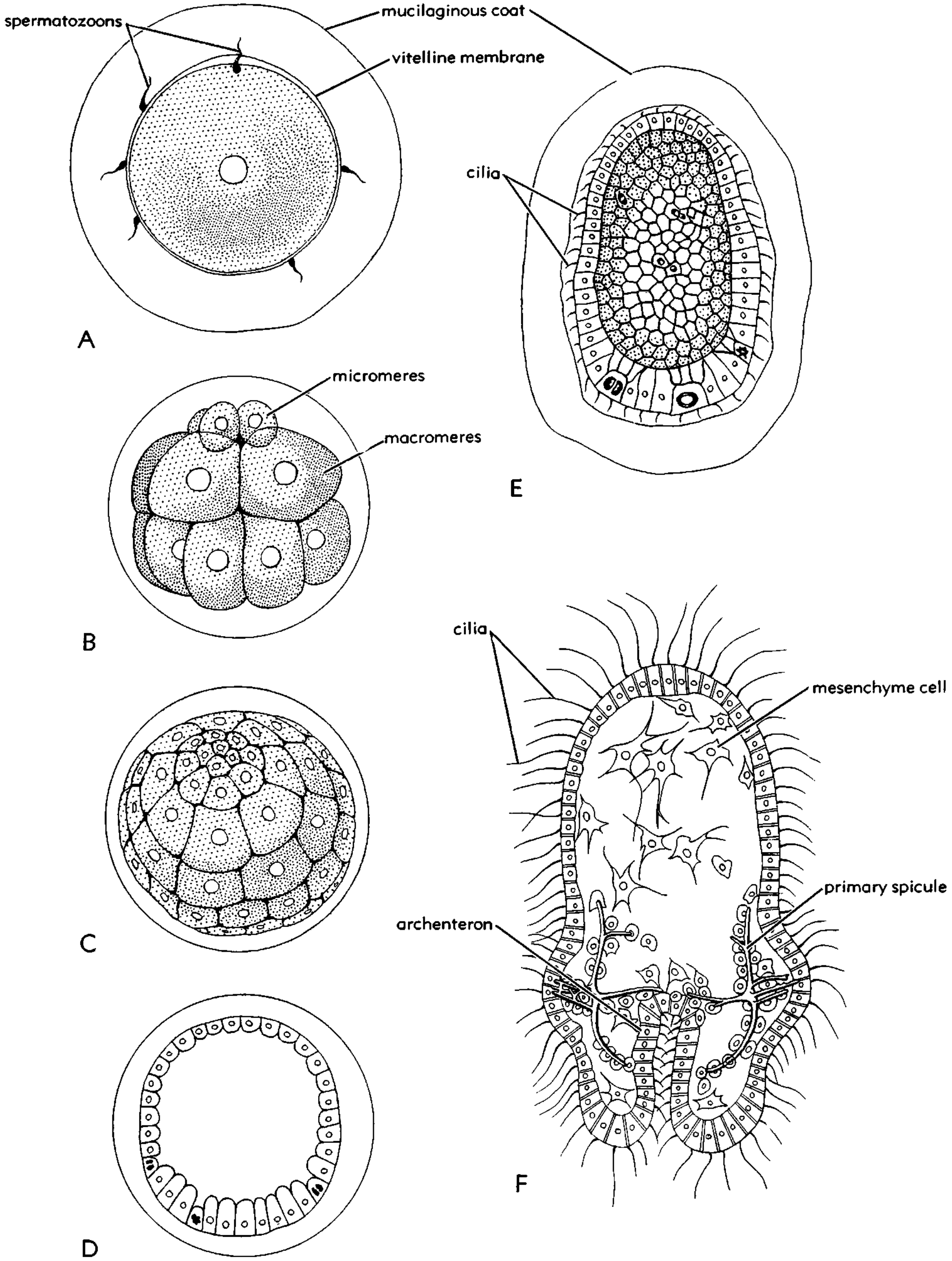

FIG. 10. Early ontogenetic stages of *Echinocyamus pusillus* (echinoid) (Théel).——*A*. Mature ovum at moment of impregnation, with one spermatozoon entering yolk and vitelline membrane beginning to separate, ×410.——*B*. Cleavage stage with 16 cells, ×400.——*C*. Later cleavage stage, at about three hours after fecundation, ×400.——*D*. Optical section through coeloblastula seven hours after fecundation, ×300.——*E*. Same at 13 hours after fecundation, ×300.——*F*. Optical section through gastrula changing into larva, 40 hours after fecundation, ×275.

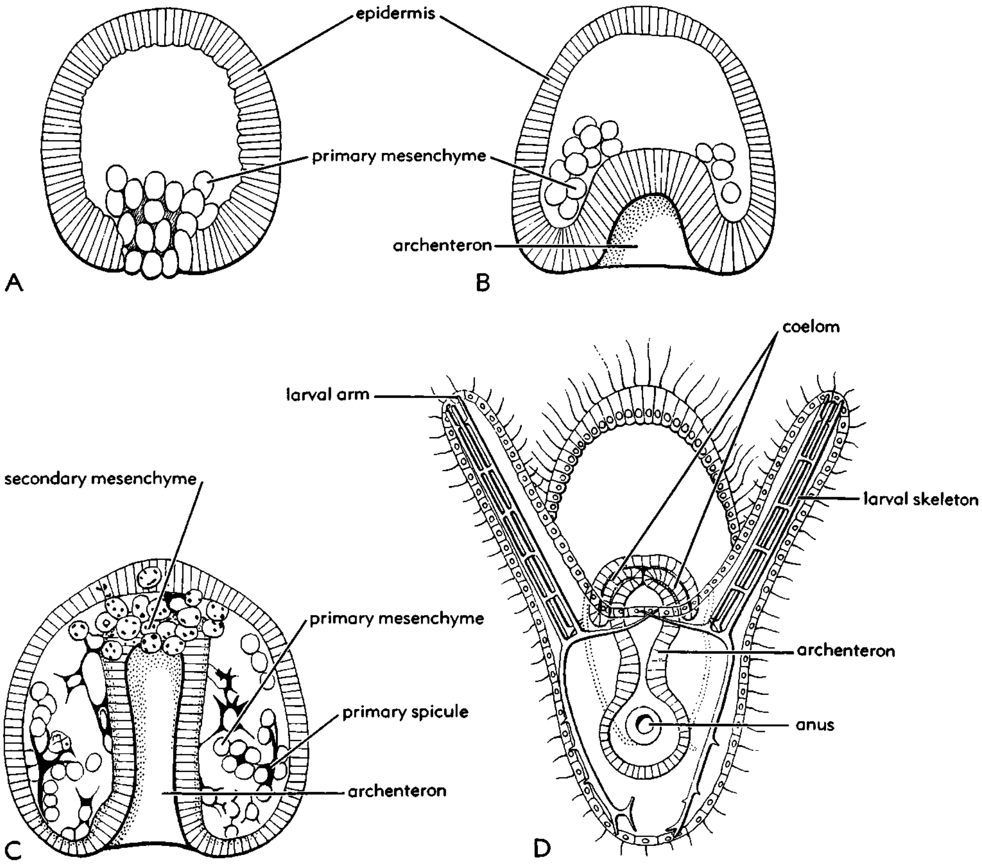

FIG. 11. Optical sections showing three stages *(A-C)* in formation of gastrula and mesenchyme of *Paracentrotus lividus* (echinoid) (Boveri); and young pluteus larva *(D)* of *Echinocyamus pusillus* (echinoid) showing formation of coeloms, ×270 (Théel).

paired; the right hydrocoel is ordinarily absent or represented only by a transitory rudiment, whereas the right axocoel (absent in holothuroids and crinoids) remains much less developed than the left one. Moreover, the separation of the axocoels and hydrocoels is by no means always sharp and they may more or less function as though they constituted a single unity. We see, then, that the embryo exhibits a profound **asymmetry** which appears very early, since it is already manifest in initial stages and even in the nonsegmented egg of some species. This is considered to be **secondary asymmetry,** however, because abnormal larvae are known that show either a division of the coelom as perfect on the right as on the left side or the development of the functional hydrocoel, not on the left but on the right side.

The ultimate fates of the diverse coelomic compartments are very dissimilar. The left axocoel remains in direct communication (except among crinoids where communication is established later on) with the left hydrocoel by means of a canal **(stone canal)** while it gives off a tubelike diverticulum **(hydroporic canal)** that opens dorsally on the left side in an orifice **(hydropore).** It is seen, then, that the hydrocoel, lacking a pore of its own, can communicate with the outside only by means of the axocoel. The right axocoel regresses, but not without having budded off a small contractile vesicle that will become, as observed later, the **dorsal sac** or **madreporic vesicle** of the axial organ. While normally the right hydrocoel, when present, plays no part in organogenesis, the left hydrocoel develops to form the water-vascular system of the adult (whence

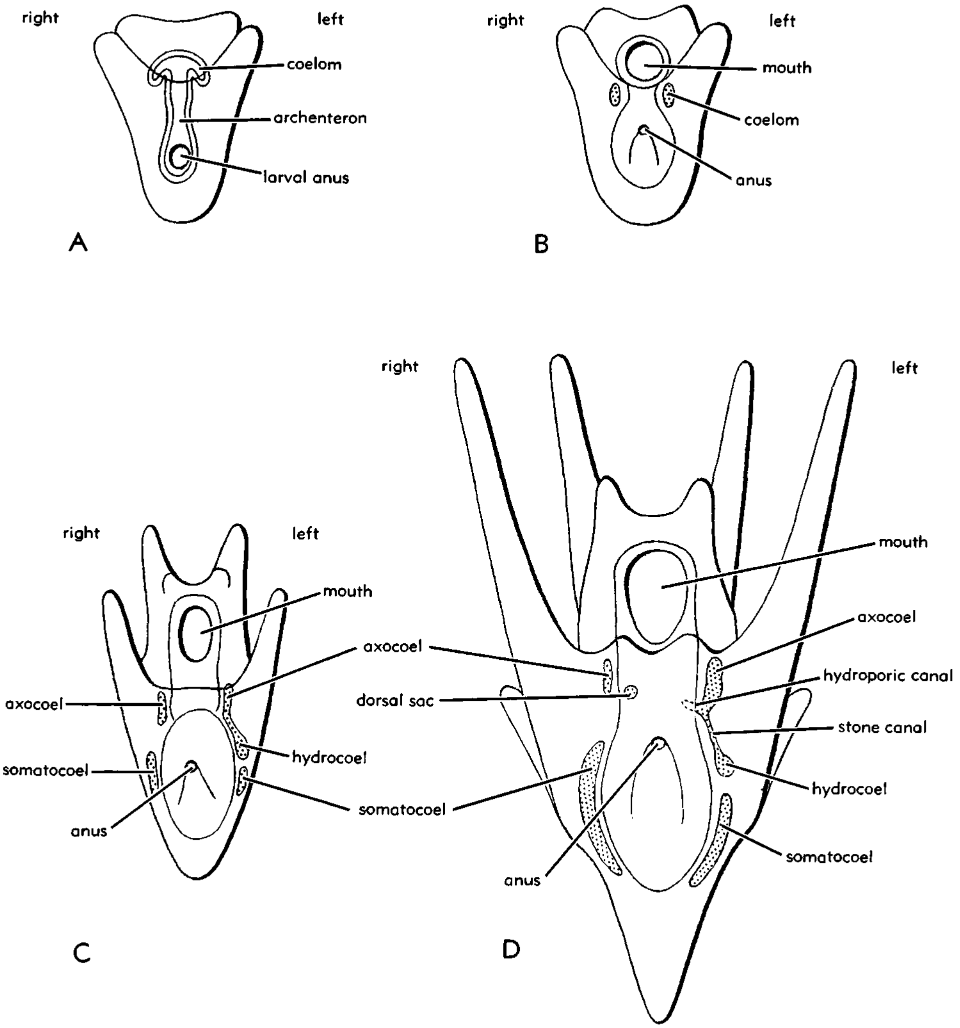

FIG. 12. Formation and first evolution of coeloms in echinoid larva (diagram.) (von Übisch).

its name). The two somatocoels, both well developed (but the left generally larger than the right) have symmetrical positions in some but strongly asymmetrical in others; where they adjoin, their walls combine to form the **principal mesentery.**

The different function allotted to each of the coelomic compartments proves that division of the coelom in no way corresponds to segmentation in the strict sense. Further, it is not accompanied by segmentation or repetition in series of any of the body structures. The mesoblast especially shows no fundamental tendency to give rise to somites. Therefore, HYMAN (1955) is entirely correct when she insists on the nonsegmented nature of the echinoderm body.

LARVAE

Notwithstanding the strong asymmetry of its coelomic elements, the embryo becomes transformed into an externally symmetrical larva. The part of the archenteron not involved in forming the coelom becomes the larval digestive tube, entirely formed of entoderm. The blastopore, which remains open (except in crinoids, where

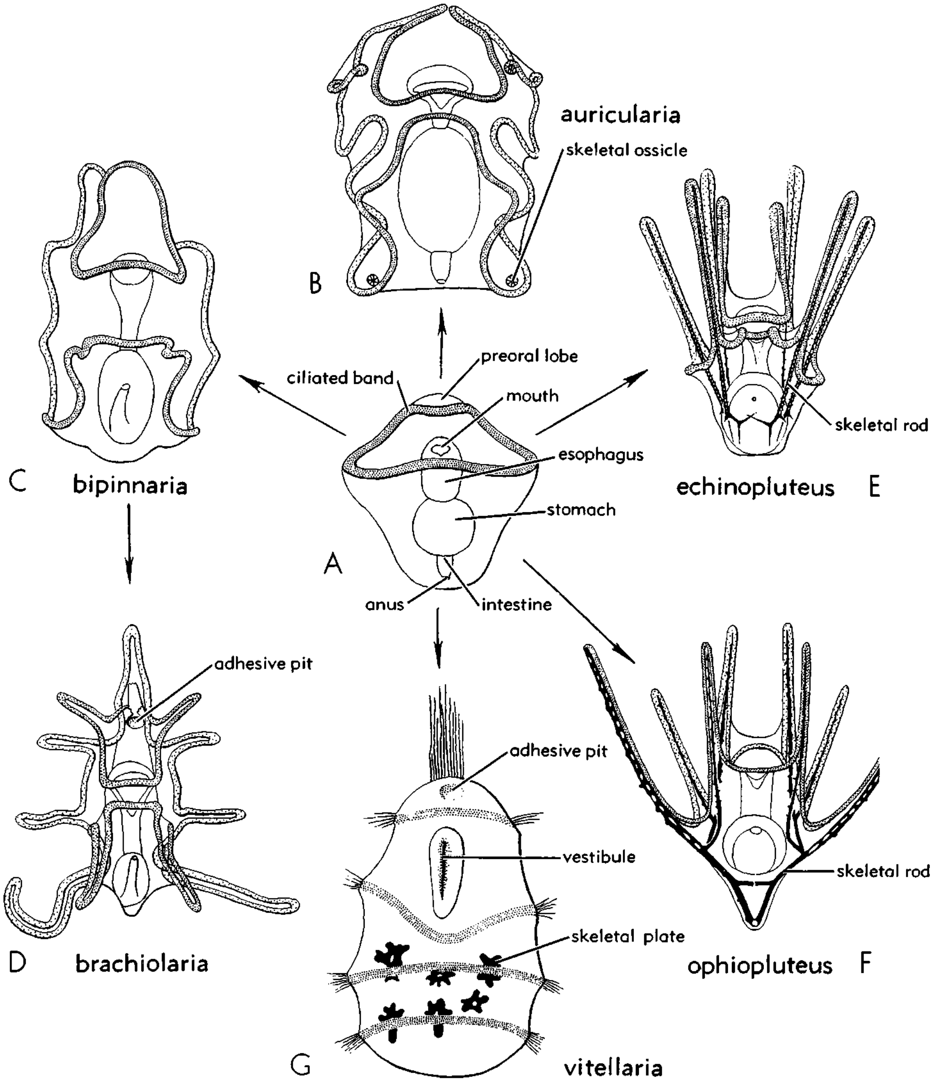

Fig. 13. Morphological relations between theoretical dipleurula larva *(A)* and other echinoderm larvae *(B-G)* (Ubaghs, n).

it is closed), becomes the larval anus and this serves to place the echinoderms among true Deuterostomia. The other extremity of the archenteron curves backward and opens to the exterior by way of the **mouth.** The appearance of this new orifice determines the **ventral face** of the larva, to which the anus, at first apical, soon becomes transferred. Finally, the digestive tube, which has become curved inward dorsally, is divided into an esophagus, a stomachic expansion, and an intestine (Fig. 13,*A*).

On the initially ovoid ventral face of the larva, a shallow, saddle-like depression is formed that encloses the mouth but leaves the anus outside of its limits. Accompanying disappearance of general ciliation, an ectodermic rim provided with flagella or cilia is produced, completely surrounding the ventral depression, following all of its sinuosities. The portion of the larval body in front of the mouth comprises the **preoral lobe.** A sensory plate, provided with nerve elements and sometimes a tuft of cilia, may be differentiated at its apex. The larva, thus characterized, belongs to the dipleurula stage of development (Fig. 13,*A*). Noteworthy is the absence of any sort of nephridial apparatus. It is active and feeds on microplankton.

Truthfully, this so-called **dipleurula** stage has no real existence, for, as shown by MÜLLER (1848), it rather represents the common characteristics or the basic pattern of the diverse sorts of swimming larval forms which externally are strongly differentiated from one another and highly varied as to the order and degree of development of their internal structures. They provide for the dispersal of species having very restricted powers of locomotion in adults and are to be regarded as special adaptations.

These larave, considered formerly as distinct organisms, have received special names; they are: **auricularia** of the Holothuroidea (Fig. 13,*B*), **bipinnaria** (Fig. 13,*C*) and **brachiolaria** (Fig. 13,*D*) of the Asteroidea, **echinopluteus** (Fig. 13,*E*) of the Echinoidea, and **ophiopluteus** (Fig. 13,*F*) of the Ophiuroidea. All have characteristic small lobes on the surface and many exhibit very long projections (larval arms), which in ophiopluteus and echinopluteus are supported by a very complex larval skeleton; this skeleton is only slightly developed in auricularia and entirely lacking in bipinnaria and brachiolaria.

Another type of larva exists in crinoids, certain holothuroids and a few ophiuroids. They are the barrel-shaped larvae or **vitellaria** (Fig. 13,*G*) of FELL, characterized by their subcylindrical form, as well as opacity of their walls (owing to presence of deutoplasm), complete absence of arms, and replacement of the continuous ciliated band by several ciliated or flagellated parallel belts. The barrel-shaped larva, which is only slightly active and cannot feed itself, is generally considered as a larval dipleurula profoundly modified by coenogenetic characters.

We may notice finally that the free larval phase characteristic of the **indirect development** of echinoderms may be much altered or (a single case known) entirely omitted, development working in a condensed manner termed **direct development**; this may be observed in the ontogeny of species having large yolk-rich eggs. Since ordinarily, however, direct development is accompanied by appearance of structures characteristic of the larvae, one admits generally that it is secondary as compared to indirect development.

METAMORPHOSIS

GENERAL CHARACTERS

The transformation **(metamorphosis)** of the larva into the definitive young organism, is effected in various ways that cannot be described here. Discussion is limited to consideration only of fundamental aspects of metamorphosis and principal features of organogenesis.

Metamorphosis of crinoids and numerous asteroids is preceded by fixation of the larva to the substratum, whereas the larvae of other echinoderms are transformed while continuing to swim about. The whole body of the larva of holothuroids participates in the formation of adult structures; among other echinoderms, a larger or smaller part of this larval body is rejected or resorbed.

In agreement with HEIDER (1912), several phases may be distinguished in metamorphosis of the echinoderms.

ASYMMETRIC PHASE

After an initial larval phase characterized by a more or less perfect bilateral symmetry (Fig. 14,*1a,b*), an **asymmetric phase** appears. We have already taken account of the preponderant development of the left anterior coeloms in the embryo. At beginning of the metamorphosis, the mouth, which was located in the mid-ventral plane of the larva, tends to be shifted toward the left side of the body (Fig. 14,*2a,b*). This displacement, very slight in holothuroids and ophiuroids, amounts to nearly 90 degrees in asteroids and echinoids, among which the mouth becomes actually lateral in position. When the larval mouth turns into the definitive mouth, the displacement is real; but the larval mouth and esophagus may also be replaced by a mouth and esoph-

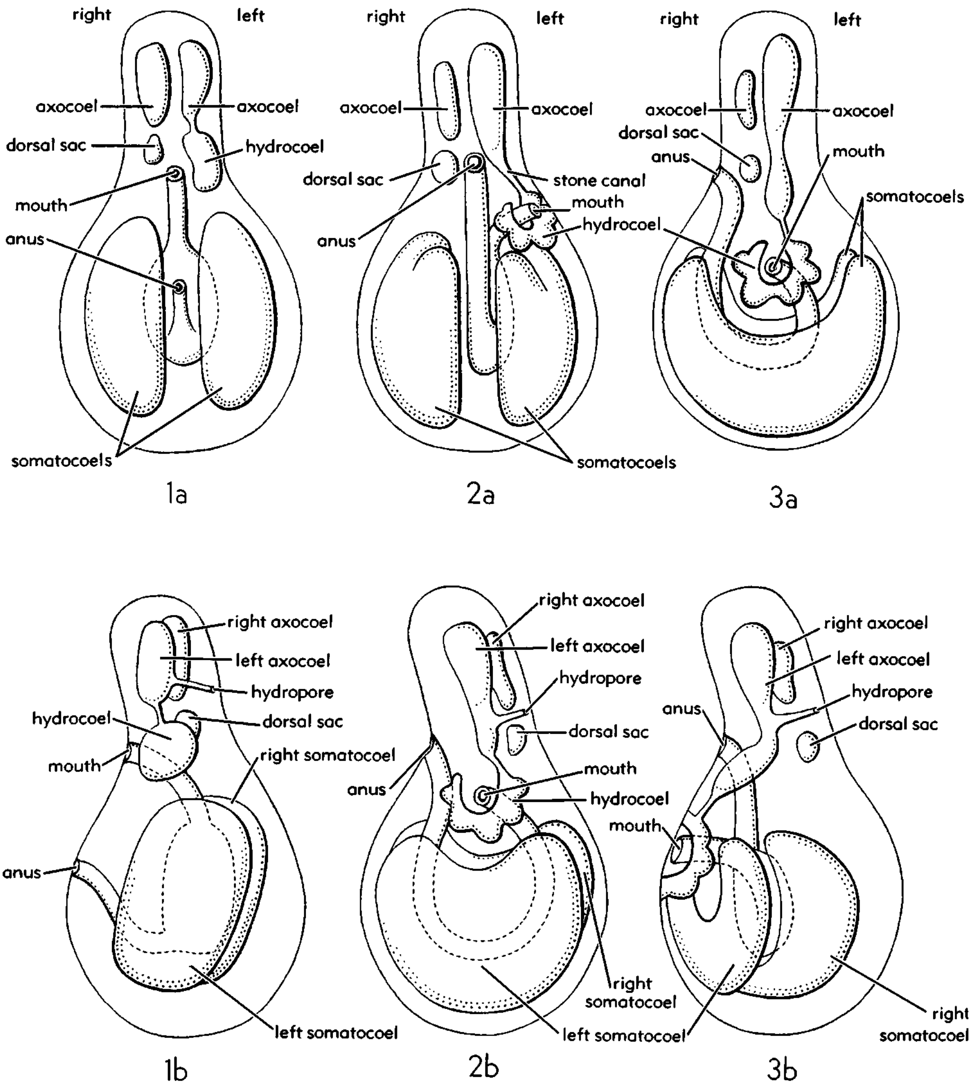

FIG. 14. First phases of metamorphosis in echinoderms (diagram.), upper row showing larvae from ventral side and lower row from left side.——*1a,b.* Initial symmetrical phase.——*2a,b.* Asymmetrical phase.——*3a,b.* Phase of secondary symmetry (Heider).

agus newly formed on the left side of the larval body, as especially seen in echinoids and asteroids. Whatever the way this change is accomplished, it produces a leftward deviation of the front part of the digestive tube, very characteristic of all echinoderms. As for the anus, whether it remains in the mid-plane of the body, being pushed strongly forward, or, as is generally the case, undergoes a shift toward the right, its displacement is in a direction opposite to movement of the mouth. The digestive tube takes then the form of a loop turned around on itself.

The displacement of the mouth carries with it the left hydrocoel, which acquires a horseshoe shape and tends to grow around the esophagus. Likewise, the two somatocoels take on a crescent shape, with development of terminal horns that play an im-

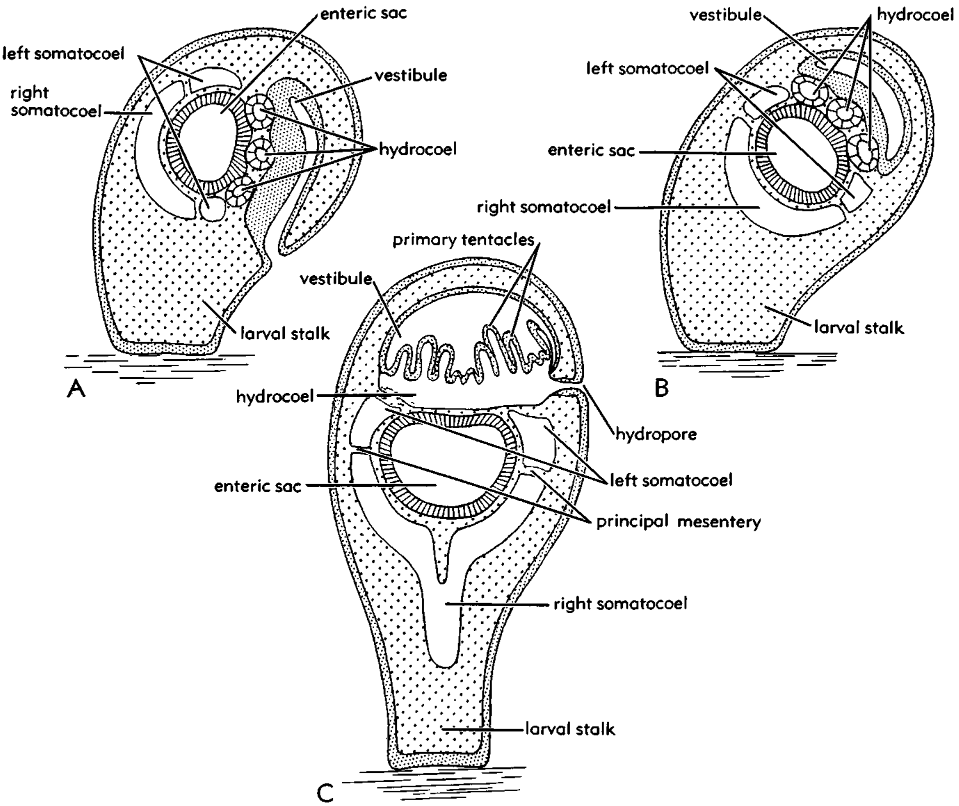

FIG. 15. Diagrammatic sections showing successive stages (*A-C*) of elevation among crinoids (mod. from Barrois).

portant role in organogenesis, as we shall observe.

The larva, arrived at this stage, no longer presents a bilateral symmetry. It has become asymmetrical. A new median plane, marked by the mouth and hydrocoelic crescent, tends to be distinguishable, however. This does not coincide with the midplane of the larva but makes a more or less large angle with it, which in asteroids and echinoids may attain approximately 90 degrees (Fig. 14,*2b*).

PHASE OF SECONDARY SYMMETRY

The phase of asymmetry is followed by one in which **secondary symmetry** is developed. The mouth tends to return to the ventral surface and to recover more or less the medioventral position that it occupied in the dipleurula larva (Fig. 14,*3a,b*). This return, however, is accompanied by displacement of the hydrocoel and the two somatocoels. All together, this amounts to what HEIDER has termed a torsion of the entire visceral complex around the longitudinal axis of the larval body, so that the median plane of the echinoderm in course of development comes to coincide with the primitive mid-plane of the larva. However, the symmetry thus produced does not correspond to the primitive bilateral symmetry. The digestive tube is no longer found in the median (sagittal) plane of the dipleurula larva, but rather extends in its frontal plane; the principal mesentery is not now dorsoventral but is also frontal; the originally left somatocoel is moved to the oral side, while the originally right one becomes aboral.

ELEVATION AND FLEXION

The further course of development differs among the classes of echinoderms. We will

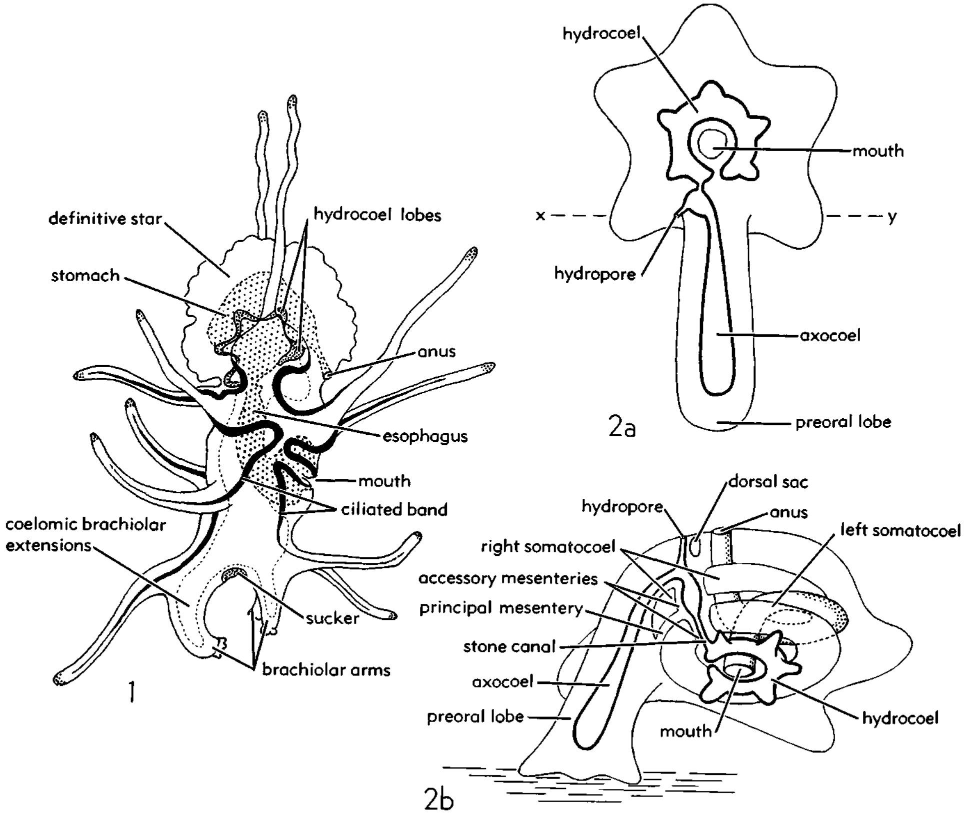

FIG. 16. Early stages in asteroid development.——*1*. Brachiolaria of *Asterias forbesi* in attached position, from left side, with definitive star formed from larval posterior region presenting its oral face to observer (Mead).——*2a,b*. Successive stages of flexion among asteroids, showing transverse axis *(x-y)* around which flexion operates (diagram.) (mod. from Heider and Dawydoff).

here consider only crinoids and asteroids having fixed larvae, because of phylogenetic significance commonly accorded to these larvae.

Among crinoids, and especially comatulids (a very specialized group but the only one for which we have knowledge of development), the larva becomes fixed by an adhesive pit carried on the ventral surface of the anterior part of its body, and this part thus becomes the attached or aboral surface, while the morphologically posterior part of the larva, with all its organs concentrated in it, turns 90 degrees about a transverse axis so as to become oriented toward the upper pole, now the free oral end of the larva (Fig. 15). The two somatocoels and the mesentery between them (principal mesentery) are disposed horizontally. Their crescentic form is accentuated and their blind extremities become located in the neighborhood of what was the original mid-ventral line, forming two short vertical mesenteries termed **accessory mesenteries.** HEIDER has used the term **elevation** for this process by which the fixed larva becomes erect and takes the inverted vertical position characteristic of crinoids and other fixed echinoderms.

On the other hand, HEIDER has designated as **flexion** (bending) the morphogenetic movements of asteroids which pass through a fixed stage. Here also the echinoderm body turns around a transverse axis in relation to the preoral lobe which assures temporary fixation of the organism (Fig. 16). This movement is accomplished in an opposite sense to that of crinoids, however; it bends the body toward the provisional peduncle (flexion), turning first the mouth toward it and then deflecting the body downward (Fig. 16). By this displacement, the organ of fixation comes to be planted on the side of the mouth that forms the oral face of the young starfish, whereas in crinoids it is inserted at the center of the aboral face. The anus appears subsequently on the aboral face and the somatocoels, by reason of their location with respect to the digestive tube, become distinguished as hypogastric (left) and epigastric (right). The principal mesentery is also disposed horizontally and the junction of their terminal projections produce accessory mesenteries perpendicular to the principal mesentery (Fig. 16,*2b*). These accessory mesenteries are important, for they determine the madreporite interray *(CD)* and are closely associated with the axial sinus (derived from the left axocoel), as well as the axial organ (mesenchymentous origin), the madreporic vesicle (derived from the right axocoel), the stone canal, and the madreporite; in brief, they are the seat of the axial complex.

ROTATIONS

Internal morphogenetic movements of rotational nature may be produced in the course of ontogenetic development of echinoderms. For example, in certain asteroids a rotation of the hydrocoelic ring has been described with displacement in a clockwise direction, accompanied by an opposite displacement of the aboral parts of the arms. Among holothuroids, the hydrocoelic ring undergoes a rotation that modifies relations of the radial canals and radii.

PENTARADIAL SYMMETRY

Fivefold radial symmetry is introduced in the echinoderm organism in the course of development by very special evolution of the left hydrocoel (see below) and by its morphogenetic influence on neighboring regions, serving to determine a final identical distribution of food grooves (or epineural canals), ectoneural radial cords, endoskeletal structures joined to the ambulacral apparatus, and hyponeural canals.

DEVELOPMENT OF PRINCIPAL ORGANS

VESTIBULE

In the larvae of all echinoderms, except asteroids, a deep ectodermal invagination is formed in front of the mouth, sheltering development of the first radial structures of the water-vascular apparatus. This is the **vestibule** (improperly called amniotic sac in echinoids) (Figs. 13; 15; 17,*B,C*).

COELOMS

Right axocoel. A small vesicle, termed **dorsal sac** or **madreporic vesicle,** located beneath the madreporite and enclosing the aboral extremity of the axial organ is derived from the right axocoel, either directly or through the medium of mesenchyme.

Left axocoel. Derived from the left axocoel are: 1) the hydroporic canal, 2) a small ampulla located at its junction with the stone canal, 3) the **axial coelom** or **sinus,** and 4) in asteroids, the internal ring of the circumoral sinus (the external ring being hyponeural, i.e., produced by the left somatocoel).

Right hydrocoel. In normal echinoderm larvae, the right hydrocoel disappears without taking any part in organogenesis.

Left hydrocoel. The water-vascular system, including all its dependent structures, is derived from the left hydrocoel. The original left hydrocoelic vesicle, very early in development, is bent into a horseshoe shape around the esophagus and tends to be closed in a complete ring (future **oral ring** of the water-vascular apparatus). Five diverticula representing the five **primary tentacles** (forerunners of the radial canals) are extended from the outer border of the hydrocoel vesicle. These five tentacles push back the subjacent integument (floor of the vestibule where this structure exists) and acquire in this way their ectodermic covering; thus the radii begin to be defined. On the other hand, the oral ring preserves its relations with the exterior by means of the larval stone canal and the left axocoel. Regression of this latter, however, permits the placement of the stone canal and hydroporic canal of the larvae end to end. In this way, finally, the water-vascular system opens directly to the exterior and at the junction of the two canals a small ampulla, as we have seen, may persist as a remnant of the left axocoel. The polian vesicles and Tiedemann's bodies, like the radial canals, are outgrowths of the oral ring. The podia are developed as evaginations from the radial canals.

Somatocoels. We have seen that the two somatocoels are displaced in such manner that the right becomes the aboral (epigastric) part of the principal coelom or general cavity of the adult and the left the adoral (hypogastric) part (Figs. 15; 16,*2a,b*). We have observed also that the principal mesentery is disposed horizontally and that terminal horns of each produce, on meeting, the accessory mesenteries perpendicular to the principal mesentery (Fig. 16,*2b*).

The right (aboral) somatocoel presents little complication; among crinoids it sends into the mesenchyme which invades the cavity of the stem, the five tubes of the **chambered organ**; these tubes, from the beginning of metamorphosis, are separated from the cavity in which they are developed. The left (oral) somatocoel produces in the interradii caecal evaginations that come to be placed above the hydrocoel ring, themselves joined in a ring and giving rise to the ensemble of the hyponeural sinus. The left somatocoel also participates in forming the **genital coelom** of free forms and among echinoids produces between the five lobes of the hydrocoel five diverticula (the dentary sacs), which represent the primordium of the masticatory apparatus (called Aristotle's lantern).

DIGESTIVE TUBE

The digestive tube of the definitive echinoderm organism is more or less developed from that of the larva. Among crinoids, the cavity of the digestive sac, closed in the larva, connects to the exterior by an esophagus produced by meeting through the hydrocoel ring of an ectodermic diverticulum and an entodermic diverticulum produced by its wall; only later on is the anal opening developed within the madreporic interradius near the hydropore. Among holothuroids, the digestive tube of the larva becomes that of the adult, but the larval anus (blastopore) disappears and the definitive anus is opened near the site of the blastopore without an ectodermic invagination. In asteroids and echinoids the larval mouth closes, and the larval esophagus, mostly resorbed, is replaced by an esophagus produced by an evagination of the stomach on the original left side of the larva through the hydrocoel ring; in asteroids this evagination opens directly to the outside; in echinoids it joins an ectodermic invagination which it meets; in various groups the new anus is produced (very belatedly) on the aboral face. In the ophiuroids, the larval anus and intestine become atrophied and entirely disappear; the mouth of the adult may be derived directly from the larval mouth or in some species may be a newly developed feature; a part of the larval esophagus seems to persist and to give rise to the definitive esophagus.

HEMAL SYSTEM AND AXIAL ORGAN

The hemal (or blood lacunar) circulatory system is produced by the mesenchyme. The axial gland is produced from connective tissues accumulated along the wall of the axial sinus in the accessory mesentery, surrounded by a fold of the wall of this sinus. Its aboral portion is intimately related to the madreporic vesicle (derived from the right axocoel), which surrounds it like a hood; in addition, it communicates (though secondarily) with the genital stalk, the origin of which we shall see is quite different.

GENITAL ORGANS

In the larvae of crinoids, a transitory first indication of the gonad appears in the principal mesentery close to anus and hydropore—accordingly in the madreporic interradius. This primordial structure is replaced by that of the definitive gonad, which seemingly lacks relation with the first. This second structure is differentiated from the aboral vertical or accessory mesentery in close association with the peritoneum of the right somatocoel. It gives rise to a compact cellular cord which migrates into the arms where it buds off the true gonads.

Among holothuroids, the genital structure makes appearance and develops in the dorsal mesentery in the neighborhood of the stone canal and in contact with the left

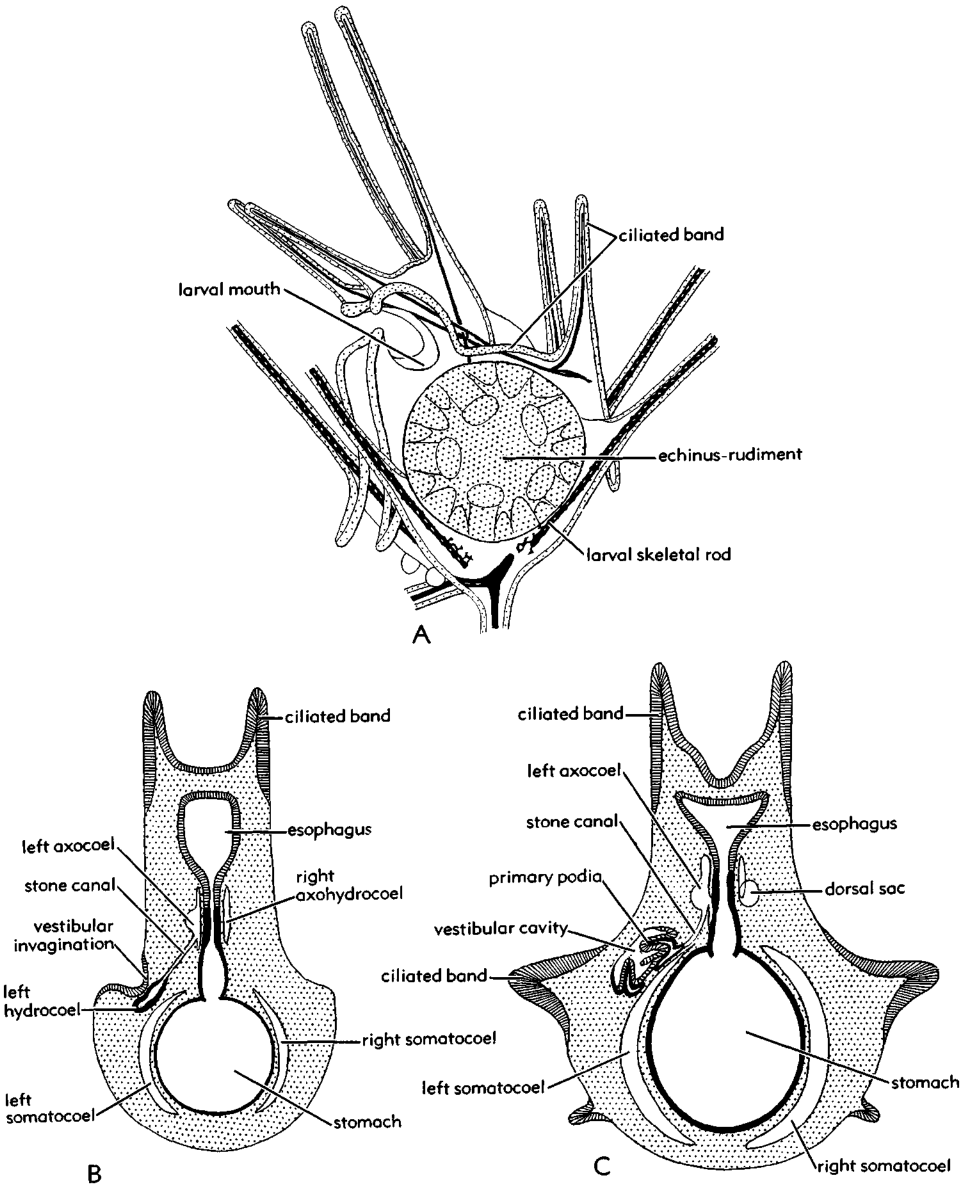

FIG. 17. Larval stages of echinoids.——*A*. Fully formed echinopluteus of *Arbacia punctulata* (LAMARCK) seen from left side, showing echinus rudiment (stippled area), ×100 (Gordon).——*B,C*. Diagrammatic frontal section through echinoplutei showing development of echinus rudiment on left side of larva (Macbride).

somatocoel, therefore with almost the same morphologic position as the gonad of crinoids.

In other echinoderms, one finds the first genital cells in the aboral (vertical) accessory mesentery, located in the madreporic interray (*CD* interray) and in close relation with the wall of the left somatocoel. After its differentiation this structure gives rise to a cellular cord, the genital stolon or stalk. This cord pushes toward the aboral surface inside a coelomic evagination of the left somatocoel so that a space, completely separated from the coelom that produced it, becomes a genital sinus. The genital stalk, with its coelomic envelope, forms a ring beneath the aboral pole and from this ring the true gonads are budded off into the interradii.

ENDOSKELETON

The first indications of the definitive endoskeleton appear before, during, or after metamorphosis. In echinoids, calcium carbonate of the pluteus larval rods is used for construction of the elements. We have already noted how the secretion of endoskeletal ossicles is produced by lime-depositing cells in the mesenchyme.

Comparable, but not necessarily homologous, development is found in the living echinoderms, except the holothuroids, producing a somewhat similar arrangement of plates around the apex of young echinoderms (Fig. 18). This arrangement persists more or less undisturbed in the adult stages of crinoids and echinoids but in the majority of ophiuroids and asteroids the primary plates are either resorbed or lost among a host of intercalary plates which arise around or between them. Among crinoids, around the larval stem, appear two cycles of five plates, both interradial in position, encircling the viscera: an aboral cycle of **basal** plates and an oral cycle of **oral** plates; generally also, inserted between the basals and the stem, are three to five small radially located plates, the **infrabasals,** that soon are resorbed or fused with the proximal skeletal piece of the stem or **centrodorsal.** Somewhat later on, five **radial** plates arise in the radii between the basals and the orals, prior to the outgrowth of the arms from the periphery of the oral surface. As the arms grow, **brachial plates** are formed in linear succession with the radials.

Among asteroids, on the aboral side of the young star, one may observe, around a **central plate,** five conspicuous interradial plates or basals, one of which incorporates the hydropore; there are no plates equivalent to the radials of crinoids and ophiuroids, but in later stages, just as in crinoids, infrabasals are introduced between central and basals, and then lost again. Early in the development appear also five radially located plates, the **terminals,** which, when the animal grows, move distally to the extremity of the arms, where they surround the terminal tentacle. The first **ambulacrals** are laid down on the oral side of the young star in close relation with the hydrocoel lobes and the first pairs of podia.

Among ophiuroids, the primary skeleton of the aboral side consists of a **central plate** and five **radials,** many species develop also a circle of interradially located **basals** between the central and the radials. Five **terminals** appear early; they are carried away to the arm tips. **Vertebrals,** representing fused ambulacrals, are secreted immediately adoral to the terminals; in adults, they constitute an internal row of ossicles supporting the arms.

Among echinoids, five interradial plates, termed **basals** or **genitals,** appear on the dorsal surface of the pluteus, and on the outer side of the primary podia, which they later surround, develop five radially situated **terminals** or **oculars.** Genitals and oculars remain in close contact, making a special system of plates (called the **apical system**) around the aboral end of the test in the adult. One of the genitals embraces the hydropore and becomes the **madreporite.**

GROWTH AFTER METAMORPHOSIS

The growth stages following metamorphosis and ending in the adult organism have very great interest for paleontologists. First, this is because they are the only ontogenetic stages that can be collected from geologic formations, but also it is because growth stages reveal important morphologic changes in endoskeletal elements—changes in form, proportions, number, placement, and topographic relations—and these changes may especially illuminate problems relating to homology and phylogeny.

An interesting application of CHILD's concept of axial gradients to the growth patterns exhibited by the endoskeletal elements and the soft parts more directly related to the endoskeleton of echinoderms recently has been made by FELL (196). He has shown that two major patterns of dominant gradients are to be recognized among echinoderms: a meridional pattern as exemplified in echinoids and holothuroids, a radial pattern as exemplified in crinoids and stelleroids. In young echinoids and young holothuroids, during metamorphosis, the hydrocoel encircles the esophagus, and sends five meridional water tubes which encircle the body cavity. Thereafter the endoskeleton, the nervous system, and part of the coelom differentiate under the same influence, and the whole body becomes more or less globose. In young crinoids and asterozoans, on the other hand, the five primary tentacles, which become the radial canals, instead of growing meridionally, are radiating more or less horizontally from the oral ring, carrying the body wall, coelom, nervous system, and the largest part of the endoskeleton with them, and resulting in a star-shaped body with arms. Then transverse growth gradients emerge from the main radial gradients, giving a pinnate structure to the arms, as well exemplified by the pinnulate arms of crinoids or the frondlike arms of somasteroids.

PHYSIOLOGY

Movements of echinoderms are provided by the podia, spines, or work of muscles. The podia are especially utilized by holothuroids, echinoids, and asteroids, but their locomotive function is weak or lacking in ophiuroids and entirely absent in crinoids. Only echinoids make use of spines for locomotion; otherwise these may serve many functions such as digging, burrow-building, protecting, harboring the developing larvae or as tactile and defensive organs. Creeping movements are effected in certain holothuroids by the general musculature of the body wall, while muscles interposed between the endoskeletal pieces govern movements of the rays of ophiuroids and the arms of crinoids; in the last-mentioned group, action of these muscles combined with the antagonistic action of ligamentary fibers may result in swimming or creeping motion (Comatulida).

LOCOMOTION

The locomotive function of the podia has been especially well studied in the asteroids by J. E. Smith (1948). The movements of protraction, retraction, and bending of each podion are controlled by a motor nerve located in the neck of the ampulla and connected with Lange's nerves and radial nerves. When the animal is moving, podia are extended first in the direction of locomotion until attached by their terminal sucker disc to the substratum, and then shortened in a backward direction so as to carry the animal forward. After contraction, the podia relax their adhesion and extend forward again. Progress of the animal requires that activities of the podia be coordinated. This coordination is accomplished by the radial nerves and the nerve ring, although a certain degree of coordination exists among the podia of an isolated arm. Presumably, a coordination center is located at the junction of each radial nerve with the nerve ring. Each center controls the longitudinal muscles that work unilaterally in a given direction, but the center that directs activity of the arm placed in the direction of forward progress exercises a temporarily dominant action. Thus, direction of movement is determined by the particular center having control at a given moment.

Individual movements of the radioles or spines of echinoids are governed by the action of muscles attached to their base and locally controlled by nerve-fiber bundles of the subepidermic system. The indispensable coordination of their movements in locomotion, however, is assured by the radial nerves.

NUTRITION

Most echinoderms are nourished by minute food particles (plankton and detritus), but some are active predators or scavengers which ingest large particles or capture living prey. They display a large array of feeding mechanisms, none of which are restricted to any particular group; furthermore each group, including many species, may use several ways of getting food.

MUCOCILIARY MECHANISMS

Among crinoids, powerful play of vibratile cilia produce centripetal currents that transport mucus-imbedded food particles along the ambulacral grooves toward the mouth. The tube feet produce and spread a mucus net in the surrounding water; then they collect the net loaded with food particles and discharge it into the groove. The same type of nutrition occurred probably in most, if not all, fossil-attached echinoderms. Among stelleroids, microphagous ciliary feeding, performed by the action of pinnate food grooves, is a fundamental feature of somasteroids. Some asteroids, e.g., *Porania, Ctenodiscus*) feed also by the mucociliary method, the food particles being entangled in mucus strands that are carried into the digestive tract. In many living starfishes, mucus protects the surface of the body and serves to collect small particles which may be carried by ciliary currents into the mouth. The mucociliary method of feeding has been also described among clypeasteroid and spatangoid echinoids; in numerous species mucus secretion and ciliary currents on the surface of the body are part of the feeding mechanisms.

TENTACULAR MECHANISMS

As just mentioned, tentacles or tube feet play an essential role in catching food particles in crinoids. Many holothuroids living in crevices or buried in mud entangle plankton and fine particles by means of the sticky tentacles surrounding the mouth; at intervals, the tentacles are thrust into the mouth and the adhering food is wiped off and ingested. Some ophiuroids are plankton-feeders, fishing with tube feet extended from the arms as they are swept through the water. Possibly the "carpoid" echinoderms used a similar feeding method.

INGESTION OF BOTTOM MATERIAL

Many holothuroid species push bottom material into the mouth with the buccal tentacles and burrowing forms swallow the mud in large quantity as they crawl along. The heart urchins (spatangoids) live buried in sandy bottoms. By means of specialized tube feet of the buccal region, they explore the walls of their burrow and catch small particles which are directed to the mouth. The digestive tract of the many species examined is invariably stuffed with bottom material. Most ophiuroids appear to be selective detritus-feeders, burrowing in the soft substrate for organic material. The starfish *Ctenodiscus* (see above) feeds primarily on mud particles which are stuck together with mucus and are carried along special grooves between the marginal plates to the podia and then to the mouth. Its stomach is generally distended with swallowed mud.

SCRAPING

Numerous echinoids equipped with strong teeth nibble on plants or masticate mostly sessile and encrusting animals. Similarly, some starfishes feed on coral polyps or sponges.

CAPTURE OF PREY

Most asteroids are predators, feeding on bivalves, gastropods, crustaceans, polychaetes, other echinoderms, sponges, and the like. Some swallow their prey whole, but others evert their stomach through the mouth and digest the captured animal externally. Most of the starfishes which feed in this way are able to capture bivalved molluscs, which are too big to be swallowed. To open the shell they use strong but intermittent pulls on the valves by means of their podia and they insinuate their stomach through tiny gaps between the valves. The use of toxins to produce relaxation of the adductor muscles of the prey is a possibility that is not yet supported by conclusive evidence. Many ophiuroids are carnivorous, preying on small worms and crustaceans, less commonly on young echinoderms and mollusks. The seizing of prey may be effected by an arm loop and the carrying of it to the mouth either by coiling of the arm or by the podia. The gorgonocephalids, which have extremely ramified and flexible arms, form an open bow-net in which small swimming animals become entrapped.

CIRCULATION

The coelomic cavities, including those of the water-vascular system, are carpeted by an endothelium, generally ciliated, vibratile movements of the cilia assuring slow circulation of internal fluids. Since echinoderms are generally in osmotic equilibrium with their environment, these fluids have a composition very close to that of sea water, except that they include products of metabolism and may contain numerous floating coelomocytes of varied sorts that perform diverse functions. These cells penetrate all tissues and all organs and one may find them also in the hemal system. Throughout the body, the liquids of internal cavities show a large degree of homogeneity.

The fact that the hemal system shows its greatest development in connection with the digestive tube and, further, that this system exhibits close relationships with important organs such as the podia and gonads, seems to indicate that it plays a considerable role in the distribution of the products of digestion. Recently, BOOLOOTIAN & CAMPBELL (1964) have demonstrated that a pulsating vessel occupying the lumen of the axial organ and terminating aborally in a compartmented contractile chamber pulses several times a minute and thus moves coelomic fluid from the perivisceral cavity into and throughout the hemal system of the sea urchin *Strongylocentrotus purpuratus*.

The cavities of the water-vascular system, which is involved in locomotory, feeding, respiratory, and burrowing activities, enclose a liquid that differs very little from the coelomic liquid. Observations of *Strongylocentrotus purpuratus* have shown that a direct communication exists between the lumina of the axial organ and the stone canal which contracts simultaneously with the pulsating vessel of the axial organ. The rhythmic contraction of this vessel, together with pulsating of the stone canal, may be important in moving fluids throughout the entire water-vascular system (3a).

RESPIRATION

Echinoderms possess a few specialized organs that function for respiration. Some gaseous exchanges can be effected through the body wall when it is sufficiently thin, as among certain holothuroids, or by means of local infolds or outfolds of this wall. Infolds (invaginations) include: 1) the ten **pouches** or **branchial sacs (bursae)** of ophiuroids, opening toward the exterior by slits placed along the bases of the arms and constantly traversed by water currents maintained by ciliary action and (in some species) by body movements that pump water in and out; 2) probably also the **hydrospires** of blastoids; and 3) the **pore rhombs** of rhombiferan cystoids. Outfolds (evaginations) are represented by: 4) the **podia** (see below); 5) the **papulae** or dermal gills of asteroids, which are simple or divided pockets that project exteriorly between plates of the skeleton, each enclosing a diverticulum of the general body cavity; 6) the external **gills** of echinoids (except cidaroids and irregular echinoids), containing branches of the peripharyngeal coelom; and 7) the organs (possibly like papulae) which probably covered the **diplopores** of diploporitan cystoids and the **sutural pores** and **epispires** of eocrinoids and some other archaic forms.

The digestive tube also may play a role in respiration. This is especially so in the case of the holothuroids (except Elasipodida and Apodida) which possess two very thin-walled, extremely ramified tubes, the respiratory trees, originating in the rearmost (cloacal) part of the digestive tube and extending into the general body cavity. By rhythmic contractions, the respiratory trees are alternately filled and emptied of water introduced into the cloaca through the anus. The rectum of living crinoids, enclosed in a conical projection **(anal tube)** developed on the oral surface of the animal, offers comparable activities; it alternately takes in and ejects sea water, thus producing a current that may be presumed to have some respiratory functions. Among certain fossil crinoids, the anal tube is enormously developed, its endoskeleton being provided with numerous perforations or very thin-walled infolds through which exchange between the exterior environment and the interior medium could be effected.

In most echinoderms which lack special respiratory structures, the tube feet are probably the main organs to have a respiratory function. In such asteroids as *Asterias,* half respiratory exchange takes place through the tube feet. When they are extended, the walls of the tube feet become extremly thin, and exchanges of gases take place between the sea water and the fluid filling the lumen; when the tube feet are retracted, exchanges take place between the fluid of the ampullae (or other internal parts of the water-vascular system if ampullae are lacking) and the fluids of the general body cavity. Maintenance of a current within the tube feet and ampullae is therefore advantageous: in many tube feet two bands of cilia, beating in opposite directions inside the lumen, and in most echinoids two canals connecting each tube foot and its ampulla are features of probably respiratory significance.

In many forms, especially in burrowing species, respiration (and other functions such as nutrition and sanitation) is greatly assisted by ciliary currents on the body surface or by special devices. For instance, in the phanerozone starfishes, the dorsal surface is covered by closely set plates, the **paxillae,** that consist of raised ossicles, each with a crown of more or less movable spinelets; these spinelets when lying horizontally form a covering under which an open space is maintained for purpose of respiration, feeding, and excretion. In the asteroid family Pterasteridae, the spinelets are united by a membrane; they form the outer roof of a brooding chamber that is aerated by pumping of water. In echinoids of the order Spatangoida, closely set minute spines, the **clavulae,** that carry longitudinal bands of cilia and occur in narrow tracts, or **fascioles,** create water currents that assist in respiration, feeding, and removing of foreign particles.

EXCRETION

Echinoderms possess no excretory system, although the function of excretion may seem to be quite active. Waste is generally evacuated by the coelomocytes or by cells having large capacity as phagocytes, the principal exits being by way of the podia, stone canal, madreporite (especially in echinoids), papulae of asteroids, pouches of ophiuroids, digestive tube, gonads, and respiratory trees of holothuroids. This eliminative action, however, does not always suffice to rid the organism entirely of its waste products; the deposition of melanoid pigments in the tissues, a feature which becomes more pronounced with increasing age, may be related also to an excretory activity. Most nitrogenous matter excreted by echinoderms occurs in the form of ammonia, with little urea and purines and only traces of uric acid; large quantities of amino acids are loosed also.

BIOCHEMISTRY

Studies in comparative biochemistry have led to formulation of conclusions of phylogenetic character. We will here consider only problems introduced by the distribution of phosphagens and sterols in animal groups, including echinoderms.

PHOSPHAGENS

Until a few years ago, it was believed that most invertebrates possessed a type of phosphagen (arginin phosphate), whereas vertebrates have another kind (creatin phosphate). The presence of phosphocreatin and phosphoarginin both in echinoderms and stomochordates seemed then to indicate that these groups were connected with one another and with the Chordata. We know now that other phyla (Porifera, Sipunculoidea, Annelida) also show this character and that the distribution of phosphagens in several phyla is by no means constant; instead, it varies among related genera, among species of the same genus, and even in different organs of the same animal. Consequently, the type of phosphagen found in a given phylum cannot be regarded as a useful criterion in considering phyletic relationships.

STEROLS

According to the nature of their contained sterols, echinoderms examined to date may be divided into two large groups: one, characterized by the presence of delta-7 sterols, comprises the asteroids and holothuroids; the other, characterized by the presence of delta-5 sterols, includes the ophiuroids, echinoids, and crinoids. This grouping is conformable to that suggested by comparative characters (excluding crinoids) of larval forms belonging to these classes. It is seen to be completely discordant with other evidence, however, especially that based on comparative anatomy and paleontology, according to which the asteroids and ophiuroids are much more closely related to one another than either of them to the echinoids.

PHYLOGENY

Remains of authentic echinoderms are found throughout the geologic column from the Lower Cambrian upward. The oldest known representatives of the phylum, already diversified and showing essential characteristics of the group, throw no light on the affinities and origins of the echinoderms, or on the manner in which their essential organization has been developed. Embryology (and in smaller degree comparative anatomy) provide more precise evidence bearing on these questions, which calls, however, for great caution in interpretation.

AFFINITIES OF ECHINODERMS

Retention of the blastopore or its emplacement as the definitive anus and the enterocoelic formation of the coelom accompanied by its division into three pairs of sacs, are characters generally considered to comprise a trustworthy basis for assignment of echinoderms with deuterostomian invertebrates, which include (in addition to echinoderms) the Stomochorda (or Hemichorda), and perhaps the Pogonophora. Inclusion of the Chordata (Protochordata and Vertebrata) in this assemblage presents another problem foreign to present considerations.

The most probable relationships of echinoderms are, in the judgment of many zoologists, with the Stomochorda (Enteropneusta, Pterobranchia, ?Graptolithina). The early larval stage of echinoderms (dipleurula larva), in fact, offers striking similarities with the tornaria larva of Enteropneusta, for these have the same general aspect, including: 1) similar placement of the circumoral ciliated band, 2) the same emplacement of the apical sensory plate, 3) the same shape and subdivisions of the digestive tract, 4) the same mode of appearance and division of the coelom, 5) identical presence of a coelomoduct with asymmetrical external orifice connecting the anterior coelom with the exterior, 6) the same general behavior of the dorsal pulsatile vesicle (madreporic vesicle of echinoderms, cardiopericardial vesicle of Stomochorda) developed from the anterior coelom, and finally, 7) absence in both of any sort of nephridial apparatus. If, moreover, the ambulacral system of echinoderms—the most distinctive feature marking these organisms—is to be compared with any other structure, it is with the lophophore of Pterobranchia, since both are derived from the middle coelom and both one and the other have the form of coelomic tentacle-bearing evaginations. Such complete resemblances can hardly be construed as fortuitous. They suggest real affinities existing between the Stomochorda and Echinodermata, but beyond this, alignment together is not justified, because the nature of complex modifications impressed on the latter in the course of their metamorphoses and the fact that no close comparison between adult echinoderms and other groups of the animal kingdom is possible sufficiently prove that at a certain stage in their history the echinoderms became radically and definitively separated from the ancestral type that possibly united them with the Stomochorda. It seems evident, moreover, that all adult echinoderms, both living and fossil, as well as larvae, in so far as we know them, are much too specialized to have been able, through later evolution, to give rise to another phylum.

Numerous authors have noted or now admit the possibility of genetic relationships between chordates (Protochordata and Vertebrata) and echinoderms. We will not undertake here a review of arguments, mainly based on embryological and biochemical considerations (see above) advanced in favor of this hypothesis. If we refer to it, it is because certain authors have judged that among some Paleozoic echinoderms indication of a common parentage between these two phyla can be found. GREGORY (1934, 1951) has drawn attention to the resemblance that exists between the theca of the stylophorans *Placocystites* or *Mitrocystella* and the body covering of a

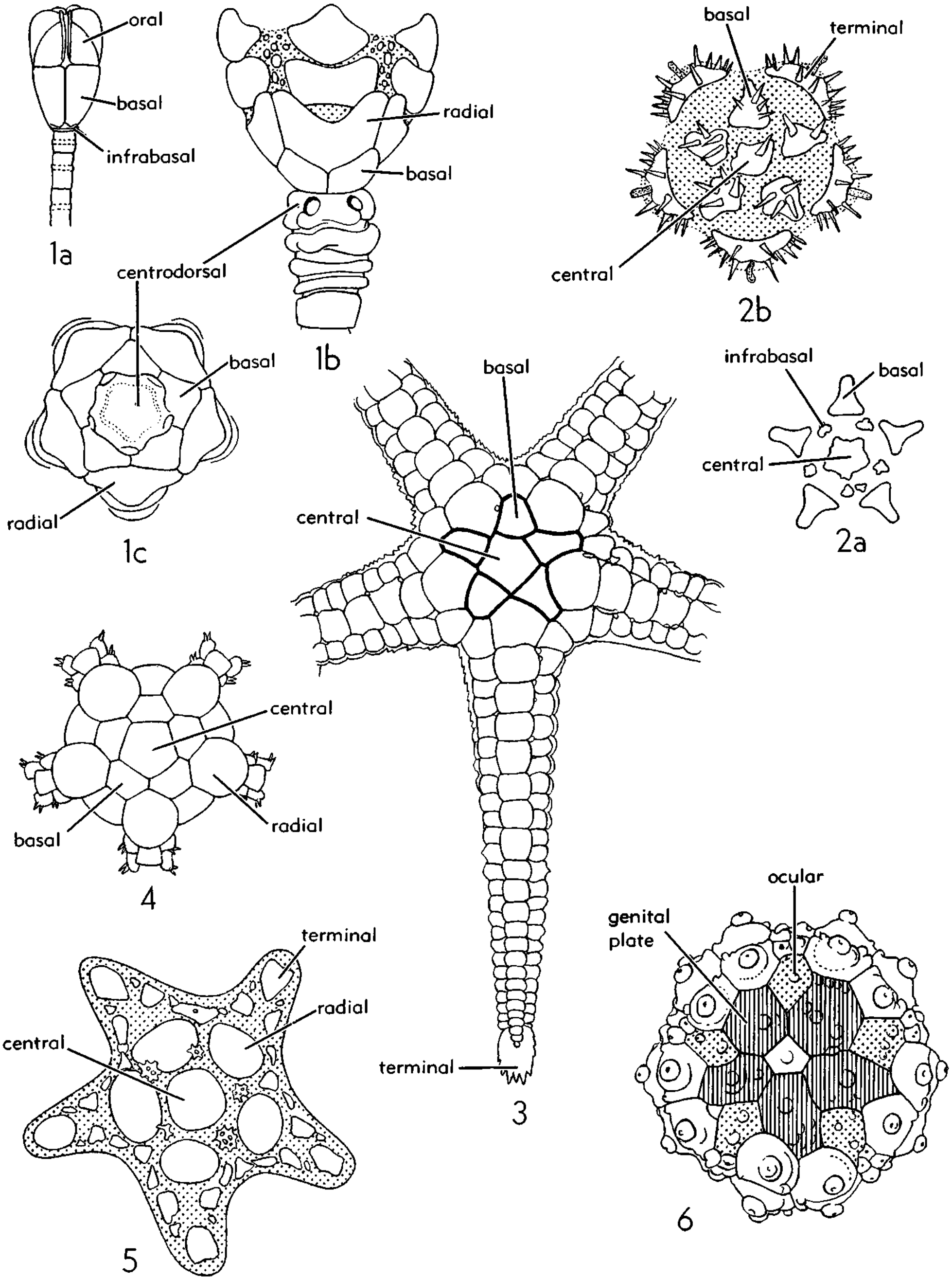

FIG. 18. Comparison of aboral endoskeletons of echinoderms.——*1. Promachocrinus kerguelensis* (crinoid); *1a,* very young larva, ×48 (Clark); *1b,c,* lateral and dorsal views of 2-year pentacrinoid stage, ×8 (Fell).——*2. Asterina* sp. (asteroid); *2a,b,* two stages, ×10 (Fell).——*3. Cnemidaster wyvillii* (asteroid), ×3 (Sladen).——*4. Ophiosteria echinulata* (ophiuroid), immature specimen, ×4 (Fell).——*5. Amphipholis squamata* (ophiuroid), very young individual, enl. (Cuénot, after Ludwig).——*6. Austrocidaris canaliculata* (echinoid), immature specimen, ×26 (Lovén).

Devonian ostracoderm, *Drepanaspis*. In the view of Gislén (1930), the asymmetries in organization of the "carpoids," especially in the position of the multiple orifices of the upper face of *Ceratocystis* and *Cothurnocystis,* offer close resemblances with the asymmetries and arrangement of the branchial slits of *Amphioxus* larvae. These comparisons are based either on superficial analogies or on erroneous interpretations of the "carpoid" organization. Equally objectionable is the assertion by Spencer (1938) that the polygonal canaliculated plates of certain cystoids (e.g., *Aristocystites*) closely resemble the bony scales (tesserae) in the armor of ostracoderms or the view of Caster & Eaton (1956) that plates of the stylophoran *Paranacystis* exhibit a microstructure like that of the superficial layer of plates of the ostracoderm *Procephalaspis oesolensis.* As a matter of fact, the plates of echinoderms and tesserae of ostracoderms show entirely different histologic structure, quite aside from the fact that the bones of vertebrates and stereom of echinoderms have fundamental distinctions that should not be forgotten.

ORIGIN AND DEVELOPMENT OF ECHINODERM ORGANIZATION

The origin of echinoderms and the manner in which their organization (structure) has developed have been subjects of numerous speculations. For the ancestor and for representatives of initial phases in the history of the phylum rather widely diverse pictures have been proposed. Figures 19-20 represent some of these. The best-known, almost classic representation is the dipleurula, a hypothetical pre-echinoderm stage which should be reproduced in ontogeny (Fig. 13,*A*). All these representations help in understanding the genesis of the organization of echinoderms; this is their virtue. There is trouble, however, in distinguishing in them the part that is purely speculative from well-justified interpretation of facts. It seems more in accord with modern scientific procedures to be limited by interrogating in critical manner the diverse sources of our information and by drawing from them guidance in efforts to clarify somewhat initial phases in the history of the phylum.

The important foundation of common characters presented by the first ontogenetical stages of living forms and the organization of the only zoological group to which one may usefully compare echinoderms—that is to say, the Stomochorda—lead us to agree that echinoderms are derived from free bilaterally symmetrical forms with three pairs of coelomic pouches (or perhaps only two pairs, for division of the anterior two pairs is not always sharp) and that these pouches are developed by unequal division of a pair of sacciform evaginations of the archenteric wall. We may still agree that from the beginning the three (or two) pairs of coeloms were more or less well differentiated and, as in the Pterobranchia, of quite different size. Also generally acceptable is the conclusion that the coeloms in each pair were probably equally developed from the beginning, although in Recent larval forms only the left anterior coelom undergoes a complete division. As we have seen, certain observations from embryology require that we regard this asymmetry as secondary. Nevertheless, it constitutes a fundamental ontogenetic character which controls all stages of development, and which may be traced back to the egg. This precocity and its organogenetic importance leads to query as to whether the bilateral symmetry of the ancestral forms was not already disturbed. In any case, asymmetry must have been acquired very early by the phylum.

As an indication of this, we find no fossil echinoderms possessing two hydropores, which would allow the conclusion that two functional hydrocoels existed. The endoskeleton of "carpoids" and helicoplacoids, which probably may be considered as the most primitive of all known echinoderms, since they have no radial symmetry, lacks bilateral symmetry; although in some "carpoids" it tends to acquire a certain bilaterality, this never masks its profound and multiple asymmetries. If, then, a pre-echinoderm symmetrically bilateral stage existed, it could only have been well before the beginning of Cambrian time. It is surprising, then, that Whitehouse (1941) judged that in an enigmatic Middle Cambrian fossil of

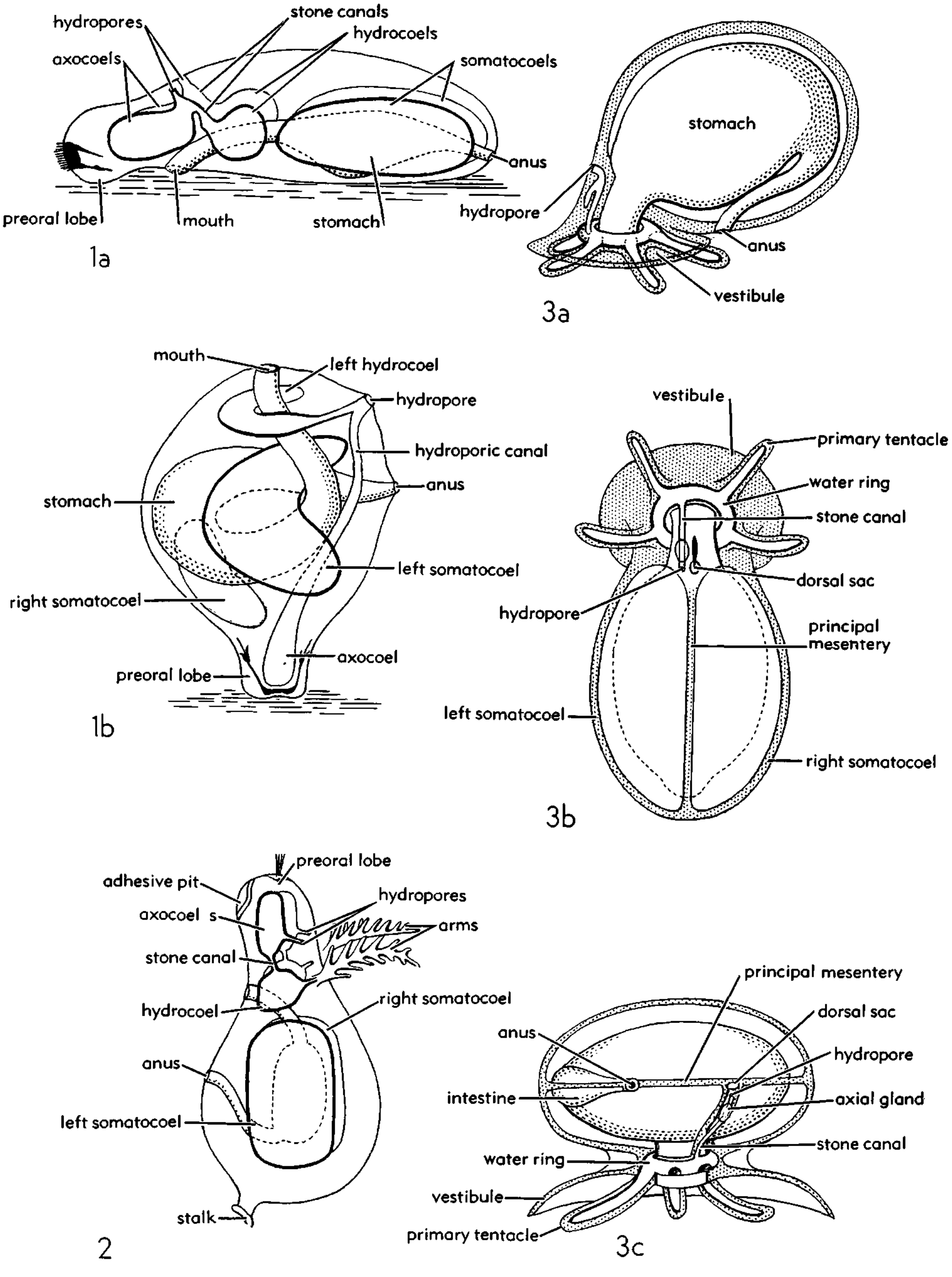

FIG. 19. Theoretical reconstructions of echinoderm ancestor.——*1.* Dipleurula ancestor; *1a,b,* from left side and after fixation (primitive pelmatozoic ancestor) (Bather).——*2.* Dipleurula ancestor (Heider).——*3.* Pentactaea ancestor; *3a-c,* from left side, dorsal view, and after torsion to radial stage (half of vestibule and two tentacles supposedly removed) (Bury).

Queensland *(Peridionites)* he had found a form corresponding morphologically to the stage of dipleurula in larval development of the phylum, a quite erroneous and improper interpretation, as shown clearly by GISLÉN (1947), HYMAN (1955), NICHOLS (1962), and others.

In order to explain the morphologic and ontogenetic peculiarities of echinoderms, it is commonly supposed that their ancestors have passed through a fixed stage. This condition refers to (1) the radial organization of the adults, (2) the asymmetrical development of many structures, (3) the rotations and torsions undergone by organs during ontogeny, (4) the possession of a calcareous well-developed endoskeleton necessary to protect a sessile organism, and (5) the fixation that actually precedes or accompanies the metamorphosis of the larvae of crinoids and numerous asteroids and that one generally agrees to recognize as having great phylogenetic importance.

In order to explain the preponderant development of organs belonging to the left half of the body, at expense of those of the right half, and the displacement of the mouth to the left of the larva, diverse authors (BÜTSCHLI, LANG, BATHER, VON ÜBISCH) have supposed further that fixation was effected by the right part of the anterior extremity or that the ancestral forms came to rest on the right side of the body or became fixed with that side (GISLÉN).

As a consequence of this, it is supposed that (1) the preoral part of the body became elongated in a peduncle, undeveloped or entirely lost in most free echinoderms; (2) the mouth was displaced toward the left and eventually to the morphologically posterior pole; (3) the principal organs underwent a torsion by which the originally left side became the oral part of the developed organism, and the originally right side, the aboral part; (4) the structures in the right anterior part of the body were reduced, with preponderant compensatory growth of the left half. In summation, if we follow the most generally accepted interpretation, the event marking the origin of the echinoderm phylum would have been adaptation to a sessile or sedentary mode of life.

This hypothesis, of course, cannot be founded on present paleontological evidence. As a matter of fact, the "carpoids" and the Helicoplacoidea, which are probably the most primitive known echinoderms, were not attached to the sea bottom. But this does not imply that their ancestors were not fixed. It does simply show that, if a fixed stage ever existed in the common history of the phylum, this stage must belong to such remote past that it is unlikely that it could be represented in the fossil record. It is true that certain Ordovician cystoids (e.g., *Aristocystites*) have been considered sometimes (BATHER, 1900, 1901, 1929) as presenting the structure of this primordial form forecast by theory. But it appears more and more evident that cystoids in general and the Aristocystitidae in particular comprise a specialized group that does not possess this generalized organization from which could be derived the basic structure of *all* other echinoderms.

The above theory is almost entirely founded on ontogenetic considerations. It postulates that the changes which occur in the development of Recent echinoderms possess, at least to some extent, a recapitulative significance. It must be noted, however, that (1) the morphologic orientation and asymmetry of the embryo are found to be already determined in the egg of certain echinoderms, then *before* any development; (2) all traces of a fixed stage have disappeared from the ontogeny of holothuroids, echinoids, ophiuroids, and even many asteroids; (3) the fixation of asteroid larvae is regarded by some zoologists as a cenogenetic specialization without phylogenetic significance; (4) the attachment of the crinoid and asteroid larvae takes place in the middle line (not on the right side) of the anterior part of the larval body; (5) the appearance of a protective endoskeleton probably results less from a special cause such as the discovery of the bottom by direct ancestors of echinoderms than from a more general factor responsible for the production of skeletal structures in many unrelated invertebrates in late Precambrian time or at about the beginning of the Paleozoic Era.

The appearance and development of radial symmetry in echinoderms generally is also attributed to adaptation for a fixed

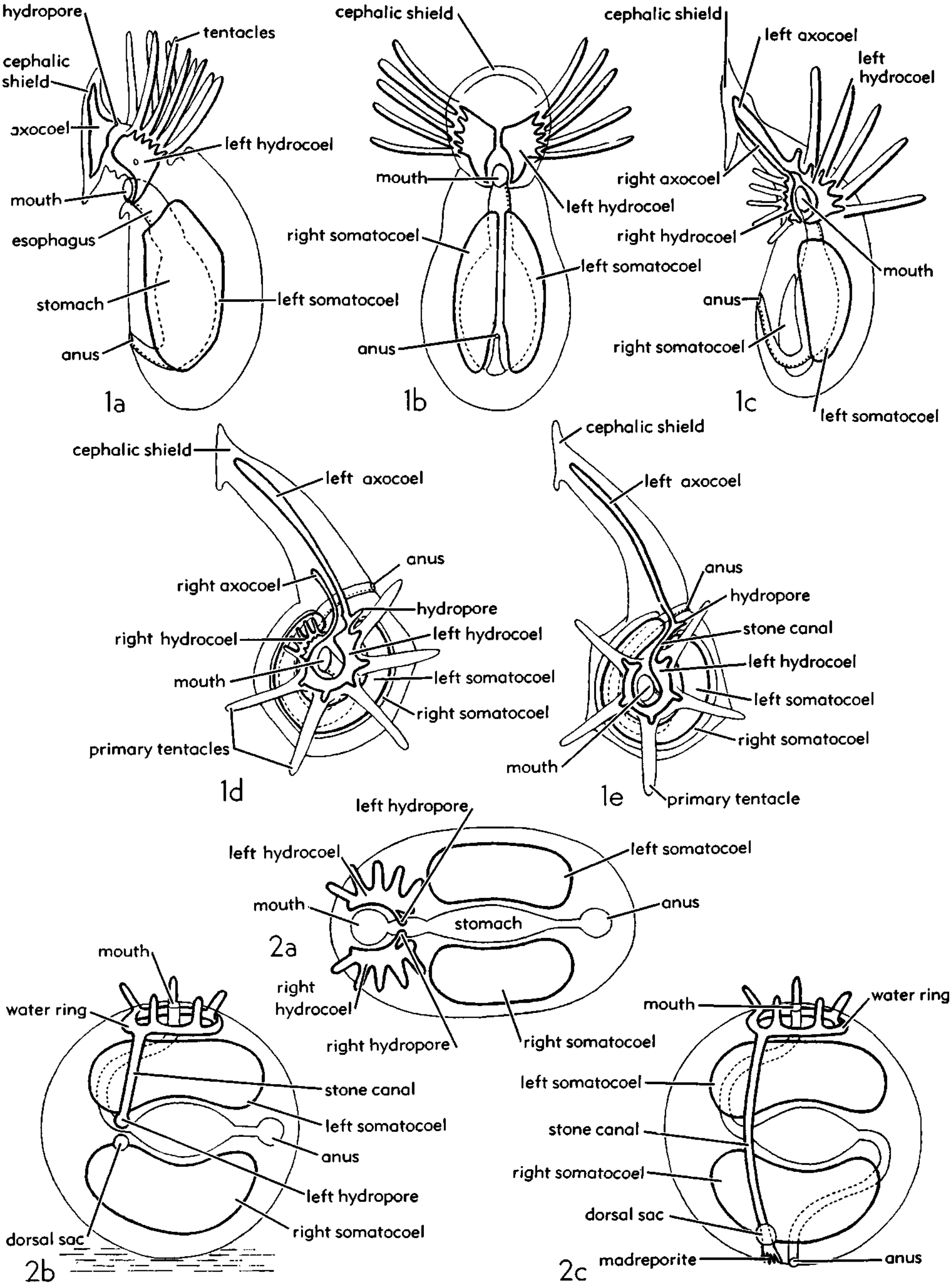

FIG. 20. Theoretical reconstructions of echinoderm ancestor (continued).——*1. Cephalodiscus*-like ancestor; *1a,b,* from left side and ventral view; *1c-e,* progressive stages in transformation to echinoderm, from left side (Grobben).——*2.* Echinoderm ancestor; *2a,* free-living bilateral form, ventral view; *2b,* radial condition after fixation; *2c,* echinoid condition, again free-living (von Übisch).

mode of life. Such a conclusion is not obligatory, however, since fixed organisms exist which are not radial and radial organisms are found, which, like the ctenophores, probably never have been sessile. In addition, radial symmetry of the echinoderms is superimposed in the course of ontogeny on asymmetry of free-swimming, as well as fixed, larvae. For the rest, if a fixed mode of life is attributed to ancestors of the echinoderms, it is not so much for explaining their radial symmetry as for taking account of the hypertrophy in growth of the left side as compared to the right side, correlated with torsions shown by the organs in the course of metamorphosis. What embryology suggests appears to be entirely different. It indicates that radial symmetry is introduced by development of the left hydrocoel and by the morphogenetic modifications that this part of the coelom exercises on other organs, as well shown by RUNNSTRØM (1918). Now the left hydrocoel develops the water-vascular apparatus, which in initial stages of its growth is represented by the five primary tentacles and resembles the lophophore of pterobranchs. At most, we can suppose that fixation of the free bilaterally symmetrical ancestor by the right anterior part of the body and accompanying reduction of the right hydrocoel provided the conditions needed for the left hydrocoel to grow around the esophagus into a ring from which proceeded the five primary radial structures. In this way, we may recognize the possibility of some indirect relation between radial symmetry and the presumed passage through a fixed stage during the history of the phylum, but all the same nothing in this assumption explains why the left hydrocoel acquired a fivefold (rather than a three-, four-, or sixfold) organization.

BATHER (1900, 1901, 1929), followed by HEIDER (1912), has maintained the view that the pentamerous condition of the echinoderms must have been preceded by a triradiate condition of the subvective system. This opinion is based on interpretation of a morphological series consisting of certain attached fossil echinoderms (cystoids) and on some theoretical considerations. Initially, three food grooves (three arms, according to HEIDER, two primitive lophophores and a third added later) would be spread out on the theca diverging from the mouth, one in a direction opposed to the anus, and the other two on each side of the mouth; the development of a groove on the posterior side would have been prevented by the presence of anus and hydropore. Eventually, the two lateral grooves would be divided, increasing the number of alimentary furrows to five. These grooves, fringed by tentacles (podia) produced from the left hydrocoel, would gradually lengthen outward. Other coelomic extensions would accompany them, serving as blood vessels, while the ciliated epithelium covering the floor of the grooves would produce the five radial ectoneural cords. The tentacles would remain as small soft structures, or contrariwise, would be enlarged and come to be supported by endoskeletal plates. The ciliated grooves would then be extended along these giant podia developed as brachioles. Finally, this pentactiny, at first superficial, would have gradually affected internal organs and eventually the whole organism.

Two sorts of objections may be opposed to these considerations. The first is that they find no support in embryology. The other objections are based on paleontology. A triradiate condition of the subvective system observed in a very small number of fossil echinoderms, represents a secondary character, without doubt. Archaic fixed forms show an important range of variation in the number of brachioles and food grooves. Moreover, the cystoids to which BATHER referred comprise a strongly specialized group preceded in time by other classes, namely that of the helicoplacoids, "carpoids," edrioasteroids, and eocrinoids. Now, only one food groove starts from the mouth in helicoplacoids, and in mitrate, cornute, and solute carpoids. The edrioasteroids exhibit a well-defined pentamerism from the time of their first appearance in the Lower Cambrian and the eocrinoids possess multiple brachioles generally distributed in five groups. We may add that in all earliest known representatives of the blastoids, crinoids, stelleroids, echinoids, and ophiocistioids, pentaradial symmetry is already very well developed. This indicates that paleontology offers no solution to the problem of the origin of the pentamerous condition in echinoderms. In fact most representations of the source stock of echinoderms admit the existence in it of either two tentacles-bearing arms, as in *Rhabdopleura* (HEIDER) (Fig. 19,*2*), or a group of five tentacles (*Pentactaea* of SEMON and of BURY) (Fig. 19,*3a-c*), or two groups of tentacles, one right and the other left (BÜTSCHLI, GROBBEN, VON ÜBISCH) (Fig. 20,*1-2*).

The entirety of the preceding consideration brings out more what is not known than what is known. It is true that the phylogenetic phases that we have tried to trace must belong much farther back in geological time than the earliest terrains found to contain fossils. Interpretations based on embryology cannot, for the most part, be confirmed by this evidence; in no case should they be considered as a certainty. The phylogenetic theories, even the most ingenious, may be useful as working hypotheses, but one cannot minimize the important part of speculation which they contain.

ORIGIN AND INTERRELATIONS OF ECHINODERM CLASSES

The differentiation of classes among echinoderms belongs to Precambrian time, or, at least, was accomplished during the earliest Paleozoic. Remains of Helicoplacoidea, Edrioasteroidea, and Eocrinoidea are found in the lower half of the Lower Cambrian. Slightly later, but still in the Lower Cambrian, occur two genera (*Camptostroma* and *Lepidocystis*) which may represent two other classes. In Middle Cambrian, other major groups are recorded: Homostelea, Stylophora, along with the enigmatic Australian forms *Cymbionites* and *Peridionites*. Homoiostelea, Crinoidea, Stelleroidea and Ophiocistioidea are first observed in the Uppermost Cambrian or in the Lower Ordovician. All other classes of echinoderms, including Holothuroidea (identified by isolated spicules), are known from the Middle or Upper Ordovician onward, and no new class has been introduced since the close of that period.

Next, we may observe that these classes, from the time of their appearance in the geologic record, are generally well delimited in fundamental and distinctive characters. The assignment of a fossil to one of these classes is rarely doubtful if its morphology has been adequately elucidated. It is true that forms reputed to be intermediate between the defined classes exist, for they combine certain structural characters considered as distinctive of the different classes. But these so-called intermediate forms, although relatively numerous among early echinoderms, are only morphological intermediates; none of them indicate true phylogenetic links between the classes (REGNÉLL, 1960). The origin of the classes is unknown.

Another very important observation relates to the great antiquity of the architectural plan on which each of the echinoderm classes is constructed. The earliest crinoids and first echinoids, for example, exhibit structural organization essentially similar to that of living crinoids and echinoids. Without doubt, in the course of phylogeny of each of these groups, important transformations that represent functional and morphological adaptations to different modes of life have been introduced as response to ecologic conditions. But fundamental anatomical plans have remained unchanged throughout the history of these classes. Even structures as complex as the Aristotle's lantern of echinoids may be traced back to the very distant past.

Extreme antiquity of essential structures of the classes is matched by like antiquity of their main systematic divisions. As soon as they appear, the "carpoids" are represented by three classes (Homostelea, Homoiostelea, Stylophora) and the cystoids by their two orders (Rhombifera, Diploporita); the Crinoidea (already in the Middle Ordovician) by three of their four subclasses (Camerata, Inadunata, Flexibilia); the Echinoidea by two of their orders (Bothriocidaroida, Echinocystitoida); the Stelleroidea, by their three subclasses (Somasteroidea, Asteroidea, Ophiuroidea). This so-very-early diversification carries far back in time the actual origin of the classes and shows that their differentiation must be much earlier than the moment represented by actual remains found in rock strata.

Another observation seems worthy of record, namely, that from the time of their appearance in the stratigraphic record, the echinoderms have been distributed into two large groups according to their habits with respect to environment—free forms, such as the mitrate and cornute "carpoids," stelleroids, and echinoids, and attached forms, such as the crinoids, cystoids, and blastoids. Already in earliest Cambrian time, free-living (helicoplacoids) and sessile forms (eocrinoids, edrioasteroids) were represented. The attached mode of life is generally referred to as **pelmatozoic**[1] (from *Pelmatozoa,* a term proposed by LEUCKART, 1848, and meaning animal, *zoon,* provided with a stalk, *pelma*) and the free mode of life as **eleutherozoic** (from *Eleutherozoa*, a name introduced by BELL, 1891, and meaning animal that moves freely, *eleutheros*). Typically pelmatozoic mode of life characterizes those echinoderms which, during the whole or at least the early portion of their existence, are attached either directly by the aboral surface or by an aboral jointed stalk; their oral surface is directed upward; their podia serve primarily as food-catching organs, their regimen is microphagous and their ambulacra, acting as food-grooves, carry food particles to the mouth by mucus-ciliating mechanisms; their anus generally opens on the oral surface or laterally, but never aborally. On the other hand, adoption of a free-living or eleutherozoic habit means that the animal develops locomotor mechanisms and a mode of nutrition which generally is nonciliary; the oral surface is directed downward or is located at one end of the body (holothuroids); the anus, if present, is typically aboral.

Customarily such contrasting characters as those just mentioned have been used as a basis for a division of the phylum Echinodermata into two subphyla, the Pelmatozoa and the Eleutherozoa. It has become more and more evident, however, that this grouping is less supported by real genetic affinities than by structural and functional analogies. Pelmatozoan and eleutherozoan characters have probably arisen independently, and at different times, in various echinoderm groups. Therefore, it does not seem possible to build a natural classification on the basis of the described characters alone (FELL, 1963, 1965).

Evidence furnished by comparative anatomy, embryology, and paleontology suggests that symmetry and patterns of dominant gradients of growth, which may be considered as innate features initially independent of the environment, probably constitute a better criterion for grouping of the classes in more comprehensive units. On such grounds, for subphyla[2] recently have been recognized by FELL (1965). They have been adopted in the present *Treatise,* as indicated in the following table.

Subphyla of Echinodermata

Subphylum HOMALOZOA. Echinoderms without radial symmetry and with fundamentally asymmetrical body. Included classes: HOMOIOSTELEA, HOMOSTELEA, STYLOPHORA (these three classes collectively called "carpoid" echinoderms), and possibly MACHAERIDIA.

Subphylum CRINOZOA. Echinoderms with radial symmetry, showing a partial meridional pattern of growth tending to produce an aboral cup-shaped or globoid plated test (theca) and a partial radially divergent pattern of growth forming appendages (brachioles or arms) which carry exothecal extensions of feeding ambulacra. Included classes: BLASTOIDEA,

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[1] More rarely, statozoic (from Statozoa, a name coined by BELL, 1891, and meaning animal which is stationary, *statos*).

[2] Many other groupings of echinoderm classes have been proposed in the past. Most of them deserve no more than historical interest. Some seem worth recording because they have played a part in shaping basic concepts of the present classification. In the famous work in which he demonstrated that the echinoderms are to be regarded as a main division of the animal kingdom, LEUCKART (1848) divided the phylum into three classes, termed Pelmatozoa (including *"Cystideen"* and *"Crinoideen"* as orders), Actinozoa (including *"Echiniden"* and *"Asteriden"* as orders) and Scytodermata (including Holothuriae and Sipunculida as orders). In 1891, BELL proposed a rather complicated classification, in which the term Eleutherozoa (used for the first time) is opposed to the term Statozoa (practically a synonym of Pelmatozoa). This procedure seems to have initiated the dualistic division into Pelmatozoa and Eleutherozoa, popularized by BATHER (1899, 1900) and adopted in most treatises and textbooks published subsequently. In presenting his classification, BATHER was fully aware of the phylogenetic heterogeneity of the Eleutherozoa, but he judged the Pelmatozoa to comprise a closely related group. In 1929, however, he recognized the nonpelmatozoan nature of the "carpoids" (invariably placed among the Pelmatozoa until then) and recommended that they should be separated (along with the Machaeridia) from all other echinoderms. This led WHITEHOUSE (1941) to propose a new subphylum, Homalozoa, for both the "carpoids" and the machaeridians. On the other hand, ZITTEL (1895), following HAECKEL, recognized three subphyla—Pelmatozoa, Asterozoa, and Echinozoa, distributing the free-living echinoderms in two subphyla instead of one. A similar grouping was advocated by JAEKEL (1918), MATSUMOTO (1929), and especially by FELL (1962), who furnished evidence of the fallacious nature of the presumed significant similarities of the eleutherozoans.

CRINOIDEA, CYSTOIDEA, EDRIOBLASTOIDEA, EOCRINOIDEA, PARABLASTOIDEA, PARACRINOIDEA, and LEPIDOCYSTOIDEA.

Subphylum ASTEROZOA. Echinoderms with radial symmetry, showing a radially divergent pattern of growth which produces projecting rays and a star-shaped body. Included class: STELLEROIDEA, containing subclasses Somasteroidea, Asteroidea, and Ophiuroidea.

Subphylum ECHINOZOA. Echinoderms with radial symmetry, meridional pattern of growth producing an essentially globoid body, but no arms or projecting rays. Included classes: CYCLOCYSTOIDEA, ECHINOIDEA, EDRIOASTEROIDEA, HELICOPLACOIDEA, HOLOTHUROIDEA, OPHIOCISTIOIDEA, and CAMPTOSTROMATOIDEA.

The stratigraphic distribution of the subphyla and classes of the Echinodermata is shown graphically in Figure 21. However, this diagram has not been redrawn to include newly recognized classes defined by DURHAM—the curious CAMPTOSTROMATOIDEA (L.Cam.), added to the Echinozoa, and LEPIDOCYSTOIDEA (L.Cam.), assigned to the Crinozoa. Also, the Holothuroidea possibly range into the Ordovician.

MAIN DIVISIONS OF ECHINODERMATA

HOMALOZOA

The subphylum Homalozoa—a term proposed by WHITEHOUSE (1941) and meaning flat *(homalos)* animal *(zoon)*—comprises the exclusively fossil group (Middle Cambrian to Middle Devonian) of "carpoid" echinoderms and perhaps the enigmatic Machaeridia (Fig. 21).

As stated previously, the Homalozoa lack any trace of radial symmetry, a feature the importance of which had already been emphasized by BATHER (1930), who proposed to divide the Echinodermata into two contrasted groups: the Echinoderma bilateralia comprising the "carpoids" and Machaeridia, and the Echinoderma radiata, containing all the other echinoderms. If the concept is sound, the term "bilateralia" is inappropriate, for it fails to recognize another of the most important features of these echinoderms, namely, their fundamental asymmetry.

The Machaeridia were marine animals with body enclosed in an elongate, bilaterally symmetrical shell composed of an even number of longitudinal columns of plates. They have been referred to the Mollusca, Annelida, Arthropoda, and (because their plates are composed of crystalline calcite showing, in at least one genus, the cleavage characteristic of echinoderms) to the Echinodermata. Among echinoderms, they have been regarded either as a distinct group representing an early offshoot from the echinoderm stem (BATHER) or as isolated parts of the body of forms belonging to other classes. On this last hypothesis, some of them have been considered as the stem of "carpoids" (WOODWARD), the cover plates enveloping the spines of mitrate "carpoids" (POPE), or the tube feet of ophiocistioids (NICHOLS).

If the assignment of Machaeridia to Echinodermata remains an open question, the same doubt regarding the "carpoids" would not be permissible, for (1) their stereom is formed of crystalline calcite displaying the reticulate microstructure characteristic of this phylum, and (2) most of them possess an ambulacral groove organized according to the typical echinoderm pattern.

The "carpoids" have been and still are commonly classed with the pelmatozoan echinoderms. No morphologically intermediate forms are known between them and the other echinoderms, however. They constitute a very isolated group, characterized primarily by their asymmetry, on which radial symmetry has never been imposed. This lack of radial symmetry is probably related to the fact that their water-vascular system did not produce five primary tentacles, but sent only one extension into a single ambulacrum, which may be looked upon as an unpaired lophophore structure. All of them are depressed and they seem to have experienced some sort of eleutherozoic existence. They probably belong to another and apparently much more primitive adaptive radiation than those that produced the radiate echinoderms.

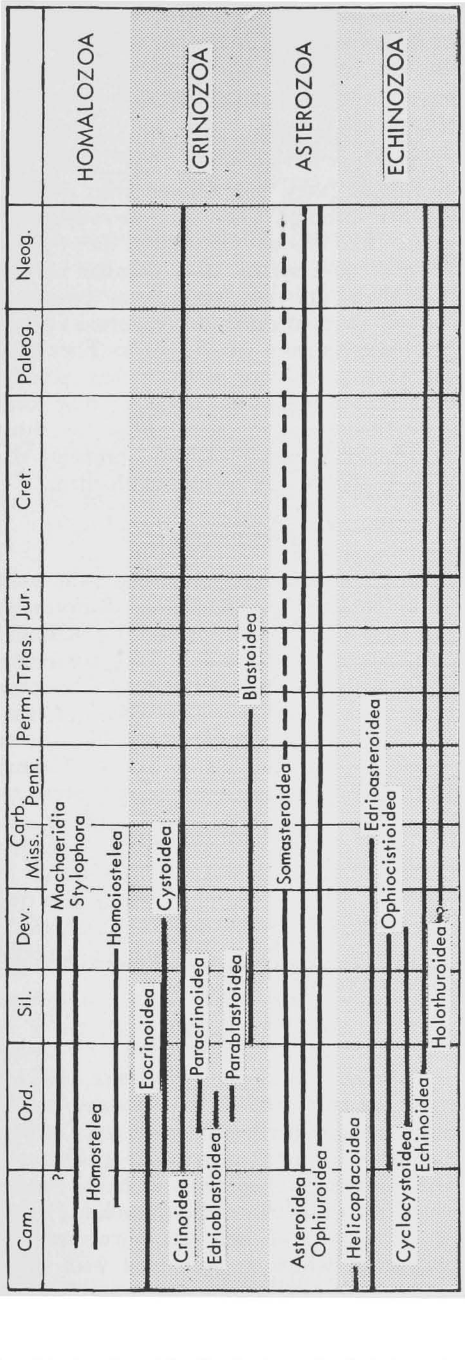

Fig. 21. Stratigraphic distribution of subphyla and class of Echinodermata (Ubaghs, n). [Added groups include the echinozoan class Camptostromatoidea (L. Cam.) and crinozoan class Lepidocystoidea (L. Cam.).]

The "carpoids" were first recognized as an independent class by Jaekel (1901), who divided it later (1918) into four orders: Cincta, Cornuta, Mitrata, and Soluta. To these, Gekker (1938) added the new order Digitata to include *Rhipidocystis.* Now it appears that this assemblage is quite heterogeneous. Firstly, *Rhipidocystis* differs from all other "carpoids" in having strongly developed brachioles and other crinozoan features; it seems preferable to place it among the Eocrinoidea (Ubaghs, 1961). Secondly, whereas the Cornuta and the Mitrata present the same basic organization, they differ as much from the Cincta and Soluta as the two latter differ between themselves. These orders, except the two first ones, are so widely apart that relationships between them cannot be satisfactorily proven. They may represent unrelated, or at least remote, remnants of an early preradiate echinoderm stock. Therefore, it seems better to treat them as separate classes: Homostelea, containing the Cincta; Homoiostelea, comprising the Soluta; and Stylophora, grouping together the Cornuta and Mitrata.

CRINOZOA

The Crinozoa, a name proposed by Matsumoto (1929), are echinoderms which are 1) affected in varying degree by radial (generally pentamerous) symmetry; 2) typically characterized by a globoid, pyriform, or cup-shaped body (theca) enclosing the visceral mass or the main part of it, and 3) provided with food-gathering appendages which are either simple exothecal projections (brachioles of noncrinoid Crinozoa) or evaginations of the body wall carrying extensions of the coeloms and various systems of organs with them (arms of crinoids). In the theca, the meridional pattern of growth appears dominant, whereas in the food-gathering appendages (particularly the arms of crinoids), it is the radially divergent pattern which is prevalent. Crinozoa are attached more or less permanently to the substrate, either directly by their aboral surface, or more generally by an aboral jointed stalk. Their oral surface is typically directed upward. Their podia serve primarily as food-catching organs; their regimen is microphagous and their ambulacra act as food grooves. The anus generally opens on the oral surface and, though it may be found on the side of the theca, is never strictly aboral. All members of this subphylum, except crinoids, are exclusively Paleozoic.

The subphylum Crinozoa, as here defined, corresponds to the subphylum Pelmatozoa of many other classifications, except that it does not include the "carpoids," which are classified among the Homalozoa, and the classes Edrioasteroidea and Cyclocystoidea, which are transferred to the Echinozoa. As so restricted, it comprises eight classes: Eocrinoidea, Paracrinoidea, Cystoidea, Blastoidea, Parablastoidea, Edrioblastoidea, Lepidocystoidea, and Crinoidea. Such classes seem to have unequal value, whether one considers numbers of their representatives, diversity within each group, distribution in geologic time, or importance in stratigraphic paleontology. To judge them according to purely morphological criteria, certain classes, such as the Crinoidea and Blastoidea, seem to form natural groups having well-defined morphological attributes, but others may well represent artificial or heterogeneous assemblages.

EOCRINOIDEA

The oldest known crinozoans are Lower Cambrian members of the Eocrinoidea (Fig. 21). This group, introduced by JAEKEL (1918) as a subclass of the Crinoidea, was elevated to class rank by REGNÉLL (1945). It comprises heterogeneous assemblage of genera, some of which are still inadequately known. Though the organization of at least many of their representatives is essentially cystoid-like, they differ from typical cystoids either in their entire lack of thecal pores or in the presence of sutural pores which are basically different from the diplopores and pore rhombs of the true cystoids. On the other hand, most of their so-called crinoidal features are demonstrably homoplastic resemblances—especially one cannot homologize their brachioles with the arms of crinoids. Therefore, it does not seem possible to refer eocrinoids to the Cystoidea, as now restricted, and still less to the Crinoidea. Thus, it appears convenient to regard them, at least provisionally, as a separate class. Remains of Eocrinoidea have not been found in terrain younger than Middle Ordovician.

PARACRINOIDEA

The Paracrinoidea are exclusively Middle Ordovician in age (Fig. 21). Like the eocrinoids, they are neither true cystoids nor true crinoids. Their theca is constructed mainly like that of cystoids, but they possess a thecal pore system of a peculiar nature, and their uniserial or biserial pinnulate "arms" seem to differ as well from cystoid brachioles as from crinoid arms. They may represent a line of development parallel with that of these groups or they may form an artificial entity. Recognition of them as a separate class constitutes probably the most practical way to deal with them.

CYSTOIDEA

The Cystoidea comprise one of the most important classes of the Crinozoa. Formerly they included in addition to all noncrinoid Crinozoa, the "carpoids," Edrioasteroidea, and Cyclocystoidea. Nowadays, the class generally is restricted to noncrinoid Crinozoa that possess special pores piercing the thecal skeleton (diplopores, pore rhombs) and biserial brachioles; radial symmetry affects their food grooves and, only in advanced members, the thecal plates. Patterns of growth are dominantly meridional in many of them. They are divided into two orders, the Rhombifera and the Diploporita, of unknown origin, which may have developed independently.

BLASTOIDEA

Blastoidea are a fairly distinct class of Crinozoa characterized by 1) their highly developed pentamerous symmetry, 2) prevailing meridional pattern of growth, 3) uniformity of arrangement of their 18 to 21 thecal plates in four definite cycles, 4) specialized nature of their recumbent ambulacral areas, which are provided with great many small biserial brachioles, and 5) particularly distinctive structures and localization of their hydrospires (calcareous infolds of the thecal wall which hang into the body cavity beneath each ambulacrum). They are known from Silurian to Permian (Fig. 21). It has been maintained mainly by JAEKEL (1918) and REGNÉLL (1945) that the blastoids should be considered as a subclass or order of the Cystoidea, especially because the hydrospires may be regarded as a variety of thecal pores and because biserial brachioles are present in both groups. While thecal pores and biserial brachioles exist also in many Eocrinoidea, the distinctiveness of the Blastoidea as a whole and the very special structure and arrangement of their hydrospires make it desirable to separate the group as a class, as now usually is done.

PARABLASTOIDEA

The Parablastoidea are a very small group erected by HUDSON (1907) (as an order of the Blastoidea) for the Middle Ordovician (Chazyan) genus *Blastoidocrinus* BILLINGS (Fig. 21). This form, which recalls the Blastoidea in many respects, differs from them in important features, such as number of thecal plates and structure of the ambulacra. Of unknown ancestry and descent, these echinoderms may well represent an aberrant and unsuccessful offshoot of an early blastoid stock.

EDRIOBLASTOIDEA

The Edrioblastoidea contain so far a single genus, *Astrocystites* WHITEAVES, from the Middle Ordovician of North America (Fig. 21). This genus, of an exclusively meridional pattern of growth, differs from all other Crinozoa in lacking arms and brachioles and in having ambulacral pores, as in the Edrioasteridae, a family of Edrioasteroidea. It is separated, however, from typical members of this class in being provided with a well-defined jointed stem and in having a theca superficially like that of blastoids. Customarily it has been placed among the Edrioasteroidea, but FAY (1961) erected a new class, the Edrioblastoidea, to receive it.

CRINOIDEA

The Crinoidea constitute the most diversified class of the Crinozoa. They are stalked or (but secondarily) stalkless pentamerous echinoderms. Their theca, reduced to an aboral cup covered orally by a vault or tegmen, bears radially outspread food-gathering arms, which generally are branched. Therefore, the theca alone retains the meridional pattern of growth. The arms differ fundamentally from brachioles of noncrinoid Crinozoa. Whereas brachioles are simple external processes of the theca supported by their own small endoskeletal pieces, crinoid arms are evaginations of the body wall containing extensions of the food grooves, coelom, and nervous, water-vascular, hemal, and reproductive systems, and they are supported by plates directly continuous with the radial plates of the theca. The fact that crinoid arms and the brachioles of noncrinoid Crinozoa are not homologous renders particularly puzzling the problem of the origin of the crinoids. They first appear in the Lower Ordovician with all of their essential features, and no morphological intermediates are known which suppress or reduce the gap existing between them and older, more primitive crinozoans. The crinoids, like other classes of Crinozoa, flourished especially during the Paleozoic Era, contributing in large areas to the formation of thick sedimentary deposits. Since the Early Triassic, they have been represented only by the Articulata, one of the four subclasses which may be distinguished among them (Fig. 21).

The morphologic and phylogenetic hiatuses that separate the classes of the subphylum Crinozoa from one another are probably not of the same importance. Some are widely apart, whereas others seem to be somewhat closely allied. The precise origin of all of them is unknown and their interrelationships are very puzzling. Yet the unity of general crinozoan organization supports judgment that the classes may be derived from a common, though uncertain, source belonging undoubtedly to the very distant past. The eocrinoids sometimes have been interpreted as such a possible source. This concept finds support in the fact that they precede known representatives of other classes in time. They may indeed contain ancestors of the cystoids, from which some of them are kept apart by rather artificial distinctions. But possible relationships with other classes, and particularly with the crinoids, remain purely conjectural. The so-called crinoidal features of eocrinoids seem generally based on superficial resemblances.

One does not know any intermediate between eocrinoids and crinoids, or between eocrinoids and paracrinoids, blastoids, parablastoids, and edrioblastoids. It must be emphasized that the time of origin of all classes, each of which possesses its distinctive features from first appearance in the geological record, must be much more remote than it is presently known. The problem of origins remains an open question.

ASTEROZOA

The Asterozoa are radiate free echinoderms that possess a depressed, pentagonal or star-shaped body, consisting of a central disc and typically five rays or arms. This shape results from the fact that growth operates in the horizontal plane along five radially divergent axes around the oral pole, and not, as in Echinozoa, along meridional directions. As a rule the mouth is inferior and always central in position. The tube feet are restricted to the undersurface of the rays. The radial water canals and other radial structures lie on the oral side of the ambulacral plates.

They comprise the asteroids, ophiuroids, and somasteroids. Among modern animals, the asteroids and ophiuroids constitute two well-separated groups, to which most zoologists accord the rank of class. The ophiuroids, however, after metamorphosis, pass through an asteroid stage, characterized among other things by an aboral skeleton closely comparable to that of a juvenile asteroid. Comparative anatomy also shows that the two groups are constructed essentially on the same plan and indicates, with the full support of paleontology, that they converge toward the same source (somasteroids) from which the segregation of asteroid and ophiuroid characters seems to have developed in progressive, divergent manner. It appears, therefore, advisable to consider the somasteroids, asteroids, and ophiuroids as subclasses of a single class, the Stelleroidea, rather than as separate classes.

Some zoologists, in opposition to this view, completely separate the ophiuroids from asteroids so as to align them with the echinoids. This is based on 1) resemblance of the ophiopluteus and echinopluteus larval stages, 2) the existence of a vestibule in the larvae of echinoids and vestiges of it in the larvae of ophiuroids, whereas this structure is absent in the larvae of asteroids, 3) the presence of an epineural canal (instead of the open ambulacral furrow of asteroids) in echinoids and ophiuroids, and 4) observation previously noted that the sterols of ophiuroids (at least of examined species) belong to the same type as those of studied echinoids, whereas the sterols of asteroids are of a different type. These arguments do not seem to be convincing. Indeed, they lend to embryologic and biochemical analogies a phylogenetic meaning that remains to be demonstrated, and they overlook allowance of the possibility that the common features just mentioned between ophiuroids and echinoids could have been acquired independently. As a matter of fact, they strongly conflict with all other evidence, such as that derived from postlarval ontogeny, morphology, and paleontology. Paleontological observations, in particular, suggest a very clear morphological convergence of ophiuroids and asteroids in the direction of a common source, whereas comparison of the history of ophiuroids and echinoids shows that the two groups have followed very distinct pathways since their known initial appearance.

Jaekel (1918), Bather (1901, 1915), and others have postulated the Edrioasteroidea as a possible source of the Asterozoa. It is the nature of their ambulacral furrows, the presence of pores interpreted as ambulacral pores, and the absence of free arms and brachioles that seems to bring them nearer the asterozoans in the same degree as these characters separate them from crinozoans. Besides, the first edrioasteroids considerably precede in time the earliest known asterozoans, and if some of them were firmly attached to the substratum, others could have simply rested on the sea bottom. However this may be, the transformation of an edrioasteroid into an asterozoan would have implied very considerable structural and adaptative modifications, as shown by Bather (1915) with considerable ingenuity. This hypothesis, we must say, has not received the confirmation that discovery of the most ancient known stelleroids by Spencer (1951) should have furnished in its support. Contrariwise, as demonstrated by Fell (1963), the endoskeleton of archaic asterozoans has a fundamental pinnate structure entirely different from that shown by edrioasteroids. If, therefore, some superficial resemblance exists between edrioasteroids and asterozoans, it seems to be ascribed to convergence, rather than genetic relationship.

According to FELL (1963), analysis of the growth patterns exhibited by the endoskeletal elements and related soft structures in fossil and extant stelleroids allows recognition of the original characters of the class. These characters, as illustrated by somasteroids, are exclusively crinozoan. They indicate that the Asterozoa must have arisen from some pinnulate crinozoan stock, namely from some pinnulate crinoid. Indeed, the oral skeleton of the arms of somasteroids resembles that of a pinnulate arm of crinoids to some extent. It is built of elongate rods *(virgalia)* arranged in obliquely transverse rows on either side of the axial series of ambulacral ossicles, as are pinnular ossicles to the brachial ossicles of crinoids. The rows of virgalia form the lateral walls of intervening grooves, protected by cover plates inserted on adjacent virgalia. In these grooves ciliary activity conveys water currents to the main radial groove, and thence to the mouth. Thus, a microphagous ciliary feeding, involving pinnately arranged food grooves, is found in archaic asterozoans, as in pinnulate crinoids.

The analogy is admittedly great, but, to my mind, of a rather superficial nature. Virgalia and pinnulars differ in many respects. The pinnate food grooves of somasteroids have not the same organization as those of the pinnules of crinoids, for 1) they are not carried *on* the virgalia, but lie *between* them; 2) they are not accompanied by extensions from the water-vascular and other systems of organs or cavities as are the food grooves of the pinnules of crinoids, but are just ciliated furrows; 3) they are not small arms, like the pinnules of crinoids, which morphologically are dwarfed arms, and 4) they are apparently of a primary origin, whereas the pinnules of crinoids are demonstrably of secondary origin. Many other and important differences exist between the general anatomy of somasteroids and that of crinoids, and earliest known representatives of the two groups, associated in the same Lower Ordovician beds, far from showing a closer resemblance, appear more distinct than their extant relatives. However appealing they may be, such explanations as those given by FELL remain hypothetical to a large extent, and as long as one has to rely only on them, it seems advisable to reserve judgment.

ECHINOZOA

Echinozoa are typically radiate echinoderms, with a cylindrical, ovoid, fusiform, pyriform, globose, cordiform, or discoid body. Divergent radial axes of growth never arise, but a meridional pattern of development appears to be a fundamental feature of the subphylum. The Echinozoa differ radically from the Asterozoa in their complete lack of outspread rays and from Crinozoa in never having feeding appendages, such as the arms of crinoids or brachioles of cystoids projecting from the body. Most of them are free-moving, but some, like the cyclocystoids and edrioasteroids, are pelmatozoic animals. According to the classification adopted in the present *Treatise,* they comprise seven classes—Helicoplacoidea, Holothuroidea, Ophiocistioidea, Cyclocystoidea, Edrioasteroidea, Camptostromatoidea, and Echinoidea.

HELICOPLACOIDEA

Helicoplacoidea comprise a few genera from the Lower Cambrian *Olenellus* zone of California, Nevada, and Canada. They were free-living echinoderms, characterized by a fusiform (when expanded) to pyriform (when contracted) spirally coiled and heavily plated body, with an expansible and flexible test and with oral and apical poles at opposite extremities. The lack of arms, shape of the body, the origination of new plates from the apical pole and the free-living character suggest that these echinoderms are related to the subphylum Echinozoa. They differ however from all other known Echinozoa by the presence of generally single ambulacrum—a character which they share with the "carpoid" echinoderms Stylophora and Homoiostelea—the spiral arrangement of both the ambulacral and "interambulacral" columns of plates, and the nature of the ambulacrum, covered by a pavement of small plates. Podial pores arranged in a row on each side of the ambulacrum which indicate the presence of an internal "radial" water vascular canal have recently been recognized. The origin of Helicoplacoidea is unknown and their relation with other echinoderms problematical. They may well represent an aberrant offshoot from some Precambrian echinoderm stock.

EDRIOASTEROIDEA

The Edrioasteroidea appear also in the Lower Cambrian, with all of their typical features (Fig. 21). Their origin is not known. They are pelmatozoic echinoderms, and it is in the subphylum Pelmatozoa that they have been included customarily. They differ however from most representatives of this now rejected subphylum in having a purely meridional pattern of symmetry—they lack arms, brachioles, or protruding rays—and in having ambulacral pores which suggest the existence of tube feet provided with ampullae, as in many echinozoans and asterozoans. Besides, they are stemless, or at least never have a typical stem, such as characterizes crinoids and cystoids; some of their earliest representatives may even have rested loose on the sea bottom. In some dendrochirote holothuroids the pharyngeal skeleton is not unlike the calcareous oral ring and the associated ambulacral plates of some edrioasteroids—an analogy regarded by Fell (1965) as suggesting that the Edrioasteroidea, like the Holothuroidea, descended from a common echinozoan stock. The inclusion of edrioasteroids in Pelmatozoa has been questioned by Matsumoto (1929), Lameere (1931), and Fell (1965), who consider that their pelmatozoan features are purely secondary responses to adoption of a sessile mode of life. Reasons for including them (and Cyclocystoidea) in the Echinozoa are given in Part U of the present *Treatise*.

HOLOTHUROIDEA

The origin and relationships of the other classes included in the subphylum Echinozoa offer problems for which no satisfying answers have been given. From a morphological point of view, the holothuroids, which do not move about on their oral surface and have only a single gonad, are unlike other free-living radiate echinoderms which travel on their oral surface and exhibit a genital system (at least in Recent representatives) influenced by radial symmetry. The Holothuroidea are identified as primitive in having only a single gonad and the observation that their gonopore and hydropore have retained original positions in the *CD* interray. The fact that their ambulacra are closed does not indicate any particular relationship, since this feature has been independently acquired in ophiuroids and echinoids. Comparative study of the internal endoskeleton of the pharyngeal region of dendrochirote holothurians suggests, however, that this endoskeleton possibly represents invaginated remnants of ambulacral ossicles similar to those found in some edrioasteroids (Fell, 1965). Nevertheless, the existence of real connections between these two classes remains hypothetical, since the paleontological history of the Holothuroidea is very inadequately known.

ECHINOIDEA

Echinoids form a well-defined group and no known representatives, fossil or living, exhibit features suggesting close relationships to any other class of echinoderms. As rightly observed by Durham & Melville (1957), the ancestral form of echinoids should have evolutionary potentialities able to produce in the Late Ordovician two types as different as *Bothriocidaris* and *Aulechinus*. This observation requires reference of the origin of the class to such a remote time that knowledge of it is at present conjectural. Diverse hypotheses have been formulated, such as derivation of the echinoids from edrioasteroids, from a primitive holothurian stock, or from diploporite cystoids. Each of these hypotheses has received appropriate critical review and none appears convincing at the present time.

OPHIOCISTIOIDEA

The class of the ophiocistioids include five genera, exclusively Paleozoic, the general organization of which does not seem expressed by that of other echinoderm classes. An affinity of the ophiocistioids with ophiuroids has been suggested by several authors, but the points of similarity between the two groups are demonstrably superficial. The resemblance to archaic echinoids seems somewhat greater, but it is with the very young echinoids, in process of metamorphosis or just after metamorphosis, that they show the most remarkable likeness. One may question whether they are not neotenic Echinozoa. Yet the differences from other classes are such as to warrant the appropriateness of regarding the ophiocistioids as a distinct group that became extinct without leaving known descendants.

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ECHINODERM ONTOGENY

By H. BARRACLOUGH FELL

CONTENTS

GENERAL FEATURES

Development in echinoderms may be indirect, involving pelagic, bilaterally symmetrical, larval forms, or more or less direct, with the larval stage either reduced or omitted. Of the extant classes, only the Echinoidea are characterized by being predominantly of the type with indirect development. The main features of development and the interrelationships of echinoderm larvae were elucidated by JOHANNES MÜLLER (30), who demonstrated that four chief types of larvae exist, and that in each the final larval form arises from a preceding simpler form, now known as the **dipleurula.**

The fundamental plan of development is represented in Figure 22. The dipleurula arises from the preceding gastrula stage by the formation of a ciliated (or vibratile) band (Fig. 22,*1*) which forms a closed loop about the mouth. A simple alimentary canal is present, comprising stomodeum, archenteron or stomach, and proctodeum; the anus is generally, but not invariably, formed from the blastopore. In its subsequent development the dipleurula undergoes a transformation varying in accordance with the systematic position of the parent species.

In the Echinoidea and Ophiuroidea, the development of paired processes, or arms on either side of the body, upon which the ciliated band becomes extended, leads to formation of the simple **pluteus** (Fig. 22,*2*). Further development of paired arms, strengthened by internal calcareous rods, leads to the final larval forms, distinguished by MORTENSEN (1898) as **echinopluteus** and **ophiopluteus.**

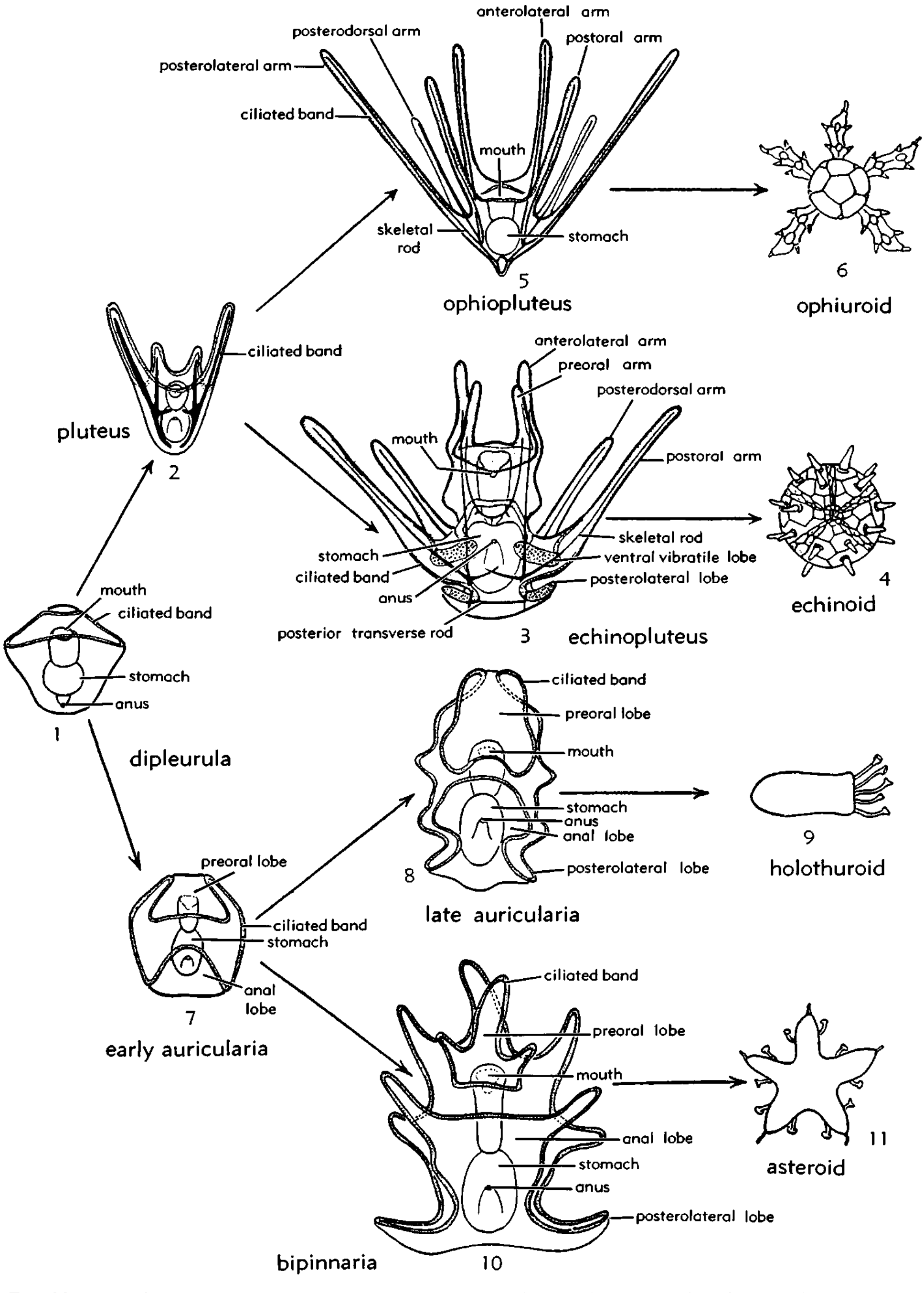

Fig. 22. General scheme illustrating relationships between bilaterally symmetrical larvae of echinoderms inferred from their morphology. *1*, Dipleurula; *2*, pluteus; *3*, echinopluteus, which metamorphoses into *4*, young echinoid; *5*, ophiopluteus, which metamorphoses into *6*, young ophiuroid; *7*, early auricularia; *8*, fully developed auricularia, which metamorphoses into *9*, young holothuroid; *10*, bipinnaria, which metamorphoses into *11*, young asteroid (8).

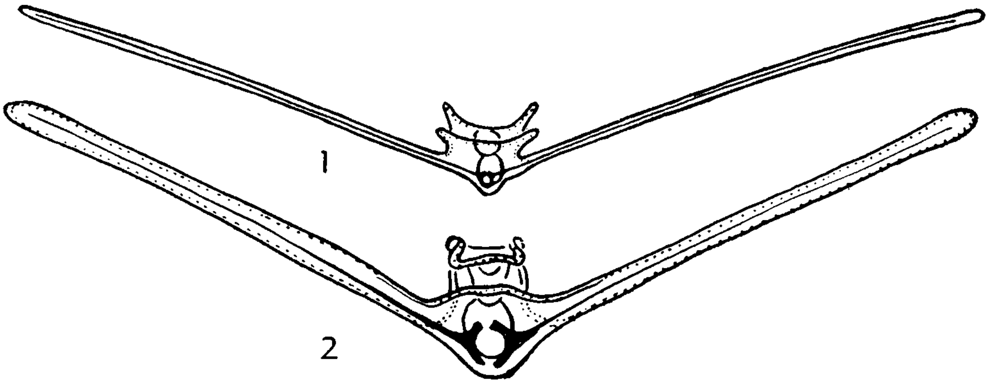

FIG. 23. Convergent larval forms. *1*, Ophiuroid, *Ophiothrix; 2*, echinoid, *Diadema* (8).

The echinopluteus usually possesses four pairs of arms (Fig. 22,*3*), though more or fewer may be present in certain forms. The four principal pairs of arms comprise two anterior pairs, the anterolateral and preoral pairs, and two posterior pairs, the postoral and the posterodorsal pairs. In addition, at the extreme posterior end of the body are commonly found a pair of posterolateral processes, which may be elongated to form distinct posterolateral arms. Anterodorsal arms occur in certain forms as a still further complexity (compare Fig. 29,*11*, a spatangoid echinopluteus). These various arms are supported by slender calcareous rods, which may form a mesh about the archenteron at their inner extremities within the body; commonly a special posterior transverse rod is formed between the posterolateral processes. Certain portions of the ciliated band may become thickened dorsally and ventrally to form the paired dorsal and ventral vibratile lobes; or these may become separated from the main band to form prominent epaulets (see Fig. 29,*7*).

The ophiopluteus (Fig. 22,*5*), if fully developed, is of rather similar appearance, having four pairs of arms, which, however, do not correspond altogether to the four pairs commonly present in the echinopluteus. It is usual that the most prominent and enduring arms are those termed the posterolateral pair, which MORTENSEN has shown to be homologous with the posterolateral lobes of the normally formed echinopluteus. The other arms are the anterolateral, postoral, and posterodorsal pairs, respectively. The preoral arms of the echinopluteus are not represented. The internal skeleton takes the form of a pair of calcareous rods in the body, each sending branches into the four arms on its corresponding side; the posterior transverse rod is not represented.

In larvae of the Holothuroidea and Asteroidea no comparable development of paired arms occurs. Initially the dipleurula becomes rather barrel-shaped (Fig. 22,*7*), and the ciliated band is thrown into folds in an anterior and posterior loop. Further sinuous growth of the ciliated band leads to the characteristic larval forms designated as **auricularia** in holothurians and **bipinnaria** in asteroids.

The auricularia (Fig. 22,*8*) is characterized by the formation of two lobes bordered by the folded ciliated band, the preoral lobe anteriorly, and the anal lobe posteriorly, the latter bearing the anus. The mouth lies in a depression on the ventral side, between the preoral and anal lobes. Smaller posterolateral lobes occur in the same relative position as in the preceding larvae.

The bipinnaria is much more variable in structure. In some, especially primitive starfish, it is scarcely distinguishable from the simple auricularia. More frequently the sinuous lobes of the ciliated band become drawn out into prominent arms (Fig. 22,*10*) which, however, lack skeletal rods. Consequently, they are not rigid and are utilized as flexible swimming organs. Posterolateral lobes are usually found as in the auricularia. Median arms often appear anteriorly to the mouth, on the preoral lobe. It is usual for the bipinnaria stage to be followed by what is termed a brachiolaria larva, distinguished principally by the development of median sucking arms (or disc) anterior to the mouth, by means of which the larva may become temporarily attached.

Metamorphosis in each case involves either discarding or absorbing the paired larval structures, while a secondary radial symmetry is initiated through encirclement of the gut by the five lobes of the hydrocoel.

The embryology of crinoids, so far as known, does not include a comparable bilaterally symmetrical larva, and the mode of development is so different that it cannot be treated in the scheme just outlined. Many echinoderms other than crinoids also undergo development of an entirely different character from the basic plan described above. In species with large yolky eggs the larva is commonly a simple cylindrical form with a number of transverse ciliated bands. This type, which is sluggish and does not take food, has been termed the **vitellaria.** It is formed variously, and the internal organogeny differs according to the class. Echinoderm larvae occasionally grow to a considerable size. Thus the bipinnaria of *Luidia sarsi* reaches a length of 2.4 cm.

The above facts offer interesting problems. The general occurrence of a pelagic bilaterally symmetrical dipleurula stage in four of the existing classes has been interpreted as a recapitulation of the hypothetical dipleurula form from which all echinoderms are supposed to have descended. This view has not been seriously questioned and remains acceptable to taxonomists and embryologists alike. But beyond this point matters are less clear. Are the succeeding larval stages to be interpreted in the same light? If so, we would be led to conclude that ophiuroids and echinoids, with their similar pluteus stages, are more closely related to each other than to any of the remaining classes. Neither taxonomic nor paleontological evidence supports such a deduction. The only alternative is to regard the characteristic postdipleurula larval stages as digressions from the original path of development, which have arisen independently in the various classes. They may have arisen in response to the need for a temporary food-gathering stage as a preliminary to further development; for they almost invariably arise from eggs which are deficient in yolk and cytoplasm.

A more specific examination of modes of echinoderm development also leads inevitably to the conclusion that special larval evolution has occurred, often quite independently of natural groupings, as the following cases illustrate.

It is instructive to compare the larval development of an ophiuroid such as *Ophiothrix* with that of echinoids of the genus *Diadema*. The echinopluteus of the latter is greatly modified through unusual development of the postoral arms and reduction of the other arms, so that it superficially resembles an ophiopluteus (Fig. 23). This case, in which adults conspicuously distinct and only remotely related possess surprisingly similar larval forms, permits of only one interpretation: convergent embryonic evolution has occurred in the echinoid, which temporarily resembles an ophiuroid stage.

Even more striking is the case of the vitellaria larva (Fig. 24). This characteristic cylindrical larva with ciliated annulations, derived from a yolky egg, occurs in three classes, holothurians and crinoids commonly, and ophiuroids rarely. Although GRAVE (17) regarded this larva as representing an original primitive form, this view has received much less attention than it deserves.

Divergent evolution in larval development is also strikingly illustrated throughout the phylum. In ophiuroids, for example, quite diverse modes of development occur (Fig. 25). The case of *Amphiura* is illustrative. Two closely related species of this genus develop so differently that, were the adults unknown, the young stages could hardly be recognized as belonging to the same class, certainly not to the same genus. Nor is this an isolated case, for examples can be found in other genera, such as *Ophiura*.

The conclusion to be drawn from such data is that embryos and larvae of echinoderms are extremely plastic, often exhibiting convergence, divergence, and adaptation susceptible to evolutionary modifications of structure which may act quite independently of the adult stage. Ancestral structure cannot be deduced from such forms.

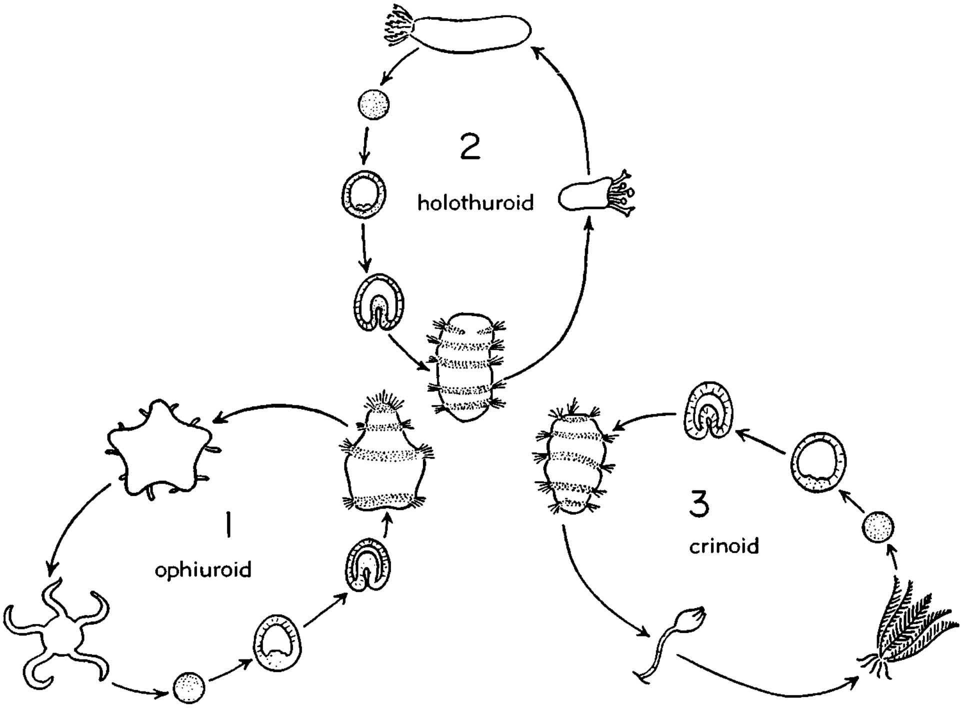

FIG. 24. Convergent patterns of development in unrelated echinoderms. *1*, Ophiuroid *(Ophioderma)*; *2*, holothuroid *(Cucumaria)*; *3*, crinoid *(Antedon)*. In each the larva is a banded vitellaria, which is a widely shared larval form now known to occur in three families of ophiuroids, most holothuroids, and four families of crinoids (8).

LARVAL FORMS AND PHYLOGENY

The auricularia larva presents close and striking resemblances to the tornaria larva of some enteropneusts; the enterocoelous development of the coelom parallels that found in primitive chordates. Hence echinoderms and chordates have long been regarded as related groups. This conclusion, though well established in the literature, is hardly as well grounded on fact, and at present is in dispute.

The significance of similarities in the larvae of echinoderms and protochordates may be viewed in the following context. If the echinoderms are arranged to express their inferred relationships on the basis of their larval similarities and differences, the result places the ophiuroids near the echinoids, and apart from the asteroids. But this totally disagrees with evidence from paleontology and morphology, both of which indicate that ophiuroids and asteroids are closely related taxa. Further, the paleontology of echinoids, at least as well known as that of any other group of animals, indicates that echinoids have followed an entirely independent development since the early Paleozoic. On the other hand, ophiuroids and asteroids share common early Paleozoic ancestors. Therefore, the resemblances between larvae of echinoids and ophiuroids, striking though they may be, can be the result only of convergent larval evolution. Similarly, differences between the larvae of ophiuroids and asteroids, certainly very great differences, must be the result of a secondary larval divergence, because the fossil history of these two groups shows a common derivation at a later date than the divergence of the other groups of echinoderms. It follows inevitably therefore that within the phylum Echinodermata larval characters are no guide to phylog-

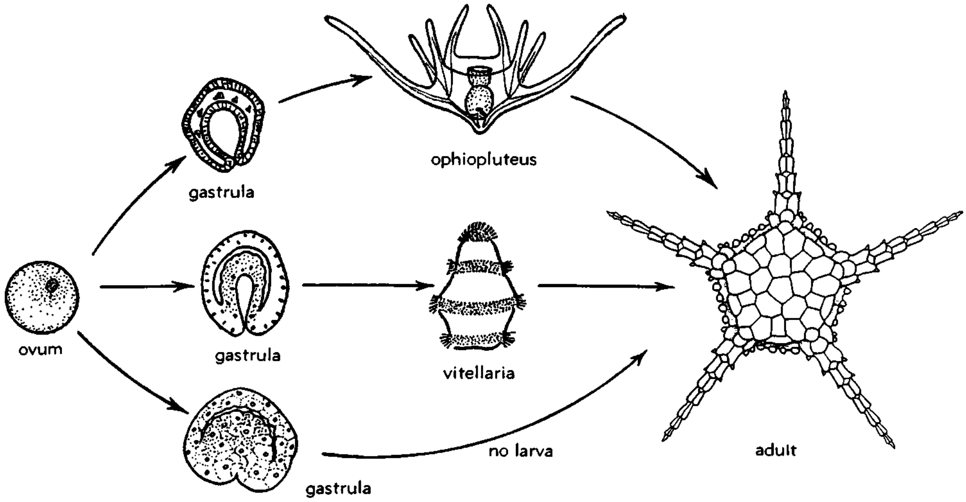

FIG. 25. Divergent patterns of development in ophiuroids. Above, with ophiopluteus larva, as in Ophiothricidae, some Amphiuridae, Ophiocomidae, and some Ophiuridae. Middle, with vitellaria larva, as in Ophiodermatidae, Ophionereidae, and some Ophiuridae. Below, with no larval form, as in Ophiomyxidae and probably most (or ?all) Phrynophiurida (Fell, n).

eny, and, indeed, run contrary to phylogeny. Since ontogeny does not reflect phylogeny within the phylum, it is obviously inadmissible to try to extrapolate beyond the phylum, or to infer phylogenetic affinity between hemichordates and echinoderms solely because the auricularia closely resembles the tornaria. The foregoing analysis, with detailed evidence, has been put forward by FELL (8) and subsequently has been accepted and supported on other grounds by N. J. BERRILL (3). E. MARCUS (21), although differing from FELL in believing that indirect development must be prototypical for echinoderms and protochordates, agreed that the asteroids and ophiuroids must be closely related, and that broad phylogenetic conclusions therefore cannot be drawn on the basis of their larvae. MARCUS, like FELL, considered any embryological or biochemical theory implying that some groups of eleutherozoan echinoderms are more closely related to enteropneusts and vertebrates than the four classes of the former are to one another, to be necessarily absurd. HYMAN (18) has dissented from this view, but failed to account for the evidence of intermediate forms which link ophiuroids with asteroids. HYMAN grouped the extant eleutherozoans together, as their larval similarities suggest, and concludes that the "arrangement recently adopted by paleontologists (e.g., UBAGHS, 1953), according to which asteroids and ophiuroids derive from a common somasteroid ancestor and hence are to be united into one class, must be somehow wrong." HYMAN further stated that FELL's views are based on modified ontogeny in forms with yolky eggs and shortened development; in point of fact, FELL arrived at his conclusions from a consideration of every species of echinoderm for which the development had been investigated, and his reasoning depends almost entirely on larval evidence, as stated clearly by him in 1948, and as summarized above. In the present context it is unnecessary to list the very numerous cases that were then adduced, since a full documentation is available in the work cited (8).

Phylogenetic influences have also been drawn from certain biochemical data which have been held to support the view that echinoderms and chordates are related taxa. As they have a direct bearing on the problem discussed in this chapter, a brief summary is appropriate here.

Biochromes are organic pigments which occur in all echinoderms. D. L. FOX (14) defined three principal groups: (1) echino-

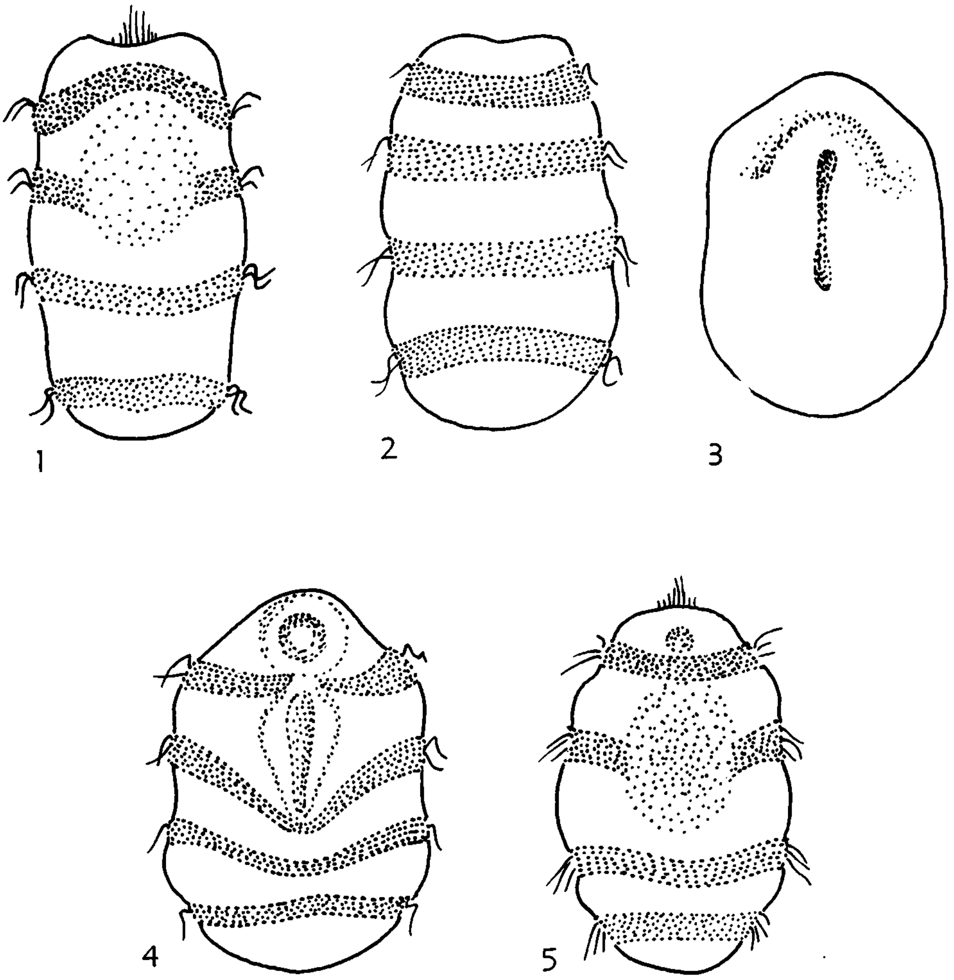

Fig. 26. Vitellaria larvae of comatulid crinoids.—*1. Tropiometra carinata* (Lamarck), Tropiometridae, ×160 (23).—*2. Heterometra savignyi* (J. Müller), Himerometridae, ×240 (28c).—*3. Notocrinus virilis* Mortensen, Notocrinidae, ×24 (28a).—*4. Isometra vivipara* Mortensen, Antedonidae, ×75 (23).—*5. Compsometra serrata* (A. H. Clark), Antedonidae, ×160 (23).

chromes (including spinochromes), purple, red or green naphthoquinones known only from sea urchins and some homopterous insects; (2) dark melanoids which occur in ophiuroids, sea urchins and holothurians; and (3) carotenoids, which occur in the integument of all echinoderms. They are typically red or orange, but if conjugated with a protein they may be green, blue, or purple. Alcohol denaturizes the protein, so that the carotenoid reverts to red or orange.

Phosphagens are of two types in echinoderms (1). These are arginine phosphate in crinoids, asteroids, and holothurians; creatinine phosphate in ophiuroids; and both types in echinoids. Creatinine phosphate is also reported from hemichordates and vertebrates, whereas arginine phosphate is known from mollusks and arthropods. Hyman (18) has accepted these results as supporting the theory that echinoderms are related to chordates. Fell (8) considered the biochemical evidence inconclusive, not only because it conflicts with paleontological evidence, but also because it is self-contradictory. Thus, echinochromes occur in insects and in echinoids, yet not in any other echinoderms; sterols of one type occur in echinoids and ophiuroids, and a similar type in orinoids, whereas sterols of a different type occur in asteroids and holothurians. Marcus (21) has pointed out that ophiuroids and echinoids cannot possibly be more closely related to vertebrates than to other eleutherozoan echinoderms, yet such is the implication of the occurrence of arginine phosphate. Phylogenetic speculation based on such data would result in chaos.

To summarize, although one may postulate that the dipleurula stage of Asteroidea, Ophiuroidea, Echinoidea, and Holothuroidea recapitulates a common ancestral dipleurula, it is no longer possible to regard any of the other types of echinoderm larvae as anything but specialized forms that lack broad phylogenetic significance.

If larval stages of echinoderms are interpreted as recapitulating ancestral stages, the conclusions reached are seriously discordant with other evidence. Therefore, it is unsafe to base phylogenetic interpretations on larval stages alone.

LARVAL TAXONOMY

Researches leading to the conclusion that definite relationships can exist between the structure of adult echinoderms and that of their larvae have been carried out by Mortensen (23-29). Thus, in the Echinoidea, the extant orders and frequently families can be characterized by the nature of the echinopluteus. To a lesser extent a similar relation is seen in the other classes. These results, in conjunction with other relevant studies, are summarized in the following survey.

Subphylum HOMALOZOA

Nothing is known of the embryonic development of organisms classed as Homalozoa or whether a larval form occurred in any of these Paleozoic forms.

Subphylum CRINOZOA

Our knowledge of embryonic (prelarval and larval) development in crinozoans is restricted to the single surviving class, Crinoidea, and even here we have no information on the mode of development in any group other than the Comatulida, among the Articulata. In all cases so far investigated, the larva has proved to be the vitellaria. This is a transversely ringed cylindrical form, similar to the doliolaria, which follows the auricularia stage of a holothurian, but differs in arising directly from the late gastrula, as the primary larva of a yolk-laden embryo. Representative crinoid larvae are illustrated by forms classed in the suborder Oligophreatina.

Suborder OLIGOPHREATINA

Larvae of two families (Fig. 26,*1*,*2*) are known. In *Tropiometra* (Tropiometridae) four transverse bands are seen on the body. *Heterometra* (Himerometridae), although having very small eggs (diam., 0.15 mm.), yield a typical vitellaria.

Suborder MACROPHREATINA

The Macrophreatina (Fig. 26,*3*-*5*) include *Notocrinus* (Notocrinidae) which has a vitellaria with uniform ciliation, lacking definite bands, and which arises in a viviparous genus. Another genus, *Isometra* (Antedonidae) is also viviparous and yet yields a temporary larval stage, as does *Notocrinus*, having fully developed ciliated bands, in addition. Two other genera of the Antedonidae, *Compsonetra* and *Antedon*, are known to have banded vitellariae, the former with four bands, the latter with four or five bands.

Subphylum ASTEROZOA
Class STELLEROIDEA
Subclass SOMASTEROIDEA

As yet, nothing is known of the embryonic development or larval in this subclass. However, the extant genus *Platasterias* may be expected to yield data very shortly.

Subclass ASTEROIDEA

The larva, if present in development, is initially at least, always a bipinnaria. A more complex larval form, the brachiolaria,

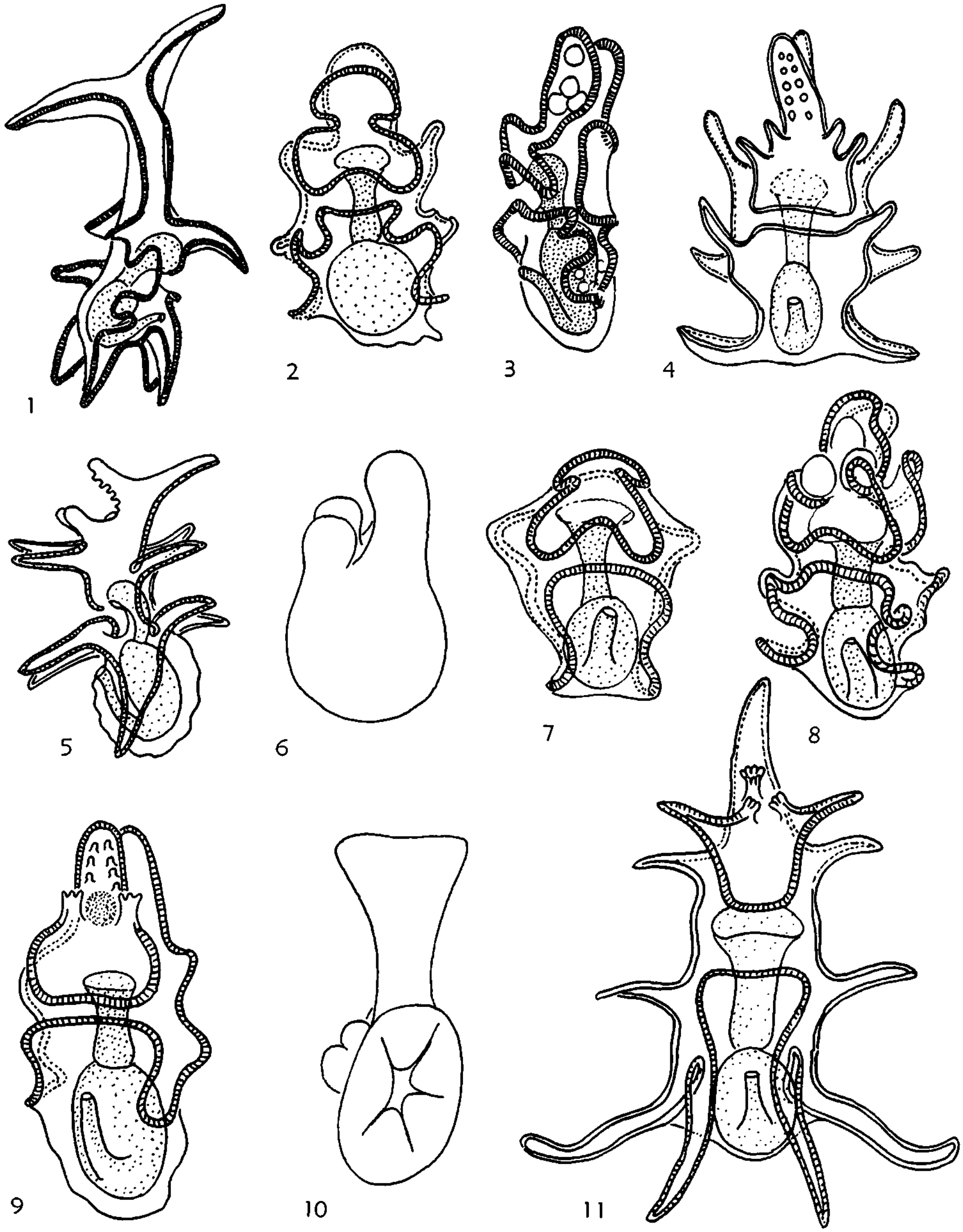

FIG. 27. Larvae of asteroids; bipinnariae *(1,2,7)* and brachiolariae *(3-6, 8-11)*.—*1. Luidia* sp. (*?sarsi* DÜBEN & KOREN), Platyasterida, Luidiidae, ×18 (15).—*2. Astropecten scoparius* MÜLLER & TROSCHEL, Paxillosina, Astropectinidae, ×48 (24).—*3. Archaster typicus* MÜLLER & TROSCHEL, Valvatina, Archasteridae, ×72 (28a).—*4. Pentaceraster mammillatus* (AUDOUIN), Valvatina, Oreasteridae, ×30 (28c).—*5. Linckia multifora* (LAMARCK), Valvatina, Ophidiasteridae, ×38 (28c).—*6. Fromia ghardaqana* MORTENSEN, Valvatina, Linckiidae, ×30 (28c).—*7. Asteropsis carinifera* (LAMARCK), Valvatina, Poraniidae, ×90 (24).—*8. Acanthaster planci* (LINNÉ), Spinulosida, Acanthasteridae, ×72 (28a).—*9. Patiria pectinifera* (MÜLLER & TROSCHEL), Spinulosida, Asterinidae, ×60 (24).—*10. Echinaster purpureus* (GRAY), Spinulosida, Echinasteridae, ×30 (28c).—*11. Asterias rubens* LINNÉ, Forcipulatida, Asteriidae, ×12 (26).

usually follows. The order Platyasterida (with the sole surviving family Luidiidae) and the family Astropectinidae in the order Phanerozonida both stand apart from all other known asteroids; in so far as known the larva never proceeds beyond the bipinnaria stage. All other asteroids appear to possess a brachiolaria, though this may be much reduced in cases of direct development (28c). Variations in larval development of asteroids, in so far as they can be correlated taxonomically, may be summarized in the following way.

Order PLATYASTERIDA

Although this order until recently was supposed to be extinct, it is now realized that the Luidiidae are members; accordingly, the characteristic larva of that family may throw more light on the origin of asteroid larval forms than was formerly realized (Fig. 27,*1*).

The general characters of the *Luidia* larva appear to include a more or less pronounced elongation of the anterior part (median lobes) and the total absence of brachiolarian arms and sucking disc. This larva differs from that of *Astropecten* in its more developed arms and elongation of the median lobes.

The development is known in three species of *Luidia*—one five-armed and two seven-armed—the latter showing considerable disturbance of normal calyx symmetry immediately after metamorphosis.

Order PHANEROZONIDA

Suborder PAXILLOSINA

Representatives of the Paxillosina are grouped in three families (Fig. 27,*2*).

Astropectinidae. The larval forms of five species of *Astropecten* are known with certainty and all are so similar as to be scarcely distinguishable. MORTENSEN (23) concluded that the Astropectinidae possess a distinctive larva, which is bipinnaria having the special characteristics of broad, round anterior lobes. There is no brachiolaria. The larval body is completely absorbed during metamorphosis. Of other genera, *Psilaster* (with yolky eggs) and *Ctenodiscus* and *Trophodiscus* (brood-protecting forms), are all presumed to have no larva.

Porcellanasteridae. Nothing is known of the development, but at least forms with large yolky eggs (e.g., species of *Ctenodiscus*) may be inferred to have direct development.

Benthopectinidae. Nothing is known of the development, but forms such as *Pontaster,* with yolky eggs, probably have direct development.

Suborder VALVATINA

Here, as also in the orders Spinulosida and Forcipulatida, a brachiolaria larval stage apparently is the normal sequel to a preliminary bipinnaria larva (Fig. 27,*3-7*); if the brachiolaria stage is not developed, then at least a vestige of the stage seems to occur. However, direct development may occur at all grades.

Archasteridae. The brachiolaria stage occurs in *Archaster*.

Goniasteridae *(sensu lato):* No larval forms are definitely associated with any member of this large family; the occurrence of large yolky eggs in *Hippasteria, Ceramaster,* and *Mediaster* suggests that in some species, at least, direct development probably occurs. Unpublished observations by J. FREEMAN CLARK show that the eggs of *Hippasteria phrygiana* rise to the surface after release, a fact which suggests that the deep-water genus spends the initial part of its life at the surface.

Oreasteridae. *Pentaceraster* is known to have a bipinnaria followed by a brachiolaria of the type in which a series of papillae occurs along sides of the ventral lobe, with a short series along the brachiolaria arms (which do not have a terminal crown of papillae). *Culcita* probably has a similar development.

Ophidiasteridae. The type genus *Ophidiaster* is known to include a bipinnaria, at least in its life history; with a brachiolaria probably following, but this is not yet certain. *Fromia* has yolky eggs, and very much modified brachiolaria, but is able to swim, however. *Linckia* passes through an initial larval stage very similar to that of *Luidia,* but later this (bipinnaria) gives place to a brachiolaria of seriopapillate type, as in *Pentaceraster.*

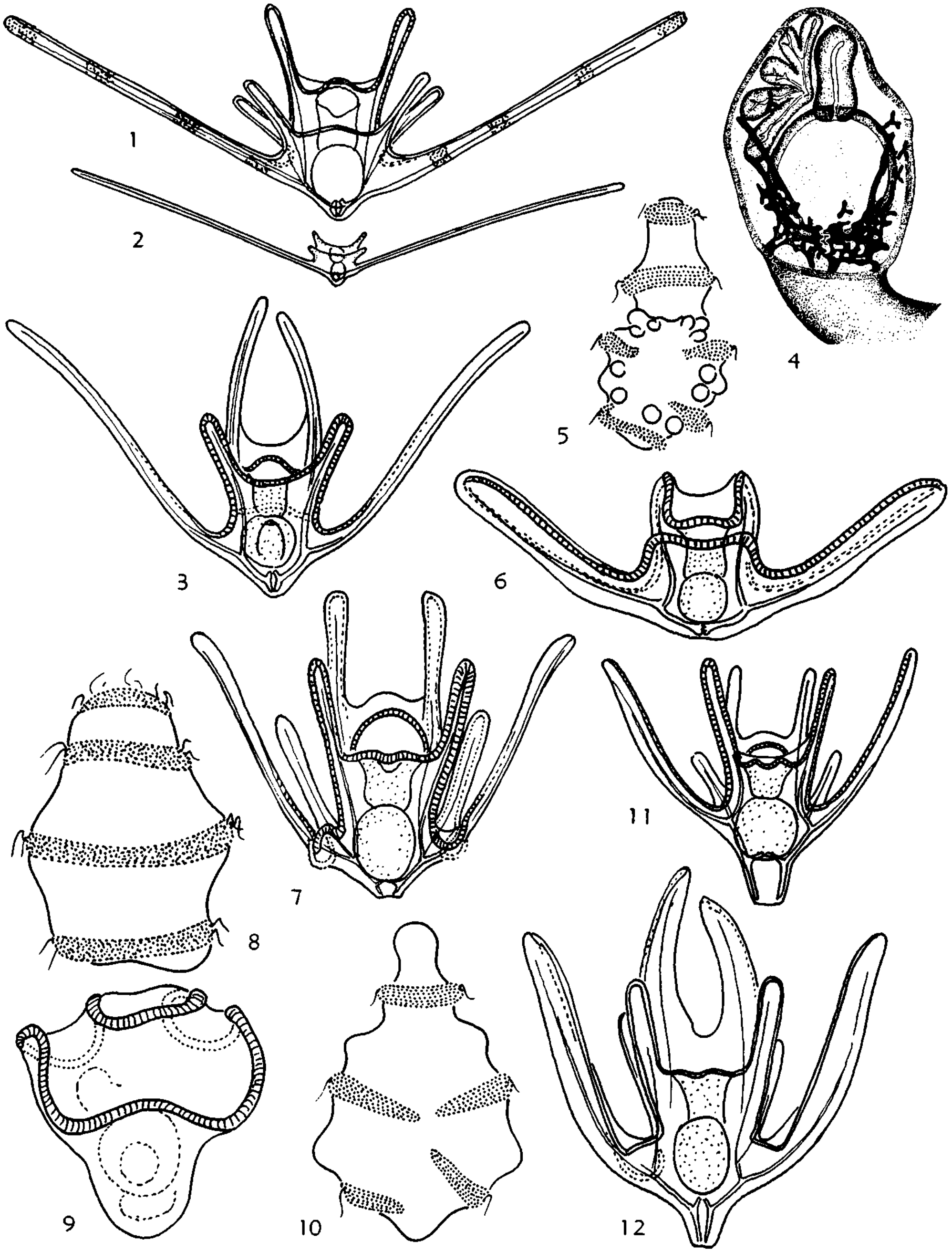

FIG. 28. Larvae of ophiuroids, ophioplutei *(1-4, 6,7,9,11,12)* and vitellariae *(5,8,10)*. All belong to order Ophiurida, larvae being unknown from other orders.—*1,2*. Ophiothricidae; *1, Ophiothrix savignyi* (Müller & Troschel), ×72 (28c); *2, Ophiothrix* sp., ×22 (24).—*3,4,* Amphiuridae; *3, Icalia filiformis* (O. F. Müller), ×60 (28a); *4, Amphipholis squamata* (Delle Chiaje), ×144, vestigial pluteus with embryonic attachment to parental bursa (7).—*5,* Ophionereididae; *Ophionereis squamulosa* Koehler, ×48 (24).—*6,7.* Ophiocomidae; *6, Ophiocoma echinata* (Lamarck), ×90 (28a); *7, Ophiocomina nigra* (Abildgaard), ×60 (28a).—*8.* Ophiodermatidae; *Ophioderma brevispinum* (Say), ×78 (17).—*9-12,* Ophiuridae; *9, Ophionotus hexactis* (E. A. Smith), (lobes of ciliated band not always so conspicuous), ×90 (24); *10, Ophiolepis cincta* Müller & Troschel, ×90 (28c); *11, Ophiura texturata* Lamarck, ×60 (28a); *12, Ophiura albida* Forbes, ×60 (28a).

Poraniidae. *Porania* has a development similar to that of *Pentaceraster*, with seriopapillate brachiolaria. *Asteropsis* is known to have at least a bipinnaria, and in all probability it includes also a brachiolaria of seriopapillate type.

Order SPINULOSIDA

Representatives of the Spinulosida are illustrated in Figure 27,*8-10*.

Acanthasteridae. *Acanthaster,* with small eggs (0.1 mm.), includes both bipinnaria and brachiolaria larval stages in the life history.

Asterinidae. *Patiria* is known to include bipinnaria and brachiolaria (of seriopapillate type) in the life span and it includes at least two species. Very probably a similar sequence occurs in *Patiriella,* though as yet only the bipinnaria stage has been demonstrated in the New Zealand species; in an Australian species of the genus *(P. exigua)* a shortened development occurs, with vestiges of brachiolarian processes; a similar shortened development is seen in the European *Asterina gibbosa.*

Pterasteridae. Shortened development occurs in some species of *Pteraster* and *Hymenaster,* the young normally retained within a dorsal marsupium, opening to the exterior by an osculum. Unpublished observations by Fu-Shiang Chia indicate, however, that on the northwest coast of the USA *Pteraster tesselatus* is a nonbrooding species, laying large yolky eggs (diam. 1.2-1.6 mm.), from which a free-swimming ciliated modified brachiolaria develops; metamorphosis is completed within one month of fertilization (Chia, personal communication).

Echinasteridae. Shortened development is characteristic here. Some species of *Henricia* protect the brood, and have no larval stage at all; others have yolky eggs and a modified brachiolaria larva, and the same circumstance has been reported in *Echinaster.*

Solasteridae. Shortened development of echinasterid type occurs here.

Order FORCIPULATIDA

The Forcipulatida are illustrated by Figure 27,*11*.

Asteriidae *(sensu lato)*. The normal pattern of development, if fully expressed, apparently includes a bipinnaria stage, followed by a brachiolaria of the terminopapillate type. Genera include *Asterias, Marthasterias, Orthasterias,* and *Pisaster.* A bipinnaria at least is known to occur in *Coscinasterias, Evasterias,* and *Pycnopodia;* in many genera (e.g., *Leptasterias*), brooding is performed, and no larval stages are produced.

CONCLUSIONS

The foregoing survey implies that the bipinnaria must be the older type of larva among asteroids, and the more widespread occurrence of the brachiolaria can be no more than a reflection of the fact that extant asteroids belong mainly to the specialized, later groups of asteroids which are now dominant surviving forms. The brachiolaria stage was probably evolved at about the same time that suctorial tube feet first arose in the (postastropectinid, postporcellanasterid) phanerozonid asteroids. The older views maintained by MacBride (20a), that the brachiolaria is the original larva and represents a stalked pelmatozoan ancestry, cannot be maintained.

Subclass OPHIUROIDEA

As stated above, the typical larva of ophiuroids is the ophiopluteus, though development in very many cases is direct, without a larva; and in a number of cases the larva is the vitellaria, of the same type as occurs in Holothuroidea and Crinoidea. The following is a systematic survey of embryological data so far known.

Order STENURIDA

Development unknown, all extinct.

Order OEGOPHIURIDA

Although now known to have a living representative in the Indonesian genus *Ophiocanops* (Ophiocanopidae), the development is at present unknown.

Order PHRYNOPHIURIDA

Suborder OPHIOMYXINA

Ophiomyxidae (Fig. 28). No larva is known, development being absolutely direct, in at least two species without slightest vestige of larva. Viviparous forms with direct development include species of *Ophiomyxa, Ophioscolex.*

Suborder EURYALINA

Gorgonocephalidae. *Astrochlamys,* and probably *Astrothorax,* includes viviparous species, with presumably direct development. Species of *Gorgonocephalus* probably have direct development, with young stages feeding in alcyonarian polyps, but it is possible that some free-swimming stage (?gastrula) occurs.

The development of the other three families is virtually unknown, though believed to be direct.

Order OPHIURIDA

Hemieuryalidae. *Ophiochondrus* is viviparous, but nothing is known as to the existence or otherwise of a larval stage.

Ophiacanthidae. *Ophiacantha* (five species) and *Ophiomitrella* (five species) are both known to be viviparous, probably without larval stages.

Ophiothricidae (Fig. 28,*1,2*). Species of *Ophiothrix* have ophiopluteus larvae in which the posterolateral arms form a long pair of rods, much larger and more conspicuous than other rods; also, during and after metamorphosis, these long arms remain unresorbed, and are eventually thrown off after metamorphosis.

Ophiactidae. The ophiopluteus is well developed and peculiar in having a double recurrent calcareous rod; only the type genus *Ophiactis* has been studied.

Amphiuridae (Fig. 28,*3,4*). Well-developed ophiopluteus, though in some species assuming the peculiar form (previously known as "*Ophiopluteus mancus*") in which the posterodorsal arms are missing; viviparity, and consequential direct development, occurs in *Amphipholis* (two species), *Amphiodia* (one species), *Amphiura* (three species), *Monamphiura* (seven species), *Icalia* (two species), *Pandelia* (one species), *Nullamphiura* (two species).

Ophionereididae (Fig. 28,*5*). A vitellaria larva occurs in *Ophionereis squamulosa,* and another species of *Ophionereis* is viviparous; otherwise, the development is unknown.

Ophiocomidae (Fig. 28,*6,7*). Extremely broad arms are evidently characteristic of the ophiopluteus of *Ophiocoma.* This feature is not seen in *Ophiocomina.* Both genera have enlarged ciliated lobes at the bases of the two posterolateral arms, but some evidence of the same feature occurs in *Ophiura,* so it is not, in itself, distinctive of the family Ophiocomidae. It is possible that *Ophiocomina* is wrongly classified with the Ophiocomidae, and should this prove to be the case, then presumably the broadened arms will be the main familial character.

Ophiodermatidae (Fig. 28,*8*). The only larva so far known from the family is the vitellaria, first described for *Ophioderma brevispina* by GRAVE (14); similar larvae have since been found in American waters, and are provisionally attributed to other species of *Ophioderma.* In other genera of the family direct development occurs, associated with viviparity, namely in *Cryptopelta* (two species), *Pectinura* (two species), and *Ophioconis* (one species).

Ophiuridae (Fig. 28,*9-12*). A variety of larval forms, and of modes of development, occur in the Ophiuridae (i.e., Ophiolepididae auctt.). A larva of vitellaria type characterizes *Ophiolepis.* An auricularia-like larva (however, with traces of rods of a pluteus-type arm skeleton) is characteristic of *Ophionotus*; this is apparently never free-swimming, as the development is completed within the bursa in the one species *(O. hexactis)* in which this peculiar larva has been observed (Fig. 28,*9*). As in other hexamerous and polymerous forms, the symmetry of the calycinal system is seriously disturbed in the newly metamorphosed form. A normal ophiopluteus occurs in the various species of *Ophiura,* but its range of variation is so great between species of the genus that one might well suppose them to belong to different families, as MORTENSEN (28a) has commented. Viviparity, with consequent direct or partly direct development, is known in a considerable number of genera of this family, namely *Ophiotjalfa, Ophiolebella, Ophioceres, Ophiozonella, Ophiomages, Ophiosteira, Ophiurolepis,* and *Ophionotus,* each with a single species, and *Ophiura, Amphiophiura, Stegophiura,* each with two species.

Subphylum ECHINOZOA
Class ECHINOIDEA

In the Echinoidea larval evolution seems to have occurred subsequently to separation of the main orders and families. Within relatively small groups larval evolution has followed similar trends, so that characteristic larvae occur in various subgroups, where the young stages may follow similar ontogenies; but such independent evolution tends to obscure the phylogenetic relationships between the class as a whole and the other classes.

Order CIDAROIDA

Until 1937 the development of cidaroids was known only very incompletely, and no general conclusions could be drawn as to its nature. The genera *Cidaris* and *Eucidaris* had been studied. In addition, MORTENSEN had shown that the development of *Phyllacanthus parvispinus* is probably direct. In 1937 MORTENSEN (28b) published his account of *Eucidaris metularia,* and the following year (28c) that of *Prionocidaris baculosa,* which was studied through metamorphosis. The two latter accounts are the most important, and together with the earlier data enabled the conclusion to be drawn that a distinctive cidaroid larval form exists (Fig. 29,*1*). This is an echinopluteus characterized by very long, smooth fenestrated postoral and posterodorsal rods, by having the posterior transverse rod provided with long, slender median processes dorsally and ventrally, and by strong development of the ciliated lobes. A larval muscular system is present in the two latter species, enabling the two pairs of long arms to be moved backward and forward, and no doubt this feature is also generally characteristic of the cidaroid larva.

A further feature of morphological interest is that in the newly metamorphosed urchin of *Prionocidaris* a pluriserial interambulacrum occurs, as in Palaeozoic echinoids. The supernumerary plates are later resorbed, as in *Archaeocidaris.*

Order DIADEMATOIDA

Knowledge of the development of these is due mainly to MORTENSEN (Fig. 29,*2,3*). Four species belonging to *Diadema* and *Echinothrix* have been investigated. The larvae of these have proved to be types earlier described under the name *Echinopluteus transversus* (24), the parental form being at that time unknown. This is notable for great development of the postoral arms, other arms being absent save for small anterolaterals which may be present. The larva thus strongly resembles an ophiopluteus. The ciliated band is not strongly developed, in sympathy with reduction of the arms, and no vibratile lobes or epaulets are observed. Other skeletal peculiarities do not need to be specified here.

Order ARBACIOIDA

The development of three species of the genus *Arbacia* has been studied (Fig. 29,*4*). The arbaciid larva has a basket skeleton at first. In its second stage of development a posterior transverse rod is present, ending in a pair of long posterolateral arms which are similar to the other arms. Postoral and posterodorsal rods are fenestrated. Large ventral and dorsal lobes occur, but no epaulets.

Order PHYMOSOMATOIDA

The development of *Stomopneustes* is known to resemble that of the Echinometridae as noted subsequently.

Order TEMNOPLEUROIDA

Temnopleuridae. In this family the development is known for species of *Temnopleurus, Temnotrema, Mespilia,* and *Salmacis.* In the first stage no basket structure of the skeleton is seen. In the second stage (Fig. 29,*5*) a posterior transverse rod is formed and short branched posterolateral rods may or may not issue from it. Four vibratile epaulets are found, but no vibratile lobes. The arms commonly present a highly characteristic bloated appearance (24).

Toxopneustidae. Among genera belonging to this group the species of *Toxopneustes, Lytechinus, Nudechinus, Tripneustes, Sphaerechinus,* and *Pseudocentrotus.* The echinopluteus of this assemblage possesses in its first stage a short body, usually with a basket structure of the skeleton. In its second stage (Fig. 29,*6*) a posterior transverse rod is introduced. Postero-

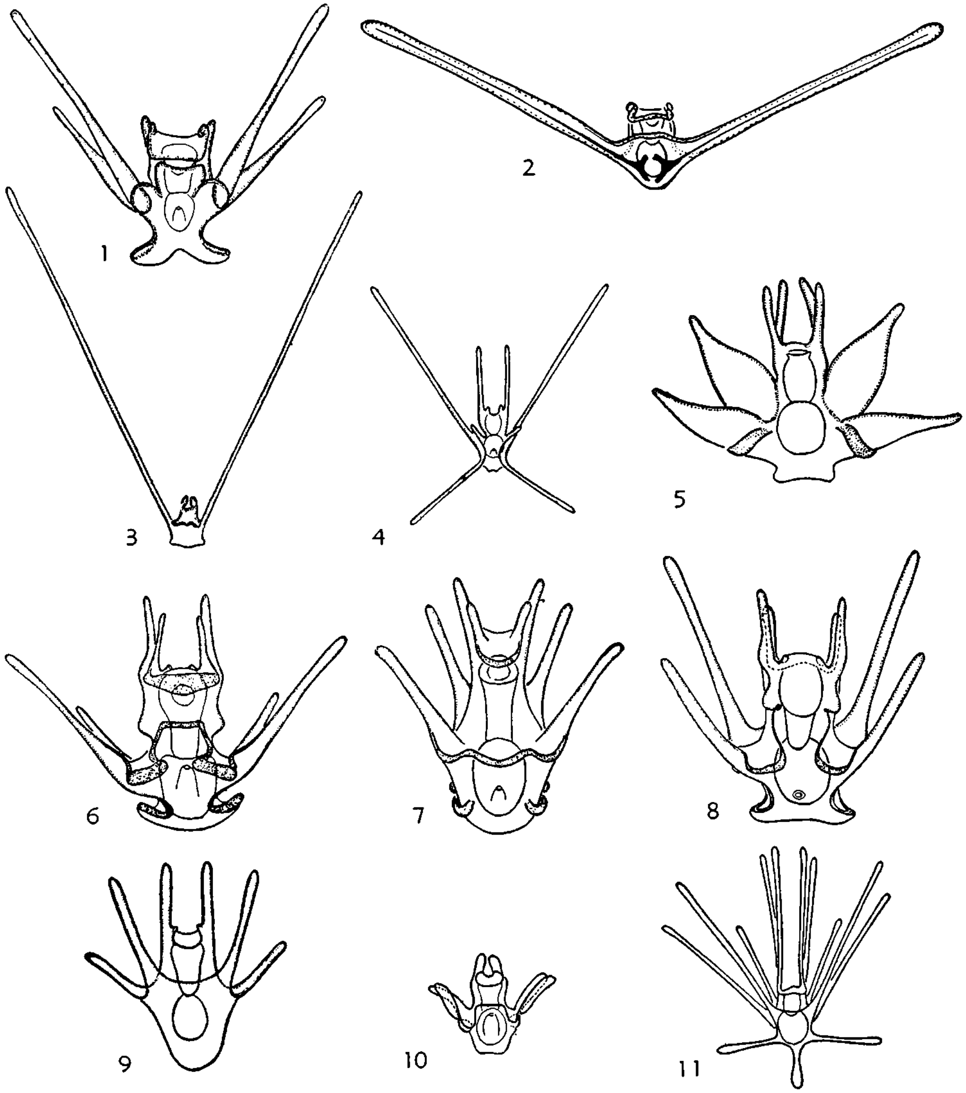

Fig. 29. Echinopluteus larvae of echinoids.—*1. Prionocidaris baculosa* (Lamarck), Cidaroida, Cidaridae, ×30 (28c).—*2. Diadema setosum* Gray, Diadematoida, Diadematidae, early larva, ×42 (28a).—*3.* Same, later stage (28b).—*4. Arbacia stellata* (Blainville), Arbacioida, Arbaciidae, ×24 (24).—*5. Mespilia globulus* (Linné), Temnopleuroida, Temnopleuridae, ×30 (31).—*6. Lytechinus variegatus* (Lamarck), Temnopleuroida, Toxopneustidae, ×42 (24).—*7. Echinus esculentus* Linné, Echinoida, Echinidae, ×60 (24).—*8. Echinometra lucunter* (Linné), ×54 (24).—*9. Arachnoides placenta* (Linné), Clypeasteroida, Arachnoididae, ×48 (24).—*10. Apatopygus recens* (Milne-Edwards), Nucleolitoida, Apatopygidae, ×30 (24).—*11. Echinocardium cordatum* (Pennant), Spatangoida, Loveniidae, ×22 (28a).

lateral arms and vibratile lobes occur, and epaulets are seen at the bases of the four main arms. The rods of the main arms may be either simple or fenestrated (24). *Strongylocentrotus,* now placed in a family by itself, has a development similar to that of the Toxopneustidae.

Order ECHINOIDA

Echinidae. The larval development of echinids is known for species of *Echinus, Psammechinus, Paracentrotus, Parechinus,* and *Sterechinus.* In its first stage the larva has a short body, usually with a basket structure of the skeleton. In the second stage (Fig. 29,7) a posterior transverse rod is present; posterolateral and vibratile lobes occur, and also epaulets at bases of the four main arms; the rods of the main arms may be either simple or fenestrated.

Echinometridae. The development is known for species of *Echinometra, Colobocentrotus, Heterocentrotus, Evechinus, Heliocidaris,* and *Echinostrephus.* The development of *Heliocidaris erythrongramma* is direct, or partially so. The echinometrid larva has in the first stage a short, obliquely truncate body supported by a complex basket structure. In its second stage (Fig. 29, *8*) a posterior transverse rod is present. Posterolateral and vibratile lobes occur, but no epaulets. The rods of the main arms are fenestrated (24).

Order CLYPEASTEROIDA

The development is known of 15 species belonging to the genera *Clypeaster, Fibularia, Echinarachnius, Peronella, Arachnoides, Fellaster, Encope, Mellita, Astriclypeus, Laganum,* and *Echinodiscus* (Fig. 29, *9*). In the clypeasteroid larva the body skeleton forms a prominent basket structure of distinctive character. This commonly takes the form of a large, complex, fenestrated plate in the posterior end of the body.

Order CASSIDULOIDA

Mortensen's (24) account of *Apatopygus recens* suggests affinity between its larval development and that of the clypeasteroids. The fully developed larva is as yet unknown, but Mortensen's oldest stage is illustrated (Fig. 29,*10*).

Of the other surviving Cassiduloida, the development is unknown.

Order SPATANGOIDA

The spatangoids are characterized by possessing a highly distinctive echinopluteus which bears a median unpaired armlike process (Fig. 29,*11*). In addition, the anterodorsal arms are well developed. Mortensen (24) has further suggested that it may ultimately be found that the families Spatangidae and Brissidae have distinctive larvae, as from the data available it appears that the former possess posterolateral arms, whereas the latter lack these structures. The genera which have been studied include *Spatangus, Lovenia, Echinocardium, Moira, Brissus, Brissopsis,* and *Meoma.*

SUMMARY OF ECHINOIDS

It may be inferred from the foregoing discussion that larval evolution of the echinopluteus must have occurred subsequent to separation of the main orders and families of echinoids, and within any one group of echinoids larval evolution has followed similar trends. Thus, within relatively small groupings it is true to say that the young stages of related species show similar ontogenies. It is obvious that, with independent larval evolution occurring simultaneously in the many orders and families of echinoderms in general, the phylogenetic relationship between major groups, such as the classes, will become ever more and more obscured in so far as it is reflected in embryology. In his main study, Mortensen (24) wrote as follows:

> The Echinopluteus affords the greatest diversity of forms of all Echinoderm larvae, and several well-marked types are to be distinguished. It does not immediately appear which of these represents the more primitive type. Considering, however, the fact that the larvae in which the body skelton in the first stage forms a basket structure, and which have in their second stage a posterior transverse rod and more or less developed posterolateral processes are characteristic—so far as we know—of the Cidarids, Diadematids and Arbaciids, that is to say of the more primitive forms of Echinoids, it can hardly be disputed that we have to regard this larval type as the more primitive form. Consequently the larval type characteristic of the family Echinidae s. str., with the elongated, club-shaped body rods, with the recurrent rod rudimentary or absent, and without a posterior transverse rod or posterolateral processes, is highly specialized. It is therefore not at all justifiable to make this larval type represent the Echinoid larva in general as is done in most text-books.
>
> Characteristic of the larval body of the primary type are the vibratile lobes; in the more specialized types, the larva of the Echinidae s. str., and of the Spatangoids, these lobes have disappeared, while the Clypeastroid larvae have retained them to some degree. A further specialization from the lobes are the epaulets occurring in the higher types of the Regularia.
>
> Both the vibratile lobes and the epaulets evidently serve to increase the floating power of the larva. This object is attained to a still higher de-

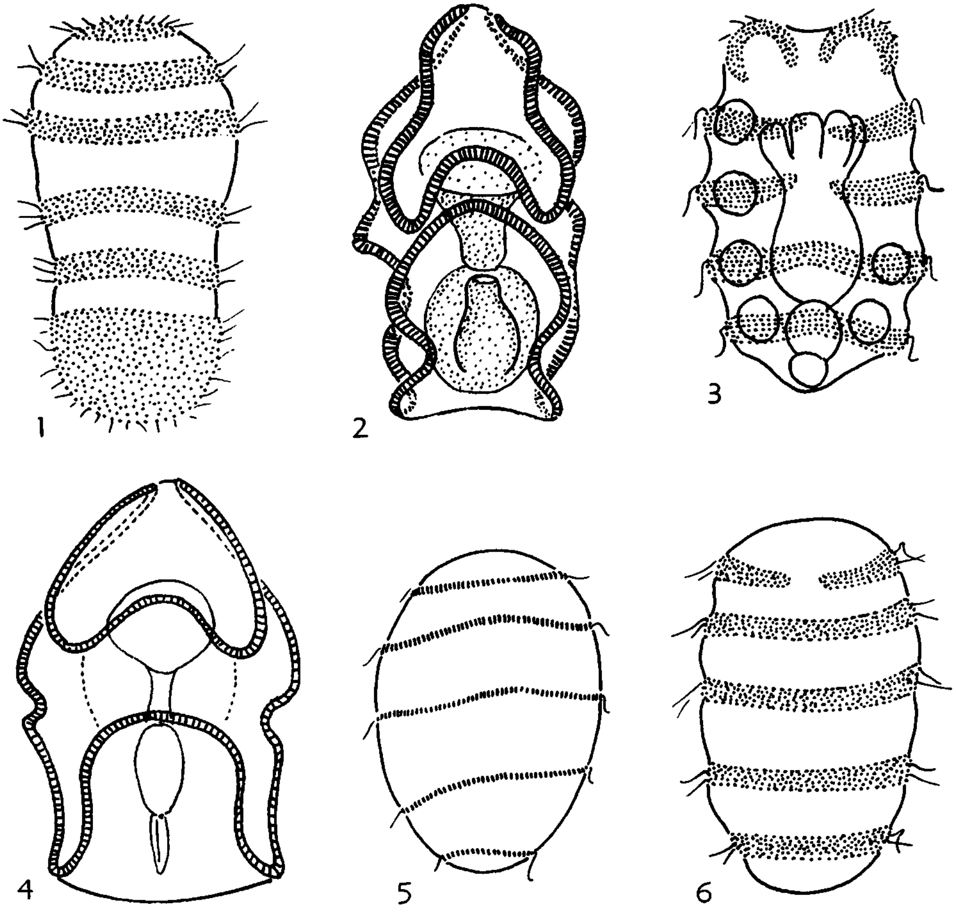

Fig. 30. Vitellaria larvae (doliolaria) *(1,3,5,6)*, and auricularia larvae *(2,4)* of holothuroids.—*1*. Dendrochirotida, *Cucumaria planci* von Marenzeller, Cucumariidae, ×135 (32).—*2*. Aspidochirotida, *Stichopus californiensis* (Stimpson), Stichopodidae, ×56 (24).—*3*. Aspidochirotida, *Holothuria impatiens* (Forskål), Holothuriidae, metamorphosing doliolaria derived from a preceding auricularia stage, ×75 (28c).—*4-6*. Apodida, Synaptidae; *4, Opheodesoma grisea* (Semper), ×90 (28c); *5, Synaptula vittata* (Forskål), ×60 (28c); *6, Labidoplax* sp., ×75 (28c).

gree in several larval forms of Regular Echini and Clypeastroids in which muscles connect the lower ends of the rods of the four main arms, so that these arms become actively movable. These larvae, when floating, keep the four main arms in a more or less horizontal position, raising them when disturbed. This is not yet an active swimming movement, the muscular apparatus being too simple for performing regularly repeated movements. Only one Echinoid larva appears to be able to swim actively, viz., the remarkable Echinopluteus transversus (of Diadematidae), in which a complicated muscular system has developed, the body-skeleton being most extraordinarily adapted for serving as a support to the muscles. . . .

As regards the skeleton it is a noteworthy fact that the fenestrated rods represent a primary structure, as must be concluded from the fact that this type of rods (always confined to the four main arms) is found in the larvae of the more primitive forms. . . .

Class HOLOTHUROIDEA

The larval forms of holothurians are either vitellariae or auriculariae, and the occurrence of transitional stages between the auricularia and a secondary larva (doliolaria or pupa), in which the ciliated loops are gradually transformed into transverse rings, shows that no sharp distinction between the vitellaria and auricularia is to be made (Fig. 30). This is significant, for in the other classes of echinoderms the vitellaria seems to stand as an independent form, lacking transitional stages to link it with other larval types. In many holothurians the development must be quite direct, no larval form having ever been reported. The following paragraphs present a review of the known evidence.

Order DENDROCHIROTIDA

The only larvae reported from dendrochirotes are vitellariae, either of the annulated doliolaria type, or uniformly ciliated cylindrical forms; auriculariae are unknown (Fig. 30,*1*).

Cucumariidae. *Cucumaria planci* and other species have a transversely ringed vitellaria which is independently formed as the primary larva, not as the doliolaria of an auricularia. Other species of *Cucumaria* (e.g., *C. saxicola, C. frondosa*) are ciliated all over, evidently comprising a form of vitellaria derived directly from the late gastrula. No larva at all occurs in *Thyone.* In both *Thyone* and *Cucumaria* viviparity occurs.

Psolidae. In *Psolus phantapus* a uniformly ciliated vitellaria occurs. Viviparity occurs in *Psolus, Psolidium,* and *Thyonepsolus.*

Rhopalodinidae, Phylloporidae. No reliable information is available on the development of these families.

Order ASPIDOCHIROTIDA

An auricularia is known to occur in some aspidochirotes, with transversely annulated doliolaria stages occurring at metamorphosis. Otherwise, the development appears to be direct (Fig. 30,*2,3*).

Synallactidae. The development is unknown in these deep-water forms, but the prevalence of large yolky eggs suggests that direct development is probably usual.

Stichopodidae. An auricularia is known for *Stichopus californicus.*

Holothuriidae. Auriculariae of simple type occur in *Microthele* and *Holothuria impatiens.* Absolutely direct development occurs in *H. floridana.*

Order MOLPADIIDA

The only larva recorded is a vitellaria in *Paracaudina.*

Order ELASIPODIDA

Larval development is unknown in any of the five families of the order.

Order APODIDA

The widest range of larval forms occurs in this specialized order, with vitellariae and doliolariae, auriculariae (elaborate in some), as also direct development (Fig. 30, *4,5*).

Synaptidae. Larvae may occur, but in some genera they are omitted. An auricularia (with subsequent doliolaria) arises in species of *Synaptula, Opheodesoma grisea,* and *Labidoplax digitata.* Partially direct development occurs in *Leptosynapta inhaerens,* where a vitellaria arises (despite the small size of the eggs in that species). A vitellaria also occurs in *Labidoplax buskii.* Coelomic incubation is known to occur in species of *Synaptula.*

Chiridotidae. Coelomic incubation occurs in species of *Chiridota, Trochodota,* and *Taeniogyrus.* No other information is on record as to mode of development, or larvae.

Myriotrochidae. Although nothing is recorded on the development of this family, the large planktonic "Auriculariae nudibranchiatae" are presumably referable to it, for the wheel-shaped deposits illustrated by Chun (1896) appear to be of myriotrochid type, having numerous spokes (D. L. Pawson, pers. commun., unpubl.).

DIRECT DEVELOPMENT

Until recently it had come to be generally assumed that all typical echinoderms have an indirect mode of development; however, a survey of the known embryological data of particlular faunas indicates that no special mode of development can be taken as the general rule for the phylum. The egg of echinoderms is liable to undergo changes in volume. Increase of volume is directly related to increase in cytoplasm and its product, the yolk material. Such increases have led to direct development. Increase in cytoplasm and yolk has not greatly affected the cleavage process, which is almost always total. A distinction between micromeres and macromeres frequently results. With increasing cytoplasm, the wall of the blastula becomes thicker, and in extreme cases the blastocoel is reduced to a vestige in the animal hemisphere. The mesenchyme fails to separate as such, but projects as a solid mass into the blastocoel. Invagination is reduced to a solid inpushing of cells, and epiboly may ensue. The archenteron may become vestigial, in which case the definitive enteron is excavated in the solid endoderm by splitting. The enterocoel becomes reduced or lost, and the coelom and its adjuncts may arise by schizocoelous splitting in mesenchyme.

It may be regarded as reasonably proven that the accumulation of yolk and cytoplasm in the egg is in some way responsible for suppression of the larval form. The salient features of the sequence of reduced larvae studied above are (1) a progressive reduction in size and number of the paired larval arms, followed by loss of the arm skeleton; (2) an increase in the amount and importance of mesenchyme, within which ultimately the coelom is excavated in place of coelomic pouches from the enteron; and (3) bilateral symmetry is lost completely. The order in which these reductions occur, in terms of increasing yolk mass, suggest progressive inhibitions in metabolism along the axes of a bilaterally symmetrical body. By convergent evolution among echinoderms with yolky eggs, a special vitellaria larva has arisen independently in Holothuroidea, Ophiuroidea, and Crinoidea. The vitellaria is characterized by its barrel shape, and the transmutation of the ciliated band into annuli. In the Crinoidea this is the only larva yet known.

In Ophiuroidea a succession of stages in reduction of the ophiopluteus may be seen, suggesting a recession backward in time of the moment at which metamorphosis is initiated. In extreme cases the gastrula itself becomes radially symmetrical and the larva is completely lost. Viviparity is of interest in echinoderm reproduction owing to the modifications of development which usually accompany its occurrence. Commonly eggs of viviparous species are large and yolky. The relationship between parent and young is often extremely intimate, with marsupia forming in the mother, an embryonic attachment developing, and even nutritive substances sometimes being supplied to the embryo by the parent. Larval stages are vestigial or suppressed altogether.

Among asteroids simple brood protection is illustrated by *Calvasterias suteri* from New Zealand. The eggs are laid and the numerous young are carried in a large cluster about the mouth, apparently in the later stages living as commensals. In the astropectinid *Leptychaster kerguelensis,* the young stars are hatched in the oviducts and later adhere to re-entrant angles between rays of the parent. *Leptasterias groenlandica* is reported to hatch its young in its stomach, a very surprising circumstance. In species of *Echinaster,* the young are carried in the ambulacral grooves with the side of the arms folded over them. More complex conditions are seen in *Pteraster* and *Hymenaster* where a dorsal marsupium occurs, held up by modified paxillae and opening dorsally by a special osculum. A marsupium is known also in *Granaster nutrix*. In the starfish *Anasterias antarctica* the embryo is joined to the parent by an attachment.

In ophiuroids all degrees of brood protection and viviparity are found; the condition is very common in Antarctic species, of which MORTENSEN (29) recorded 31 as viviparous. A very interesting example has been recorded in Britain by SMITH (33) who found numerous young individuals of *Ophiothrix fragilis* clinging to the spines and tube feet of adults, larger young ones occurring separately in the parental bursae. As the species has nonyolky eggs and well-developed pelagic larvae, this is an unexpected instance that indicates how viviparity might arise in such forms. SMITH regarded the occurrence as equivalent to natural crevice sheltering. In truly viviparous ophiuroids the eggs are usually large, and either many young may be found in the bursa (e.g., *Ophiomyxa brevirima,* from New Zealand, 4) or several (e.g., *Pectinura cylindrica*), or only a few (e.g., *Amphipholis squamata*). The last-mentioned species, as others of the same genus, is notable in having an embryonic attachment to the parent. This structure is not nutritive; there are reasons for believing that a nutritive fluid is secreted by the bursal wall (7).

In comatulid crinoids, where the eggs are large and rich in yolk, as a general rule the young adhere to and develop on pinnules of the parent. In some species, however, the eggs are free (e.g., *Tropiometra carinata, Antedon petasus*). True viviparity, involving special marsupia, is found in Antarctic crinoids (e.g., *Isometra vivipara, Phrixometra nutrix*). In *Notocrinus virilis* it appears that the young are nourished by an albuminous secretion from the wall of the marsupium (23).

Similar degrees of brood protection and of viviparity are observed in the holothurians, where the incidence in Antarctic species is as pronounced as in other echinoderm classes. In the simplest type the embryos merely rest on the surface of the body. In other species small alveoli may form in the integument, enclosing the eggs. In some the eggs develop within the oviducts, or within the coelom. In others an invagination or evagination of the body wall forms a marsupium. Genera showing viviparity include *Cucumaria, Thyone, Psolus,* and *Phyllophorus* among Cucumariidae, and *Chiridota, Synaptula,* and *Leptosynapta* among Synaptidae.

Since echinoids are distinguished from other echinoderms by possessing generally small eggs and pelagic larvae, viviparity is necessarily of limited incidence in this class. Among cidarids *Goniocidaris umbraculum,* of New Zealand, carries the young in the partly sunken peristome, covered over by oral spines, thus forming a marsupium. In other cidarids the spines of the apical part of the test form a marsupium. Among the spatangoids the sunken petals frequently serve as marsupia, as in *Schizaster, Hemiaster,* and others. In Antarctic genera a sexual dimorphism of the test is a consequence of this condition.

It is clear that brood protection and viviparity can influence development considerably. Larval stages can be effaced or at least reduced. New embryonic organs may evolve, such as the attachment stalks between embryo and parent. New modes of nutrition may arise, involving a change from ingestion of planktonic food in a functional alimentary canal to surface absorption of fluid material by the outer epithelia of the embryo. Yet in these the end result is the same—an adult echinoderm arises quite as typical of its group as an oviparous form. Here, then, is one more illustration of the potency of evolution in acting upon embryonic stages without significantly affecting the adult.

GROWTH GRADIENTS AND PHYLOGENY

The foregoing discussion, based entirely on larval forms, leads to a purely negative result, since the only deduction possible is that larval forms in echinoderms are specialized and cannot throw any direct light upon the question of origin and interrelationships of the various groups included within the phylum. This situation was apparent by 1948 (8).

A more positive approach subsequently has become possible as a result of detailed studies of growth patterns and growth gradients, particularly the postmetamorphic changes which the skeleton undergoes during its development. The results have been reported in a series of papers (Fell, 9-13), which cover a program of comparative studies carried out over the past decade. A brief summary of the conclusions is relevant in the present context, as it provides a general frame of reference within which echinoderm larvae can be viewed.

The analysis begins with asterozoans, is then extended to pelmatozoans, and thence taken forward to echinozoans. The following are the main steps in the inquiry.

(1) The rod-shaped skeletal structures known as **virgalia,** which occur in lower Paleozoic somasteroids, can be shown to be direct homologues of major skeletal elements in modern asteroids and ophiuroids, and the homologies can be specified.

(2) The axes along which the major skeletal elements differentiate in asteroids are found to show progressive alterations in strength and direction, so that the various

families can be arranged in a sequence. Direct fossil evidence indicates the older end of the series, which accordingly can be oriented in time. When the soft structures are correlated, they, too, fall in a progressive linear sequence, coordinated with the hard parts. The inferred chronology may therefore be accepted as an initial working hypothesis.

(3) Using this frame of reference, progressive eliminations enable the most archaic asteroids to be isolated. The final residual group proves to comprise the Luidiidae, the members of which are shown to be surviving representatives of the order Platyasterida, hitherto known only as lower and middle Paleozoic fossils. The order can thus be more precisely defined, the soft structures inferred, and its relationship to other asteroids indicated.

(4) Proceeding from this basis, the inference is drawn that the Luidiidae probably arose from somasteroids through certain hypothetical changes which can be specified. However, the extant asterozoan *Platasterias* ought, on the evidence of its recorded structure, to fall in an early position within the inferred sequence. Detailed study of the structure of *Platasterias* has confirmed its archaic nature and showed it to be a surviving representative of the supposedly extinct somasteroids, though at the same time clearly related to luidiid asteroids. Thus all inferences up to this juncture have been confirmed, and they can therefore be transferred to the working data.

(5) It was thereby established that (a) The oldest asteroids had dominant transverse growth axes in the arm, causing *inter alia* the skeletal plates to lie in transverse rows, and that therefore the entry into the arm of dominant longitudinal growth axes must have been a post-luidiid change. (b) The oldest asteroids had no intestine or anus, the appearance of these structures being a post-luidiid change, coinciding with the astropectinid grade of evolution. (c) The oldest asteroids had nonsuctorial tube feet, the appearance of suckers being a post-astropectinid change. (d) The oldest asteroids had small, double ampullae, inherited from a pre-asteroid ancestry (identified with platasteriid somasteroids), and the subsequent enlargement of the ampullae coincided with the permanent invagination of the ambulacral furrow, which occurred at the platyasterid grade of evolution, with simultaneous enlargement of the tube feet. (e) The single ampullae of Porcellanasteridae are thus a specialized simplification of formerly double ampullae and, being of post-luidiid origin, cannot be primitive. (f) The madreporite was originally placed at the margin of the disc.

(6) The mode of origin of ophiuroids from lower Paleozoic somasteroids can now be deduced, in accordance with theoretical methods used for the asteroids. These predict the existence of ophiuroids with the same pinnate skeletal structure as occurs in archaic asteroids. This inference, tested by dissection of the internal skeleton in representatives of extant families, has been confirmed, and surviving (as well as extinct) genera with pinnate structure have been isolated; further, the homologies of the skeletal elements with somasteroid virgalia have been demonstrated in detail.

(7) Accordingly pinnate structure of the skeleton is shown to be fundamental to all asterozoans, that of ophiuroids and of asteroids being inherited directly from somasteroid precursors.

(8) Next, the soft structures of ophiuroids are to be correlated with the inferred sequence of skeletal changes, as was done in the case of the asteroids. Study of this sort has led to the following inferences. (a) Gastric caeca must once have extended far out into the arms of ophiuroids, for this condition is found in all asteroids and has been demonstrated in the somasteroid *Platasterias*. (b) The gonads in ophiuroids originally must have been confined to the arms, arranged in approximately paired series along either side of the dorsal coelomic canal, for this condition is shown to be primitive in other asterozoans. Since all these conditions are known to occur in the extant genus *Ophiocanops*, this ophiuroid immediately came under suspicion as an archaic form, possibly wrongly classified. Investigation of the endoskeleton of this genus immediately confirmed that it is, in fact, archaic, and agrees in every major feature with that already known in the zeugophiurine Oegophiuroidea, hitherto supposedly extinct since the Late Carboniferous. Accordingly, *Ophiocanops* was rec-

ognized as a surviving representative of the Oegophiurida, and its distinctive soft-part characters could be interpreted as characters of that order. There are no bursae, no genital plates, no dorsal or ventral arm plates, and the madreporite is situated at the margin of the disc.

(9) Drawing upon all the foregoing data, one can now determine which characters of ophiuroids and asteroids are of ancient origin, and which are of late, and therefore secondary, origin, subsequent to differentiation of the two groups from their common somasteroid ancestry. The secondary features can be isolated and catalogued.

(10) Extracting this isolate from overall characters of the Asterozoa, one obtains a residue which yields the inferred original characters of ancient asterozoans. The residual morphological attributes include certain soft-part characters, as well as numerous features related to the skeletal system, and these may be amplified by direct reference to the extant somasteroid *Platasterias* and its fossil precursors, the Chinianasteridae. They prove to comprise characters which are exclusively pelmatozoan, having no near parallel in any known group of echinoderms other than pinnulate crinoids. The embryonic structure of the asterozoan disc conforms fundamentally to that of the crinoid calyx,[1] the plates initially comprising a centrodorsal, five basals, five radials, and in some infrabasals also. Interpinnular grooves in somasteroids are inferred to have arisen from an earlier pelmatozoan condition, in which the food grooves were originally carried on the pinnules. The transformation is attributed to a change in the attitude of the cover plates of the food groove, which turned outward so as to overhang the interpinnular space, with a simultaneous development of interpinnular integument. Pinnular ossicles of crinoids are therefore considered to be homologues of somasteroid virgalia, since both are essentially rod-shaped elements produced in identical pinnate axial sequences, and bearing a double row of cover plates on the oral surface. In the surviving somasteroid *Platasterias* the cover plates (and their supporting webs) are erectile, and in the erected condition apparently return to their ancient attitude, simulating a (nonfunctional) food groove on the pinnule.

(11) Somasteroids are thus interpreted as a group transitional in character between other Asterozoa and Crinozoa and are thought to have arisen from some pinnulate pelmatozoan stock, which cannot at present be precisely identified. The approximate nature of the inferred pelmatozoan ancestry is indicated, however, and points to a pinnulate crinoid. The characters of the hypothetical "protosomasteroid" fall very near to those of a biserial crinoid. Since somasteroids themselves are antecedent to other asterozoans, it follows that all star-shaped echinoderms constitute an independent genetic stock, with no relationship to any other group of echinoderms except pinnulate pelmatozoans.

(12) Embryological data are utilized to derive an hypothesis accounting for the manner in which asterozoans might have arisen from a pelmatozoan ancestry similar to pinnulate crinoids. The hypothesis postulates an initial dislocation in adoral direction of the main radial growth axis at the junction of the radial calycinal plate and the first brachial ossicle. The dislocation is inferred to have arisen in a pentacrinoid stage of development of some pinnulate pelmatozoan. Evidence that such dislocation has occurred in the past is adduced from the embryology of extant asterozoans. The dislocation is comparable in nature, though greater in magnitude, to that exhibited in the transverse growth axes of *Platasterias,* where the second virgalium in each metapinnule is occluded, and thus ejected from the growth axis in which it initially belonged, to become the superambulacral ossicle; in postastropectinid asteroids the occluded element vanishes, and the general dislocation of the entire transverse growth axis is initiated, or even completed.

(13) Extending the analysis to crinoids, their somasteroid-like features have been isolated and catalogued. The residual characters are of ancient, generalized type, like those of eocrinoids or cystoids. Crinoids thus seem to be late pelmatozoans which have (a) retained the original meridional

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[1] The homology of asteroid and ophiuroid primary plates with the calyx of crinoids, and their fundamental difference from the apical system of echinoids, has been demonstrated by MORTENSEN, *Systematiske Studier over Echinodermlarver,* 1897, p. 169.

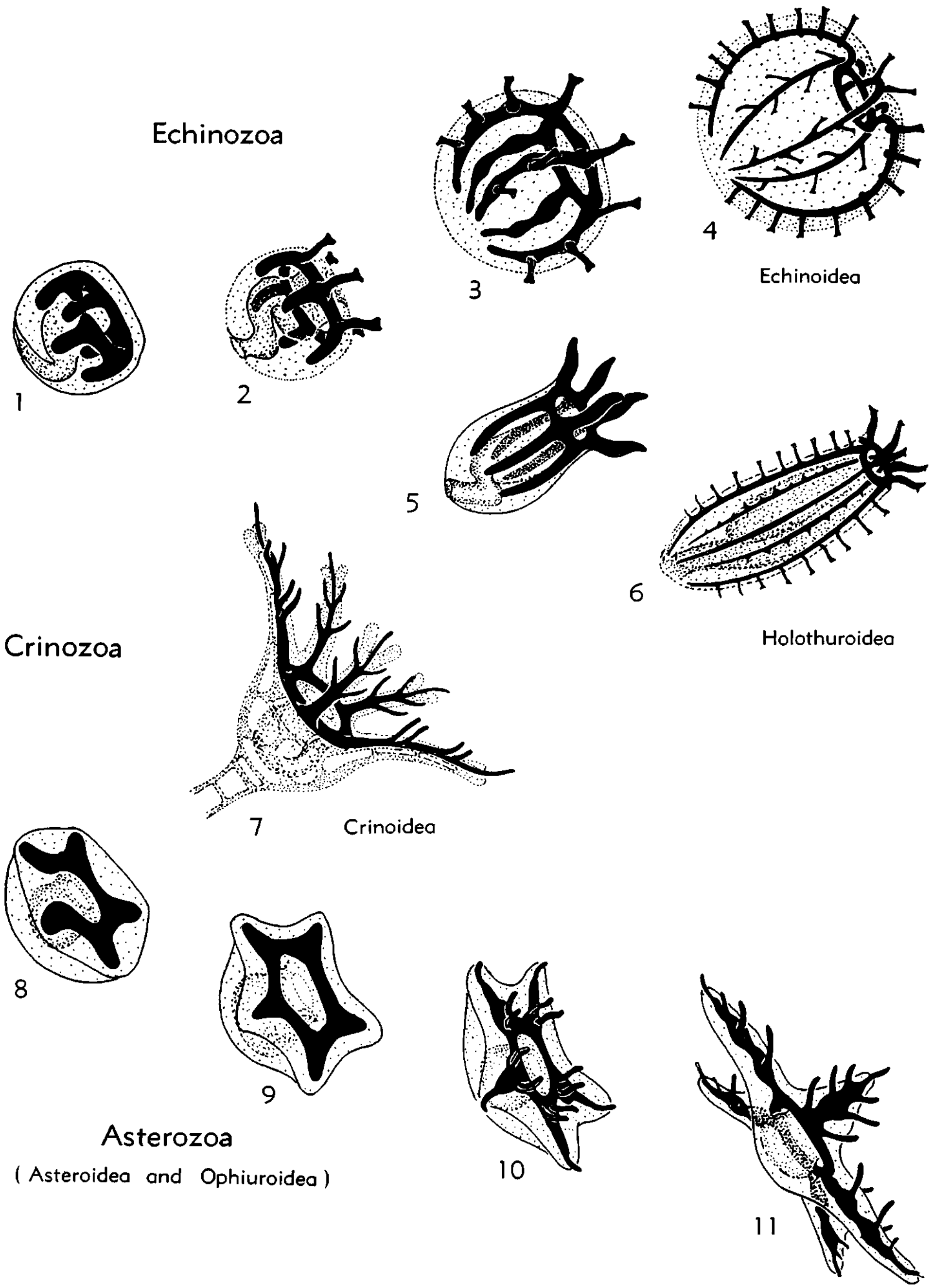

Fig. 31. Major patterns of growth gradients initiated by the hydrocoel during metamorphosis and immediately following it (hydrocoel shown in solid black). Echinozoa *(1-6)* display meridional patterns, whereas Crinozoa *(7)* and Asterozoa *(8-11)* exhibit divergent radial patterns (10) (Fell, n).

patterns of growth in the calyx, as an inheritance from early pelmatozoans; (b) in addition, acquired five, radially directed, divergent axes of growth, leading to the outgrowth of arms and, later on, to secondary acquisition of pinnular subsidiary axes. Somasteroids represent a further term in this progression, in which character (a) is diminished, and (b) is exploited.

(14) The axes of growth of early pelmatozoans are closely comparable with those of echinozoan groups (echinoids, ophiocistioids, holothurians). All are either meridional patterns, or quite disordered. None have radial divergent components.

(15) The Echinozoa are viewed accordingly as archaic derivatives of a still more ancient globoid pelmatozoan stock, the Ophiocistioidea perhaps representing transitional forms. The Echinozoa can have no closer relationship to the Asterozoa than that implied by their derivation ultimately from common ancient globoid pelmatozoans. On the other hand, the Asterozoa present numerous fundamental resemblances to Crinoidea, so great as to imply a close genetic affinity. Consequently, the conventional association of Asterozoa and Echinozoa under one head (Eleutherozoa) is unjustified. The characters supposedly shared by eleutherozoans are, in fact, shared only by demonstrably late groups of Asterozoa, and demonstrably early groups of Echinozoa. The subphylum "Pelmatozoa" is polyphyletic, and must be abandoned as a unit of formal classification.

Figure 31 illustrates the two major patterns of dominant gradients which we may recognize in echinoderms. The upper diagrams show the essentially meridional pattern established in young Echinozoa. The hydrocoel, during metamorphosis, encircles the gut, and then sends out five meridional water tubes which traverse the body. The whole skeleton and nervous system thereafter differentiates under the same meridional gradients. The lower diagrams show the contrasted pattern of dominant radial gradients, found in the Crinoidea and in the Asterozoa. Instead of growing along meridians, the five water tubes are thrust radially outward in the horizontal plane, carrying the body wall and coelom with them, and thus they produce the divergent, radiating arms. The whole skeletal and nervous system differentiates thereafter under the control of such dominant radial gradients, with the calyx alone retaining the ancient meridional system, inherited from the oldest known fossil pelmatozoans. Thus, it now appears that these postlarval gradient systems are a better clue to the phylogeny of post-Cambrian echinoderms. The conventional classification which groups echinoids, holothurians, starfishes, and brittle stars in one assemblage, set apart from crinoids, cannot possibly accommodate the facts as now known.

(16) These inferences, though based mainly on postlarval embryology and comparative morphology, are not entirely dependent on such data, for the fossil record supports them in most respects. The major phylogenetic differentiations here deduced are provisionally dated as not later than Tremadocian time, though some may have been earlier (fossil evidence being inadequate). Persistent transitional forms may be expected at later horizons. In one respect the fossil evidence at present diverges from these results in that the hypothesis predicts the existence of mid-Cambrian pinnulate pelmatozoans, whereas such forms have not yet been found earlier than the Early Ordovician; however, such negative evidence need not be treated as significant until an exhaustive search has been made for pinnulate pelmatozoans in (for example) Indo-Pacific sediments of Cambrian age, and of suitable facies.

(17) The pluteus and auricularia larval stages of echinoderms known to possess them cannot be indicative of phylogenetic affinities, for they imply relationships which are demonstrably false. The larvae may have arisen as a response to similar temporary food-gathering phases in the life-histories of groups not closely related. The evolution of such phases awaits clarification. On the other hand, the ontogeny of the postlarval stages is entirely consistent with morphological evidence from adult echinoderms and with paleontological evidence.

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CRINOZOANS

By H. H. Beaver, J. W. Durham, R. O. Fay, R. V. Kesling, D. B. Macurda, Jr., R. C. Moore, Georges Ubaghs, and †Johannes Wanner

In addition to chapters on cystoids, paracrinoids, edrioblastoids, parablastoids, blastoids, and eocrinoids, the description and discussion of lepidocystoids given in the Addendum (p. S627) belong in this section. Crinoids are allotted entirely to Part T of the *Treatise.*

CYSTOIDS

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[Museum of Paleontology, University of Michigan]

CONTENTS

GENERAL FEATURES

Cystoids are extinct pelmatozoan echinoderms characterized by having a theca of numerous plates provided with distinctive pores. The animals may be presumed to have led an essentially sedentary existence, feeding on microscopic organisms or detritus gathered by their armlike appendages, termed brachioles. Most kinds were anchored by a short column (Fig. 32).

As a group, the Cystoidea are not notable as guide fossils. Let it be understood that most cystoids were small populations, restricted within small geographic provinces. Very few left a record of abundant specimens, and many species are so rare that they are known only from the holotype. *Echinosphaerites aurantium* (GYLLENHAAL), it is true, achieved widespread distribution and phenomenal numbers, but it is properly stressed as the exception. In most formations, cystoids are a very minor faunal element.

What cystoids lack in abundance they make up for in diversity. Their differences are so pronounced that most kinds of cystoids can readily be fitted into a taxonomic key. The hierarchy of suprageneric categories is defensible. At first glance, the classification seems to be too involved, with too many superfamilies for the number of families and too many families for the number of genera; however, this impression is misleading, and each taxon is justified. The unusually high ratio of families to genera does reflect and emphasize the paucity of the paleontologic record. The cystoids made known to science in the last half century have filled in details in some vague sections of the cystoid picture; but they have also disclosed unexpected new extents of the panorama. In the light of the heterogeneity of cystoids already described, one anticipates the discovery of additional genera, quite possibly additional families and superfamilies.

The Cystoidea have invited comparison with several other groups of echinoderms. Several paleontologists have speculated upon the possible ancestry of the cystoids and their relation to other taxonomic units. By their symmetry and shape, cystoids resemble blastoids; by their organization of plates into circlets, some show similarities to crinoids; and by their thecal division into ambulacral and interambulacral areas, some are like echinoids. Nevertheless, cystoids are none of these. They lack such complicated respiratory structures as the hydrospires of the blastoids, they are encased in a theca unlike the calyx and tegmen of the crinoids, and they have a covered peristome, not an open mouth like that of the echinoids. Other differences could be mentioned. The column and the ambulacra, for example, are uniquely developed in the cystoids. Hence, the Cystoidea constitute a discrete class.

Certain authors have suggested that the early cystoids were ancestors of the blastoids and echinoids. Others would not commit themselves to as strong a position, but maintained that the primitive blastoids were very similar to *Cystoblastus* or *Asteroblastus,* and primitive echinoids to *Lepidocalix* or related cystoids. The implication is that the cystoids or their immediate forebears gave rise to other taxa of echinoderms. This realm of supposition generated schools of proponents for this or that genus as the special progenitor of another class. Until more echinoderms are intensively investigated, evolutionary hypotheses involving classes remain inconclusive.

For one reason or another, most paleontologists have avoided the cystoids. Significant advances in studies of morphology and taxonomy have been sporadic. Because of the very few workers who have devoted much effort to classification of cystoids, the literature is not extensive. It is scattered, however, through several journals and textbooks and over a protracted period. The most important contributions have been made by GYLLENHAAL (56), who recognized the animal nature of the fossils and placed them in the echinoderms; by VON BUCH (29-31), who set the cystoids apart as a taxon; by MÜLLER (90), who outlined the primary bases for classification; by BATHER (8-15), and JAEKEL (68-72), who presented detailed systems of classification; and more recently by REGNÉLL (99-105), who filled in details of cystoid morphology and clarified pelmatozoan taxonomy. Other workers

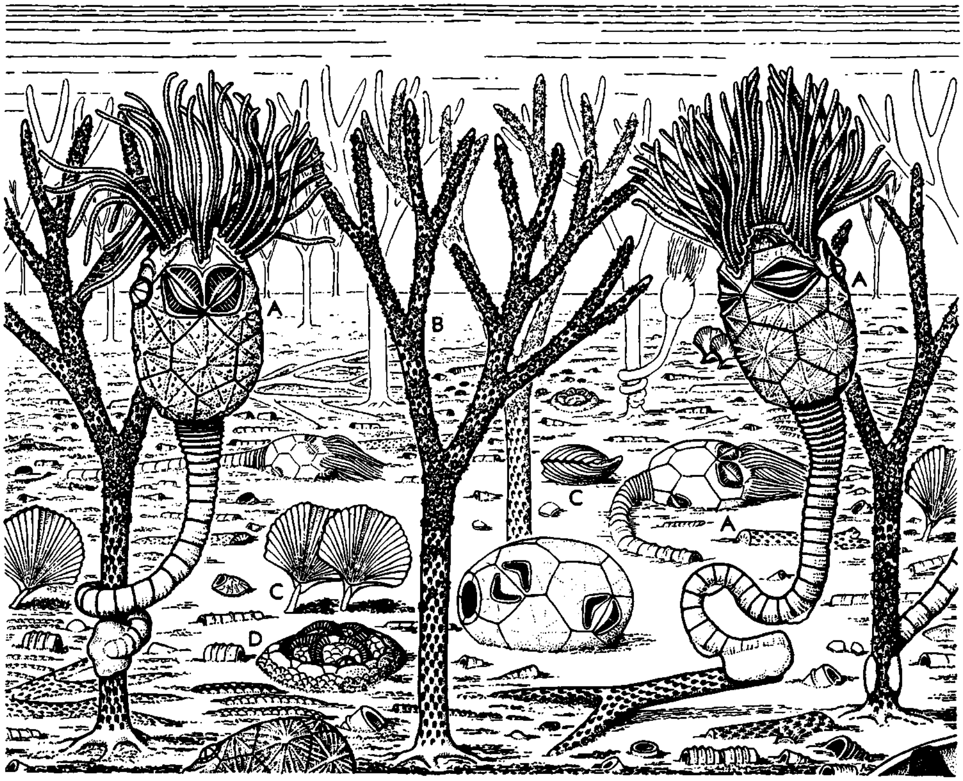


FIG. 32. Reconstruction of sea floor in southern Indiana during Richmond (Late Ordovician) time, showing *(A) Lepadocystis moorei* (MEEK), *(B)* ramose bryozoans, *(C)* small brachiopods, and *(D)* edrioasteroids in natural association (75).

advanced cystoid studies from time to time, but generally they were concerned with descriptions of new species or with particular divisions of the Cystoidea.

In recent years, the only paleontologists who have attempted concerted investigations of cystoids are Prof. GERHARD REGNÉLL, of the Paleontologisk-Geologiska Institutionen at Lunds Universitet, Sweden, and Prof. R. F. GEKKER [HECKER], of the Paleontologiskii Institut of the Akademiya Nauk, Moscow, Russia. Both have very graciously offered suggestions on classification. Prof. GEORGES UBAGHS, of the Laboratoire de Paléontologie of the Université de Liège, Belgium, has kindly presented his opinions on certain dubious cystoids and provided me with latex casts which clarify the position of *Rhombifera*. To each of these authorities, assistance given is gratefully acknowledged.

The aspects which have best support are the intricate relationships among genera and suprageneric taxa. Of special interest is the sudden culmination of the Cystoidea. The first unquestioned cystoids appeared in Early Ordovician time. In the following epoch, more than three-fourths of the families were represented. For the most part, the 22 families and seven superfamilies of Cystoidea are clear-cut entities.

Whereas the classification of cystoids is now reasonably satisfactory, despite some dubious genera, the paleontologist can plausibly anticipate refinements. The most deficient field of our knowledge centers on the paleoecology of cystoids. Progress has been halting, and likely will so continue. The position of the Cystoidea among Paleozoic echinoderms can only be set forth on the basis of morphology; the degree to which this reflects phylogeny will not be soon decided. Nevertheless, the known variety of shapes, thecal pores, ambulacra, plate arrangements, and forms of periproct, hydropore, and gonopore will undoubtedly increase as new cystoids are discovered. At the same time, the evolutionary trends within families will assume sharper definition. As stated by REGNÉLL (105), "Some future finds may have far-reaching consequences. But isn't it so that what makes Palaeontology such a fascinating study is, in part, the very fact that so much of the Past remains to be revealed in the Future?"

MORPHOLOGY

THECAL PORES

Whether or not they are considered to be the sole criterion for the class, thecal pores must be granted precedence in any discussion of cystoid morphology. Certainly, within the Crinozoa the nature of thecal perforations assumes taxonomic significance, and within the Cystoidea it is used to differentiate the two orders. Thecal pores are here discussed according to their form, their supposed function, and the manner in which they operated.

FORM OF PORES

Thecal pores are in one or the other of two main forms: those in which complete units are confined in most specimens to one thecal plate (Fig. 33,*8*) and those in which each unit is invariably shared by adjacent plates (Fig. 33,*9*). The first is characteristic of the Diploporita and the second of the Rhombifera. Although the two types have been called diplopores and pore rhombs, these designations are somewhat misleading, for not all pores confined to individual plates are paired and not all pores shared by plates are arranged in rhombs. For convenience, nevertheless, these terms will be employed.

DIPLOPORES

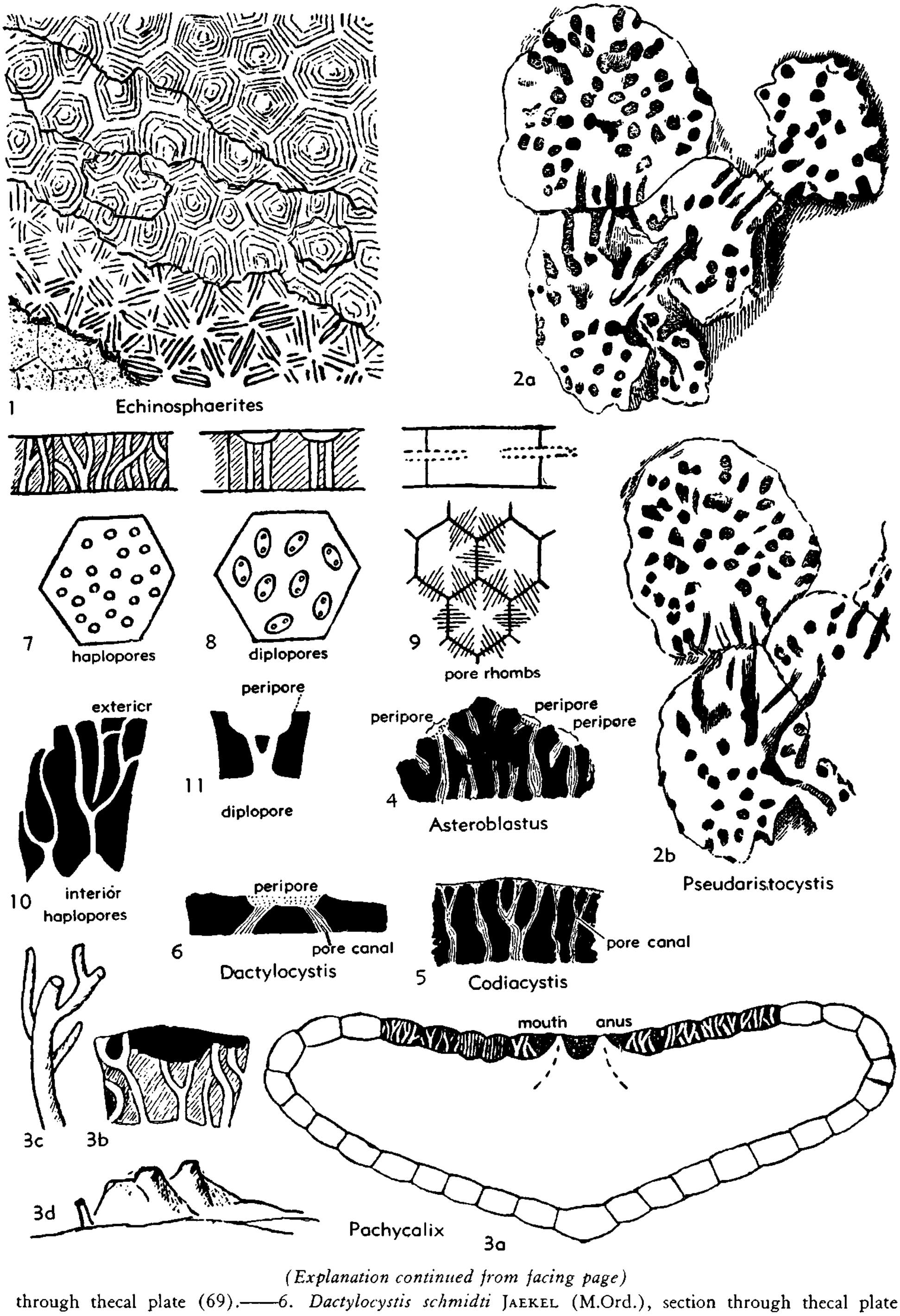
The diplopore type of thecal pores may well be older than pore rhombs, despite the reference by REGNÉLL (99) to "the fact that the Rhombifera appeared, as far as known, earlier than the Diploporita." The Middle Cambrian doubtful genera *Lapillocystites* and *Pilocystites* from Bohemia appear to be related to the diplopore-bearing genera of the Aristocystitidae. If these Bohemian forms are remains of cystoids, then the Diploporita are definitely older than the Rhombifera.

The classic development of diplopores is found in such genera as *Asteroblastus* (Fig. 33,*4*), *Sphaeronites,* and *Glyptosphaerites,* in which the pores are not only distributed in pairs, but each pair lies within a distinct depressed area (the *"Porenhof"* of JAEKEL, 69; *"fossette"* of CHAUVEL, 33), and the association is further emphasized by a surrounding rim (Fig. 33,*6*). In whatever orientation or wherever present on the theca, the pores are invariably paired in such cystoids, leading to the conclusion that the two pores of each pair acted as a unit. In most fossils, the canals leading to the openings have the form of a Y set normal to the surface of the plate in which they occur (Fig. 33,*11*).

Not all pore units confined to single plates are so regular. In fact, a large spectrum can be assembled to illustrate various degrees of irregularity. The most irregular of the pores have been termed haplopores (Fig. 33,*10*). Neither "diplopore" nor "haplopore" precisely express the development of thecal pores in some cystoids, which have intermediate stages with some pores more or less paired and others obviously not paired at all (Fig. 33,*5*).

In *Aristocystites bohemicus,* JAEKEL (69) described the **peripores** as bent, twisted, meandering, and branched, so that the

FIG. 33. Structure of thecal pores and plates.——*1. Echinosphaerites* (L.Ord.-U.Ord.), with outer layers scaled off to show ornamentation of epitheca and underlying tangential pore canals (69).——*2. Pseudaristocystis dagon* (BATHER) (M.Ord.); *2a,b,* polished surfaces to show pores in thecal plates (11).——*3. Pachycalix halli* (ROUAULT) (M.Ord); *3a,* section through theca showing mouth and anus; *3b,* enlarged section through thecal plate; *3c,d,* casts of thecal pores (34).——*4. Asteroblastus foveolatus* (EICHWALD) (L.Ord.), section through thecal plate (69).——*5. Codiacystis bohemica* (BARRANDE) (M.Ord.), section



(Explanation continued from facing page)

through thecal plate (69).——*6. Dactylocystis schmidti* Jaekel (M.Ord.), section through thecal plate showing pore canals and peripore (69).——*7-9.* Generalized cross sections and surfaces of thecal plates bearing haplopores *(7)*, diplopores *(8)*, and subepithecal pore rhombs *(9)* (34).——*10,11.* Generalized sections through haplopores and a diplopore (125).

paired pores are more distant than in *Mesocystis* and *Codiacystis,* and some peripores have supernumerary pores. The related descendant in America, *Trematocystis,* has a complicated set of surficial grooves with irregularly spaced pores. In his discussion of peripores or fossettes, CHAUVEL (34) differentiated various kinds according to their arrangement, (1) more or less radially disposed pores on each plate (e.g., *Calix, Sinocystis*), (2) pores placed more or less parallel to the long axis of a plate (e.g., *Sphaeronites lobiferus*), and (3) pores arranged horizontally on adambulacrals (e.g., *Protocrinites, Dactylocystis*). CHAUVEL also noted the different shapes of peripores as elliptical (e.g., *Calix*), subcircular (e.g., *Codiacystis*), horseshoe-shaped (e.g., *Hippocystis*), vermicular (e.g., *Aristocystis*), polygonal (e.g., *Tholocystis*), and in pustules (e.g., *Sinocystis*).

Some pores are nearly or quite closed over by an epithecal layer. This occurs in *Trematocystis* in much the same fashion, according to JAEKEL (69), as epitheca covers the tangential pore canals in the rhombiferan *Echinosphaerites.* The nature of epitheca became the subject of disagreement between REED (98) and BATHER (13) regarding cystoids from Yunnan. REED differentiated *Sinocystis* from *Ovocystis* partly on the basis of the presence of an epithecal covering of diplopores in the former and its absence in the latter. BATHER studied the type species of *Sinocystis* and reported on the rounded elevations containing the pore pairs that "as it grows upwards there is certainly a tendency for the epistereom to block the pores, but I was unable to convince myself that it ever actually succeeded." In consequence, he made *Sinocystis* and *Ovocystis* synonyms, and stated that if epitheca did close diplopores, it should be interpreted as a character of old age. According to BATHER, the pore canals of *Sinocystis* became ensconced in epitheca, in some specimens a pair of pores opening at the summit of a tubercle and in others several pairs occurring in a fused structure which he termed a turret.

In the Sphaeronitidae, an inverse correlation appears to be recognizable between size and number of the pores, whereby pores tend to be small and numerous or large and few.

Another trend is for pores to become localized. An outstanding example is found in the Dactylocystidae, in which the diplopores are limited to the brachiole-bearing "adambulacrals." The peripores are mostly horizontal, set between brachiole facets. On the "adambulacrals" the individual pores are larger, longer, more nearly aligned parallel, and much fewer in the Dactylocystidae than in the Protocrinitidae. In the Asteroblastidae the pores are concentrated on interambulacral plates in the adoral part of the theca; this is especially well demonstrated in the five special pore-bearing plates of *Asteroblastus.* In *Glyptosphaerites leuchtenbergi* the pores are concentrated in the adoral part of each plate, as illustrated by REGNÉLL (99), and in species of *Eucystis* the diplopores are mostly limited to the adoral half of the theca.

It may be emphasized that diplopores occur in both ambulacral and interambulacral positions. In the Protocrinitidae they are about as numerous on the interambulacral plates as on the "adambulacrals," and in the Glyptosphaeritidae they are distributed about evenly in the two positions. Where localization occurs, the diplopores may be restricted to ambulacral positions, as in the Dactylocystidae, or concentrated in interambulacral plates, as in the Asteroblastidae.

In the multiplated Aristocystitidae, some specimens show diplopore-free areas of irregular shape and magnitude on the sides of the theca, as illustrated by BARRANDE (3). Cystoids attached by the base of the theca lack diplopores on the "sole" or area of attachment. Furthermore, CHAUVEL (34) claims to have observed pores near the base in *Codiacystis moneta* much more developed than those on the rest of the theca.

A peculiar disposition of pores occurs in a cystoid from the very low Middle Ordovician strata of Burma described by BATHER (11) as *Aristocystis dagon.* This species was made the type of *Pseudaristocystis* by SUN (123) and the type of *Dagoncystis* by CHAUVEL (34), who refused to acknowledge SUN's genus on the ground that the form of the name suggested a lack of true relationship to *Aristocystites;* irrespective of its being appropriate, *Pseudaristocystis* has priority. The remarkable circumstance in the pores of *P. dagon* is that the canals in the central area of each plate perforate it at right angles to the surface, but those in the marginal area curve to become normal to the suture and lead to adjacent plates (Fig. 33,*2a,b*). Thus each plate contains two kinds of pore canals, one nearly perpendicular and resembling a haplopore and the other with more horizontal development and resembling a unit of a pore rhomb. In view of its stratigraphic position, *Pseudaristocystis* cannot be the ancestor of both the Diploporita and Rhombifera, but its existence lends support to the very tempting supposition that a similar cystoid may have held such a distinction.

PORE RHOMBS

Just as not all pores confined to one thecal plate conform to the classic concept of diplopores, not all pore rhombs are expressed as **pectinirhombs.** The canals of some are concealed by epitheca, and the pores in others are not arranged in a rhomb. Each unit of a pore rhomb, however, is shared by two adjacent thecal plates. Such a unit and its openings were termed **dichopores** by Jaekel (69, 71), who substituted Dichoporita for Rhombifera as the name of the order. In general, each of the four superfamilies of Rhombifera—the Glyptocystitida, Hemicosmitida, Polycosmitida, and Caryocystitida—possesses a distinctive type of pore rhomb.

In many of the Glyptocystitida, the rhombs have long slits for openings, so that Forbes (51) called them "pectinated rhombs," and others have since termed them "pectinirhombs." In many genera (e.g., *Cheirocrinus*, Fig. 34,*2*, *Glyptocystites*, most callocystitids) the long, narrow, parallel slits bear a strong resemblance to the slots in a comb; but in other genera of the superfamily (e.g., *Echinoencrinites, Erinocystis*) some species have the openings reduced to small ovals. The slits are always paired, one in each plate, and the two halves of a rhomb are approximately mirror images (Fig. 34,*1,2*). The number of pores varies greatly; some species of *Erinocystis* have only a few in each half-rhomb, whereas *Pseudocrinites gordoni* has more than 100 in a half-rhomb.

Most pore rhombs have the shape of a rhomb, each half-rhomb occupying a sector of the polygonal plate, a triangle bounded by two radii and one side of the plate. Some rhombs, however, are reduced to just half of this area, each half-rhomb filling half of a sector. These are called **demirhombs,** and the pores in a demirhomb form a chevron more or less symmetrical with respect to the plate suture. Demirhombs are mostly limited to genera with numerous pore rhombs (e.g., *Cheirocrinus, Glyptocystites, Cystoblastus*).

Whether developed as full rhombs or as demirhombs, the pectinirhombs can be classified by the distribution of pores. In some cystoids (e.g., *Leptocystis*) the two pores are confluent in each unit of the rhomb, so that open slits extend from one plate into the other (Fig. 34,*1*). According to the classification proposed by Bather (12), such pore rhombs are **conjunct** (Fig. 35). In contrast, pore rhombs in which each unit or dichopore has a distinct and separate opening in each plate are said to be **disjunct** (e.g., *Cheirocrinus penniger* and the majority of other Glyptocystitida, Fig. 34,*2*). In *Cheirocrinus interruptus* (and perhaps in one or more other cystoids with which I am not acquainted), each unit has more than one pore in each plate and the pores are so arranged as to form concentric rhombs; this rare type Bather called **multidisjunct** (Fig. 35). To these types, Sinclair (118) added **montidisjunct,** to apply to disjunct pore rhombs in which one of the half-rhombs has a rim surrounding the pores (Fig. 36,*1b,c*). Most of the Silurian and Devonian Glyptocystitida are montidisjunct, but the outstanding example is *Jaekelocystis,* in which one half-rhomb of each pair is reduced to a small subcircular opening provided with a spoutlike rim.

During the geologic history of the Glyptocystitida, the number of pore rhombs was reduced to three and the positions of these rhombs were stabilized along the sutures between plates designated as basal *2* and infralateral *2(B2/IL2),* lateral *1* and radial *5 (L1/R5)* and lateral *4* and radial *3 (L4/R3)*. An Ordovician species of *Glyptocystites* has as many as 14 pectinirhombs, and some Ordovician cystoids of the family Cheirocrinidae have even more. In contrast, none of the Glyptocystitida younger than Early Silurian have more than three rhombs.

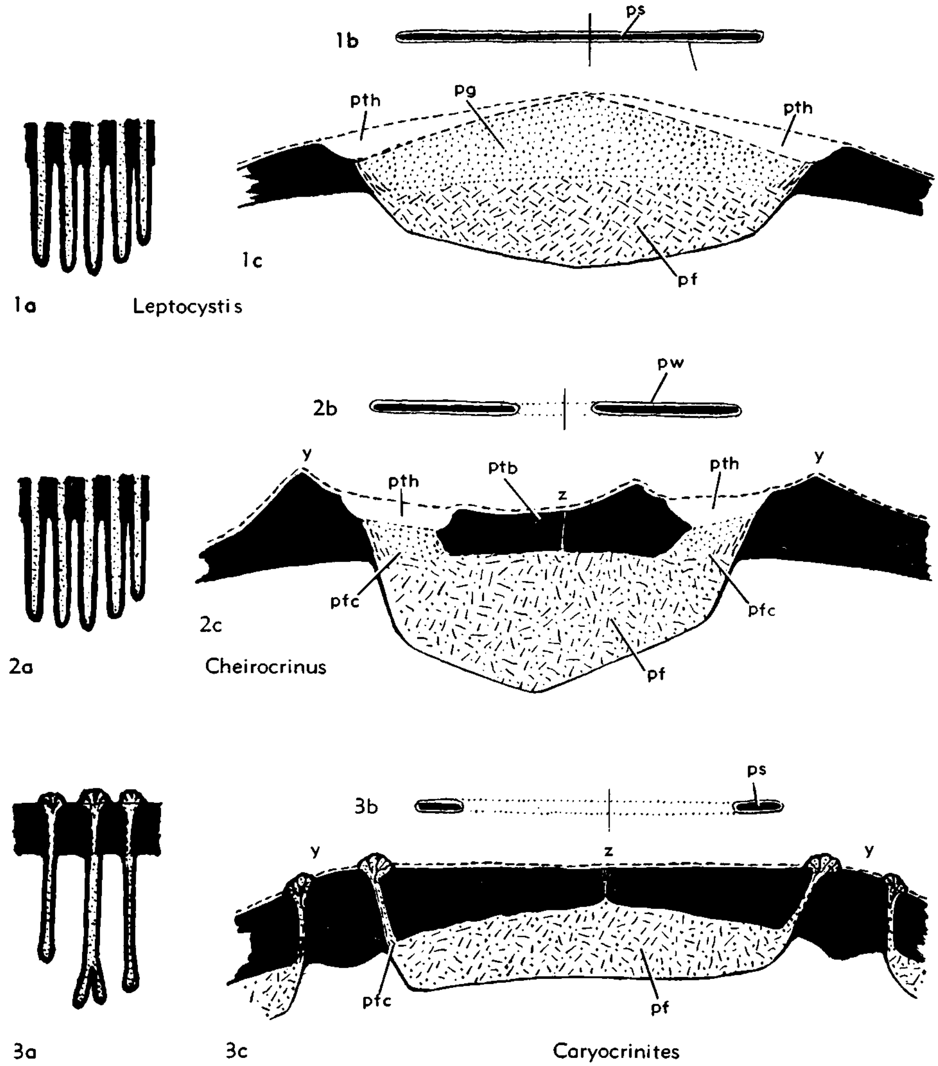


Fig. 34. Diagrammatic sections across pores *(1a, 2a, 3a)*, top views of pores *(1b, 2b, 3b)*, and sections along pores *(1c, 2c, 3c)* in selected cystoids.——*1. Leptocystis* (L.Ord.-L.Sil.), typical of conjunct pectinirhombs in Glyptocystitida.——*2. Cheirocrinus* (L.Ord.-U.Ord.), typical of disjunct pectinirhombs in Glyptocystitida.——*3. Caryocrinites* (M.Ord.-M.Sil.), typical of pore rhombs in Hemicosmitida (69). [Explanation: *pf,* inner pore folds; *pfc,* internal end of pore canal; *pg,* pore canal; *ps,* pore slit; *ptb,* intra-slit space; *pth,* external pore; *pw,* pore wall; *y,* plate center; *Z,* suture.]

The stable positions of the three show an unusual relationship in the theca: in the adoral half of the theca, rhombs *L1/R5* and *L4/R3* are on opposite sides in posterior and anterior areas, and the third rhomb, *B2/IL2,* is at the aboral left, diagonally opposite to the periproct. As thus arranged, the alignment of the pore units is such that those in each rhomb are nearly at right angles to those of the other two.

Very little information is available on the actual nature of the internal extensions of the pores. From the few reports of structures, the units seem to be folds projecting inward from the thecal wall. Inasmuch as these folds are seldom preserved, they ap-

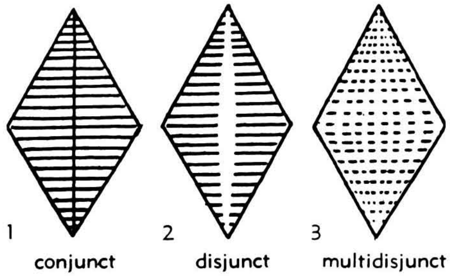


FIG. 35. Three principal types of pectinirhombs (12).

pear to be uncalcified in most specimens and to be replaced post-mortem in the few examples in which they are found. The descriptions of these folds leave considerable doubt as to whether they are composed of inward extensions of the epitheca or of an inner hypothecal layer of plate material.

It should be pointed out that the intrarhombic platform which separates the pores of one plate from those of the other in disjunct pectinirhombs attains only about half the thickness of the rest of the thecal plate, as illustrated by KESLING & MINTZ (75) in *Lepadocystis moorei* and by KESLING (74) in *Rhombifera bohemica.* Possibly, the two pores of each unit were connected by a canal or tube that did not project into the thecal cavity but, instead, lay close under the intrarhombic platform.

A second type of pore rhombs is found in the Hemicosmitida and exemplified by *Caryocrinites.* It strongly resembles the pectinirhomb type except that the pores terminate externally in tubercles covered by epitheca (Fig. 34,*3*). The canals leading into the tubercles are branched near their distal ends in some species; as a result, weathered specimens in which the epitheca has been removed are described as having **sievelike end pores.** In *Caryocrinites,* the units were evidently quite regular, since each pore-bearing tubercle is directly opposed to its mate in the adjacent plate. In some species of *Hemicosmites,* however, the pores are irregularly distributed, so that it is impossible to match pores of one plate with those in another, at least with any degree of assurance.

A third type has horizontal tubes within the plates which curve inward at each end to the interior of the theca. These are termed **tangential pore canals.** They typify the Caryocystitida. The whole of the rhomb structure is concealed by the epitheca, and the nature becomes apparent only in weathered specimens in which the outer

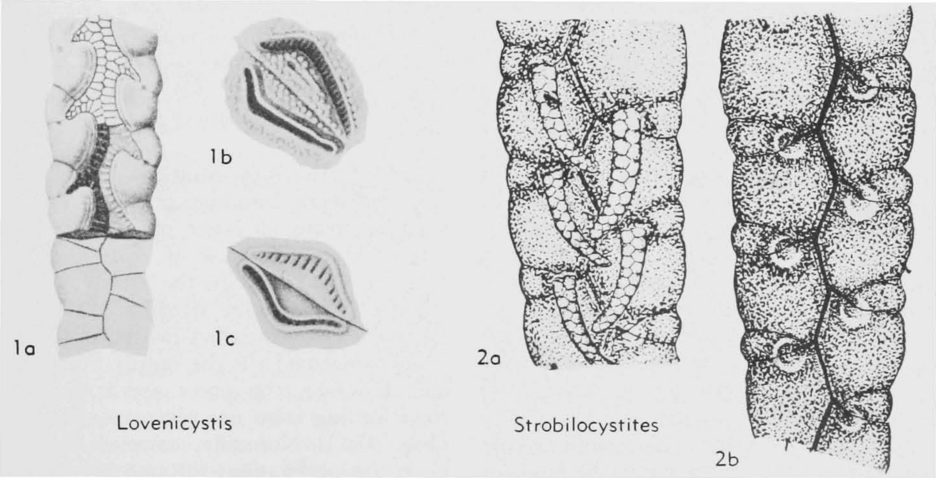


FIG. 36. Ambulacral and pore-rhomb structures of cystoids.——*1. Lovenicystis* (U.Sil.); *1a,* ambulacrum, covering plates in upper (proximal) section, flooring plates removed to show impressions on thecal plates in lower (distal) section; *1b,c,* examples of montidisjunct pectinirhombs (99).——*2. Strobilocystites* (M.Dev.-U.Dev.); *2a,* section of ambulacrum with brachioles restored; *2b,* ambulacrum showing two kinds of alternating flooring plates, ambulacral groove, and lateral branches leading to brachiole facets (120).

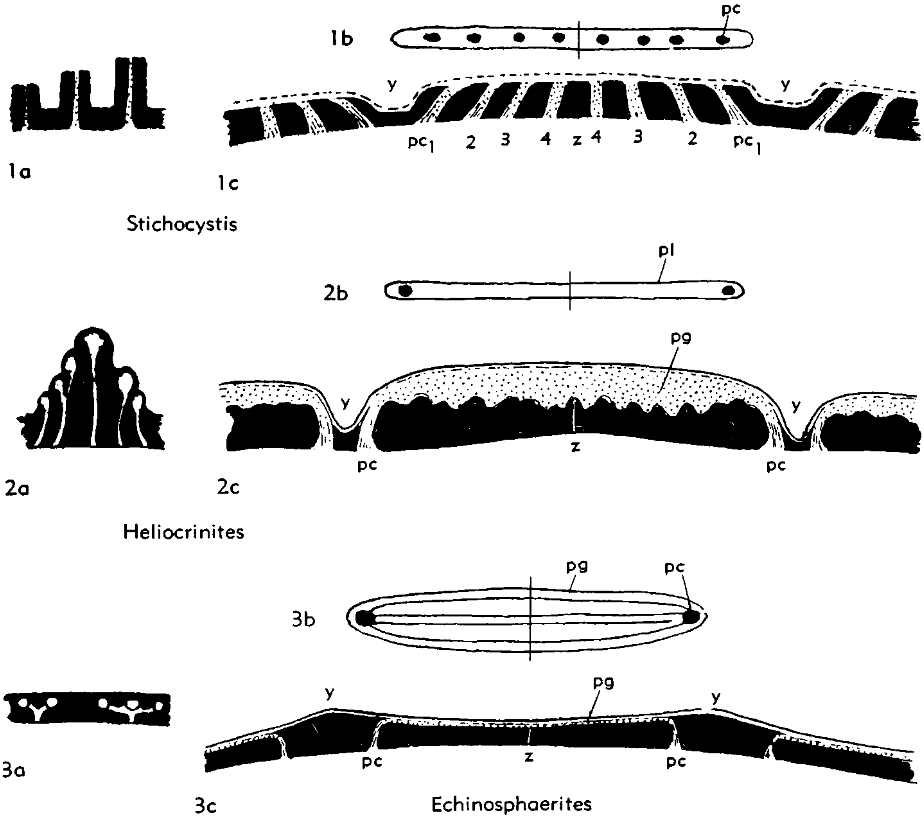


FIG. 37. Diagrammatic section across pores *(a)*, top view of a pore *(b)*, and section along a pore *(c)* in selected cystoids. ——*1. Stichocystis* (M.Ord.), typical of pore rhombs in Polycosmitida.——*2. Heliocrinites* (L.Ord.-U.Ord.), typical of simple tangential pore canals in Caryocystitida.——*3. Echinosphaerites* (L.Ord.-U.Ord.), typical of compound tangential pore canals in Caryocystitida (69). [Explanation: *pc*, pore; *pg*, pore canal; *pl*, pore canal wall; *z*, junction of plates; *y*, center of plate.]

covering has been removed. Within this type of pore rhomb are two subtypes. In the first, the terminal portions of the canals, more or less vertical, are connected by a single tangential canal (Fig. 37,*2*); this subtype is exemplified by *Heliocrinites.* In the second, the terminal portions are connected by more than one canal, so that the number of tangential pore canals outnumbers the terminal sections leading to the interior (Fig. 37,*3*); this subtype is exemplified by *Echinosphaerites.* In the latter, the epitheca in some specimens is very thick and the plates bear concentric markings, revealing nothing of the kind of pores present (Fig. 33,*1*).

The last-cited type of pore rhombs is the most difficult to interpret. As preserved in cystoids of the Polycosmitida, the pore system consists of a number of inclined canals, with no trace of inner or outer covered tubes connecting those of one plate with those of the other. In the family Polycosmitidae the pores are irregularly arranged, lacking clear association on the two thecal plates concerned. In the family Stichocystidae, however, the pores are arranged in rows leading from one plate onto the other (Fig. 37,*1*). Normally, as preserved, the pores are perforations through ridges, with the same number on one side of a suture as on the other. Those farther from the suture are more inclined, suggesting that each ridge of pores may have developed in the Stichocystidae in much the same manner that the pores formed in the Caryocystitida, but with repetition of inclined canals leading to the interior; neither epitheca nor canals connecting pores have ever been observed.

FUNCTION OF PORES

Although most authors ascribe a respiratory function to thecal pores, there is not yet universal agreement. The use for respiration was stressed by many authors—PANDER (93), VON BUCH (31), VOLBORTH (136), MÜLLER (90), BILLINGS (23), JAEKEL (69), and others. Some differences of opinion on the mode of fulfilling this function are noted below.

BATHER (10) suggested that in large canals of the haplopore type, connective tissue or stroma gained access from within the theca to the outside, where it spread out as a thin covering layer. This was endorsed by DELAGE & HÉROUARD (37).

KIRK (76) supposed that free-living cystoids may have developed tube feet for locomotion, inasmuch as the brachioles were poorly suited for this purpose. Evidence in support of this possibility was offered by CHAUVEL (34).

In 1941, GENEVIÈVE DELPEY (who married HENRI TERMIER and with him published many joint papers and books) proposed that pectinirhombs were balancing organs (38). She was impressed by the arrangement of the dichopores in the three rhombs of late Rhombifera at right angles or nearly so. SINCLAIR (118) discussed this theory, noting that even in the most specialized of the Glyptocystitida, he could not ascertain exact perpendicularity of the three sets of pores, as would be the probable disposition for organs of balance. He further declared

> Even in *Pleurocystites,* which seems most specialized for a vagrant life and therefore most in need of accurate knowledge of its position, there is no precise arrangement of the rhombs. . . . It is essential for an organ of balance that the otoliths be shielded from any influence other than the movement of the animal. Usually the otocysts are either completely within the body or open to the exterior by a very small pore. In *Callocystites* we find the rhombs open for most of their length, and each rhomb surrounded by about 40 ciliated brachioles each creating a current of water. . . . I think the contrast between this structural arrangement and that necessary for a functioning proprioceptor is too great for reconciliation.

TERMIER & TERMIER (125) again suggested a balancing function for pectinirhombs.

BATHER (10) published a figure of a hypothetical glyptocystitidan cystoid in which he included pore rhombs in all locations known on the theca. In this composite, he supposed that the lack of pore rhombs signified the course of the gut. In 1913, BATHER (12) corrected his figure to add additional rhombs, and in 1948, SINCLAIR (118) noted another. The accompanying illustration (Fig. 38) includes still others that have been reported in the Glyptocystitida. BATHER (10, 12) thought that pressure of the gut against the thecal wall prevented formation of pore rhombs.

SINCLAIR (118) explained the distribution as an association of pore rhombs and internal coelomic pouches. He pointed out that the gut is adequately supplied by water and that the water-vascular system is furnished contact with the outside by the hydropore, but that the coelom, being internal, is in need of a special respiratory mechanism. From BATHER'S (10) reconstruction of the imagined primitive pelmatozoan ancestor, SINCLAIR proposed that the basal pore rhomb, on the suture between basal *2* and infralateral *2 (B2/IL2),* served to aerate the right posterior coelom and that upper rhombs aerated the left posterior coelom. With regard to the rhomb-free zone around the theca, he stated, "There are no rhombs along its [the gut's] course, not because pressure inhibited them, but because the presence of the gut precluded that of the coelom, and the rhombs were functionally connected with the latter." In Figure 38 one or the other of the alternative courses for the rhomb-free zone are present in any selected species.

A very positive expression of conviction was that of REGNÉLL (99), who said, "Nor can it be doubted nowadays that they [the pores] performed a respiratory function, being—besides the ambulacral and alimentary systems, the only organs by which aërated water could come into contact with the body-fluids for oxygenation by osmosis. And it is likely that the main respiration took place by the pores."

OPERATION OF PORES

The interpretation of how the pores functioned is dependent upon the interpretation

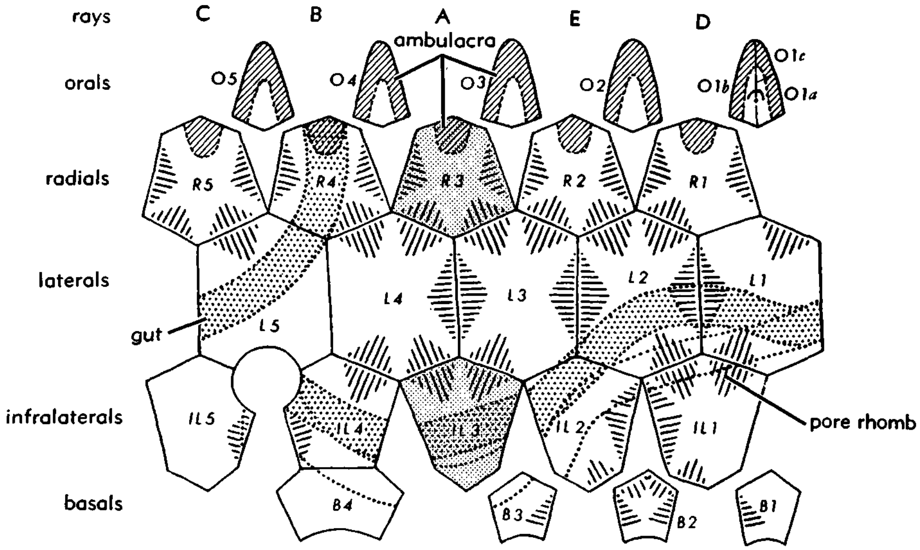


Fig. 38. Generalized plate diagram of a glyptocystitidan cystoid, with plate designations by Regnéll (adopted in the *Treatise*): *B,* basal; *IL,* infralateral; *L,* lateral; *O,* oral; *R,* radial. Ambulacra are indicated by oblique ruling on orals and radials. Pore rhombs are shown in all positions known in the Glyptocystitida. Alternative hypothetical courses of the gut are indicated by dotted lines along one or another rhomb-free path present on each cystoid. Plates of *A*-ray shaded (10,12 mod.).

of the epitheca, of the external appendages associated with pores, and of the ambulacral system. Various combinations of reasoning on these factors have led to strongly divergent conclusions.

First, the epitheca (or epistereom, as termed by some writers) has been interpreted, according to Chauvel (34), as (1) membranous, in some instances mineralized after death of the cystoid, (2) the site of calcification more or less advanced, or (3) a continuous calcareous layer. In this connection, Reed (98) considered that a thick layer of epitheca covered the tubercles and concealed the openings of diplopores in *Sinocystis,* whereas Bather (13) stated,

> It is difficult to believe that the closing of true diplopores by epistereom can ever have been a normal character of the adult in any species: the structures seem so clearly adapted for the passage of some aërating organs (papulae) through the test; and the very fact that the epistereom does grow up in tubercles and turrets indicates the constant outward extension of those organs.

Depending upon whether one accepts or rejects the hypothesis of a continuous calcareous epitheca, two alternative explanations of the circulation of fluids may be advanced with respect to respiration: external, with water introduced from outside (Billings, 23), or internal, acting as reservoirs (Bernard, 17).

The epitheca in *Echinosphaerites,* for example, seems so thick and distinctively ornamented (Fig. 33,*1*) that it is difficult to conceive of it as the post-mortem calcification of a soft membrane on the surface of the theca. On the other hand, it is equally puzzling to explain the functioning of pore rhombs in many cystoids if the epitheca was a dense layer of calcareous deposits. It is worthy of note here that, were it not for the presence of the epitheca in the Hemicosmitida and Caryocystitida, all types of pore rhombs would show rather close resemblance.

Kirk (76) thought that contact with an exterior object promoted the growth of secondary stereom, thus accounting for the layer covering over the diplopores in the area of attachment for certain specimens of *Aristocystites.*

The nature of external appendages, if any, has occasioned much speculation. The theories are predicated upon the interpretation of the epitheca. In the original assignment of cystoids to the animal kingdom, GYLLENHAAL (56) took the diplopores as attachments for ambulacral feet, so that he compared the globular *Sphaeronites* to echinoids. MÜLLER (90) astutely noted the interambulacral position of diplopores in many Diploporita, and therefore denied that diplopores were ambulacral pores. Nevertheless, LOVÉN (81) continued to regard GYLLENHAAL's interpretation as a brilliant deduction, and stated (translation by REGNÉLL, 99),

> There seems also to be little reason for doubting the pedicellar character of the geminous pores in *Sphaeronis, Eucystis, Glyptosphaera, Protocrinus, Mesites,* the less so since the want of a decisive proof in this regard is supplied, in some degree at least, by the occasional preservation of the actual pedicels in a contemporary form of Echinoids, *Botryocidaris Pahleni*. . . .

Whereas the taxonomic position of *Bothriocidaris* may be open to question, its structure does not corroborate the nature of diplopores in the Diploporita, as stressed by REGNÉLL (99).

KIRK (76) also supposed that free-living cystoids may have developed tube feet for locomotion. His interpretation has received recent support. CHAUVEL (34) reported that in *Codiacystis moneta,* canals of the aboral corona are larger than those on the rest of the theca, a situation that he analyzed as robust tube feet or tentacles by which the animal could attach itself for support or release itself at will, the rest of the theca being covered by respiratory structures. Inasmuch as the brachioles are inadequately constructed for propulsion, CHAUVEL was convinced that fixation and movement could have been taken over by tube feet in forms that were unattached as adults.

The respiratory function of external tube feet or tentacles connected with the ambulacral system through diplopores was suggested long ago by PANDER (93), VON BUCH (31), and others.

BATHER (13) reached the conclusion that canals served to conduct a liquid (probably coelomic) in osmotic connection with the surrounding medium, the fluid entering at one pore and leaving by another terminating distally in a papilla. He did not, it must be remembered, think the epitheca constituted an impervious, continuous layer. Later, BATHER (14) referred to the hypothetical external structures as papulae and compared them with the podia of echinoids, saying that both "subserve aëration by an up-and-down current of the contained fluid."

REGNÉLL (99) considered that a papula or papilla may have projected from each diplopore, with a circulation through the canals quite independent of the ambulacral system.

CHAUVEL (34) presented two hypotheses whereby the structures associated with diplopores (and possibly pore rhombs as well) could have an ambulacral origin: (1) the internal ambulacral system in the primitive cystoid had ramified canals and numerous podia distributed over all the theca, which by specialization came to constitute one group of ciliated tentacles devoted to feeding and another, little changed, used for respiration; or (2) the primitive echinoderm may have had two absolutely independent systems, one a number of ciliated grooves for feeding and the other an ambulacral system; in the Asterozoa, radial symmetry early affected both systems equally, so that they came to be associated (food grooves and ambulacra in radial positions); but in the cystoids, resistant to pentamerism, only the food grooves were affected and the ambulacral system remained diffused and leading to podia. The restriction of diplopores to ambulacral areas in *Dactylocystis* and *Estonocystis* were cited as examples favoring the second hypothesis, wherein the pentamerism was extending its influence to diplopores as well as food grooves.

These hypotheses, as admitted by CHAUVEL, have against them the fact that cystoids show no traces of water canals under plates forming the ambulacral grooves, such as occur in all living echinoderms, from which proliferations lead to the podia.

Still another suggestion on diplopores has emerged. From the pustular form of the diplopores in certain cystoids, CHAUVEL (34) was moved to raise the question of the possibility that some of the Diploporita possessed an appendicular skeleton, provided with movable spines like those of echinoids. Later, TERMIER & TERMIER (125) interpreted *Lepidocalix* as a cystoid bearing such spines.

No final conclusion regarding the nature of external protuberances, the origin and operation of diplopores, or the limits of the ambulacral system can be attained at this time. The form of fossil cystoids strongly suggests a respiratory system operating through the pores and completely separate from the feeding system.

THECA

SHAPE AND SIZE

The theca varies drastically in shape. Some of the rather bizarre forms have taxonomic value, so that the quadrate-spindle shape is unique to the Rhombiferidae, the asymmetry caused by a protuberant periproct is characteristic of the Echinoencrinitidae, and the pentremite shape sets the Cystoblastidae apart from all other families of the Rhombifera.

Many authors have stressed that the primitive cystoid was saclike. Perhaps, if the Middle Cambrian *Lapillocystites* and *Pilocystites* really represent cystoids, this is true. Among unquestioned cystoids, however, the Lower Ordovician forms include the ovate *Cheirocrinus,* the strongly asymmetrical *Erinocystis* with protruding periproct, the subspherical *Echinosphaerites* and *Sphaeronites,* and the pentremite-shaped *Asteroblastus.* It would be difficult to defend any of these as typical of the ancestral cystoid.

The size of the theca shows great range. It is difficult, to be sure, to determine that a small specimen is an adult, but *Cystoblastus leuchtenbergi* appears to have matured with a height of theca less than 7 mm. On the other hand, *Calix* reaches a height of 40 cm.; this is an extreme, and the majority of cystoids do not exceed a few cm. in height, exclusive of the column and brachioles.

THECAL OPENINGS

In most cystoids, the theca has five openings in addition to the thecal pores. These are mouth (with peristome), anus (with periproct), hydropore, gonopore, and opening at base leading into the column. The mouth and periproct are invariably present, in one form or other. Some cystoids have no detectable hydropore, a few lack any trace of a gonopore, and some have no basal opening, either having no column at all or casting it off while very young and sealing the opening by a cicatrix.

The **mouth** is usually at the oral pole, although there are exceptions. It is covered by a roof of small plates continuous with those of the ambulacra, displaying varying degrees of regularity in the biserial arrangement. The shape of the opening may be subquadrate and large (e.g., *Trematocystis*), long and narrow (e.g., *Schizocystis*), or relatively small (e.g., Callocystitidae). In the Caryocrinitidae, the mouth is hidden by a "tegmen" of specialized plates, giving it the appearance of a crinoid.

The position and the size of the **periproct** are subject to extreme variation. Insofar as is known, the gut in all cystoids discharged through a valvular anal pyramid. In some, this pyramid filled the periproct. In the Pleurocystitidae, in contrast, the periproct filled nearly all of one side of the flattened theca, the small anal pyramid situated in an embayment in the aboral right corner, and the remainder of the vast area plated by numerous (as many as 1,500) tiny plates called "periproctals." In many of the Callocystitidae, the anal pyramid was bordered by a ring of small quadrate plates called **accessory plates.**

The periproct in *Sphaeronites* is situated quite close to the mouth, separated by only a narrow bar of plate material; it is in such close proximity that the anal pyramid is in contact with the covering plates of the peristome. In contradistinction, the periproct in *Erinocystis* surrounds an opening at end of a prolongation formed by thecal plates, directed aborally, so that the periproct may be farther removed from the mouth than is the column. Between the two extremes, most cystoids have the periproct slightly above mid-height. The position of the periproct is used in generic diagnoses in some families.

THECAL PLATES

The thickness of the thecal plates also shows extremes. A few cystoids have such thin plates that the specimens suffer from distortion. The plates in most species are less than 2 mm. thick. In contrast, *Pachy-*

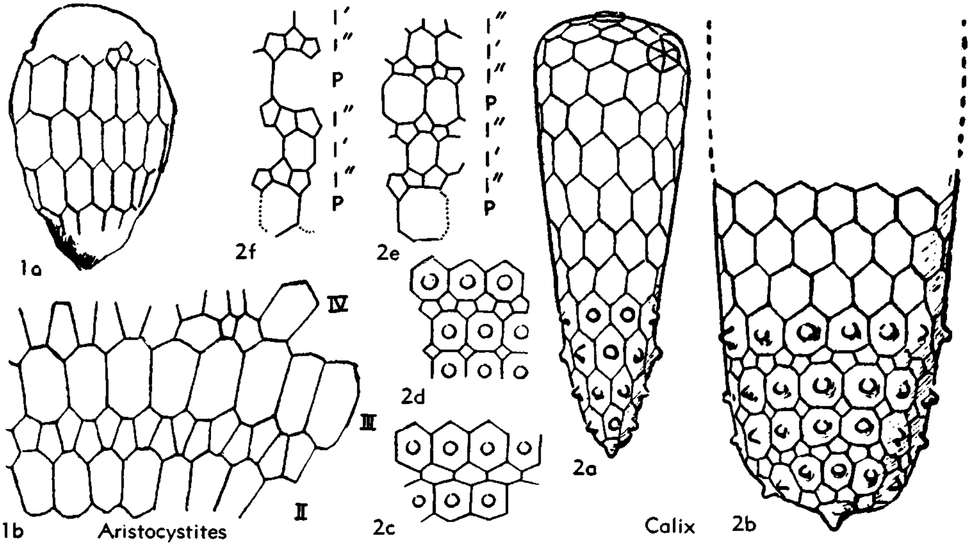


FIG. 39. Growth by interstitial addition of plates.——*1. Aristocystites bohemicus* BARRANDE (M.Ord.); *1a,* stage 1, in which plates are subequal, ×0.8; *1b,* stage 2, in which secondary plates have been inserted in circlets.——*2. Calix sedgwicki* ROUAULT (M.Ord.); *2a,* stage 1, ×1; *2b-d,* stage 2, in which secondary plates develop as rhombs, pentagons, or hexagons, ×1; *2e-f,* stage 3, in which circlets of plates are introduced between primary and secondary circlets. [*P*—primary plates; *i′*—secondary plates; *i″*—tertiary plates] (34).

calix pachytheca, as reconstructed by TERMIER & TERMIER (129), is aborally very thick, with plate material occupying more than half of the total diameter near the base; they report a thickness of 2 cm.

In the cystoids, the number of plates comprising the theca, exclusive of the many-segmented brachioles, ambulacra, peristomial covering plates, anal pyramid and periproctals, and columnals, is strongly stabilized in some families and diverse in others. The Glyptocystitida have a pattern of 24 basic plates in such regularity that exceptions are noteworthy. The Hemicosmitida are also remarkable for the consistency of plate number and arrangement in its genera. On the other hand, *Calix* is known to have about 2,000 small plates in its theca. Numerous genera have over 100 plates in the theca.

As discussed below under "Ontogeny," cystoids show two growth patterns, one in which the individual plates increase by peripheral additions, and the other in which new plates are added interstitially. All cystoids with numerous thecal plates in the adult stage show evidences of the second pattern at some stage of development, with large initial plates and smaller secondary plates (Fig. 39). In some, the secondary plates are inserted in cycles between the initial plates, and even tertiary plates may be introduced in cycles.

In the Glyptocystitida, with 24 basic plates in the theca, the genera can be closely compared and distinguished by the plate arrangement. For convenience, a system of plate designations is used. Long ago, FORBES (51) introduced a system of numbering that still finds adherents (Fig. 40). Starting with the plate in the aboral circlet which is normally provided with a half-rhomb, he numbered the plates consecutively in sequence spiraling adorally to the right; thus the four plates of the basal circlet are numbered *1* to *4,* those in the next are *5* to *9,* and the oral circlet contains *20* to *24.* Perhaps the most prominent, and certainly the most persistent, devotee of this system was BATHER. The greatest difficulty in using this system occurs in cystoids in which plates of two adjacent circlets are intercalated; the numbers have significance as a series only in cystoids which conform

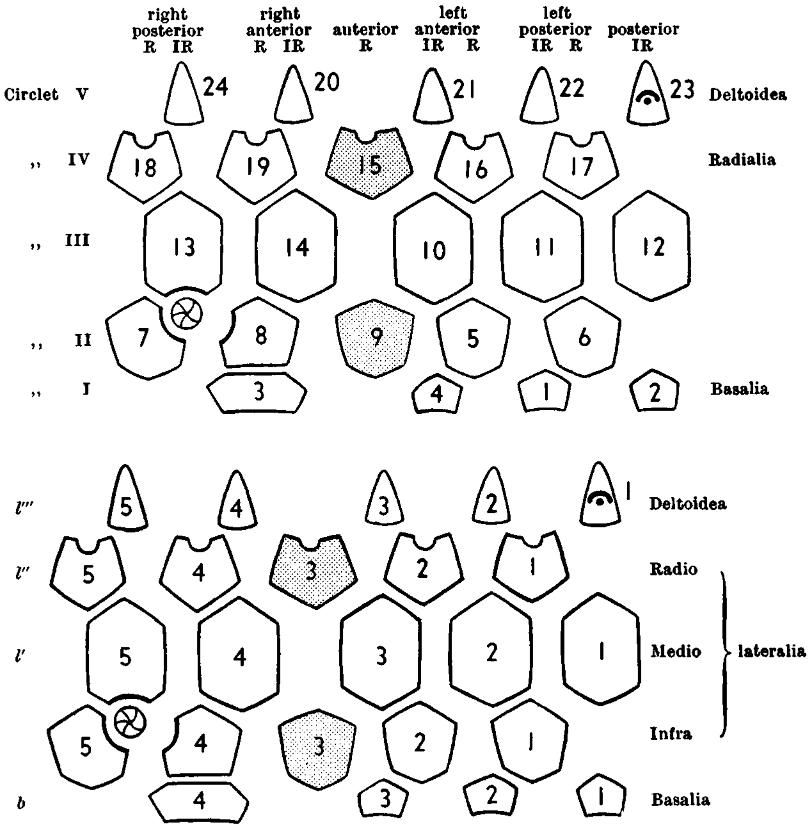


FIG. 40. Generalized plate diagrams of glyptocystitidan cystoids (plates of *A*-ray shaded), with designations by FORBES and BATHER (above) and by JAEKEL (below) (12).

to a rather idealized pattern, and the precise location of any given plate is hard to remember.

DESIGNATIONS OF PLATES

JAEKEL (69) introduced a system of designations recognizing the association of thecal plates in circlets (Fig. 40), calling the aboral circlet basalia *(b)*, and succeeding circlets infralateralia *(l)*, mediolateralia (l'), radiolateralia (l''), and deltoidea [*sic*] (l'''). Within each circlet, the plates were numbered in sequence from right to left, starting with the posterior region for basalia, mediolateralia, and deltoidea [*sic*] and with the left posterior ambulacral region for infralateralia and radiolateralia. By this method, the hydropore-bearing plate became l'''_1 and the hexagonal basal plate b_4.

Essentially the same system but with more conveniently written symbols was proposed by REGNÉLL (99), and his system is followed in this study (Fig. 38). The basals are designated as *BB*, infralaterals as *ILL*, laterals as *LL*, radials as *RR*, and orals or deltoids as *OO*. The singular is formed by dropping the terminal letter. Thus, the hydropore-bearing plate is *O1* and the hexagonal basal is *B4*.

Considerable difficulty is encountered in applying this system to the Hemicosmitida. The problem centers upon the question of whether the plates of this superfamily are homologous to those in the Glyptocystitida. MOORE (89) favored homology, and used FORBES' system of numbered plates in *Hemicosmites* and *Caryocrinites*. The possibility remains, however, that through evolution the Hemicosmitida and Glyptocystitida had diverged so far, by the time the fossil record is known, that homologies are obscure and confused. In emphasizing the resemblance of these cystoids to the crinoids, BATHER (10) called plates of the aboral circlet in *Caryocrinites* and *Hemicosmites* infrabasals, of the next basals, and of the next radials. The smaller plates in excess of five in the radial circlet were referred to as interradials. In *Heterocystis,* the ten plates of the second circlet were designated according to the nearest ambulacrum. Regardless of the symbols employed, it is obvious that the Hemicosmitida do not have plates unquestionably homologous with those in the Glyptocystitida.

Similar problems are met with in trying to accommodate the plate system of the Glyptocystitida to that of the Asteroblastidae. Whereas the plates generally conform to the glyptocystitidan pattern, the circlets of *Asteroblastus* contain extra or supernumerary plates in the region of the periproct. This "anal series" has no counterpart in other cystoids.

AMBULACRAL SYSTEM

GENERAL FEATURES

By ambulacral system is meant the structures housing conduits leading to the oral opening presumed to be the mouth. Presumably, the chief function was food gathering, but in cystoids in which the gonopore is atrophied, the appendages may have played a role in reproduction, as do the arms and pinnules of crinoids. The latter function cannot be disproved, although it seems unlikely that the genital system could have been hypothecal in some and exothecal in other cystoids that were morphologically similar in most respects. There is no assurance that the ambulacral system of cystoids was homologous in its entirety to that of other pelmatozoans. The possibility that the thecal pores may constitute part of the ambulacral system has already been discussed.

The ambulacral system, as treated here, includes the **brachioles**—biserial erect appendages—and the **ambulacra**—structures upon the theca housing conduits leading from the brachioles to the mouth. The conduits or passageways for food are covered over by small biserially disposed plates, both in the brachioles (Fig. 36,*2a*) and in the ambulacra (Fig. 36,*1a*). The parts lying within the ambulacra are called the **ambulacral grooves** (Fig. 36,*2b*).

Brachioles in most genera are long, tapering, unbranched appendages, consisting of biserial platelets arranged to form a trough and smaller biserial platelets serving as covering plates. A surprising exception is *Caryocrinites ornatus* SAY. In this species, FOERSTE (47) discovered pinnulate free arms, in which both brachials and pinnulars are biserial. The biserial character of the pinnules readily differentiates them from the uniserial pinnules of crinoids.

Wherever a brachiole is disarticulated from the rest of the cystoid, as happens in numerous specimens, its juncture with the ambulacrum is marked by a **brachiole facet** (Fig. 36,*2b*). The configuration of this facet strongly suggests that musculature controlled the movement of the brachiole.

The number of brachioles varies greatly. *Pleurocystites* possessed only two, which were strongly constructed and as long or longer than the theca (Fig. 41). In contrast, *Mesocystis* had about 1,000 brachioles, which were short and delicate (Fig. 42). The number of brachioles can only be stated as commonly occurring within the family, inasmuch as those families with an extensive representation contain some cystoids which depart appreciably from the average for the family.

Nearly all ambulacra are on the outer surface of the theca. The only discrepancy from this usual location may be *Cystoblastus.* According to JAEKEL (69), the ambulacra are inserted in clefts in the radial plates so that they extend to the inside of the theca. JAEKEL was strongly impressed by this supposed arrangement, and concluded that *Cystoblastus* was the most remarkable cystoid known, admirably displaying all the structures requisite for an ancestor of the blastoids; indeed, in 1918 he placed it as a *"Vorform"* in the Blastoidea. From specimens subsequently discovered, YAKOVLEV (143, 145) presented a new interpretation of *Cystoblastus,* wherein the force of JAEKEL's contention of blastoid-like structures was seriously weakened. The possibility exists that the ambulacra of *Cystoblastus* were deeply entrenched within the thecal plates, but did not actually penetrate completely through them; the answer to the condition of the ambulacra lies in finding additional specimens, carefully sectioning the ambulacral areas, and studying the preservation.

Apart from *Cystoblastus,* cystoids have two types of ambulacra. In the first, the groove lies within **flooring plates** which are attached to the surface of the theca. In the second, the groove is incised in thecal plates themselves. Both types have tiny **covering plates.**

Flooring plates are well developed in the Glyptocystitidae and the Callocystitidae.

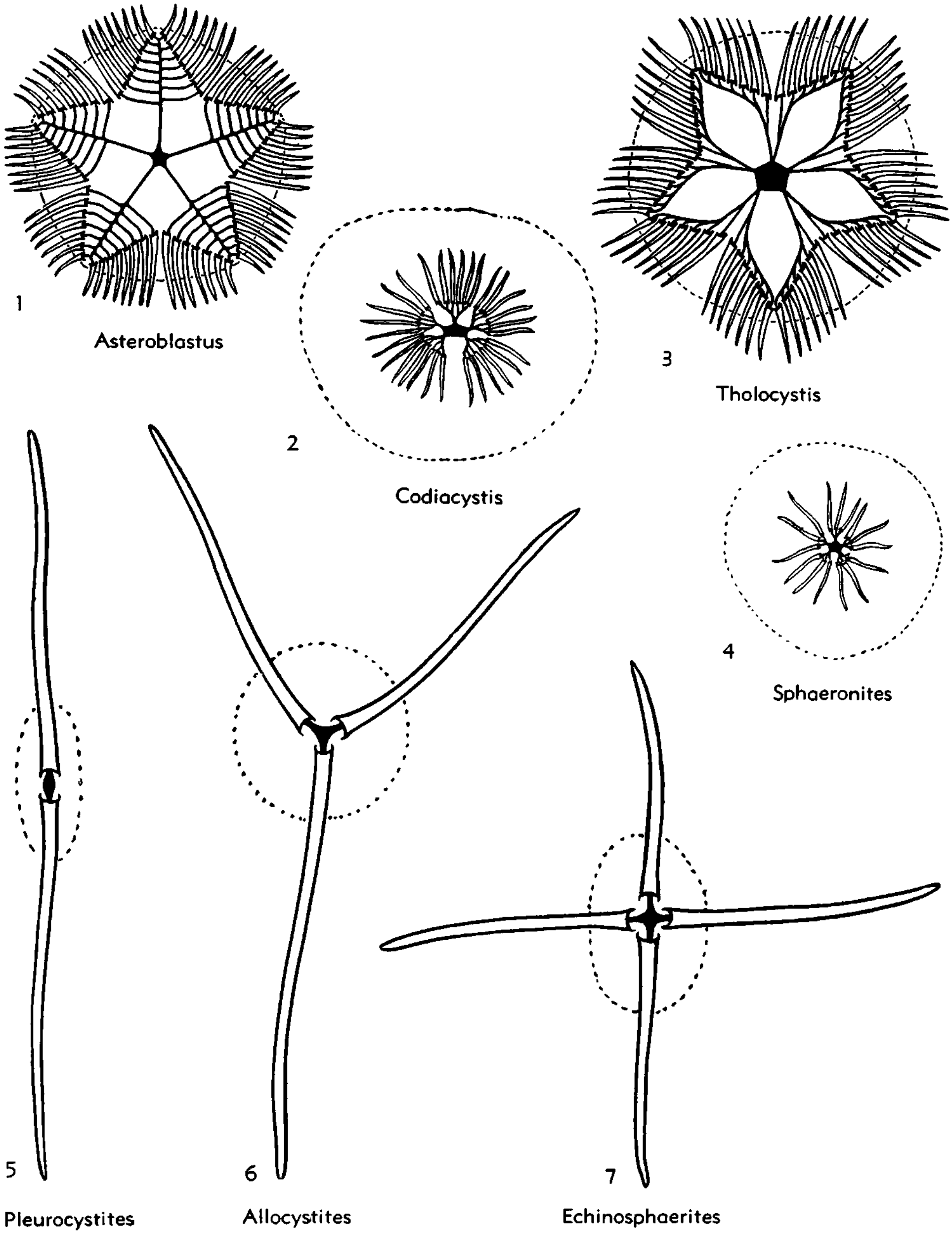


Fig. 41. Diagrammatic oral projections of ambulacral systems (69, Kesling, n).

Characteristically, they consist of large and small plates alternating on each side, with a large plate on one side opposite a small one of the other to produce a kind of biserial placement (Fig. 36,*1a*). Many special forms evolved. In *Pseudocrinites,* the flooring plates attained remarkable thickness, whereby the ambulacral groove was perched rather far out on a palisade of flooring plates. In *Jaekelocystis,* the flooring plates were also thick, but so deeply entrenched in the thecal plates that the ambulacra were nearly flush with the general surface of the theca. In *Glyptocystites,* the flooring plates are thin and loosely attached to the theca, from which they readily scale

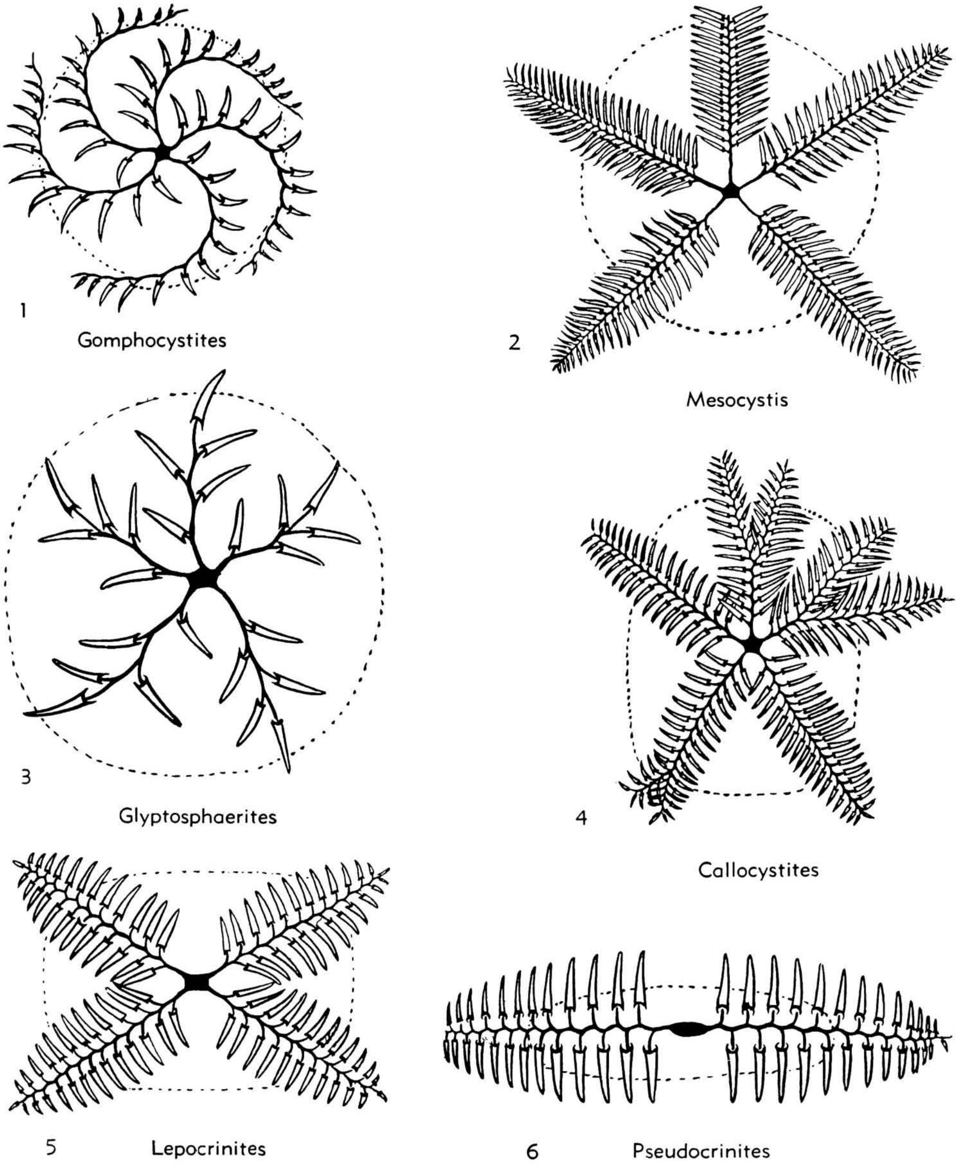


FIG. 42. Diagrammatic oral projections of ambulacral systems (69).

off with weathering. In *Cheirocrinus,* the flooring plates, if they exist, are very thin and indistinct.

In those cystoids which lack flooring plates, the ambulacral grooves may wander over thecal plates indiscriminately, as in *Glyptosphaerites,* or they may be confined to series of regularly alternating special thecal plates called **adambulacrals,** as in *Dactylocystis, Estonocystis, Protocrinites,* and others.

Whether flooring plates are present or lacking, the ambulacra vary in length. In *Pseudocrinites* and *Revalocystis,* the ambulacra not only extend from the mouth to the aboral end of the theca, but in some specimens are even known to encroach onto the column. In contrast, the brachioles of *Pleurocystites* and many of the Sphaeronitida rise in close proximity to the mouth, so that the ambulacra, if any can be distinguished, are very short. Many families (e.g., Echinoencrinitidae, Cheirocrinidae, Glyptosphaeritidae, Gomphocystitidae) have ambulacra of intermediate length.

BRANCHING OF AMBULACRA

The character of branching in ambulacra has considerable taxonomic significance. In the Glyptocystitida, branching of the main grooves occurs normally only in the family Callocystitidae; the set of flooring plates divides into two sets of flooring plates, commonly at some distance down on the theca, and these may subdivide further so that the ambulacral grooves assume a dendritic pattern (Fig. 42, *Callocystites*). *Schizocystis* presents a special case in which the lateral branches are short, curved, and irregular. The spiral ambulacra of the Gomphocystitidae extend short branches only from the convex side (Fig. 42, *Gomphocystites*). The Dactylocystidae and Protocrinitidae send out very short lateral branches to the alternating adambulacral plates. In the Sphaeronitidae, the ambulacra branch immediately from the peristome, extending relatively short branches in a distinctive pattern; those in *Sphaeronites* splay out fanwise (Fig. 41), those in *Archegocystis* all curve clockwise, and those in *Codiacystis* extend subparallel in each ambulacral area (Fig. 41).

One interesting and curious aspect of ambulacral branching is the manner in which the brachiole facets of both *Asteroblastus* and *Tholocystis* come to be arranged in the shape of a star, yet by drastically different methods. In *Asteroblastus,* the main ambulacral groove in each ambulacrum is straight; at an appreciable distance from the mouth, each main groove sends out lateral branches, nearly at right angles, more or less alternating, and decreasing in length distally (Fig. 41). As a result, the ambulacral pattern of each ambulacral area bears sharp resemblance to the branching of a tree. On the other hand, *Tholocystis* has two main branches from each corner of the peristome, diverging slightly at first and then more sharply, with branches extending from the outer side of the two main branches (Fig. 41). Whereas both genera have the brachioles in the form of a star, each of the five apices in *Asteroblastus* is formed by one ambulacrum and lies in an ambulacral position, but each apex of *Tholocystis* is formed by two ambulacra and lies in an interambulacral position.

Most species are represented by too few specimens to establish variation in ambulacral development. In *Jaekelocystis hartleyi,* study of 41 well-preserved specimens (KESLING, 73) revealed one in which an ambulacrum was branched and three in which an ambulacrum was not fully developed (Fig. 43). It is doubtful that any two specimens have their four ambulacra in precisely the same positions relative to the ambulacral plates; the general location is nearly constant, but the ambulacra occupy slightly different parts of the corresponding plates and may obscure different sutures. The specimen selected by SCHUCHERT (116) as holotype and only known representative of the type species of his genus *Trimerocystis* may be interpreted as a *Pseudocrinites* with a supernumerary third ambulacrum (KESLING, 73).

The ambulacra increase by distal extension over the theca. As shown in *Lepadocystis, Brockocystis,* and *Glyptocystites,* the presence of a pore rhomb or rhombs athwart the path of an ambulacrum normally seems to prevent its further development. Some specimens, however, show the "smothering" of part of a rhomb by an ambulacrum. This

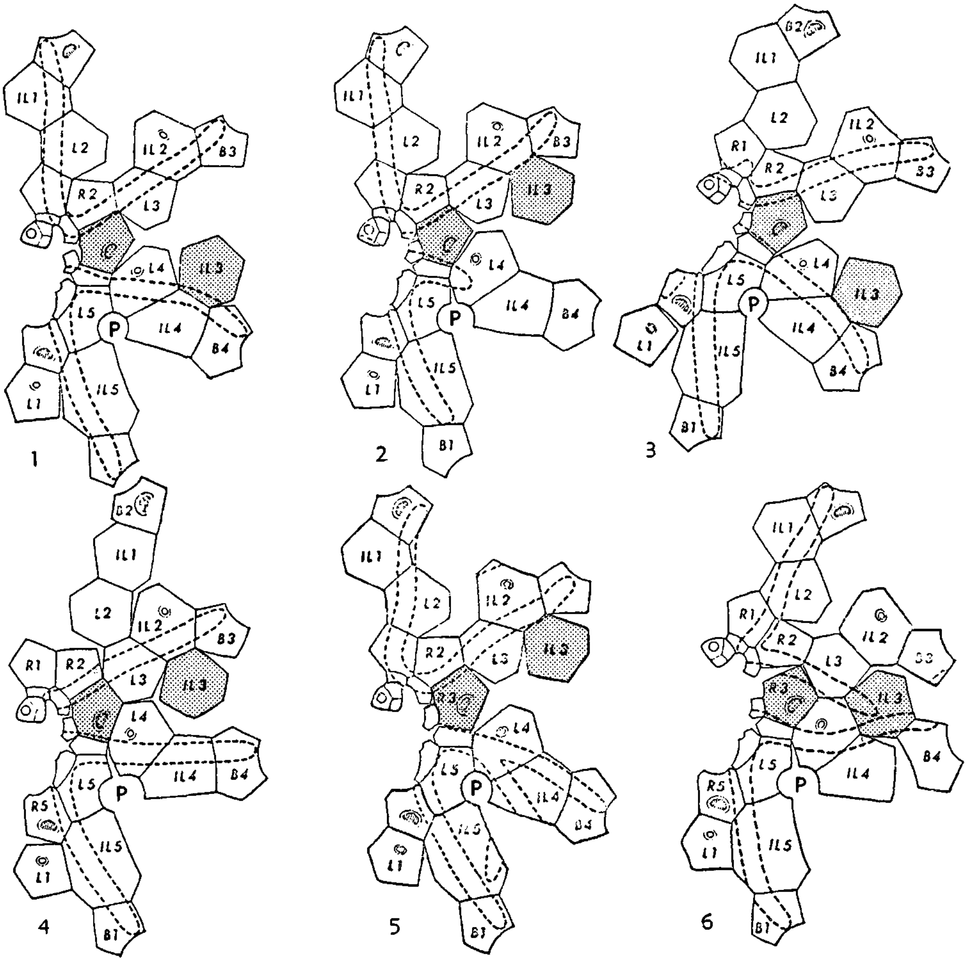


FIG. 43. Variations in ambulacra in *Jaekelocystis hartleyi* SCHUCHERT (L. Dev.); *1,* ambulacra typically developed; *2,* ambulacrum *IV (B)* short; *3,* ambulacrum *I (D)* deformed; *4,* ambulacrum *I (D)* aborted; *5,* ambulacrum *IV (B)* bifurcate; *6,* ambulacrum *II (E)* abutting on *IV (D)* (73). [Plate designations as in Figure 38.]

physiological struggle between two systems is discussed under "Ontogeny."

Certain published comments on ambulacra are misleading. JAEKEL (69) stated that the ambulacra of *Cheirocrinus* are inserted in indentations or "cut-outs" of the radials; instead, I find that the oral plates, on which the ambulacra rest, have acuminate tips on their junctures, which are set nearly horizontally on steeply inclined median folds of the radial plates. The concept of ambulacral insertion apparently stemmed from the illusion engendered by the rather flat crown set atop steep sides of the theca. Some authors have referred to the long ambulacra of certain Glyptocystitida as "recumbent"; actually, all ambulacra are recumbent, in that they lie on the surface of the theca. Others have sought to distinguish the ambulacra of certain cystoids as "exothecal"; this is no distinction at all, since all ambulacral grooves have access into the theca only through the mouth.

DESIGNATION OF RAYS

In designating particular ambulacra, several methods have been suggested. The

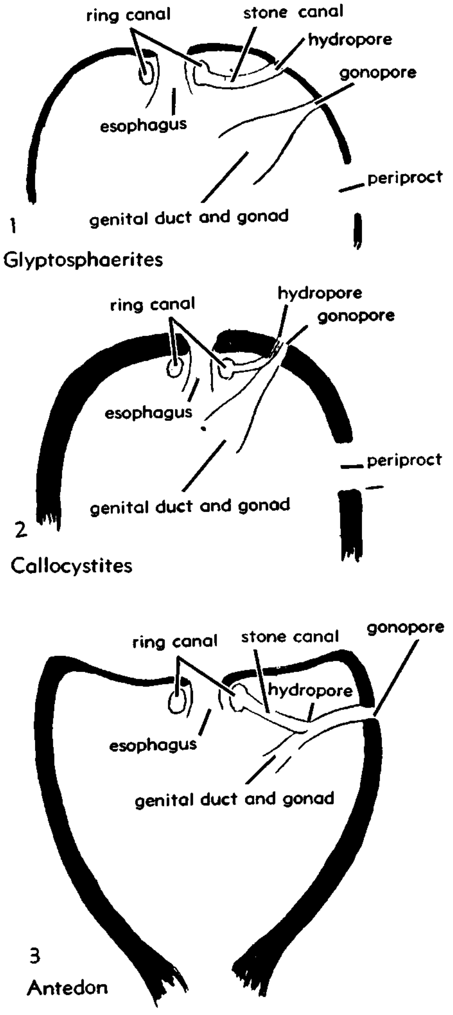


Fig. 44. Cross sections through peristome, hydropore, gonopore, and periproct.——*1,2.* Hypothetical reconstructions of *Glyptosphaerites* (L.Ord.-U.Ord.) and *Callocystites* (M.Sil.).——*3.* Young stage of *Antedon* (Rec.) (69).

hydropore occupies the posterior interambulacrum. One system (introduced by Carpenter, 1884), applied also to other echinoderms, designates the ambulacrum opposite the hydropore by the letter *"A,"* and in clockwise direction (as the theca is viewed orally) and others are marked *"B"* through *"E."* Bather (10) gave distinct rules for orientation, with the ambulacrum opposite the hydropore designated "anterior" and the others "left anterior," "left posterior," "right anterior," or "right posterior," according to their relative position. As noted by Jaekel (71), the terms "right" and "left" introduce confusion, since the cystoid must always be placed mouth upward with hydropore-bearing interambulacrum next to the observer in order for the terms to be applied in consistent fashion. Jaekel (68, 69) introduced a simple system using Roman numerals, in which *"I"* indicates the first ambulacrum to the left of the hydropore and the others are numbered in sequence clockwise. As explained in Bather's (13) critique, Reed (98) described cystoids from Yunnan in extremely confused terms of orientation.

HYDROPORE AND GONOPORE

Inasmuch as the **hydropore** and **gonopore** appear to be combined in certain cystoids, they are here discussed under the same heading. Some authors call them the primary pores. The two structures never occur far removed from one another. Neither is farther than the periproct from the mouth, and typically both are close to the oral pole. In *Glyptosphaerites,* the cystoid in which the two are probably farthest apart, the hydropore and gonopore are about equally spaced between the peristome and periproct (Fig. 44,*1*). In many of the Glyptocystitida, the gonopore lies within the crescent formed by the curved hydropore; and in such genera as *Jaekelocystis* there is but one opening. As Jaekel (69) stated (translated), "Here we must consider the possibility that, in the examples in which only one of these primary pores is present, it represents the opening of both canals."

As outlined by Regnéll (99), the gonopore was misinterpreted for many years. Gyllenhaal (56), who first recognized the echinoderm affinities of the cystoids, referred to the gonopore of *Echinosphaerites aurantium* as the anus. His interpretation was followed by Hisinger (65), Wahlenberg (139), von Buch (29, 31), Eichwald (42, 44), Forbes (51), Hall (60), Billings (20), with question by Barrande (3), and in part by S. A. Miller (85, 86). The nature of the opening is said to have been established first by Roemer (1851). It was recognized as a genital pore by Lovén (80), Angelin (1), Carpenter (32), Haeckel

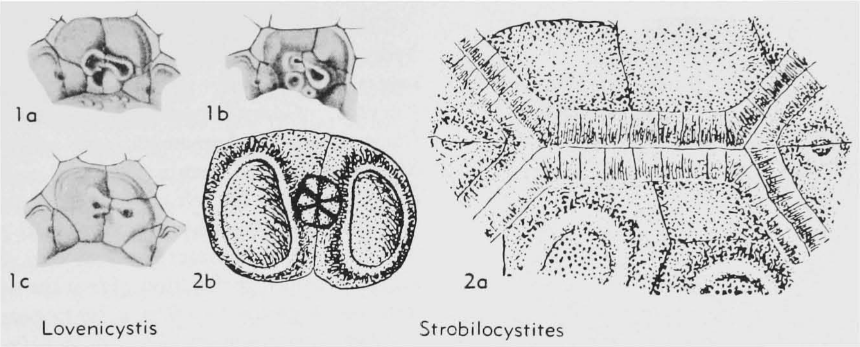


FIG. 45. Hydropore and gonopore features.——*1. Lovenicystis* (U.Sil.); *1a-c,* posterior sector or oral region showing various forms of hydropore and gonopore.——*2. Strobilocystites* (M.Dev.-U.Dev.); *2a,b,* peristome and bipartite hydropore and pyramid-closed gonopore (99, 120).

(58), JAEKEL (69, 71), BATHER (10), and subsequent authors. Contrary to previous authors, who had correctly identified the hydropore (under various names), S. A. MILLER (85) interpreted it in part as the anal opening. BARRANDE (3) and HAECKEL (58) called the structure the fourth opening, although presuming, with question, its function as a hydropore.

HYDROPORE-GONOPORE-DEFINED GROUPS

The cystoids were divided by JAEKEL (69) into three groups according to the development of the gonopore, (1) the gonopore situated below the hydropore, (2) the gonopore combined with the hydropore, and (3) the gonopore atrophied. To these, YAKOVLEV (146) added (4) gonopore to the left of the hydropore.

Much of the discussion of the hydropore and gonopore has involved their possible relation to a parietal septum. Some sort of structure is indicated in a few cross sections of specimens of *Caryocrinites* and on steinkerns of *Glyptosphaerites, Echinosphaerites,* and *Echinoencrinites.* These examples are rare among the numerous cystoids that have been studied. In the cross sections, the structure is indicated by dark markings, and on the steinkerns by a groove. It was interpreted by JAEKEL (69) as a parietal septum, a kind of mesentery forming an internal meridional wall. From its position in the posterior interambulacrum, the parietal septum has been assumed to have a close relationship to the gonopore. A detailed investigation of *Echinosphaerites,* however, induced GEKKER [HECKER] (53) to question the mesenteric interpretation, primarily because of branching and ductlike circular passageways of unknown significance.

Both the hydropore and gonopore occur along sutures, although the fusion of thecal plates in some specimens may tend to obscure the presence and location of sutures. This is undoubtedly the result of the plates growing around the pores and their canals during the ontogeny of the cystoid.

The difference between group 1 (gonopore below or aboral to the hydropore) and group 4 (gonopore to the left of the hydropore) may not be as strong as emphasized by YAKOVLEV (146). Even in such typical representatives of group 1 as *Pleurocystites, Glyptocystites,* and *Lepadocystis,* the gonopore is situated to the aboral left of the hydropore, rather than directly aboral to it. The main distinction involves the location of the two openings relative to the three plates that commonly occur in the posterior oral region. In group 1, the two are shared by the middle and left plate; in group 4, the gonopore is shared by the middle and left plate and the hydropore by the middle and right plate.

In the Glyptocystitida, which exemplify group 1, the gonopore is a small circular opening in nearly all genera, but the hydropore exhibits an evolutionary trend. In *Glyptocystites* (M.Ord.) and *Pleurocystites* (M.Ord.) the hydropore is an open cres-

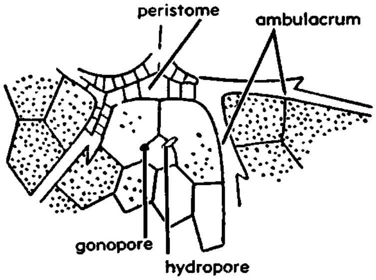


FIG. 46. *Protocrinites fragum* (EICHWALD) (L. Ord.). Diagrammatic plan of the posterior part of the oral region (146).

centic slit curved around the gonopore; in *Lepadocystis* (U.Ord.) bars develop across the slit to form a grating; in *Lovenicystis* (U.Sil.) the ends of the slit are greatly dilated, so that the hydropore assumes a dumbbell shape (Fig. 45,*1*); and in *Lipsanocystis* (M.Dev.) and *Strobilocystites* (M.Dev.-U.Dev.) the central part of the slit is absent and the expanded ends are left as two separate openings, one in each of the pair of plates, with each provided with a complex sieve structure (Fig. 45,*2b*).

The hydropore in *Glyptosphaerites* consists of irregular crenulate slits in a thickened triangular field. From the examples illustrated by various authors, the hydropore in this genus may occur on the same suture as the gonopore or on a suture to the adoral right; thus *Glyptosphaerites* appears to span groups 1 and 4. In *Archegocystis,* the hydropore is a curious hatchet-shaped opening between the round gonopore and the mouth. This structure finds expression in *Calix* as a lobed plate with superficial grooves.

The trend in the Callocystitidae for the hydropore to divide into two parts has a parallel in the gonopore. In certain specimens of *Lovenicystis,* as illustrated by REGNÉLL (99), the gonopore comprises two distinct round openings, one in each of the adjacent plates (Fig. 45,*1b*). The gonopore in several cystoids, including *Pseudocrinites* and *Echinosphaerites,* has been found to be closed by a tiny pyramid of triangular plates (Fig. 45,*2b*). Possibly, other cystoids had such closure of the gonopore, but the pyramids have not been preserved.

Group 2, in which the gonopore and hydropore seem to be combined, is found in several unrelated cystoids—*Jaekelocystis, Eucystis, Gomphocystites, Hemicosmites, Caryocystites, Sphaeronites,* and others. In *Sphaeronites,* the opening is small and circular, located at the left of the anal pyramid, which in this genus lies in exceptional proximity to the peristome; the size and shape of this porelike perforation give it the aspect more of a gonopore than a hydropore. In contrast, the single opening of *Jaekelocystis* is large and provided with a sieve structure, very much like half of the bipartite hydropore in the related *Lipsanocystis* and *Strobilocystites.* The majority of cystoids with combined hydropore-gonopore openings, however, are more nearly similar to *Sphaeronites.*

Of the examples given by JAEKEL (69) of group 3, those cystoids in which the gonopore is atrophied or absent, the only genus which has not been shown to belong to other groups is *Caryocrinites.* In this cystoid, the oral region is covered by a "tegmen" of specialized plates, so that details of this part of the theca are obscured. Possibly, a small opening is present in the complicated crown, and will yet be discovered. With all, however, one cannot discount the possibility that the crinoidal tendencies of *Caryocrinites* in thecal organization, "tegmen," arms, and column went even further, and that the genital system was no longer internal, but rather like that of living crinoids—located in the arms. This seems highly unlikely, but this genus has other features unique among cystoids.

The best examples of group 4 are *Protocrinites* and *Cystoblastus,* as established by YAKOVLEV (146). The hydropore of *Protocrinites* is a slit, not unlike that in its contemporaries of group 1 (Fig. 46). But that of *Cystoblastus* is a large space perforated like a sieve, in contact with the plate on the right. As pointed out by YAKOVLEV, the lateral locations of the openings in *Protocrinites* can scarcely be reconciled with an association with a vertical septum, as presumed by JAEKEL (69).

The antiquity of the four groups is not firmly established, and which is the primitive or ancestral form is a guess.

FUNCTIONS OF HYDROPORE AND GONOPORE

The function of the hydropore is presumed to have been like that of the corresponding structure in modern echinoderms, to admit water to the water vascular system through the stone canal. What use the cystoid made of a water vascular system is undetermined. As discussed above, suggestions have been made that the system was ramified and connected to thecal pores, or that it had nothing whatsoever to do with the thecal pores but served in food gathering in some manner.

The presumed function of the gonopore to discharge products of internal gonads is based on comparison with the gonopore connected by a duct with the genital organs in holothurians or with the dorsal organ of the sexual system in crinoids, echinoids, asteroids, and ophiuroids. Although granting the connection of the orifice and the sex system in cystoids, JAEKEL (69) nevertheless chose to call it the *"Parietalporus,"* mainly on account of the fusion with the hydropore in certain genera.

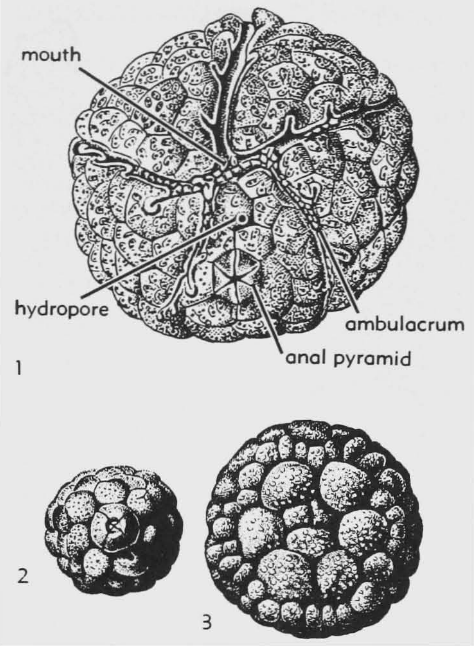


FIG. 47. *Protocrinites oviformis* EICHWALD (M. Ord.); *1,* oral view, ×1.5; *2,3,* aboral views of very young and adult individuals, showing ontogenetic changes in which traces of the cicatrix of columnar attachment are eradicated, ×1 (10).

COLUMN

The presence or absence of a column has limited taxonomic significance, as does the form of the column. Because the columns are detached from many thecae, and numerous columns are dissociated into columnals, the structure is unknown or incompletely known in many genera. Nevertheless, it appears possible to group cystoids into three categories: (1) those which lose the column during youth, or perhaps never develop one at all; (2) those in which the column is flared at the junction with the theca, containing a wide lumen; and (3) those in which the column is of about the same diameter throughout its length, with a very small lumen.

Protocrinites oviformis EICHWALD is known to have a columnar facet in very young specimens, but shows no trace of the facet in adult specimens; the plates at the aboral pole become strongly modified during ontogeny, eradicating even a cicatrix at the former position of the column (Fig. 47,*3*). Columns are absent in nearly all genera of the Aristocystitidae. *Calix* has an aboral terminal tubercle or spine. The aboral end of *Aristocystites* is indented and cuplike or retains the impression of the object to which it was attached. Some specimens of *Aristocystites* and *Pseudaristocystis* have the aboral end crooked, logically interpreted to be so formed because the base was attached and the remainder of the theca bent down to live more or less prostrate on the sea floor. In the Sphaeronitidae, columns are never prominently developed either. *Eucystis* occurs either with or without a column; if present it is very short, and if absent the aboral end bears markings of the object of attachment. *Tholocystis* is noted for its kettle-shaped theca, with large flat base or sole; it shows no traces of a column. The enlargement of diplopores in the aboral circlet of plates in *Codiacystis,* as reported by CHAUVEL (34), has already been discussed.

Among the rhombiferans, some cystoids have weak columns. This is particularly applicable to the Caryocystitidae, in which

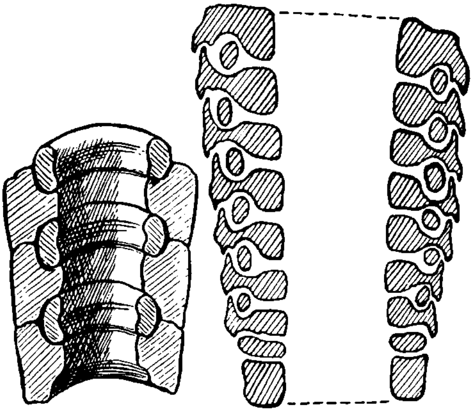


FIG. 48. Sections through proximal parts of the column, showing association of two alternating kinds of columnals.——*1. Cheirocrinus* (L.Ord.-U.Ord.).——*2. Strobilocystites* (M.Dev.-U.Dev.) (12, 120).

Caryocystites and *Heliocrinites* have small facets at their aboral poles to which the columns were presumably attached.

A few cystoids appear to have developed substitutes for the column. *Arachnocystites* has a thin, stemlike aboral protuberance of alternating rows of tiny hexagonal plates. To a lesser degree, *Sinocystis* possesses a prolongation of the base as an unspecialized stemlike section. *Calix* probably utilized stout tubercles in the aboral region for support, and *Pachycalix pachytheca,* as restored by TERMIER & TERMIER (128), may have kept upright by the sheer weight of the thecal plates in the aboral region, like a weighted flask.

The column in the Glyptocystitida and a few other cystoids is wide at the junction with the theca and tapers drastically in the proximal part. The columnals differ considerably within each column; those close to the theca are short, wide, and bear a broad lumen, whereas those in the distal section are high, narrow, and have a very small lumen. Furthermore, in at least some cystoids, the distal end of the column is specialized to keep the animal anchored. Thus, in *Lepadocystis moorei,* as reported by KESLING & MINTZ (75), the terminus of the column is variously modified by lobate processes which became attached to foreign objects, growing around them for a firm hold (Fig. 32). HALL (62) noted the curious termination of the column in the related genus *Lepocrinites.* In *L. gebhardii,* the distal 15 or about that number of columnals are ankylosed to form a club-shaped process, which was interpreted by KIRK (76) as a ballast or drag.

The broad lumen may well have housed musculature to control the attitude or position of the theca; such use in adjustment was proposed by KIRK (76). The junctions of the columnals in the proximal region is such that great freedom of movement was possible. An unusual arrangement of the proximal columnals was described by JAEKEL (69) for *Cheirocrinus* and by STAINBROOK (120) for *Strobilocystites* (Fig. 48). In these cystoids, the columnals in the flexible section are of two sizes, alternating; the wider rings have rims or flanges that more or less conceal the narrower. Probably, the disposition of the two kinds made it possible for the larger columnals to move over the outer surface of the smaller, in sleeve fashion, while still maintaining the strength and protection of a continuous series of columnals. Perhaps this arrangement exists in other cystoids, but has not been discovered.

Another bizarre form of proximal columnals is found in *Brockocystis,* as noted by FOERSTE (48), wherein the column tapers rapidly for about 12 columnals, the lower end being set deeply in a cup formed of about four greatly expanded columnals, beyond which the column tapers rapidly to a very narrow diameter; the whole structure strongly resembles a kind of ball-and-socket joint.

In sharp contrast to these broad-lumened, tapering columns, the stem of *Caryocrinites* strongly resembles that of a crinoid. It is long, nearly constant in diameter, and has a very small lumen. This form of its column is only one of the ways in which *Caryocrinites* approached the Crinoidea; it also developed a "tegmen," arms, and a stout, compact theca similar to the calyx of the Camerata.

GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO CYSTOIDEA

Relative importance of terms is indicated by the type in which they appear: first rank by boldface capital letters, second rank by boldface small letters, and third rank (including obsolete terms, terms having cross references, and synonyms) by italic small letters.

abactinal. See aboral.

aboral. Located away from mouth; in direction away from mouth; also called abactinal.

aboral pole. End of theca opposite mouth, in most cystoids marking end to which column is attached.

actinal. See oral.

adambulacral. One of brachiole-bearing plates which regularly alternate in paired vertical rows in Dactylocystidae and Protocrinitidae.

adoral. Located toward mouth; in direction toward mouth.

AMBULACRAL. (1, adj.). Referring to zone in which an ambulacrum is present, as contrasted with *interambulacral.* (2, adj.). Referring to an ambulacrum or to ambulacra collectively, as in *ambulacral system.* (3, n.). Broader of two types of flooring plates, especially in Glyptocystitida; *see* ambulacral flooring plates.

ambulacral covering plates. Tiny plates biserially arranged and covering over ambulacral groove, in some forms readily dislodged and rarely preserved.

ambulacral flooring plates. Biserially arranged plates of ambulacrum containing ambulacral groove and attached to underlying thecal plates (with possible exception of *Cystoblastus,* in which they may be inserted in cleft in radial plate). Plates are of two sizes, one broad and one narrow, arranged biserially, whereby broad and narrow plates alternate in each row, a broad plate being aligned with a narrow plate in row on opposite side of ambulacrum, thus forming a zigzag line; broad plates called ambulacralia, ambulacrals, or side-plates, and narrow plates called parambulacralia, parambulacrals, or outer side-plates.

ambulacral groove. Groove through which food was conveyed from brachioles to mouth, covered by ambulacral covering plates; in some cystoids lying within flooring plates as zigzag trough (Glyptocystitida), but in others lying directly in surface layer of thecal plates (Glyptosphaeritida) or concealed by a "tegmen" (Caryocrinitidae).

ambulacralia. Broader of two types of ambulacral flooring plates; also called ambulacrals or side-plates.

AMBULACRUM. Structure in which food was conveyed from brachioles to mouth, always on surface of theca, never erect, exothecal (with possible exception of *Cystoblastus,* in which ambulacra may be in contact with interior of theca owing to a cleft in thecal plates). Five ambulacra in many cystoids, but number may be reduced to 2. Length of ambulacra varies greatly, from very short conduits, where brachioles are clustered near mouth (Aristocystitidae), to medium, where brachioles are limited to crown of theca (Cheirocrinidae), to very long, in some extending to base (Callocystitidae). Each ambulacrum consisting of ambulacral groove enclosed by biserial covering plates; some ambulacra provided with flooring plates, others with groove entrenched into thecal surface.

ANAL PYRAMID. Valvular structure of triangular plates in periproct serving to close anus.

anal series. Plates in interambulacrum bearing periproct in Hemiscosmitida and Asteroblastidae, so called because they appear to be supernumerary when plate system is compared with that of Glyptocystitida; not recommended, since plate homologies are only inferred.

anterior. Located on side of theca opposite hydropore, or gonopore, or both.

anus. Exit of alimentary canal or gut, including tissues as well as anal pyramid.

aperture. Any of major openings through theca, commonly referring to mouth or anus but also by some authors including hydropore and gonopore.

arm. Major element in food-gathering structure of *Caryocrinites,* which, unlike other cystoids with simple unbranched brachioles, has arms of biserially arranged plates bearing biserial pinnules.

auxiliary plate. One of tiny plates bordering anal pyramid and forming ring around inner edge of periproct, present in many cystoids of Glyptocystitida.

axial ridge. See radial ridge.

BASAL. (1, n.). Plate in aboral circlet, especially one of 4 plates in this circlet in Glyptocystitida and Hemicosmitida, designated as *B1, B2,* etc., plural, *BB.* (2, adj.). Referring to aboral part of theca.

base. Aboral part of theca, by some restricted to columnar facet but by others expanded to include thecal plates of basal circlet or aboral circlets.

bipartite. Divided into 2 parts, especially used to refer to glyptocystitidan in which one plate of classic series is represented by 2 plates, as some species of *Cheirocrinus* have *R1* bipartite (2 plates in position occupied by *R1* in most other species of the superfamily).

BRACHIOLE. One of erect structures by which food is gathered and transmitted to ambulacrum. Brachioles reduced to 2 large tapering structures in Pleurocystitidae, but numerous in most Glyptocystitida, especially Callocystitidae, and abundant in Mesocystidae, with as many as 1,000 in *Mesocystis.* Each brachiole composed of biserial plates and unbranched. Two rows of dorsal plates include brachiole groove, and 2 rows of tiny ventral plates (also biserially arranged) roof it over.

BRACHIOLE FACET. Indentation where brachiole was attached, commonly subcircular. Brachiole facets on thecal plates in cystoids lacking ambulacral flooring plates (e.g., Glyptosphaeritida) otherwise shared by an ambulacralium and parambulacralium (e.g., Glyptocystitida).

cicatrix. Scar, usually used for former position of column in cystoids which apparently molt it (e.g., *Protocrinites*).

CIRCLET. Plates which form ring around theca, or which in classic type of Glyptocystitida form such ring. Thus, *B, IL, L, R,* and *O* circlets are present in glyptocystitidans; they are called *complete,* if circlet extends entirely around theca, and *interrupted,* if plate of another circlet intervenes in such manner as to separate 2 plates adjacent in the circlet.

coelom. Supposed major unit of body comparable with that known in living echinoderms.

COLUMN. Stemlike structure attached to aboral end of most cystoids, fairly rigid in *Caryocrinites* but in most other forms having proximal section flared and flexible. Column presumably used for anchoring cystoid, distal end known to be variously modified in some species.

columnal. Unit ossicle composing column. Columnals in many species varying according to position in column, distal columnals longer, cylindrical, with narrow central canal, and proximal columnals shorter, ringlike, with wide lumen. Certain proximals strongly modified in some cystoids (e.g., *Brockocystis*).

columnar facet. Indentation in basal plates of theca to accommodate proximal end of column, normally circular.

complete. See circlet.

compound. See tangential pore canal.

conjunct. See pectinirhomb.

covering plate. See ambulacral covering plate *and* peristomial covering plate.

crown. Oral region, especially applied to cystoids having sharp boundary between steep lateral sides and blunt, flat or gently convex oral region (e.g., *Cheirocrinus*), in which theca is adorally truncate, with flat-lying *OO* forming lidlike cap atop steep *RR.*

deltoid. See oral.

DEMIRHOMB. Kind of pectinirhomb in which pores are arranged in chevron, formed when successive pores are developed on only one side of first pore; rare except in Glyptocystitidae, Cheirocrinidae, and Cystoblastidae.

diameter. Distance from point on theca to point opposite, mostly used to indicate greatest distance across theca equatorially.

DICHOPORE. Structure in pore rhomb, originally proposed for complete unit of 2 terminal openings and their connection, but sometimes applied to only terminal pore or slit in pectinirhomb. Dichopores differ in superfamilies of Rhombifera, as explained in "Morphology," but each kind extends from one thecal plate to another.

DIPLOPORE. Structure penetrating thecal plate and mostly confined to that plate; classic example, as figured in texts, consisting of Y-shaped branching canal or tube with 2 openings at outer end, but canals which do not branch or which branch irregularly are also included in diplopores by some workers. Unbranched canals may be separated as haplopores.

disjunct. See pectinirhomb.

divided. As applied to ambulacra, signifying that ambulacral groove (exclusive of lateral branches) bifurcates, each branch complete with flooring and covering plates; taxonomically significant in Callocystitidae.

EPITHECA. Outermost thin calcareous layer of thecal plates, especially noted in Caryocystitida, in which it covers tangential pore canals so that pore rhombs are apparent only in specimens having epitheca weathered off. Epitheca in *Echinosphaerites* composed of several thin laminae bearing concentric lines (probably growth lines).

epithek. See epitheca.

exothecal. Outside theca, secreted by integument not connected with that of theca. Ambulacra in nearly all cystoids physically separated and distinct from thecal plates and lying outside them. In *Cystoblastus,* however, ambulacra may extend through clefts in *RR* to interior of theca; nevertheless, integument which secreted ambulacra undoubtedly had form of 5 flaps apart from that of theca and folded back to fit into clefts or recesses in *RR,* so that even in this genus ambulacra could be technically called exothecal.

flooring plate. See ambulacral flooring plate.

food groove. See ambulacral groove.

genital pore. See gonopore.

GONOPORE. Small opening in posterior region, usually close to mouth, penetrating thecal plates. Gonopore not detected in all cystoids; in Glyptocystitida, lying on suture within plate *O1.* Some gonopores closed by small valvular pyramid of few pieces or plates.

gut. Supposed alimentary canal similar to that known in living echinoderms. Course of gut inferred; *see* rhomb-free area.

HALF-RHOMB. That part of pore rhomb lying within one thecal plate.

haplopore. Unbranched pore lying normally within one thecal plate; sometimes included under broad interpretation of diplopore.

height. Distance between oral and aboral poles.

HYDROPORE. Opening or openings through thecal plates in posterior region in vicinity of mouth, variously developed as slit, group of irregular slits, or sieve. In most cystoids, hydropore lies between gonopore and mouth, yet in some it is offset to one side, in which case it is not farther from mouth than gonopore. In Glyptocystitida, hydropore lies within plate *O1*. Hydropore also known as primary pore, madrepore, madreporite, and water pore.

INFRALATERAL. One of circlet of 5 plates in Glyptocystitida lying adoral to *BB* and aboral to *L* circlet, designated as *IL1, IL2,* etc., plural *ILL.*

integument. Supposed exterior layer of tissue in cystoids which secreted thecal and other plates, similar to layer known in living echinoderms.

INTERAMBULACRAL. Referring to zone between ambulacra, especially to thecal plates found there.

INTERAMBULACRUM. Part of theca between ambulacra, in most cystoids present as meridional zone or lune but in Gomphocystitidae strongly modified by spiral ambulacra. Interambulacra distinctly bordered in some families (e.g., Dactylocystidae).

intercalation. In Glyptocystitida, arrangement of thecal plates wherein those of one circlet extend into zone of another circlet, separating plates or parts of plates; extending plates sometimes said to be "inserted" into other circlet.

interrupted. See circlet.

LATERAL. (1, n.). One of circlet of 5 plates in Glyptocystitida lying between *IL* and *R* circlets, thus about equatorial in many cystoids, designated as *L1, L2,* etc., plural *LL.* (2, adj.). Located on side of theca, as contrasted to oral and aboral areas.

lateral branches. Short grooves from brachioles to main ambulacral groove, roofed by tiny biserial covering plates; in Glyptocystitida lying upon flooring plates.

lumen. Central open space, applied particularly to wide space in proximal columnals of many cystoids.

madrepore. See hydropore.

madreporite. See hydropore.

montidisjunct. See pectinirhomb.

MOUTH. Aperture at oral pole through which food entered body from ambulacra, covered by peristomial covering plates similar and continuous with those of ambulacra.

multidisjunct. See pectinirhomb.

ORAL. (1, n.). One of circumoral circlet of 5 plates in Glyptocystitida, designated as *O1, O2,* etc., plural *OO*; *O1* containing hydropore and gonopore, normally tripartite. Sutures between *OO* in most cystoids obscured by ambulacra.

oral pole. End of theca containing mouth.

oral projection. Protuberance of oral pole, in *Echinosphaerites* set off by constriction, whereby theca has phialine lip at mouth.

orifice. Any major opening through theca; used in general sense, like aperture.

ornament. See ornamentation.

ornamentation. Surface features of thecal plates (e.g., ridges, granules, tubercles, nodes, spines).

outer side-plate. See ambulacral flooring plates.

papilla. Surficial mound associated with pore.

parambulacral. See ambulacral flooring plates.

parambulacralia. See ambulacral flooring plates.

parietal pore. See gonopore.

parietal septum. Longitudinal wall extending inward from theca in posterior region, seldom preserved but traces observed.

PECTINIRHOMB. Type of pore rhomb found in Glyptocystitida, with units or dichopores terminating in perforations through thecal plates, either as round pores or, more commonly, as slits. If slits from one plate are continuous with those of another, pectinirhomb is conjunct; if slits of one plate are separated from those of other by slit-free area, pectinirhomb is disjunct; if each dichopore has line of slits in each plate, instead of terminal slit only, pectinirhomb is multidisjunct (rare, known in *Cheirocrinus interruptus*); and if slits in one half-rhomb are surrounded by rim, pectinirhomb is montidisjunct.

peripore. Small rimmed fossette associated with pores, commonly applied to rim enclosing pair of diplopores.

PERIPROCT. Major thecal tract containing anal pyramid and, in many species, additional plates; extreme development attained in Pleurocystitidae, in which periproct nearly fills one side of compressed theca. In many Callocystitidae, periproct is filled by small anal pyramid and surrounding ring of auxiliary plates.

periproctal. Any of small plates filling area between anal pyramid and border of periproct, particularly used in descriptions of Pleurocystitidae.

PERISTOME. Thecal tract associated with mouth, especially peristomial covering plates.

peristomial covering plate. Any of small plates covering mouth and continuous with ambulacral covering plates which they resemble.

peristomial projection. See oral projection.

piece. Sometimes used for one of small triangular plates in valvular pyramid, either anal pyramid or small pyramid over gonopore.

pinnule. One of branches of food-gathering system in *Caryocrinites,* biserial, and thus differing from pinnules of crinoids; homologous to simple brachiole in other cystoids.

plate. Any calcareous ossicle, normally flat, in cystoid; by some used only for thecal plates, but all calcareous bodies formed serve as framework of support for soft parts and constitute plates.

pole. See aboral pole *and* oral pole.

pore. General term for perforations in thecal plates. It is better to use pore for openings of these perforations and pore canal for perforation, but usage has been confused on this distinction.

pore canal. Perforation in thecal plate.

PORE RHOMB. Group of perforations in thecal plates, of which each end of perforation lies in one of 2 adjacent plates. Ends may be exposed (Glyptocystitida) or covered by epitheca (Hemicosmitida), and canal from one opening to other may pass through stereotheca (Caryocystitida) or under it (Glyptocystitida, Hemicosmitida).

pore slit. Form of pore in pectinirhomb. *See* dichopore.

posterior. Applied to interambulacrum containing hydropore, in some forms also containing periproct.

primary pore. See hydropore.

RADIAL. (1, n.). One of circlet of 5 plates in Glyptocystitida lying adoral to *LL* and aboral to *O* circlet, designated as *R1, R2,* etc., plural *RR.* Most ambulacra extend to or over corresponding radial. (2, adj.). Used as synonym of ambulacral to signify zone in which ambulacrum is present; use not recommended.

radial ridge. Ridge on thecal plate passing from umbo to side and commonly continuous with similar ridge on adjacent plate; also called axial ridge.

ray. Abulacrum.

"recumbent." Applied to long ambulacra, such as those in Callocystitidae, but misleading, inasmuch as all ambulacra extend back on theca and are therefore recumbent.

rhomb. See pore rhomb.

rhomb-free area. Zone around theca of glyptocystitidan cystoid from mouth to periproct which contains no pectinirhombs, interpreted as marking course of gut.

sculpture. Ornamentation of thecal plates, especially strongly developed ornamentation.

side plate. See ambulacral flooring plates.

simple. See tangential pore canal.

skeleton. All calcareous parts of cystoid.

stem. See column.

stereom. Calcareous material of cystoid, in particular that comprising thecal plates.

STEREOTHECA. Inner layer of thecal plate, thicker than epitheca, containing tangential pore canals in Caryocystitida.

stereothek. See stereotheca.

subepithecal. Lying below epitheca, used in reference to location of tangential pore canals.

subvective appendage. See ambulacrum.

subvective groove. See ambulacral groove.

SUTURE. As used by most workers, boundary line marking junction between 2 plates; in reality, area of contact between 2 plates.

tangential pore canal. Subepithecal pore canal in Caryocystitida which runs parallel to surface of thecal plates and connects 2 pore canals normal to inner surface of different plates; each tangential pore canal extends through stereotheca of 2 adjacent thecal plates. If 2 pores normal to surface and leading to interior of theca are connected by only one tangential pore canal, that canal is said to be simple; but if 2 are connected by more than one, tangential pore canals are compound.

"tegmen." Structure in *Caryocrinites* and related genera which covers mouth and ambulacral grooves as plated roof; probably not homologous to tegmen of a crinoid.

test. See theca.

THECA. Enclosure of plates in which body of cystoid was housed.

THECAL PLATE. One of plates composing theca.

thickness. Distance through plate normal to its surface.

tripartite. Divided into 3 parts; in Glyptocystitida, *O1,* consisting of 3 plates, is said to be tripartite.

umbo. Central projection on thecal plate, part of ornamentation.

valvular pyramid. Either anal pyramid or pyramid covering gonopore in some species.

valvule. One of triangular plates or pieces making up anal pyramid or pyramid covering gonopore.

water pore. See hydropore.

ONTOGENY

THECAL GROWTH

MODES OF GROWTH

Two distinct plans of thecal growth can be distinguished among cystoids. Insofar as the theca alone is concerned, growth proceeded by peripheral additions to plates already present or by interstitial insertion of plates. In the first plan, the total number of plates appears to have formed very early in the life cycle, each plate increasing in size by holoperipheral growth. In the second plan, the total number of plates can be roughly equated with the ontogenetic stage attained by the individual; the first-formed plates tended to grow by peripheral increase in such manner as to attain a much larger size than plates interstitially inserted later (Fig. 39). The mode of growth is an important concept, for it seems certain that the nature of pores and other features were directly related or even controlled by it.

Thecal growth by peripheral additions to plates is exemplified by cystoids of the superfamily Glyptocystitida, in which departures from the basic 24 thecal plates is so exceptional as to be worthy of note. It is true, of course, that a few specimens have been found with anomalous fusion of two plates or division of one or more plates, but no species is known to have irregular intercalation of supernumerary plates. In this superfamily, a few genera exhibit a reduction of plates (e.g., *Cystoblastus,* with only four laterals; *Glaphyrocystis,* lacking radial *4*; *Proctocystis,* lacking radial *5*; perhaps *Pleurocystites,* which seems to lack lateral *5,* and *Sphaerocystites,* which has very small radials *1* and *4* or neither of these plates). Some glyptocystitids possess a bipartite radial *1* (e.g., certain cheirocrinid species and possibly *Glyptocystites*). All such variations are accorded taxonomic significance, attesting to the remarkable constancy of the number of plates in the widespread and diverse Glyptocystitida.

This superfamily is also noted for the constancy of its pore rhombs, both in number and in thecal position, by which genera are distinguished. Each unit, called a **dichopore** by some, first appeared as a pore on a suture, and became elongate perpendicular to the suture by peripheral growth of the two plates which shared it; each pectinirhomb consisted of several to many dichopores. Plainly, the existence and maintenance of rhombs of this kind were possible only in thecae with peripheral plate growth; they would have been interrupted and destroyed by insertion of additional plates along the suture. Rhombs will be discussed in more detail below. It suffices here to point out that rhomb-bearing plates of the Glyptocystitida show concentric growth lines, from which the shape and number of dichopores in the rhomb can be deduced at successive growth intervals of the plates.

The superfamily Hemicosmitida is likewise noted for the constancy of plate number and arrangement. Although the rhombs are perhaps not as perfected as those in the Glyptocystitida, the dichopores similarly extend from one plate to the next, and owe their continued development to peripheral plate growth.

In the other two superfamilies of the Rhombifera, the Polycosmitida and the Caryocystitida, the number of plates is not constant for a species, insofar as known. From the variation in plate size noted for certain specimens of *Echinosphaerites,* for example, it appears that some of the smaller plates were interstitially added after the larger. In neither of the two superfamilies were pore rhombs strongly developed; instead, they were numerous, present on nearly all sides of each plate. From selected illustrations, one is led to the impression that the rhombs are dissimilarly developed on the various sides of a plate. It seems logical to presume that as soon as an additional plate was inserted in the theca, it started forming dichopores with adjacent plates, and that peripheral growth proceeded at the same rate in all plates, regardless of their time of formation; as a result, the size of a rhomb would be proportional to the size of the smaller plate sharing it (or to the length of the suture between the plates) but not comparable with all other rhombs of the specimen. This was apparently the case.

Among the diplopore-bearing cystoids, both types of growth also took place. The ultimate expression of interstitial insertion seems to have been in species of *Holocystites* and related aristocystitids, whereby the initial plates attained very large size, resembling platters set in a mosaic of small pieces. By contrast, *Asteroblastus* possessed a plate stability comparable to that of the rhombiferan *Cystoblastus.*

From this discussion, the following conclusions are derived: (1) diplopores could form irrespective of the kind of plate growth; (2) pectinirhombs could develop only with peripheral plate growth; and (3) small, dissimilar pore rhombs were characteristic of thecae with interstitial plate insertion.

CHANGES IN SHAPE

Regardless of mode of growth, the theca could change shape somewhat during ontogeny. In particular, the largest (and presumably gerontic) specimens commonly differ from other adults. This change was expressed in most species by progressive elongation, so that spherical juveniles and adults became pyriform in old age. Many cystoids tended to become prolonged aborally. The alterations in shape were produced in cystoids having peripheral growth by differential rates in various plates, and in those having the interstitial insertions by addition of more plates in the oral region than the aboral.

DEVELOPMENT OF PORE RHOMBS

In considering the manner in which rhombs formed, it is necessary to bear in mind that the thecal plates were undoubtedly encased in an integument, a layer of "living skin" like that of present echinoderms. All calcareous deposits constituting the fossil were secreted, at one time or another, during the lifetime of the cystoid. In the Glyptocystitida, the complex and very regular **pectinirhombs** began, undoubtedly, as a single pore on the suture between plates. Stages with only a few pores in each rhomb have been found. As the plates increased peripherally, as shown by growth lines, the spot at the pore received no deposits from either plate, and gradually was left as a dichopore slit from one plate into the other. At the same time, as the length of the suture increased, other pores appeared along the suture on each side of the slit. Thereafter, the process continued, with periodic additions of new pores at each end of the suture. Thus the **conjunct rhombs** were developed. The pore slits extending farthest from the suture lie at the obtuse angles of the rhomb and were the first-formed; the pairs at the ends of the suture are closest together and were the last-formed.

The **disjunct rhombs** required an additional step. After the slit had grown to a length characteristic of the species, the integument began secreting a thin surficial calcite along the edge of the plate, sealing off the slit and creating a platform area within the rhomb; this proceeded to apply at intervals to dichopore slits on either side, so that the intrarhombic platform area also came to have a rhomb shape. In the rather rare occurrences of **multidisjunct rhombs,** such as in *Cheirocrinus interruptus,* the integument alternately secreted and failed to secrete along the sites of the pores, with the result that additional slits were left along the line connecting the distal (original) paired dichopores. The multidisjunct rhomb can be described as a series of concentric rhombs, but this is misleading in terms of its genesis; a more fitting description is a pectinirhomb in which each dichopore is represented by a row of slits.

No evidence of extensive alteration of dichopores by subsequent resorption and resecretion can be cited. Once formed, a pore retained its position as the plate extended peripherally. So it is not surprising that the spacing of dichopore slits is constant for all specimens of a species, regardless of their size.

With reference to the time of rhomb formation, certain anomalies are instructive. A specimen of *Pseudocrinites* described by SCHUCHERT (116) as *P. abnormalis* shows the lower rhomb developed along the suture between infralaterals *1* and *2* instead of the normal basal *2* and infralateral *2,* accompanied by necessary alterations in shape of aboral plates to accommodate the large rhomb in the anomalous position. SINCLAIR (117), mentioned a specimen of *Glyptocystites multipora* with a rhomb on the lateral *1*-radial *1* suture instead of the nearby normal lateral *1*-lateral *2* position. This supports SINCLAIR's statement: "It seems that the position of a rhomb was not fixed with reference to a particular suture, but only with reference to a given area of the theca." If this is true, pores initiating the rhombs developed in the very young cystoid before the thecal plates assumed their definitive form.

Another point in connection with the ontogeny of pore rhombs concerns the "smothering" of rhombs by ambulacra. In some specimens, a part of a rhomb area may be covered by an ambulacrum; invariably, if pores on one side of the rhomb were prevented from forming, their counterparts in the plate opposite did not develop. One may interpret this, in terms of growth, as an instance wherein the exothecal ambulacrum transgressed the plate suture at a time when a dichopore was being formed. Both the thecal plates and the ambulacral flooring plates were coated with a layer of integument, so that the initial bond between the thecal plates and extending ambulacral plates was not strong. When an ambulacrum grew as far as a pore rhomb, a physiological conflict appears to have developed between the functions of respiration through the pores and food-gathering by the ambulacrum. In the cases cited above, the ambulacrum was victorious and grew right on across the pore area; but these were probably exceptions. In most other cases, the rhombs provided effective blockades for ambulacral extension. Thus, in *Lepadocystis* with two half-rhombs on radial *3,* ambulacrum *III* grew only as far as the rhombs, or projected its tip onto the narrow ridge separating the two rhombs. Similarly, ambulacrum *III* in *Glyptocystites* was effectively blocked by the transverse lateral *3*-radial *3* rhomb, to which it extended and then apparently stopped distal growth. One may judge that whichever occupied the part of the theca first, rhomb or ambulacrum, thenceforth prevented the other from utilizing the particular area.

In large specimens of some species, the process of pore addition ceased, and the half-rhomb on each plate was moved farther away from the half-rhomb opposite. In certain of the Callocystitidae, for example, one of the half-rhombs came to be completely enclosed by a rim in the adult theca. In a few Glyptocystitida (e.g., *Jaekelocystis*) the pores in adjacent plates developed in different fashion, although they were paired, of course.

Rhombs of the type found in the Hemicosmitida fall into this same ontogenetic pattern, as do the rhombs with simple tangential canals in the Caryocystitida. In the rhombs of *Echinosphaerites,* which possess compound tangential canals, the formation was somewhat more complicated. After each pore was formed along the suture, the integument proceeded to secrete small bars across this area, then wider bars; the pore canals, therefore, instead of developing as single tangential tunnels through the plates, became divided into several subparallel connections between each pair of pores.

DEVELOPMENT OF AMBULACRA

As the size of the theca increased, the ambulacra kept pace by (1) increasing the diameter or lateral extent by peripheral additions, and (2) extending the length by addition of new terminal elements. Numerous excellent examples to illustrate this mode of growth can be found in the Callocystitidae, in which the ambulacra are small and short in the small specimens of the species and larger and longer in more mature specimens.

In many groups (e.g., Cheirocrinidae, Pleurocystitidae, Caryocystitidae, Echinosphaeritidae, and others) the ambulacra are short, limited to the crown or apex of the theca. Their ontogenetic development proceeds slowly, with more emphasis on peripheral extension than on terminal additions.

In such groups as the Glyptocystitidae, and Callocystitidae, however, the ambulacra grow in length more rapidly than in lateral extent. In *Lepadocystis moorei,* for example, juvenile specimens have short ambulacra on the crown of the theca, mature individuals have ambulacra extending to the level of the upper rhombs, and gerontic forms have some ambulacra reaching below this level (75); hence, the ambulacra grew more rapidly than the theca. In *Glyptocystites, Callocystites, Pseudocrinites, Sphaerocystites,* and other genera, the ambulacra of the adults reach almost or quite to the column, crossing the entire theca meridionally; their ambulacra are sometimes called "recumbent," though this term is exceedingly misleading. The spacing of the brachiole facets along the course of the ambulacrum does not change much through ontogeny, proof that the growth of the ambulacral plates is mostly lateral, rather than in direction of the length. In this group, however, the adult has many more brachiole facets than the juvenile. The significant mode of ambulacral growth, therefore, is by addition of terminal plates. The lateral growth of long ambulacra evidently slows up, for many of the callocystitid cystoids have ambulacra with subparallel sides.

Inasmuch as the brachiole facets on the ambulacral flooring plates retain nearly their original spacing, the growth and expansion of thecal plates must have required continuous readjustment and repositioning beneath the nonexpanding bases of the flooring plates (Kesling, 73). This accounts, in part at least, for the rather loose attachment of ambulacra in most genera.

Branching of the main ambulacra, involving addition of new flooring plates, is progressive (Fig. 49,*5-9*). Young individuals have simple ambulacra; branches are added later.

COLUMN

Certain cystoids (e.g., *Protocrinites oviformis*) have immature specimens with a facet for column attachment and adults with the base completely altered to obliterate all signs of such attachment (Fig. 47). Presumably, as suggested by Jaekel (69), the disappearance of the column marked the entry of the individual into a free ex-

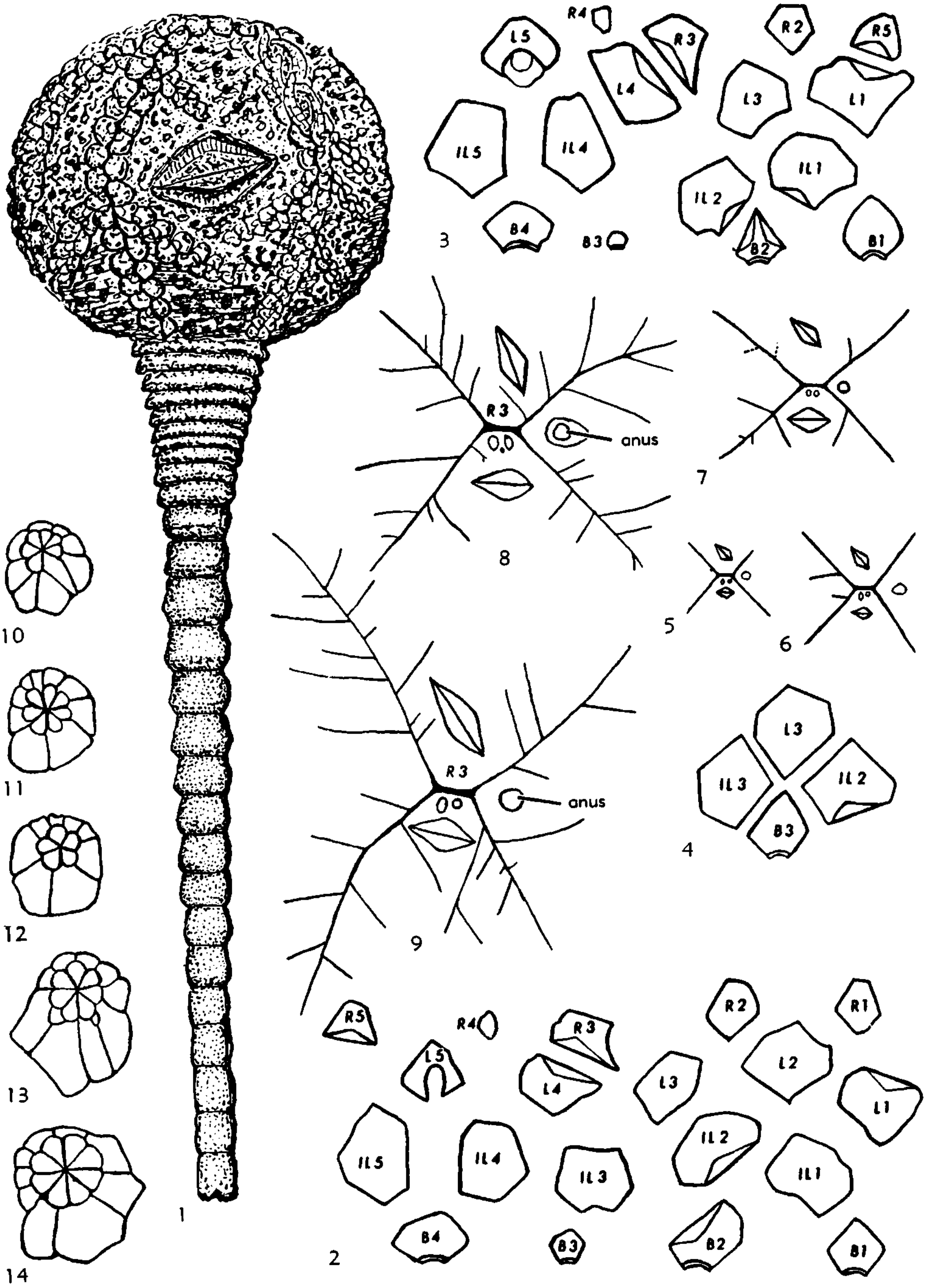


FIG. 49. Structures of *Strobilocystites* (M.Dev.-U.Dev.) and their variations.——*1. S. calvini* WHITE (M. Dev.), restoration, ×2.——*2.* Diagram of plates in nearly average specimen, except that *B3* (4) is rather small (plates of *A*-ray shaded).——*3.* Diagram of plates of anomalous specimen in which *IL3, L2,* and *R1* are not developed (plates of *A*-ray shaded).——*4.* Anomalous reduction of sutures at *B3-IL2-IL3-L3* juncture.——*5-9.* Ontogenetic series showing progressive branching of ambulacra.——*10-14.* Variations in anal pyramid and circlet of auxiliary plates (120). [Plate designations as in Figure 38.]

istence. In *Protocrinites* the stem had been cast off and only a scar remained in a specimen 11 mm. in diameter.

Certain of the Aristocystitidae probably never possessed a column, for their flexible aboral region is found variously conforming to the shape of objects to which they were attached.

On the other hand, the column of *Caryocrinites* grew relatively very long, much more like the stem of a crinoid than the generally short, tapering column in cystoids of other families.

PERISTOME AND PERIPROCT

The major thecal openings of the mouth and anus commonly are surrounded by rather small, irregularly arranged plates which are classed as belonging to the peristome and periproct, respectively. These areas required alterations in the curvature of bordering plates in order to increase in size. It must be reasoned that the plates adjacent to the peristome and periproct could undergo some marginal resorption, as well as differential peripheral growth.

PALEOECOLOGY

It should be understood from the start of discussion that paleoecological literature on cystoids is fragmentary, mostly in the form of annotations or remarks appended to systematic descriptions. It should be further admitted that the occurrences of cystoids are not generally reported with details of the burial attitude, associated fauna, lithology of the enclosing strata, or distribution throughout a sequence of beds. Without such basic data, a comprehensive treatment of paleoecology cannot be accomplished.

Certain factors may be considered. In more than a century of purposeful collecting, several species are known from only one or two specimens; some of these are types of the only known species of their genera. Only a few species are known to have widespread geographic distribution. One species may be locally abundant. Many cystoids were able to exist without a column. Columns, where developed, are of several kinds. Brachioles are not powerfully constructed elements of cystoids. Food could enter the ambulacral system only through the gap between opened tiny biserial plates on the brachioles. The number of thecal pores varies greatly, both as diplopores and haplopores in the Diploporita and as pore rhombs in the Rhombifera. Thecae occur in laterally compressed, elongate, and spherical shapes with drastic extremes in symmetry. These differences in abundance, distribution, and morphology have been studied independently and irregularly, whereas they probably have coherent relationships.

Even if one is convinced that evolution of cystoids resulted from dramatic mutations, monogeneric families based on monospecific genera can scarcely be explained except as evidence of poor paleontologic record. Conversely, widespread and abundant species (e.g., *Echinosphaerites aurantium*) may be well represented because of very fortunate circumstances of preservation and discovery. Nevertheless, insofar as reports are concerned, some species appear to have been represented by small, restricted populations and others to have been cosmopolitan and prolific.

From the narrow openings present in the brachioles, even when the covering plates were fully opened, one must conclude that the cystoids could only ingest microscopic particles. Irrespective of their possible motility, none of the cystoids could have fed upon large animals. Kesling & Mintz (75) noted that *Lepadocystis moorei* was preserved in excellent condition on slabs bearing bryozoans, small brachiopods, and edrioasteroids, other "filter-feeders," and theorized that current eddies may have provided a more or less continuous rain of microscopic life or debris to the community. This implies that cystoids may have thrived only in restricted areas where food was abundantly provided. Sinclair (119) described numerous *Cheirocrinus* in close proximity as probably living in colonies with the distal end of the column embedded in the soft bottom sediment. Stainbrook (120) had interpreted the abundant *Strobilocystites* as inhabitants of a quiet sea bottom on which fine mud was accumulating, associated with small brachiopods, bryozoans, and auloporoid corals but no nektonic or planktonic forms.

The crowding together in a favorable area was noted by Billings (20), who studied 60 specimens of *Glyptocystites multipora* well-preserved on a shale slab two yards square. He offered the opinion that they formed a colony growing at considerable depth in clear water, and were buried alive. Specimens of *Echinosphaerites* occurring in great banks, densely packed in certain strata containing more clay than adjacent cystoid-free beds, were differently interpreted by Hadding (57), who thought their environment to be quiet water near the shore.

One of the principal problems of paleoecology is eleutherozoic adaptations of the cystoids, including the means and extent of their motility. Kirk (76) made a special investigation of such tendencies for all the Paleozoic pelmatozoans, dividing them into three groups: (1) those retaining jointed columns throughout life, but not using them for permanent attachment; (2) those losing most or all of the column at some stage of development; and (3) those possessing no true jointed column, but attaching the theca by a base of varying morphological nature. The cystoids (which Kirk used in a broad sense) were placed in group 1, but with some explanation that there were technical difficulties in the separation; within group 1, three types were distinguished: (1a) no true columns, attached by an outgrowth of the thecal wall, if at all; (1b) columns prehensile, the animal attached at will; and (1c) propulsion along the bottom by means of brachial appendages and possibly by columns—this included only the "carpoids." Type 1a included the Echinosphaeritidae and Aristocystitidae as used by Bather, approximately the Caryocystitida, Protocrinitidae, and Sphaeronitida in modern taxa, to judge from the genera cited. Type 1b included most of the Glyptocystitida. Kirk's advocacy of adaptations for free existence was enthusiastic, as witnessed by his statement, "Whether there ever existed a stalked Pelmatozoan that was sedentary from the time of its attachment is a question that must unfortunately be forever open."

Aristocystites has come up for consideration of its mode of life. Bather (10) stated, "The animal usually fixed itself to some solid body by a portion of the theca at or near the lower pole." Kirk (76) distinguished three kinds of specimens of *Aristocystites*: (1) those with an aboral depression covered by secondary stereom, thought to signify that the animal was fixed until the time of death; (2) those with aboral depression and theca entirely porous, no secondary stereom, the animal presumably preserving the marks of its pelmatozoan existence; and (3) those with the aboral extremity rounded, lacking a depression, no secondary deposits, some with an apical plate distinguishable, considered to have been only briefly fixed while very young, the apical plate being the sole souvenir of this state. Chauvel (34) suggested that fixation may have been principally by means of aboral diploporitic "tentacules," a sort of tube feet. In many specimens of *Aristocystites,* the base is strongly twisted to one side. This distortion of the silhouette was shown in certain older reconstructions as the result of the base remaining fixed and the heavy oral section falling over to lie prostrate on the sea floor. Kirk and Chauvel concluded that these organisms tended to detach themselves and travel about. Termier & Termier (125) believed they could detect eleutherozoic tendencies in reduction of ambulacral grooves and in the presence of a sort of calcareous epidermis corking up the diplopores on all or part of the theca in *Aristocystites* and related genera.

Other features have been cited to demonstrate the adoption of a free existence, such as flattening of the theca in *Pleurocystites,* the deciduous column of *Protocrinites* leaving scarcely a cicatrix in the adult, if at all, and others. An unusual suggestion was put forth by Termier & Termier (125) for *Campylostoma* (translated): "The mouth . . . is arcuate, sinuous, and presents two lips, as if they had a function more active than the mouth of a fixed form." This is exceedingly difficult to comprehend, for the peristome was presumably arched over by covering plates, like those known to be present and fixed in other cystoids.

Not all cystoids have been regarded as eleutherozoic. Many authors of the 19th century looked upon all cystoids as anchored by a column, and therefrom inferred a relationship to crinoids. With regard to the exceptional find of *Glyptocystites multipora* already alluded to, BILLINGS (20) said, "There is good reason to believe that they lived and died upon this spot. . . . It is quite clear that they could not have been at all drifted about the bottom after death, otherwise they would at least have lost their columns and pinnulae. It is more probable that they formed a little colony, growing on this spot at a considerable depth, . . . and that the shale consists of a deposit showered down upon them from a superficial current, literally burying them alive." CHAUVEL (34) said that *Calix* may have lived with the aboral end buried, the spines of that region giving the theca anchorage; he also suggested that *Pachycalix* may likewise have lived submerged in the bottom sediments. In their reconstruction of *Pachycalix pachytheca,* TERMIER & TERMIER (129) showed it to be flask-shaped, thin-walled in the tapered oral end and much-thickened and heavy at the rounded base, causing the theca to be weighted like a child's tumble-doll.

Echinosphaerites aurantium GYLLENHAAL) has inspired considerable speculation on its life habits because it is found in many parts of the world and because certain limestone strata are crammed with thecae. No other Ordovician echinoderm was more ubiquitous. A salient point for reconstruction of their environment is whether the remarkable occurrences are biocoenoses or thanatocoenoses. Both views have had adherents. DEECKE (35) thought that they lived in immense colonies at or quite near their burial site. This concept received the endorsement of HADDING (57) and REGNÉLL (99). On the other hand, KIRK (76) and BATHER (14) promoted the idea of burial at considerable distances from the living arena. They differed somewhat in their suppositions on the mode of life. KIRK emphasized the thin thecal walls and consequent light weight of the animal and took them to indicate an adaptation to a floating existence; but BATHER conceived of these cystoids as anchored like captive balloons by their flexible columns, broken away from their moorings when deceased or at times while living, and concentrated in great masses along the shore by currents and winds. Both authors were attempting to discover a peculiarity of *Echinosphaerites aurantium* as an animal that would explain its wide dispersal as a species. Both claimed that dissemination took place with the adults, since, if larvae were involved, all other species would have similar distributions. This was countered by REGNÉLL (104), who expressed the opinion that the *Echinosphaerites*-bearing beds were autochthonous and that larvae of this species could readily have been spread by currents; supposition that the larvae of other species did not accomplish widespread dispersal could not be accepted in REGNÉLL's opinion, as an argument against such a factor for *E. aurantium.*

KIRK (76) reported a flattening on one side of *Cheirocrinus* by "excessive multiplication of circum-anal plates," a curious relationship of cause-and-effect. In it he claimed to see a lineage leading to *Pleurocystites* and negating any claims that *Glyptocystites* descended from *Cheirocrinus.* The prostrate habit he also assigned to *Erinocystis,* the periproct being produced by hypertrophy of the bordering plates so as to shift the anal opening outward and backward.

In *Pleurocystites,* KIRK (76) claimed that the rhombs were on the dorsal convex side, whereas BATHER (12) thought them to have belonged on the underside of the animal. According to BATHER, the column coiled loosely around some upright object and the animal stretched out horizontally with the periproct uppermost. Clogging of the pore rhombs on the underside by sediment induced the periproct to assume a respiratory function. Thus, BATHER hoped to derive an explanation that would satisfy two phylogenetic trends—reduction in size and number of pore rhombs and great enlargement of the multiplated periproct.

The manner of accomplishing locomotion is another matter of debate. MÜLLER (90) suggested the presence of "suctorial feet" in the cystoids, but assumed a close proximity to the ambulacral grooves. KIRK (76) admitted the possibility of podia in *Protocrinites* and other Diploporita similar to those suspected in *Bothriocidaris.* This theme was followed by CHAUVEL (34), who argued that the brachioles were too weak for propulsion in *Codiacystis moneta* but concluded that (translation) "the aboral corona of canals is more developed than on the rest of the theca, a situation that may be interpreted as robust tube feet or tentacles that permitted the animal to attach for support or release itself at will." On the other hand, KIRK (76) called attention to the stout brachioles of *Arachnocystites* which conceivably could have served as "fairly effective swimming organs." He also proposed that the brachioles of *Pleurocystites* may have acted like flagella for locomotion. Still another mode of movement was postulated by CHAUVEL (34). He compared the papillae associated with the diplopores with those of echinoids and raised question as to the presence of movable spines in the cystoids. TERMIER & TERMIER (125) assumed the existence of such spines in their reconstruction of *Lepidocalix.*

The column of the Glyptocystitida is modified in bizarre ways. The proximal section is wide and contains a large lumen; judging from its structure, this section was undoubtedly very flexible. The column tapers and distally is narrower and less flexible. Some of the accounts have implied that the animal sculled along like a one-armed brittle star. KIRK (76) claimed that the eleutherozoic habit was a mark of "decadence" in *Pleurocystites,* "and the animals crawled about, dragging an all but useless stem behind them." If, as KIRK supposed in the same publication, the brachioles acted as flagella in *Pleurocystites,* one is hard pressed to imagine them "crawling."

In some Glyptocystitida, at least, the column is terminally specialized. *Lepocrinites* has the distal columnals fused to form a clavate appendage, which may have served as a ballast or drag. *Lepadocystis moorei* has processes grown around objects of attachment, presumably extending as soft integument and calcifying later. These genera may be thought of as utilizing musculature housed in the lumen of the flexible column to adjust and shift the attitude of the theca, rather than for locomotion.

No clear consensus on paleoecology has emerged. I am inclined to agree with REGNÉLL (105) that the cystoids were practically sedentary, some perhaps moving sluggishly on the bottom ooze. Spread of a species over great distances was accomplished, therefore, by the active larvae. Favorable areas were soon saturated with individuals. There is some evidence that different species preferred different depths and bottom conditions.

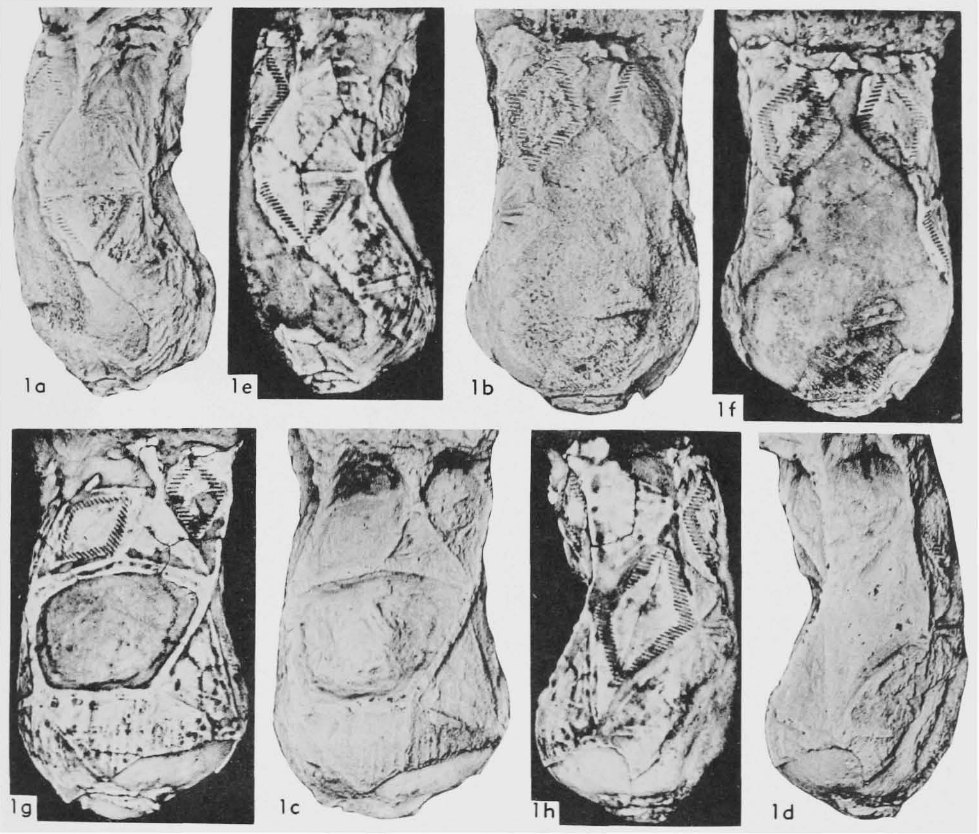
TECHNIQUES FOR PREPARATION AND STUDY OF CYSTOIDS

FIELD METHODS

Cystoids are in general so rare and so fragile that considerable care must be exercised in collecting them. Before going into the field, the paleontologist should take cognizance of certain characteristics of cystoids. These concern the structures of the specimens, the distribution of specimens, and the paleoecological setting in which they occur.

Certain structures are so weakly attached to the theca that they are liable to be left behind in the rock unless special attention is given to their recovery. The brachioles and the column are such structures. If they are present in the fossil, it may be necessary to quarry the slab on which the specimen rests, delaying further exhumation until it reaches the laboratory. In the Glyptocystitidae and Callocystitidae, the ambulacral plates in many species are so loosely fastened to the theca that they readily flake off; further, these plates are so small and so similar that they can be reassembled, if at all, only after tedious efforts. It is wise to leave the theca encased in as much matrix as possible until it can be cleaned under a binocular microscope.

In certain occurrences that have been described, numerous specimens have been found associated in a rather small area. The finding of one cystoid should be the signal to examine the exposure for others before proceeding with quarrying operations. It may also be borne in mind that a species does not necessarily attain its greatest abundance in the oldest strata. After the initial discovery, the search should be ex-



Homocystites

FIG. 50. Four views of a specimen coated with sublimated ammonium chloride and the same submersed in xylol, all photographed in high contrast. *Homocystites anatiformis* (HALL), M.Ord.(Trenton), Mich.; *1a-d,* four lat., ×2, coated; *1e-h,* same, submersed; only part of specimen shown in *1b* was exposed; the remainder was exhumed from limestone matrix with vibrotool and needles (Kesling, n).

tended stratigraphically as well as geographically.

Much of the information requisite to paleoecology can be obtained only in the field. Detailed notes on the burial attitude of the cystoids, the associated fauna, and the lithology should be set down for each find.

WORK ON SPECIMENS

PREPARATION

Depending upon rarity of the species, the nature of preserved structures, and characters of the rock matrix, a specimen may be fully exhumed or left partly embedded in a slab. If the cystoid appears to be new, especially of the Glyptocystitida, the theca should be entirely removed from matrix for the purpose of exposing the thecal plates, periproct, peristome, thecal pores, and other structures of diagnostic value. This does not mean that brachioles and column must be destroyed, however, because they can be carefully preserved during the cleaning procedure and later restored to their normal position.

Each kind of matrix demands its special treatment. Limestone may be so dense that it can be removed only with vibratool and small chisels. Great skill and practice are needed when the matrix is harder than the thecal plates. All work should be done under magnification. If the matrix is soft

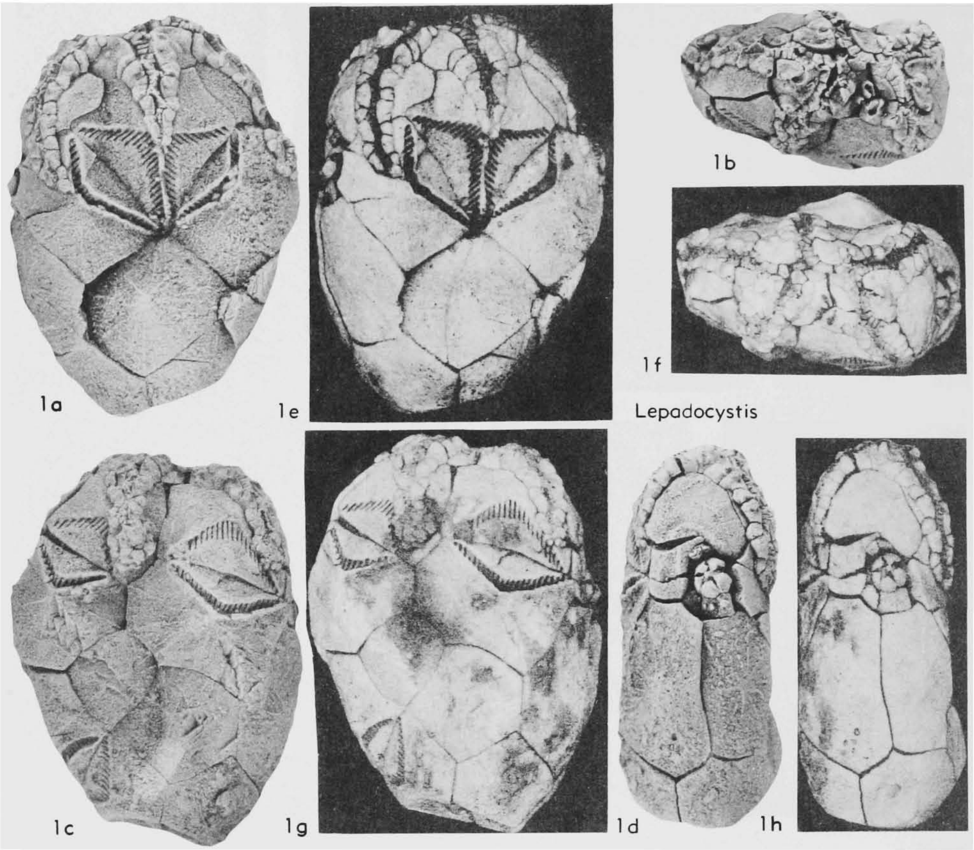


FIG. 51. Four views of a specimen coated with sublimated ammonium chloride and the same submersed in xylol, all photographed in low contrast. *Lepadocystis moorei* (MEEK), U.Ord.(Cincinnati.), Ind.; *1a-d,* lat. *(III),* oral, lat. (post) and lat. (anal), ×4, coated; *1e-h,* same submersed; this specimen has anomalous bipartite *IL1* (75).

shale, it can be removed by brushing while wet. It may happen that similar material forms the steinkern, or part of the steinkern, in which instance prolonged soaking will loosen the thecal plates. Calcareous shales are difficult or impossible to dislodge by brushing, but they tend to break down with application of potassium hydroxide pellets. The reaction is rather extreme, and should be under surveillance. Inspection will indicate when the matrix has been softened sufficiently to be removed. When the hydroxide treatment is complete, the specimen must be soaked at length in slightly acidified water, then clear water, to prevent future reaction that could disintegrate the fossil.

With mechanical scraping, chipping, and gouging, or with chemical treatment, the application of ultrasonic vibration may be a helpful supplement. It has the unfortunate disadvantage of dislodging loose thecal and ambulacral plates and brachioles. No matter how the cystoid is handled in the initial stages of exhumation, normally some additional touches of needle and brush are needed to clean sutures, ambulacra, rhombs, and other tiny parts. A toothpick is helpful in final steps of preparation.

Parts that are dislodged or intentionally removed can be reassembled with glue. The opposing faces should be carefully cleaned and the parts positioned under a binocular microscope. The choice of glue depends

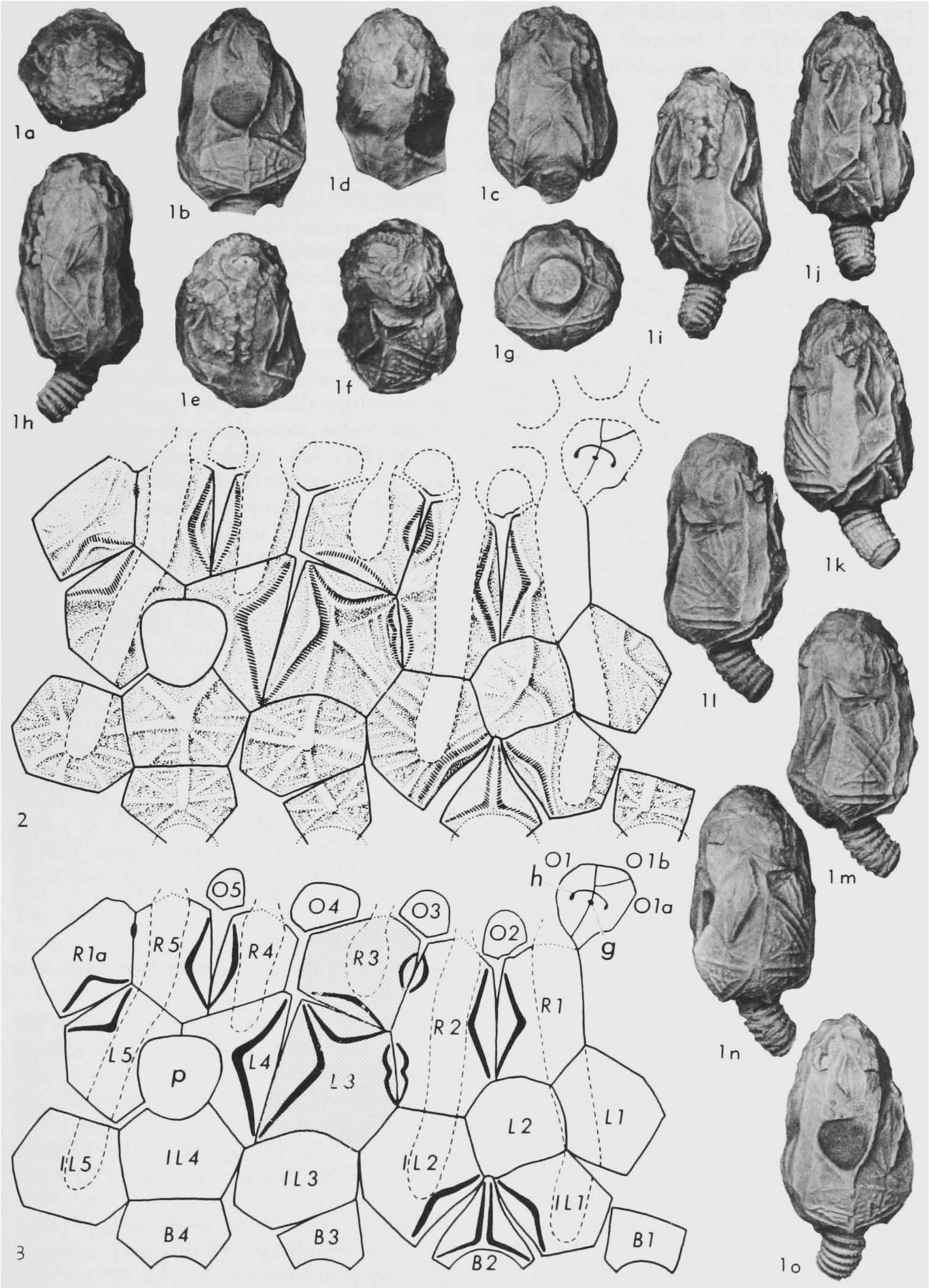


FIG. 52. *Glyptocystites ehlersi* KESLING, M.Ord.(Trenton.), Mich.; *1*, photographs, all ×1; *1a*, oral view; *1b,c*, aborally inclined views of interambulacra *4* and *1*; *1d-f*, orally inclined views of ambulacra *V (C)*, *I (D)*, and *III (A)*; *1g*, aboral view; *1h-o*, lateral views, *h* on interambulacrum *5* (posterior), *i on* ambulacrum *I (D)*, *j* on interambulacrum *l*, *k* on ambulacrum *II (E)*, *l* on interambulacrum *2*, *m* on ambulacrum *III (A)*, *n* on interambulacrum *3*, *o* on interambulacrum *4*.——*2*. Plates drawn with camera lucida.——*3*. Simplified plate diagram, plates of *A*-ray shaded (*p*, periproct; *h*, hydropore; *g*, gonopore) (73). [Plate designations as in Figure 38.]

partly upon the solutions in which the specimen may be submersed for study. In most cases, the glue should be applied in adequate quantity, and any excess removed immediately or with cautious use of a solvent later.

OBSERVATION

To see the details of thecal pores, hydropore, gonopore, ambulacra, and such small structures, it may be necessary to submerge the specimen in a liquid or to stain it, or both. The sutures of most cystoids show to advantage when submersed and soaked in glycerine, xylol, or various other substances. The slits of a pectinirhomb are normally filled with shaly matrix, and can be strongly emphasized by staining with organic dyes. The same treatment may be used for other thecal openings and sutures.

PHOTOGRAPHY

The cystoid may be lightly coated with sublimated ammonium chloride to show the general form (Fig. 50). If details of pore rhombs are to be illustrated, they can be photographed while submersed (Fig. 51). The diverse diagnostic structures in cystoids require various views and magnifications for adequate substantiation. The films employed for coated specimens normally have greater contrast than those for submersed specimens. Exposures for submersed specimens are very long.

SPECIAL PROBLEMS

In cystoids having an epithecal layer, it becomes essential to grind off a small area to reveal the thecal pores in the stereom.

If numerous specimens are available, internal structures can be sought by a series of polished surfaces. These may be recorded photographically or by preparation of peels.

Some species are known from parts preserved in several incomplete specimens. A reconstruction can be attempted for a species by drawing individual plates or sections with the aid of a camera lucida. Each plate must be drawn to a selected scale and from a direction normal to its surface. In proper relationship, these plates form a diagram of the theca expanded and reduced to a plane (Fig. 52). Such diagrams are essential to study of the Glyptocystitida, and they are helpful for many other kinds of cystoids.

UNPROMISING TECHNIQUES

No vital information has been disclosed by thin sections that is not equally clear on polished surfaces. The application of hydrofluoric acid to make thecal plates translucent has not been explored, especially with reference to the extent of thecal pores. Grinding down a few thecal plates appears to be a more satisfactory method of determining the precise level of subsurface pore structures. This should not be taken to mean that such methods of examination should not be further explored, but that they have not yet been found helpful.

OCCURRENCE OF CYSTOIDS

STRATIGRAPHIC DISTRIBUTION

ORDOVICIAN ROCK DIVISIONS

Cystoids attained their zenith in diversity during the Ordovician in Europe. Therefore, any attempt to arrange related forms chronologically to reveal phylogeny or routes of dispersal must first resolve the complex stratigraphy of Ordovician deposits in Europe, particularly the Baltic region.

Inasmuch as European stratigraphers have points of difference, it is necessary to be somewhat arbitrary in correlation. The lack of universal agreement on the Lower-Middle and the Middle-Upper boundaries is natural —the sequence of sediments in most European sections lacks major interruptions corresponding to the boundaries recognized in North America and on which the *Treatise* terms Lower, Middle, and Upper Ordovician are based.

The correlation table presented here (Fig. 53) is a compilation from many authors, foremost of whom are Bouček (25), Öpik (92), Størmer (122), Regnéll & Hede (106), and Thorslund & Jaanusson (132). The critical boundaries adopted here are those of Thorslund (*in* Thorslund & Jaanusson, 132), who in central Sweden places the base of the Ordovician at the base of the *Dictyonema desmograptoides* zone, the Lower-Middle boundary at the top of the *Didymograptus bifidus* zone, the Middle-Upper boundary at the top of the *Dicranograptus clingani* zone, and the top of the Ordovician at the top of the *Dalmanatina* Beds.

In Bohemia, the designations of Barrande (3) have been found to have serious deficiencies arising from the discontinuity of exposures used in compiling his proposed sequence. In present stratigraphic terms, the Middle Ordovician begins at the base of the Šárka Beds, and the Upper at the base of the Bohdalec Beds, which lie in the *Pleurograptus linearis* zone; thus, the Middle-Upper boundary occurs within the Zahořany Series.

In Britain, the current hexapartite division of the Ordovician does not contain boundaries that fit those in North America. The Lower-Middle boundary lies within the Llanvirn Series, between zones 6 and 7, and the Middle-Upper within the Caradoc Series, between zones 12 and 13. In the Girvan district of Scotland, the cystoid-bearing Drummuck Group lies in zone 15, the *Dicellograptus anceps* zone, of the Ashgill Series.

In Norway, the debated Lower-Middle boundary is here placed, by correlation with the Swedish section, within the Upper *Didymograptus* Shale, between $4\alpha_1$ and $4\alpha_2$. The Middle-Upper boundary is more distinct, corresponding to the boundary of the *Chasmops* and *Tretaspis* Series.

In the so-called shelly facies of Sweden, the Lower-Middle division line comes between the *Gigas* Limestone (top of the *Vaginatum*) and *Platyurus* Limestone, and the Middle-Upper between the *Macrourus* Limestone and Slandrom Limestone. In the graptolitic facies, the latter boundary is between Middle and Upper *Dicellograptus* divisions.

In Estonia, the Lower-Middle boundary is placed between the Upper Linsen (C_{1a}) and *Echinosphaerites* (C_{1b}) in terms of Schmidt (113, many others). In the classification of Öpik (92), it is between the $C_1\alpha$ and $C_1\beta$; it therefore comes within the Azeri, Duboviki, and Volkhovstroy succession of the Estonian and the Leningrad region, Russia. The Middle-Upper boundary, as in Scandinavia, is more sharply expressed, lying between the Wasalemm and Wesenberg (D_3 and E) with their variant spellings. In eastern Estonia, the E zone is called the Rakvere. In placing the Upper Ordovician limit, the table follows Öpik (92) and Sarv (111) in assigning the Borkholm or Porkuni (F_2) to the Lower Silurian, rather than uppermost Ordovician, as classified by Rõõmusoks (108).

Correlation of these strata with Ordovician deposits in other parts of the world contains elements of doubt, irrespective of the means used. The classification of the cystoid-bearing beds in Burma and southern China is especially important, as it bears on the origin of *Heliocrinites* and *Hemicosmites*. Here, the Naunkangyi Beds of northern Burma, the Shihtien Beds of Yunnan, and the Shihtzepu Shale of Kweichou, China, are considered to be approximate equivalents; a review of the suggested correlations in the three areas has been offered by Regnéll (101). Following Reed (97) and Regnéll (100), the Naungkangyi Beds are correlated with the $C_1\beta$-$C_1\gamma$ of the eastern Baltic region, and are thus considered to be lower Middle Ordovician.

In North America, the Trenton Group is regarded as the same in age as zone 12 (*Dicranograptus clingani* zone) of Britain, the Upper *Chasmops* Limestone of Norway, the *Macrourus* Limestone of Sweden, and the Wasalemm Beds (and possibly the Kegel) of Estonia. The Richmond is equivalent to the zone 15 (*Dicellograptus anceps* zone) of the British section.

EARLIEST CYSTOIDS

The oldest occurrence of unquestioned cystoids is Early Ordovician. In Arenig and lower Llanvirn strata in the Baltic region, cystoids belonging to the Glyptocystitida, Caryocystitida, Sphaeronitida, Asteroblastida, and Glyptosphaeritida have been found. Thus, within one epoch, all superfamilies of the Diploporita and half the superfamilies of the Rhombifera left a fossil record. Such diversity at this taxonomic level may be regarded as strong evidence for a long period of evolution antedating the Ordovician.

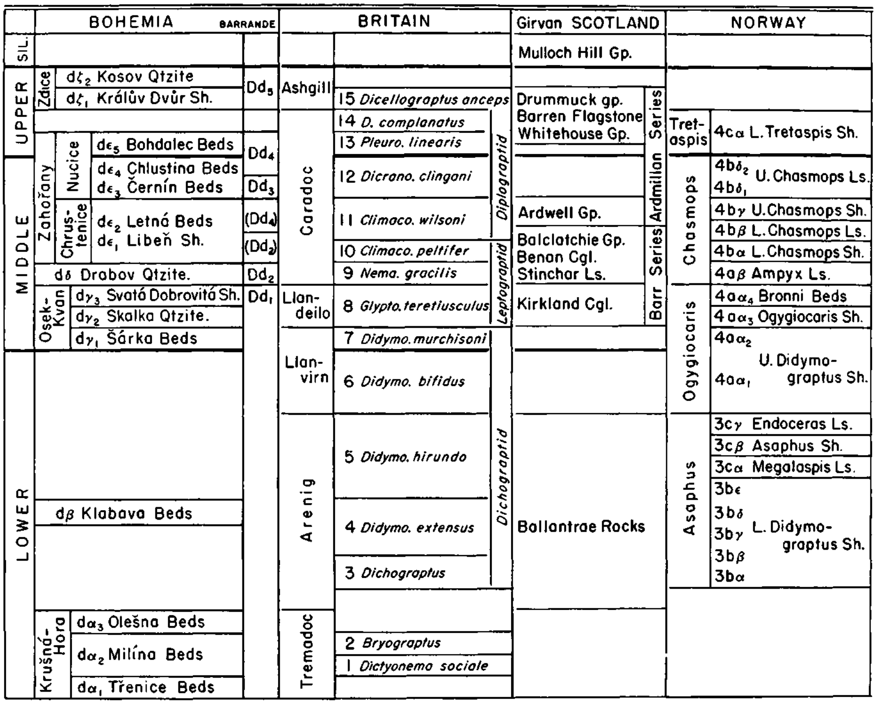


FIG. 53. Correlations of Ordovician formations in parts of Europe. Lower-Middle-Upper boundaries from THORSLUND (1960); other data from BOUČEK (1938), ÖPIK (1952), STØRMER (1953), REGNÉLL & HEDE (1960), and THORSLUND & JAANUSSON (1960).

Lowermost Ordovician outcrops in Bohemia, the Třenice Beds ($d\alpha_1$), contain *Paleosphaeronites*. These strata are early Tremadoc in age (Fig. 53).

Cheirocrinus holmi REGNÉLL is the oldest cystoid mentioned by REGNÉLL (101) in his excellent contribution, "An Outline of the Succession and Migration of Non-Crinoid Pelmatozoan Faunas in the Lower Paleozoic of Scandinavia." The only specimen of this species occurs in the *Planilimbata* Limestone of the Island of Öland, Sweden, correlated with the 3bα zone of Norway.

Some of the cystoids from the eastern Baltic region are only a little younger. ÖPIK (92) listed *Mesocystis pusirefskii* (HOFFMAN) and *Echinoencrinites angulosus* (PANDER) from the Estonian $B_{II}\gamma$ zone, about equivalent to the Norwegian 3cα *Megalaspis* Limestone. From the B_2 Volkhov (Walchow in older reports), the literature records the occurrence of *Asteroblastus sublaevis* JAEKEL, *A. volborthi* SCHMIDT, *Echinoencrinites interlaevigatus* (JAEKEL), and *Leptocystis gigantea* (LEUCHTENBERG); and listed as from either the Volkhov or Kunda (B_3) are *Asteroblastus stellatus* EICHWALD, *Echinoencrinites simplicatus* PHLEGER, *E. sphaeroidalis* PHLEGER, *Eutretocystis acutirostris* PHLEGER, *E. similis* PHLEGER, *Glyptosphaerites leuchtenbergi* (VOLBORTH), and *Heliocrinites echinoides* (LEUCHTENBERG). Although *Echinosphaerites*, so abundant in early Middle Ordovician strata, is generally stated to appear in the $C_1\beta$ of Estonia, *E. ellipticus* EICHWALD has been noted in the Estonian B_3 (BASSLER & MOODEY, 7). From strata of this age in Estonia and the Leningrad region, reported cystoids include *Erinocystis sculpta* JAEKEL, *E. volborthi* JAEKEL, *Heliocrinites radiatus* (EICHWALD), *Metasterocystis micropelta* JAEKEL, *Scoliocystis pumila* (EICHWALD), and *S. thersites* JAEKEL.

Elsewhere, *Sphaeronites pomum* (GYLLENHAAL) occurs in profusion in strata of the 3cβ zone in Norway. From equivalent beds in Sweden, REGNÉLL (99) described

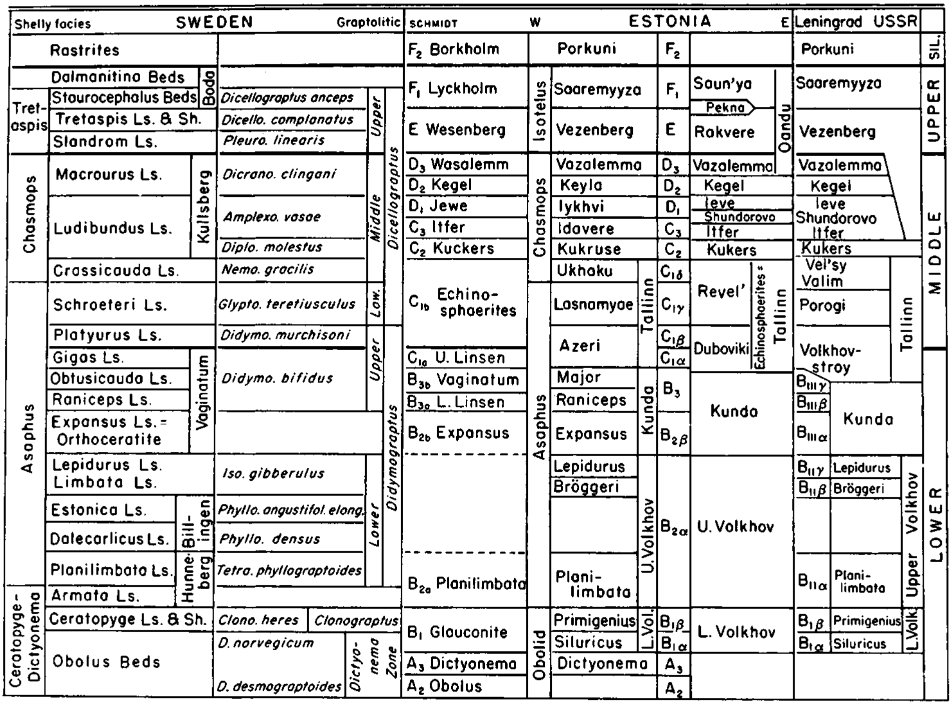


FIG. 53 *(Continued).*

Proctocystis monstruosa. The *Vaginatum* Limestone has yielded *Protocrinites fragum* (EICHWALD). *Glyptosphaerites ferrigenus* (BARRANDE) from Bohemia is said to be Lower Ordovician.

In brief summary, the following cystoids are considered to have lived during Early Ordovician time.

Lower Ordovician Cystoids

Order RHOMBIFERA
- Cheirocrinidae—*Leptocystis, Cheirocrinus.*
- Echinoencrinitidae — *Echinoencrinites, Erinocystis, Eutretocystis, Proctocystis, Scoliocystis.*
- Caryocystitidae—*Heliocrinites.*
- Echinosphaeritidae—*Echinosphaerites.*

Order DIPLOPORITA
- Glyptosphaeritidae—*Glyptosphaerites.*
- Protocrinitidae—*Protocrinites.*
- Asteroblastidae—*Asteroblastus, Asterocystis, Metasterocystis.*
- Mesocystidae—*Mesocystis.*

RHOMBIFERA

As can be readily seen in Table 1, the Rhombifera had a great taxonomic expansion in Middle Ordovician, with 11 of the 14 families recorded during that epoch. By gradual decline during the Late Ordovician, Silurian, and Early Devonian, the number of families dwindled until only one survived in Middle and Late Devonian time. Only three families appeared after the Middle Ordovician. It is interesting to note

TABLE 1. *Number of Families of Cystoidea Known in Each Epoch.*

[Doubtful records not included.]

Order	Ordovician			Silurian			Devonian			Total Known Families
	Early	Middle	Late	Early	Middle	Late	Early	Middle	Late	
Rhombifera	4	11	9	6	5	4	3	1	1	14
Diploporita	5	6	5	3	3	1	1	0	0	8
Total	9	17	14	9	8	5	4	1	1	22

TABLE 2. *Percent of Total Families of Cystoidea Known in Each Epoch.*
[Doubtful records not included.]

Order	Ordovician			Silurian			Devonian			Total Known Families
	Early	Middle	Late	Early	Middle	Late	Early	Middle	Late	
Rhombifera	18	50	41	27	23	18	13	5	5	64
Diploporita	23	27	23	14	13	5	5	0	0	36
Total	41	77	64	41	36	23	18	5	5	100

TABLE 3. *Number of Genera of Cystoidea Known in Each Epoch.*
[Doubtful records not included.]

Order	Ordovician			Silurian			Devonian			Total Known Genera
	Early	Middle	Late	Early	Middle	Late	Early	Middle	Late	
Rhombifera	9	19	14	5	8	9	8	2	1	51
Diploporita	8	21	8	2	5	1	4	0	0	35
Total	17	40	22	7	13	10	12	2	1	86

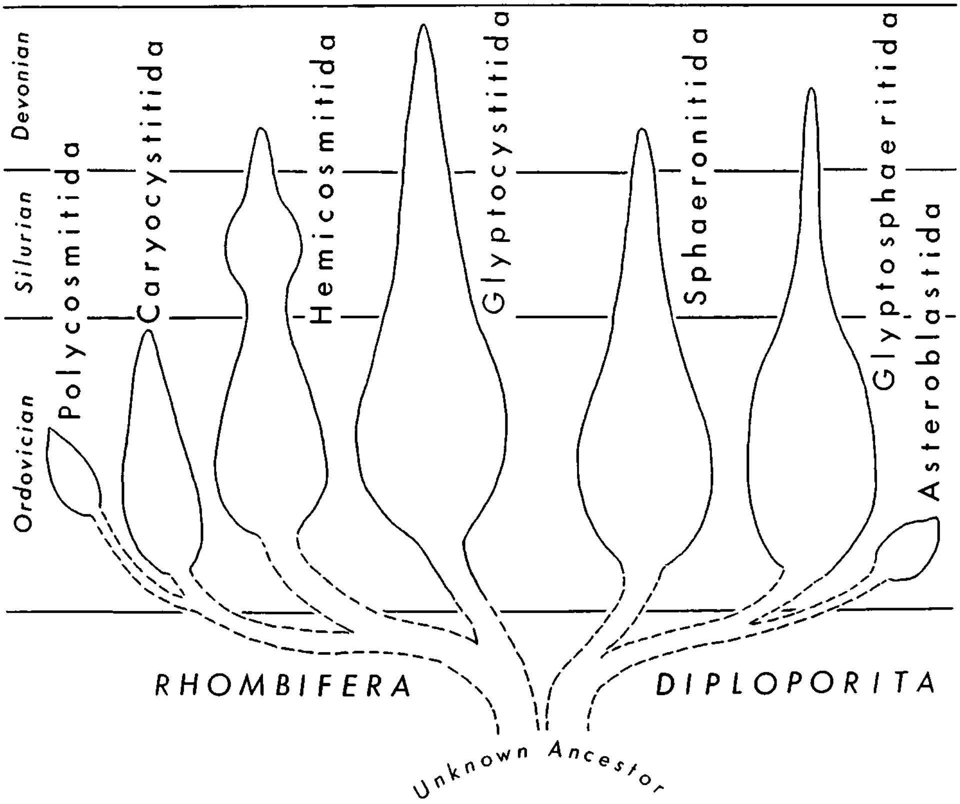


FIG. 54. Diagram representing stratigraphic distribution and inferred relationships of orders and superfamilies of Cystoidea (Kesling, n).

(Table 2) that half of all known cystoid families are represented among Middle Ordovician Rhombifera.

On a generic basis (Table 3), the Middle Ordovician expansion of cystoids and their subsequent decline are not so clearly portrayed, primarily because the family Callocystitidae, which attained its zenith in Late Silurian and Early Devonian time, has been divided into numerous genera. Another factor tending to distort the record is the paucity of good Early Silurian faunas.

Whereas the Cheirocrinidae is the oldest known family of undisputed Rhombifera, it may not necessarily be the ancestor of all the others. The recorded appearance of the families Echinoencrinitidae, Caryocystitidae, and Echinosphaeritidae from formations only slightly younger indicates familial divergence at a considerably remote time.

Within the Rhombifera, each of the superfamilies created its own pattern of stratigraphic distribution by diversity, abundance, decline, and extinction (Fig. 54). The relationship of one superfamily to another must be inferred. In the Polycosmitida, the pores perforating the thecal plates are inclined outward toward the suture separating the paired plates. Logically, one is led to suppose that tangential canals, if they existed in this taxon, were outside the preserved stereom and were covered by integument or perhaps by thin fragile epitheca that did not survive fossilization. By this arrangement, the Polycosmitida are closely allied to the Caryocystitida, lacking the preserved tangential canals and epitheca of the latter. The fossil record is too sketchy to determine when the Polycosmitida became a distinct entity. The superfamily has been recorded only from Middle Ordovician rocks. Specimens are rare. Each of the two families is represented only by the type genus, *Polycosmites* and *Stichocystis;* undoubtedly, numerous genera remain to be discovered.

CARYOCYSTITIDA

The Caryocystitida began in the Early Ordovician with *Heliocrinites* of the eastern Baltic region, and survived until the Late Ordovician (Fig. 55). Each of the two families has the same range, although the Echinosphaeritidae appeared later in Early Ordovician time than the Caryocystitidae.

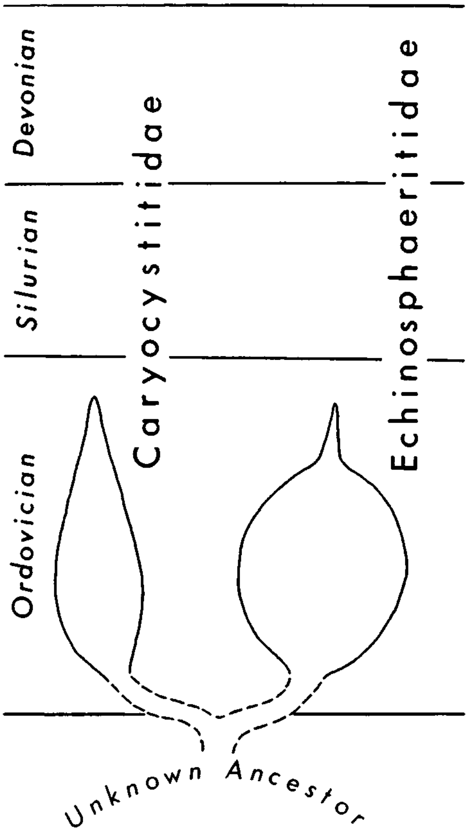


FIG. 55. Diagram representing stratigraphic distribution and inferred relationships of families of the Caryocystitida (Kesling, n).

Although relatively short-lived, this group of cystoids was widespread and abundant. *Echinosphaerites* is particularly prominent in lowermost Middle Ordovician deposits of the Baltic, being tightly packed in some strata of the $C_1\beta$ and $C_1\gamma$ zones and their equivalents. There is no reason to doubt that formations containing this cystoid in other parts of the world are about the same in age. *Heliocrinites* was also prolific, so that part of the C_2 Kukruse Beds of the East Baltic Provinces are crammed with *H. balticus* (EICHWALD). This species or closely related forms, or both, are found also in Sweden, Norway, and Britain in *Chasmops* and Caradoc beds.

HEMICOSMITIDA

The Hemicosmitida appear to be intermediate between the Glyptocystitida and

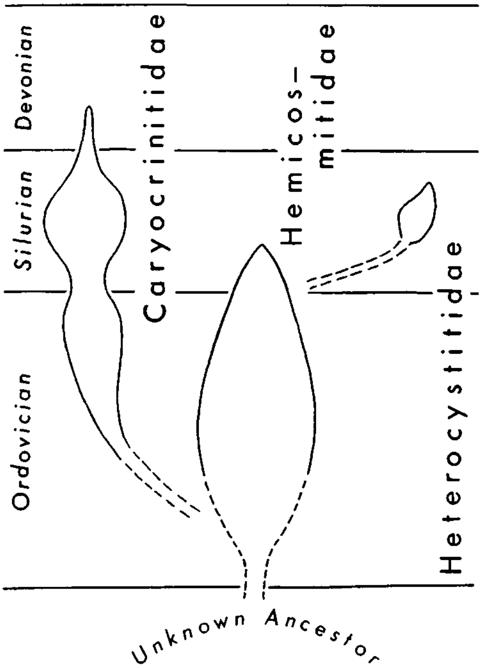


FIG. 56. Diagram representing stratigraphic distribution and inferred relationships of families of the Hemicosmitida (Kesling, n).

Hemicosmitida in development of thecal pores, which could be adequately described as having internal linkage of paired pores like the Glyptocystitida and a covering epithecal layer like the Caryocystitida. With respect to the regularity of the thecal plates, the Hemicosmitida stand closer to the Glyptocystitida. The superfamily ranges from Middle Ordovician to Early Devonian. Two significant expansions are indicated by the fossil record, each representing a success of one of the two larger families (Fig. 56). The Hemicosmitidae, notably the type genus, is present in considerable numbers and species in Middle Ordovician formations; the sudden culmination of the family after its oldest geologic record is taken to signify a long period of development for which no fossil evidence has been discovered. *Hemicosmites* survived until the Early Silurian. *Corylocrinus* is known from Late Ordovician rocks and *Tricosmites* from the Early Silurian, but neither genus is distinguished for abundance or diversity. The Caryocrinitidae attained their maximum during the Middle Silurian Epoch in North America. *Caryocrinites* is the longest-lived of the genera, from Middle Ordovician to Middle Silurian. *Juglandocrinus, Oocystis,* and *Ptychocosmites* are Upper Ordovician genera containing only a few species. *Stribalocystites* is very similar to *Caryocrinites,* originating in the Middle Silurian and continuing into Early Devonian, the last of the family. The Heterocystitidae appear to be taxonomically distinct, although based only on the Middle Silurian type genus, itself founded on one species represented by an incomplete specimen. This family is probably an offshoot from the Hemicosmitidae (Fig. 56).

GLYPTOCYSTITIDA

The Glyptocystitida are the rhombiferan superfamily containing the greatest number of genera. Partly this may be attributed to fortuitous collecting, but mostly it is the result of closer taxonomic discrimination, which is made possible by the standard number of their thecal plates and conspicuous differences in their ambulacra and pore rhombs. The superfamily began in Early Ordovician time, attained its zenith in the Middle and Late Ordovician, and included the last surviving cystoid in the Late Devonian. Of the seven families into which the Glyptocystitida have been divided (Fig. 57), the Callocystitidae contain 15 genera, Echinoencrinitidae eight, Cheirocrinidae and Pleurocystitidae three each, Cystoblastidae two, and Glyptocystitidae and Rhombiferidae one each. In Ordovician strata, seven genera are represented in the Lower, eight in the Middle, and six in the Upper; in Silurian strata, two are present in the Lower, five in the Middle, and eight in the Upper; and in Devonian rocks, seven genera are in the Lower, two in the Middle, and one in the Upper. This distribution of genera does not accurately reflect the importance of the superfamily during any selected epoch, for in two of the families large gaps are encountered in the record.

The Cheirocrinidae constitute such a closely knit group of cystoids that generic boundaries are discerned and fixed rather arbitrarily, without much significance. *Cheirocrinus,* the type and oldest member of Rhombifera, ranged from Early to Late Ordovician; *Homocystites,* with a more cos-

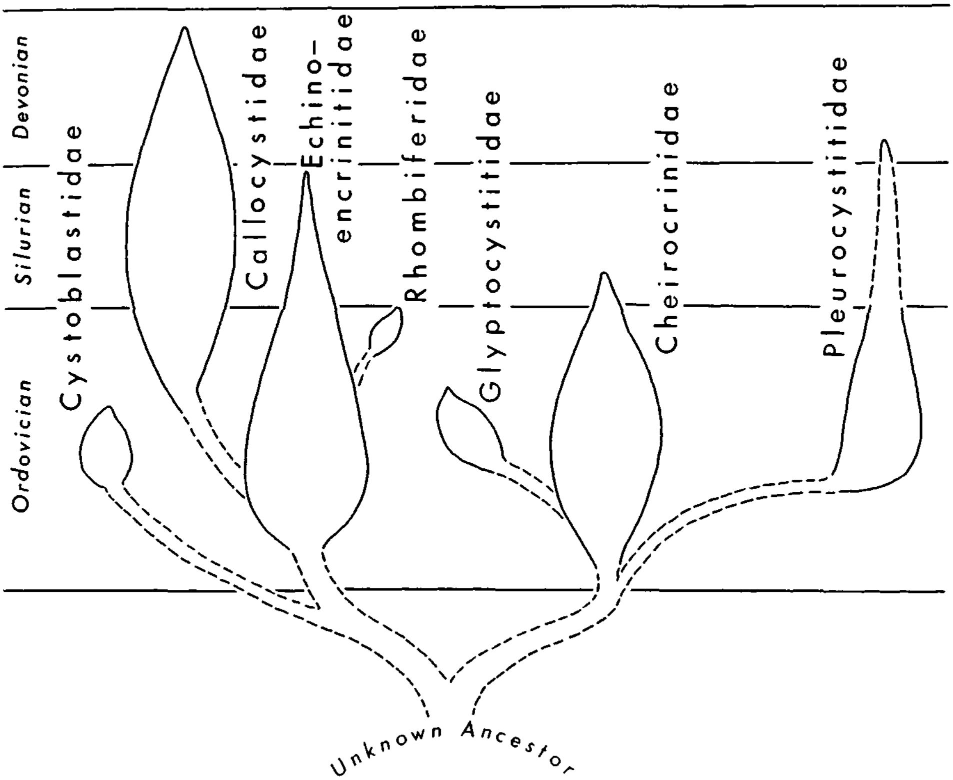


FIG. 57. Diagram representing stratigraphic distribution and inferred relationships of families of the Glyptocystitida (Kesling, n).

mopolitan distribution, was confined to the Middle Ordovician; and *Leptocystis* occurred in both Late Ordovician and Early Silurian time. The Echinoencrinitidae have a strange record—five genera are known in Lower Ordovician formations, one in Upper Ordovician, and two in Upper Silurian, yet not a single specimen has been found in Middle Ordovician, Lower Silurian, or Middle Silurian strata. From Lower Ordovician beds, *Echinoencrinites, Erinocystis, Eutretocystis, Proctocystis,* and *Scoliocystis* all seem to be well founded and distinct, although *Eutretocystis* may be an anomalous *Echinoencrinites.* At any rate, these genera all agree in having a rather small periproct, short ambulacra, ovate theca, large radials, and plates bordering the periproct that form a large protuberance serving to direct the opening outward and aborally. The last feature is not nearly so prominently developed in the Late Ordovician *Glaphyrocystis* or the Late Silurian *Prunocystites* and *Schizocystis,* but the other characters are present and no valid reason is seen to remove the three genera as a separate family. Should *Prunocystites* and *Schizocystis* be set apart from the Echinoencrinitidae, it would be most difficult to explain the derivation of these cystoids with short ambulacra from the only other Glyptocystitida that were their near contemporaries—the Callocystitidae, with very long ambulacra, or the Pleurocystitidae, with strongly compressed thecae and extremely large periprocts. Hence, the most satisfactory treatment is to maintain the Echinoencrinitidae as a family, despite the spotty log of its contained genera.

The Cheirocrinidae and Echinoencrinitidae (Fig. 57) are representative of the two major groups of families in the Glyptocystitida, those with large periprocts containing numerous small plates and those with small periprocts containing at most a small ring of plates around the anal pyra-

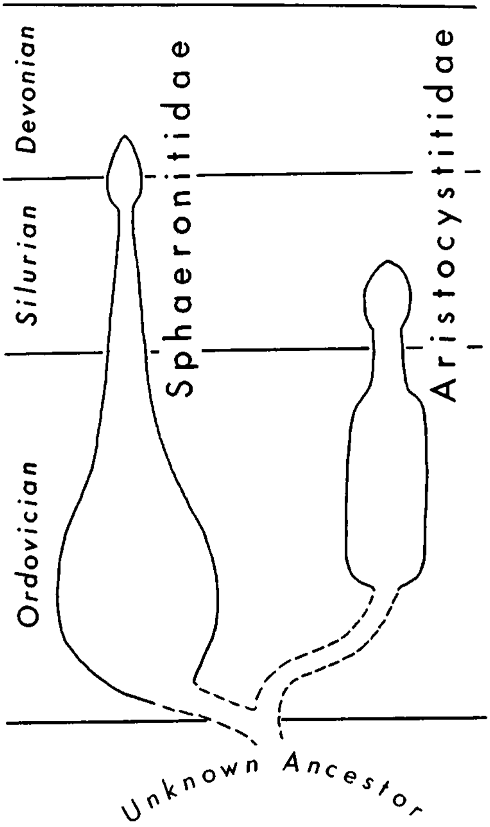


FIG. 58. Diagram representing stratigraphic distribution and inferred relationships of families of the Sphaeronitida (Kesling, n).

mid. Intermediate development of the periproct is unknown, so that divergence of the two groups evidently was accomplished prior to the geologic record of the superfamily. By Middle Ordovician time, the cheirocrinid stock gave rise to two other families, the short-lived Middle Ordovician Glyptocystitidae and the long-lived Pleurocystitidae, which continued into the Early Devonian. The Glyptocystitidae are known only from the type genus. The Pleurocystitidae, morphologically rather far removed from other cystoids, contain the well-known *Pleurocystites* (M.Ord.-U.Ord.), the enigmatic *Amecystis* (M.Ord.), and the surprising *Regulaecystis* (L.Dev.); not a single pleurocystitid has been discovered in Silurian deposits. The placement of *Regulaecystis* in the family, nevertheless, cannot reasonably be questioned.

In addition to the Echinoencrinitidae, the echinoencrinitid stock, characterized by small periprocts, seems to have produced the Cystoblastidae (M.Ord.), Rhombiferidae (U.Ord.), and Callocystitidae (U.Ord.-U. Dev.). The first two are rare from the standpoint of number of species, number of specimens known, and formations in which they occur. The Callocystitidae, on the other hand, are extensive and heterogeneous to such a degree that they are separated into three subfamilies. The Callocystitidae began, in so far as the record goes, with the Late Ordovician *Lepadocystis moorei* (MEEK), followed by the Early Silurian *Brockocystis*. The Middle Silurian is marked by the appearance of *Callocystites, Coelocystis, Hallicystis, Apiocystites,* and *Tetracystis,* of which the first three are limited to the Middle Silurian and the latter two endured until Early Devonian time. In the Late Silurian, four additional genera evolved: *Lovenicystis, Staurocystis, Lepocrinites,* and *Pseudocrinites.* In Europe none of these outlasted the epoch; in North America the last two are found in the Keyser and Coeymans Limestones, here included in Lower Devonian. These beds also yielded *Sphaerocystites* and *Jaekelocystis. Lipsanocystis* occurs in the Middle Devonian. *Strobilocystites* extends from the Middle Devonian Cedar Valley Limestone into the Upper Devonian Shell Rock Limestone of Iowa, and is the last known survivor of the cystoids. Whereas the subfamilies Callocystitinae and Staurocystinae have brief and uneventful histories, the subfamily Apiocystitinae displays some interesting trends in reduction of the number of pectinirhombs, loss of an ambulacrum, complexity of the hydropore, and shifting of the periproct.

DIPLOPORITA

The accepted Diploporita extend from Early Ordovician to Early Devonian. The Sphaeronitida and Glyptosphaeritida attained their maxima during the Middle Ordovician. The third superfamily, the Asteroblastida, is limited to Early Ordovician. In both symmetry and ambulacral development, the Asteroblastida stand closer to the Glyptosphaeritida than to the Sphaeronitida (Fig. 54).

TABLE 4. *Percent of Total Genera of Cystoidea Known in each Epoch.*

[Doubtful records not included.]

Order	Ordovician			Silurian			Devonian			Total Known Genera
	Early	Middle	Late	Early	Middle	Late	Early	Middle	Late	
Rhombifera	11	22	16	6	9	11	9	2	1	59
Diploporita	9	25	9	2	6	1	5	0	0	41
Total	20	47	25	8	15	12	14	2	1	100

Tables 1 and 2 portray the rise, culmination, gradual curtailment, and final disappearance of the Diploporita. The Middle Ordovician climax of the diploporitan cystoids was less spectacular than that of the Rhombifera at the same time, primarily because ephemeral little taxa have not been conceded the stature of families. This approach has much in its favor, inasmuch as discrete groups do not stand out among the genera now included. If more kinds of diploporitans should be discovered, it is likely that further divisions could be made on the basis of thecal symmetry, which is far advanced in *Tholocystis*, for example. The generic tabulation (Tables 3, 4) shows the Middle Ordovician diversification to advantage, but it also stresses the paucity of Silurian faunas. The Diploporita and Rhombifera seem to have classifications which progressed in comparable fashion, since the familial ratio of 36:64 is nearly the same as the generic ratio of 41:59 (Tables 2, 4).

SPHAERONITIDA

The Sphaeronitida (Fig. 58) contain the families Sphaeronitidae (L.Ord.-L.Dev.) and Aristocystitidae (M.Ord.-M.Sil.). Of the former, *Paleosphaeronites* and *Sphaeronites* lived during the Early Ordovician; of the two, *Sphaeronites* became very prolific at certain times; it did not die out until Late Ordovician. *Archegocystis, Codiacystis,* and *Tholocystis,* established for a very modest number of specimens, are confined to the Middle Ordovician. *Haplosphaeronis* and *Eucystis* occur in Middle and Upper Ordovician rocks, and the latter is also found in Lower Devonian beds. Strangely, no genera are known from Lower or Upper Silurian strata, and the only Silurian member with a fossil record is *Allocystites,* poorly represented, from the Middle Silurian. In Early Devonian time, a final proliferation occurred before the Sphaeronitidae became extinct. *Carpocystites, Proteocystites,* and *Bulbocystis* have been described from Lower Devonian beds, although some authors consider them to resemble the contemporary *Eucystis* so closely as to be merely junior synonyms.

The Aristocystitidae (Fig. 58) comprise a potpourri of genera unequivocally disparate except for their abridged ambulacra. Many genera are poorly understood and more refined taxonomy must await the finding of better specimens. At this time, the phylogeny of these cystoids is obscure. Nine genera have been recorded from Middle Ordovician formations, of which only one *(Calix)* extends into the Upper Ordovician. In addition to this genus, *Campylostoma* and *Holocystites* occur in the Late Ordovician, the latter generating numerous species in the Middle Silurian. *Trematocystis* is the only other genus known in Middle Silurian strata.

GLYPTOSPHAERITIDA

The Glyptosphaeritida are essentially an Ordovician superfamily (Fig. 54). Three of the families (Fig. 59) are restricted to this period and the other lasted until at least Middle Silurian time. Probably, the oldest of the Glyptosphaeritida is *Glyptosphaerites leuchtenbergi* (VOLBORTH), reported from B_2 or B_3 rocks of the Baltic region. This type and only genus of the family Glyptosphaeritidae has good representation, so that the family is prominent, despite its being monogeneric. It lived until Late Ordovician time. The Protocrinitidae, allied to the Glyptosphaeritidae by weak symmetry and possession of interambulacral diplopores, range from Early to Middle Ordovician. In Middle Ordovician deposits the type genus was joined by *Eumorpho-*

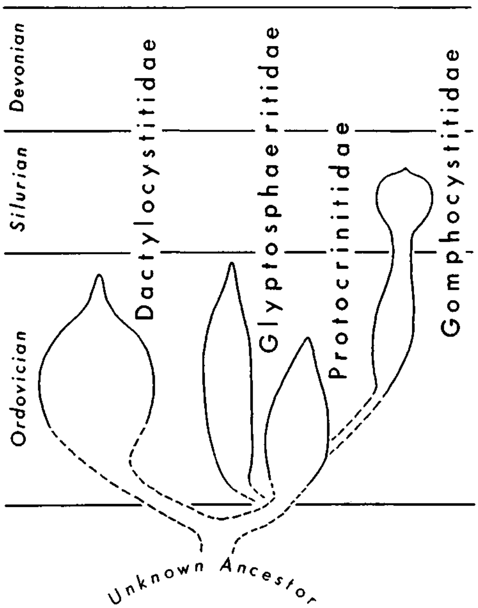


FIG. 59. Diagram representing stratigraphic distribution and inferred relationships of families of the Glyptosphaeritida (Kesling, n).

cystis, Fungocystites, and *Regnellicystis.* Examples of these three genera are rare. The Gomphocystitidae, also related to the Glyptosphaeritidae more closely than to the Dactylocystidae, have an interrupted record. No cystoids of the family have been found between the Middle Ordovician *Pyrocystites* and the Middle Silurian *Gomphocystites.* The questioned species *G. californicus* was described by STAUFFER (1930) from the Kennett Formation at Kearsarge, California. The age is no longer regarded as Middle Devonian, but instead as Middle Silurian.

The Dactylocystidae, with advanced symmetry and restriction of thecal pores to the adambulacrals, stand apart from other families of the Glyptosphaeritida (Fig. 59). The assemblage includes *Dactylocystis* and *Estonocystis* of Middle Ordovician age, and *Revalocystis,* of the Late Ordovician. Although this family excites considerable interest in its resemblance to echinoids, it is not known from many examples.

ASTEROBLASTIDA

The Asteroblastida flourished and withered within the Early Ordovician (Fig. 54). They exhibit stronger resemblances to the Glyptosphaeritida than to the Sphaeronitida, particularly in the well-developed ambulacra and clear pentameral symmetry, but no forms are known to have thecal organization intermediate between the Asteroblastida and the Glyptocystitida. Hence, phylogenetic division occurred prior to deposition of the $\mathrm{B_{II}}\gamma$ zone, which contains the oldest of the Asteroblastida, *Mesocystis pusirefsķii* (HOFFMAN). The superfamily has been much discussed as a possible ancestral stock of the blastoids, but no form morphologically closer to the latter has been discovered than *Asteroblastus.* The two families, Asteroblastidae (with *Asteroblastus, Asterocystis,* and *Metasterocystis*) and the Mesocystidae (with *Mesocystis*) are distinctive, even though their existence was brief. If the stratigraphic determination of TERMIER & TERMIER (126) is correct, fragments identified as *Asteroblastus* occur in Llandeilo strata of Morocco.

GEOGRAPHIC DISTRIBUTION

MODE OF DISPERSAL

As reasoned by REGNÉLL (104), adult cystoids were capable of very little moving about from one place to another. They were sedentary or sluggish bottom-dwellers. Before they settled down to become benthonic, however, the larvae were free to invade wide areas. Extension of a cystoid species into new places appears to have been accomplished by larval migration or transport. If cystoid larvae could survive for as long as crinoid larvae, that is, from two to 12 days, then widespread areas could potentially be populated in a few generations.

The paleontological record, admittedly fragmentary and probably inaccurate, reveals only one species, *Echinosphaerites aurantium,* that achieved intercontinental distribution. On the other hand, several genera are known to be widespread, and most families occur on more than one continent. From this, one is led to believe that dispersal was, on the whole, a very slow process, or that the larvae could survive only under restricted conditions. Conceivably, both factors may have operated to keep populations localized, except for very hardy species. What limitations were imposed genetically and what were at-

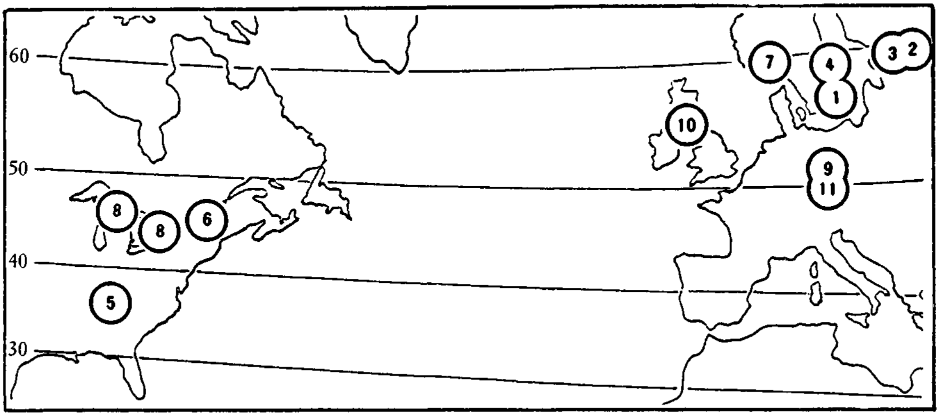


FIG. 60. Sequence and geographic distribution of cystoids of the family Cheirocrinidae.——*1. Cheirocrinus holmi,* L.Ord.*(Planilimbata),* Sweden(Öland).——*2. Leptocystis gigantea, Homocystites* spp., L.Ord. (B_2-B_3), USSR(Leningrad region).——*3. Cheirocrinus radiatus, C. ornatus,* etc., L.Ord.-U.Ord., Eu. (Est).——*4. Cheirocrinus leuchtenbergi,* L.Ord.(*Expansus* beds), Sweden(Sodermanland).——*5. Homocystites angulatus,* M.Ord.(Chazy.), USA(Tenn.).——*6. Homocystites forbesi,* M.Ord.(Crown Point-Aylmer), USA(N.Y.)-Can.(Que.).——*7. Cheirocrinus nodosus,* M.Ord.*(Ogygiocaris* beds), Norway.——*8. Homocystites anatiformis, H. walcotti,* M.Ord.(Trenton), USA(N.Y.-Mich.)-Can.(Ont.).——*9. Homocystites alter,* M.Ord.(Dd_4), Eu.(Czech.).——*10. Leptocystis constricta,* U.Ord.(Craighead), Scot.——*11. Leptocystis tertia,* L.Sil.(E_1-E_2), Bohemia (Kesling, n).

tributable to ecology are matters for conjecture.

RHOMBIFERA

Because the ancestry of the order Rhombifera cannot be established, each of the superfamilies must of necessity be considered separately. The selection of the very ancient cystoid, *Cheirocrinus holmi,* from Norway, as typical of the ancestral stock would be a presumption.

GLYPTOCYSTITIDA

Within the superfamily Glyptocystitida, more than one interchange between Europe and North America seems to have occurred. The **Cheirocrinidae** appeared in Early Ordovician time in Europe, where they continued until the Early Silurian. During the earliest part of Middle Ordovician time, the first cheirocrinid reached North America, where members of the family lived only through the remainder of the epoch. Another emigration from one continent to the other took place in the **Cystoblastidae,** but correlations are not accurate enough to determine whether *Cystoblastus* of Europe or *Hesperocystis* of North America is the older.

The **Pleurocystitidae** presumably developed from cheirocrinid ancestors. The oldest of the family, however, seems to be a species of *Pleurocystites* from China, where no cheirocrinids are known. The Pleurocystitidae flourished in North America during late Middle Ordovician time, and spread to Europe during the Late Ordovician. Although no post-Ordovician pleurocystitids have been discovered in North America, the family survived in Europe until the Early Devonian.

A definite migration from North America to Europe involved the **Callocystitidae,** which evolved in North America during Late Ordovician time from unknown ancestors and thrived to become the last of the cystoids in the Late Devonian. During the Late Silurian one genus traveled from America to Europe, and during the Early Devonian another came from Europe to America. Of the other three families of the Glyptocystitida, the Echinoencrinitidae and Rhombiferidae did not escape from Europe, nor the Glyptocystitidae from North America.

Within families, the cystoids appear to have had strong geographic preferences at certain times. The **Cheirocrinidae** furnish

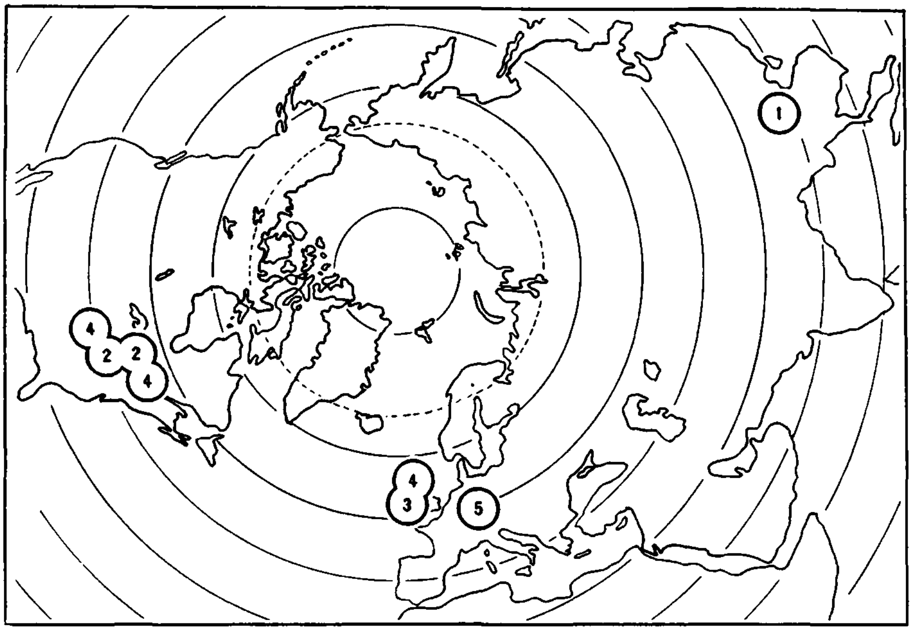


FIG. 61. Sequence and geographic distribution of cystoids of the family Pleurocystitidae.——*1. Pleurocystites bassleri,* M.Ord., China.——*2. P. elegans, P. filitextus, P. squamosus,* etc., *Amecystis,* M.Ord. (Trenton.), Can.(Que.-Ont.)-USA(Wis.-Minn.-Mich.-Ky.-N.Y.).——*3. P. anglicus, P. rugeri,* M.Ord. (Caradoc), Eu.(Eire-Wales).——*4. P. anticostiensis, P. beckeri, P. foriolus, P. gibbus,* etc., U.Ord. (Richmond.-Maquoketa-Craighead), Can.(Anticosti I.)-USA(Iowa)-Eu.(Scot.).——*5. Regulaecystis pleurocystoides,* L.Dev.. Eu.(Ger.) (Kesling, n).

good examples (Fig. 60). *Cheirocrinus* was restricted to the Baltic region. The oldest species are from Norway: *C. holmi* REGNÉLL (3bα) and *C. hyperboreus* REGNÉLL (3cβ). During Early Ordovician (B_3) time, the genus extended to western Russia in Estonia and the Leningrad region, *C. radiatus* (JAEKEL), *C. ornatus* EICHWALD, and *C. volborthi* (SCHMIDT). Estonia remained a favorable locale during the Middle and Late Ordovician, with *C. granulatus* (JAEKEL) (C_2) and *C. penniger* (EICHWALD) (E). The report by BATHER (12) of *C. interruptus* in Upper Ordovician deposits of Scotland raises doubt about the B_2 or B_3 occurrence in Russia reported by BASSLER & MOODEY (7), from what source cannot be learned; at any rate, it poses a longevity of this species inconsistent with those known for other cystoids, incredibly long. Other occurrences of *Cheirocrinus* are in Sweden, *C. leuchtenbergi* (ANGELIN) (the Lower Ordovician *Expansus* Limestone), in Norway, *C. nodosus* (JAEKEL) (the Middle Ordovician *Ogygiocaris* Shale), and in Belgium, *C. dilatus* REGNÉLL (the Upper Ordovician Fosse Shales).

Another cheirocrinid genus, *Homocystites,* began in the Leningrad region, where *H. sculptus* (SCHMIDT), *H. degener* (JAEKEL), and *H. striatus* (JAEKEL) occur in the Lower Ordovician B_3 Kunda Formation. Early in the following epoch, *Homocystites* came to America as *H. angulatus* (WOOD), found in the Chazyan of Tennessee. Other cheirocrinids, all of this genus, evolved during the Middle Ordovician in North America: *H. forbesi* (BILLINGS) in the Aylmer Formation of Quebec and the Crown Point Limestone of New York, *H. anatiformis* (HALL) in the Trenton of New York, and *H. walcotti* (JAEKEL) in the Trenton limestones of Ontario and Michigan. The last of *Homocystites* is the rather isolated occurrence of *H. alter* BARRANDE in the Dd_4 of Bohemia.

The last cheirocrinid genus, *Leptocystis,* migrated about Europe. The oldest species are reported from the Leningrad region in Early Ordovician formations, *L. gigantea* (Leuchtenberg) (B_2) and *L. atava* (Jaekel) (B_3). The next appearance of *Leptocystis* is in Scotland, *L. constricta* (Bather) in the Upper Ordovician Craighead Limestone. The final species is the type, *L. tertia* Barrande, in the Lower Silurian E_1 and E_2 of Bohemia.

All of the **Echinoencrinitidae** are European. The early history centers around western Russia and the late history around England. Many species have been described from Lower Ordovician beds in Estonia and the Leningrad region, from $B_{II}\gamma$, *Echinoencrinites angulosus* Pander; from B_2, *E. interlaevigatus* (Jaekel); from B_2 or B_3, *E. fenestratus* (Leuchtenberg), *E. simplicatus* Phleger, *E. sphaeroidalis* Phleger, *Eutretocystis acutirostris* Phleger, and *E. similis* Phleger; and from B_3, *Echinoencrinites angulosus comptus* (Jaekel), *E. angulosus quadratus* (Jaekel), *E. laevigatus* Jaekel, *E. lahuseni* Jaekel, *E. reticulatus* Jaekel, *E. striatus* Pander, *E. senckenbergii* Meyer, *Erinocystis angulata* Jaekel, *E. sculpta* Jaekel, *E. volborthi* Jaekel, *Scoliocystis thersites* Jaekel, and *S. pumila* (Eichwald). Other Early Ordovician echinoencrinitids include *Echinoencrinites senckenbergi acutangulus* Regnéll and *Erinocystis broggeri* Regnéll, from the Oslo region (3cβ), *Proctocystis monstruosa* Regnéll, from Sweden (*Expansus* Limestone), and *P. rossica* Regnéll, from Russia.

Glaphyrocystis occurs only in Estonia, *G. woehrmanni* Jaekel and *G. compressa* Jaekel, both being restricted to Upper Ordovician F_1. All Late Silurian echinoencrinitids are from England, in the Dudley Limestone: *Prunocystites baccatus* (Forbes), *P. fletcheri* Forbes, and *Schizocystis armata* Forbes.

The **Glyptocystitidae** are all North American, the five species of *Glyptocystites* occurring in Trenton rocks of Ontario, Quebec, and Michigan. The **Rhombiferidae** include only *Rhombifera bohemica* Barrande from Bohemia. No close relatives of the two families have been recognized.

The **Pleurocystitidae** (Fig. 61) may have begun with *Pleurocystites bassleri* Sun from the early Middle Ordovician of China; Regnéll (104) referred to it as "a somewhat doubtful species." Oklahoma has yielded *P. watkinsi* Strimple from the Middle Ordovician Bromide Formation. In late Middle Ordovician time in North America, *Pleurocystites* proliferated into numerous species recorded from Ontario, Quebec, Wisconsin, Minnesota, Michigan, Kentucky, and New York: *P. elegans* Billings, *P. exornatus* Billings, *P. filitextus* Billings, *P. squamosus* Billings, *P. robustus* Billings, *P. matutinus* (Ruedemann), and *P. mercerensis* Miller & Gurley. The genus continued to thrive on this continent in the Late Ordovician, with *P. anticostiensis* Billings, recorded on Anticosti Island and *P. beckeri* Foerste, *P. clermontensis* Foerste, *P. slocomi* Foerste, and *P. multistriatus* Ulrich & Kirk, from Iowa. The first emigrants to Europe were *P. anglicus* Jaekel, of Ireland, and *P. rugeri* Salter, of Wales, found in Caradoc strata. The species from the Craighead Limestone in Scotland were described by Bather (12), *P. foriolus, P. gibbus, P. procerus,* and *P. quadratus.* With these Late Ordovician species, *Pleurocystites* came to an end. The unique and perplexing *Amecystis laevis* (Raymond) occurs in Ontario and Michigan in the late Middle Ordovician Trenton rocks, with unknown ancestors or descendants. With no known Silurian forms, *Regulaecystis pleurocystoides* Dehm, from the Lower Devonian Hunsrück Slates, near Bundenbach, Germany, was unexpected, but insofar as known, closed the record of the family.

The **Cystoblastidae** include *Cystoblastus leuchtenbergi* Volborth from the Leningrad region (C_1), *C. kokeni* Jaekel, from Estonia (C_2), and *Hesperocystis deckeri* Sinclair, from Oklahoma (Bromide Formation, upper Chazy and lower Black River). Whether the American or Russian occurrences are earlier is open to question.

In the **Callocystitidae** (Fig. 62), the subfamily Apiocystitinae commence registry with *Lepadocystis moorei* (Meek), from Ohio and Indiana, in the Upper Ordovician Richmond beds. North America remained the stronghold of the subfamily until its extinction. The Early Silurian *Brockocystis* is known by *B. nodosaria* Foerste, from Ohio, and *B. huronensis* (Billings) and *B. tecumsethi* (Billings), from Ontario. *Hallicystis imago* (Hall) occurs in Wisconsin, Illinois, and Ohio in Middle Silurian Ni-

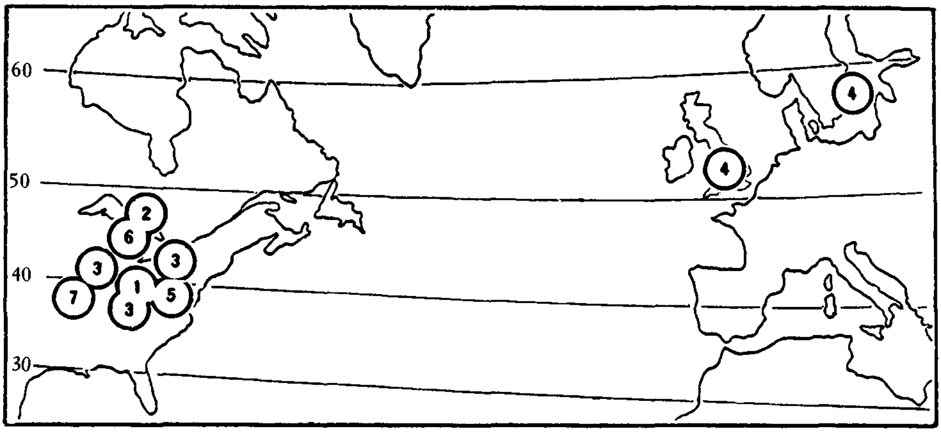


FIG. 62. Sequence and geographic distribution of cystoids of the family Callocystitidae. ——*1. Lepadocystis,* U.Ord., USA(Ind.-Ohio).——*2. Brockocystis,* L.Sil., Can.(Ont.)-USA(Ohio).——*3. Apiocystites, Hallicystis, Tetracystis,* M.Sil.(Niagaran), Can.(Ont.)-USA(N.Y.-Wis.-Ill.-Tenn.).——*4. Apiocystites, Lovenicystis, Lepocrinites,* U.Sil., Eu.(Gotl.-Eng.).——*5. Jaekelocystis, Leptocrinites, Tetracystis,* L.Dev., USA (W.Va.-Md.).——*6. Lipsanocystis,* M.Dev., USA(Mich.).——*7. Strobilocystites,* M.Dev.-U.Dev., USA (Iowa) (Kesling, n).

agaran strata. Other Niagaran cystoids of the subfamily are *Apiocystites elegans* HALL, from New York and Ontario, and *Tetracystis fenestratus* (TROOST), from Tennessee. Early Devonian species include *Apiocystites anna* SAFFORD, from Tennessee, *Lepocrinites gebhardii* CONRAD, from New York, Maryland, and Virginia, and several species described by SCHUCHERT from West Virginia and Maryland: *Tetracystis chrysalis, Lepocrinites manlius, Jaekelocystis avellana, J. hartleyi,* and *J. papillata.* Michigan was the homeland of all described species of the Middle Devonian genus *Lipsanocystis.* In Iowa, *Strobilocystites calvini* WHITE, *S. polleyi* CALVIN, and *S. schucherti* THOMAS are reported from the upper Middle Devonian Cedar Valley Limestone, and the last-named species extends into the lower Upper Devonian Shell Rock Limestone. In Late Silurian time, the Apiocystitinae reached to Europe, with *Apiocystites pentrematoides* FORBES and *Lepocrinites oblongus* (FORBES), in England, and *Lovenicystis angelini* (JAEKEL), in Sweden. The invading stock did not become firmly entrenched, and no later European species have been found.

The subfamily Callocystitinae did not migrate beyond North America. *Callocystites canadensis* BILLINGS and *C. jewetti* (HALL) resided in New York and Ontario and *C. jewetti elongatus* FOERSTE in Ohio during the Middle Silurian. The contemporaneous *Coelocystis subglobosa* (HALL) was in Wisconsin, Illinois, and Ohio. Species of *Sphaerocystites* are limited to the Lower Devonian Keyser Formation, and are found in Pennsylvania, West Virginia, and Maryland.

The subfamily Staurocystinae reversed the route of the Apiocystitinae, developing first in Europe and emigrating to North America. In England, the Upper Silurian Dudley Limestone contains *Staurocystis quadrifasciata* (PEARCE), *Pseudocrinites bifasciatus* PEARCE, and *P. magnificus* FORBES. *Staurocystis* seems to have produced no more species; but *Pseudocrinites* reached its climax in North America during the Early Devonian, with seven species described by SCHUCHERT from the Keyser Formation in Pennsylvania, West Virginia, and Maryland.

The pattern of migrations is a little enigmatic. During Late Silurian time, England was receiving immigrants of the Apiocystitinae from North America at about the same time that it was dispatching emigrants of the Staurocystinae to North America. If currents were responsible for the spread of

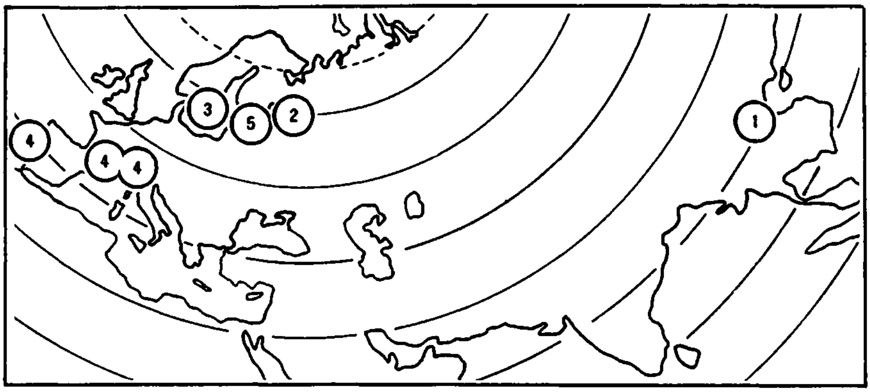


FIG. 63. Sequence and geographic distribution of cystoids of the family Hemicosmitidae.——*1. Hemicosmites jaekeli,* M.Ord., China.——*2. H. malum, H. oblongus,* M.Ord. ($C_1\beta$), Eu.(Baltic).——*3. H. oelandicus,* M.Ord.(L.*Chasmops*), Sweden.——*4. Corylocrinus elongatus, C. occidentalis, C. carnicus,* U. Ord., Eu.(Fr.-Port.-Carnic Alps).——*5. H. grandis, Tricosmites tricornis,* L.Sil.(F_2), Eu.(Est.) (Kesling, n).

cystoids, there was ample time in this epoch, of course, for reversals of direction.

HEMICOSMITIDA

The superfamily Hemicosmitida was dispersed throughout the northern hemisphere. In the **Hemicosmitidae** (Fig. 63), the genus *Hemicosmites* probably began in the Orient. The oldest described species may be *H. jaekeli* SUN, from China; nevertheless, it was nearly contemporaneous with some Baltic species, *H. malum* (PANDER) ($C_1\beta$) and *H. laevior* JAEKEL and *H. oblongus* (PANDER) (reported only as C_1). The last-named species has also been recorded from Wales. The exact age of *H. squamosus* FORBES, from Wales, has not been stated. *H. oelandicus* REGNÉLL occurs in Sweden in Lower *Chasmops* strata. Numerous species come from Estonia, including *H. altus* JAEKEL, *H. pulcherrimus* JAEKEL, and *H. pocillus* JAEKEL (D_1), *H. porosus* EICHWALD and *H. rudis* JAEKEL (D_3), *H. verrucosus* EICHWALD (F_1), and *H. grandis* JAEKEL (Lower Silurian, F_2), the youngest species found. *H. extraneus* EICHWALD has been discovered in Estonia and Russia (D_1 or D_3) and in Sweden (Kullsberg Limestone). The other two genera included in the Hemicosmitidae are restricted to Europe. *Corylocrinus* is represented in Upper Ordovician deposits of Russia, *C. olli* YAKOVLEV; France, *C. elongatus* JAEKEL and *C. europaeus* (QUENSTEDT); Portugal, *C. occidentalis* JAEKEL; and the Carnic Alps, *C. carnicus* BATHER. *Tricosmites* contains only the type species, *T. tricornis* (JAEKEL), from Estonia, where it occurs in the F_2 Borkholm Limestone with *Hemicosmites grandis* JAEKEL.

The second family of Hemicosmitida, the **Caryocrinitidae**, also seems to have originated in the Far East (Fig. 64). From the lower Middle Ordovician Naungkangyi Beds of northern Burma BATHER (11) described *Caryocrinites aurorus, C. avellanus,* and *C. turbo.* The Late Ordovician *C. septentrionalis* REGNÉLL is from Sweden. Other named species are all from Middle Silurian strata and, with one exception, from North America. Niagaran rocks of east-central United States and adjacent areas of Canada have yielded *C. milliganae* (MILLER & GURLEY), *C. gorbyi* (MILLER & GURLEY), and *C. indianensis* (MILLER), from Indiana; *C. persculptus* SPRINGER and *C. globosus* TROOST, from Tennessee; *C. missouriensis* (ROWLEY), from Missouri; and *C. ornatus* SAY, from Ontario, New York, Indiana, Iowa, and Wisconsin. The only other species known is from France, *C. ornatus europaeus* (QUENSTEDT). *Stribalocystites,* closely related to *Caryocrinites,* is exclusively North American. Middle Silurian species include *S. sphaeroidalis* (MILLER & GURLEY) and *S. tumidus* (MILLER), from Indiana, *S. bulbulus* (MILLER & GURLEY), from Tennessee, and *S. kentuckiensis* (MIL-

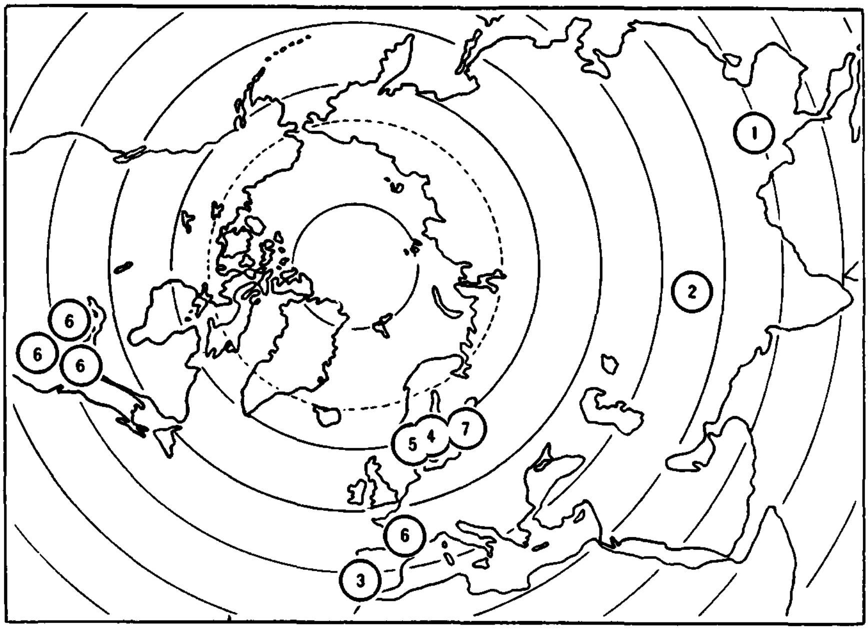


FIG. 64. Sequence and geographic distribution of cystoids of the genus *Caryocrinites.*——*1. C. aurorus, C. avellanus,* M.Ord.(Naugkangyi beds), Burma.——*2. C.* sp., M.Ord., Asia(Karakorum).——*3. C.* sp., M.Ord.(Llandeilo or Caradoc), Eu.(Port.).——*4. C. septentrionalis,* U.Ord., Sweden(Dalarna).——*5. C.* sp., L.Sil. (5b), Norway(Oslo).——*6. C. ornatus, C. milliganae, C. persculptus, C. ornatus europaeus,* M.Sil., Can.(Ont.)-USA(N.Y.-Ind.-Iowa-Wis.)-Eu.(Fr.).——*7. "C. ornatus"* of SCHMIDT (1858), U.Sil. (Wenlock, L.Oesel or Jaani beds), Eu.(Est.) (Kesling, n).

LER & GURLEY), from Kentucky. The last of the family is the Early Devonian *S. elongatus* (ROWLEY), from Missouri.

During the Late Ordovician, the Caryocrinitidae produced three short-lived genera, restricted stratigraphically to the epoch and geographically to western Europe. *Juglandocrinus crassus* KOENEN, *Oocystis major* DREYFUSS, and *O. vulgaris* DREYFUSS come from France; *Oocystis rugata* (FORBES), from Wales and England; and *Ptychocosmites sardinicus* JAEKEL, from Sardinia.

The family **Heterocystitidae** rests only on *Heterocystites armatus* HALL, from Niagaran rocks of New York.

POLYCOSMITIDA

In the superfamily Polycosmitida, only two species are involved, each the type of a genus that is type of a family. Both are Middle Ordovician, *Polycosmites bohemicus* JAEKEL, from Bohemia, and *Stichocystis geometrica* (ANGELIN), from Scandinavia and from drift in Germany. SUN (123) reported *Stichocystis* from China, as *S. geometrica* or a very similar species. The Chinese specimens are earliest Middle Ordovician, whereas the European are latest Middle Ordovician, supporting REGNÉLL'S (1948) contention that the genus migrated westward.

CARYOCYSTITIDA

The superfamily Caryocystitida achieved widespread distribution. The **Caryocystitidae** inhabited Asia and Europe. As recorded (Fig. 65), *Heliocrinites* began as *H. echinoides* (LEUCHTENBERG) in Russia (B_2). This species was followed by *H. radiatus* (EICHWALD) in Estonia and the Leningrad region (B_3). *H. granatum* (WAHLENBERG) from Sweden is said to be in the *"Orthoceras"* Limestone, presumably used in the broad sense for Lower and Middle Ordovician limestones. Early Middle Ordovician occurrences in the Orient are *H. fiscellus* (BATHER), *H. qualus* (BATHER), and *H. rugatus* (BATHER), in Burma, *H. subovalis*

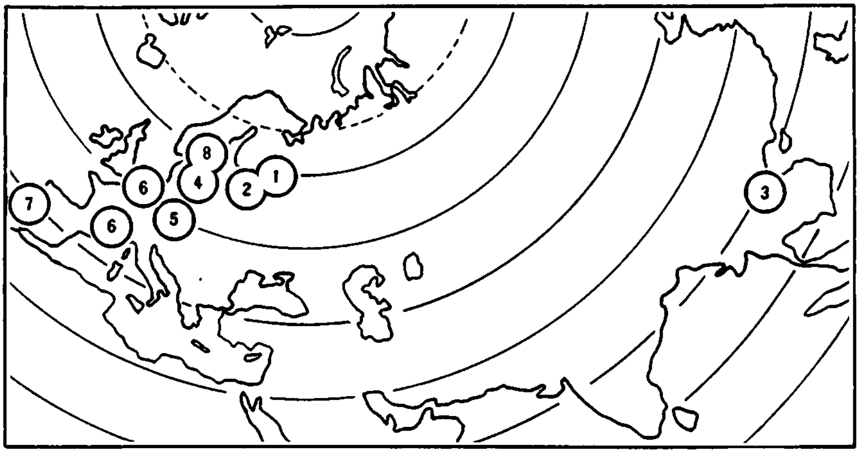


Fig. 65. Sequence and geographic distribution of cystoids of the genus *Heliocrinites.*——*1. H. echinoides,* L.Ord.(B$_2$), USSR(Leningrad region).——*2. H. radiatus,* L.Ord. (B$_3$), Eu.(Est.-Leningrad region).——*3.* H. *fiscellus, H. qualus, H. kweichouensis,* M.Ord., Burma-China(Yunnan-Kweichou).——*4. H. granatum, H. augustiporus, H. ovalis,* M.Ord.(L.*Chasmops,*) Sweden(Scania-Östergötl.-Jamtl.).——*5. H. confortatus,* M.Ord.-U.Ord.(Dd$_4$-Dd$_5$), Eu.(Czech.).——*6. H. rouvillei, H. malaisei,* U.Ord., Eu.(Fr.-Belg.).——*7. H. burdigalensis,* U.Ord., Eu.(Port.-Spain).——*8. H. stellatus, H. variabilis,* U.Ord., Sweden (Dalarna) (Kesling, n).

(Reed), in Yunnan, China, and *H. kweichouensis* (Sun), at Kweichou, China. At about the same time, the genus appeared in Estonia as *H. araneus* (von Schlotheim) in Estonia and Sweden (C$_1$) and *H. balticus* (Eichwald) in Estonia and Wales (C$_2$). The age of *H. ovum* (von Schlotheim) from near Reval, Estonia, is not given, but may be presumed to be about C$_1$. In Sweden, several species occur in the *Chasmops* series, *H. granatum* (Wahlenberg), *H. guttaeformis* Regnéll, *H. ovalis* (Angelin), *H. prominens* (Angelin), and *H. tenuistriatus* (Angelin). During the Late Ordovician, *Heliocrinites* continued in Sweden as *H. stellatus* Regnéll and *H. variabilis* Regnéll, and spread southward to Thuringia and Bohemia as *H. confortatus* (Barrande), to Belgium as *H. malaisei* Regnéll, to France as *H. rouvillei* (Koenen), and to Portugal as *H. burdigalensis* (Jaekel).

Caryocystites also has its earliest history centered in the Baltic and in China, but which area yielded the older fossils cannot be decided until greater stratigraphic accuracy is attained in correlation. *C. bicompressus* (Reed) comes from the Shih-tien Beds of China, *C. esthoniae* (Jaekel) from the C$_2$ of Estonia, and *C. laevis* Gekker from C strata of the Leningrad region. Elsewhere, *C. davisi* M'Coy occurs in Llandeilo rocks of Wales and England, *C. angelini* (Haeckel) in *Chasmops* beds of Sweden, and *C. lagenalis* Regnéll from the Swedish Kullsberg Limestone, which Regnéll (1945) regards as "Middle and (basal) Upper Ordovician." Bassler (1919) mentioned cystoid plates which he assigned to *Caryocystites* as abundant in his "*Caryocystites* bed" at the base of the Chambersburg Limestone in Pennsylvania and Maryland; no specifically determinable specimens have been described.

Other caryocystitid genera are from Middle and Upper Ordovician strata. *Orocystites helmhackeri* Barrande is found in Bohemia and Portugal (M.Ord.), *O. helmhackeri thuringae* (Jaekel) in Thuringia (M.Ord.), and *O.* sp. cf. *O. helmhackeri* in Belgium (U.Ord.). The inadequately described *Ulrichocystis eximia* Bassler is from Tennessee.

The **Echinosphaeritidae** are of particular interest because one species has been recognized in Europe and in North America. *Echinosphaerites ellipticus* Eichwald from Estonia (B$_3$) is the oldest known species of the family (Fig. 66). The famous *E. aurantium* (Gyllenhaal), including the

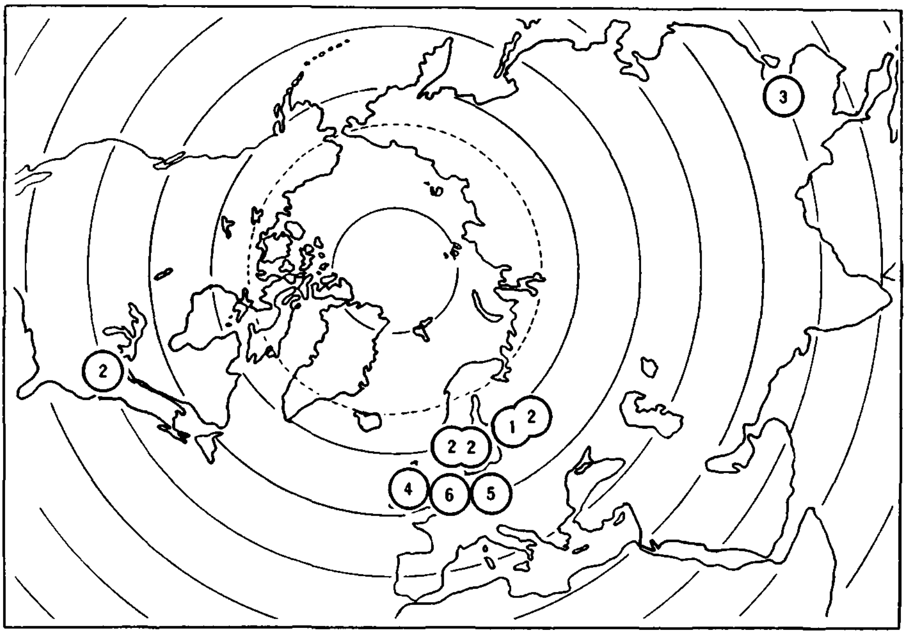


FIG. 66. Sequence and geographic distribution of cystoids of the genus *Echinosphaerites*.——*1. E.* sp., *E. ellipticus,* L.Ord.(B_2-B_3), Eu.(Est.).——*2. E. aurantium,* M.Ord., USA-Eu.(Sweden-Norway-Leningrad region).——*3. E. sinensis,* M.Ord., China.——*4. E. granulatus,* M.Ord.(Caradoc), Eire.——*5. E. barrandei,* M.Ord.(Dd_4), Eu.(Czech.).——*6. E. barrandei belgicus,* U.Ord.(Fauquez Sh.), Eu.(Belg.) (Kesling, n).

several subspecies and mutations erected, is present in Middle Ordovician deposits of the Leningrad region, Estonia, Sweden, Norway, Wales, and eastern United States (Pennsylvania, Virginia, and Tennessee). In the Baltic, this species ranges from C_{1b} to C_3. It bears a close resemblance to *E. sinensis* (REED) from China. *E. pogrebowi* GEKKER occurs in the Leningrad region (C_2). *E. grandis* JAEKEL, in Estonia and the Leningrad area, is perhaps from the C_2; in Sweden, it comes from the Kullsberg Limestone. From the C_3 of Estonia, two species were described by JAEKEL, *E. difformis* and *E. pirum.* In Ireland and Scotland, *E. granulatus* M'COY is found in the Caradoc Series. *E. barrandei* JAEKEL has been described from the Dd_4 of Bohemia and recognized in Norway, and *E. barrandei belgicus* JAEKEL, from the Upper Ordovician Fauquez Shales of Belgium. The age remains in doubt for *E. gyllenhahli* QUENSTEDT of Sweden and Russia, *E. globosus* JAEKEL, of Estonia, *E. globosus anglicus* JAEKEL, of Ireland, and *E. kloedeni* JAEKEL, from the drift of Estonia and northern Germany. *Arachnocystites infaustus* (BARRANDE) is from Bohemia (Dd_1-Dd_4).

DIPLOPORITA

Cystoids of the order Diploporita have been collected in southeastern Asia, Europe, northern Africa, and North America. The lack of finds in the southern hemisphere may be explained by absence of concerted collecting.

GLYPTOSPHAERITIDA

The superfamily Glyptosphaeritida may not have given rise to many species, but it spread over a considerable area. The family **Glyptosphaeritidae** contains only the type genus. One wishes to know whether *C. ferrigenus* (BARRANDE) from Bohemia (Dd_1) or *G. leuchtenbergi* (VOLBORTH) from the Baltic region (B_3 to C_{1b}) is older, but no conclusion is obtainable (Fig. 67). *G. suecicus* (ANGELIN) in Sweden is latest Middle Ordovician, and *G. mariae* JAEKEL in the drift of northern Germany is of unknown age.

The **Gomphocystitidae** began with *Pyrocystites orientalis* (Reed) in China. The genus has also been determined in Bohemia by Barrande, with *P. patulus* and *P. incertus* (D_1) and *P. pirum* (D_1 and D_4). No lineage leading to *Gomphocystites* has been discovered. *Gomphocystites* is a Middle Silurian genus, primarily North American. From Niagaran strata, *G. bownockeri* Foerste has been described from Ohio, *G. clavus* Hall from Wisconsin, *G. glans* Hall from Wisconsin and Illinois, *G. indianensis* Miller from Indiana, and *G. tenax* Hall from New York and Kentucky. This cystoid fauna has not been found in Michigan and Ontario. *"G.? californicus"* Stauffer, from the Kennett Formation in California, was thought to be Middle Devonian, but recent evaluations of stratigraphy place it in Middle Silurian. The only species outside North America is *G. gotlandicus* (Angelin) from the Högklint Limestone of Gotland. It is Middle Silurian, but its age relationship to the Niagaran species cannot be established.

The **Protocrinitidae** are widely dispersed (Fig. 68). *Protocrinites* begins its record with *P. fragum* (Eichwald) in the Baltic area (Vaginatum through Wasalemm). *P. sparsiporus* (Bather) occurs in Burma (Naungkangyi Beds). In Estonia, *P. oviformis* (Eichwald) is known from D_3 beds. Middle Ordovician protocrinitids from North America include *Eumorphocystis multiporata* Branson & Peck from Oklahoma and *Regnellicystis typicalis* Bassler from Virginia. The known species of *Fungocystites, F. rarissimus* and *F. solitarius,* were described from Bohemia by Barrande.

The family **Dactylocystidae** is based on very unusual but very rare cystoids from Estonia: *Dactylocystis schmidti* Jaekel (D_1), *Estonocystis antropoffi* Jaekel (D_1), and *Revalocystis mickwitzi* Jaekel (E).

SPHAERONITIDA

Cystoids of the superfamily Sphaeronitida are found in many places in the northern hemisphere, but they are especially characteristic of central and southern Europe. In fact, Termier & Termier (127) called this area the "province à Amphorides" because of the predominance of the Aristocystitidae.

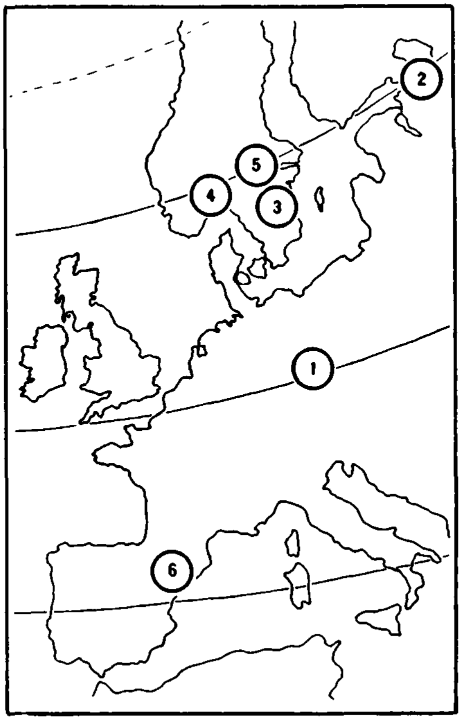


Fig. 67. Sequence and geographic distribution of cystoids of the genus *Glyptosphaerites*.——*1. G. ferrigenus,* Ord. (Dd_1), Eu. (Czech.).——*2. G. leuchtenbergi,* L.Ord. (B_3-C_1), Eu. (Baltic).——*3. G. leuchtenbergi,* M.Ord. (*Platyurus* Ls.), Eu. (Sweden).——*4. G.* sp., M.Ord.(*Chasmops* Ls.), Norway(Oslo region).——*5. G. suecicus,* M.Ord. (*Macrourus* Ls.), Sweden(Dalarna).——*6. G. leuchtenbergi hispanicus,* U.Ord., Eu.(Spain) (Kesling, n).

The family **Sphaeronitidae** contains some genera that became diverse and left an ample record and some that are understood only from a few specimens. Generic boundaries are not sharply drawn, adding to the difficulty of searching out the geographic extent of a particular genus.

Insofar as known, the ancestor of the family is the earliest Ordovician *Paleosphaeronites* from Bohemia. It is closely related to the slightly younger *Sphaeronites.*

For much of its content, *Sphaeronites* is taxonomically bound to the fate of the genera poorly established by Haeckel (58), *Pomosphaera, Pomonites,* and *Pomocystis.* These are here suppressed, and *Sphaeronites* is acknowledged as one of the senior syn-

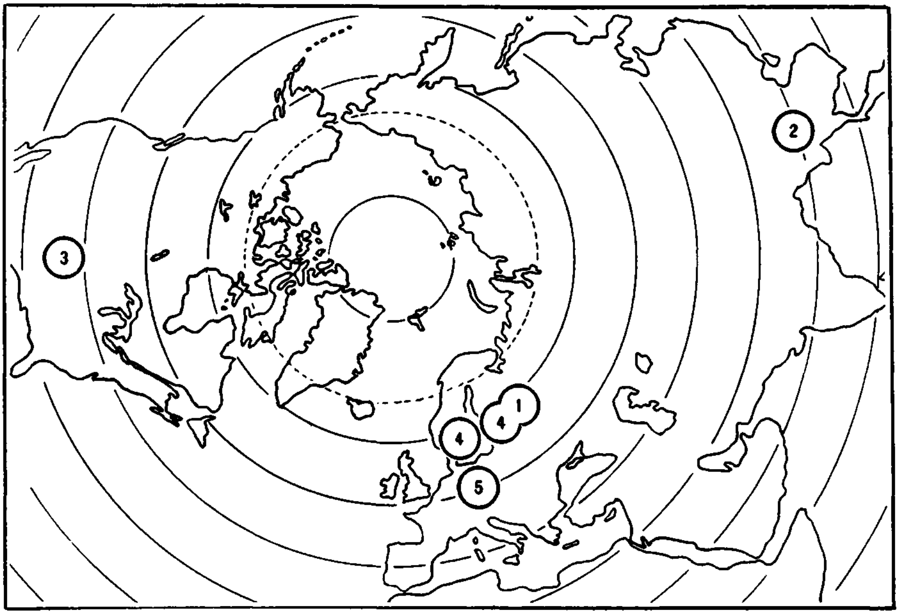


Fig. 68. Sequence and geographic distribution of cystoids of the family Protocrinitidae.——*1. Protocrinites fragum,* L.Ord.(*Vaginatum* beds or C_1), Eu.(USSR).——*2. P. sparsiporus,* M.Ord.(Naungkangyi beds), Burma.——*3. Eumorphocystis,* M.Ord.(Bromide), USA(Okla.).——*4. P. oviformis, P. fragum,* M.Ord.(D_3), Eu.(USSR-Est.-Scand.-Ger.).——*5. Fungocystites,* M.Ord.(Dd_4), Eu.(Czech.) (Kesling, n).

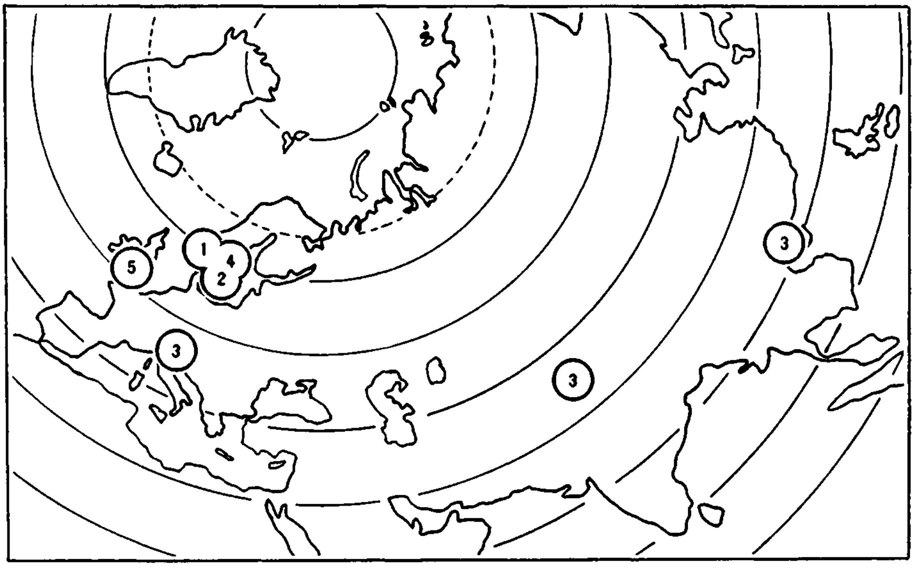


Fig. 69. Sequence and geographic distribution of cystoids of the genus *Sphaeronites.*——*1. S.* sp., L.Ord., Norway.——*2. S. pomum,* L.Ord., Sweden(Öland).——*3. S. shihtiensis,* M.Ord., Asia(China-Karakorum)-Eu.(Italy).——*4. S. globulus,* M.Ord.(L.*Chasmops* beds), Sweden (Västergötland-Östergötland-Dalarna).——*5. S. stelluliferus,* Caradoc, Eu.(Wales) (Kesling, n).

onyms involved. Its oldest occurrence (Fig. 69) is in the 3cβ of Norway (100). The prolific *S. pomum* (GYLLENHAAL) is found in the *Asaphus* Limestone of Sweden in strata equivalent to the 3cβ. *S. shihtienensis* (REED) is an eastward extension of the genus during early Middle Ordovician, being recorded in Yunnan, China, and the central Asian Karakorum region. In Sweden, the genus continued as *S. globulus* (ANGELIN) in the Lower *Chasmops*. The westernmost extent is in Wales, where *S. stelluliferus* SALTER is found in Caradoc beds and *S. punctatus* FORBES and *S. pyriformis* (FORBES) are found in the Ashgillian Rhiwlas Limestone. The stratigraphic position of *S. dalecarlicus* (ANGELIN) in Sweden, *S. pentactaeus* (HAECKEL) in Scandinavia, and *S. tesselatus* PHILLIPS in England is not known. The closely related *Haplosphaeronis* makes its debut in the Shihtien Beds of southeastern China as *H. lobifera* (REED). In Sweden, *H. oblonga* (ANGELIN) is known from lower *Chasmops* strata. REGNÉLL (101) gave the Swedish range of *Haplosphaeronis* as at least from Kullsberg to Boda (Fig. 53). From Norway comes the Middle Ordovician *H. kiaeri* JAEKEL and *H. kiaeri norvegica* JAEKEL and from Belgium the Late Ordovician *H. proiciens* REGNÉLL.

Eucystis lacks clear separation from certain Early Devonian cystoids, which could be interpreted as species either of the genus in a broad sense or of strongly similar genera derived from *Eucystis*. The latter disposition is followed in the *Treatise*. The oldest species known was described from Yunnan, China, as *E.* sp. cf. *E. raripuncta* REED (98), from the early Middle Ordovician Shihtien Beds (Fig. 70). The species probably is not *E. raripuncta* ANGELIN, which occurs in the Boda Limestone of Sweden. *E. litchi* (FORBES) from Wales (Caradoc) was said by REGNÉLL (100) to be atypical of *Eucystis*. In addition to *E. raripuncta*, the Boda Limestone of Sweden has yielded *E. angelini* REGNÉLL, *E. acuminata* REGNÉLL, and *E. quadrangularis* REGNÉLL. The Lower Devonian of Germany, France, Bohemia, and Morocco contains cystoids of the late *Eucystis* complex. *E. hercynica* JAEKEL from Germany is retained provisionally in *Eucystis*. *Carpocystites soyei* OEHLERT from France and *Proteocystites flavus* BARRANDE, *P. barrandenus* (HAECKEL), and *Bulbocystis mira* RUŽIČKA from Bohemia are tentatively placed in their respective genera.

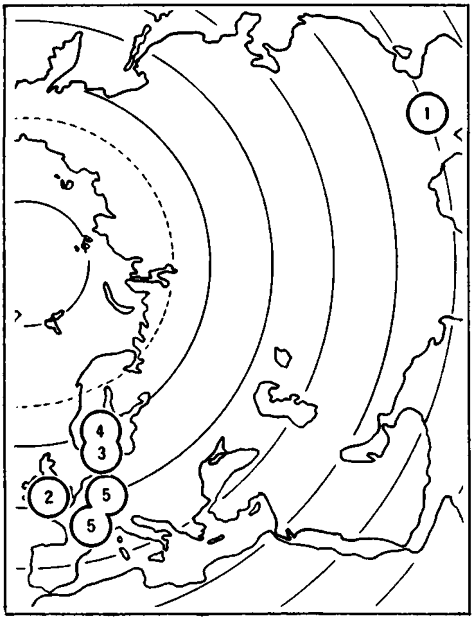


FIG. 70. Sequence and geographic distribution of cystoids of *Eucystis* and related genera.——*1.* "*Eucystis* cf. *raripuncta*" of REED (1917), M.Ord., China.——*2. E. litchi*, Caradoc, Eu.(Wales).——*3. E. quadrangularis, E.* sp., U.Ord.(L.Boda beds). Sweden(Scania).——*4. E. raripuncta, E. angelini, E. acuminata*, U.Ord.(U.Boda beds), Sweden (Dalarna).——*5. E. hercynica, Carpocystites soyei, Proteocystites flavus, P. barrandenus, Bulbocystis mira*, L.Dev., Eu.(Ger.-Czech.-Fr.) (Kesling, n).

Tholocystis kolihai CHAUVEL from France does not have clear affinities with any other described cystoid of the Sphaeronitidae.

Bohemia produced all the known species of *Archegocystis* and *Codiacystis*. *A. desideratus* BARRANDE has the distinction of being the oldest (Dd$_1$) Bohemian sphaeronitid. In the Chrustenitz region, BARRANDE (3) described an amazing number of species of *Codiacystis* from Dd$_4$ beds, under the original assignment to *Aristocystites (C. potens, C. sculptus)* and to *Craterina (C. absens, applanata, bohemica, consobrina, docens, embryo, excavata, excavata intermedia, idealis, infundibulum, modica, oneta, simulans, surgens,* and *tecta)*. These species have never been subjected to revision; they appear to be excessive.

Allocystites hammelli S. A. Miller from Indiana is notable for being the only Silurian cystoid of the Sphaeronitidae. It is not particularly well described or well represented.

In the **Aristocystitidae,** the generic boundaries are even more diffuse than in the Sphaeronitidae. The antiquity of the family seems to lie in the Early Ordovician species from China, *Sinocystis loczyi* Reed, *S. yunnanensis* Reed, *S. mansuyi* (Reed), and *Aristocystites sinicus* (Sun); and from Burma, *Pseudaristocystis dagon* (Bather). *Sinocystis* reached Morocco in Llandeilo time as *S. segaudi* Termier & Termier. Two species of *Aristocystites* have also been described from Morocco, *A. gigas* Termier & Termier, from Llandeilo strata, and *A. regularis* Termier & Termier, from Caradoc strata. Other species were found in Bohemia (Dd_4) by Barrande, *A. bohemicus, A. desideratus,* and *A. rudis.*

Calix is another genus associated with the so-called *Aristocystites* fauna. In France, it is represented by the Middle Ordovician *C. sedgwicki* Rouault and *C. rouaulti* Chauvel and by the Late Ordovician *C. lebesconti* Chauvel. *Pachycalix halli* (Rouault) occurs in the Middle Ordovician of Brittany, and *P. pachytheca* Termier & Termier in the Caradocian of Morocco. The somewhat doubtful *Lepidocalix pulchrum* Termier & Termier has been found in Algeria (M.Ord.). The unique *Campylostoma grandis* Dreyfuss was obtained from Upper Ordovician beds in France. The Dd_4 in Bohemia contains, in addition to the species of *Aristocystites, Amphoracystis irregularis* (Barrande), *Hippocystis subcylindrica* (Barrande), and the questionable *Baculocystites simplex* Barrande.

The Middle Silurian fauna of east-central North America seems to be the culmination of a lineage that began with *Holocystites ovalis* (Angelin) in Sweden during the Late Ordovician. It contains *Holocystites* and *Trematocystis,* the former beset by a multiplicity of species names. For specimens from Indiana, S. A. Miller alone created species for localities, *H. indianensis* and *madisonensis*; for shape and ornamentation of theca, *H. adipatus, amplus, baculus, canneus, commodus, elegans, globosus, ornatissimus, ornatus, papulosus, parvulus, parvus, perlongus, plenus, pustulosus, rotundus, scitulus, subovatus, subrotundus, tumidus, turbinatus,* and *ventricosus*; and for acquaintances, *benedicti, brauni, colletti, dyeri, faberi, gorbyi, spangleri, wetherbyi,* and *wykoffi.* One suspects that Miller was overzealous in discrimination. Other species are known from Wisconsin, Illinois, Ohio, and Tennessee, including *Holocystites abnormis* Hall, *H. affinis* Miller & Faber, *H. cylindricus* (Hall), *H. greenvillensis* Foerste, *H. gyrinus* Miller & Gurley, *H. scutellatus* Hall, *H. sphaericus* Winchell & Marcy, *H. sphaeroidalis* Miller & Gurley, *H. splendens* Miller & Gurley, and *H. winchelli* Hall. This extensive list is evidence of the abundance of these cystoids in Niagaran rocks of the United States. The closely allied *Trematocystis,* from the same strata and geographic locale, contains *T. subglobosa* (Miller) and *T. hammelli* (Miller); it may be found to have one or more additional species from Miller's replete set.

ASTEROBLASTIDA

The superfamily Asteroblastida lived in Early Ordovician time in the Baltic provinces. *Mesocystis pusirefskii* (Hoffman) is the oldest. The other species are *Asteroblastus foveolatus* (Eichwald), *A. regularis* Jaekel, *A. sublaevis* Jaekel, *A. volborthi* Schmidt, *Asterocystis globulus* Jaekel, *A. tuberculatus* (Schmidt), *Metasterocystis micropelta* Jaekel, and *Mesocystis jaekeli* Yakovlev. Fragmentary specimens from Morocco identified by Termier & Termier (126) as *Asteroblastus* were said to come from Llandeilo strata. The stratigraphic accuracy is not known.

MIGRATIONS

The whole undertaking of establishing migration routes is fraught with uncertainties. All taxonomic determinations are not accurate, and correlations are not reliable. Even some geographic occurrences have been cited incorrectly. As Regnéll (105) stated, "To be sure, it is no easy task to recognize the individual threads in this entangled web . . . the pictures of palaeobiogeographic features in remote times which we endeavour to envisage are poor in details, on account of scanty information."

To simplify the geographic factor, five areas can be designated which have had distinctive cystoid faunas—(1) Burma and adjacent parts of China, (2) Scandinavia and the eastern Baltic region, (3) central and southern Europe and the Mediterranean region, (4) the British Isles, and (5) eastern North America. These areas are particularly prominent during the Ordovician, the time of maximum diversity and distribution of the cystoids.

Regnéll (101), from a detailed study of the succession of cystoids, concluded that many of the significant faunal elements came from the Far East or that they originated in the Arctic and spread to both the Far East and to Europe. The picture of cystoid migration that emerges in the light of the Ordovician correlations adopted in this section of the *Treatise* in part substantiates, in part deviates from that which he depicted.

From inspection of the known ranges of the families (Fig. 71), it is apparent that the late Early Ordovician and early Middle Ordovician were times when specialized stocks evolved; they were also times when old lineages spread into new territories. Hence, this interval is one of extreme importance in unraveling the origins of the suprageneric taxa and their prime routes of dispersal.

Much of the available information on the sequence of recorded first appearances of various taxa in the five principal regions is summarized in Table 5. This is a compilation of the cystoid distribution in time and space insofar as known. In analyzing these data, one must not lose sight of the small percentage of sediments of a particular age that are exposed, the lack of persistent collecting from many outcrops, and the possibility that many key species lived in small populations.

Nevertheless, in the examples selected in Table 5, eight taxa made their appearance in the Baltic region, six in the China-Burma region, one in North America, and none in the British Isles or southern Europe. Thus, two centers emerge as significant. Many of the Early and Middle Ordovician migrations appear to have been interchanges between these two centers.

Several taxa originated in the Baltic during the late part of Early Ordovician and spread to Burma and China during the early part of Middle Ordovician: *Heliocrinites* (Fig. 65), *Echinosphaerites* (Fig. 66), *Protocrinites* (Fig. 68), and *Sphaeronites* (Fig. 69). On the other hand, some taxa developed in the Far East during the early part of Middle Ordovician and quickly migrated westward to the Baltic region: *Haplosphaeronis, Eucystis* (Fig. 70), *Stichocystis,* and possibly *Caryocrinites* (Fig. 64). A plausible explanation of this pattern was suggested by Regnéll (100), that the evolutionary center may not have been at either the Baltic or Far East occurrences of cystoids, but situated instead in the Arctic Sea, whence the faunal elements dispersed, some arriving first in the Baltic and others arriving first in the Far East.

The families Cheirocrinidae and Asteroblastidae are exceptions among the cystoids appearing first in the Baltic during Early Ordovician. Neither reached Burma or China. The Cheirocrinidae (Fig. 60) extended to North America and southern Europe during the Middle Ordovician, and the Asteroblastidae seem to have spread to the Mediterranean region at that time. Conversely, the Pleurocystitidae (Fig. 61) begin their record in China, if Sun's (124) identification is correct, and spread to North America (Middle Ordovician), to Britain (Late Ordovician), and to Germany (Early Devonian), but never reached the Baltic region.

Some of the occurrences are interrupted, and little can be inferred about intermediate locales. This applies to *Holocystites* from the Baltic (U.Ord.) to North America (M. Sil.). The Echinoencrinitidae have no representation during the Middle Ordovician or Early and Middle Silurian, the Sphaeronitidae and Caryocrinitidae during Early or Late Silurian, or the Pleurocystitidae during all of the Silurian.

The supposed Scottish-Hungarian barrier separating the Baltic region from the "province à Amphorides" may have been an influence in guiding cystoid migrations. For example, *Heliocrinites* (Fig. 65) and *Echinosphaerites* (Fig. 66), which have a considerable fossil record, seem to have gone from the Baltic to Britain before extending to Bohemia. The same route may have been followed later by *Caryocrinites* (Fig. 64), which has a record in the Baltic in

TABLE 5. *Sequence and Time of Recorded Appearances in Various Regions of Selected Families and Genera of Cystoids.*

[Where considerable doubt exists as to which of two occurrences is the older, both are assigned the same sequence number. Where the occurrence itself is dubious, the entry is followed by a question mark.]

	North America	British Isles	Baltic	Southern Europe	China-Burma
Cheirocrinidae					
Cheirocrinus		6 U.Ord.	1 L.Ord.		
Homocystites	4 M.Ord.		3 L.Ord.	5 M.Ord.	
Leptocystis		6 U.Ord.	2 L.Ord.	7 L.Sil.	
Echinoencrinitidae					
Echinoencrinites			1 L.Ord.		
Glaphyrocystis			2 U.Ord.		
Prunocystites		3 U.Sil.			
Pleurocystitidae					
Pleurocystites	2 M.Ord.	3 U.Ord.			1 M.Ord.?
Amecystis	2 M.Ord.				
Regulaecystis				4 L.Dev.*	
Callocystitidae					
Apiocystitinae					
Lepadocystis	1 U.Ord.				
Brockocystis	2 L.Sil.				
Hallicystis	3 M.Sil.				
Tetracystis	3 M.Sil.				
Apiocystites	3 M.Sil.	4 U.Sil.			
Lovenicystis			4 U.Sil.		
Lepocrinites	5 L.Dev.	4 U.Sil.			
Jaekelocystis	5 L.Dev.				
Lipsanocystis	6 M.Dev.				
Strobilocystites	7 M.Dev.				
Callocystitinae					
Callocystites	3 M.Sil.				
Coelocystis	3 M.Sil.				
Sphaerocystites	5 L.Dev.				
Staurocystinae					
Staurocystis		4 U.Sil.			
Pseudocrinites	5 L.Dev.	4 U.Sil.			
Hemicosmitidae					
Hemicosmites		2 M.Ord.	1 M.Ord.		1 M.Ord.
Corylocrinus			3 U.Ord.	3 U.Ord.	
Tricosmites			4 L.Sil.		
Caryocrinitidae					
Caryocrinites	4 M.Sil.	3 U.Ord.	2 M.Ord.?	4 M.Sil.	1 M.Ord.
Juglandocrinus				3 U.Ord.	
Oocystis		3 U.Ord.		3 U.Ord.	
Ptychosmites				3 U.Ord.	
Stribalocystites	4 M.Sil.				
Polycosmitidae					
Polycosmites				2 M.Ord.	
Stichocystis			3 M.Ord.		1 M.Ord.
Caryocystitidae					
Heliocrinites		3 M.Ord.	1 L.Ord.	4 U.Ord.	2 M.Ord.
Caryocystites	3 M.Ord.?	3 M.Ord.	3 M.Ord.		2 M.Ord.
Orocystites			3 M.Ord.	3 M.Ord.	
Echinosphaeritidae					
Echinosphaerites	3 M.Ord.	4 M.Ord.	1 L.Ord.	5 M.Ord.	2 M.Ord.
Arachnocystites				2 M.Ord.	
Gomphocystitidae					
Pyrocystites				2 M.Ord.	1 M.Ord.
Gomphocystites	3 M. Sil.		3 M.Sil.		
Protocrinitidae					
Protocrinites			1 L.Ord.		2 M.Ord.
Eumorphocystis	3 M.Ord.				
Fungocystites				4 M.Ord.	

TABLE 5 *(continued)*

	North America	British Isles	Baltic	Southern Europe	China-Burma
Sphaeronites		3 M.Ord.	1 L.Ord.		2 M.Ord.
Haplosphaeronis			2 M.Ord.		1 M.Ord.
Eucystis		3 M.Ord.?	2 M.Ord.	4 L.Dev.	1 M.Ord.
Holocystites	2 M.Sil.		1 U.Ord.		
Asteroblastus			1 L.Ord.	2 M.Ord.?	

*Germany

Middle Ordovician, Britain in Late Ordovician, and France in Middle Silurian.

Within the subfamily Apiocystitinae, *Apiocystites* occurs first in the Middle Silurian rocks of the United States and then in the Upper Silurian rocks of Britain, but *Lepocrinites* appears first in the Upper Silurian of Britain and extended to America in Early Devonian time. In this migration, *Lepocrinites* was joined by *Pseudocrinites*. Only during Late Silurian did callocystitids send out emigrants from North America. The easternmost extent of this minor wave was Sweden.

Despite these invasions and extensions, the regions produced distinctive faunas. The Middle Ordovician cystoids of North America are dominated by *Pleurocystites* and *Homocystites*. The fauna of this age in the Baltic consists primarily of *Heliocrinites, Echinosphaerites,* and *Caryocystites,* although other cystoids are present. The Early and Middle Ordovician faunas of Estonia contain many rare genera. The majority of Ordovician cystoids in central and southern Europe are Aristocystitidae. The Silurian cystoids of North America are mostly *Holocystites, Caryocrinites,* and Callocystitidae. Other examples could be cited.

In summary, the cystoids evolved as distinctive faunas, probably because each population was closely attuned to the ecological factors in a particular province. Only rarely did a species develop a range of tolerance sufficient to thrive over a broad intercontinental area.

CLASSIFICATION

INTRODUCTION

Taxonomy of cystoids has not followed a consistent trend. For the class as a whole, additions and deletions have been piecemeal and have lacked universal acceptance, despite the comprehensive works of JAEKEL (69, 71) and BATHER (10). Major contributions have been sporadic, and very few changes have been made in recent years.

From new discoveries of fossil cystoids, through the years, new genera were made known and accommodated into the suprageneric framework. From sharper discrimination, sometimes astute and sometimes picayune, additional genera have been created by splitting the old. For the most part, attempts to assess the genera, even within a superfamily, have been perfunctory. Many authors have been reluctant to eliminate genera; this criticism may apply to the *Treatise,* wherein several genera of dubious taxonomic value have been retained because time was insufficient to locate and evaluate types of the assigned species, particularly of cystoids described in the previous century.

The long-dominant concept of Cystoidea including any and all pelmatozoans not definitely classed as crinoids led to an amalgamation of echinoderms having such diverse morphology that they fell far short of constituting a definable class. The Cystoidea attained its present state by major excisions. Removal and diagnosis of the Edrioasteroidea were early accomplished by BILLINGS (20) and confirmed by the major contribution of JAEKEL (69) and BATHER (9, 10). This was followed by separation of the Carpoidea by JAEKEL (70), the Eocrinoidea by JAEKEL (71), the Paracrinoidea by REGNÉLL (99), and the Edrioblastoidea by FAY (45). Not all workers have accepted these efforts to reduce the Cystoidea.

The position of the Blastoidea is still debated. Rather firm positions for including and for excluding them from the Cystoidea have been taken in the past decade. In the *Treatise,* the Blastoidea are classed as a separate taxon.

To identify the echinoderms that have appeared in literature as cystoids but are here classified otherwise, a list is offered of "Echinoderms Formerly Included in Cystoidea."

Some of the problems of classification have been of a nomenclatural nature. An especially perplexing area of concern is the publication by Haeckel (58) of genera based on previous accounts, *nomina nuda,* and hypothetical genera. This creation of names for possible cystoids that could have developed on theoretical grounds, coupled with his general unreliability for according authorship of species, makes it difficult to do justice to his work. Nearly all of his genera are extremely weakly founded, but one must decide if they are recognizable at all and whether they were even based on specimens. Lists are presented herein of Junior Synonyms, Nomina Nuda, Preoccupied Names, and Unrecognizable Genera.

DEVELOPMENT OF CLASSIFICATION

The cystoids *Sphaeronites pomum* and *Echinosphaerites aurantium* are so abundant in the *Asaphus* and *Chasmops* Limestones of Sweden, respectively, that some exposures yield a wealth of these spherical fossils, which are closely packed in certain strata. Linné (79) mentioned them as *"Crystall-äplen"* and Wallerius (140) as *"Spat-klot,"* both authors expressing the current belief that such crystal-apples and lime-balls were of inorganic origin.

EARLY WORK

The brilliant, pioneer work of Johan Abraham Gyllenhaal, a Swedish miner, was published in the journal of the Royal Swedish Academy of Science (Kgl. Vetenskap Academiens Handlingar) in 1772 (56). (His name was misspelled as Gyllenhahl at the heading of the paper, and has been so cited many times.) In it he illustrated these two common species and named them *Echinus pomum* and *E. aurantium,* regarding them as sea urchins "of the genus *Echinus,* or its nearest relatives" (translated from the title by Regnéll (99), who presented annotations and commentary on the work). He correctly interpreted the peristome and periproct in *Sphaeronites pomum,* but identified the periproct as the peristome and the gonopore as the periproct in *Echinosphaerites aurantium.* The significant contribution was Gyllenhaal's recognition of these objects not only as organic but also as representing echinoderms.

Whereas several additions of genera were published in the succeeding 70 years, only two bear much taxonomic interest in that the idea of cystoid relationship to echinoids was changed. Thomas Say (112) described *Caryocrinites* from North America as a crinoid, and Hisinger (66) stated that cystoids were intermediate between "Encrinites" (crinoids) and "Echinites" (echinoids) because they were provided with a stem (column) and yet displayed similarities to sea urchins.

In 1846, Leopold von Buch (31) published a paper that he had read earlier, in which he recognized for the first time the independence of the cystoids from other echinoderms. He called them *"Cystideen."*

MÜLLER

The most important attempt at classification, however, was that of Johann Müller (90). He devised an outline of classification which was not completed with taxonomic names until years after his time.

Cystoid Taxa with Index Numbers for Sequence Given on Figure 71

Aristocystitidae—3
Asteroblastida—10
Asteroblastidae—12
Callocystitidae—24
Caryocrinitidae—30
Caryocystitida—14
Caryocystitidae—15
Cheirocrinidae—18
Cystoblastidae—21
Dactylocystidae—8
DIPLOPORITA—1
Echinoencrinitidae—19
Echinosphaeritidae—16
Glyptocystitida—17
Glyptocystitidae—20
Glyptosphaeritida—5
Glyptosphaeritidae—6
Gomphocystitidae—9
Hemicosmitida—28
Hemicosmitidae—29
Heterocystitidae—31
Mesocystidae—11
Pleurocystitidae—22
Polycosmitida—25
Polycosmitidae—26
Protocrinitidae—7
RHOMBIFERA—13
Rhombiferidae—23
Sphaeronitida—2
Sphaeronitidae—4
Stichocystidae—27

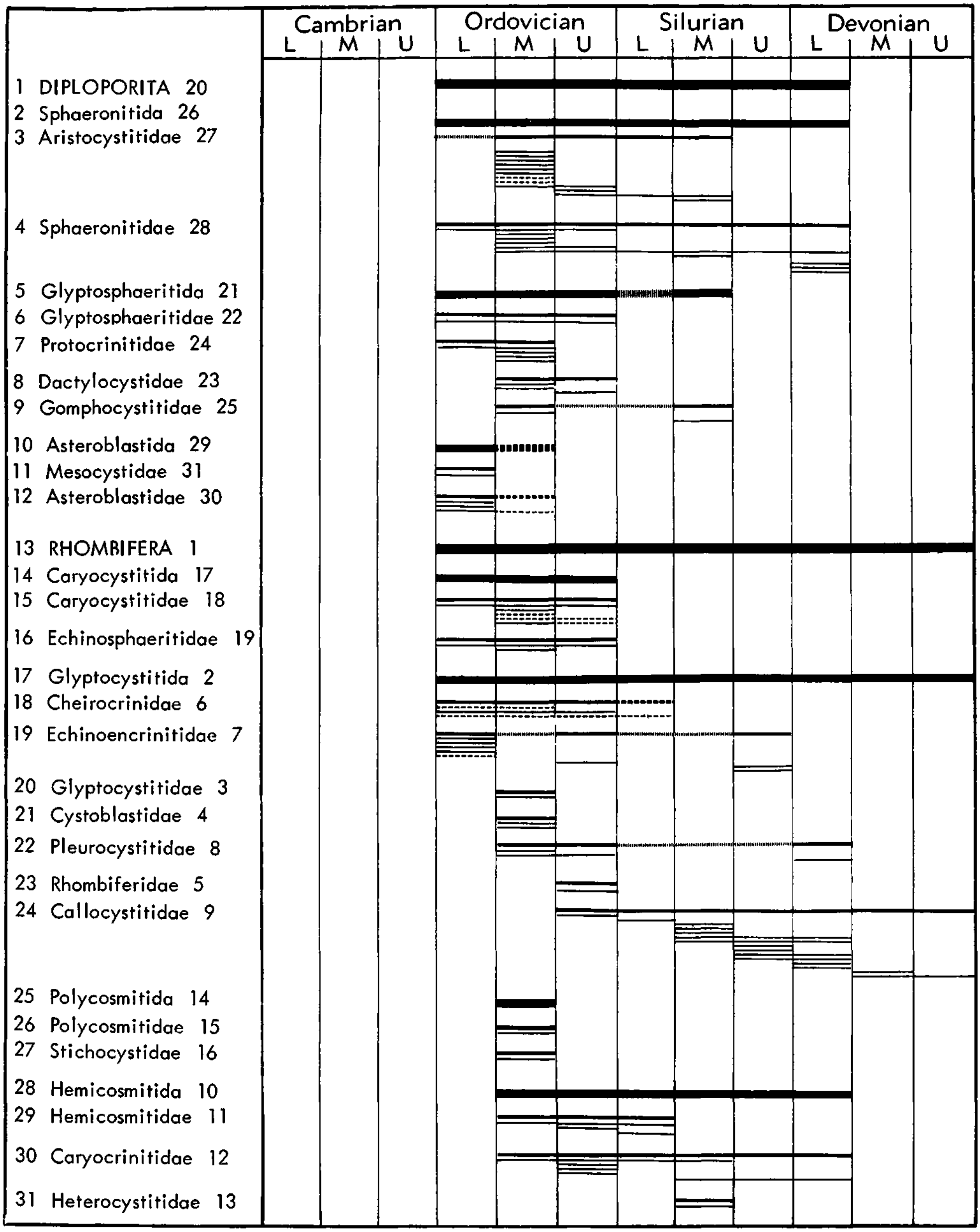


Fig. 71. Stratigraphic distribution of suprageneric cystoid taxa; geologic periods indicated only to epoch. The numbers following the names of taxa indicate systematic placement as given in the preceding tabular outline of cystoid classification. Also, an alphabetical list of taxa is accompanied by index numbers referring to the serially arranged numbers that precede the names of taxa on the diagram; this facilitates location of any selected family as plotted with respect to stratigraphic occurrence. [Range of orders (capital letters) and superfamilies indicated by heavy black lines, that of families by intermediate-weight lines, and individual genera by thinnest lines.]

He divided cystoids into two groups, those with *"Doppelporen,"* which were restricted to individual plates, and those with *"Porenrauten."* The first he called the *"Diploporiten"* and the second he left unnamed. In the following summary of his outline, the present taxa are indicated in brackets.

Classification of Cystoids by Müller

1. Cystoids with pore rhombs [Rhombifera].
   a. Rhombs without external openings for the pores, *Hemicosmites, Caryocrinites* [Hemicosmitida].
   b. Pores linked by an outer rod [actually a pore canal beneath epitheca], *Caryocystites* [Caryocystitida, Caryocystitidae in part].
   c. Pores linked by several outer rods [actually multiple pore canals beneath epitheca], *Echinosphaerites* [Caryocystitida, Echinosphaeritidae in part].
   d. With few pore rhombs, *Echinoencrinites, Pseudocrinites, Apiocystites, Prunocystites* [Glyptocystitida].
2. Cystoids with double pores, which occur on the same plate (Diploporiten), *Sphaeronites, Protocrinites, Glyptosphaerites* [Diploporita].

Müller's worthy system, which with additions and slight emendation serves as the order-superfamily classification now in use, was not readily accepted for nearly a half century.

EICHWALD

The next contribution to taxonomy was by E. von Eichwald (44), who sought to formalize his concepts of the cystoids. He created four "orders," written as family names, which he assigned to the Crinoidea. Of these, his Rhombiporitidae was said to contain *Cheirocrinus* and *Gonocrinus* [=*Echinoencrinites*], and corresponds to the Glyptocystitida of the Rhombifera. His Diploporitidae is the order Diploporita. His order Taxiporitidae is an admixture of Rhombifera and Crinoidea; it contained the cystoids *Heliocrinites, Caryocystites,* and *Echinosphaerites* [Caryocystitida] and *Hemicosmites* [Hemicosmitida]. His last order, the Aporitidae, contained only the eocrinoid *Cryptocrinites.*

Classification of Cystoidea by Eichwald, 1860 (44)

[As orders of Crinoidea]

Order Diploporitidae *(Sphaeronites, Protocrinus, Glyptosphaerites)*
Order Taxiporitidae *(Echinosphaerites, Caryocystites, Heliocrinus, Hemicosmites, Cyclocrinus)*
Order Rhombiporitidae *(Gonocrinus, Cheirocrinus)*
Order Aporitidae *(Cryptocrinus)*

QUENSTEDT

A simple division was proposed by F. A. Quenstedt (96) in which he divided cystoids into the "Serti" and the "Tricati." The first contained few and mostly large plates, to which he assigned *Caryocrinites, Hemicosmites,* and an "entire host of Rhombocystiden" (here translated); hence it corresponds to the Glyptocystitida and Hemicosmitida of the Rhombifera. The second, which Quenstedt admitted contained essentially different forms, contained *Echinosphaerites* of the Rhombifera and various genera of the Diploporita.

ANGELIN

N. P. Angelin (1) divided the cystoids into three groups. His Apora was so named because the pore canals were obscured in *Echinosphaerites* and *Caryocystites* [now included in the Caryocystitida]; he added *"Megacystis"* [=*Holocystites*], apparently because pores were not discerned on the steinkerns. His Gemellipora (twin-pores) corresponds to the Diploporita. His last group, Pedicellata, contained *Glyptocystites* and *Lepocrinites* (under other names), and hence is equivalent to the Glyptocystitida, insofar as one may judge from the content rather than the name.

Classification of Cystoidea by Angelin, 1878 (1)

Apora *(Echinosphaera, Caryocystis, Megacystis)*
Gemellipora *(Sphaeronis, Glyptosphaera)*
Pedicellata *(Glyptocystis, Lepadocrinus)*

ZITTEL

Karl A. von Zittel (147) used a tripartite division, each part of which he ascribed to J. Müller. The group Aporitidae were carpoids, edrioasteroids, and eocrinoids. The Diploporitidae included the Diploporita. The Rhombiferi were subdivided according to Müller's classification, although some carpoids, eocrinoids, crinoids, and a blastoid were included along with cystoids. The Rhombiferi appeared for the first time in the stem form of the Rhombifera.

Classification of Cystoidea by Zittel, 1879 (147)

Group Aporitidae J. Müller
Group Diploporitidae J. Müller
Group Rhombiferi J. Müller

BARRANDE

Joachim Barrande (3), in his monumental work on cystoids of Bohemia, divided the Cystoidea according to their supposed number of thecal openings. Many of his determinations of openings were in error. He did not, however, formally declare these divisions to be taxa, and he may perhaps have regarded them merely as a utilitarian aid in identification.

NEUMAYR

Melchior Neumayr (91) proposed a classification of "groups" (written informally as families with *-iden* termination) and "orders" (written with a subfamilial *-inen* termination). It is important not for the overall treatment, but for the first appearance of the stems from which Sphaeronitidae, Aristocystitidae, Echinosphaeritidae, and Pleurocystitidae were derived.

Classification of Cystoidea by Neumayr, 1889 (91)

Group Sphaeronitiden
  Order Sphaeronitinen
  Order Aristocystinen
  Order Mesitinen
Group Echinosphaeritiden
Group Pleurocystiden

MILLER

S. A. Miller (85) published a list of 12 families, the first 11 in alphabetical order and the last called "Family uncertain." By present standards, seven of the families contained noncystoid echinoderms. Miller's work did establish the families Caryocrinitidae and Gomphocystitidae.

Classification of Cystoidea in Families by S. A. Miller, 1889 (85)

Amygdalocystidae
Anomalocystidae
Caryocrinidae
Comarocystidae
Echinocystidae
Eocystidae
Gomphocystidae
Holocystidae
Hybocystidae
Lepadocrinidae
Platycystidae
Family Uncertain

STEINMANN

G. Steinmann (121) expressed taxonomically the conviction held by several workers in that century that cystoids were intermediate forms giving rise to other echinoderms. In the following key, his Eucystoidea contains both Rhombifera and Diplorita, his Cystechinoidea was created for one cystoid and one echinoid, his Cystasteroidea for an edrioasteroid, and his Cystocrinoidea for a unit of the Glyptocystitida, a unit of the Hemicosmitida, and a crinoid.

Classification of Cystoidea by Steinmann, 1890 (121)

A. No sharp border present between upper and lower sides of theca. No distinct free arms, instead mostly developed as ambulacral grooves or fields.
  a. Plates either numerous and irregular or less numerous and arranged in various circlets like those in crinoids, *Glyptosphaerites, Echinosphaerites, Lepocrinites* .... Eucystoidea
  b. Part of thecal plates arranged in meridional rows, *Cystocidaris, Mesites* .... Cystechinoidea
B. Upper and lower sides of theca different; several free arms developed like those of crinoids.
  a. Theca flat, with 5 arms fused onto a disc, *Agelacrinus* .... Cystasteroidea
  b. Theca beaker-shaped; free arms at junction of upper and lower sides, *Echinoencrinites, Caryocrinites, Porocrinus* .... Cystocrinoidea

BERNARD

Bernard (17) included the cystoids in his "groupe des Eucystidés," which he divided into six families. He introduced the Glyptosphaeritidae and Callocystitidae, although their definitions would scarcely suffice in modern taxonomy. The former included, in addition to *Glyptosphaerites, Protocrinites* of the Protocrinitidae, *Proteocystites* of the Sphaeronitidae, and an eocrinoid; it was based on the presence of diplopores, small brachioles, and ambulacral grooves. Apart from the Eucystidés, Bernard placed *Cystoblastus* and *Asteroblastus* as transitional to the blastoids; he also listed "Cystocrinoides," supposedly intermediate between cystoids and crinoids, but containing an eocrinoid and two crinoids as listed genera.

Classification of Cystoidea (Cystidés) in Families by Bernard, 1895 (17)

Aristocystidés
Échinosphaeritidés
Glyptosphaeritidés
Caryocrinidés
Callocystidés
Pleurocystidés

HAECKEL

The work of E. Haeckel (58), notorious for serious misconceptions and factual errors and liberally supplied with hypothetical genera, introduced a classification that divided the majority of cystoids into those with numerous plates and those with few. It is remembered, however, for the introduction of the Amphoridea, an assemblage of cystoids, eocrinoids, paracrinoids, and carpoids that found favor with certain subsequent authors and long delayed trimming the cystoids to a definite taxon. The families and their divisions (presumably subfamilies) added little to classification.

Classification of Cystoidea by Haeckel, 1896 (58)

Class Amphoridea
  Family Eocystida—hypothetical.
  Family Anomocystida or Pleurocystida—*Pleurocystites* and carpoids.
  Family Aristocystida or Holocystida—diploporites, rhombiferans, and carpoids.
  Family Palaeocystida or Archaeocystida—cystoids, carpoids, and crinoids.
Order Microplacta or Eucystidea—numerous thecal plates, irregularly arranged.
  Family Pomocystida (Sphaeronitida, Proteocystida).
  Family Fungocystida (Glyptosphaerida, Malocystida).
  Family Agelacystida (Hemicystida, Asterocystida).
  Family Ascocystida—forms transitional to holothurians.
Order Megaplacta or Parcystidea—few thecal plates, regularly arranged.
  Family Callocystida (Acanthocystida, Apiocystida, Pseudocrinida).
  Family Glyptocystida (Hexalacystida, Sycocystida).

KOKEN

Also in 1896, Koken (78) presented a key to the cystoids in his "Leitfossilien." Because he based his primary division on the extent of the ambulacra, the Diploporita and Rhombifera appear in each of the two major groups.

Classification of Cystoidea by Koken, 1896 (78)

A. Brachiata—brachioles near the mouth.
  1. Numerous thecal plates,
    With diplopores: *Holocystites, Sphaeronites.*
    With pore rhombs: *Echinosphaerites, Caryocystites.*
  2. Few thecal plates, arranged in circlets,
    With simple pores: *Cryptocrinites, Hypocrinus* (eocrinoid, crinoid).
    With numerous pore rhombs: *Caryocrinites, Hemicosmites.*
    With few pore rhombs: *Echinoencrinites.*
B. Abrachiata—long ambulacra radiating from the mouth.
  1. Numerous thecal plates,
    With pores absent: *Agelacrinites* (edrioasteroid).
    With diplopores: *Mesites, Protocrinites, Glyptosphaerites.*
  2. Few thecal plates,
    With numerous pore rhombs: *Glyptocystites.*
    With few pore rhombs: *Lepocrinites, Callocystites.*

BATHER AND JAEKEL

It was a coincidence that the two most influential, penetrating, substantial classifications were in preparation simultaneously but independently, by Bather (9) and by Jaekel (69), and both appeared in the same year, 1899. It is an even more astonishing coincidence that the two classifications agreed on nearly all major divisions.

Both authors recognized the order Rhombifera and Diploporita with many of the same families. Both used families Glyptocystitidae, Callocystitidae, Caryocrinitidae, Echinosphaeritidae, Glyptosphaeritidae, Gomphocystitidae, Sphaeronitidae, Aristocystitidae, and Mesocystidae, in various spellings and taxa.

The main difference between Bather (9) and Jaekel (69) lies in the inclusion by the former of the order Amphoridea (for the Aristocystitidae and carpoids) and the order Aporita (for some eocrinoids). Although they both put *Dactylocystis* and *Protocrinites* into one family, Bather called it Protocrinidae and Jaekel called it Dactylocystidae; actually, the two genera are representative of separate families. Although both put *Rhombifera* and *Tiaracrinus* into one family, Bather called it Tiaracrinidae and Jaekel called it Tetracystidae; actually, *Rhombifera* is the type of a cystoid family and *Tiaracrinus* is a crinoid. BATHER's subfamily Echinoencrininae of the Glyptocystidae is approximately equal to JAEKEL's family Scoliocystidae. Hence, for the most part, even the differences are those of taxonomic names rather than content.

BATHER's classification appeared slightly earlier than JAEKEL's, and has priority. BATHER introduced the following taxa (with variant spellings and ranks): Glyptocystitidae, Echinoencrinitidae, Mesocystidae, and Protocrinitidae. JAEKEL introduced Cheirocrinidae, Cystoblastidae, and Dactylocystidae.

Classification of Cystoidea (Called Cystidea) by Bather, 1899 (9)

- Order Amphoridea
  - Aristocystidae
  - Dendrocystidae
  - Anomalocystidae
- Order Rhombifera
  - Echinosphaeridae
  - Macrocystellidae
  - Tiaracrinidae
  - Malocystidae
  - Glyptocystidae
    - Echinoencrininae
    - Callocystinae
    - Glyptocystinae
  - Caryocrinidae
- Order Aporita
  - Cryptocrinidae
- Order Diploporita
  - Sphaeronidae
  - Glyptosphaeridae
  - Protocrinidae
  - Mesocystidae
  - Gomphocystidae

Classification of Cystoidea by Jaekel, 1899 (69)

- Order Dichoporita
  - Regularia
    - Chirocrinidae
    - Cystoblastidae nov.
    - Pleurocystidae
    - Scoliocystidae nov.
    - Callocystidae BERNARD
      - Glyptocystinae
      - Apiocystinae
      - Staurocystinae
      - Callocystinae
  - Irregularia
    - Caryocrinidae nov.
    - Echinosphaeridae nov.
    - ?Tetracystidae nov.
- Order Diploporita
  - Mesocystidae
  - Sphaeronidae
  - Aristocystidae nov.
  - Gomphocystidae nov.
  - Glyptosphaeridae
  - Dactylocystidae

BATHER's (10) treatment of the Cystoidea in LANKESTER's *A Treatise on Zoology* was published in 1900, after he had the opportunity to examine JAEKEL's (69) classification briefly. For intent and purpose, however, BATHER followed his taxonomy of the previous year. He added the family Eocystidae to the Amphoridea and the family Comarocystidae to the Rhombifera. Therewith, he emphasized an important distinction between his system and that of JAEKEL; we may note that BATHER's concept of the cystoids was very broad, including the carpoids and other pelmatozoans, whereas JAEKEL's concept was more restricted, approaching the modern content of the class.

Classification of Cystoidea (Called Cystidea) by Bather, 1900 (10)

- Order Amphoridea
  - Aristocystidae
  - Dendrocystidae
  - Eocystidae
  - Anomalocystidae
- Order Rhombifera
  - Echinosphaeridae
  - Comarocystidae
  - Macrocystellidae
  - Tiaracrinidae
  - Malocystidae
  - Glyptocystidae
    - Echinoencrininae
    - Callocystinae
    - Glyptocystinae
  - Caryocrinidae
- Order Aporita
  - Cryptocrinidae
- Order Diploporita
  - Sphaeronidae
  - Glyptosphaeridae
  - Protocrinidae
  - Mesocystidae
  - Gomphocystidae

Also in 1900, a classification of cystoids appeared in the ZITTEL textbook (translation by EASTMAN). It took no cognizance of the significant changes introduced by BATHER (9) and JAEKEL (69).

Classification of Cystoidea in Families by Zittel-Eastman, 1900

- Aristocystidae
- Sphaeronitidae
- Camarocystidae
- Echinosphaeritidae
- Cryptocrinidae
- Caryocrinidae
- Anomalocystidae
- Callocystidae
- Agelacrinidae

Jaekel (70) formally set up the class Carpoidea, which he had used the year previously as a *nomen nudum*; the current concept of these echinoderms, however, includes only the Heterostelea of Jaekel. Then, Bather (11, in Reed) defended his classification, including the Amphoridea, and presented it once again, with slight modification, in 1913.

The classification closest to the one in the *Treatise* was published by Jaekel in 1918 (71). The families Hemicosmitidae, Heterocystitidae, Polycosmitidae, Stichocystidae, and Caryocystitidae came into being. Jaekel's subclasses Dichoporita and Diploporita are the orders Rhombifera and Diploporita recognized here. His orders and suborders were strangely named and used in the sense of superfamilies. In this important contribution, the blastoids were included as a subclass of the cystoids, in the same rank as "Dichoporita" and Diploporita; this close affinity of cystoids and blastoids was to become a point of taxonomic controversy. It should be mentioned that Jaekel at the same time refined his definition of Carpoidea and set up the Eocrinoidea, which he made a subclass of the Crinoidea.

Classification of Cystoidea by Jaekel, 1918 (71)

- Subclass Dichoporita
  - Order Regularia
    - Chirocrinidae
    - Cystoblastidae
    - Scoliocystidae
    - Pleurocystidae
    - Callocystidae
      - Glyptocystinae
      - Schizocystinae
      - Apiocystinae
      - Staurocystinae
      - Callocystinae
  - Order Irregularia
    - Suborder Hemicosmites, nov.
      - Hemicosmitidae
      - Caryocrinidae
      - Heterocystidae
    - Suborder Polycosmites, nov.
      - Polycosmitidae
      - Stichocystidae
    - Suborder Caryocystites, nov.
      - Caryocystidae
      - Echinosphaeridae
  - Order Tetracystida
  - Order ?Pentacystida
- Subclass Diploporita
  - Order Asterocystida
    - Asterocystidae
    - Mesocystidae
  - Order Seriolata
    - Estonocystidae, nov.
    - Protocrinidae
    - Glyptosphaeridae
    - Gomphocystidae
  - Order Sphaeronita
    - Sphaeronidae
    - Aristocystidae
- Subclass Blastoidea
  - "*Vorform: Cystoblastus*"
  - "*Aberrante Versuchsform* (Parablastida)"
    - Blastocystidae
  - Order Radiolata
    - Suborder Spiraculata
      - Troostoblastidae
      - Pentremitidae
      - Nucleoblastidae
        - "*Anhang: Eleutherocrinus*"
      - Granatoblastidae
        - "*Anhang: Pentephyllum, Zygocrinus*"
    - Suborder Fissiculata
      - Orophocrinidae
      - Codasteridae
  - Order Coronata
    - Stephanoblastidae

BROILI

In the Zittel-Broili textbook (21), the Cystoidea were divided into three orders corresponding to edrioasteroids, carpoids, and cystoids in the sense used here. The last was called the Hydrophoridea.

Classification of Cystoidea in Zittel-Broili (21)

- Order Thecoidea Jaekel (Edrioasteroidea Billings, *emend.* Bather)
  - Edrioasteridae Jaekel
  - Steganoblastidae
  - Cyathocystidae
  - Agelacrinidae Hall (*emend.* Jaekel)
- Order Carpoidea Jaekel (Amphoridea Bather)
  - Anomalocystidae H. Woodward (Heterostelea Jaekel)
- Order Hydrophoridea Zittel
  - Suborder Rhombifera Zittel, *emend.* Bather (Dichoporita Jaekel)
    - Echinosphaeritidae Neumayr

Caryocrinidae Jaekel
Macrocystellidae Bather
Chirocrinidae Jaekel
Scoliocystidae Jaekel
Pleurocystidae Miller & Gurley (*emend.* Jaekel)
Callocystidae Bernard
Cystoblastidae Jaekel
Suborder Diploporita
  Aristocystidae Neumayr (*emend.* Jaekel)
  Sphaeronidae Jaekel (Pomocystae Haeckel)
  Gomphocystidae Jaekel
  Glyptosphaeridae Jaekel
  Protocrinidae Bather (Dactylocystidae Jaekel)
  Mesocystidae Jaekel

Bather (15) in his last published classification, in the *Encyclopaedia Britannica,* 14th ed., abandoned the Amphoridea and treated the Cystoidea and Blastoidea as distinct but closely related.

BASSLER

Bassler (5) in the "Pelmatozoa Palaeozoica" for the *Fossilium Catalogus,* and Bassler & Moodey (7) in *Bibliographic and Faunal Index of Paleozoic Pelmatozoan Echinoderms* turned back taxonomy to the 1900 concepts of Bather, enlarging somewhat on the unwieldy Amphoridea and altering the Rhombifera and Diploporita to a degree, but nevertheless reviving a general system that Jaekel (71) had condemned and Bather (15) had come to abandon.

Classification of Cystoidea by Bassler & Moodey, 1943 (7)

Order Amphoridea Haeckel
  Eocystitidae Bassler (Eocystidae Bather)
  Aristocystitidae Bassler (Aristocystidae Neumayr)
  Anomalocystitidae Bassler (Anomalocystidae Meek)
  Dendrocystitidae Bassler (Dendrocystidae Bather)
  Cothurnocystidae Bather
  Malocystitidae Bassler (Malocystidae Bather)
  Comarocystitidae Bassler (Comarocystidae Bather)
Order Rhombifera Zittel
  Echinosphaeritidae Neumayr (Echinosphaeridae Jaekel)
  Caryocrinitidae Bassler (Caryocrinidae Bernard)
  Callocystitidae Bassler (Callocystidae Bernard)
  Cheirocrinidae Jaekel
  Pleurocystitidae Bassler (Pleurocystidae Jaekel)
  Echinoencrinitidae Phleger (Echinoencrinidae Bather)
  Cryptocrinitidae Bassler (Cryptocrinidae Zittel)
  Macrocystellidae Bather
Order Diploporita Zittel
  Sphaeronitidae Neumayr (Sphaeronidae of authors)
  Glyptosphaeritidae Bassler (Glyptosphaeridae Jaekel)
  Protocrinitidae Bassler (Protocrinidae Bather)
  Gomphocystitidae Bassler (Gomphocystidae Jaekel)
  Eumorphocystidae Branson & Peck

Regnéll (99) criticized Bassler (5) and Bassler & Moodey (7) for their classification, and elected to follow Jaekel (71) in including the blastoids in the Cystoidea. He also corrected some of the taxonomic names of earlier authors, and presented a general critique of noncrinoid Pelmatozoa. Regnéll set up the Paracrinoidea to receive certain forms that had been assigned by some to the cystoids.

Moore (89) gave a summary of Pelmatozoa, and stated that "the relegation of blastoids to rank as a subclass of the cystoids, as recently proposed by Regnéll (99), is a backward step which is not accepted." Regnéll (104) rebutted Moore's contention by saying, "Now, the way of classification is a purely technical question and a matter of personal judgement and taste." He then referred to previous interpretations of *Cystoblastus, Asteroblastus,* and *Tholocystis* as possible intermediate forms between the cystoids (in a restricted sense) and the blastoids.

Other papers could be discussed here; but these above have treated the Cystoidea as an entity, whereas many lesser contributions have been concerned with only a part of the class.

CLASSIFICATION ADOPTED IN TREATISE

GENERAL DISCUSSION

The classification adopted here differs in some respects from any previously presented. Except for the inclusion of the Blastoidea, Jaekel's (71) diagnoses were mostly sound and his criteria clearly stated, insofar as suprageneric taxa were concerned. Unfortunately, the generic content of each taxon was not complete, and generic distinctions were sketchy or omitted.

No single morphological character will suffice to differentiate all the families. Criteria employed for the families in one superfamily are not applicable to those in another superfamily. To judge from the morphological extremes included therein, some superfamilies are taxonomically more discrete than others. Similarly, some families are composed of very diverse genera, whereas others contain closely similar genera. Monofamilial superfamilies and monogeneric families serve to emphasize the inadequacy of the fossil record. Our knowledge of the Callocystitidae, probably the best understood of families, appears to have been the result of fortuitous availability of good specimens rather than innate qualities of the cystoids concerned.

Inasmuch as cystoids became extinct in the mid-Paleozoic, their physiology, specific variation, and diagnostic features must be inferred, in many cases from an insufficient sample of the population. The criteria based on the fossils are undoubtedly artificial to some degree. Nevertheless, the separation of the two orders on the basis of the thecal pores has been granted wide acceptance. As it has subsequently developed, the choices of names for them have priority but little else in their favor.

The Rhombifera have thecal pores extending from one plate to another, but not all genera exhibit rhombic arrangements. And the Diploporita have thecal pores confined to individual plates, but not all genera have these developed as diplopores. Both orders contain some cystoids with very regular disposition of thecal plates and some with irregular. The number of thecal pores varies greatly in each order. Some Rhombifera and some Diploporita have no column in the adult.

Criteria for dividing the Rhombifera into superfamilies are not the same as those for dividing the Diploporita. The four superfamilies of the Rhombifera are differentiated by the sort of thecal pores and the regularity of the thecal plates. The three superfamilies of the Diploporita are distinguished by the development of the ambulacral system and, to a lesser degree, by the nature of the column and the distribution of thecal pores.

Within superfamilies, the families are defined on various characters, such as number and arrangement of thecal plates, shape of theca, size of periproct, development of ambulacra, number of brachioles, number and location of rhombs or diplopores, and development of column.

Although the effort may be somewhat discretionary, the Systematic Descriptions contains in the Cystoidea a key to all families and in each family a key to the firmly established genera. These should prove useful to the beginning student and may be valuable to the advanced worker in gauging the validity of the current classification and in formulating additional emendations. The keys constitute a compendium of the taxonomy adopted in the *Treatise.*

ORDER RHOMBIFERA

The Rhombifera are a group of cystoids in which the thecal pores extend from one plate to another, being normally shared equally by the two plates. Most cystoids of the order have the pores, called dichopores, aligned in rhombs, but the Polycosmitidae are an exception. The Rhombifera were clearly separated from the Diploporita when the fossil record starts in the Lower Ordovician (Fig. 54), so that a previous long history may be inferred. The order reached its maximum diversity in Middle Ordovician, but continued to produce new genera throughout the Silurian and much of the Devonian. The last surviving cystoid was the rhombiferan *Strobilocystites* from the Upper Devonian of Iowa.

The basis for differentiating superfamilies was indicated long ago by MÜLLER (90). It is rather remarkable that, among the relatively few cystoids known in his time, he had representation of the different superfamilies, and that he was discerning enough to discover the key character. Subsequently, taxonomic names were devised to fit the categories set up by MÜLLER.

SUPERFAMILY GLYPTOCYSTITIDA

The thecal pores of the Glyptocystitida are pore rhombs, typically developed as pectinirhombs. In all the pores are open to the outside, but some have pores that are subcircular, rather than parallel slits, so that the rhombs do not fit the textbook concepts of pectinirhombs.

In addition to the form of the pores, the Glyptocystitida have thecae composed of 24 basic plates (although rare exceptions are found in which one or more plates may be bipartite or tripartite). These plates are disposed more or less in circlets of four basals *(BB),* five infralaterals *(ILL),* five laterals *(LL),* five radials *(RR),* and five orals or deltoids *(OO).* Because of the constant number of the thecal plates, species and genera can be compared in greater detail than those of other superfamilies.

The Glyptocystitida are divisible into two groups (Fig. 57), one characterized by large periprocts containing numerous plates in addition to the anal pyramid and another distinguished by small periprocts containing not more than a single circlet of auxiliary plates around the anal pyramid. The first group includes the Pleurocystitidae, Cheirocrinidae, and Glyptocystitidae. Of these, the Pleurocystitidae is distinctive for having a strongly compressed theca, extremely large periproct, and few pore rhombs. The Cheirocrinidae can be differentiated from the Glyptocystitidae by their shorter ambulacra and fewer brachioles.

The second group, with small subcircular periprocts, includes the Echinoencrinitidae, Callocystitidae, Cystoblastidae, and Rhombiferidae. The first two both have subovate thecae, but can readily be distinguished by shortness of the ambulacra and (in most) the protuberant nature of the periproct region in the Echinoencrinitidae. The Cystoblastidae have a pentremite shape that cannot be confused with that of any other Rhombifera; the theca bears such resemblance to a pentremite blastoid that Jaekel (68, 69, 71) repeatedly emphasized the derivation of the Blastoidea from this family of cystoids. The Rhombiferidae contains only the type genus, *Rhombifera,* which also has a unique shape; the spindle-like theca is futher conspicuous in having the laterals set directly atop the infralaterals with the radials reduced to small plates alternating with the orals, an arrangement not met with in any other cystoid.

SUPERFAMILY HEMICOSMITIDA

The cystoids of the Hemicosmitida exhibit a degree of regularity in the plate pattern, although not as prominent as that in the Glyptocystitida. The chief character lies in the nature of the rhombs, which are numerous and internally like pectinirhombs, but have the pores covered by epitheca. The Hemicosmitida bear close resemblances to crinoids, some more than others, in form of the column and organization of the theca. This similarity is interpreted here as convergence, rather than indicative of close genetic affinity.

The division into families (Fig. 56) is not as sharply defined as in other superfamilies. The Heterocystitidae are readily identified by the 10 plates in the circlet above the basals, as contrasted with the six in the Hemicosmitidae and Caryocrinitidae. Insofar as *Hemicosmites* and *Caryocrinites* are concerned, the differences are clear; in the latter, the brachioles lie at the borders of a "tegmen" formed by modified covering plates, which roof over the ambulacral grooves. The other genera of the same families, however, are not so definitely of one or the other type; the "tegmen" of some is much reduced and the ambulacra rather closely set, so that classification becomes a matter of preference. As a result, the contents of the Hemicosmitidae and Caryocrinitidae in the *Treatise* do not conform in all respects to any previously presented. The taxonomic treatment of these cystoids offers fertile ground for further investigation.

SUPERFAMILY POLYCOSMITIDA

Of all superfamilies of the Rhombifera, the Polycosmitida is the one least known because of the scarcity of complete specimens and well-preserved structures. The thecal pores are the openings of inclined canals, disposed symmetrically with respect to plate sutures but not connected by preserved inside or outside tangential pore canals. Pore rhombs are numerous and apparently present on all sides of thecal plates.

In the Polycosmitidae the pores are arranged in rows that outline rhombic areas, whereas in the Stichocystidae they are irregularly placed within sectors of the plates so as to fill the rhombic areas. *Polycosmites,* the only genus of its family, is known only from isolated plates. If complete thecae are found, perhaps other criteria may enter into the familial diagnoses.

The pore structure, on which this superfamily is based, seems to be intermediate between that of the Hemicosmitida and that of the Caryocystitida. The paleontological record, however, does not suffice to warrant phylogenetic conclusions.

SUPERFAMILY CARYOCYSTITIDA

In the Caryocystitida, the ends of the dichopores open to the interior of the theca and the tangential canals linking paired pores lie beneath a layer of epitheca. Pairs of pores may be linked by a single tangential canal (simple) or by more than one (compound). Where the epitheca is not preserved, the tangential canals display a superficial resemblance to the pore slits in conjunct pectinirhombs of the Glyptocystitida, although they are more numerous and are underlain by stereotheca.

Two families (Fig.55) are distinguished by the number of thecal plates, the Caryocystitidae with 30 to 120 plates and the Echinosphaeritidae with 200 to more than 800. Other differences are not so incisive. In the Caryocystitidae, the epitheca is seldom preserved and presumably was thinner or more incompletely calcified than that of the Echinosphaeritidae, but this has not been proved; the theca is elongate in many genera, but some are ovate and approach the spherical shape of the Echinosphaeritidae; also, the plates tend to be arranged in circlets and to be disposed in alternating position, as opposed to the irregular pattern of the tiny plates in the other family.

ORDER DIPLOPORITA

The Diploporita are a group of cystoids in which the thecal pores are nearly all confined to individual plates. Commonly, these pores are paired as diplopores, but in some genera the canals are irregular, do not divide in two, and are called haplopores. It is unsafe to assert that diplopores or haplopores are the ancestral form of cystoid pores, for the record is too fragmentary to support either contention.

Certain incompletely preserved fossils from the Middle Cambrian of Bohemia may belong to the Diploporita, and they are assigned with question in the *Treatise*. Unquestionable Diploporita are present in Lower Ordovician deposits. The order extends into the Lower Devonian. Like the Rhombifera, the order attained maximum diversity in the Ordovician.

The three superfamilies (Fig. 54) are classified by form of the ambulacra, which are very short in the Sphaeronitida, long in the Glyptosphaeritida, and intermediate and quite regular in the Asteroblastida. Other superfamilial characters are the shape of the theca, distribution of the thecal pores, and development of the column.

SUPERFAMILY GLYPTOSPHAERITIDA

Genera of the Glyptosphaeritida (Fig. 59) have long ambulacra, variously developed in the families. The theca varies in shape from irregular and saclike to ovate or globular with a high degree of symmetry. Pores are present as diplopores, typically with peripores highly developed, invariably found in the ambulacra-bearing plates and in some cystoids on the interambulacral areas as well.

Ambulacra are spiral in the Gomphocystitidae, long, straight, and regularly provided with short lateral branches in the Dactylocystidae, long and zigzag, with regularly alternating branches in the Protocrinitidae, and long, irregularly branched in the Glyptosphaeritidae. The Glyptosphaeritidae also have an apple-shaped theca, anchored by a short, small column; except for the peristomial covering plates, these cystoids show weak expression of symmetry. The Gomphocystitidae, shaped like an inverted pear, have no true column, although the theca is aborally prolonged as a stemlike section. The Protocrinitidae and Dactylocystidae have a high degree of pentameral symmetry, especially the latter; both have the ambulacra resting on special alternating thecal plates known as adambulacrals. Primary distinction lies in the distribution of diplopores, which occur in interambulacral and ambulacral plates in the Protocrinitidae, but are restricted to the adambulacrals in the Dactylocystidae. In addition, the main ambulacral grooves in the latter are very straight, and the bordering adambulacral plates are regularly shaped and distinctly different from the interambulacral plates.

SUPERFAMILY SPHAERONITIDA

The brachioles are closely set around the peristome in representatives of the Sphaeronitida so that the ambulacra, if any can be distinguished, are quite short. Most of the cystoids are attached by the base of the theca, at least as adults, and show no trace of a column. Thecal pores are developed either as diplopores or as haplopores.

The two families (Fig. 58) are separated on the basis of the ambulacra. In the Sphaeronitidae, the ambulacra branch directly from the corners of the peristome, in characteristic patterns for the genera; in the Aristocystitidae, however, no extensions of any kind are known for the food grooves, and the brachiole facets are set adjacent to the peristome. Whereas the Sphaeronitidae are rather similar in form, the Aristocystitidae contain a heterogeneous assemblage showing extremes not only in shape of the theca but also in kinds of thecal pores. Many of the genera are poorly known. Any key to the established genera is highly artificial at this time.

The inconsistent order Amphoridea, conceived by HAECKEL (58) to embrace markedly dissimilar echinoderms, including some of his imaginary genera, met with obstacles to acceptance from the start. The association of the Aristocystitidae with carpoids, eocrinoids, and paracrinoids was unnatural, so that JAEKEL (69) was fully justified in removing so-called amphorideans to the Diploporita. From time to time, BATHER (10-13) defended the Amphoridea, but at last dropped the group in his final (15) classification of the cystoids. Nevertheless, BASSLER & MOODEY (7) retained it in their compilation of Paleozoic Pelmatozoa. REGNÉLL (99) stoutly denied the desirability for such a "fatal" taxon, and it seems to have been suppressed effectively.

SUPERFAMILY ASTEROBLASTIDA

Cystoids placed in the Asteroblastida have in common a bud- or pentremite-shaped theca, small column, straight ambulacra, diplopores confined to interambulacral plates, and a high degree of pentameral symmetry. The superfamily is of particular interest because some authors have proposed that it contains the ancestral form of the blastoids. Undoubtedly, the thecal shape and strong symmetry convey an impression of a blastoid lacking only the hydrospires. This particularly applies to *Asteroblastus,* just as it did to *Cystoblastus* among the Rhombifera. As early as 1874, SCHMIDT (114) concluded that *Asteroblastus* was a transitional form. BERGOUNIOUX (16) included the genus in his chapter of the *Traité de Zoologie* on the blastoids. WANNER (1951) thought that, if blastoids did originate from known cystoids, only the Asteroblastidae contained the required structures. On the other hand, JAEKEL (71) was quite as firmly convinced that the Blastoidea descended from *Cystoblastus.*

In the Asteroblastidae, the ambulacra are broad, the brachioles relatively few, and the thecal plates organized comparable to those in the Glyptocystitida. In direct contrast, in the Mesocystidae, the ambulacra are very narrow, the brachioles numerous (as many as 1,000), and the thecal plates exceptionally numerous, tiny, and irregularly disposed. Insofar as known, both families are present in Early Ordovician, and the Cystoblastidae may have lived on into Middle Ordovician time.

SUMMARY OF CHARACTERS

The main characters of the orders and superfamilies of cystoids recognized in the *Treatise* are summarized in Table 6 on p. S164. Certain other characters are used in diagnoses of superfamilies in one order but not in the other. These appear in the Key to Orders, Superfamilies, Families, and Subfamilies on p. S167.

ECHINODERMS FORMERLY INCLUDED IN CYSTOIDEA

Acanthocystites BARRANDE, 1887 [=*Acanthocystis* BATHER, 1889 (*nom. van. pro Acanthocystites* BARRANDE, 1887), *non* CARTER, 1863, *nec* HAECKEL, 1887 (*nom. null. pro Acanthocyrtis* HAECKEL, 1881), *nec* HAECKEL, 1896 (*nom. nud.*)] .... Eocrinoidea

Achradocystites VOLBORTH, 1870 [=*Achradocystis* HAECKEL, 1896 (*nom. van.*)] .. Paracrinoidea

Amygdalocystites BILLINGS, 1854 [=*Amygdalocystis* CARPENTER, 1891 (*nom. van.*); *Ottawacystites* WILSON, 1946] .... Paracrinoidea

Anatiferocystis CHAUVEL, 1941 .... Stylophora

Anomalocystites HALL, 1859 [=*Anomalocystis* BATHER, 1889 (*nom. van.*); *Anomocystis* HAECKEL, 1896 (*nom. null. pro Anomalocystites* HALL)] .... Stylophora

TABLE 6. *Characters of Cystoid Orders and Superfamilies*

Order	RHOMBIFERA				DIPLOPORITA		
Superfamily	Glypto-cystitida	Hemicos-mitida	Polycos-mitida	Caryo-cystitida	Glypto-sphaer-itida	Sphaer-onitida	Astero-blastida
Thecal plate arrangement	Regular	Regular	Irregular	Irregular	Irregular	Irregular	Some regular
Kind of pores	Pectini-rhombs, pores open	Inner tan-gential canals, pores covered	No inner or outer tangenti-al canals calcified	Subepi-thecal tangential canals, pores inside	Diplo-pores, dispersed or ambul-acral	Diplo-pores or haplo-pores, dispersed	Diplopores on special interamb-ulacral plates
Number of pore units	Few in most	Many	Numerous	Very numerous	Numerous	Numerous	Relatively few
Column	Present, normally flared at theca	Present, much like crinoid column	Weakly developed	Weakly developed, absent in some	Small, absent in some	Absent	Present, weakly developed

Anomocystis Jaekel, 1918 [*non* Haeckel, 1896 (*nom. null. pro Anomalocystites* Hall, 1859)] .... Stylophora

Archaeocystites Barrande, 1887 [=*Archaeocystis* Haeckel, 1896 (*nom. van.*)] ?Eocrinoidea

Ascocystites Barrande, 1887 [=*Ascocrinus* Barrande, 1887, *non* Tromelin & Lebesconte, 1876 (*nom. nud.*); *Ascocystis* Bather, 1889 (*nom. van.*)] .... Eocrinoidea

Astrocystites Whiteaves, 1897 .... Edrioblastoidea

Ateleocystites Billings, 1858 [=*Ateleocystis* Lindström, 1888; *Atelecystis* Bather, 1889 (*nom. null.*); *Atelocystis* Haeckel, 1896 (*nom. null.*)] .... Stylophora

Balanocystites Barrande, 1887 [=*Balanocystis* Haeckel, 1896 (*nom. van.*)] .... Stylophora

Batherocystis Bassler, 1950 .... Eocrinoidea

Belemnocystites Miller & Gurley, 1894 [=*Belemnocystis* Bather, 1900 (*nom. van.*); *Myeinocystites* Strimple, 1953] .... Homoiostelea

Billingsocystis Bassler, 1950 .... Paracrinoidea

Bockia Gekker, 1938 .... Eocrinoidea

Canadocystis Jaekel, 1900 [=*Sigmacystis* Hudson, 1911] .... Paracrinoidea

Cardiocystites Barrande, 1887 [=*Cardiocystis* Haeckel, 1896 (*nom. van.*)] .... Eocrinoidea

Ceratocystis Jaekel, 1900 .... Stylophora

Cigara Barrande, 1887 .... Eocrinoidea

Columbocystis Bassler, 1950 .... Eocrinoidea

Comarocystites Billings, 1854 [=*Comarocystis* Carpenter, 1891 (*nom. van.*)] .... Paracrinoidea

Cothurnocystis Bather, 1913 .... Stylophora

Crinocystites Hall, 1867 [=*Crinocystis* Haeckel, 1896 (*nom. van.*)] .... Crinoidea

Cryptocrinites von Buch, 1840 [=*Cryptocrinus* Geinitz, 1846 (*nom. van.*)] .... Eocrinoidea

Cyclocystoides Billings & Salter, 1858 .... Cyclocystoidea

Decacystis Gislén, 1927 .... Homostelea

Dendrocystites Barrande, 1887 [=*Dendrocystis* Bather, 1889 (*nom. van.*)] .... Homoiostelea

Dendrocystoides Jaekel, 1918 .... Homoiostelea

Enoploura Wetherby, 1879 [=*Enopleura* Springer, 1913 (*nom. van.*)] .... Stylophora

Eocystites Billings, 1868 [=*Eocystis* Bather, 1900 (*nom. van.*) *non* Haeckel, 1896 (*gen. hypoth.*)] .... Eocrinoidea

Foerstecystis Bassler, 1950 Eocrinoidea

Gogia Walcott, 1917 .... Eocrinoidea

Gyrocystis Jaekel, 1918 .... Homostelea

Iowacystis Thomas & Ladd, 1926 .... Homoiostelea

Kirkocystis Bassler, 1950 .... Stylophora

Lagynocystis Jaekel, 1918 .... Stylophora

Lapillocystites Barrande, 1887 .... Eocrinoidea

Larites de Gregorio .... Unrecognizable

Lepidocystis Foerste, 1938 .... Lepidocystoidea

Lichenoides Barrande, 1846 [=*Lichenocystis* Haeckel, 1896 (*nom. van.*)] .... Eocrinoidea

Lingulocystis Thoral, 1935 .... Eocrinoidea

Lodanella Kayser, 1885 .... Crinoidea

Lysocystites S. A. Miller, 1889 [*nom. subst. pro Echinocystites* Hall, 1865, *non* Thomson, 1861] [=*Lysocystis* Bather, 1897 (*nom. van.*); *Echinocystis* Haeckel, 1896 (*nom. van. pro Echinocystites* Hall), *non* Gregory, 1897 (*nom. van. pro Echinocystites* Thomson); *Aethocystites* S. A. Miller, 1892; *Aethocystis* Bather, 1900 (*nom. van.*)] .... Eocrinoidea

Macrocystella Callaway, 1877 .... Eocrinoidea

Malocystites Billings (in Chapman), 1857 [=*Malocystis* Carpenter, 1891 (*nom. van.*)] .... Paracrinoidea

Mimocystites Barrande, 1887 [=*Mimocystis* Carpenter, 1891 (*nom. van.*)] .... Eocrinoidea

Mitrocystites Barrande, 1887 [=*Mitrocystis* Bather, 1889 [*nom. van.*] .... Stylophora

Narrawayella Foerste, 1920 .... Cyclocystoidea

Neocystites Barrande, 1887 [=*Neocystis*

Bather, 1889 *(nom. van.)*] .... Probably a root
Palaeocystites Billings, 1858 .... Eocrinoidea
Peltocystis Thoral, 1935 .... Stylophora
Phyllocystis Thoral, 1935 .... Stylophora
Pilocystites Barrande, 1887 .... Eocrinoidea
Placocystella Rennie, 1936 .... Stylophora
Placocystites de Koninck, 1869 [=*Placocystis* Haeckel, 1896 *(nom. van.)*] .... Stylophora
Platycystites S. A. Miller, 1889 [=*Platycystis* Bather, 1900 *(nom. van.), non* Léger, 1892] .... Paracrinoidea
Polyptychella Jaekel, 1918 .... Eocrinoidea
Protocystites Hicks, 1872 [*non* Salter, 1865 *(nom. nud.)*; =*Protocystis* Bather, 1900 *(nom. van.), non* Wallich, 1862] .. ?Eocrinoidea
Rhenocystis Dehm, 1932 .... Stylophora
Rhipidocystis Jaekel, 1901 .... Eocrinoidea
Savagella Foerste, 1920 .... Cyclocystoidea
Schuchertocystis Bassler, 1950 .... Paracrinoidea
Sinclairocystis Bassler, 1950 .... Paracrinoidea
Springerocystis Bassler, 1950 .... Eocrinoidea
Staurosoma Barrande, 1887 .... Crinoidea
Syringocrinus Billings, 1859 .... Homoiostelea
Tiaracrinus Schultze, 1867 .... Crinoidea
Trachelocrinus Ulbich, 1929 .... ?Eocrinoidea
Trochocystites de Verneuil & Barrande, 1860 [*non* Barrande, 1859 *(nom. nud.)*; =*Trigonocystis* Haeckel, 1896; *Trochocystis* Haeckel, 1896 *(nom. van.)*] .... Homostelea
Trochocystoides Jaekel, 1918 .... Homostelea
Wellerocystis Foerste, 1920 .... Paracrinoidea

JUNIOR SYNONYMS

Aethocystites S. A. Miller, 1892 [=*Lysocystites* S. A. Miller, 1889] .... Eocrinoidea
Amorphocystites Jaekel, 1896 = *Caryocystites* von Buch, 1846
Anthocystis Haeckel, 1896 = *Callocystites* Hall, 1852
Citrocystis Haeckel, 1896 = *Echinosphaerites* Wahlenberg, 1818
Crystallocystis Haeckel, 1896 = *Echinosphaerites* Wahlenberg, 1818
Dagoncystis Chauvel, 1941 (obj.) = *Pseudaristocystis* Sun, 1936
Deutocystites Barrande, 1887 = *Echinosphaerites* Wahlenberg, 1818
Dipleurocystis Jaekel, 1918 = *Pleurocystites* Billings, 1854
Dorycystites Kloucek, 1917 = *Calix* Rouault, 1851
Ennaecystis Haeckel, 1896 = *Caryocrinites* Say, 1825
Eocrinus Jaekel, 1918 [=*Gogia* Walcott, 1917] .... Eocrinoidea
Gonocrinites Eichwald, 1840 = *Echinoencrinites* von Meyer, 1826
Heliopirum Haeckel, 1896 = *Heliocrinites* Eichwald, 1840
Hexalacystis Haeckel, 1896 = *Hemicosmites* von Buch, 1840
Leucophthalmus Koenig, 1825 = *Echinosphaerites* Wahlenberg, 1818
Meekocystis Jaekel, 1899 = *Lepadocystis* Carpenter, 1891
Megacystites Hall, 1865 = *Holocystites* Hall, 1864
Ovocystis Reed, 1917 = *Sinocystis* Reed, 1917
Palmacystis Haeckel, 1896 = *Eucystis* Angelin, 1878
Phacocystis Haeckel, 1896 (obj.) = *Pseudocrinites* Pearce, 1842
Sycocystites von Buch, 1846 = *Echinoencrinites* von Meyer, 1826
Trimerocystis Schuchert, 1904 = *Pseudocrinites* Pearce, 1842
Trinemacystis Haeckel, 1896 = *Echinosphaerites* Wahlenberg, 1818

NOMINA NUDA

Genera which clearly lack description, notes, or illustration are designated as *nom. nud.*; genera which are described and founded on hypothetical species based on nonexistent fossils are designated as *gen. hypoth.* The latter are creations of Haeckel, 1896.

Amphoraea Haeckel, 1896 *(gen. hypoth.)*
Anthocystites Bernard, 1893 *(nom. nud.)*
Archaeocystis Haeckel, 1896 *(gen. hypoth.)*
Ascocrinus Tromelin & Lebesconte, 1876 *(nom. nud.)*
Chilocystis Perner, 1911 *(nom. nud.)*
Eocystis Haeckel, 1896 [*gen. hypoth.*; *non* Bather, 1900 (*nom. van. pro Eocystites* Billings, 1868)]
Lagarocystis Jaekel, 1899 *(nom. nud.)*
Microcystites Ulrich, 1880 *(nom. nud.)*
Palamphora Haeckel, 1896 *(gen. hypoth.)*
Pentactaea Haeckel, 1896 *(gen. hypoth.)*
Pomonites Haeckel, 1896 *(gen. hypoth.)*
Proteroblastus Jaekel, 1895 *(nom. nud.)*
Protocystites Salter, 1865 *(nom. nud.)*
Psolocystis Haeckel, 1896 *(gen. hypoth.)*
Stephanamphora Haeckel, 1896 *(gen. hypoth.)*
Thuriocystis Haeckel, 1896 [*nom. nud.* (Jena Zeitschr.); *gen. hypoth.* (Festschr. Gegenb.)]
Trochocystites Barrande, 1859 *(nom. nud.)*

PREOCCUPIED NAMES

Craterina Barrande, 1887 (*non* Bory, 1826, *nec* Curtis, 1826, *nec* Gruber, 1884) = *Codiacystis* Jaekel, 1899
Mesites Hoffman, 1866 (*non* Schoenherr, 1838, *nec* Geoffroy, 1838, *nec* Jenyns, 1842, *nec* Ludwig, 1893) = *Mesocystis* Bather, 1898

UNRECOGNIZABLE GENERA

Pomocystis Haeckel, 1896 (probably = *Haplosphaeronis* Jaekel, 1926)
Pomosphaera Haeckel, 1896 (probably = *Haplosphaeronis* Jaekel, 1926)

SUMMARY OF CLASSIFICATION AND STRATIGRAPHIC DISTRIBUTION

The tabular outline of classification that follows is accompanied by statement of the stratigraphic range of each taxon as reported and interpreted into terms of Lower, Middle, and Upper parts of periods in accordance with the correlations given in Fig. 53. The bracketed index numbers preceding each taxon are for cross reference to and from the stratigraphic-distribution diagram (Fig. 71); the first of the two numbers are in sequence in the tabular outline and follow the names of the taxa in the diagram, whereas the second numbers are in sequence in the diagram. The numbers in parentheses before the range of each taxon refer to the number of genera; the first indicates well-established genera and the second (if required) the total genera recorded in the *Treatise*.

Genera are plotted on stratigraphic-distribution diagrams in the sections of the systematic descriptions devoted to the various families. These compilations are interpreted into parts of periods in accordance with correlations on p. *S*128-*S*129, as are those for the suprageneric taxa. It is hoped that this summary, like those for other fossil groups in the *Treatise*, will be useful for various purposes.

Suprageneric Taxa of Cystoidea

Cystoidea *(class)* (81, 87). *L.Ord.-U.Dev.* (Fig. 71)
(1-13) Rhombifera *(order)* (46, 51). *L.Ord.-U.Dev.* (Fig. 71).
(2-17) Glyptocystitida *(superfamily)* (30, 33). *L.Ord.-U.Dev.* (Fig. 54, 81)
(3-20) Glyptocystitidae (1). *M.Ord.* (Fig. 57, 81)
(4-21) Cystoblastidae (2). *M.Ord.* (Fig. 57, 81)
(5-23) Rhombiferidae (1). *U.Ord.* (Fig. 57, 81)
(6-18) Cheirocrinidae (1, 3). *L.Ord-L.Sil.* (Fig. 57, 81)
(7-19) Echinoencrinitidae (7, 8). *L.Ord.-U.Sil.* (Fig. 57, 81)
(8-22) Pleurocystitidae (3). *M.Ord.-L.Dev.* (Fig. 57, 81)
(9-24) Callocystitidae (15). *U.Ord.-U.Dev.* (Fig. 57, 81)
(10-28) Hemicosmitida *(superfamily)* (9). *M.Ord.-L.Dev.* (Fig. 54, 116)
(11-29) Hemicosmitidae (3). *M.Ord.-L.Sil.* (Fig. 56, 116)
(12-30) Caryocrinitidae (5). *M.Ord.-L.Dev.* (Fig. 56, 116)
(13-31) Heterocystitidae (1). *M.Sil.* (Fig. 56, 116)
(14-25) Polycosmitida *(superfamily)* (2). *M. Ord.* (Fig. 54, 125)
(15-26) Polycosmitidae (1). *M.Ord.* (Fig. 125)
(16-27) Stichocystidae (1). *M.Ord.* (Fig. 125)
(17-14) Caryocystitida *(superfamily)* (5, 6). *L.Ord.-U.Ord.* (Fig. 54, 125)
(18-15) Caryocystitidae (3, 4). *L.Ord.-U. Ord.* (Fig. 55, 125)
(19-16) Echinosphaeritidae (2). *L.Ord.-U. Ord.* (Fig. 55, 125)
(20-1) Diploporita *(order)* (35, 37). *L.Ord.-L.Dev.* (Fig. 71)
(21-5) Glyptosphaeritida *(superfamily)* (10). *L.Ord.-M.Sil.* (Fig. 54, 131)
(22-6) Glyptosphaeritidae (1). *L.Ord.-U. Ord.* (Fig. 59, 131)
(23-8) Dactylocystidae (3). *M.Ord.-U.Ord.* (Fig. 59, 131)
(24-7) Protocrinitidae (4). *L.Ord.-M.Ord.* (Fig. 59, 131)
(25-9) Gomphocystitidae (2). *M.Ord.-M. Sil.* (Fig. 59, 131)
(26-2) Sphaeronitida *(superfamily)* (21, 23). *L.Ord.-L.Dev.* (Fig. 54, 139)
(27-3) Aristocystitidae (10, 12). *M.Ord.-M. Sil.* (Fig. 58, 139)
(28-4) Sphaeronitidae (11). *L.Ord.-L.Dev.* (Fig. 58, 139)
(29-10) Asteroblastida *(superfamily)* (4). *L. Ord., ?M.Ord.* (Fig. 54)
(30-12) Asteroblastidae (3). *L.Ord., ?M. Ord.* (Fig. 71)
(31-11) Mesocystidae (1). *L.Ord.* (Fig. 71)

SYSTEMATIC DESCRIPTIONS

Class CYSTOIDEA von Buch, 1846

[*nom. correct.* NICHOLSON, 1879 (*pro* Cystideen VON BUCH, 1846)] [=Cystideae FORBES, 1848; Cystidea HALL, 1847; Cystoidia DELAGE & HÉROUARD, 1903; Hydrophoridea ZITTEL, 1903]

Calcareous plates around body constituting theca that extends to mouth, not differentiated into dorsal calyx and ventral tegmen; thecal plates penetrated from within theca by pores, either perforating plates or terminating subepithecally, never provided with inward radial structures like hydrospires. Ambulacra recumbent on surface of theca and, with possible exception of *Cystoblastus,* exothecal, only openings being those of ambulacral or food grooves leading to mouth; flooring plates, if present, biserially arranged. Brachioles composed of biserial plates, groove covered by tiny biserial plates, unbranched except in *Caryocrinites,* in which brachioles are developed as arms (biserially plated) bearing pinnules (biserially plated). Column present in most forms, in some shed early in ontogeny, in a few perhaps never developed. *L.Ord.-U. Dev.*

To the name of this class could be appended numerous emendations, altering its content by enlargements, restrictions, and revisions, so as to approach the form here considered definitive. The foremost emendations are those of Bather in 1899 (9), who published the first comprehensive classification and review; Jaekel (69), who abandoned the Aporita and Amphoridea and omitted the Carpoidea, formally defined by him later (70); Bather (10), who gave extensive treatment of the cystoids in a textbook that strongly influenced the concept of the class for many years; Jaekel (70), who published a full classification of the cystoids with formal separation of the Eocrinoidea; Bather (15) in a review and revision of the class in the *Encyclopaedia Britannica;* and Regnéll (99), who excised the Paracrinoidea and revised the Pelmatozoa. To the list of emendations could be added those of other authors, who shaped parts of the class into definitive form: Neumayr (91), S. A. Miller (85), Bernard (17), Bather (11, 12), Broili-Zittel (27), Bassler (5), and Bassler & Moodey (7). With all these emendations to which the Cystoidea have been subjected, the class, as herein conceived, nevertheless differs in minor points from any previously published. In general, it is treated much as by Jaekel in 1918 (71) but without inclusion of the Blastoidea.

The stratigraphic distribution of supra-generic groups of cystoids is shown in Figure 71.

Key to Cystoid Orders, Superfamilies, Families, and Subfamilies

1. Thecal pores developed as rhombs, with units extending across sutures .... *Order* Rhombifera, 2

   Thecal pores developed as units normally contained within plates, commonly as diplopores, rarely extending across sutures .... *Order* Diploporita, 14

2. Theca composed of 4 *BB*, 5 *ILL*, 5 *LL*, 5 *RR*, and 5 *OO* (with rare exceptions); rhombs as distinct pectinirhombs on particular sutures, outer surface with well exposed slits *Superfamily* Glyptocystitida, 3

   Theca composed of 4 *BB*, 6 to 10 *LL*, 8 or more *LL*, several *RR*; rhombs with inner side of strong folds or laminae perpendicular to sutures, outer side of pores (covered by stereom or epitheca) each surrounded by a rim (or divided into 2 or more smaller pores) .... *Superfamily* Hemicosmitida, 10

   Theca composed of numerous, irregularly arranged plates; pore rhombs on all sides of thecal plates, pores inclined and not connected by inside or outside calcareous tubes .... *Superfamily* Polycosmitida, 12

   Theca composed of numerous, irregularly arranged plates; pores connected by outer covered tubes *Superfamily* Caryocystitida, 13

3. Periproct large, containing numerous plates 4

   Periproct small, anal pyramid surrounded by not more than one circlet of auxiliary plates 6

4. Theca strongly compressed, periproct comprising most of one side of theca, 3 rhombs or less .... *Family* Pleurocystitidae

   Theca ovate, periproct much smaller than one side of theca, numerous rhombs 5

5. Ambulacra short, limited to crown of theca, brachioles relatively few .... *Family* Cheirocrinidae

   Ambulacra long, extending down over theca, brachioles numerous .... *Family* Glyptocystitidae

6. Theca shaped like a pentremite or bud, with marked pentameral symmetry; ambulacra very large, tapering, tongue-shaped; rhombs numerous .... *Family* Cystoblastidae

   Theca ovate, spindle-shaped, globular, or biconvex, but not pentremite-shaped; ambulacra not broad and tongue-shaped; rhombs not very numerous, in many reduced to 3 7

7. Ambulacra short, restricted to crown of theca 8

   Ambulacra long, extending down over theca; periproct never produced .... *Family* Callocystitidae, 9

8. Theca with shape of quadrate spindle; *ILL* and *LL* comprising sides of theca, *RR*

and *OO* alternating small plates in circlet at crown; 3 long vertical rhombs on *LL* set directly above 3 long rhombs on *ILL*; periproct small .... *Family* Rhombiferidae

Theca ovate to subglobular; *RR* large; periproct typically produced .... *Family* Echinoencrinitidae

9\. Theca ovate or globular; 4 or 5 divided ambulacra; brachioles small, widely spaced; *LL* intercalated deeply into *ILL* circlet, as many as 3 *LL* in contact with *BB* .... *Subfamily* Callocystitinae

Theca ovate or biconvex; 2 to 4 undivided, strongly protuberant ambulacra; brachioles very numerous, closely spaced; plate circlets variously modified by shape of theca .... *Subfamily* Staurocystinae

Theca ovate; 4 or 5 undivided (except in *Strobilocystites*) ambulacra not protuberant; brachioles relatively widely spaced; *ILL* forming closed circlet .... *Subfamily* Apiocystitinae

10\. Ten *ILL* in circlet above *BB* .... *Family* Heterocystitidae

No more than 6 *ILL* in circlet above *BB* .. 11

11\. Brachioles few, clustered at top with very short ambulacral grooves; periproct lateral .... *Family* Hemicosmitidae

Brachioles at lateral borders of covering plates (so-called "tegmen"), which forms roof over ambulacral grooves; periproct at upper border of theca .... *Family* Caryocrinitidae

12\. Pores not arranged in rows .... *Family* Polycosmitidae

Pores in radial rows ...... *Family* Stichocystidae

13\. Theca ovate or elongate; 30 to about 120 plates, tending to be arranged in circlets, alternating; epitheca seldom preserved .... *Family* Caryocystitidae

Theca bullet-shaped or spheroidal; 200 to more than 800 tiny irregularly polygonal plates; epitheca preserved in many specimens as smooth, concentrically striped layer .... *Family* Echinosphaeritidae

14\. Theca ovate, saclike, pear-shaped, or globular; ambulacra radial, extending over theca, with alternating lateral branches (single or in groups) to brachioles; most forms stemmed, few becoming free as adults; diplopores restricted to ambulacral plates or spread out over rest of theca .... *Superfamily* GLYPTOSPHAERITIDA 15

Theca with one of several shapes, ovate to conical, with one or other end expanded in some; ambulacra with brachioles concentrated near mouth, not extending over theca; most attached by base of theca; pores irregularly distributed over theca .... *Superfamily* SPHAERONITIDA 16

Theca bud-shaped or bullet-shaped with flat base; ambulacra straight, pentamerally arranged, distally resting on *RR*; stemmed; diplopores only on interambulacral plates .... *Superfamily* ASTEROBLASTIDA 17

15\. Theca apple-shaped; stem short; ambulacral grooves long, twisted or zigzag, with few irregularly alternating brachioles, ends may branch to several brachioles; pores in many forms radially disposed, in some concentrated in upper parts of plates .... *Family* Glyptosphaeritidae

Theca saclike, bullet-shaped, or ovate; stemmed as young, but may be free as adult; ambulacral grooves very long, slightly zigzag, with regularly alternating branches leading to brachioles, may extend to aboral end; pores distributed over both ambulacral and interambulacral plates .... *Family* Protocrinitidae

Theca ovate to pear-shaped; stemmed or free; ambulacra long, straight, brachioles at ends of short, very regularly alternating branches, so that those of each ambulacrum are arranged in 2 straight rows; brachiole-bearing plates regularly alternating, bearing diplopores; interambulacral plates irregularly arranged, without diplopores .... *Family* Dactylocystidae

Theca shaped like inverted pear; no special columnar section known; ambulacra spiral, branches (if present) from only one side; brachioles unknown; diplopores distributed over theca .... *Family* Gomphocystitidae

16\. Ambulacral grooves distinctly branched immediately from peristome; numerous brachioles in each radius .... *Family* Sphaeronitidae

No extensions of any kind known in food grooves; at most, one brachiole in each radius, number may be reduced to 2, no brachioles or attachment known for some forms .... *Family* Aristocystitidae

17\. Theca bud-shaped; ambulacra broad, leaflike; brachioles relatively few; 4 *BB*, 6 *ILL*, other plates in circlets, and several additional intervening plates .... *Family* Asteroblastidae

Theca bullet-shaped, base rather flat; ambulacra very narrow, long, straight; numerous brachioles; plates small, exceptionally numerous .... *Family* Mesocystidae

Order RHOMBIFERA Zittel, 1879

[*nom. correct.* BATHER, 1899 (*pro* Rhombiferi ZITTEL, 1879)] [=Rhombiporitidae+Taxiporitidae EICHWALD, 1860; Dichoporita JAEKEL, 1899]

Thecal pores developed as dichopores, arranged in rhombs in which each unit or dichopore is shared by 2 adjacent plates. *L.Ord.-U.Dev.*

The structure of the rhombs varies in the order and serves as the character by which the four superfamilies can be differentiated. The number of rhombs also varies, from very few in most of the Glyptocystitida to very numerous in the Caryocystitida.

The thecal plates are regularly arranged in the cystoids included in the Glyptocystitida and Hemicosmitida, but not in the Polycosmitida and Caryocystitida. A column is present in most of the Rhombifera, but is absent in some of the Caryocystitida.

Insofar as known, the Rhombifera includes the last surviving cystoids.

Superfamily GLYPTOCYSTITIDA Bather, 1899

[*nom. transl.* REGNÉLL, 1945, p. 68 (*ex* Glyptocystidae BATHER, 1899, p. 920)] [=Regularia JAEKEL, 1899, p. 193; superfamily Glyptocystidea BATHER, 1913, p. 433]

Theca in most genera composed of four *BB*, five *ILL*, five *LL*, five *RR*, and five *OO*, although plate *O1* is tripartite in many genera and *R1* is bipartite in some; a few anomalous plate divisions known to occur in some specimens. Rhombs developed as distinct pectinirhombs, most as full rhombs and a few as demirhombs, with well-exposed pores or slits. Column present, in most forms with expanded, flexible proximal part. *L.Ord.-U.Dev.*

Within this superfamily certain trends are well demonstrated. First, the number of rhombs tends to be reduced to three: *B2/IL2*, *L1/R5*, and *L4/R3*. In the strongly modified Pleurocystitidae, the rhombs *L3/L4*, *L1/L2*, and *B2/IL2* show persistence in that order. Second, the periproct tends to show specialization; in the Pleurocystitidae and to a lesser degree in the Glyptocystitidae and Cheirocrinidae, it is enlarged and filled with numerous small plates (periproctals) in addition to the anal pyramid; in the Echinoencrinitidae it tends to be prolonged and protuberant, but with a small opening. Third, the pore rhombs become specialized, whereby one of the halves is surrounded by a rim (e.g., *Pseudocrinites, Lovenicystis*) or even reduced to a small circular opening with a tubular border (e.g., *Jaekelocystis*). Fourth, the hydropore changes from an elongate slit bisected by a suture through *O1* to two separate openings (e.g., *Lipsanocystis, Strobilocystites*) or even reduced to one large sievelike opening, perhaps combined with the gonopore (e.g., *Jaekelocystis*). On the other hand, there is no consistent progression with regard to ornamentation of plates or size of theca.

Because the plates occur with regularity, they can be compared readily from one genus to another. As a result, this superfamily is best known and understood. It also has, perhaps, the longest range, definitely so if the Cambrian Aristocystitidae are discounted as unsubstantiated cystoids; at any rate, this superfamily contains the last surviving cystoids known, from the Upper Devonian of Iowa.

The stratigraphic distribution of genera belonging to the Glyptocystitida is shown in Figure 72.

Family GLYPTOCYSTITIDAE Bather, 1899

[*nom. correct.* KESLING, herein (*pro* Glyptocystidae BATHER, 1899, p. 920)]

Theca more or less ovate, not compressed. Periproct large, containing numerous plates in addition to anal pyramid, but not comprising most of one side of theca. Pore rhombs numerous. Ambulacra long, extending down over theca ("recumbent"), provided with numerous short alternating branches to brachiole facets; one or more ambulacra extending to *BB* in adults. *M.Ord.*

This family is known only from North America. The species include the type, *G. multiporus* BILLINGS, and the more recently described *G. batheri* SINCLAIR, *G. grandis* SINCLAIR, *G. regnelli* SINCLAIR, and *G. ehlersi* KESLING. Aside from the circumstance that ambulacrum IV is much shorter in *G. regnelli* and *G. ehlersi* than in the other species, there seems no grouping that would serve a useful taxonomic purpose. The family, therefore, remains monogeneric.

Glyptocystites BILLINGS, 1854, p. 215 [**G. multiporus*; OD] [=*Glyptocystis* BATHER, 1900, p. 64 (*nom. van.*)]. Theca elongate ovate or subpyriform, with *BB* somewhat indented for junction with the column. Rhombs numerous, one-half of each normally bordered by rim ("montidisjunct"), variously developed as full rhombs or demirhombs; rhombs *B2/IL1, B2/IL2, L3/L4, L3/R3, L3/R2, R1/R2, R1/R5, R2/R3,* and *R4/R5* present in all known species, each of which bears one or more additional rhombs. Plates *B2, IL1, IL2,* and *L2* practically meeting at a point; *R2* atop *IL2,* interrupting *LL* circlet; *R1* exceptionally large, probably bipartite. Ambulacra very long except III, which terminates against transverse *L3/R3* rhomb, and IV, which is intermediate in *G. regnelli* and *G. ehlersi.* Flooring plates of ambulacra of 2 sizes, alternately placed, loosely attached to thecal plates and readily scaled off; brachiole facets numerous. Hydropore a long, broadly U-shaped slit and gonopore a small perforation immediately aboral to it, both bisected by suture through tripartite *O1.* Periproct bordered by *IL4, L4,* and *L5.* Proximal part of column with flared, telescoped columnals, apparently originally flexible. Plates ornamented chiefly by irregular radiating ridges. *M.Ord.,* Can.(Que.-Ont.) - USA (Mich.).——Fig. 52,*1-3*; 74,1. *G. ehlersi* Kesling, Trenton, USA(Mich.); 52,*1,* photographs, ×1; 52,*2,* plates drawn with camera lucida; 52,*3,* plate diagram (73); 74,*1a,b,* lat., coated with ammonium chloride and submersed in xylol, ×3.75, showing 2 half-rhombs on *B2* (73).——Fig. 73,*1*; 75,*2.* **G. multiporus,* Trenton, Que.; 73,*1a,b,* plate diagram and oral region (Kesling, n); 75,*2a-c,* oral, lat., and aboral, ×3 (69).

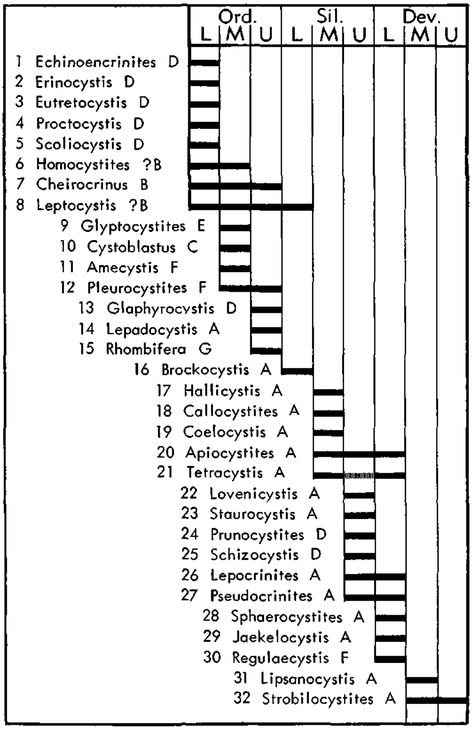


Fig. 72. Stratigraphic distribution of genera belonging to the superfamily Glyptocystitida. Classification of the genera in families is indicated by letter symbols: A—Callocystitidae, B—Cheirocrinidae, C—Cystoblastidae, D—Echinoencrinitidae, E—Glyptocystitidae, F—Pleurocystitidae, G—Rhombiferidae. The following alphabetical list of genera furnishes cross reference to the serially arranged numbers on the diagram (Kesling and Moore, n).

Family CYSTOBLASTIDAE Jaekel, 1899

[Cystoblastidae Jaekel, 1899, p. 222]

Theca shaped like a pentremite or bud, with marked pentameral symmetry. Ambulacra very large, broad and tapering, tongue-shaped, on theca appearing as petals upon radials. Rhombs numerous. *M.Ord.*

This definition of the family differs radically from the original, here translated, "Ambulacra symmetrically developed, with ambulacralia and parambulacralia lying in deep indentations of the *RR*; the last wedged in between the *LL.*"

The original author (Volborth) of *Cystoblastus* had supposed it to be a crinoid intermediate between cystoids and blastoids. From a cross section of one fragment prepared by E. Koken, Jaekel (69) interpreted the pores as leading to folds deep within the theca, the radials as forked plates to accommodate the ambulacra, and the ambulacral plates as incipient blastoid struc-

Generic Names of Glyptocystitida with Index Numbers

Amecystis—11		*Erinocystis*—2		*Leptocystis*—8		*Regulaecystis*—30	
Apiocystites—20		*Eutretocystis*—3		*Lipsanocystis*—31		*Rhombifera*—15	
Brockocystis—16		*Glaphyrocystis*—13		*Lepadocystis*—14		*Schizocystis*—25	
Callocystites—18		*Glyptocystites*—9		*Lovenicystis*—22		*Scoliocystis*—5	
Cheirocrinus—7		*Hallicystis*—17		*Pleurocystites*—12		*Sphaerocystites*—28	
Coelocystis—19		*Homocystites*—6		*Proctocystis*—4		*Staurocystis*—23	
Cystoblastus—10		*Jaekelocystis*—29		*Prunocystites*—24		*Strobilocystites*—32	
Echinoencrinites—1		*Lepocrinites*—26		*Pseudocrinites*—27		*Tetracystis*—21	

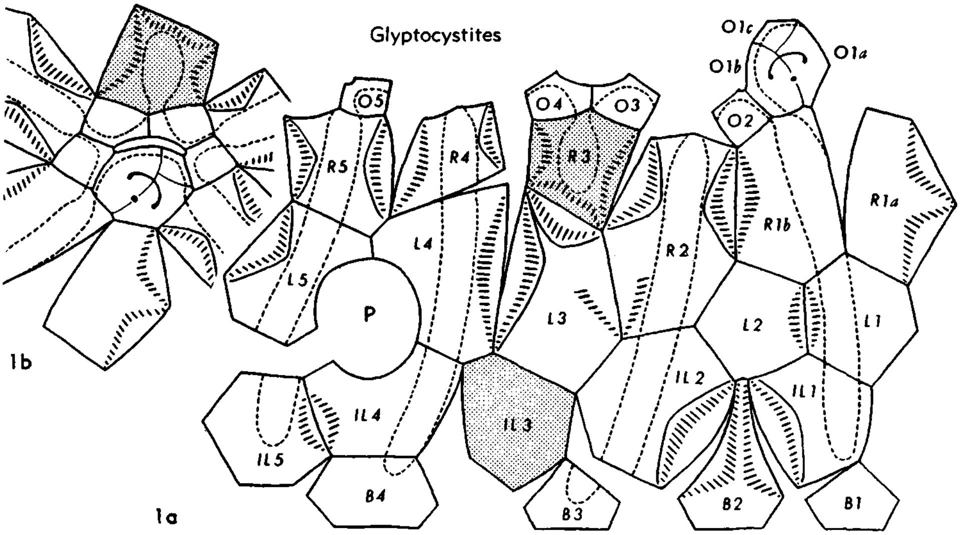


FIG. 73. Glyptocystitidae (p. *S*169-*S*170). [Plate designations as in Figure 38.]

tures. He postulated that *Cystoblastus* was the immediate ancestor of the blastoids. In the following year, BATHER wrote, "The superficial resemblance of *Cystoblastus* to certain Blastoids has led most writers to imagine a true relationship. This involves . . . the violent supposition that the horizontal transverse or tangential folds of the demi-rhombs in *Cystoblastus* originated the radial or vertical folds of the hydrospires in *Codaster*. . . ." In 1918 JAEKEL (71) elaborated on his theme, and presented a series of diagrams to compare *Cystoblastus* with *Pentremites* and *Nucleocrinus*, indicating a hypothetical stage in which all infralaterals and laterals disappeared from *Cystoblastus*, along with the troublesome rhomb-bearing *B2*. This intriguing concept was followed by MOORE (89) (Fig. 76).

Perhaps the strongest evidence bearing on the evolutionary significance of *Cystoblastus* was presented by YAKOVLEV (143), who studied additional specimens in detail. He found that the pore rhombs were comparable with those in other cystoids, and not transitional to blastoid hydrospires. It has also been pointed out that the excessive number of pores in the rhombs does not support the theory of extensive atrophy of these typically cystoidean structures.

The controversy is somewhat beclouded by the wistful and admirable desire to fit each kind of fossil into an evolutionary scheme. It appears impossible at this time to place the Cystoblastidae more precisely than within the superfamily Glyptocystitida (Fig. 77, 78). More genera, better preservation, and keener observations are required.

Key to Genera of Cystoblastidae

Only one pair of *RR* without an intervening *L*; only demirhombs on *RR*, with not more than 2 half-rhombs on any one *R* .... *Cystoblastus*

At least 2 pairs of *RR* without intervening *L*; *RR* with demirhombs and full rhombs, with 3 half-rhombs on at least one *R* ...... *Hesperocystis*

Cystoblastus VOLBORTH, 1867, p. 666 [**C. leuchtenbergi*; OD]. Theca pentremite- or bud-shaped, with marked pentameral symmetry; base indented. *BB* and *ILL* developed as in most rhombiferans, forming complete circlets except for tip of *B2* extending to that of *L2* above and possibly separating *IL1* from *IL2*; *IL4* between *B4* and periproct. [From this point, designations become confused because of different positions of the hydropore reported by VOLBORTH (137) in the type species and by YAKOVLEV (143, 144) in *C. kokeni*. The subsequent description is based primarily on the latter account.] Large *RR* intercalated with narrower *LL*, except that *R4* lies next to *R5* due to absence of *L4*; *R4* bordered below by *IL4*, *IL5*, and periproct, and all other radials with their horizontal bases upon corresponding *ILL*. Sides of *RR* tapering acutely toward mouth through most

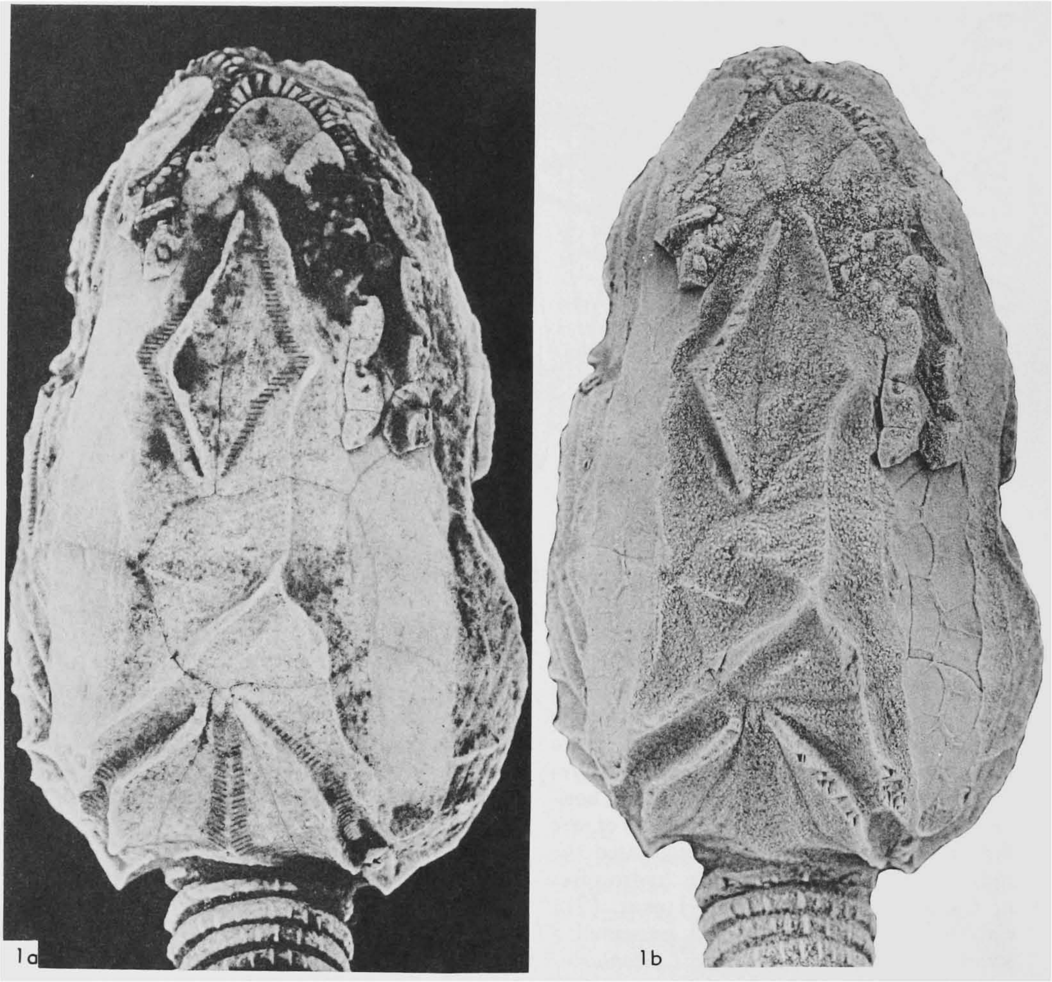
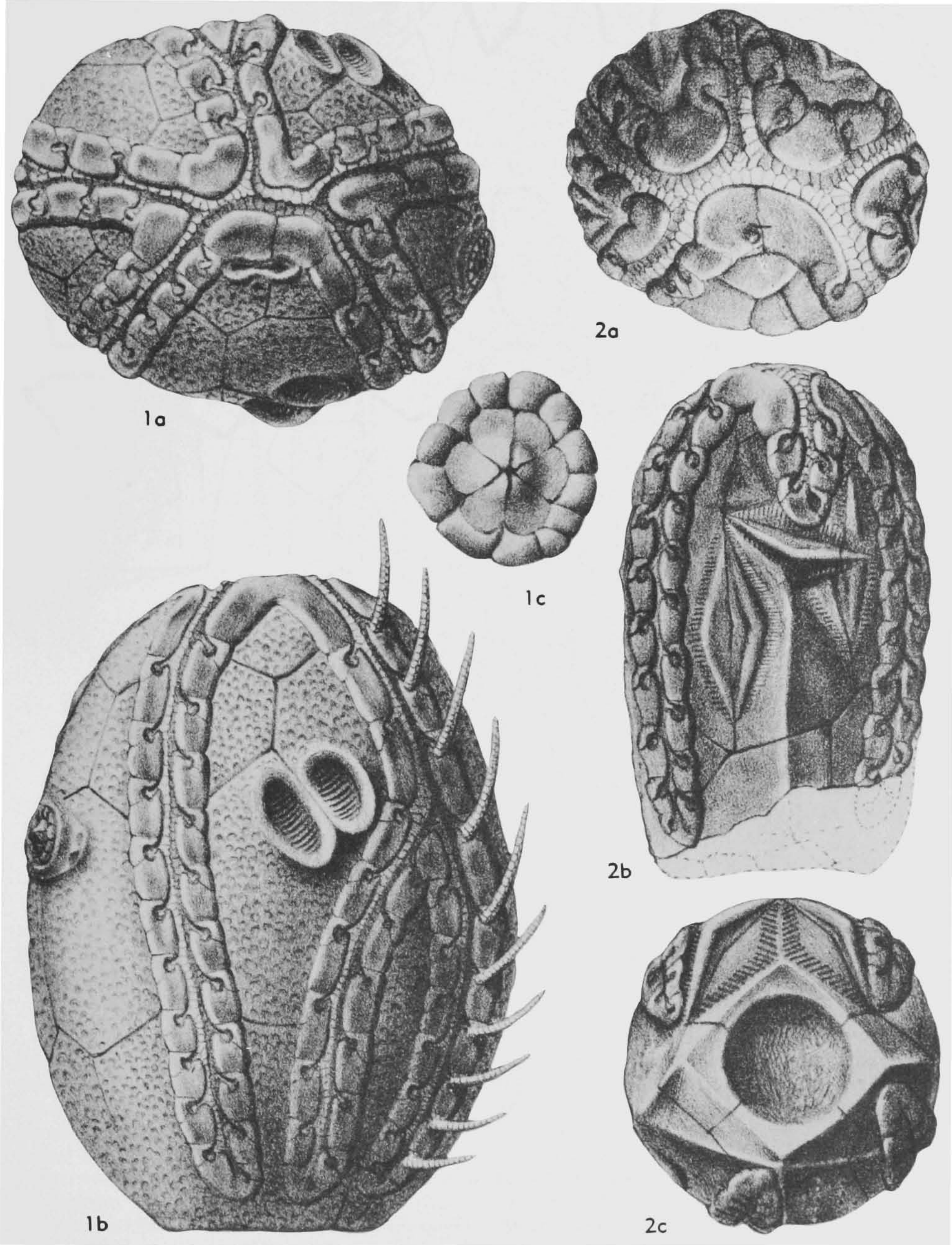


FIG. 74. Glyptocystitidae (p. S169-S170).——*1. Glyptocystites ehlersi* KESLING, M.Ord., USA(Mich.); *1a,b,* lat. view (*L2* near center, below rhomb), coated with ammonium chloride and submersed in xylol, ×3.75 *(73).*

of their length, obtusely at junction with *OO*. It appears dubious that *RR* could be forked plates, as originally described and shown in most figures, for it would necessarily follow that ambulacra in this genus are not superficial but integral parts of the theca, with no thecal plates on which to rest; this would be such a drastic departure from cystoid morphology that *Cystoblastus* might well be removed to form another class. Four *LL* kite-shaped, acutely acuminate adorally and obtusely acuminate aborally. *OO* subequal, small; one oral in type species said to have perforation at its distal corner, hydropore, situated at head of *R4/R5* suture; all other orals apparently with long narrow extensions down onto *LL* below. Two full rhombs on *B2* and adjacent *ILL*; 2 long demi-rhombs on each radial, shared with plates on either side; pore slits numerous, from 550 to about 1,800 listed. Periproct round, rather small, shared about equally by *IL4*, *L4*, and *R4*. Ambulacra tongue-shaped, with numerous alternating brachiole facets (about 60 and about 200 in the two known species). Plate designations in the type species present a dilemma, and no solution is entirely satisfactory or consistent with other cystoids. JAEKEL (69), in his elaborate discussion of the genus, showed *L1* at right of *R1* in his Fig. 42 and at left of it in his Fig. 43; he also confessed to bewilderment at position of the hydropore reported by VOLBORTH (1867), and said that he had been unable to find such a structure in his specimens. If the hydropore is present where stated, then by analogy with other cystoids it should lie between *R1* and *R5*, whereby

R5 would be the radial bordering the periproct; but the rhomb-bearing basal should by analogy *B2* and the subhexagonal basal *B4,* the lateral above *B2* should be *L2,* the radial between *L1* and *L2* should be *R1,* and the radial bordering the periproct would be *R4.* In one plate diagram, the *RR* are designated with reference to the hydropore as commonly figured in the type species and other plates with reference to the basal rhombs; in the other, the *RR* are designated with



Callocystites **Glyptocystites**

Fig. 75. Callocystitidae; Glyptocystitidae (p. *S*169-*S*170; *S*199-*S*201).

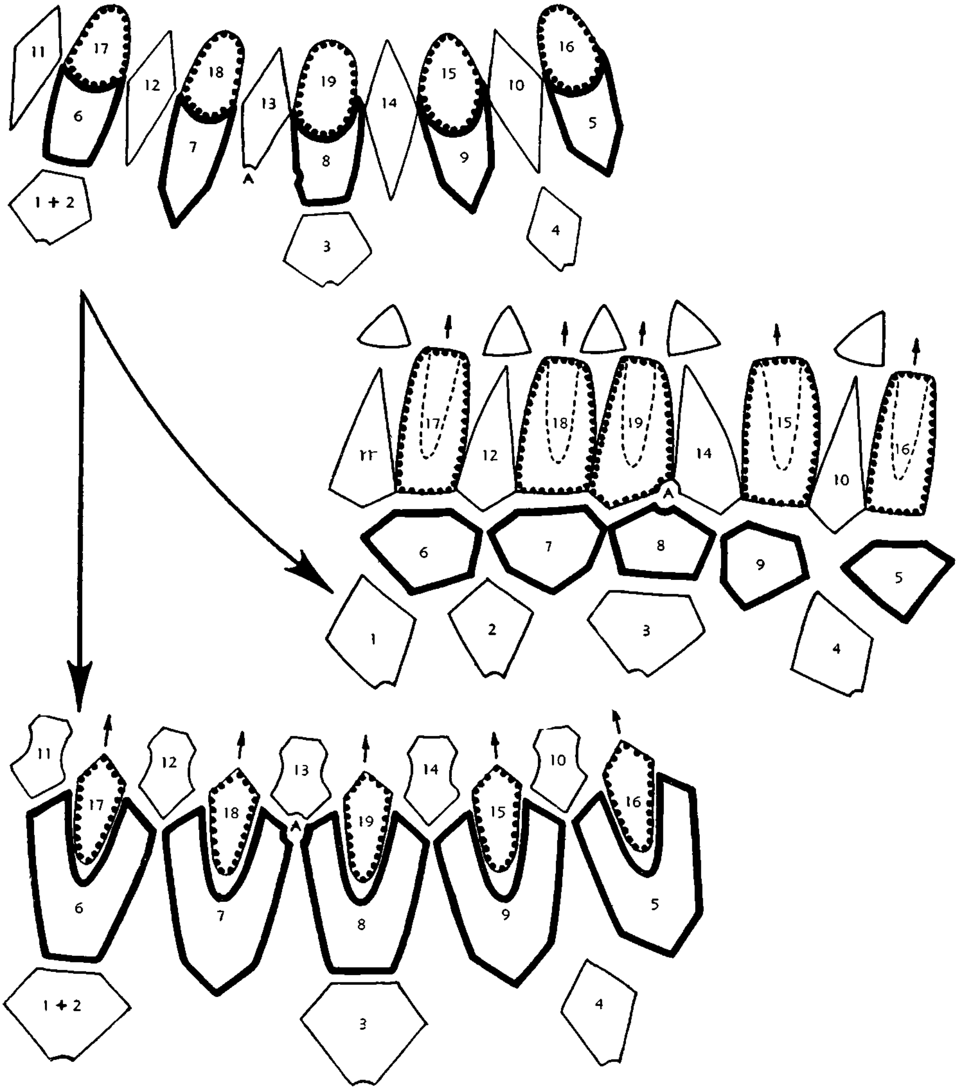


FIG. 76. Hypothetical derivation of cystoids and blastoids from a common ancestor as suggested by MOORE (1954); *1,* "hypothetical evolutionary derivative of a pre-*Cystoblastus* type"; *2, Cystoblastus; 3,* typical eublastoid with lancet plates identified as rhombiferan RR, deltoids as rhombiferan LL, and radials as rhombiferan *ILL* (89).

reference to other plates, so that they are directly adoral to corresponding *ILL*, and the reported position of the hydropore is assumed to be erroneous, as indicated by YAKOVLEV. One might suspect that VOLBORTH erred in his interpretation or description; his type specimen was already lost when JAEKEL made his study in 1899. YAKOVLEV (143-146) discovered a different situation in *Cystoblastus kokeni* JAEKEL, one which agrees with the arrangement in other cystoids of the Glyptocystitida. He found the hydropore and gonopore to be in the normal posiiton with respect to the basal pore rhombs, the missing *L* to be *L4*, and the periproct to be in the interambulacrum between III and IV. The hydropore in this species is a group of perforations forming a sieve structure more or less to the right of the small round gonopore. *M.Ord.*, Eu.(Est.-USSR).——FIG. 76. Relationship of *Cystoblastus* to blastoids (Kesling, n).——FIG. 77,*1*. **C. leuchtenbergi,* USSR; *1a-c,*

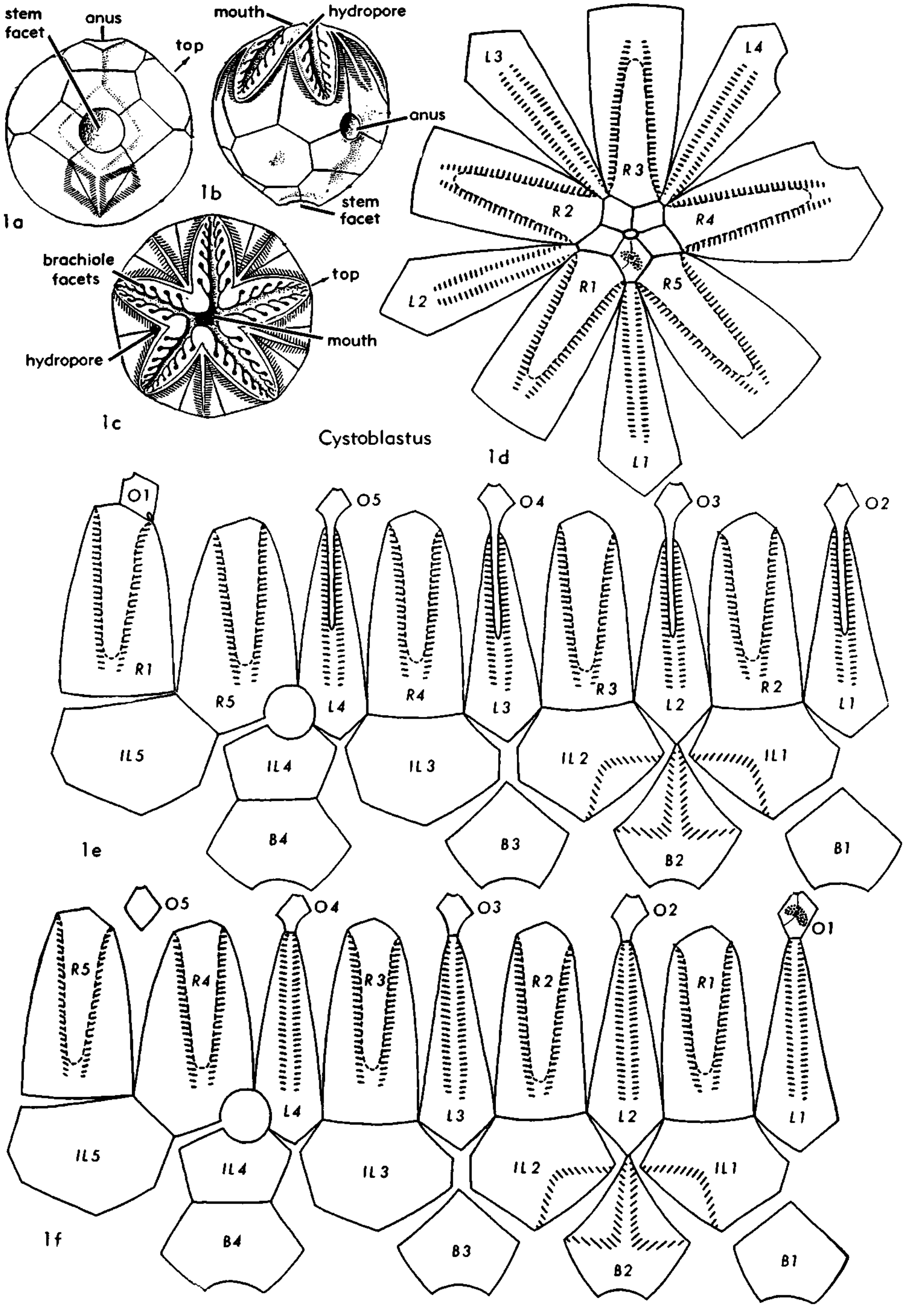


FIG. 77. Morphology of *Cystoblastus*.——*1*. **C. leuchtenbergi* VOLBORTH, M.Ord., Eu.(USSR); *1a-c,* aboral, lat., oral views of theca, ×4 (10); *1d,* oral region (diagram. reconstr.) (Kesling, n); *1e,* plate diagram to accord with VOLBORTH's original description (Kesling, n).——*1f*. *C. kokeni* JAEKEL, M.Ord., Eu. (Est. diagram); plate diagram interpreted in accordance with YAKOVLEV's description (Kesling, n). [Plate designations as in Figure 38.]

aboral, lat., oral views, ×4 (10); *1d,* oral region (diagram. reconstr.) (Kesling, n); *1e,f,* plate diagrams interpreted according to VOLBORTH's original description and according to YAKOVLEV's description of *C. kokeni* (Kesling, n).——FIG. 79. *C. kokeni* JAEKEL, Kuckers (C_2), Est.; oral view (reconstr.), approx. ×2 (Cuénot, 1953, after Yakovlev).

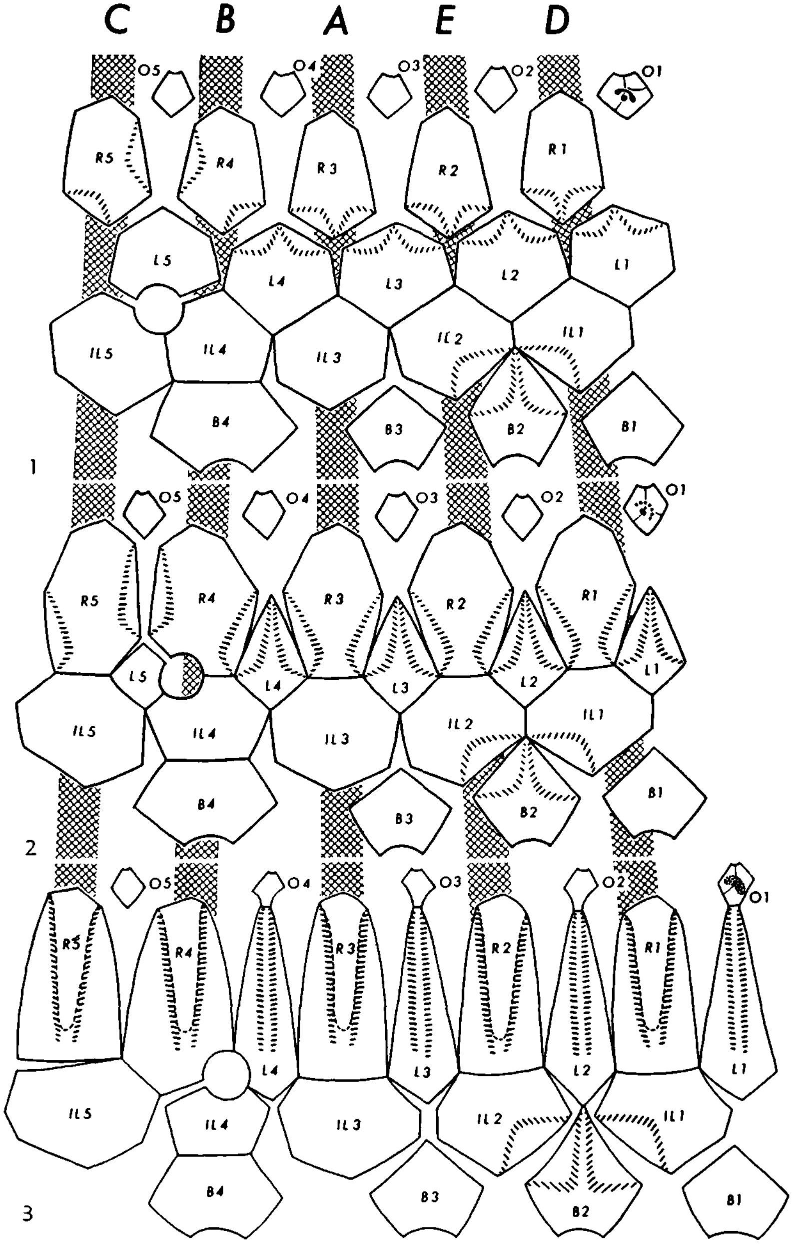


FIG. 78. Hypothetical derivation of *Cystoblastus (3)* from a generalized glyptocystitidan ancestor *(1)* with an intermediate stage (2). As shown, the evolution is supposed to have involved (1) diminution and disappearance of *L5,* (2) insertion of *RR* between *ILL* to rest atop corresponding *LL,* (3) shift of periproct from *IL5-L5-IL4* position to *IL4-R4-L4,* (4) elongation of *L1-L4* suture, and (5) modification of hydropore from simple slit to perforated area (Kesling, n). [Plate designations as in Figure 38.]

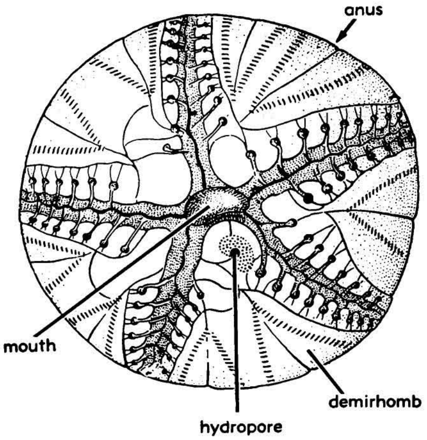


FIG. 79. Cystoblastidae (p. *S*171-*S*176). *Cystoblastus kokeni* JAEKEL, M.Ord., Eu.(Est.); oral view (reconstr.), ca. ×2 (Cuénot, 1953, from Yakovlev).

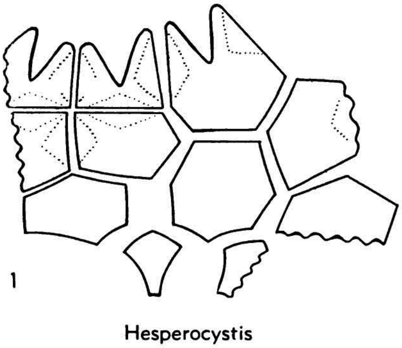


FIG. 80. Cystoblastidae (p. *S*177).——*1.* **Hesperocystis deckeri* SINCLAIR, M.Ord., USA(Okla.); plate diagram of preserved part of holotype*(117)*.

Hesperocystis SINCLAIR, 1945, p. 709 [**H. deckeri*; OD]. Theca known only from fragment preserving a few plates, which from description and figures I account as *B3*, *IL2*, *IL3*, *L3*, *R1*, *R2*, and parts of *B2*, *IL1*, *L2*, *L4*, and *R3*. No part of periproct or hydropore recorded, making orientation difficult. The 2 *BB,* from their position away from the periproct, cannot include *B4*; the left one is near center of known thecal area, and considered to be *B3*. Strangely, there is no basal rhomb; insofar as known, rhombs begin at the *LL* level; full rhombs are present as follows: *L2/?L1*, *L3/L4*, *L3/R2*, *L4/R3*, *R1/?R5*, and *R1/R2*; 3 demirhombs, one at each end of the *R2/R3* suture. *IL1*, *IL2*, and *IL3* in a continuous row; *L2* separated from *L3* by *R1/IL2* suture; *R1*, *R2*, and *R3* in a continuous row; *L3*, *L4*, *R2*, and *R3* with their right-angle corners meeting to form a +; *R1* considerably larger than other 2 *RR*. Ambulacra broad, like those of *Cystoblastus,* probably extending halfway down *RR*. [The pentremite shape of the known specimen, coupled with the broad ambulacra and rhomb-bearing *RR,* indicates a probably secure association with *Cystoblastus.*] *M.Ord.*, USA(Okla.).——FIG. 80,*1*; 81,*1*. **H. deckeri*; 80,*1*, plate diagram of holotype, only known specimen; 81,*1*, lat. and oral, holotype, ×1.5 (117).

Family RHOMBIFERIDAE Kesling, 1962

[Rhombiferidae KESLING, 1962, p. 281]

Theca extremely elongate, spindle-shaped, consisting of five *OO*, five *RR*, five *LL*, at least four *ILL* (presumably five), and probably four *BB*. Rhombs developed only between *ILL* and between *LL,* unusually large. *RR* reduced to small plates alternating with *OO* and with them forming slightly elevated ring, corona-like, around peristome. Brachioles erect, attached to facets that nearly fill *RR* plates. *U.Ord.*

As pointed out by KESLING (74), no lineage is known that indicates even faintly the relationship of the bizarre cystoid known as *Rhombifera.* The vertical align-

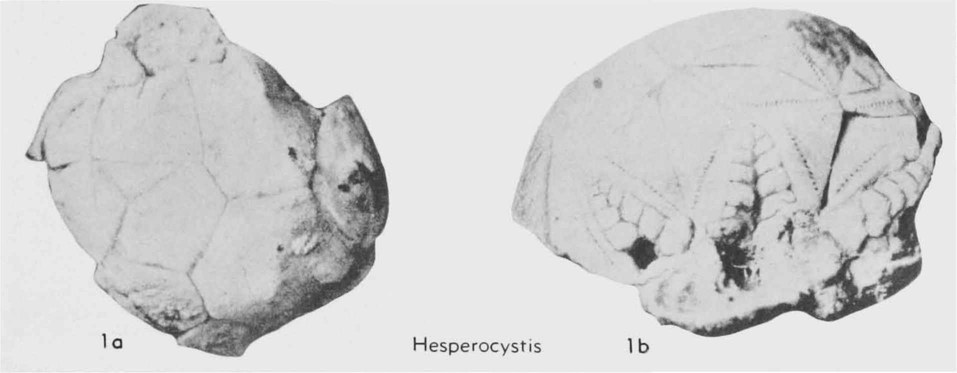


FIG. 81. Cystoblastidae (p. *S*177).

ment of *ILL* and *LL* is unique, as is the extreme reduction of *RR*. The presence and nature of pore rhombs are sufficient to assign it to the order Rhombifera, superfamily Glyptocystitida.

Rhombifera Barrande, 1867, p. 175 [**R. bohemica*; OD]. Theca shaped like a quadrate spindle, or bipyramidal, with adoral and aboral halves resembling high, square, truncated pyramids attached base to base; each face somewhat convex. Corona-like ring around mouth formed of slightly elevated alternating *OO* and *RR*. Periproct near mouth, directed upward with its aboral side extended outward, transverse subelliptical opening formed by deep indentation in *L3* and shallow one in *L4*. *BB* probably very small, to judge from steinkerns of thecae. *ILL* and *LL* large, with each of *LL* set above corresponding *ILL* and aligned with it; except for eccentric periproct, a plane of symmetry through *IL4* and *L4* and *IL1*/*IL2* and and *L1*/*L2* sutures; *IL4* and *L4* narrow vertical strips along one face of theca, and other *ILL* and *LL* each angled to form edges of quadrate spindle. Six large rhombs, each set along vertical suture: 3 full rhombs *IL1*/*IL2*, *IL1*/*IL5*, and *IL2*/*IL3*, and 3 demirhombs *L1*/*L2*, *L1*/*L5*, and *L2*/*L3*, rhombs filling most of each face of theca, provided with numerous oval pores. Brachiole facets subcircular, large, one on each *R* and filling most

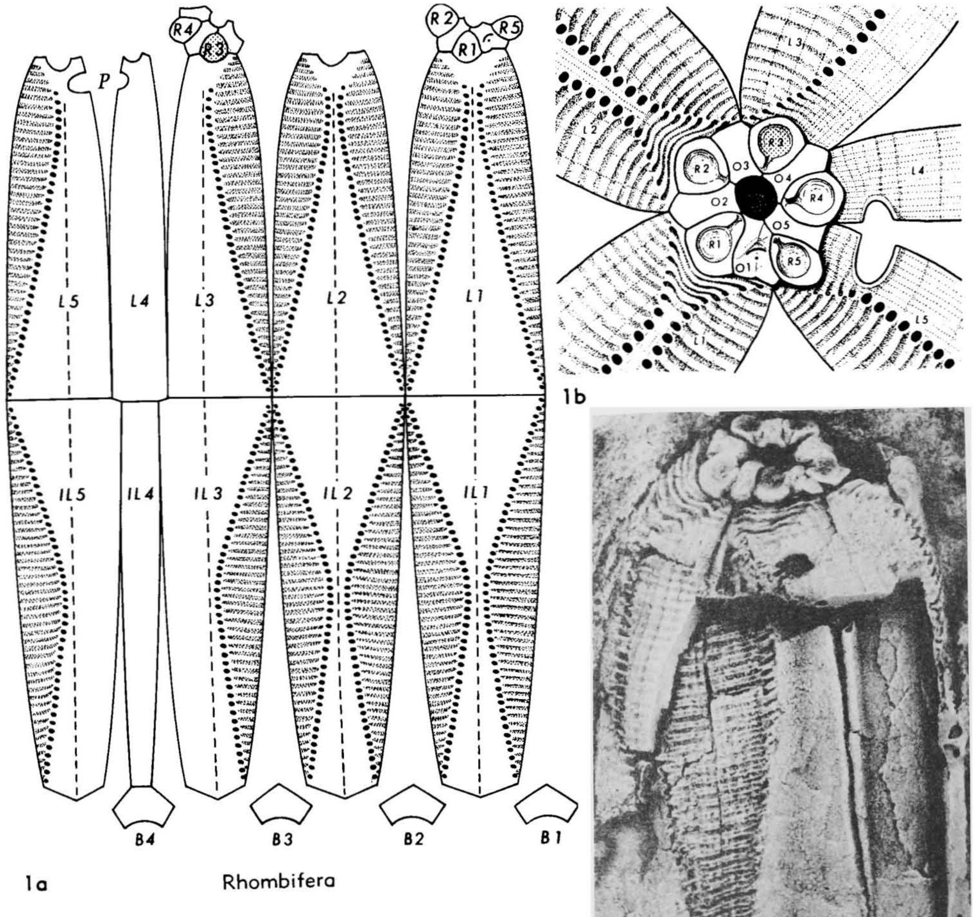


Fig. 82. Rhombiferidae (p. S178-S179).——1. **Rhombifera bohemica* Barrande, U.Ord., Eu.(Czech.); *1a*, plate diagram, ×2; *1b*, oral region, ×4; *1c*, latex cast showing part of interior on opposite side of theca, ×4 *(74)*. [Plate designations as in Figure 38.]

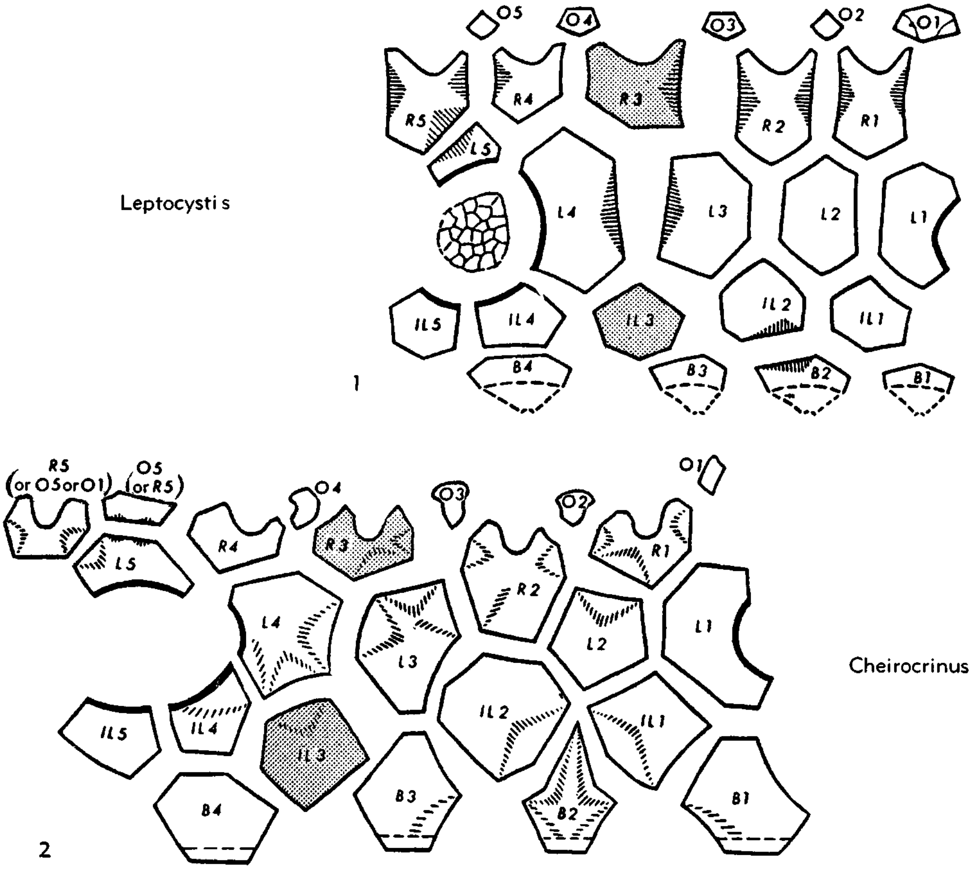


FIG. 83. Cheirocrinidae (p. S182-S184).——*1. Leptocystis constricta* (BATHER), U.Ord., Scot.; plate diagram *(12)*.——2. **Cheirocrinus penniger* (EICHWALD), L.Ord., Eu.(Est.); plate diagram *(12)*. [Plate designations as in Figure 38.]

of plate. Hydropore and possibly gonopore on *O1*, each small. *U.Ord.*, Eu.(Czech.).——FIG. 82,*1*. **R. bohemica*; *1a*, plate diagram, ×2; *1b*, oral region, ×4; *1c*, latex cast showing part of interior on opposite side of theca, ×4 (73).

Family CHEIROCRINIDAE Jaekel, 1899

[*nom. correct.* BATHER, 1913, p. 434 (*pro* Chirocrinidae JAEKEL, 1899, p. 212)]

Theca irregularly ovate, *BB* indented to accommodate junction with column. Plates of each row may form complete circlets, or *ILL* may be interrupted by aboral displacement of *L2* or *L3*, or both, or *LL* by insertion of *R2* between *L2* and *L3*; *R1* represented by two plates in many species, so that circlet of *RR* contains six plates. Periproct large, containing numerous small platelets in addition to anal pyramid. Ambulacra short, radiating from peristome atop flat or slightly arched oral region, which more or less truncates theca, each bordered by few brachioles; ambulacra never extending far, if at all, onto *RR*. Pectinirhombs numerous, developed as full rhombs or as demirhombs, conjunct or disjunct, ranging from eight to more, commonly 15 or more; rhombs *B2/IL2*, *L3/L4*, *L5/R1a*, *R1b/R2*, and *R2/R3* present on most, if not all, species; many species with rhomb *B2/IL1*, and some with rhombs between all *RR* (Fig. 83, 84). *L.Ord.-L.Sil.*

Most workers recognize only one genus, *Cheirocrinus*. JAEKEL (69) explained his reasons for creating *Leptocystis*, but later (71) ignored it completely. The genus *Homocystites* was placed in synonymy with

Cheirocrinus shortly after its erection by BARRANDE (3) and kept there. Some grounds, however, support recognition of a genus including cystoids like *Homocystites alter* BARRANDE, as distinguished from those like *Cheirocrinus penniger*

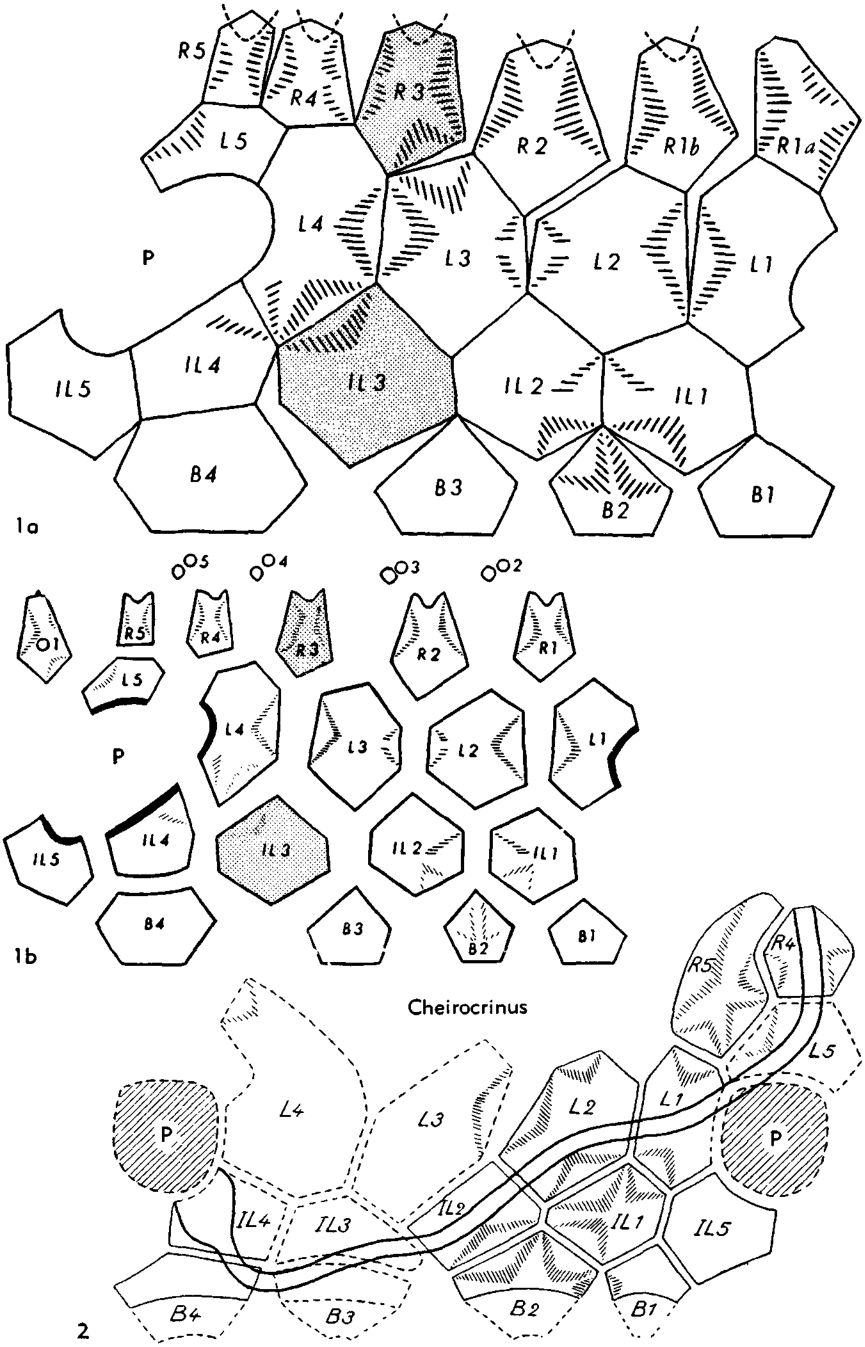


FIG. 84. Cheirocrinidae. Plate diagrams, plates of *A*-ray shaded, designations of plates as in Figure 38 (p. *S*182).

(Eichwald). Jaekel (69) divided the species having demirhombs into three groups: (1) those with only *"Spannleisten"* (ridges from centers of plates to each of the sides), (2) those with both *"Spannleisten"* and parallel *"Nebenleisten"* (ridges perpendicular to sides of plates), and (3) those with *"Gitterskulptur"* (reticulation of ridges and growth lines). Of these groups, the type species of *Cheirocrinus* represents the first and that of *Homocystites* the more highly ornamented second. Here *Homocystites* is expanded to include the third group also, which is obviously closely related to the second. It seems preferable to explain the kinds of cystoids associated with each genus than to lump all together without any recognition.

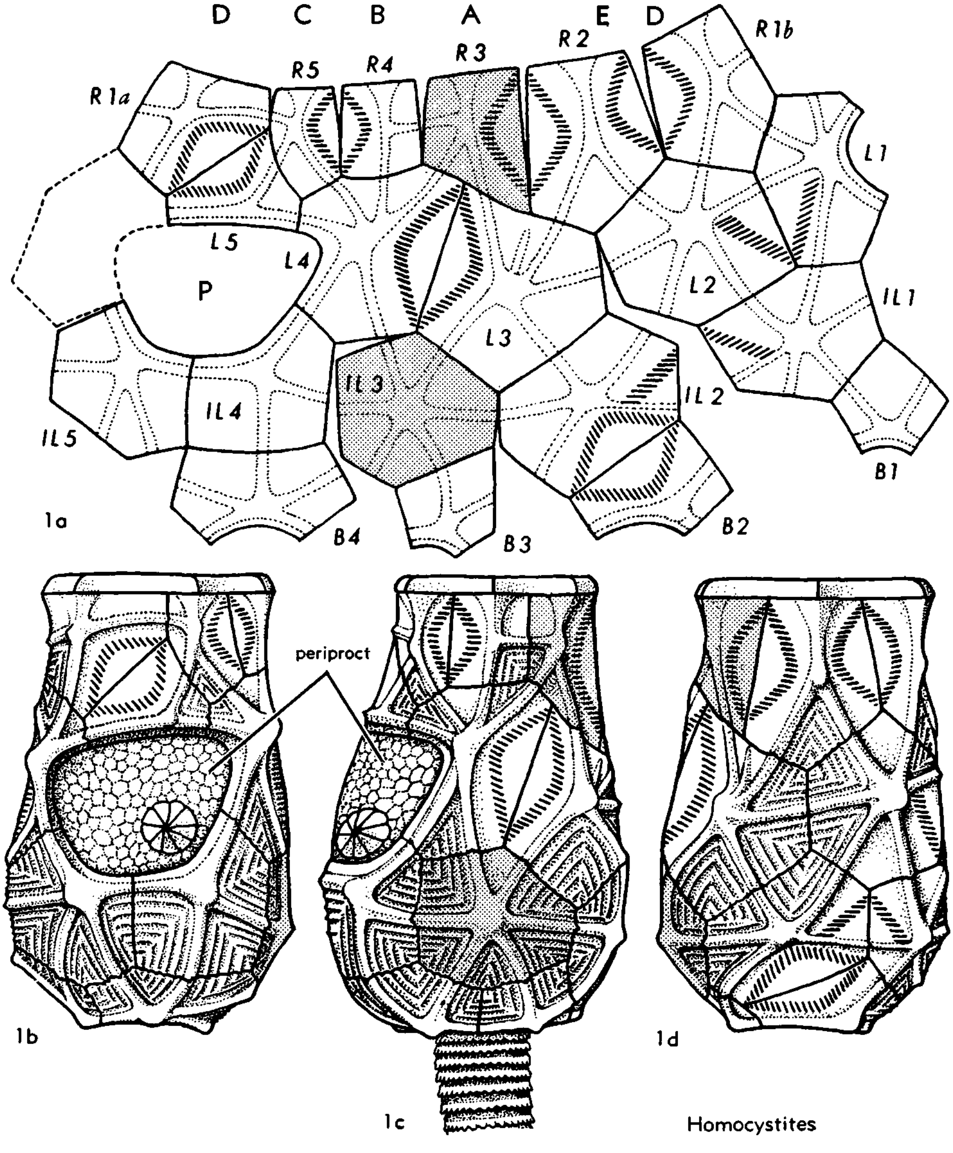


Fig. 85. Cheirocrinidae (p. S182-S184).——1. *Homocystites anatiformis* (Hall), M.Ord., USA(Mich.); *1a,* plate diagram; *1b-d,* reconstructions of theca in lateral views, ca. 2.5 *(74).* [Plate designations as in Figure 38, inferred rays of Carpenter system indicated by capital letters at top.]

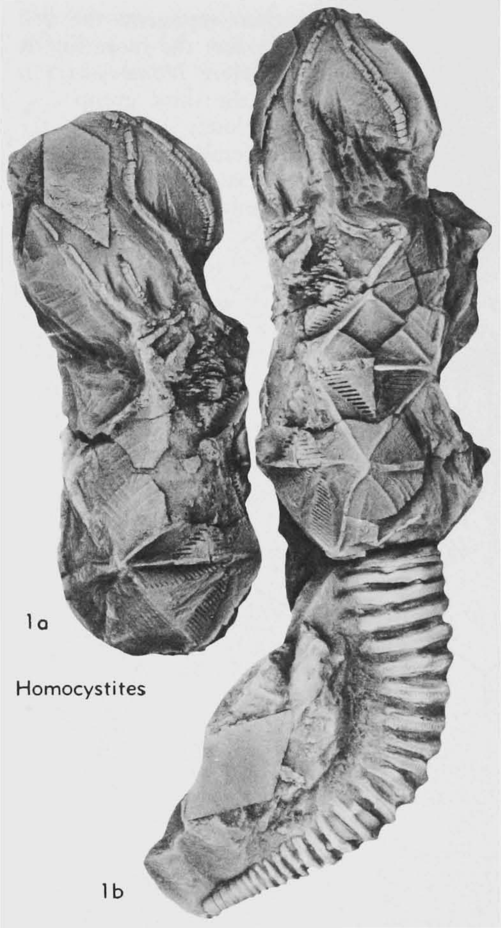


Fig. 86. Cheirocrinidae (p. S183-S184).

The crux of the taxonomic problem is whether to accredit the characters originally attributed to each genus as restrictive or to interpret and revise the description to accord with observations of the type species. Thus, Jaekel (69) noted in *Leptocystis tertius* an association of conjunct rhombs and proximal columnals that did not appear to be telescoped but all of subequal size. In the species described by Bather (12) as *Cheirocrinus constrictus,* however, conjunct rhombs are associated with strongly modified proximal columnals. I am inclined to regard the nature of the rhombs as significant, for the fact that the column is unknown in many specimens, if for no other reason.

Thus, to *Cheirocrinus* would be assigned *C. radiatus* Jaekel, *C. volborthi* (Schmidt), *C. penniger* (Eichwald), *C. granulatus* Jaekel, *C. leuchtenbergi* (Angelin), *C. nodosus* Jaekel, and probably the incompletely known *C. interruptus* Jaekel and *C. ornatus* Eichwald; to *Homocystites, H. alter* Barrande, *H. anatiformis* (Hall), *H. insignis* (Jaekel), *H. forbesi* (Billings), *H. sculptus* (Schmidt), *H. degener* (Jaekel), *H. striatus* (Jaekel), *H. angulatus* (Wood), and *H. walcotti* (Jaekel); and to *Leptocystis, L. tertius* (Barrande), *L. atavus* (Jaekel), *L. giganteus* (Leuchtenberg), and *L. constrictus* (Bather).

Key to Genera of Cheirocrinidae

1. Pectinirhombs developed as conjunct rhombs, at least on the base .... *Leptocystis*
   Pectinirhombs developed as disjunct or multidisjunct rhombs 2
2. Theca ornamented only by ridges radiating from centers to sides of plates, forming a large network of triangles ...... *Cheirocrinus*
   Theca ornamented by both large radiating ridges from centers to sides of plates and parallel lateral ridges, forming concentric triangles with the former; lateral ridges may be interrupted by growth lines to make a reticulate sculpture ...... *Homocystites*

Cheirocrinus Eichwald, 1856, p. 123 [*non* Salter in Murchison, 1859, *nec* Hall, 1860] [**Cyathocrinus penniger* Eichwald, 1842, p. 78; OD] [=*Chirocrinus* Haeckel, 1896, p. 402 *(nom. van.)*, *non* Angelin, 1878 (*nom. van. pro Cheirocrinus* Salter, *non* Eichwald)]. Pectinirhombs normally including some demirhombs as well as full rhombs, in many species varying greatly in size and shape. Thecal plates ornamented only by ridges radiating from centers to each of sides, in some forms with gentle slopes to sides and not with sharply defined boundaries. Most, perhaps all, species with 2 half-rhombs on *B2* and at least 3 rhombs shared by *RR.* Brachioles confined to crown of theca, along the sides of the ambulacra, which are short and never branch. Hydropore and gonopore, insofar as known, bisected by suture through plate *O1.* Columnals appearing to be telescoped, perhaps all columns in proximal part composed of outer columnals flexibly held by interlocking inner columnals. Periproct large. *L. Ord. - U. Ord.,* USSR - Est. - Scand. - Belg.-Scot. ——Fig. 83,*2*; 87,*1*. **C. penniger* (Eichwald), L.Ord., Eu.(Est.); 83,*2,* plate diagram (12); 87,*1a,b,* lat., two thecae, ×1 (69).——Fig. 84, *1a,b*; 88,*1*. *C. radiatus* (Jaekel), L.Ord.(Kunda, B_3), Eu.(USSR); 84,*1a,b,* plate diagrams (Kesling, n, after 12, 69); 88,*1,* lat. view, *L2* near center, ×2 (69).——Fig. 84,*2*. *C. hyperboreus* Regnéll, L.Ord($3c\beta$), Norway; diagram of known plates with heavy lines indicating inferred course of the gut (100). [See also Fig. 34,*2*, 48,*1*.]

?**Homocystites** BARRANDE, 1887, p. 160 [**H. alter*; OD] [=*Homocystis* BATHER, 1889, p. 269 *(nom. van.)*]. General shape and plate arrangement like that of *Cheirocrinus,* of which some consider this genus to be a junior synonym. Rhombs highly developed, demirhombs commonly in form of

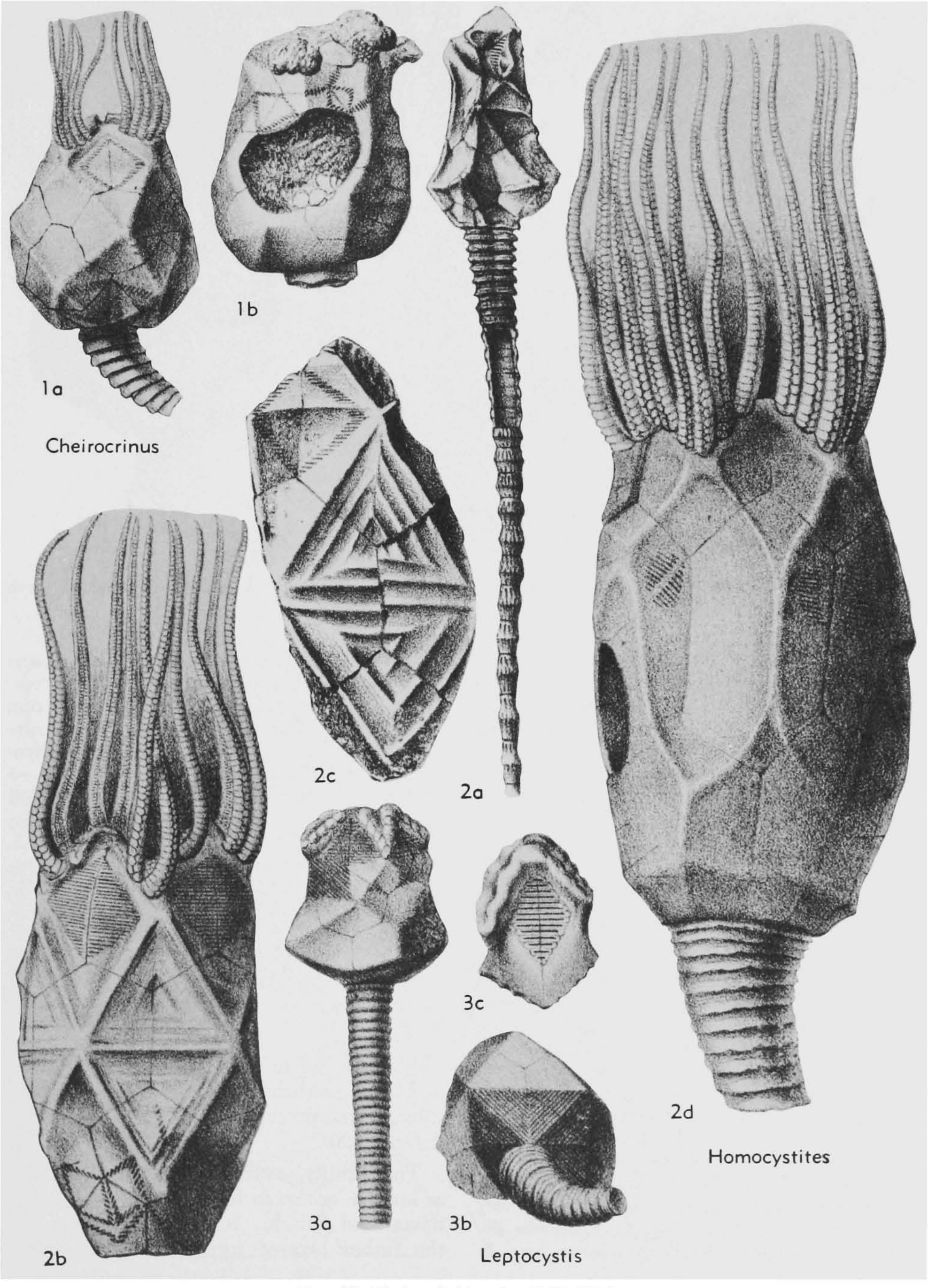


FIG. 87. Cheirocrinidae (p. *S*182-*S*184).

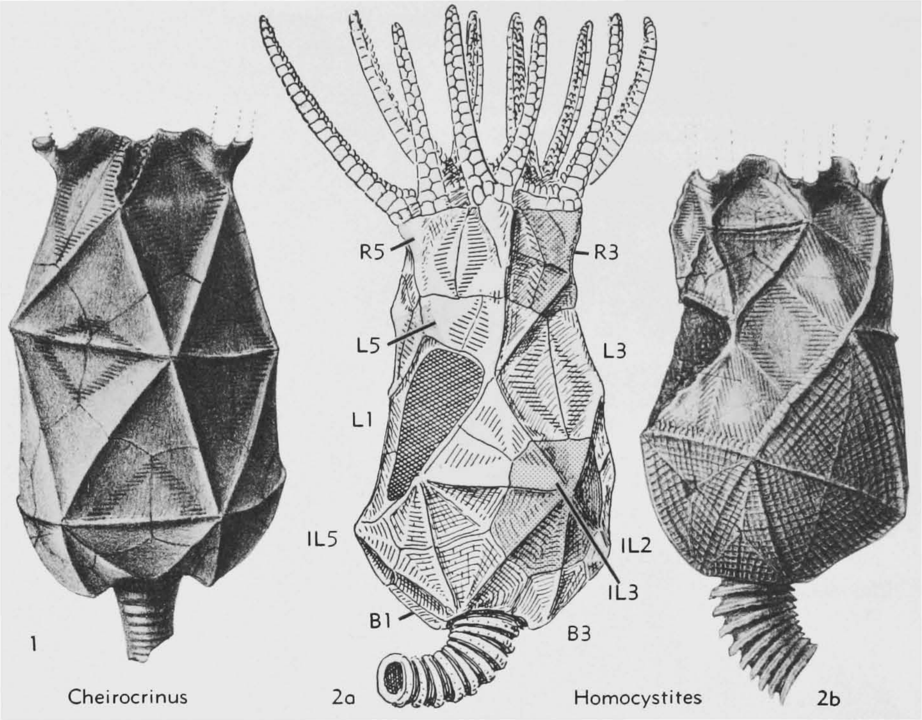


FIG. 88. Cheirocrinidae, plates of *A*-ray shaded (p. *S*182-*S*184). [Plate designations in *2a* are as given in Figure 38.]

chevron; *B2* may have only single half-rhomb instead of 2. Plates highly ornamented by parallel ridges perpendicular to sides *("Nebenleisten"),* which together with main radiating ridges *("Spannleisten")* form series of concentric triangles, or are interrupted regularly by growth lines to form a reticulation *("Gitterskulptur").* This highly ornamented group of cheirocrinids includes all known North American species. *L. Ord.-M.Ord.,* Eu.(Boh.-Port.-USSR)-N.Am.(N.Y.-Mich.-Ont.-Que.-Wis.).——FIG. 85,*1*, 86,*1*. *H. anatiformis* (HALL), M.Ord.(Trenton.), USA (Mich.) (85,*1*) and Can.(Ont.) (86,*1*); 85,*1a*, plate diagram; 85,*1b-d*, lat. views (reconstr.), approx. ×2.5 (73); 86,*1a,b*, lat. views, ×2 (Kesling, n).——FIG. 87,*2a,b*. **H. alter*, M.Ord., Boh.; *2a,b*, lat. views of 2 specimens, ×1 (69).——FIG. 87,*2c*. *H. striatus* (JAEKEL), L.Ord.(Kunda, B_3), USSR(Leningrad area); part of theca, ×2.5 (69). ——FIG. 87,*2d*. *H. walcotti* (JAEKEL), M.Ord., USA(N.Y.); lat. view (reconstr.) (69).——FIG. 88,*2*. *H. insignis* (JAEKEL), L.Ord.(Kunda, B_3), USSR; *2a,b*, lat. views, periproct at left (*2a*, reconstr.), ×2 (69). [See also Fig. 50.]

?**Leptocystis** JAEKEL, 1899, p. 222 [**Homocystites tertius* BARRANDE, 1887; OD]. Pectinirhombs developed as conjunct rhombs, at least at base. In type species, column divided by transverse sutures into nearly equal segments, not appearing "telescoped" and probably much more rigid than column of *Cheirocrinus*. [Otherwise like *Cheirocrinus*, of which this genus may be a junior synonym.] *L.Ord.-L.Sil.,* Eu.(Boh.-Scot.-USSR).——FIG. 87,*3*. *L. atava* (JAEKEL), L.Ord.(B_3), USSR (Leningrad area); *3a,b*, lat and aboral, ×3; *3c*, lat., oral part of theca, ×3 (69).——FIG. 83,*1*. *L. constricta* (BATHER), U.Ord.(Drummuck Gr.), Scot.(Girvan); plate diagram (12). [See also Fig. 34.]

Family ECHINOENCRINITIDAE
Bather, 1899

[*nom. correct.* PHLEGER, 1935, p. 194 (*pro* Echinoencrininae BATHER, 1899, p. 920)] [=Scoliocystidae JAEKEL, 1899, p. 235]

Theca ovate to subglobular, modified by typically produced periproct. Ambulacra short, restricted to crown. Pore rhombs few. *L.Ord.-U.Sil.*

This family, confined to Europe insofar as known, occurs in Russia, Estonia, Scandinavia, and Britain. It is well known from the rather bizarre forms with long periproctal extensions of the theca, but it also contains genera with less modification. The record of the family is far from complete, as attested by the lack of Lower and Middle Silurian forms. The Echinoencrinitidae probably developed in the Baltic region, where they became diverse in the Middle Ordovician. The last survivors are from Upper Silurian strata in England. The stratigraphic distribution of genera is indicated in Figure 72.

Key to Genera of Echinoencrinitidae

1. *R* circlet interrupted by adoral projection of *L5*, with *R4* very small or absent; of *ILL*, only *IL4* bordering periproct .... *Glaphyrocystis*

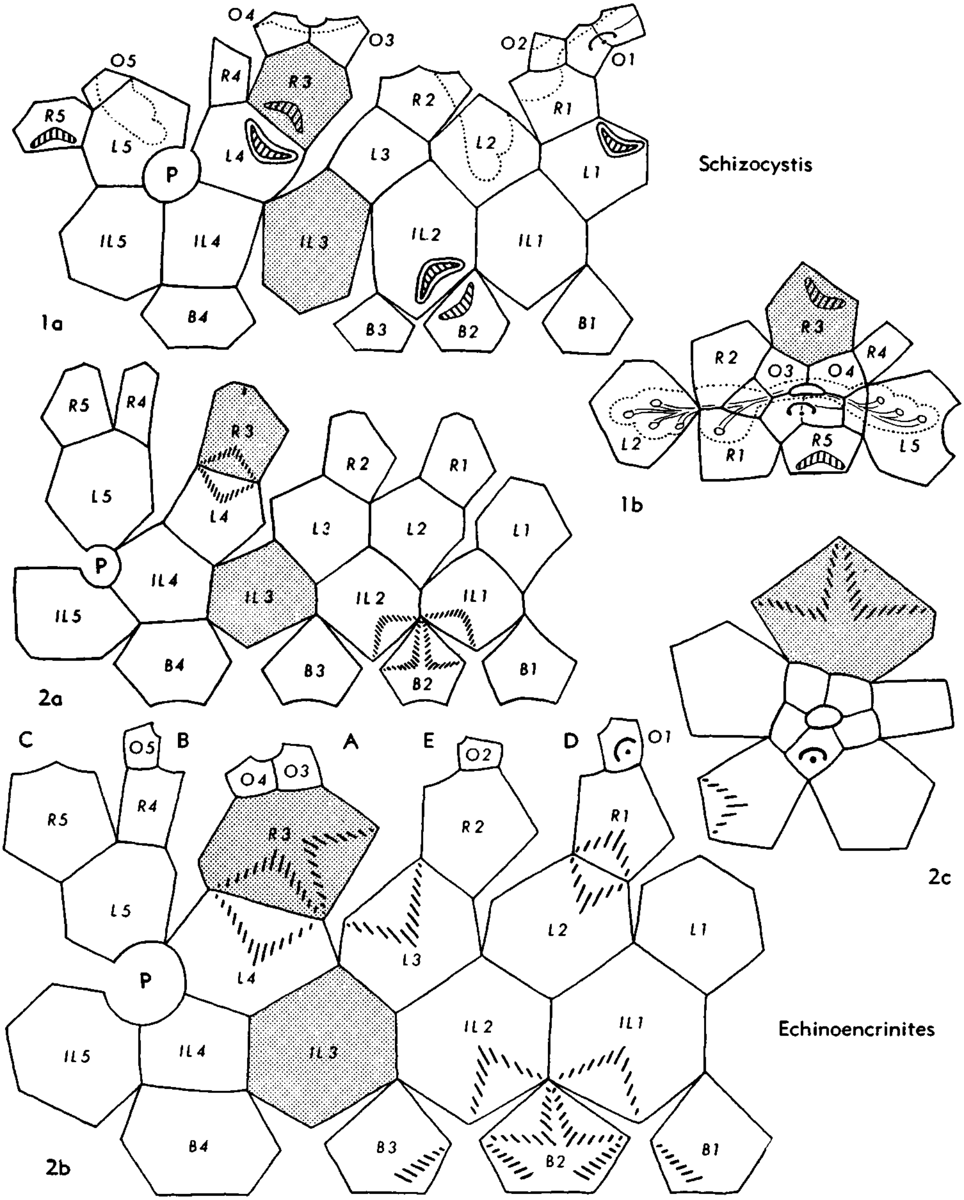


FIG. 89. Echinoencrinitidae. Plate diagrams, *A*-ray plates shaded, plate designations as in Figure 38 (p. *S*187-*S*189, *S*191).

R circlet not interrupted by any *LL*; both *IL4* and *IL5* bordering periproct 2

2. Four *RR* only, no *R5* .... *Proctocystis*

Five *RR* 3

3. Theca sharply pointed by elongate, adorally attenuated *RR*; *L3* in contact with *B3*, interrupting *IL* circlet between *IL2* and *IL3* .... *Erinocystis*

Theca not sharply pointed by attenuated *RR*; *IL* circlet complete 4

4. *B2/IL1* pectinirhomb; *BB* strongly indented to form quadrate depression for

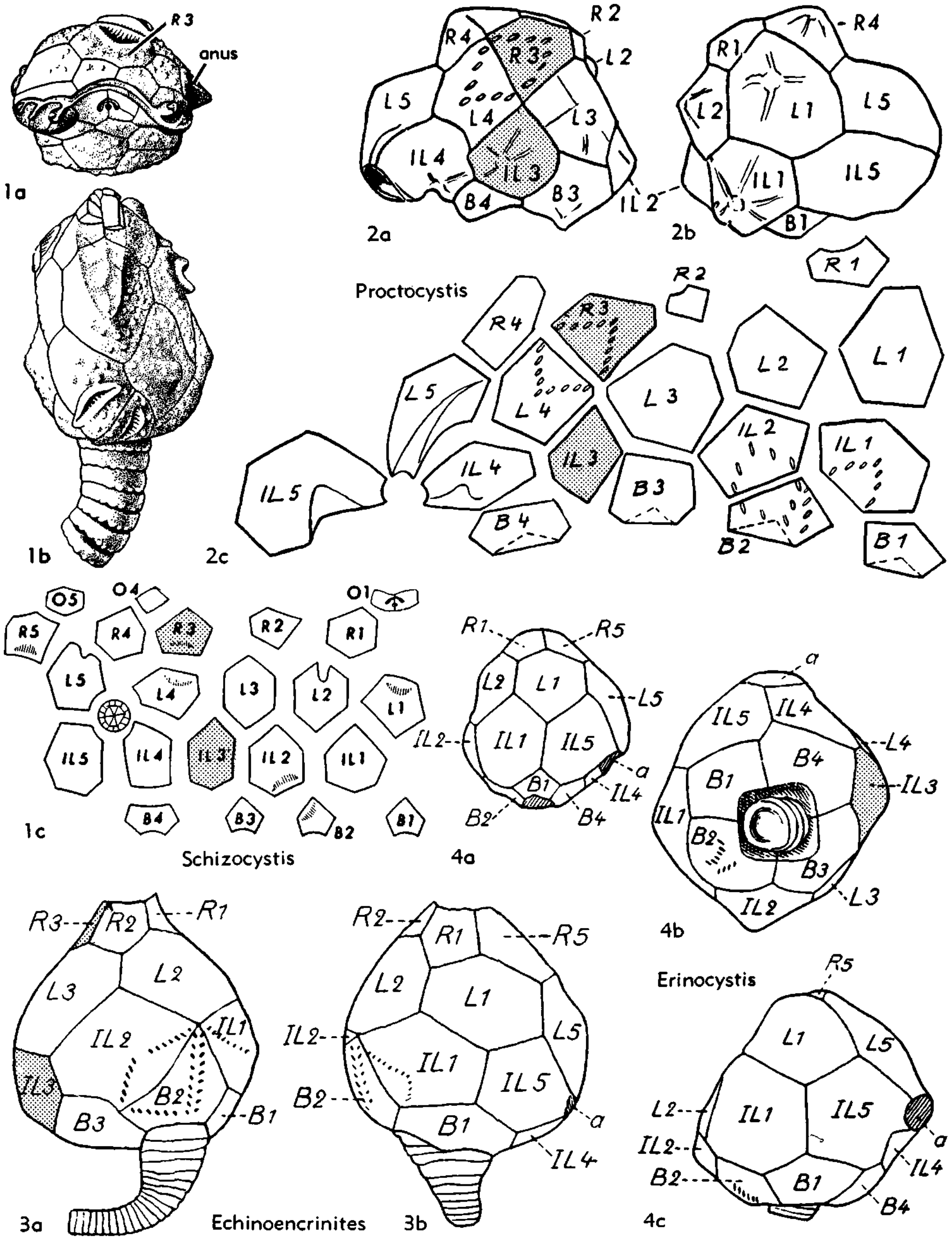


FIG. 90. Echinoencrinitidae, plates of *A*-ray shaded, plate designations as in Figure 38 (p. S187-S189, S191).

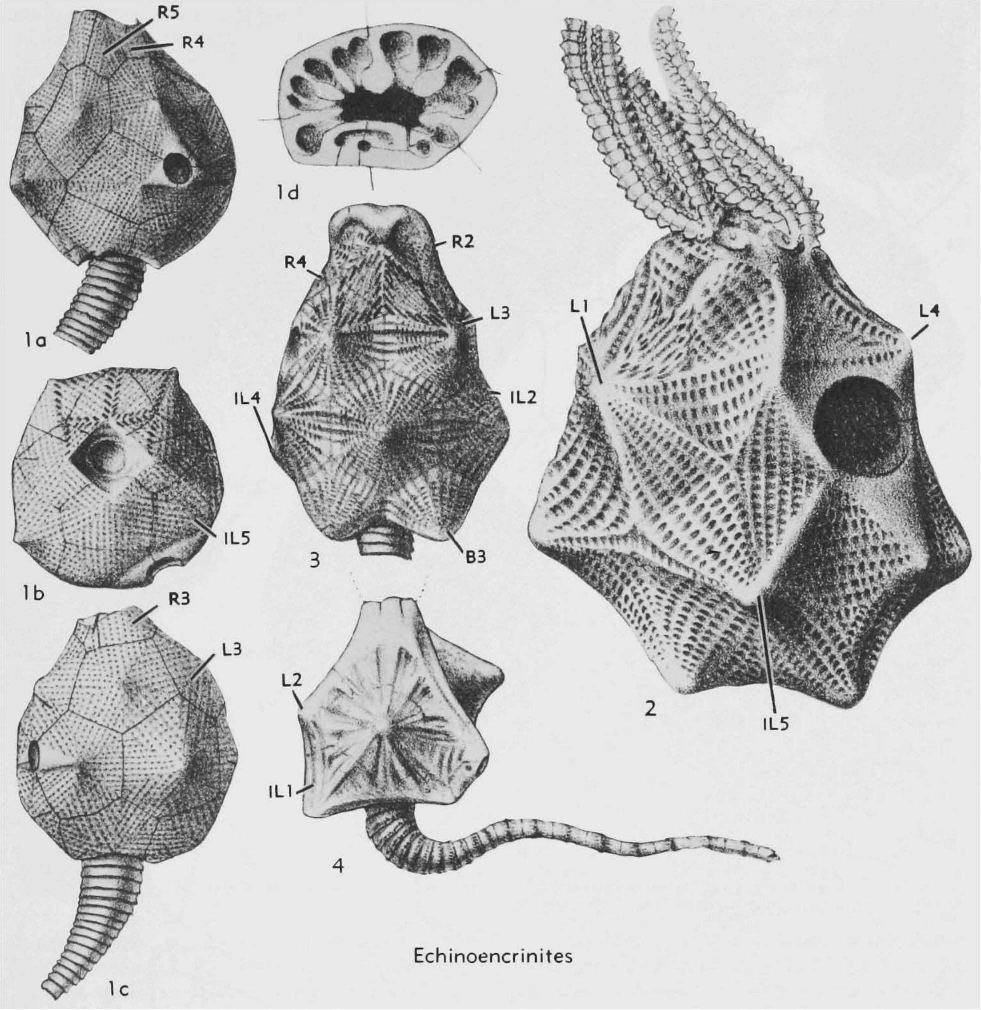


FIG. 91. Echinoencrinitidae, all L.Ord., USSR(Leningrad region), plate designations as in Figure 38 (p. S187-S189).

junction with column; periproct rather strongly protuberant 5

No *B2/IL1* pectinirhomb; *BB* only slightly indented or not at all; periproct not strongly protuberant 6

5. Extra pectinirhomb on *L3/R3* ...... *Eutretocystis*

No extra pectinirhomb on *L3/R3* .... *Echinoencrinites*

6. More than three pectinirhombs; periproct bordered by five plates *(IL4, IL5, L1, L4, L5)* .... *Scoliocystis*

Two or three pectinirhombs, *B2/IL2* and *L4/R3* invariably present, *L1/R5* in most; periproct bordered by less than five plates, never by *L1* 7

7. Brachioles clustered near peristome; theca subovate .... *Prunocystites*

Brachioles in two groups, at ends of long curved ambulacral groove across top of theca (mouth in center); theca subovate aborally, compressed in *R3-L1* plane adorally .... *Schizocystis*

Echinoencrinites VON MEYER, 1826 [**E. senckenbergii* (=*Echinosphaerites granatum* VON SCHLOTHEIM, 1826); OD] [=*Echinoencrinus* VOLBORTH, 1842 *(nom. van.)*; *Euchino-Encrinites* VON MEYER, 1826 *(nom. null.)*; *Gonocrinites* EICHWALD, 1840; *Gonocrinus* EICHWALD, 1859 *(nom. van.)*; *Sycocystites* VON BUCH, 1846; *Sycocystes* GEINITZ, 1846 *(nom. null. pro Sycocystites)*; *Cyclocystites* D'ORBIGNY, 1852 *(nom. null. pro Sycocystites)*;

Sycocystis Haeckel, 1896 *(nom. van. pro Sycocystites) non* Haeckel, 1870]. Theca subpyriform, globose aborally and tapering adorally, but not sharply pointed by attenuated *RR*; periproct slightly produced but not directed aborally; plates highly ornamented in many species, typically by concentric triangles of ridges or rows of flattened tubercles with apices directed toward centers of

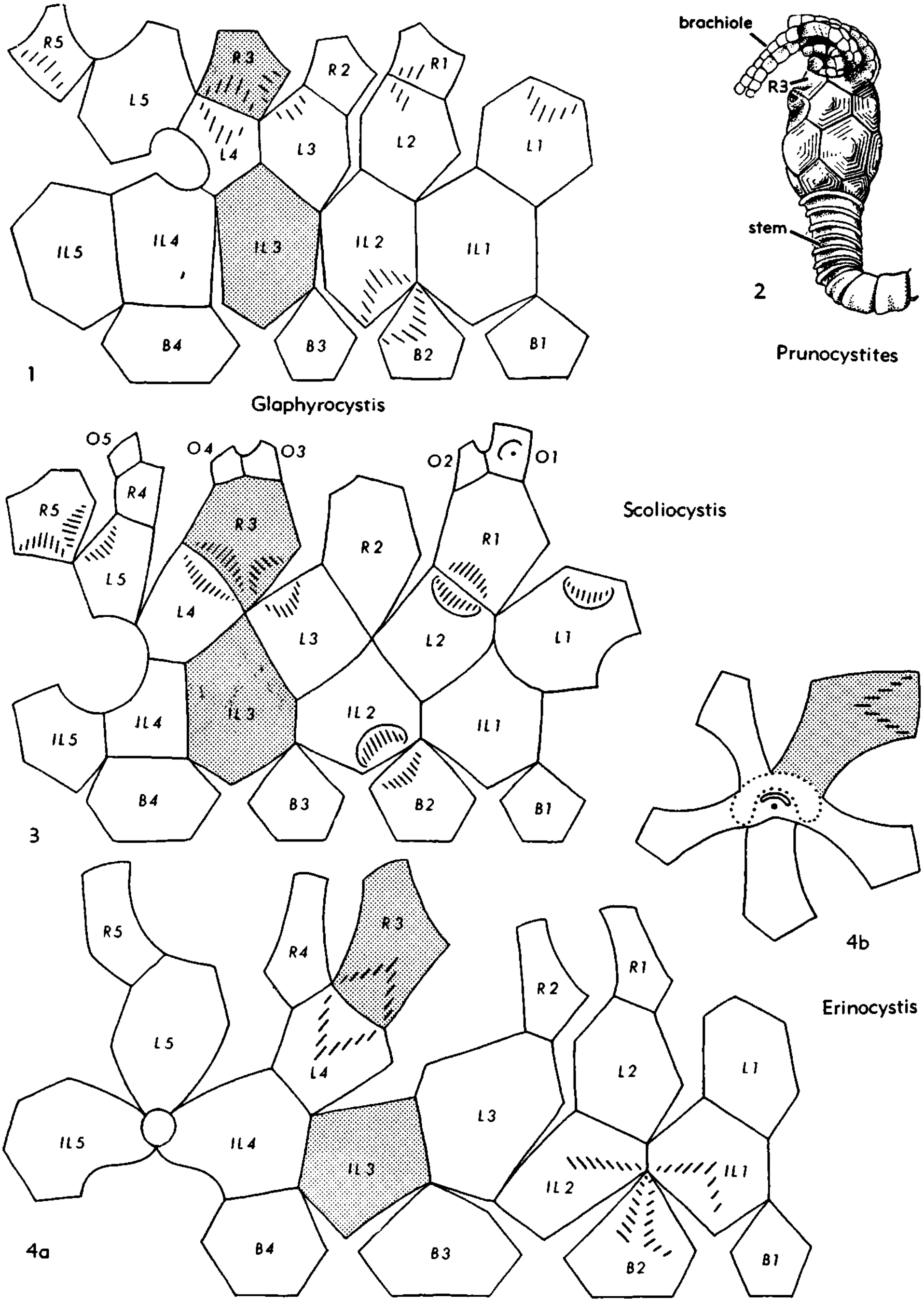


Fig. 92. Echinoencrinitidae. Plate diagrams, plates of *A*-ray shaded, plate designations as in Figure 38 (p. *S*189-*S*192).

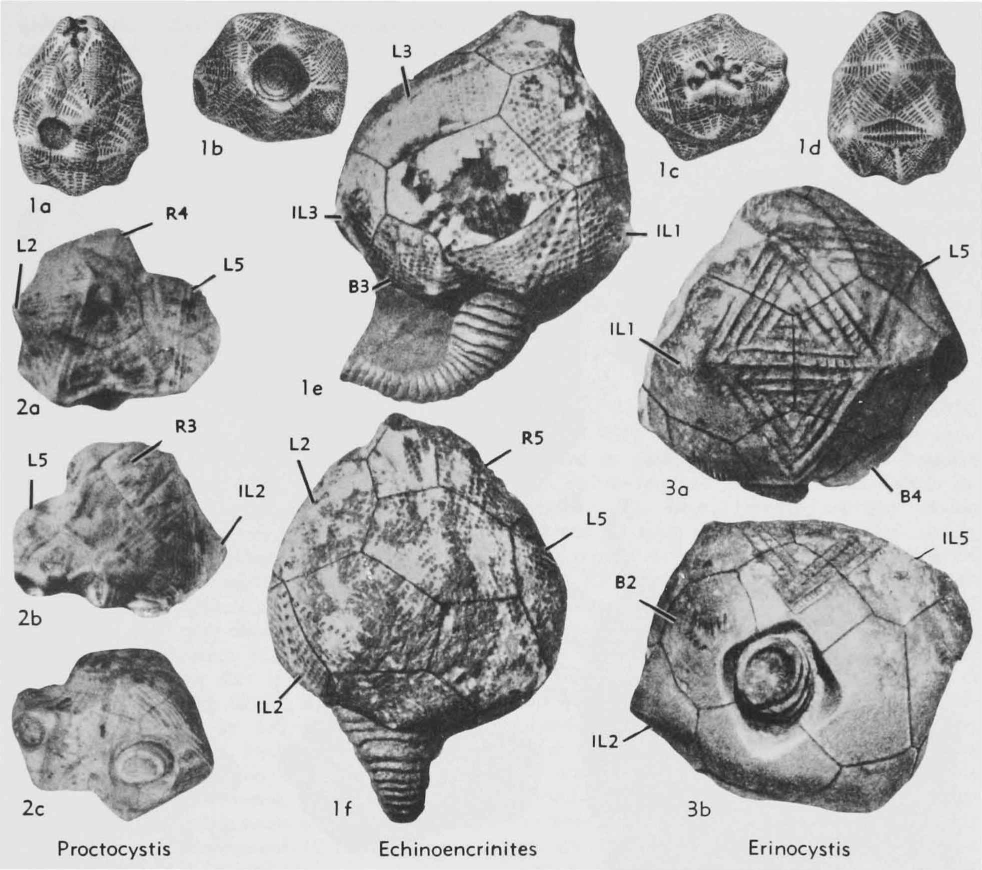


Fig. 93. Echinoencrinitidae (p. *S*187-*S*191). [Plate designations as in Figure 38.]

3 adjoining plates; all rows of thecal plates in complete circlets; *BB* well developed, indented to form quadrate depression for ample column. Brachioles 2 to 5 or more, set on short ambulacra on narrow crown. Three pore rhombs, *B2/IL1*, *B2/IL2*, and *L4/R3*. [*Eutretocystis,* created by Phleger for a specimen with an extra rhomb on *L3/R3,* may be an anomalous *Echinoencrinites.* Because many specimens are found with the proximal part of the column bent or curved, Jaekel (71) suggested that the column was prostrate and the theca erect in *Echinoencrinites.* Because specimens were not rare, and because von Meyer's publication was overlooked by subsequent workers, this cystoid was described under several names.] *L.Ord.,* Eu.(USSR-Norway-Sweden)-?Asia(Burma).——Fig. 89,*2a*; 91,*1a-d*; 93, *1a-d*. **E. senckenbergii,* Kunda(B_3), USSR(Leningrad region); 89,*2a,* plate diagram (Kesling, n, after 69); 91,*1a-c,* lat., aboral, and lat., ×1; 91, *1d,* oral region showing brachiole facets, ×3 (69); 93,*1a-d,* lat., aboral, oral, lat., ×1 (31).——Fig. 89,*2b,c*; 91,*3*. *E. lahuseni* Jaekel, Kunda (B_3), USSR(Leningrad region); 89,*2b,c,* plate diagram and oral region (Kesling, n, after 69); 91,*3,* lat., ×4 (69).——Fig. 90,*3*; 93,*1e,f*. *E. senckenbergi acutangulatus* Regnéll, *Expansus* (3cβ), Norway; 90, *3a,b,* lat., diagram., ×1.5 (100); 93,*1e,f,* lat., 2 thecae, ×2 (100).——Fig. 91,*4*. *E. angulosus* (Pander), B_2, USSR(Leningrad region); lat., ×3 (69).——Fig. 91,*2*. *E. reticulatus* Jaekel, Kunda (B_3), USSR(Leningrad region); lat., ×3 (69).

Erinocystis Jaekel, 1899, p. 252 [**E. sculpta*; OD]. Theca fig-shaped, orally strongly attenuated, base indented. *ILL* and *LL* with adjacent parts intercalated, *LL* forming complete circlet, but *ILL* interrupted by insertion of *L3* between *IL2* and *IL3*; *RR* elongate, sharply tapering to narrow crown. Periproct produced by prolongation of *IL4*, *IL5*, and *L5,* its opening rather small and directed aborally as well as outward. *OO* restricted to apex of theca, their number and arrangement obscured. Two brachioles, rather large for size of oral field, one facet atop *R1* and *R2* and other atop *R3* and *R4*. Three pore rhombs, *B2/IL1*, *B2/IL2*, and *L4/R3*, each rather high and sharply angled. Column with proximal thin-walled, circular, collar-like columnals, tapering to distal massive, compressed columnals. Thecal plates, particularly *ILL*, strongly sculptured and ornamented in some species, so much so that

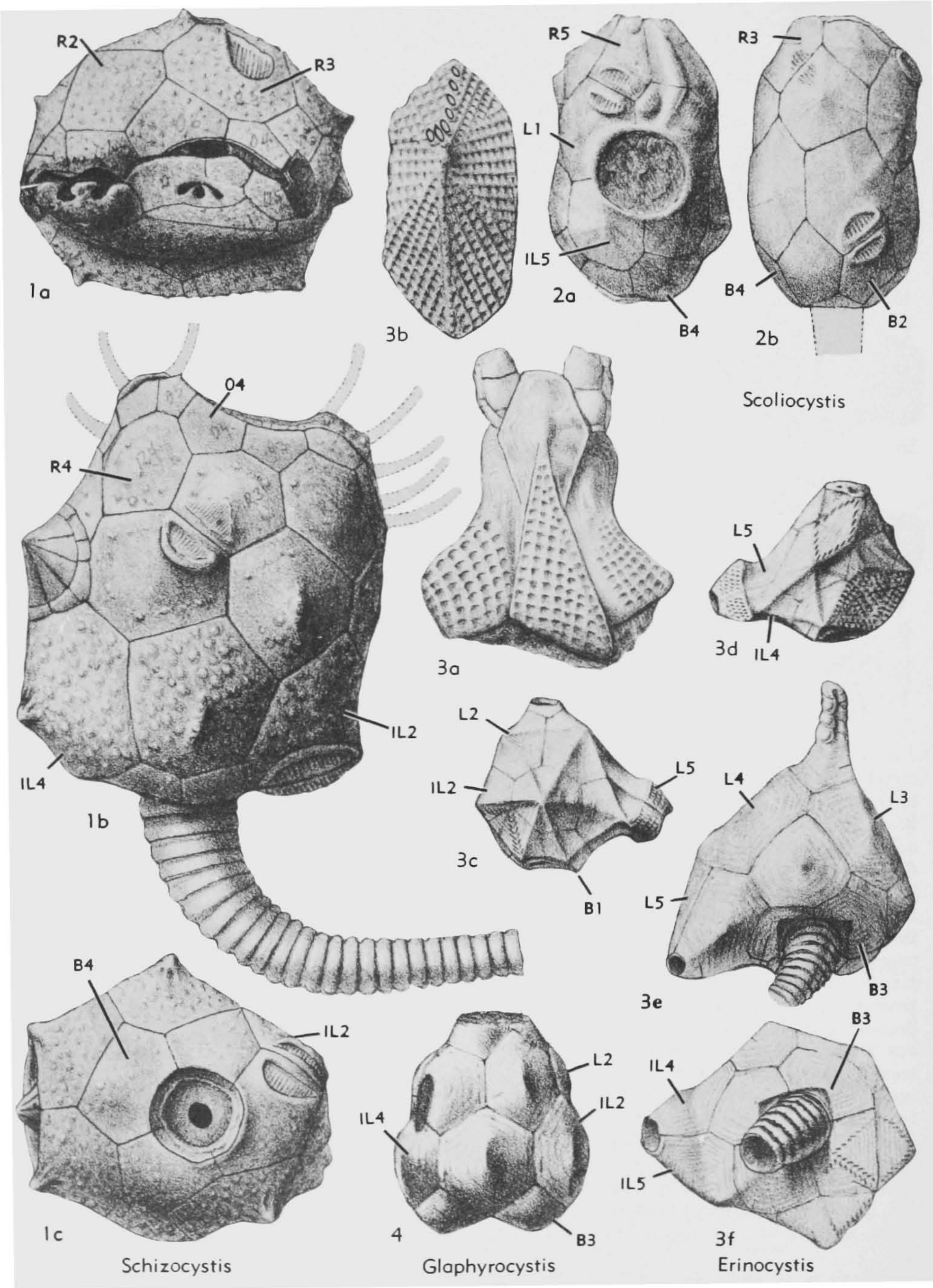


FIG. 94. Echinoencrinitidae (p. *S*189-*S*192). [Plate designations as in Figure 38.]

plate shapes and arrangements are difficult to define. *L.Ord.*, USSR-Est.-Norway.——FIG. 90,*4*; 93,*3*. *E. broeggeri* REGNÉLL, *Expansus* Ls. (3cβ), Norway; 90,*4a*, lat., small theca, ×2; 90,*4b,c*, aboral and lat., ×2 (100); 93,*3a,b*, lat. and aboral, ×3 (100).——FIG. 92,*4*; 94,*3e,f*. *E. volborthi* JAEKEL, Kunda (B_3), Leningrad; 92,*4a,b*, plate diagram and oral region (Kesling, n); 94, *3e,f*, lat. and aboral, ×1 (69).——FIG. 94,*3a,b*. **E. sculpta*, *Vaginatum* Ls., Leningrad region; *3a*, lat., ×3.5; *3b*, rhomb-bearing plate, ×5 (69). ——FIG. 94,*3c,d*. *E. angulata* JAEKEL, Kunda (B_3), Est. or Leningrad; *3c,d*, opposite lat., ×2 (69).

?**Eutretocystis** PHLEGER, 1935, p. 200 [**E. similis*; OD]. Like *Echinoencrinites* in all respects except for pectinirhomb *L3/R3*; this may well be an abnormal *Echinoencrinites* with a supernumerary rhomb. *L.Ord.*, Eu.(USSR).

Glaphyrocystis JAEKEL, 1899, p. 196 [**G. woehrmanni*; OD]. Theca irregularly ovate, narrow end oral, base indented. *IL* circlet complete in most, but some have *L3* reaching *B3*; *LL* forming complete circlet; *L5* prolonged orally between *R3* and *R5*, with *R4* rudimentary, absent, or fused with *L5*. Single basal pore rhomb, *B2/IL2*, and several upper rhombs between *LL* and *RR*; type species strongly resembling that of U.Ord. *Lepadocystis*, with rhombs *L1/R5*, *L2/R1*, *L3/R3*, and *L4/R3*. Periproct bordered by *L4*, *IL4*, and *L5*, not strongly protuberant. Hydropore and gonopore reported, but oral region mostly unknown, including brachioles. Proximal part of column with swollen, projecting columnals. *U.Ord.*, Est.——FIG. 92,*1*; 94,*4*. **G. woehrmanni*; 92,*1*, plate diagram (Kesling, n); 94,*4*, lat., ×2 (69).

Proctocystis REGNÉLL, 1945, p. 85 [**P. monstruosa*; OD]. Shape of theca very strongly influenced by large, protruding, aborally directed periproct, formed by *IL4*, *IL5*, and *L5*; only 4 *RR* present, *R5* absent; *L3* in contact with *B3*, interrupting circlet of *ILL*; *OO* apparently rudimentary; *BB* invaginated to form quadrangular depression. Three rhombs in known species: *B2/IL1*, *B2/IL2*, and *L4/R3*; few slits in each rhomb. Proximal columnals oval, with large lumen. *L.Ord.*, Sweden-USSR.——FIG. 90,2; 93,*2*. **P. monstruosa*, *Expansus* Ls., Sweden; 90,*2a,b*, lat., diagrammatic, ×2; 90,*2c*, plate diagram (99); 93,*2a-c*, 2 lat. and aboral, ×1.5 (100).

Prunocystites FORBES, 1848, p. 503 [**P. fletcheri*; OD] [=*Prunocystis* CARPENTER, 1891, p. 135 (*nom. van.*)]. Theca small, ovate, its base not indented, set atop exceptionally large column more than half as wide as theca); theca said to resemble "fruit of the dog-rose." *BB*, *ILL*, and *LL* circlets complete; *RR* circlet broken by *L5*, which, as in many genera, extends from periproct to *OO* circlet. *OO* little known, set atop somewhat truncated theca and partly obscured by clustered brachioles; FORBES' (51) description and JAEKEL'S (69) comments indicate that some plates of the short ambulacra may be incorporated into the cover of the theca. Hydropore and gonopore present. Periproct bordered by 4 plates, *IL4*, *IL5*, *L4*, and *L5*, containing an anal pyramid and ring of plates, set at mid-height. Ambulacra long, their number unknown, but according to thickness of known fragments and size of oral region, each theca had only 5 to 10 at most; segments of brachioles ("digitalia") longer than broad, with nodose enlargements. Three pore rhombs, at common locations. Proximal columnals flanged. *U.Sil.*, Eu.(Eng.).——FIG. 92,*2*. **P. fletcheri*; lat., ×4 (10).

Schizocystis JAEKEL, 1895, p. 193 (*non* LÉGER, 1900) [**Echinoencrinus armatus* FORBES, 1848, p. 507; OD]. Theca ovate aborally, adorally compressed in direction of *B1-B3*, so that periproct lies on one of small sides; base only slightly indented. *ILL* large, forming complete circlet; *L2* and *L3* more or less diamond-shaped, having little contact with adjacent *LL*; *L5* separating *R4* from *R5*; *OO* relatively large, distorted to fit elongate, narrow oral field. Long ambulacral grooves across narrow oral field, one extending from each side of mouth slot in gentle curve, irregularly branched and leading to 4 or 5 brachiole facets of various sizes. Periproct bordered by *IL4*, *IL5*, *L4*, and *L5*, rather large, with high valvular pyramid and surrounding ring of plates, not strongly protuberant. Only 2 pore rhombs, *B2/IL2* and *L4/R3*, each with moderate number of slits, basal rhomb diagonally opposite periproct on narrow side of theca. Hydropore a curved slit and gonopore a closely adjacent hole in large, elongate, tripartite *O1*, which fills most of one side of oral region. Column tapering distally, rather thick. *U.Sil.*, Eng.——FIG. 89,*1*; 90,*1*; 94,*1*. **S. armata* (FORBES); 89,*1a,b*, plate diagram and oral region (Kesling, n, after 69); 90,*1a,b*, oral and lat., ×2; 90,*1c*, plate diagram (10); 94,*1a-c*, oral, lat., and aboral, ×5 (69).

Scoliocystis JAEKEL, 1899, p. 196 [**Caryocystites pumilus* EICHWALD, 1860, p. 629; OD]. Theca irregularly elongate ovate, tapering at both ends, base not indented; all circlets of plates nearly or quite complete, definitely so in type species, but in *S. thersites* first 4 *LL* nearly separated by aboral corners of *RR* which extend to or almost to corresponding *ILL* below, so that junctions of *IL1-L1-L2-R1*, *IL2-L2-L3-R2*, and *IL3-L3-L4-R3* tend to be expressed as X's. In type species, *ILL* vertically elongate and very narrow, inducing JAEKEL (69) to describe the theca as "stunted." Periproct bounded by 5 plates, *IL4*, *IL5*, *L1*, *L4*, and *L5*, set at mid-height in *S. thersites* and rather high in *S. pumilus*, not protuberant. One basal pore rhomb, *B2/IL2*, and several between *LL* and *RR*; *S. pumilus* with *L1/R5*, *L4/R3*, and *IL2/L3*, *S. thersites* with *L1/R5*, *L2/R1*, *L3/R3*, and

L4/R3, same disposition as in *Glaphyrocystis*, its U.Ord. successor, or in *Lepadocystis*, U.Ord. callocystitid from N.Am. Ambulacra with few brachioles, concentrated near mouth. Hydropore and gonopore exactly as in *Echinoencrinites*. *L.Ord.*, USSR.——Fig. 92,*3*; 94,*2*. *S. thersites* Jaekel, Kunda (B_3), Leningrad; 92,*3*, plate diagram (Kesling, n); 94,*2a,b*, opposite lat., ×5 (69).

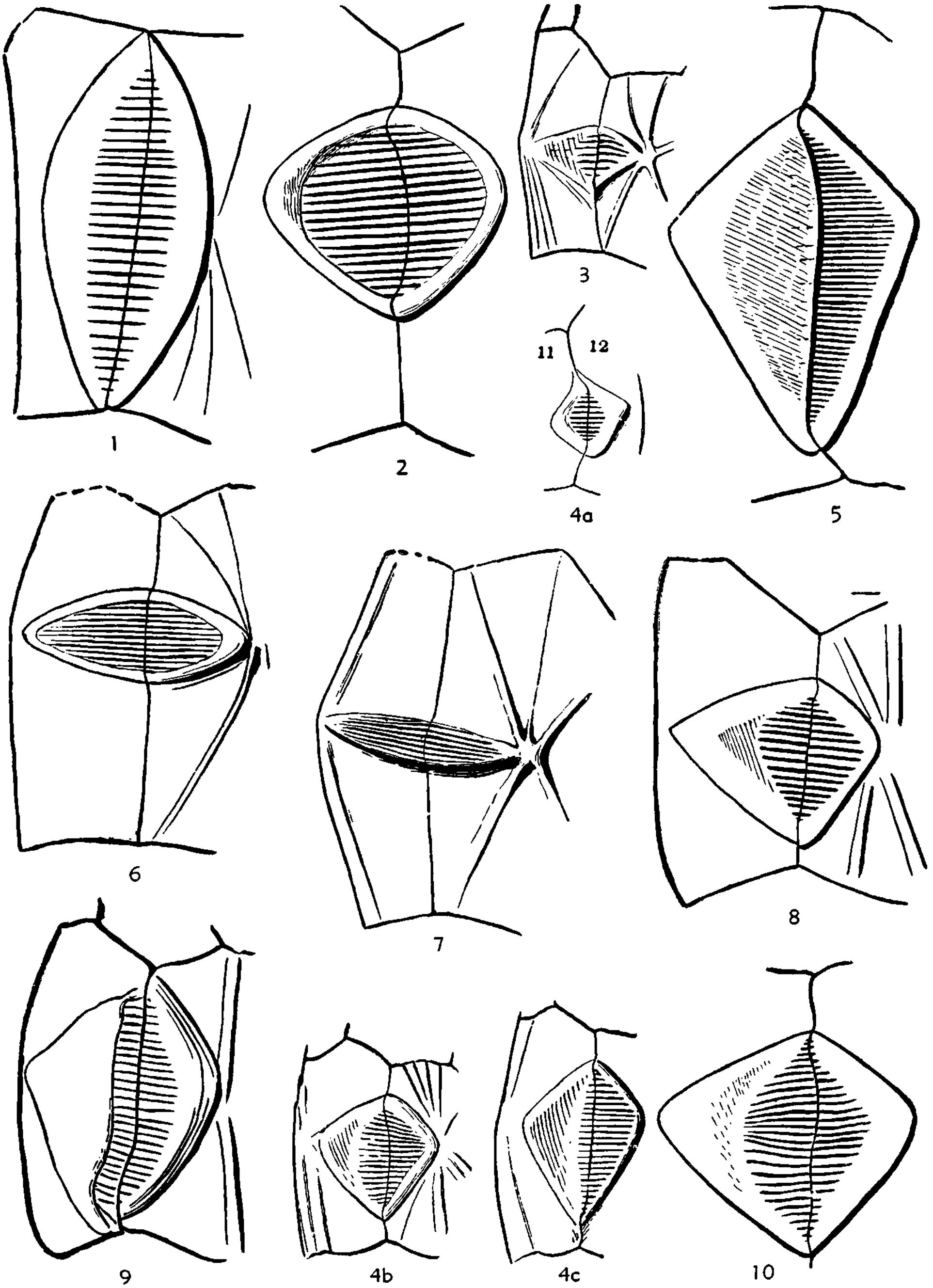


Fig. 95. Pleurocystitidae (p. *S*194-*S*199).——*1-10. Pleurocystites*, M.Ord.-U.Ord.; pectinirhomb *L1/L2* in various species, all ×5 *(12)*.

Family PLEUROCYSTITIDAE Neumayr, 1889

[*nom. correct.* BASSLER, 1938, p. 11 (*pro* Pleurocystiden NEUMAYR, 1889, p. 413)]

Theca strongly compressed, with extremely large periproct comprising most of one side. Only two brachioles, long, extending forward from sides of narrow peristome. Hydropore and gonopore on anal side. Three rhombs or less. *M.Ord.-L.Dev.*

This rather well-known family has inspired considerable speculation as to its significance in evolution of the Crinozoa, the taxonomic position of the enigmatic *Amecystis,* and precise chronological succession of species in North America, Britain, Belgium, Germany, and China. In addition, authorities have differed in their interpretation of the living position of these cystoids, their motility, and their mode of respiration.

The Pleurocystitidae appear from known records to have originated in Ontario, wherefrom they spread during the Ordovician into other parts of eastern North America—New York, Michigan, Wisconsin, Minnesota, Iowa—and eastward across the Atlantic to the British Isles and Belgium. The doubtful species *Pleurocystites bassleri* SUN is said to come from strata of Llanvirn age in China, and may represent the ancestral stock of the family. Strangely, Silurian pleurocystitids are unknown. Undoubtedly the Lower Devonian *Regulaecystis* from Germany is a member of this family.

A chronological series of *Pleurocystites* species can be selected to show any one of several trends. First, enlargement of the periproct, which attained its maximum size in British Caradocian forms and which is correlated with the spreading of adoral plates, so that *L1* and *L4* became more widely separated. Whether plate *L5* is distinct, fused to *L4,* or absent is still open to question.

A second trend concerns the number of small plates in the periproct, the so-called "periproctals." These vary from about 50 to perhaps as many as 1,500. The diminution in size of the periproctals does not appear to have been a trend throughout the history of the genus, but possibly it occurred in separate lineages at different times.

Third, the reduction in number and size of pectinirhombs. This trend, if such it be, can be strongly presented in a carefully selected series. But if all species are considered, it is somewhat less spectacular. The *L3/L4* rhomb shows progressive restriction on the suture, as well as fewer slits in the series *Pleurocystites filitextus* (Fig. 95,*1*), *P. robustus* (Fig. 95,*2*), *P. squamosus* (Fig. 95,*8*), *P. anglicus* (Fig. 95,*6*), *P. rugeri* (Fig. 95,*7*), and *P. procerus* (Fig. 95,*3*). Another series can be chosen to demonstrate the loss of slits on one-half of this rhomb, *P. filitextus, P. foriolus* (Fig. 95,*4*), and *P. gibbus* (Fig. 95,*5*); in the last-named species, BATHER (12) said that the "folds" on *L4* were "almost entirely closed by stereom." Other examples are seen in *P. elegans* (Fig. 95,*9*) and *P. quadratus* (Fig. 95,*10*). Rhomb *B2/IL2* is very small in *P. anglicus* and absent in *P. rugeri* and *P. procerus.* A drastic change also occurs in some Caradocian forms whereby the pore rhombs become elongate normal to the suture, rather than along it, attaining the ultimate expression in *P. rugeri.* It is true that Late Ordovician species all have restricted pectinirhombs, as compared with Middle Ordovician species, but the changes were evidently not attained in strict chronological sequence.

Other differences characterize species of *Pleurocystites.* The "shoulder-angle," defined by BATHER (12) as the angle formed by projection of the edges of plates *L1* and *L4*, varies from 40 to 115 degrees (at least). Ratios of height and width also exhibit an appreciable range. These are useful in description of species, but can scarcely be established as trends.

The modification, diminution, and elimination of pectinirhombs in *Pleurocystites* raise the problem of the two other genera. *Regulaecystis* seems to be a Devonian descendant in which both *B2/IL2* and *L1/L2* pectinirhombs were eliminated. But *Amecystis,* with a plate pattern almost identical with that of *Pleurocystites* but lacking any discernible rhombs or pores, originated in the Middle Ordovician and was a contemporary of *Pleurocystites elegans* and *P. filitextus.* No progression of forms is known that could have led to *Amecystis.*

Question may be raised as to whether *Amecystis* should be classed as a cystoid at all, inasmuch as it lacks thecal pores.

Dehm (36) concluded that *Amecystis* provided evidence of close affinity of cystoids with "carpoids," and proposed a Soluta-Pleurocystitidae group as an intermediary or passage from the Hydrophoridea group (true cystoids) to the Cincta-Mitrata-Cornuta group (true "carpoids"), with closer affinity to the "carpoids" than to the cystoids. This relationship, as such, has been denied by Gekker [Hecker] (54) and Regnéll (99). On the other hand, *Amecystis* is clearly not a member of any known "carpoid" lineage.

Inclusion of *Amecystis* in the cystoids produces a difficult problem in defining the taxon. Although strongly reduced, at least some thecal pores occur in *Regulaecystis,* and although roofed over by epistereom, there are pores within the thecal walls of *Hemicosmites, Polycosmites,* and *Caryocystites.* Insofar as I am aware, no attempts have been made to section plates of *Amecystis* to look for pores *within* the thecal plates. In regard to reduction of rhombs in *Pleurocystites,* Bather (12) suggested that in adapting to near-shore environment, the cystoids of this genus were confronted with a problem in respiration, and that when pectinirhombs became clogged with sand, they utilized rectal respiration, as do certain living echinoderms. Thus, he seems to have correlated increase in the periproct, at least in part, with the decrease in rhombs. If respiration was a function of the pectinirhombs, as generally conceded, and if respiration in some forms was accomplished otherwise so that the rhombs were no longer necessary or functional, and if with disuse the pectinirhombs finally disappeared—then, the position of *Amecystis* is decided, but the Cystoidea must be defined on other grounds than possession of thecal pores.

As to the position assumed by *Pleurocystites* in life, Bather (12) assumed that the column coiled loosely around some upright object and the animal stretched out parallel to the sea-floor, with the periproct or anal face uppermost. This suggestion introduces another problem: if the pectinirhombs were on the lower face of the theca, where sediment was liable to clog them, then why was the basal *(B2/IL2)* rhomb first to disappear in the evolutionary sequence? One might expect all rhombs to be affected equally. Thus, although the Pleurocystitidae has been studied from more and better specimens than most families, its ecology and evolution are poorly known.

Key to Genera of Pleurocystitidae

1. No trace of pore rhombs, at least externally .... *Amecystis*
   One to three pore rhombs, distinct, slits well defined 2
2. Two or three rhombs *(L1/L2* and *L3/L4* invariably present, *B2/IL2* in most); anal pyramid at corner of periproct, in so-called "rectal lobe" .... *Pleurocystites*
   Only one rhomb *(L3/L4)*; anal pyramid subcentral in periproct .... *Regulaecystis*

Pleurocystites Billings, 1854, p. 250 [**P. squamosus*; SD S. A. Miller, 1899, p. 272] [=*Pleurocystis* Carpenter, 1891, p. 12 *(nom. van.)* *(non Pleurocystis* Hesse, 1909); *Dipleurocystis* Jaekel, 1918, p. 95 (type, *Pleurocystites anglicus* Jaekel, 1899, p. 235)]. Pectinirhombs developed in various forms on the antanal face; *B2/IL2* smallest of rhombs, absent in some species; *L1/L2* never larger than *L3/L4,* may be conspicuously smaller; rhombs varying in degree of elongation normal to suture, number and length of slits, length of suture involved, development of bordering rim, and asymmetry of halves; *P. gibba* with slits in *L4* nearly obliterated by covering of stereom. *B1* and *B4* on anal side, forming aboral border of very large periproct, *B2* and *B3* on antanal side. *ILL* large, circlet interrupted by periproct between *IL4* and *IL5*; *LL* also well developed, particularly *L1* and *L4* which extend around edge of theca from antanal to anal sides and abut on short suture at adoral side of periproct; *L5* either absent, indistinct, or fused with *L4*. *RR* small, circlet interrupted between *R1* and *R5* by insertion of *O1*; *OO* forming complete circlet, with tripartite *O1* rather large and centered on adoral margin of anal side, *O2* giving rise to one brachiole and *O4* and *O5* to other, *O3* on antanal side directly opposite *O1*. Hydropore a curved slit and gonopore a small opening, both bisected by suture within *O1*. Periproct large, covered by 50 to about 1,500 small plates ("periproctals") with anal pyramid at aboral corner between *B4* and *IL4* in so-called "rectal lobe." Two brachioles, long, biserial as in other cystoids. Column long and tapering to very small diameter, end not known with certainty; proximal part composed of alternating inner and outer rings, probably interlocking, and distal part of longer columnals having much smaller lumen. The creation of *Dipleurocystis* by Jaekel in 1918 (71) was due to a misunderstanding of the type species of *Pleurocystites*. The type was designated by S. A. Miller (85) in 1889, as *P. squamosus*. Unaware of this action, Haeckel (58) in 1896 also selected a type, *P. filitextus. P. squamosus* has very numerous small plates in the periproct, whereas *P. filitextus* has fewer, larger, more nearly polygonal plates. BATHER (12) called attention to the correct type species; but JAEKEL (71) evidently did not understand it, for he defined *Pleurocystites* as having large periproctals and sought to create a new genus with type species *P. anglicus* JAEKEL for the species with large periproct, minute periproctals, and narrow pore rhombs. As recognized by FOERSTE (in SLOCUM & FOERSTE, 1924), and emphasized by REGNÉLL (personal communication), *Dipleurocystis* cannot be maintained because by definition it would include the type species of *Pleurocystites*.

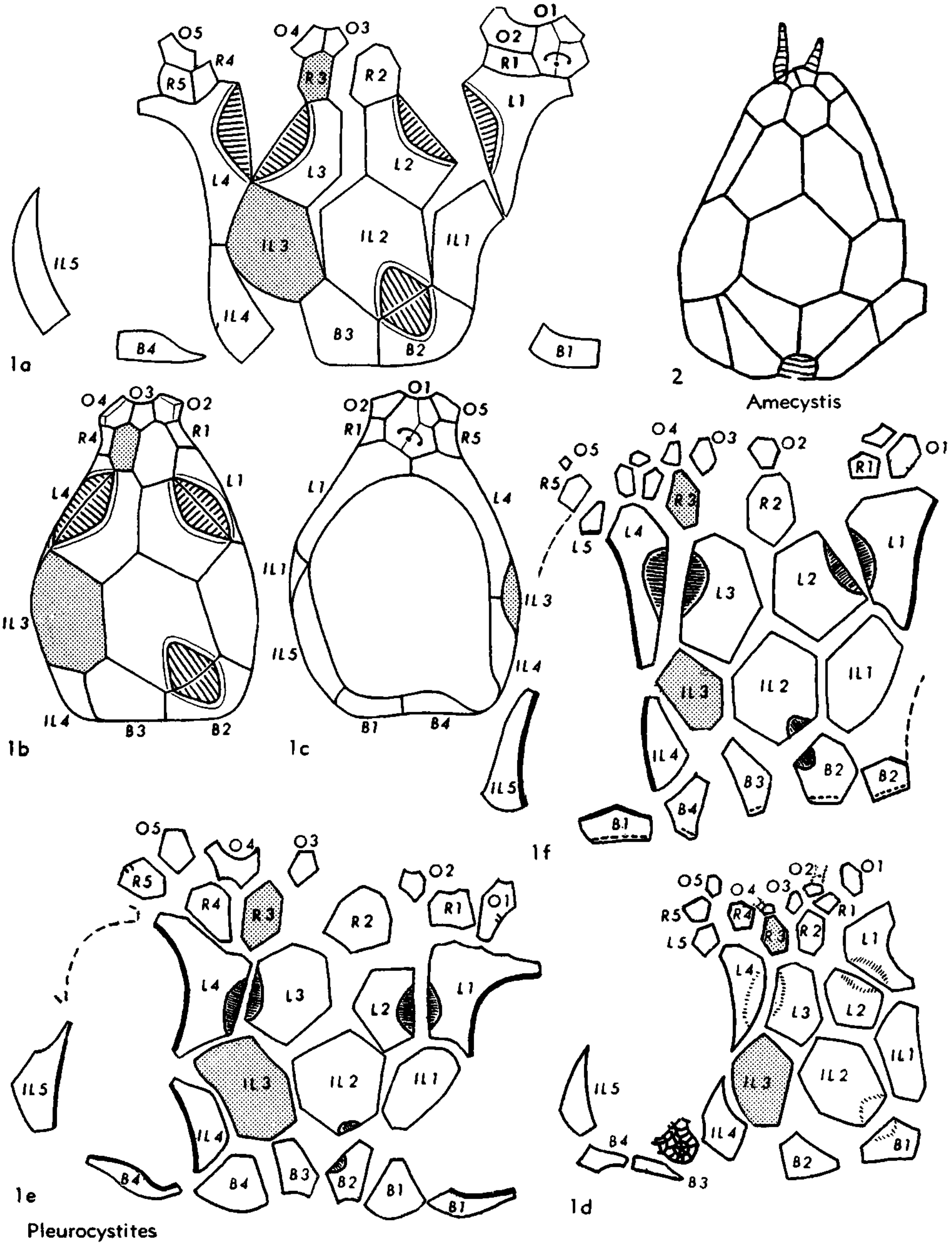


FIG. 96. Pleurocystitidae, plates of *A*-ray shaded (p. S194-S199). [Plate designations as in Figure 38.]

Further, REGNÉLL has informed me that the number of periproctals in known species falls into a nearly continuous series, with no appreciable hiatus between "few" and "numerous."] *M.Ord.-U.Ord.*, Eu.(Brit.-Belg.)-N.Am.-?China.——FIG. 95,*1-10*. Pectinirhomb *L1/L2* in various species, all ×5

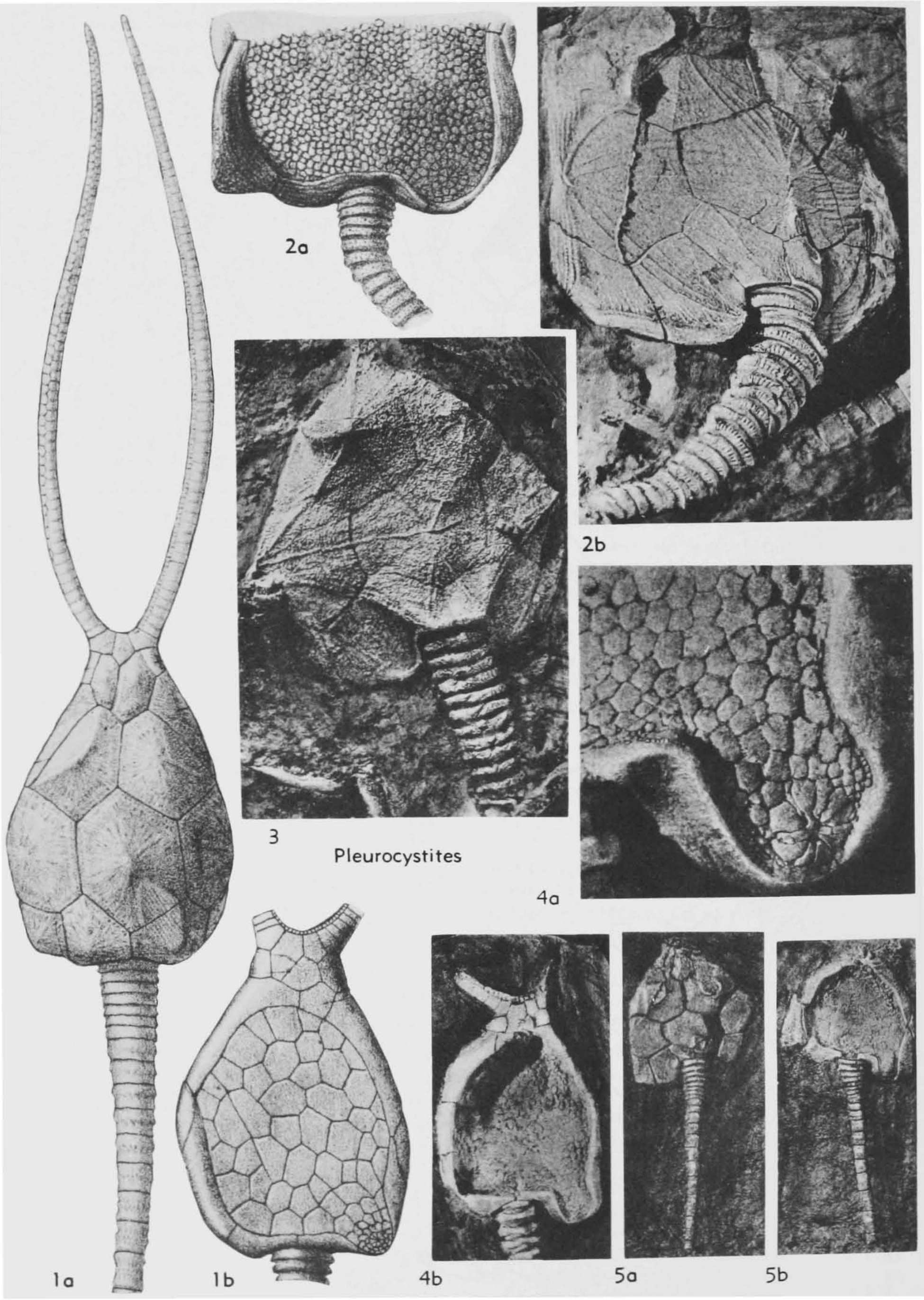


FIG. 97. Pleurocystitidae (p. S194-S199).

(12).——Fig. 96,*1;* 97,*1;* 98,*2a;* 99,*3. P. filitextus* Billings, M.Ord.(Trenton.), Ont.; 96,*1a-c,* plate diagram, antanal, and anal (Kesling, n); 96,*1d-f,* 3 plate diagrams showing various interpretations of plate number and arrangement (10, 12); 97,*1a,b,* antanal, anal views, ×2(69); 98,*2a,* antanal,

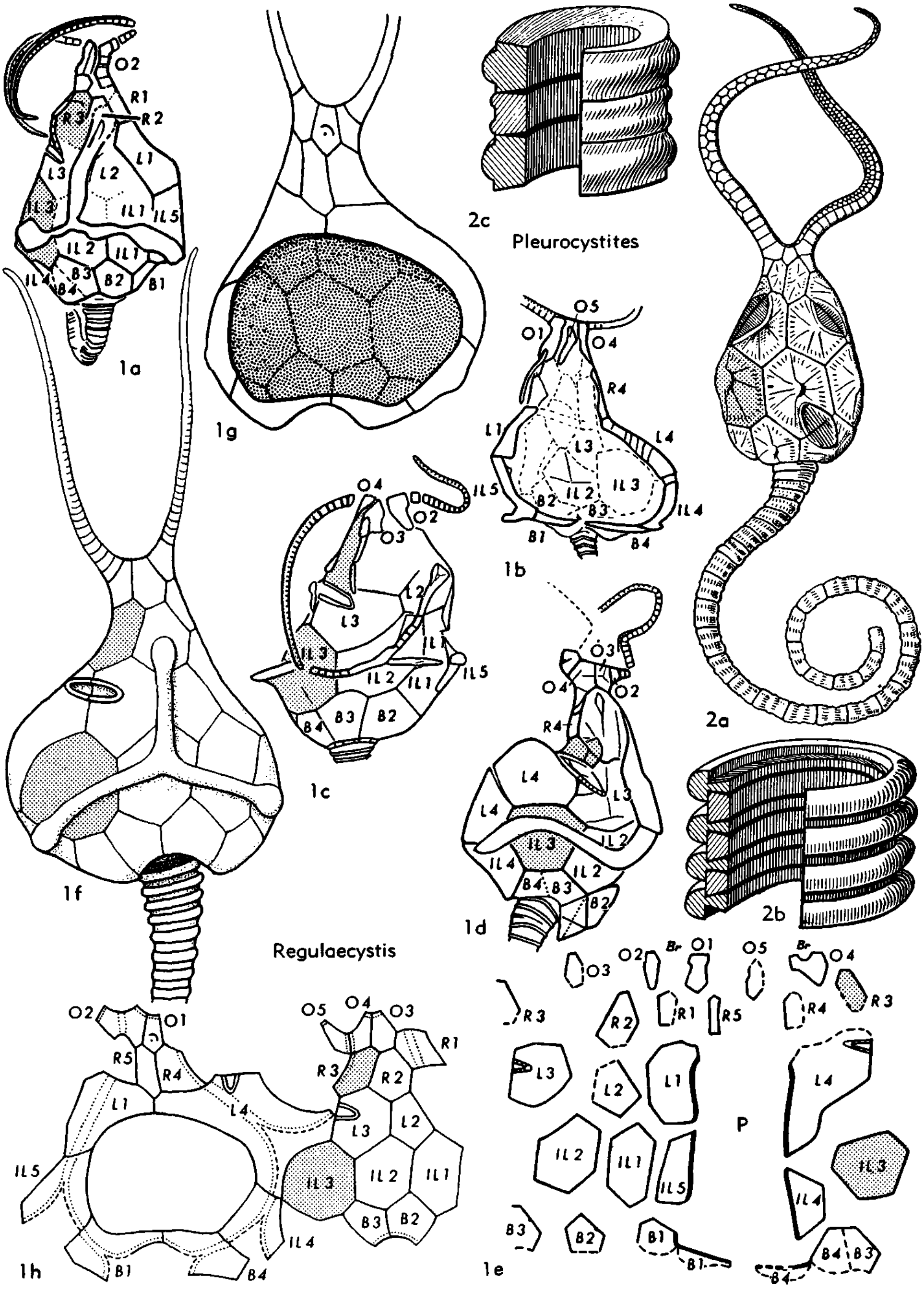


Fig. 98. Pleurocystitidae, plates of *A*-ray shaded (p. *S*194-*S*199). [Plate designations as in Figure 38.]

reconstr. (10); 99,*3a,b,* anal, antanal views, ×1 (20).——Fig. 97,*2. P. anglicus* Jaekel, U.Ord.(L. Ashgill.), Ire.; *2a,* anal, incomplete theca, ×2 (69); *2b,* antanal, ×2 (12).——Fig. 99,*2. P. elegans* Billings, M.Ord.(Trenton.), Ont.; *2a,b,* antanal, 2 thecas, ×1 (20).——Fig. 97,*5. P. foriolus* Bather, U.Ord.(Drummuck), Scot.; *5a,b,* antanal, anal views, ×1 (12).——Fig. 97,*3. P.*

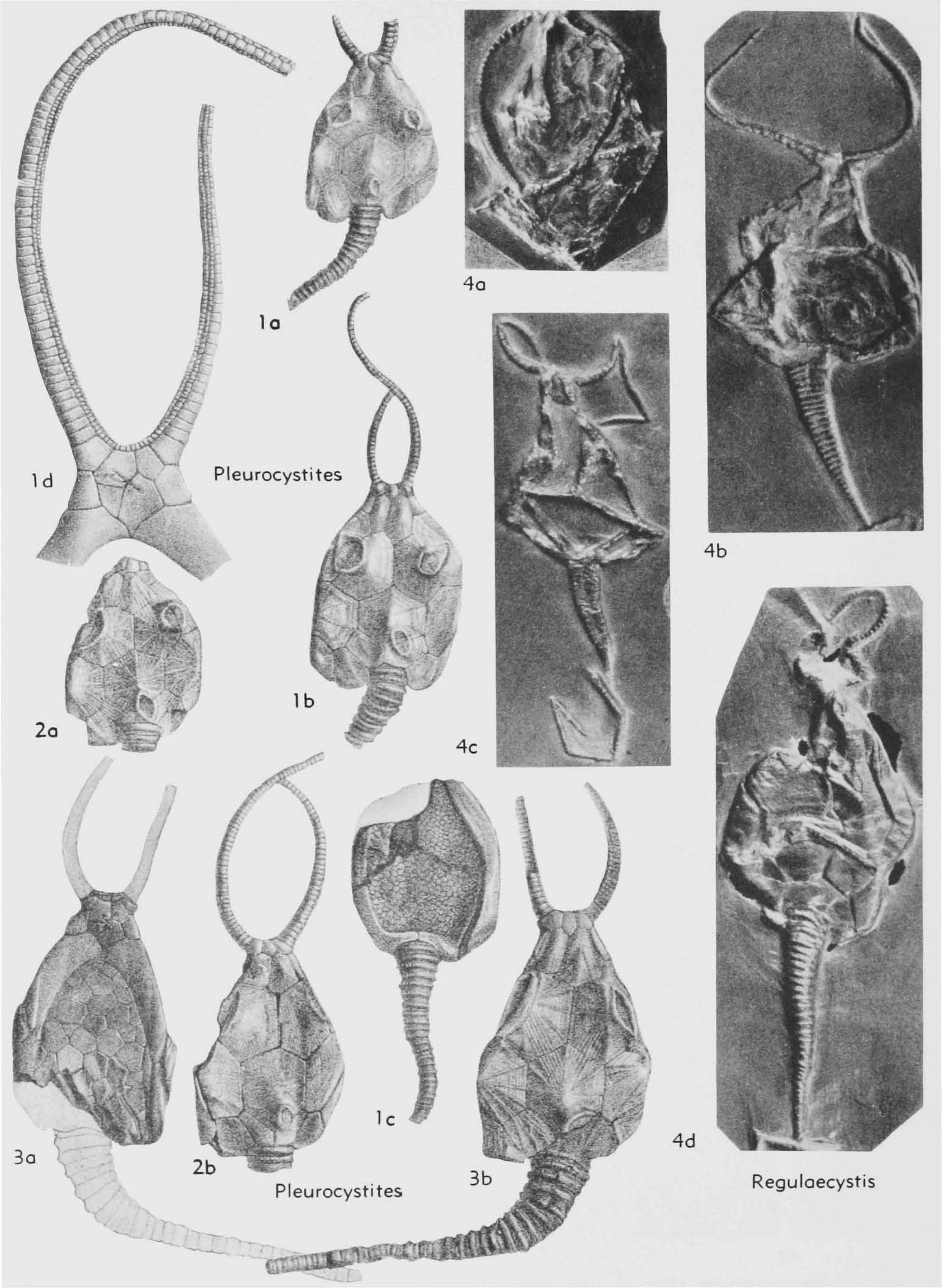


Fig. 99. Pleurocystitidae (p. S194-S199).

rugeri BATHER, M.Ord(Caradoc.), Wales; antanal, ×2 (12).——FIG. 97,*4*. *P. quadratus* BATHER, U.Ord.(Drummuck), Scot.; *4a*, "rectal" lobe of periproct with anal pyramid, ×4.5; *4b*, anal view, ×1 (12).——FIG. 98,*2b,c;* 99,*1a-d*. **P. squamosus,* M.Ord., Can.(Ont.); 98,*2b,c,* proximal and distal secs. of column (12); 99,*1a,b,* antanal, 2 specimens, ×1; 99,*1c,* anal, incomplete theca, ×1; 99,*1d,* oral regions and brachioles, enl. (20).

Amecystis ULRICH & KIRK, 1921, p. 147 [**Pleurocystites laevis* RAYMOND, 1921, p. 2; OD]. Theca with plate arrangement like that of *Pleurocystites.* No trace of pore rhombs, at least externally. [This genus is included here as a pleurocystitid despite its anomalous structure.] *M.Ord.,* N.Am.(Ont.-Minn.-Mich.-Pa.-Ky.).——FIG. 96,*2*. **A. laevis* (RAYMOND), Ont.; antanal (36).

Regulaecystis DEHM, 1932, p. 74 [**R. pleurocystoides*; OD]. Theca flattened, as in *Pleurocystites,* composed of thin, fragile plates. Four *BB* visible on antanal side, *B1* and *B4* with extensions on anal side to form lower border of periproct; *IL4, IL5, L1* and *L4* folded in thick rim, their antanal sides bordering periproct; *L4* especially large; *RR* and *OO* small. Only one rhomb, *L3/L4,* occupying short section of suture and elongate normal to suture; slits not reported. Three curious ridges radiating from center of *IL2*, to *R2*, to *IL5*, and to *IL3,* perhaps serve to give rigidity to antanal side of thin-plated theca. Periproct oval, transversely elongate. Oral end of theca very narrow, bearing 2 long, thin brachioles. Column long, tapering, with 20 to 30 columnals in proximal part and 60 to 80 in distal, structurally like column of *Pleurocystites.* Hydropore and gonopore not reported. *L.Dev.,* Ger.——FIG. 98,*1;* 99,*4*. **R. pleurocystoides;* 98,*1a-d,* sketches of 4 specimens (36); 98,*1e,* plate diagram (36); 98,*1f,g,* antanal, anal views (reconstr.) (Kesling, n); 98,*1h,* plate diagram, some sharply folded peripheral plates split (dashed lines) to show antanal and anal sides and marginal rim (dotted lines) (Kesling, n); 99,*4a-d,* 4 specimens, all distorted, ×? (36).

Family CALLOCYSTITIDAE Bernard, 1895

[*nom. correct.* BASSLER, 1938, p. 10 (*pro* Callocystidés BERNARD, 1895, p. 206)] [=Callocystidae JAEKEL, 1899, p. 266]

Rhombiferan cystoids provided with distinct pectinirhombs; periproct relatively small, not produced; theca ovate, globular, biconvex, or ellipsoidal, not spindle-shaped or resembling a pentremite; rhombs relatively few, rarely developed as demirhombs; ambulacra long, extending down over theca; column present. *U.Ord.-U.Dev.*

This family includes many of the well-known genera of rhombiferans. It was long-lived and diverse, both in Europe and in North America.

The distinctive long ambulacra, "recumbent" on the theca, tend to obscure certain of the sutures and smaller plates. For this reason, details of many cystoids can only be established from specimens in which ambulacra have been exfoliated.

Subfamily CALLOCYSTITINAE Bernard, 1895

[*nom. transl.* KESLING, herein (*ex* Callocystidés BERNARD, 1895, p. 206)] [=Callocystinae JAEKEL, 1899, p. 287 (*partim*)]

Theca ovate, ellipsoidal, or globular; four or five ambulacra, branching; brachioles small, widely spaced; *LL* intercalated deeply into *ILL* circlet, as many as three *LL* in contact with *BB*. *M.Sil.-L.Dev.*

Key to Genera of Callocystitinae

1. *R1* and *R4* very small or absent; *L2* nearly or quite reaching *B2; L4* not forming a suture with *B4,* subtrapezoidal, four-sided .... *Sphaerocystites*
   All *RR* present; *L2* distinctly separated from *B2*; *L4* in contact with *B4*, five-sided 2
2. Theca ovate to ellipsoidal; pectinirhombs rather long, provided with numerous slits .... *Callocystites*
   Theca depressed globular; pectinirhombs small, with few slits .... *Coelocystis*

Callocystites HALL, 1852, p. 238 [**C. jewetti;* OD] [=*Anthocystis* HAECKEL, 1896, p. 132 (type, *A. halliana*); *Callocystis* CARPENTER, 1891, p. 135 (*nom. van.*)]. Theca ovate to ellipsoidal, base flat or truncated but not invaginated. *L1, L3,* and *L4* atop corresponding *BB,* with *ILL* forming tier of 8 plates; *BB* large, especially *B4,* which is in contact with *IL3, L4, IL4,* and *IL5,* as well as the adjacent *BB*; *L5* above periproct, inserted between *R4* and *R5.* Five long ambulacra, broad, normally one or more subdivided at about mid-length; brachiole facets rather numerous, alternating. Periproct bordered by elongate *IL4* and *IL5* and by subtrapezoidal smaller *L5*; anal pyramid surrounded by numerous small subquadrate platelets. Pectinirhombs rather well developed, intermediate between those of *Sphaerocystites* and *Coelocystis,* with numerous slits, halves on *IL2, L1,* and *L4* surrounded by prominent walls, those on *B2, R3,* and *R5* by high outer rim and lower inner ridge. Hydropore more or less 8-shaped with expanded distal parts; gonopore adjacent and small, said to be closed by pyramid of 4 pieces. Column stout, proximal part composed of rings wide in diameter; tapering rapidly in proximal half, more slowly in distal; total length unknown but exceeding 6 cm.; proximal columnals more highly ornamented and shorter than distal. *M.Sil.,* N.Am.(Ont.-N.Y.-Ohio).——FIG. 100,*3;* 101,*2a-g.* **C. jewetti;* Niagaran, USA(N.Y.) (101,*2a-g*); Can.(Ont.) (100, *3*); 100,*3a,b,* plate diagram and oral region (Kesling, n); 101,*2a-d,* 4 lat., ×1; 101,*2e,* enlarged pectinirhomb; 101,*2f,* diagram of ambulacra, hydropore, gonopore, periproct, and pectinirhombs (60); 101,*2g,* enlarged end of ambulacrum with

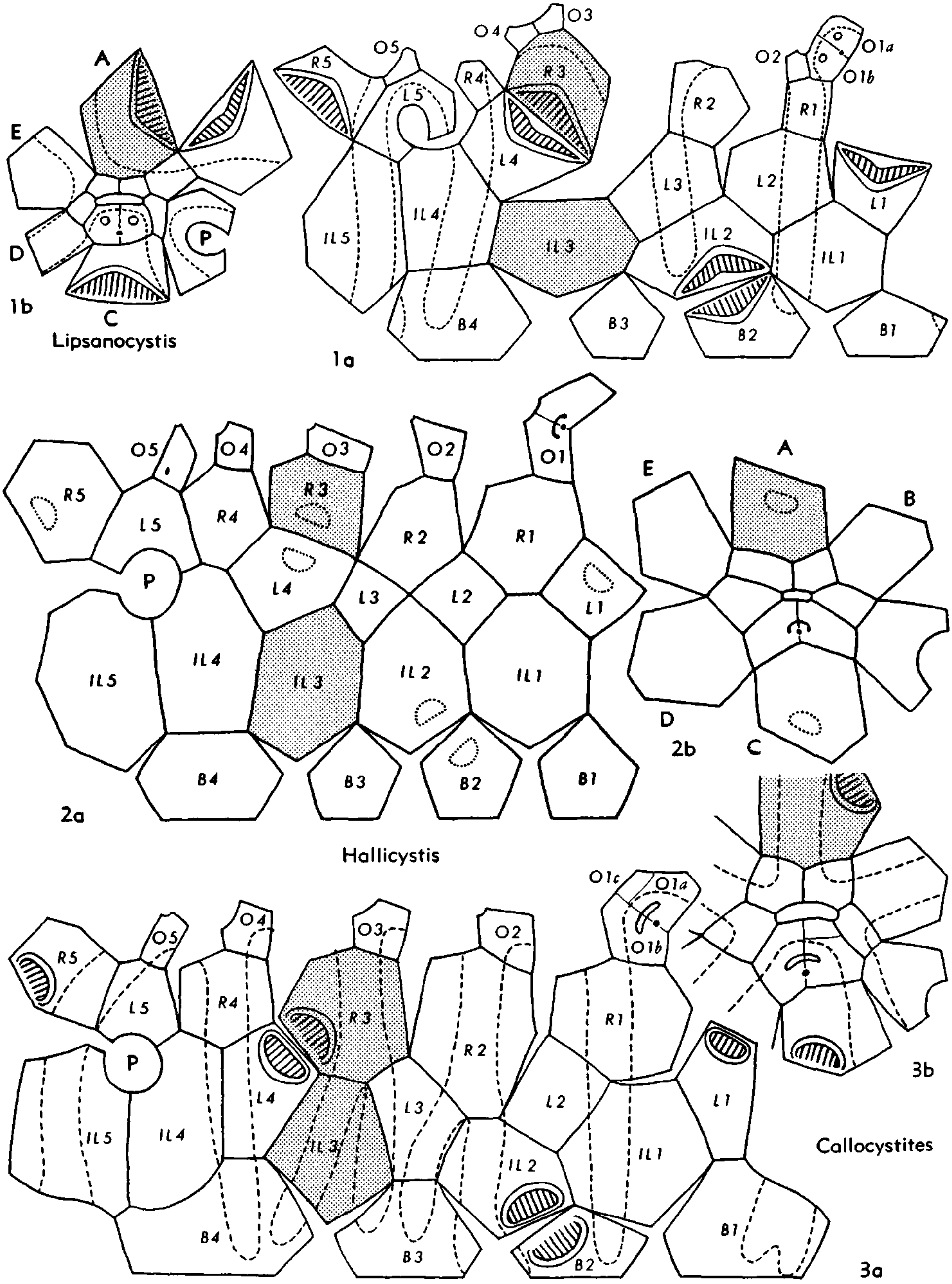


FIG. 100. Callocystitidae, Callocystitinae *(3),* Apiocystitinae, *(1,2),* plates of *A*-ray shaded (p. *S*199-*S*201, *S*209, *S*212-*S*213). [Plate designations as in Figure 38.]

1 brachiole (69).——Fig. 102,*1;* 101,*2h,i.* *C. jewetti elongatus* Foerste, Cedarville Dol., USA (Ohio); 102,*1,* plate diagram (49); 101,*2h,i,* 2 lat., steinkern, ×1 (47). [See also Fig. 44,*2;* 75,*1.*]

Coelocystis Schuchert, 1903, p. 234 [**Hemicosmites subglobosus* Hall, 1867, p. 316; OD (=*Sphaerocystis dolomiticus* Jaekel, 1899, p. 289; *Callocystites sphaeroidalis* Foerste, 1917, p. 239)]. Theca depressed globular. [Reports that the *BB* are deeply invaginated are based on stein-

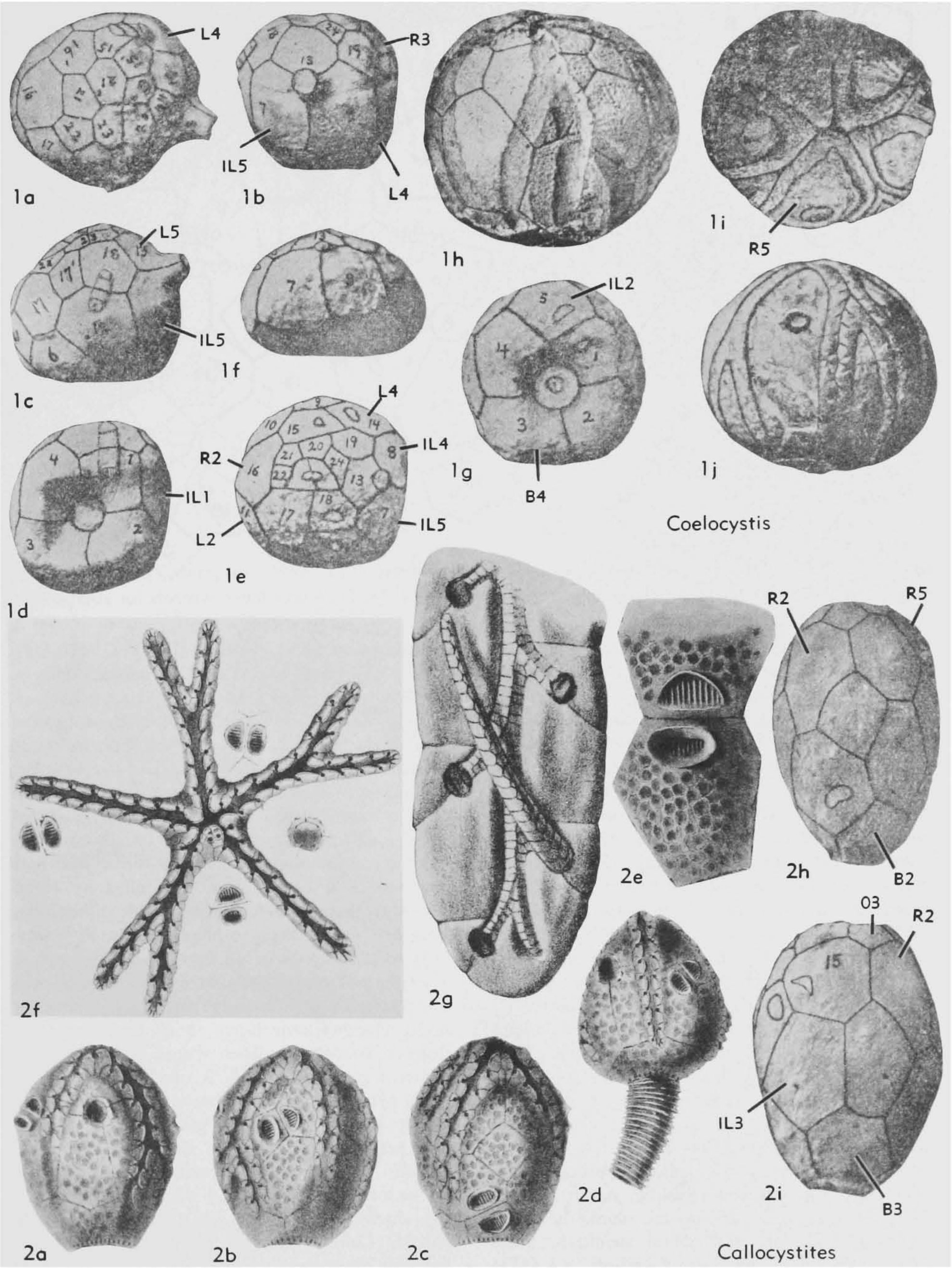


Fig. 101. Callocystitidae, Callocystitinae (p. *S*199-*S*202). [Plate designations as in Figure 38.]

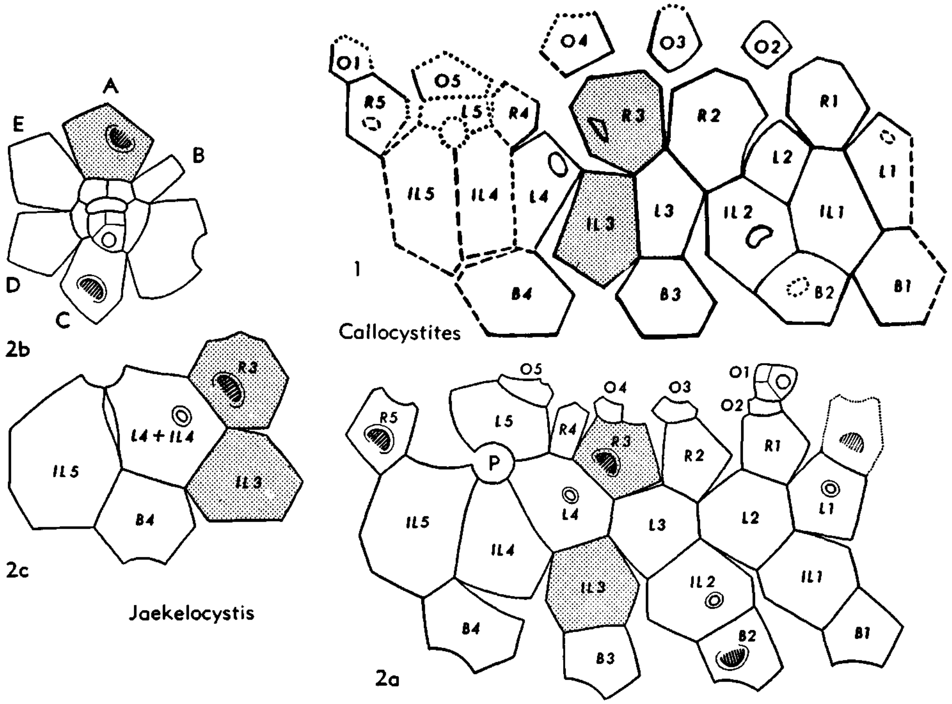


FIG. 102. Callocystitidae, Callocystitinae *(1)*, Apiocystitinae *(2)*, plate diagrams, plates of *A*-ray shaded (p. S199-S201, S209). [Plate designations as in Figure 38, Carpenter letter symbols for rays in *2b*.]

kerns; from external molds, Foerste (49) determined that at the junction with the column the plates are not indented externally but instead are much thicker in that part.] *L1* atop *B1*, *L3* atop *B3*, and *L4* atop *B4*, thus thoroughly disrupting *IL* circlet and producing second tier of 8 plates; *L2* and *L5* inserted into *R* circlet to form third tier of 7 plates; *OO* distinct but small, with *O1* bipartite (possibly tripartite?) and bearing hydropore slit and gonopore opening. Pectinirhombs small, with few slits. Five ambulacra, each rather broad and dividing into 2 to 4 branches. Anal pyramid apparently not surrounded by circle of small platelets, as in most genera of subfamily; one specimen of type species with excess plates in adoral half of theca, here accounted as bipartite *R1* and *O3* and tripartite *R3*, such occurrence perhaps being indicative of instability of depressed globular form. *M.Sil.*, N.Am.(Wis.-Ill.-Ohio).——Fig. 103,*1*; 101,*1*. *C. subglobosa (Hall), Niagaran, USA; 103,*1a,b*, plate diagram and oral region, normal theca (Kesling, n, after 116); 103,*1c,d*, plate diagram and oral region, specimen with anomalous *RR* and *OO* (Kesling, n, after 116); 101,*1a-d*, oral, 2 lat., and aboral, steinkern, ×0.8; 101,*1e-g*, oral, lat., and aboral steinkern, ×0.8 (49); 101,*1h*, lat., ambulacra flaked off, ×1 (47); 101,*1i,j*, oral and lat., ×1 (49).

Sphaerocystites Hall, 1859, p. 130 [*S. multifasciatus; OD] [=*Sphaerocystis* Carpenter, 1891, p. 5 *(nom. van.)* (*non* Leger, 1892; *nec* Chodat, 1897)]. Theca subspherical, some adults broader than high. *B2*, *L2*, *IL1*, and *IL2* with apices in contact or nearly so; *L1* and *L3* also deeply intercalated into *IL* circlet, in some species in contact with corresponding *BB*; *R1* and *R4* either absent or so small as to be obscured by ambulacra. Periproct set rather high on globular theca, with anal pyramid of 6 to 8 plates surrounded by 10 to 14 small subquadrate pieces. Four ambulacra, branched (particularly in large specimens) irregularly to produce 14 or 15 branches (maximum of 27 reported) on aboral part of theca; ambulacra narrow, with low flooring plates and numerous alternating brachiole facets on all extensions. *O1* distinct, bearing dumbbell-shaped hydropore and adjacent gonopore, which is said to be closed by small pyramid of 4 or 5 platelets; other *OO* plates small, obscured by covering plates of narrow, elongate peristome. Rhombs on *B2/IL2*, *L1/R5*, and *L4/R3*, long and filling entire suture, disjunct, halves on *IL2*, *L1*, and *L4* narrow and enclosed by sharp-edged rims; slits numerous, closely spaced. Column tapering for short distance, remainder constant in diameter, distal end terminating in rootlike processes. [The diagnosis given by

JAEKEL (69) is misleading, inasmuch as it was based on his *"S. dolomiticus,"* which is a junior synonym of *Hemicosmites subglobosus* HALL, later made the type of *Coelocystis* by SCHUCHERT (115).] *L.Dev.,* N.Am.(Pa.-Md.-W.Va.).——FIG. 104,*3a,b.* **S. multifasciatus,* Keyser F., USA

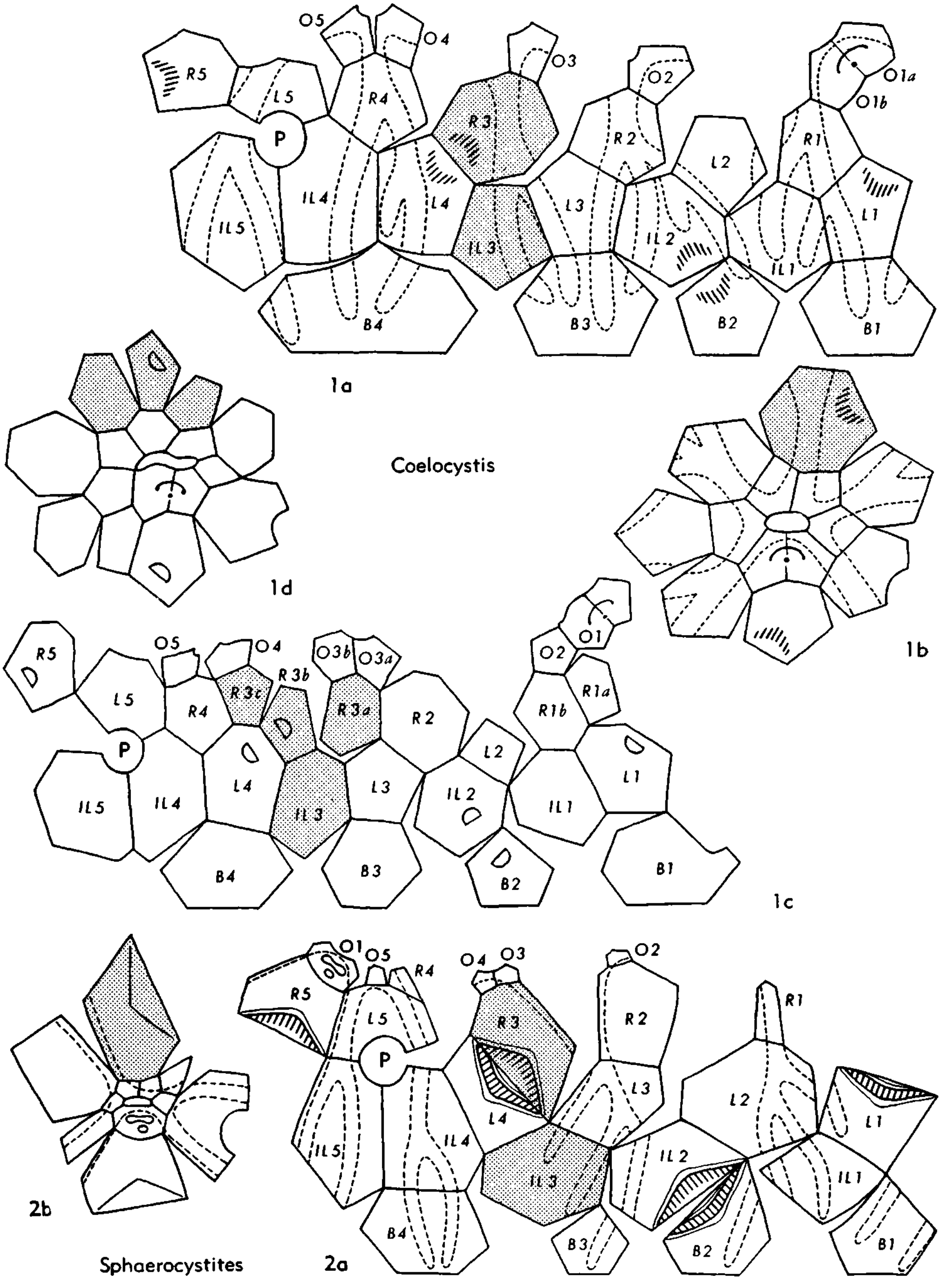


FIG. 103. Callocystitidae, Callocystitinae. Plate diagrams, plates of *A*-ray shaded (p. *S*201-*S*203). [Plate designations as in Figure 38.]

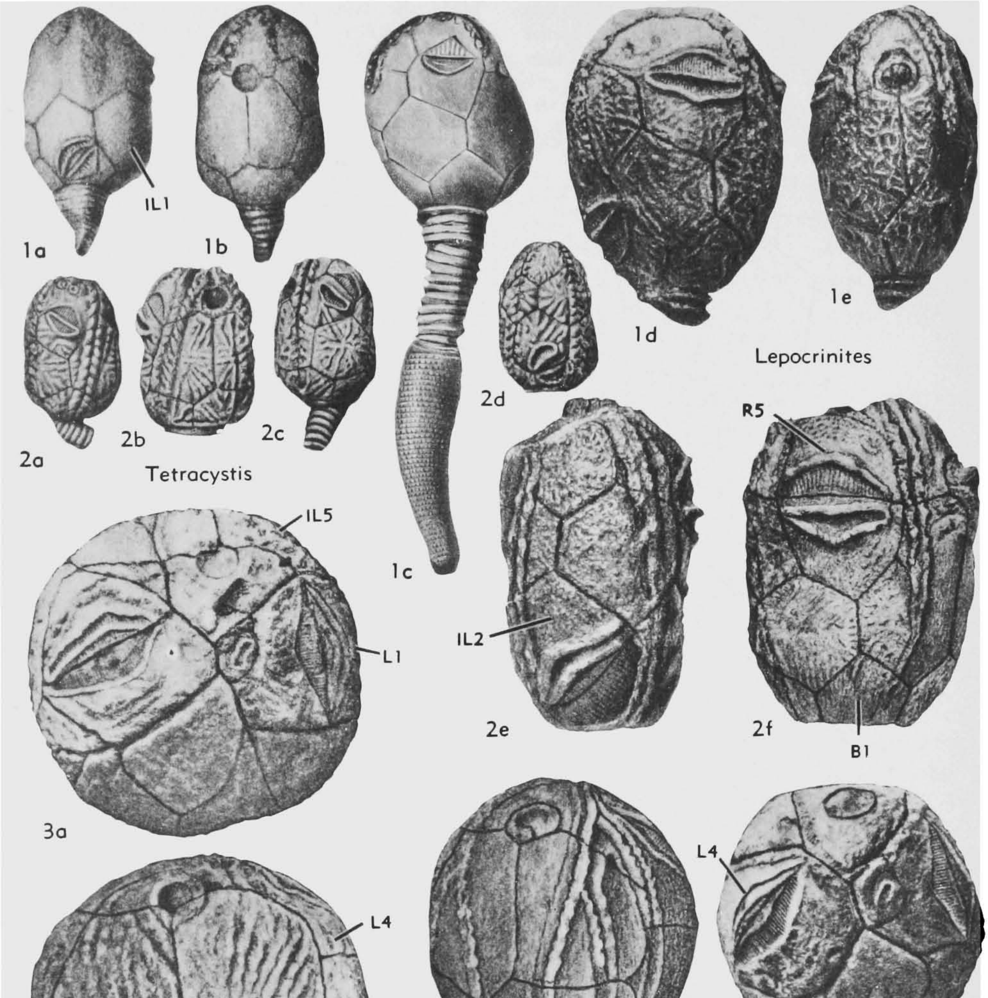


FIG. 104. Callocystitidae, Callocystitinae *(3)*, Apiocystitinae *(1,2)* (p.*S*202-*S*203, *S*211, *S*214). [Plate designations as in Figure 38.]

(Md.); *3a,b*, oral and lat., ×2 (116A).——FIG. 103,*2*; 104,*3c,d*. *S. globularis* SCHUCHERT, Keyser F., USA(Md.); 103,*2a,b*, plate diagrams, lat. and oral (Kesling, n); 104,*3c,d*, lat. and oral, ×2 (116A).

Subfamily APIOCYSTITINAE Jaekel, 1899

[*nom. correct.* KESLING, herein (*pro* Apiocystinae JAEKEL, 1899, p. 277)]

Theca ovate or ellipsoidal; four or five ambulacra, unbranched (except in *Strobilocystites*) and not protuberant; brachioles rather widely spaced; *ILL* forming a closed circlet. *U.Ord.-U.Dev.*

The position of *Strobilocystites*, the last surviving cystoid, is not clearly manifest. In branching of the ambulacra, it is allied with the Callocystitinae, but in the complete circlet of *ILL*, it shows definite affinities with the Apiocystitinae. Furthermore, the branches are only short lateral processes from the main ambulacra, not major divisions like those of *Sphaerocystites,* youngest of the Callocystitinae. In shape of thecal plates, structure of the hydropore, and general organization, *Strobilocystites* has closest resemblance to the slightly older *Lipsanocystis.* It also has ambulacra somewhat entrenched, although not to the degree present in *Jaekelocystis.* Therefore, I place it in the Apiocystitinae, contrary to previous assignments.

With inclusion of *Strobilocystites,* the Apiocystitinae portrays some interesting evolutionary trends. As recognized by JAEKEL (69), BATHER (10), REGNÉLL (99), and others, the Upper Ordovician *Lepadocystis* of southern Indiana and Ohio is the oldest known genus of the subfamily. From this ancestor, with five ambulacra and five pectinirhombs, the Lower Silurian *Brockocystis* developed in eastern North America by loss of the *L2/R1* pectinirhomb and addition of globular projections on the major thecal plates. All subsequent genera had only four ambulacra; apparently, ambulacrum *III,* already short in *Lepadocystis* and *Brockocystis* (in which it was obstructed by the two half-rhombs on *R3*), failed to form in Middle Silurian and later genera. Also in the Middle Silurian, the number of pectinirhombs stabilized at three—*B2/IL2, L1/R5,* and *L4/R3.*

Another trend involved the hydropore. In *Lepadocystis,* this structure is a long U-shaped slit, with a few crossbars to form a grating. In the Devonian *Lipsanocystis* and *Strobilocystites,* the central part of the hydropore is absent, and the ends are greatly enlarged and elevated as two separate sieve-plates. In *Tetracystis* and *Jaekelocystis,* a single large complex sieve-plate occurs, evidently representing one end of the ancestral structure. *Lovenicystis* is intermediate between *Lepadocystis* and *Lipsanocystis;* it has two openings, one piercing each of the two parts of *O1* bearing the hydropore, with a shallow groove leading from one to the other.

Certain Middle Silurian and later genera exhibit a reduction in the number of thecal plates bordering the periproct. *Tetracystis* has four, *Apiocystites* has three, and *Lipsanocystis* has the periproct nearly surrounded by *L5.* Although this may have been a trend in one lineage, the Upper Devonian *Strobilocystites* has four plates involved.

Key to Genera of Apiocystitinae

[After REGNÉLL, 1945 (99)]

1. Ambulacra five more than three pectinirhombs, with two half-rhombs on *R3* .. 2
   Ambulacra four; only three pectinirhombs, with single half-rhomb on *R3* 3
2. Pectinirhombs five; *IL4* and *IL5* elongate vertically; *R* circlet interrupted by *L5;* no globular projections on thecal plates .... *Lepadocystis*
   Pectinirhombs four; *IL4* and *IL5* not elongate; *R* circlet complete; major thecal plates with globular projections .. *Brockocystis*
3. *L* and *R* circlets complete 4
   LL and *RR* intercalated, one or both interrupted 6
4. Periproct bordered by four plates, including *L4* .... *Lovenicystis*
   Periproct bordered by three plates, not *L4* 5
5. Pectinirhombs short, with few slits; ambulacra long, nearly reaching the column .... *Apiocystites*
   Pectinirhombs long, with numerous slits; ambulacra rarely extending below *LL* .... *Lepocrinites*
6. Periproct enclosed mainly by *L5* .. *Lipsanocystis*
   Periproct bordered by three plates, not *L4* 7
   Periproct bordered by four plates, including *L4* 8
7. Pectinirhombs small, with few slits; *L1, L2,* and *L3* diamond-shaped, scarcely in contact, if at all; *ILL* much larger than *LL* .... *Hallicystis*
   Pectinirhombs large, long, with numerous slits; *L1, L2,* and *L3* large, with sutures between; *ILL* not much larger than *LL* .... *Lepocrinites*
8. Hydropore represented by two separate openings; anal pyramid very small, with aboral bordering plates very large and elongate; ambulacra divided in most mature specimens .... *Strobilocystites*
   Hydropore represented by only one opening; anal pyramid relatively large, with bordering plates (if present) subequal; ambulacra undivided in normal specimens 9
9. Pectinirhombs long, with nearly equal halves; anal pyramid with marginal ring of plates; hydropore elongate .... *Tetracystis*
   Pectinirhombs short, with half-rhombs on *IL2, L1,* and *L4* reduced to small circular

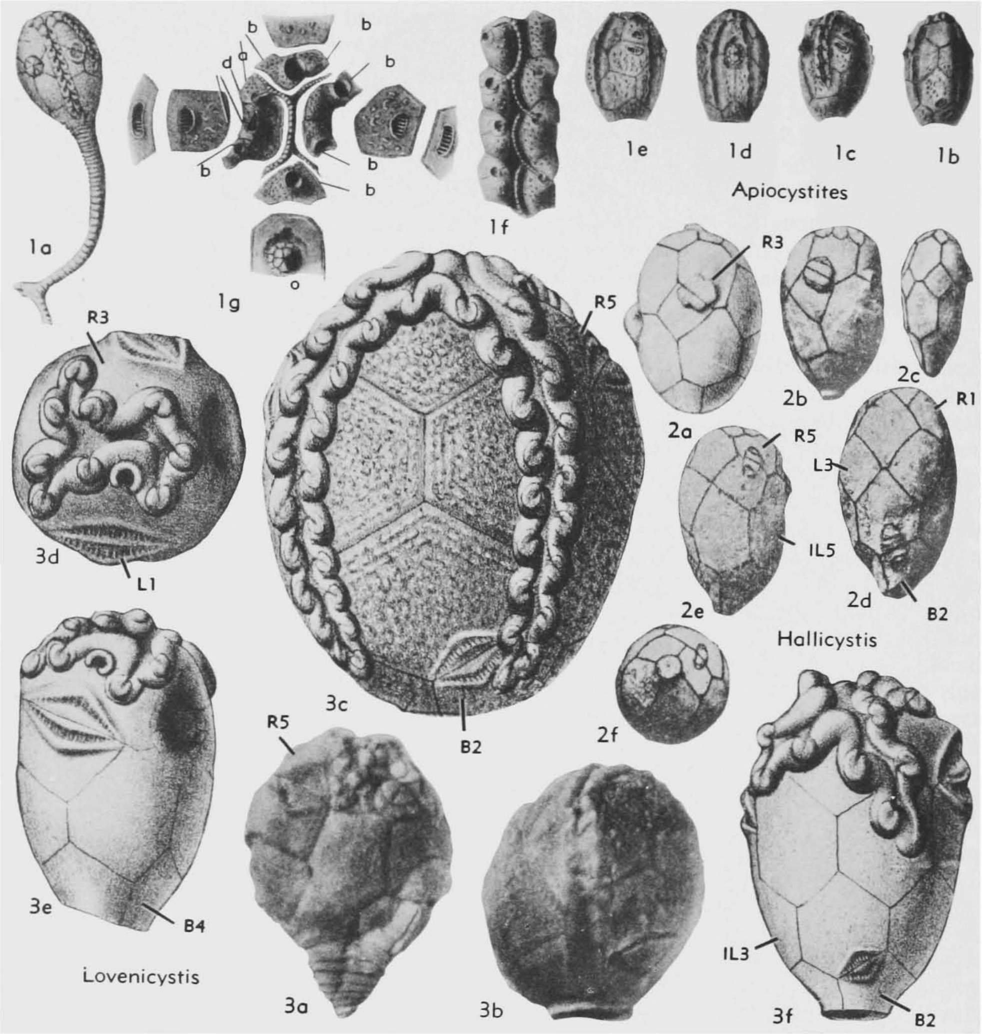


FIG. 105. Callocystitidae, Apiocystitinae (p. S206, S209, S212-S214). [Plate designations as in Figure 38.]

openings with tubular rims; anal pyramid lacking marginal ring; hydropore large, subcircular .... *Jaekelocystis*

Apiocystites FORBES, 1848, p. 501 [**A. pentrematoides;* OD] [=*Apiocystis* BATHER, 1889, p. 268 *(nom. van.)*]. Theca regularly ovate, elongate or slightly compressed, plum-shaped, with long axis not exactly vertical. *L* and *R* circlets complete. Ambulacra 4, long, attenuated, nearly reaching column, never branched or entrenched in thecal plates; brachioles spaced farther apart than in other genera of subfamily, so that each ambulacrum has only 20 to 36 facets. Pectinirhombs 3, small, short, and discrete, with few slits; no notable difference between the 2 halves of each rhomb; rhombs *L1/R5* and *L4/R3* inclined. Periproct small, bordered only by *IL4, IL5,* and *L5;* anal pyramid of 6 plates, outer ring of 9 plates. Hydropore and gonopore present on *O1;* other *OO* very small. *M.Sil.-L.Dev.,* Eu.(Eng.)-N.Am. (N.Y.-Tenn.-Ont.).——FIG. 105,*1a.* **A. pentrematoides,* M.Sil.(Wenlock), Eng.; lat., reconstr., ×1 (69).——FIG. 105,*1b-g. A. elegans* HALL, M.Sil.(Niagaran), USA(N.Y.); *1b-e,* 4 lat., ×1; *1f,* detail of ambulacrum, enl.; *1g,* plate diagram of oral region (*a,* hydropore; *b,* oral plates; *d,* gonopore; *o,* periproct) (60).

Brockocystis FOERSTE, 1914, p. 469 [**Apiocystites? tecumsethi* BILLINGS, 1866, p. 91; OD]. Theca ovate, many thecal plates strongly modified by large hemispherical protuberance occupying most of plate. *R* circlet complete; *IL4* and *IL5* not elongate; *R3* distinctive, nearly square, and like corresponding plate in *Lepadocystis* bearing 2 half-rhombs on its aboral sides, separated only by

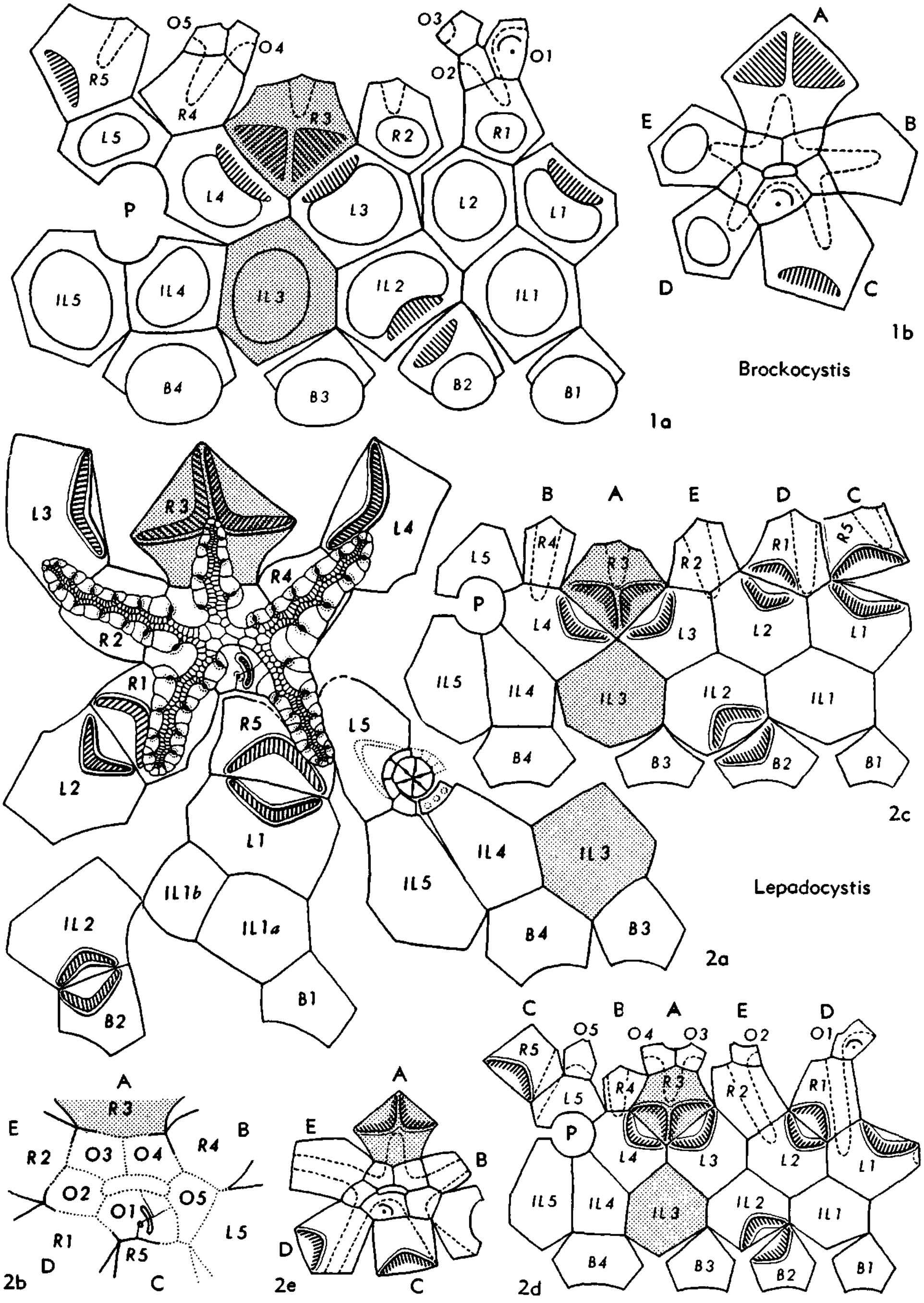


Fig. 106. Callocystitidae, Apiocystitinae, plates of *A*-ray shaded (p. *S*206-*S*211). [Plate designations as in Figure 38.]

narrow ridge; *OO* little known. Periproct large, nearly circular, its plates unknown, bordered by *IL4, IL5, L4,* and *L5.* Ambulacra 5, relatively short, few extending below *RR,* ambulacrum III short and obstructed by the close-set half-rhombs on *R3;* ambulacral grooves in trimerous arrangement in oral region; brachioles few. Pectinirhombs 4, B2/*IL2, L1/R5, L3/R3,* and *L4/R3,* each with long slits. In known examples, column tapering distally for about 12 columnals, lower end of this section set deeply in curious kind of cup formed by about 4 greatly expanded columnals, beyond which column tapers rapidly to very narrow diameter; distal end unknown. *L.Sil.,* N.Am.(Ont.-Ohio).——FIG. 106,*1;* 107,*1a-d.* **B. tecumsethi* (BILLINGS), Cataract Ls., Ont.(Manitoulin Is.);

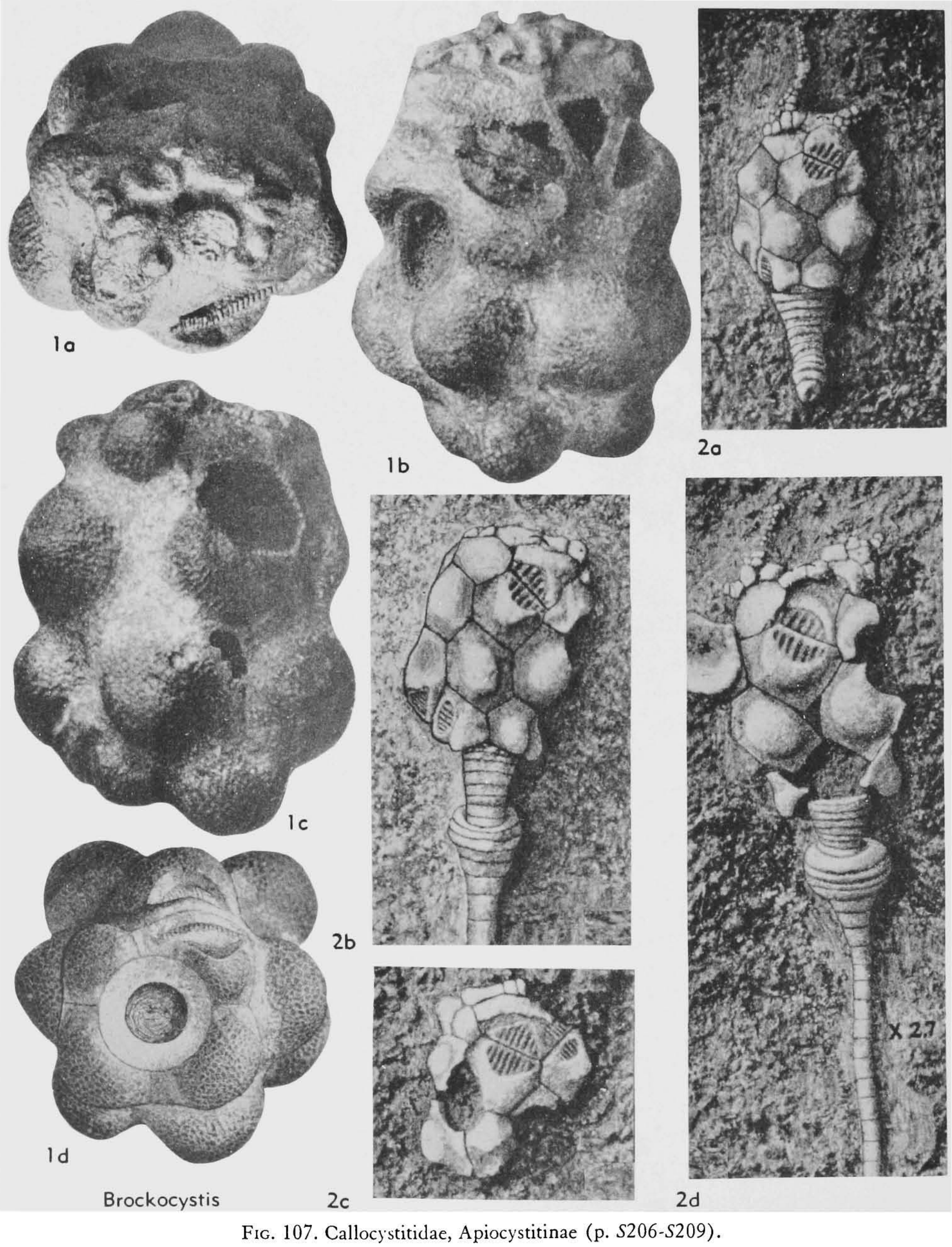


FIG. 107. Callocystitidae, Apiocystitinae (p. *S*206-*S*209).

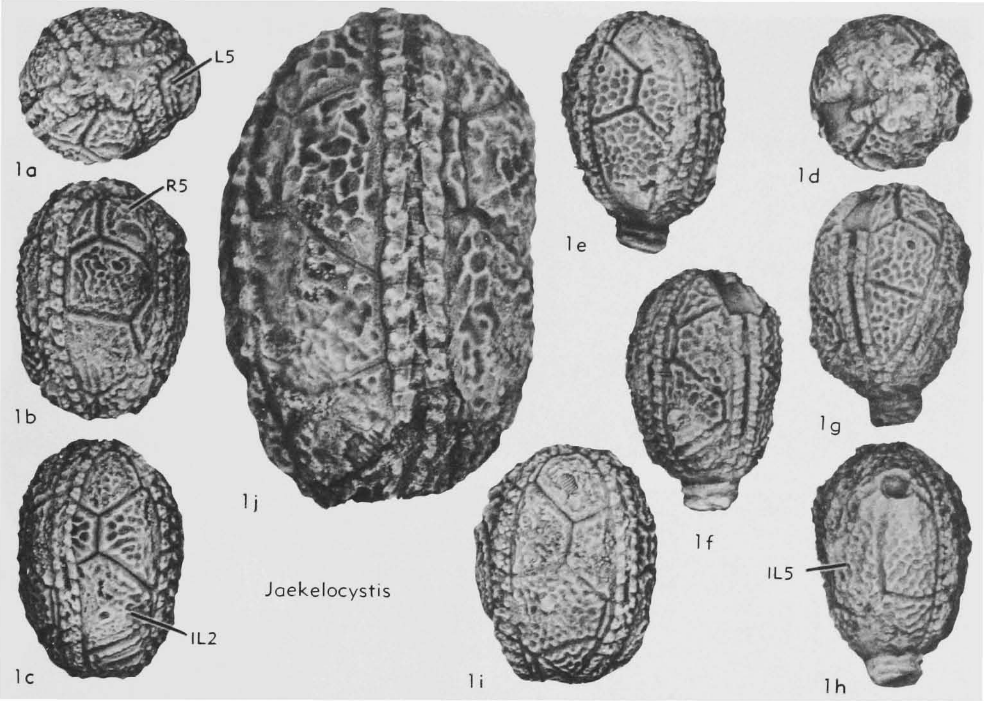


FIG. 108. Callocystitidae, Apiocystitinae (p. *S*209). [Plate designations as in Figure 38.]

106,*1a,b,* plate diagram and oral region (Kesling, n); 107,*1a-c,* oral and 2 lat., holotype, ×3 (46); 107,*1d,* aboral, holotype, ×3 (48).——FIG. 107, 2. *B. nodosaria* FOERSTE, Brassfield Ls., USA (Ohio); *2a-d,* lat., 4 thecas, ×2.7 (48).

Hallicystis JAEKEL, 1899, p. 286 [**Apiocystites imago* HALL, 1864, p. 10; OD]. Theca acorn-shaped, base not indented. *LL* and *RR* intercalated, not forming complete circlets; *L5* between *R4* and *R5; L1, L2,* and *L3* diamond-shaped, scarcely in contact, if at all; *ILL* much larger than *LL. OO* relatively large. Pectinirhombs 3, *B2/IL2, L1/R5,* and *L4/R3,* each half in form of a semicircle, with few slits. Periproct bordered by 3 plates, *IL4, IL5,* and *L5;* anal pyramid enclosed by circle of minute plates. Ambulacra 4. [Genus only known from steinkerns, but plates apparently bearing radial ridges, according to FOERSTE (1917).] *M.Sil.,* N.Am.(Wis.-Ill.-Ohio).——FIG. 100,*2;* 105,*2.* **H. imago* (HALL); 100,*2a,b,* plate diagram and oral region (Kesling, n); 105,*2a,* lat., steinkern, ×1 (69); 105,*2b,c,* 2 lat., steinkerns, ×1; 105,*2d-f,* 2 lat. and aboral, steinkerns, ×0.9 (49).

Jaekelocystis SCHUCHERT, 1903, p. 230 [**J. hartleyi;* OD]. Theca ovate to ellipsiform, some forms tending to be subquadrate in cross section. *ILL* forming complete circlet, *IL4* and *IL5* large and elongate; *R* circlet interrupted by large *L5, R4* very small, mostly concealed by ambulacrum *IV.* Periproct conspicuous, somewhat protruding in some specimens, bordered by *IL4, IL5, L4,* and *L5;* anal pyramid without surrounding accessory plates. Ambulacra long, 4 in normal specimens, flooring plates deeply embedded in thecal plates; brachiole facets discrete but numerous. Hydropore (possibly combined with gonopore) consisting of very large circular opening filled by sieve plate with vermicular, somewhat radiating slits, whole being set within *O1,* which appears to be substantially fused into single plate. Pore rhombs 3, highly specialized; halves on *B2, R3,* and *R5* nearly semicircular, provided with few, distinct slits and bordered by outer rim, but halves on *IL2, L1,* and *L4* reduced to small circular openings (at surface) with high rim, more or less tubular. [Certain significant variations can be determined from study of numerous exceptionally well-preserved specimens available. Despite deep entrenching of the ambulacra, their course across the thecal plates varies greatly. One specimen exhibits a branched ambulacrum; others have one short or completely aborted ambulacrum. Certain plate anomalies also occur.] *L.Dev.,* N.Am.(W.Va.).——FIG. 108,*1;* 102,*2.* **J. hartleyi;* 108,*1a-c,* oral and 2 lat., paratype, ×2; 108,*1d-h,* oral and 4 lat., another paratype, ×2; 108,*1i,* lat., third paratype, ×2; 108,*1j,* lat. showing details of ambulacrum *I,* ×4; 102,*2a,b,* plate

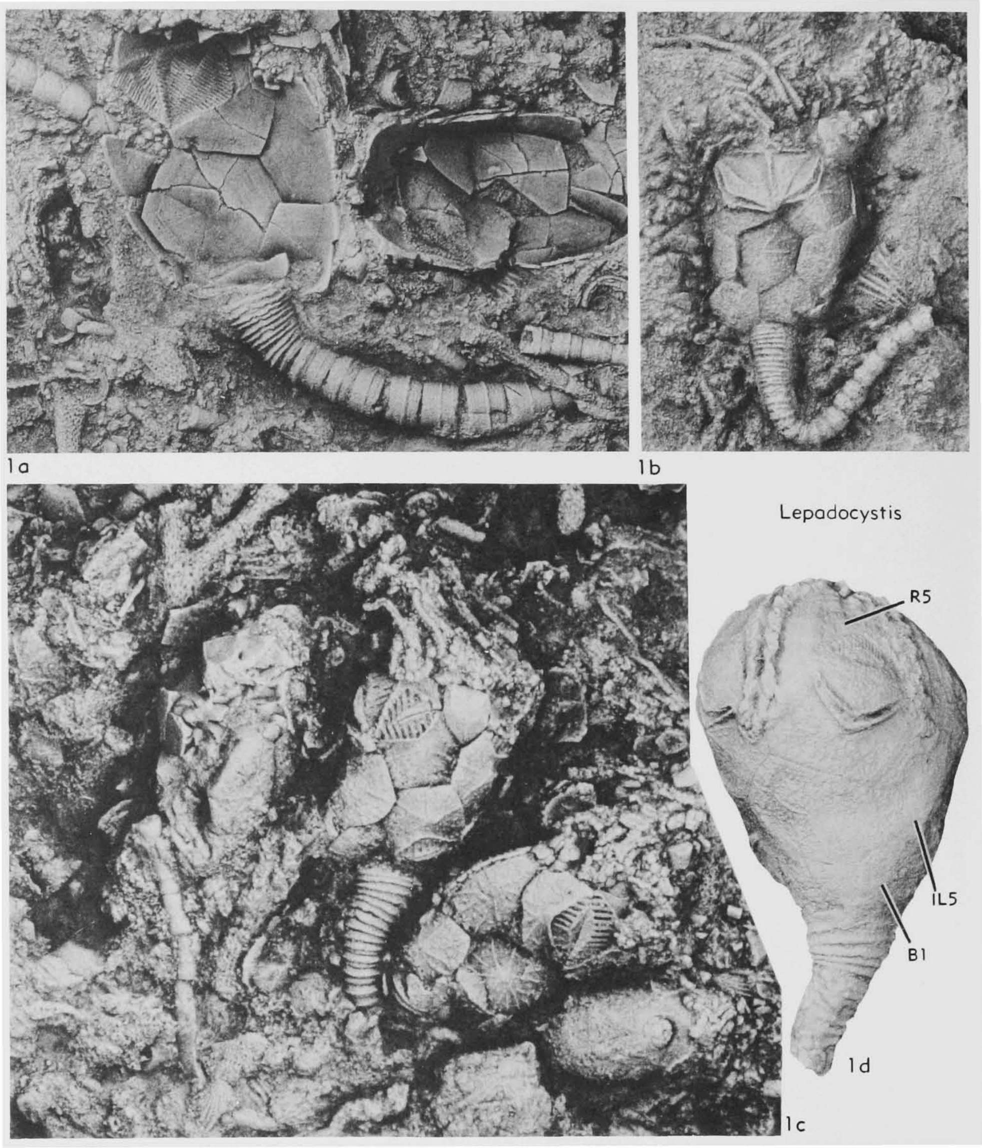


FIG. 109. Callocystitidae, Apiocystitinae (p. *S*210-*S*211).

diagram and oral region, normal specimen; 102, *2c,* anomalous plate development (73). [See also Fig. 43.]

Lepadocystis CARPENTER, 1891, p. 10 [**Lepocrinites moorei* MEEK, 1871, p. 296; OD (=*Lepadocrinites moorei* MEEK, 1871, *nom. null.*)] [=*Meekocystis* JAEKEL, 1899, p. 278 (obj.)]. Theca subovate to ellipsoidal, gerontic forms becoming pyriform and tapering to column. *R* circlet interrupted by *L5;* periproct bordered by *IL4, IL5, L4,* and *L5; IL4* and *IL5* vertically elongate; *R3* very distinctive, nearly square, with 2 half-rhombs on aboral sides of plate separated only by narrow ridge; *OO* rather large, *O1* tripartite. Ambulacra 5, relatively short, few extending below *RR,* ambulacrum III *(A)* short and obstructed by 2 half-rhombs on *R3.* Pectinirhombs 5, *B2/IL2, L1/R5, L2/R1, L3/R3,* and *L4/R3.* Gonopore and hydropore bisected by suture through *O1;* hydropore shaped like broad U, slot provided with grating or crossbars. Column with large narrow rings near theca, distally decreasing in diameter, its end variously modified for attachment to objects. Ornamentation increasing in complexity to

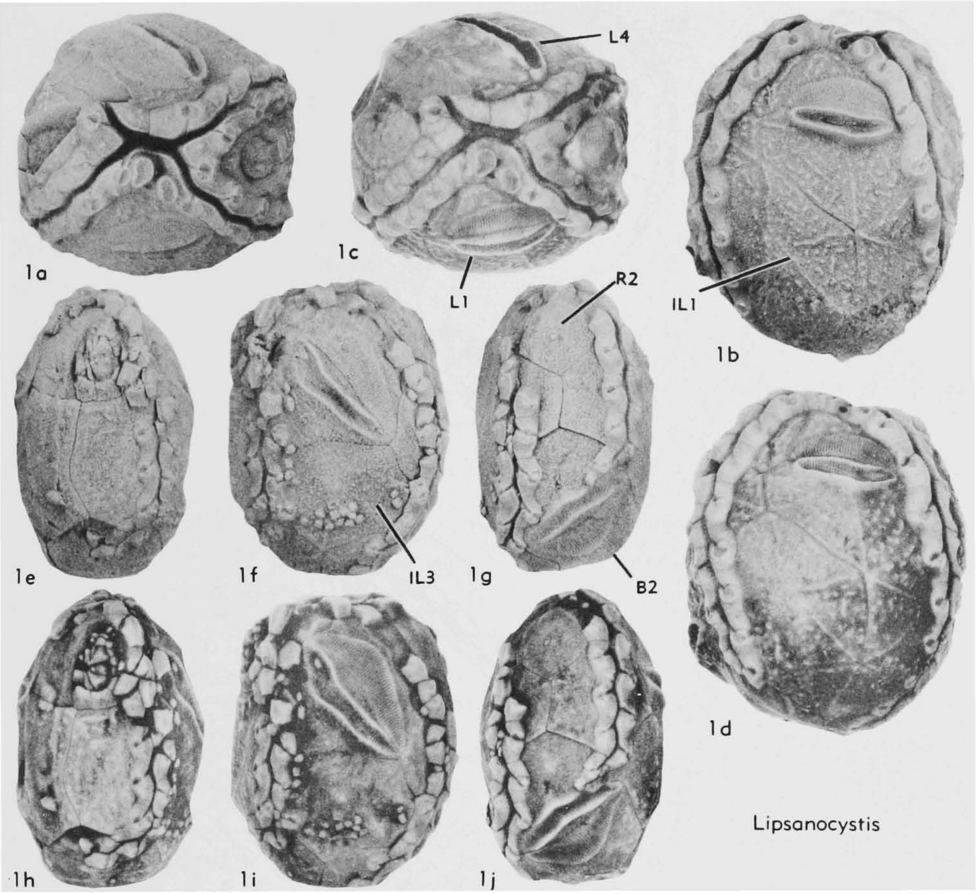


FIG. 110. Callocystitidae, Apiocystitinae (p. *S*212-*S*213). [Plate designations as in Figure 38.]

adult stage, but gerontic specimens with effaced ridges. *U.Ord.*, N.Am.(Ohio-Ind.).——FIG. 106, *2;* 109,*1*. **L. moorei* (MEEK); 106,*2a,b,* plate diagram and oral region, specimen with anomalous *IL1* (75); 106,*2c-e,* plate diagrams and an oral region, normal specimens (Kesling, n); 109,*1a,* interiors of 2 weathered specimens showing concentric growth lines, ×2.5; 109,*1b,* theca with parts of column and brachioles, ×2.5; 109,*1c,* slab containing 3 thecae and associated bryozoa and brachiopods, ×5 (compare with reconstr., FIG. 32).; 109,*1d,* lat. (post.), gerontic specimen, ×2.5 (75). [See also Fig. 32, 51,*1*.]

Lepocrinites CONRAD, 1840, p. 207 [**L. gebhardii;* OD] [=*Lepadocrinites* BILLINGS, 1854, p. 215 *(nom. van.)*; *Lepadocrinus* HALL, 1859, p. 125 *(nom. van.); Lepocrinus* HALL, 1859, p. 125 *(nom. van.)*]. Theca ovate to subpyriform, sides somewhat compressed. *BB, ILL,* and *LL* forming complete circlets, but *L5* projecting adorally between *R4* and *R5*. [The critical area is normally covered by ambulacra so that it is difficult to determine whether the *RR* are interrupted or continuous, as suggested by SCHUCHERT (1904) and REGNÉLL (1945); because this doubt exists, *Lepocrinites* appears twice in the key.] Periproct bordered by 3 plates, *IL4, IL5,* and *L5,* anal pyramid surrounded by circle of small plates. Ambulacra 4, unbranched, commonly not extending below mid-height of theca, bearing relatively few brachiole facets. Pectinirhombs 3, long, disjunct, provided with numerous closely spaced slits. Column unique; proximal part of about 15 columnals, tapering, and distal part of numerous columnals fused to form long, enlarged, club-shaped body. [Rhombs are larger, ambulacra broader, and brachioles more numerous than in *Apiocystites*.] *U.Sil.-L.Dev.,* Eu.(Eng.)-N. Am.(Va.-W. Va.-Md.-N.Y.).——FIG. 104,*1a-c.* **L. gebhardii,* L. Dev. (Coeymans Ls.), USA(Md.-N.Y.); *1a,b,* 2 lat., ×1 (116A); *1c,* reconstr., lat., ×1 (Kesling, n, after 62).——FIG. 104,*1d,e. L. manlius* SCHUCHERT,

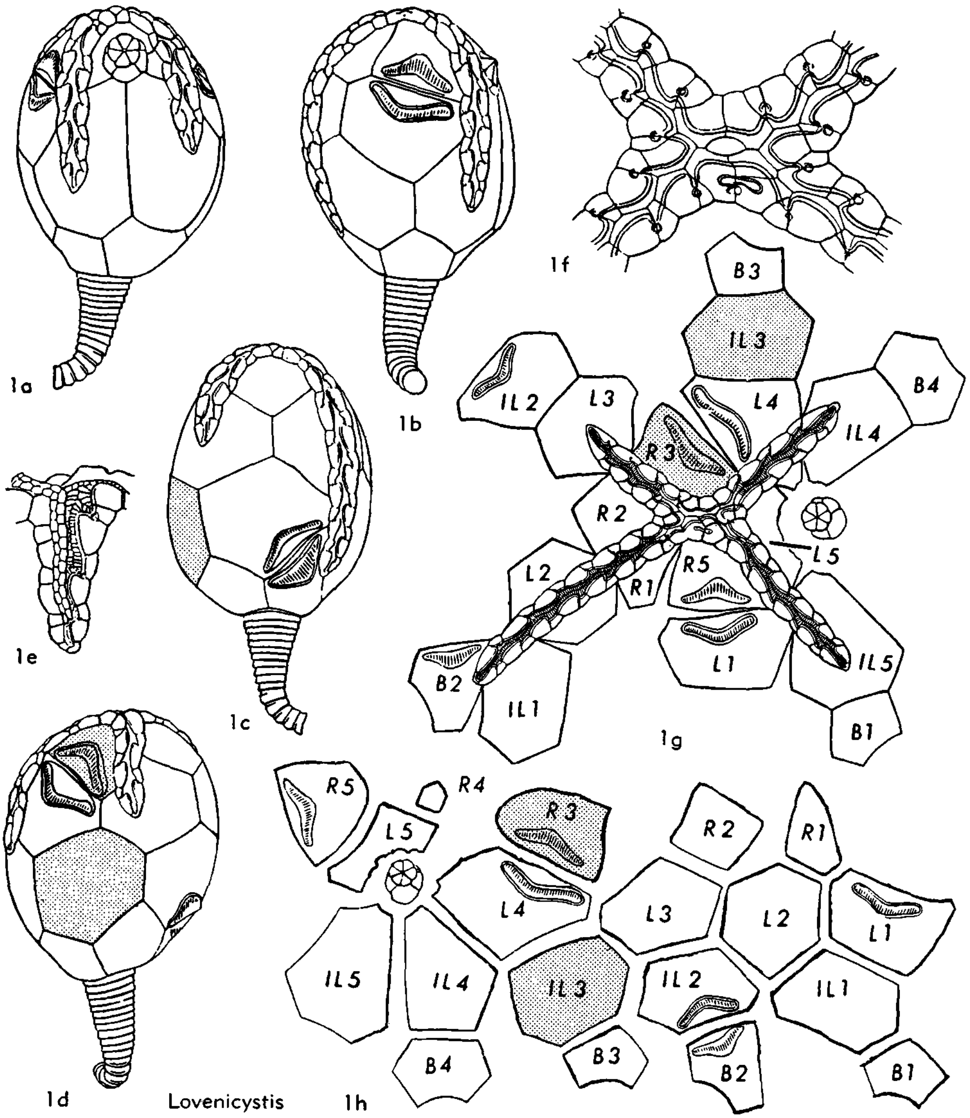


FIG. 111. Callocystitidae, Apiocystitinae. Lateral views (reconstr.) and plate diagrams; plates of *A*-ray shaded (p. *S*213-*S*214). [Plate designations as in Figure 38.]

L.Dev.(Keyser F.), USA(Md.); *1d,e,* 2 lat., ×2 (116A).

Lipsanocystis EHLERS & LEIGHLEY, 1922, p. 155 [**L. traversensis;* OD]. Theca ovate. *ILL* large, forming complete circlet, *IL4* and *IL5* elongate; *LL* nearly or quite completing circlet, *L1* and *L5* meeting at their tips; *R4* small, nearly hidden beneath ambulacra, separated from *R5* by *L5*. Periproct nearly enclosed by *L5,* its lower border touching *IL4;* ring of accessory plates around anal pyramid. Pectinirhombs well developed, long, halves on *IL2, L1,* and *L4* angulated and confined by raised margins, those on *B2, R5,* and *R3* with longer slits and outer rim only; slits numerous, closely spaced; *O1* large and bipartite, its suture bisecting small circular gonopore; hydropore consisting of definitely separated sievelike openings, subcircular, one on each half of *O1*. Ambulacra 4, broad and long, pairs branching from each end of elongate peristome, concealing most of *OO* and *R4* and considerable part of *L5*. *M.Dev.,* USA (Mich.).——FIG. 100,*1;* 110,*1*. **L. traversensis;*

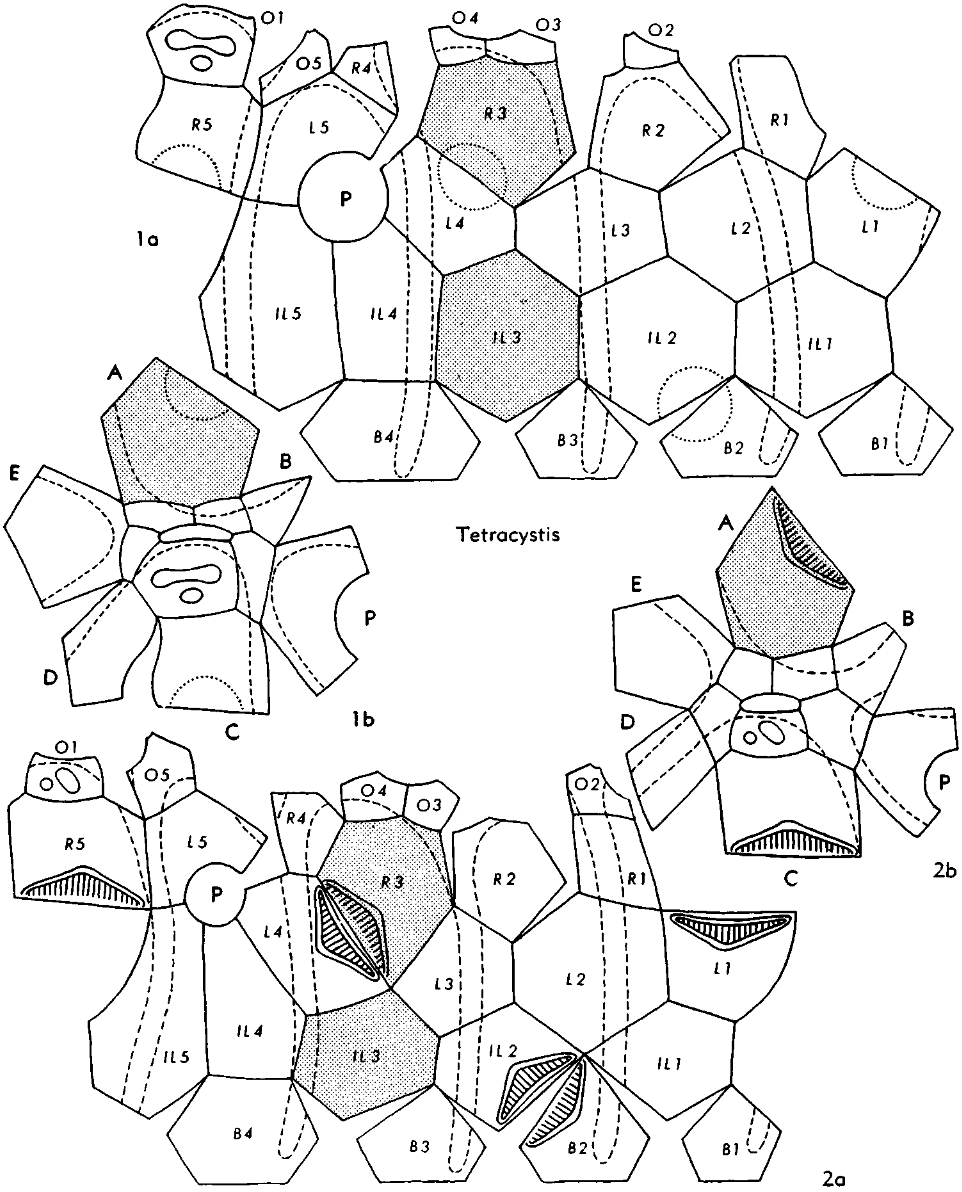


FIG. 112. Callocystitidae, Apiocystitinae. Plate diagrams, plates of *A*-ray shaded (p. S214). [Plate designations as in Figure 38, Carpenter letter symbols for rays in *1b,d.*]

100,*1a,b,* plate diagram and oral region (Kesling, n); 110,*1a,b,* oral and lat., ×2, coated with ammonium chloride; 110,*1c,d,* same, submersed in xylol; 110,*1e-g,* 3 lat., ×2, coated; 110,*1h-j,* same, submersed (Kesling, n).

Lovenicystis REGNÉLL, 1945, p. 90 [**Apiocystites angelini* JAEKEL, 1899, p. 282; OD (=*Lepadocrinus angelini* HAECKEL, 1896, p. 135, *nom. nud.*)]. Theca ovate to globular, nearly circular in cross section. *LL* and *RR* forming closed circlets; *IL4* and *IL5* vertically elongate; *O1* tripartite, with *O1a*/*O1b* suture bisecting hydropore and gonopore, each of which has 2 openings. Periproct bordered by *IL4, IL5, L4,* and *L5,* filled by anal pyramid of 6 pieces and 5 or 6 aboral bordering plates. Ambulacra 4, long, one or more extending nearly to base; brachioles numerous but not closely spaced. Pectinirhombs 3, *B2/IL2*, *L1/R5*, and *L4/R3*. *U. Sil.*, Eu.(Sweden).——Fig. 105,*3;* 111,*1.* **L. angelini* (Jaekel), L. Ludlow, Gotl.; 105,*3a,b,* lat., 2 thecae, ×2.25 (99); 105,*3c,* lat., adult, ×6; 105,*3d,e,* oral and lat., juvenile, ×6; 105,*3f,* lat., juvenile, ×6 (69); 111,*1a-d,* lat., reconstr.; 111, *1e,* short ambulacrum with flooring and covering plates; 111, *1f,* peristomial region, covering plates removed from peristome and ambulacra; 111,*1g,* plates projected radially from peristome along ambulacra; 111,*1h,* plate diagram (99). [See also Fig. 36,*1*; 45,*1*.]

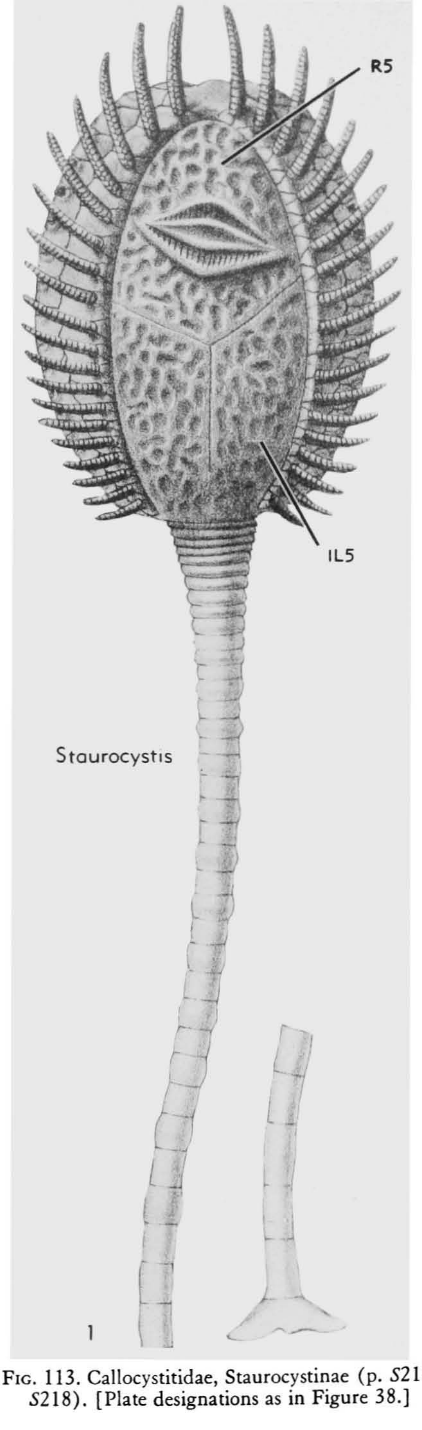


Fig. 113. Callocystitidae, Staurocystinae (p. *S*217-*S*218). [Plate designations as in Figure 38.]

Strobilocystites White, 1876, p. 28 [**S. calvini;* OD] [=*Strobilocystis* Carpenter, 1891, p. 5 *(nom. van.)*]. Theca subovate. *L* and *R* circlets complete. Periproct bordered by 4 plates, *IL4, IL5, L4,* and *L5;* anal pyramid small, subcircular, acuminate, surrounded by ring of accessory plates, of which aboral plates are exceptionally large and elongate radially to pyramid. Ambulacra 4, long, branched in adults of most known species, rather broad, slightly entrenched in thecal plates. Pectinirhombs long, provided with numerous slits, angulated, with halves on *IL2, L1,* and *L4* surrounded by prominent rim; rhomb *L1/R5* nearly horizontal, *L4/R3* exceptionally long, nearly vertical. Hydropore divided into 2 discrete parts, each nearly circular, on opposite sides of suture through *O1;* gonopore a small opening bisected by this suture. *OO* very thick, to attain level of thick ambulacral flooring plates. Branching of ambulacra and elongation of *L4/R3* rhomb emphasized in large (mature and gerontic) specimens. *M.Dev.-U.Dev.,* USA(Iowa).——Fig. 49,*1-14.* **S. calvini,* M.Dev.; 49,*1,* reconstr., ×2; 49,*2-4,* plate diagrams of normal and 2 anomalous specimens; 49,*5-9,* ontogenetic series of ambulacra; 49,*10-14,* variations in periproct (120). [See also Figs. 36,*2,* 45,*2,* 48,*2*.]

Tetracystis Schuchert, 1904, p. 217 [**T. fenestratus;* OD (=*Echinoencrinites fenestratus* Troost, 1849, p. 419, *nom. nud.*)]. Theca elongate, subquadrate in cross section, its ends subovate. *L5* interrupting *R* circlet; *ILL* and *LL* forming definite circlets in some, tenuous circlets in others in which *IL1/IL2, L3/L4,* and/or *L1/L5* contacts are reduced to points. Periproct bordered by 4 plates, rather prominent, filled by acutely pointed pyramid and numerous surrounding platelets. Pectinirhombs 3, long, bearing numerous slits. Ambulacra 4, long, narrow, one along each edge of subquadrate theca; brachioles relatively few, slender, widely separated. *M.Sil.-L.Dev.,* N.Am. (Tenn.-W.Va.)——Fig. 104,*2a-d;* 112,*1.* **T. fenestrata,* M.Sil.(Niagaran), USA(Tenn.); 104, *2a-d,* 4 lat., ×1 (Springer, 1926); 112,*1a,b,* plate diagrams, lat. and oral (*A*-ray shaded) (Kesling, n).——Fig. 104,*2e,f;* 112,*2.* *T. chrysalis* Schuchert, L.Dev.(Keyser F.), USA(W.Va.); 104,*2e,f,* 2 lat., ×2 (116A); 112,*2a,b,* plate diagrams, lat. and oral (*A*-ray shaded) (Kesling, n).

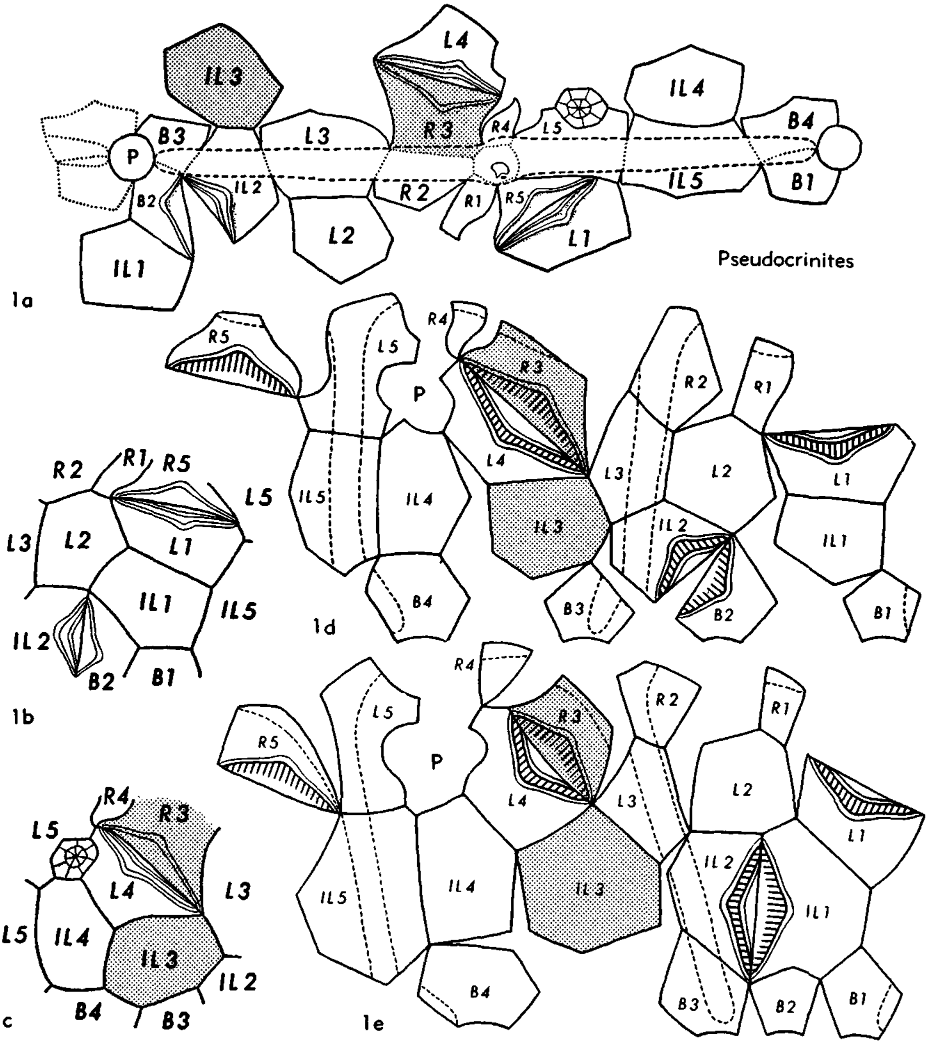


FIG. 114. Callocystitidae, Staurocystinae. Plate diagrams, plates of *A*-ray shaded (p. *S*218). [Plate designations as in Figure 38.]

Subfamily STAUROCYSTINAE Jaekel, 1899

[Staurocystinae JAEKEL, 1899, p. 282]

Theca ovate or biconvex. Shape and arrangement of plates strongly modified by shape of theca. Ambulacra two to four, undivided, strongly protuberant, provided with very numerous, closely spaced brachioles. *U.Sil.-L.Dev.*

Within the well-known *Pseudocrinites,* several anomalies occur. As KESLING (73) has pointed out, in four sets of four plates each, the plates practically meet at a point: *B2-IL2-L2-IL1, IL3-L4-R3-L3, L1-L2-R1-R5,* and *L4-L5-R4-R3.* This reduction in sutures seems to have induced instability in the theca, which fulfills its normal function by rigidity. Plate arrangements vary, at least in minor details. A specimen called *P. abnormalis* by SCHUCHERT (116) has the basal rhomb between *IL1/IL2* instead of the regular location between *B2/IL2,* with corresponding alterations in the *BB* and *ILL* to accommodate this large structure. The cystoid called *Trimerocystis* by SCHUCHERT (116) appears to have the same plate arrangement as species of *Pseudocrinites* with

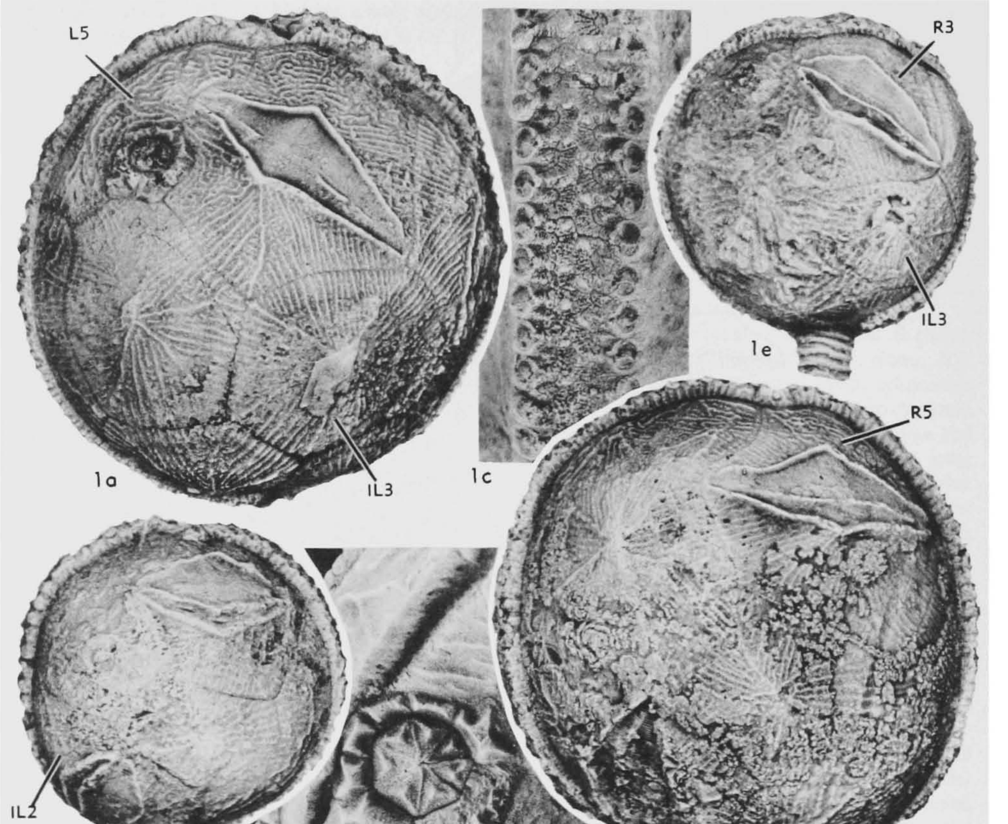


FIG. 115. Callocystitidae, Staurocystinae (p. S218). [Plate designations as in Figure 38.]

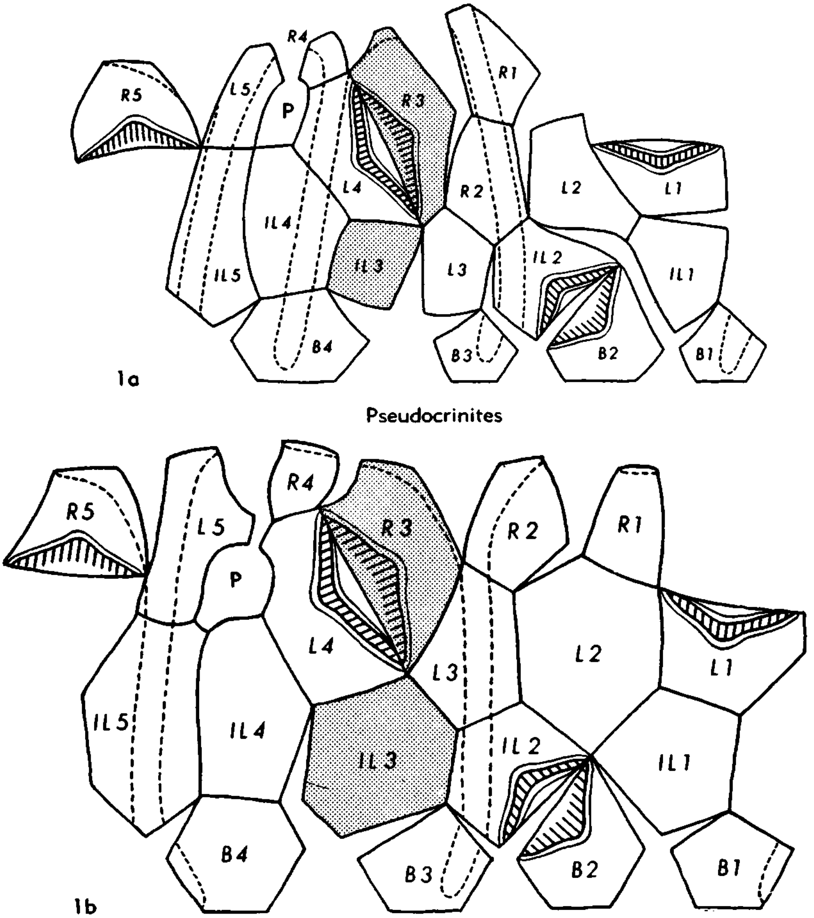


FIG. 116. Callocystitidae, Staurocystinae. Plate diagrams, plates of *A*-ray shaded (p. *S*217-*S*218). [Plate designations as in Figure 38.]

which it occurs, differing only in having a supernumerary third ambulacrum.

In the Staurocystinae, the ambulacral flooring plates are remarkably thick, so that the ambulacral groove is perched well above the level of the thecal plates. The spacing of these flooring plates, insofar as known, remains constant throughout ontogeny, indicating that the contact between these plates and the expanding thecal plates required continuous readjustment and repositioning during growth of the cystoid. The specialization of the ambulacra has obscured details of the oral region, although the *OO* were presumably also highly protuberant to receive the ambulacral groove from the ambulacra.

Key to Genera of Staurocystinae

Theca subovate; ambulacra four .... *Staurocystis*
Theca biconvex, lenslike; ambulacra two, forming thick peripheral rim .... *Pseudocrinites*

Staurocystis HAEKEL, 1896, p. 134 [**Pseudocrinites quadrifasciatus* PEARCE, 1843, p. 160; OD]. Theca subovate, suboctagonal in cross section because of strongly protuberant ambulacra; exposed part of theca in middle about twice as wide as ambulacra, gently convex. *IL1, IL2,* and *IL3* hexagonal, with distinct sutures between them; *IL4* and *IL5* vertically elongate; *IL3-L3-R3-L4* tending to meet at a point, other plates with definite sutures. All ambulacra extending to column, each with about 40 brachiole facets in adult specimens. Periproct small, subcircular, bordered by *IL4, IL5, L5,* and narrow corner of *L4*. Pectinirhombs large, long, angulated, provided with numerous slits, with

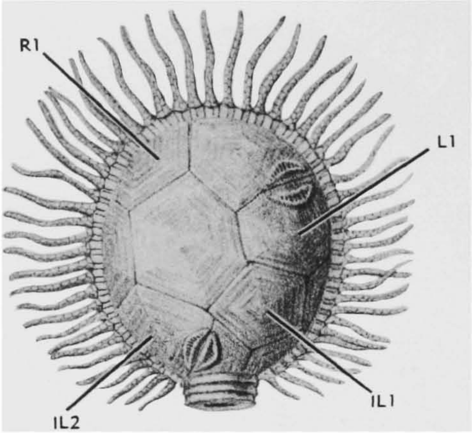


FIG. 117. Callocystitidae, Staurocystinae (p. S217-S218). [Plate designations as in Figure 38.]

halves on *IL2, L1,* and *L4* enclosed by sharply raised rim, their opposite halves with outer rim only; rhomb *B2/IL2* between ambulacra I and II, *L4/R3* between II and IV, and *L1/R5* between I and V; periproct between IV and V. Column long, as usual in family tapering rapidly distally from short wide columnals to long narrow columnals. *U.Sil.*(Wenlock), Eu.(Eng.).——FIG. 113,*1*. **S. quadrifasciata* (PEARCE); reconstr., ×5 (69).

Pseudocrinites PEARCE, 1842, p. 472 [**P. bifasciatus* PEARCE, 1843, p. 160; SD HAECKEL, 1896, p. 135 (=*P. bicopuladigiti* GARNER, 1844, p. 160)] [=*Phacocystis* HAECKEL, 1896, p. 135 *(obj.); Pseudocrinus* HAECKEL, 1896, p. 135 *(nom. van.); Trimerocystis* SCHUCHERT, 1904, p. 237 (type *T. peculiaris*)]. Theca biconvex, shaped like round or oval inflated disc, with ambulacra forming thick, heavy rim around periphery. Ambulacra 2, accounted as II and V, each composed of exceptionally thick flooring plates that raise narrow ambulacral groove well away from thecal plates, long, in many specimens attaining column, in some even longer and deflected to side of column; brachioles numerous, alternating in separate rows, those in each row close-set in circular facets; sides of ambulacral covering plates forming high palisade, obscuring details of *OO;* oral region apparently boxlike, with hydropore on top and gonopore (closed by pyramid of tiny plates) on side; other thecal plates distinct; 4 points tending to serve as junction of sets of 4 plates each, *B2-IL2-L2-IL1, IL3-L4-R3-L3, L1-L2-R1-R5,* and *L4-L5-R4-R3,* thus reducing number of sutures greatly and creating relatively unstable arrangement; *R1* and *R4* small, curved; *R* circlet interrupted by *L5* between *R4* and *R5.* Pectinirhombs large and long, with numerous slits, rimmed like those in *Staurocystis; L4/R3* exceptionally long, about 0.6 diameter of theca; rhombs *B2/IL2* and *L1/R5* on one face of theca, rhomb *L4/R3* and periproct on other. Periproct bounded by *IL4, L4,* and *L5,* not by *IL5* as in other genera of family; anal pyramid with wide border of accessory plates. *U.Sil.-L. Dev.,* Eu.(Eng.)-N.Am.(W.Va.-Md.-Pa.).——FIG. 114,*1;* 115,*1*. *P. gordoni* SCHUCHERT, L.Dev., USA (Md.); 114,*1a,* plate diagram expanded along ambulacra; 114,*1b,c,* plates on opposite sides, ambulacra not shown, about ×1 (73); 114,*1d,* plate diagram of holotype (Kesling, n); 114,*1e,* plate diagram of abnormal specimen, the "holotype" of *P. "abnormalis"* SCHUCHERT, in which rhomb *B2/IL2* is in the *IL1/IL2* position (Kesling, n, after 116); 115,*1a,b,* opposite lat., holotype (large specimen), ×2; 115,*1c,* ambulacrum, enl.; 115,*1d,* oral end of holotype, enl. to show rhomb *L1/R5* and gonopore (closed by tripartite pyramid); 115,*1e,f,* opposite lat., smaller specimen, ×2; 115,*1g,* periproct of another specimen, ×5 (73).——FIG. 116,*1b*. *P. perdewi* SCHUCHERT, U.Sil.(Manlius Ls.), USA(W.Va.); plate diagram (Kesling, n).——FIG. 116,*1a*. *P.* sp. cf. *P. perdewi,* U.Sil.(Manlius Ls.), USA(W.Va.); plate diagram of type and only specimen of *"Trimerocystis peculiaris"* SCHUCHERT (Kesling, n).——FIG. 117,*1*. *P. magnificus* FORBES, U.Sil.(Wenlock), Eng.; lat., ×1 (69).

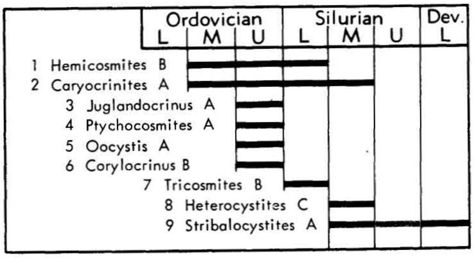


FIG. 118. Stratigraphic distribution of genera belonging to the superfamily Hemicosmitida. Classification of the genera in families is indicated by letter symbols: A—Caryocrinitidae, B—Hemicosmitidae, C—Heterocystitidae. The following alphabetical list of genera furnishes cross reference to the serially arranged numbers on the diagram (Kesling and Moore, n).

Generic Names of Hemicosmitida and Index Numbers

Caryocrinites—2
Corylocrinus—6
Hemicosmites—1
Heterocystites—8
Juglandocrinus—3
Oocystis—5
Ptychocosmites—4
Stribalocystites—9
Tricosmites—7

Superfamily HEMICOSMITIDA Jaekel, 1918

[*nom. transl.* REGNÉLL, 1945, p. 97 (*ex* Hemicosmitidae JAEKEL, 1918, p. 97)] [=suborder Hemicosmites JAEKEL, 1918, p. 97)]

Theca composed of four *BB*, six to ten *ILL*, eight or more *LL*, and several *RR*. Rhombs with inner side of strong folds or laminae perpendicular to sutures; distal end of each pore terminating in tubercle covered by epitheca (opening exposed only in weathered specimens), some ends branching into short cavities within tubercle. *M. Ord.-L.Dev.*

The designation of plates offers a problem, inasmuch as organization of the theca is different from that of the Glyptocystitida. JAEKEL (69) preferred to use the same terminology for successive circlets as he had for Glyptocystitida: basalia [*BB*], infralateralia [*ILL*], mediolateralia [*LL*], and radiolateralia [*RR*]. CARPENTER (32) and BATHER (10) used terminology comparable to that for dicyclic crinoids: infrabasalia, basalia, radialia+interradialia, and deltoidia. BATHER subsequently (1910) denoted the circlets by numerals I to IV "to avoid confusion." Whether all plates in the respective circlets in Glyptocystitida and Hemicosmitida are homologous or not, the designations of *BB, ILL, LL,* and *RR* are useful notations and can be understood to apply to thecal location only.

The stratigraphic distribution of genera belonging to the Hemicosmitida is shown in Figure 118.

Family HEMICOSMITIDAE Jaekel, 1918

[Hemicosmitidae JAEKEL, 1918, p. 97]

Theca ovate, acorn-shaped, or elongate, composed of four *BB*, six *ILL*, eight or nine *LL*, and circlet of *RR*. Brachioles few, clustered at apex of theca and connected with mouth by short ambulacral grooves. Periproct lateral, never above *LL*. *M. Ord.-L. Sil.*

The separation of the Hemicosmitidae and Caryocrinitidae is based primarily on the presence of a "tegmen" of plates roofing over the ambulacral grooves in the latter and its absence in the former. The distinction is obvious in the type genera, but not so clear in certain other genera of the two families, which to date have not been as well understood or completely known. The development of the structure known as the "tegmen" has not been satisfactorily traced, although its plates are probably homologous to the ambulacral covering plates of other rhombiferans, as suggested by JAEKEL (69).

Key to Genera of Hemicosmitidae

1. *LL* eight; periproct between two *LL*, not in contact with any *IL*; theca spindle-shaped, tapering at both ends .... *Corylocrinus*
   LL nine; periproct normally bordered by two *ILL* and one *L* plates; theca subovate 2
2. Pores in fairly regular, radiating rows; three large brachioles set close to top of theca; in many species, *ILL* and *LL* with central nodes; in some, nodes accentuated on three *LL* aligned with brachioles .... *Hemicosmites*
   Pores rather irregular; three brachioles set on three large processes on *LL*, near border of theca; plates strongly tumid or "swollen," no nodes or ridges .... *Tricosmites*

Hemicosmites VON BUCH, 1840, p. 149 [**H. pyriformis*; OD] [=*Hexalacystis* HAECKEL, 1896, p. 142 (type, *Hemicosmites verrucosus* EICHWALD, 1856)]. *BB* 4, of which 2 adjacent are pentagonal and other 2 large and hexagonal; *ILL* 6, large, 2 above hexagonal *BB* being pentagonal, 1 between hexagonal *BB* narrower than others and indented at adoral left corner for periproct, and other 3 heptagonal, with adoral indentation for juncture with 3 narrow "interradial" *LL; LL* 9, hexagonal except for 3 narrow "interradial" plates and for indentation in *L* above periproct; *RR* 9, more or less equal and pentagonal, attenuated toward mouth. Periproct small, circular, bordered by 2 *ILL* and 1 *L*, hence lateral on theca. Brachiole facets 3, large, each shared by pair of *RR;* 1 *R* without facet between each pair of facet-bearing *RR*, so that brachioles were equally spaced around mouth to form triangle; pavement of small covering plates over 3 short ambulacral grooves, converging to cover mouth. Rhombs numerous between plates of *B, IL,* and *L* circlets; pores covered, expressed as small tubercles (except in weathered specimens, in which they appear as pustules) in rows more or less radiating from umbos of plates. Rugosity near mouth in posterior position may be trace of hydropore (10), but its presence not established with certainty (69). Shape of theca varying from ovate to cuplike, depending upon development of nodes on *LL*. *M.Ord.-L.Sil.*, Asia(China-Burma)-Eu. (USSR-Est.-Sweden-Norway-Brit.).——FIG. 119, *1a*. Plates diagrammed in comparison with crinoid (*IB*, infrabasal; *B*, basal; *R*, radial; *iR*, interradial; *h*, hydropore; *ant.*, anterior; *l*, left; *r*,

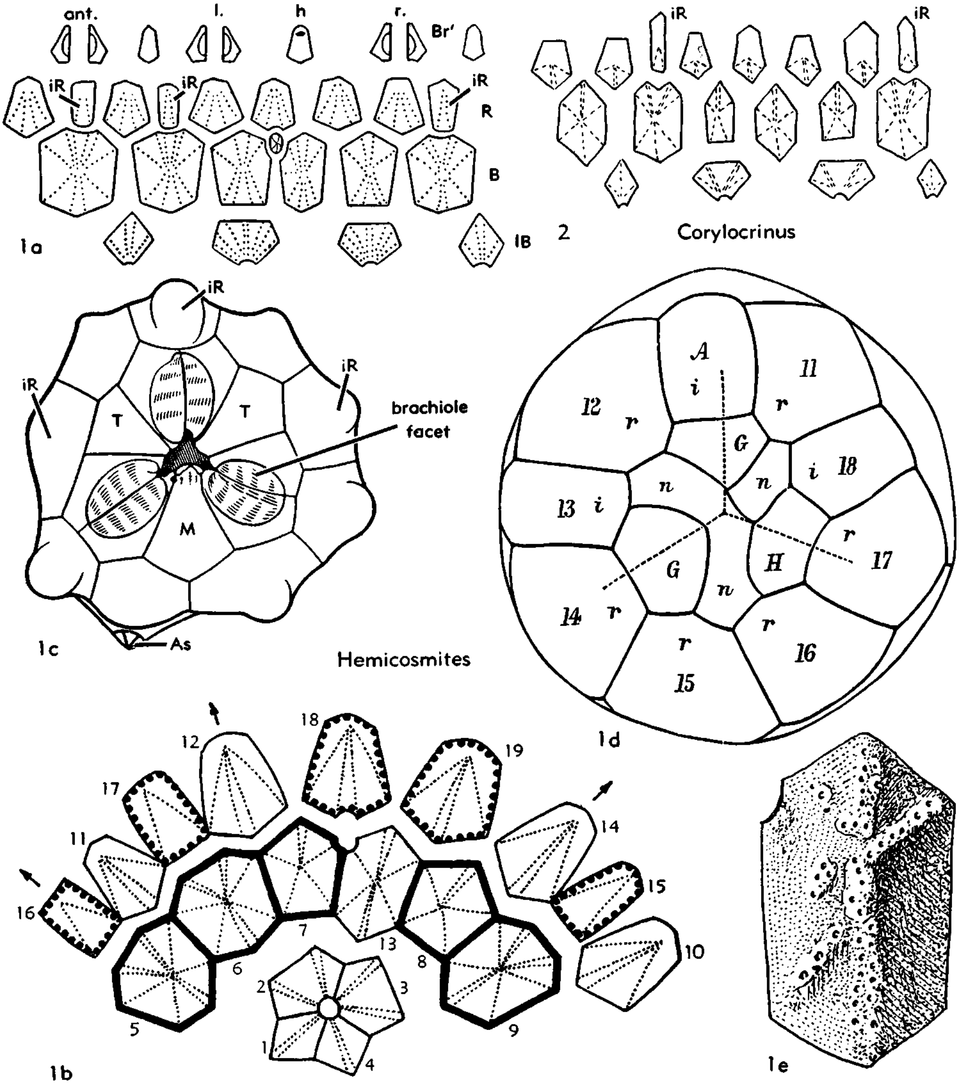


Fig. 119. Hemicosmitidae. Plate diagrams and oral views of theca (p. *S*219-*S*221). [Plate designations as in Figure 38.]

right) (10).——Fig. 119,*1b*. Plates diagrammed in comparison with Glyptocystitida (*ILL* with black borders, *RR* with dotted borders) (89).——Fig. 119,*1c*. Oral view of tegmen (*As*, periproct; *M*, plate connecting with hydropore; *T*, tegminal plate) (10).——Fig. 119,*1d*; 120,*1a,b*. **H. pyriformis*, Eu.(USSR); 119,*1d*, oral view and analysis by Carpenter (32); 120,*1a,b*, oral and lat., ×1 (31).——Fig. 119,*1e*. *H. altus* Jaekel, M. Ord.(Jewe, D_1), Est.; plate at aboral right of periproct (71).——Fig. 120,*1c-f*. *H. extraneus* Eichwald, M.Ord(Jewe), Est.; *1c,d*, oral and lat., ×0.75 (99); *1e,f*, oral and lat., ×1 (44).——Fig. 120,*1i*. *H. pulcherrimus* Jaekel, M.Ord.(Jewe), Est.; lat., ×2 (69).——Fig. 120,*1g,h*. *H. verrucosus* Eichwald, U.Ord.(Lyckholm), Est.; *1g,h*, aboral and lat., ×1 (44).

Corylocrinus Koenen, 1886, p. 249 [**C. pyriformis*; OD (=*Caryocrinus europaeus* Quenstedt, 1874, p. 665, *fide* Dreyfuss, 1939, p. 124)] [=*Cordylocrinus* Carpenter, 1891, p. 135 (*nom. null.*)]. Theca acorn-shaped to thick spindle-shaped, with rather broad "shoulders" in young specimens tending to become obscure in more rotund adults. *LL* 8, 2 most narrow set atop largest *ILL* in "interradial" positions; except for variation in

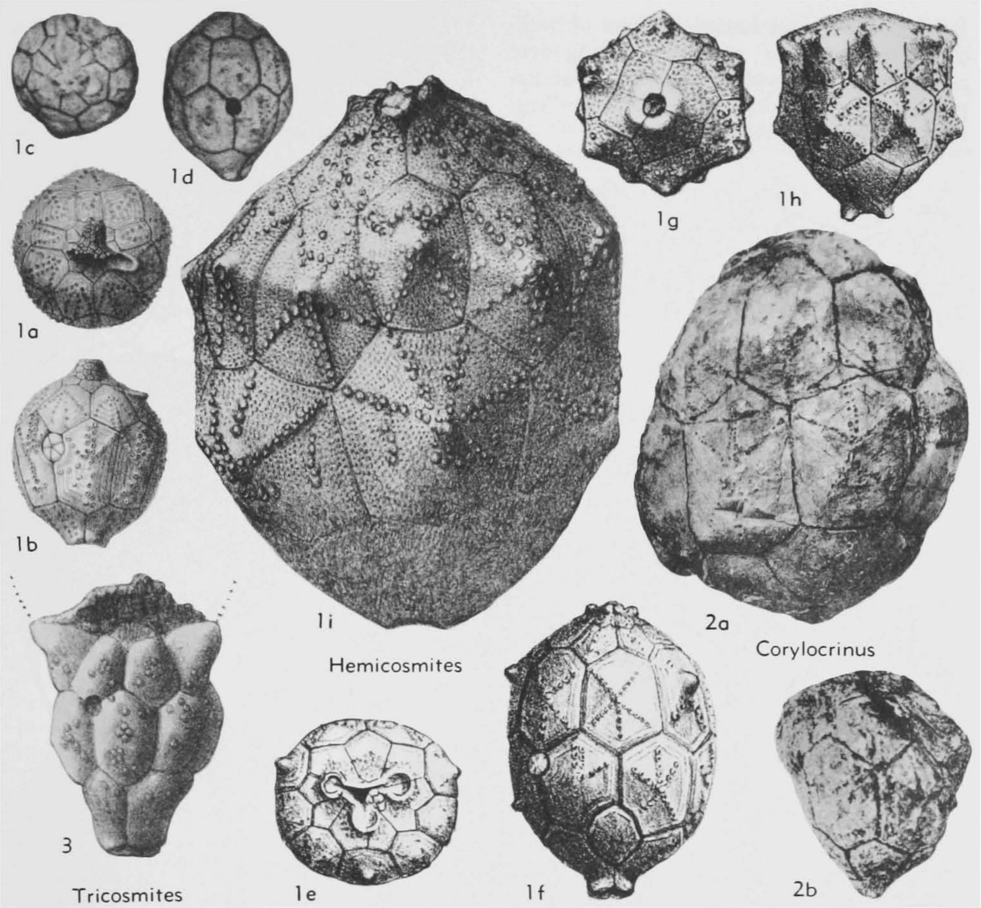


FIG. 120. Hemicosmitidae (p. *S*219-*S*221).

sizes of *LL*, first 3 circlets of plates very similar to those of *Oocystis* (Caryocrinitidae). Rhombs between all *ILL* and adjoining plates. Peristome bordered by 4 large plates, 3 bearing brachiole facets "apparently as in *Hemicosmites*" (10); 6 facets noted by YAKOVLEV (146); in spindle-like *C. elongatus*, the facets crowded together on narrow apex. Periproct between 2 *LL*, not in contact with any *IL* plate; circlets of *BB*, *ILL*, and *LL* showing plane of symmetry through periproct. [By the position of the periproct and disposition of the brachiole facets in certain species, this genus appears to be almost intermediate between the Hemicosmitidae (with low periproct and clustered brachioles) and the Caryocrinitidae (with high periproct and brachioles displaced outward by the "tegmen") (146).] *U.Ord.*, Eu.(Fr.-Alps-Port.-USSR)-N.Afr.(Alg.)-Asia(India).——FIG. 119,*2*. Plate diagram (*IR*, interradial) (39).——FIG. 120, *2*. **C. europaeus* (QUENSTEDT), Caradoc, Fr.; *2a,b*, lat., 2 thecae, ×0.9 (39).

Tricosmites JAEKEL, 1918, p. 97 [**Hemicosmites tricornis* JAEKEL, 1899, p. 311; OD]. Theca tapering toward base, somewhat urn-shaped, strongly modified near border by 3 *LL* processes which form bases for brachiole facets, plates arranged as in *Hemicosmites*. Plates strongly tumid, but without nodes or ridges. Pores rather irregular. *L.Sil.* (Borkholm F_2), Eu.(Est.).——FIG. 120,*3*. **T. tricornis* (JAEKEL); lat., ×2 (69).

Family CARYOCRINITIDAE Bernard, 1895

[*nom. correct.* BASSLER, 1938, p. 10 (*pro* Caryocrinidés BERNARD, 1895, p. 205)]

Theca composed of four *BB*, six *ILL*, eight *LL*, and several small *RR*. Rhombs with inner side of strong folds or laminae perpendicular to sutures, terminal pores nearly penetrating through plates but covered by thin layer of epitheca or stereom.

Brachiole facets at lateral borders of well-developed "tegmen" of plates roofing over ambulacra and peristome. Periproct at upper border of theca, above *LL,* near "tegmen." *M.Ord.-L.Dev.*

Key to Genera of Caryocrinitidae

1\. Plates very tumid or "swollen," without ridges; pores mostly obscure .. *Stribalocystites*
Plates not tumid, bearing ridges; pores distinct 2

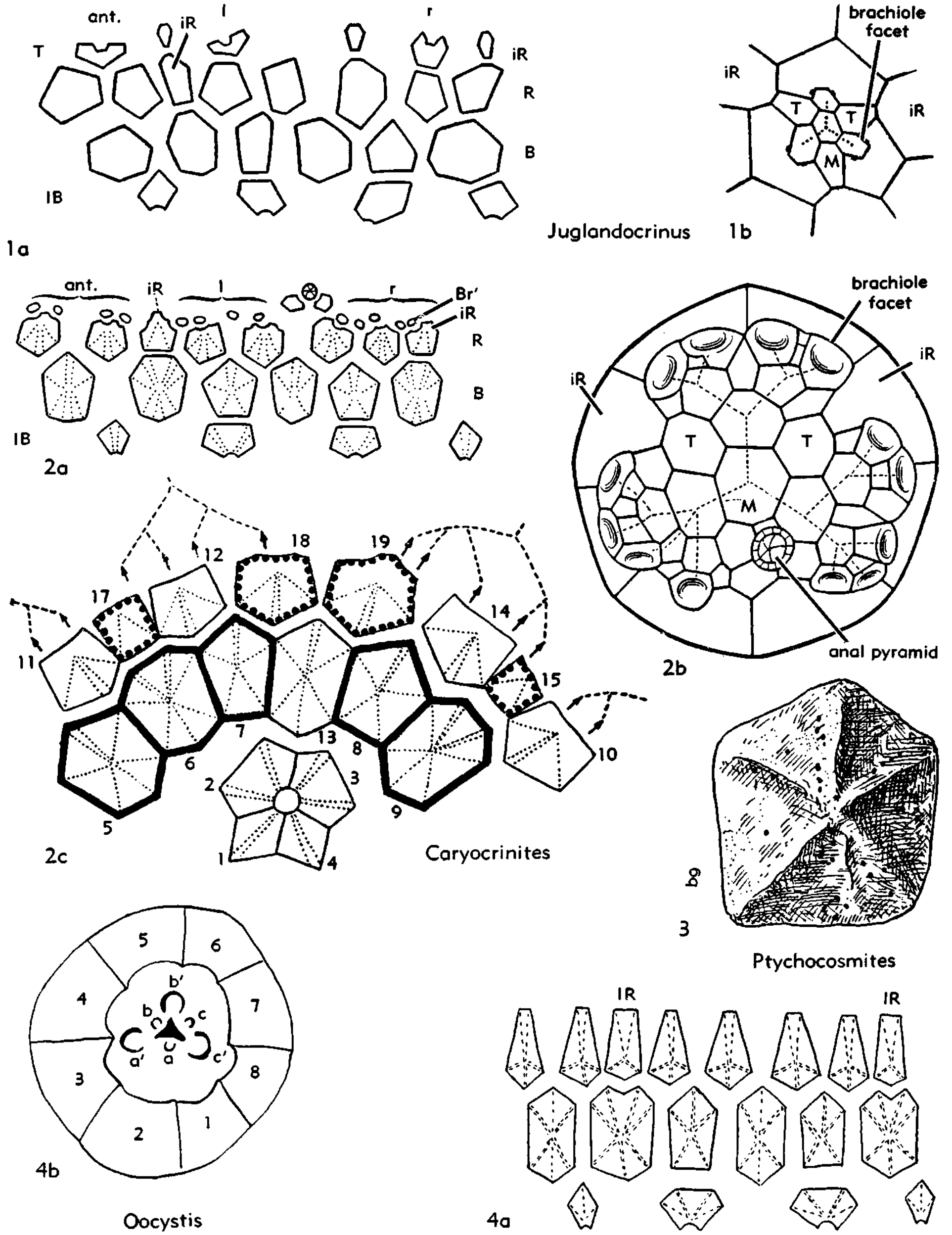


Fig. 121. Caryocrinitidae. Plate diagrams and oral views of theca (p. *S*223-*S*225).

2. Pores in areas between ridges, not arranged in rows .... *Ptychocosmites*

   Pores in rows along sides of ridges 3

3. *LL* not regularly arranged with respect to *ILL*, of several shapes .... *Juglandocrinus*

   LL regularly arranged with respect to *ILL*, six nearly identical with their lower apices between *ILL* ("radial" positions of some authors) and two of different shape set atop *ILL* ("interradial" positions) 4

4. Brachiole facets consisting of three large ones with three smaller spaced between; *LL* elongate, nearly or quite pentagonal .... *Oocystis*

   Several brachiole facets at ends of three branching ambulacra; *LL* partly covered by "tegmen," not elongate, more nearly hexagonal than pentagonal .... *Caryocrinites*

Caryocrinites SAY, 1825, p. 289 [**C. ornatus;* OD] [=*Cariocrinites* BRONN, 1834, p. 64 *(nom. null.); Caryocrinus* AGASSIZ, 1836, p. 198 *(nom. van.); Cariocrinus* AUSTIN & AUSTIN, 1845, p. 53 *(nom. van.); Enneacystis* HAECKEL, 1896, p. 143 (type, *E. buchiana*)]. Theca ovoid to acorn-shaped, with

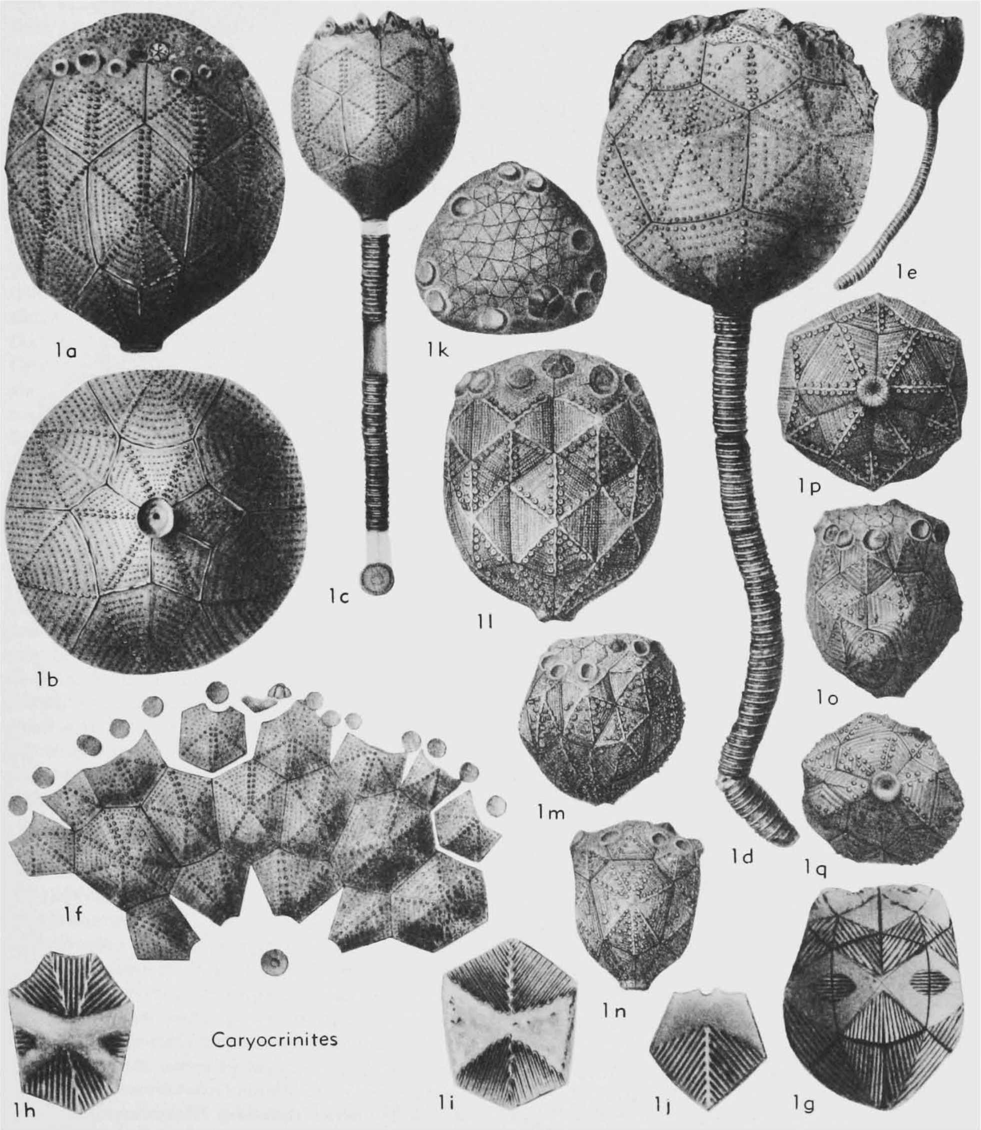


FIG. 122. Caryocrinitidae (p. S223-S225).

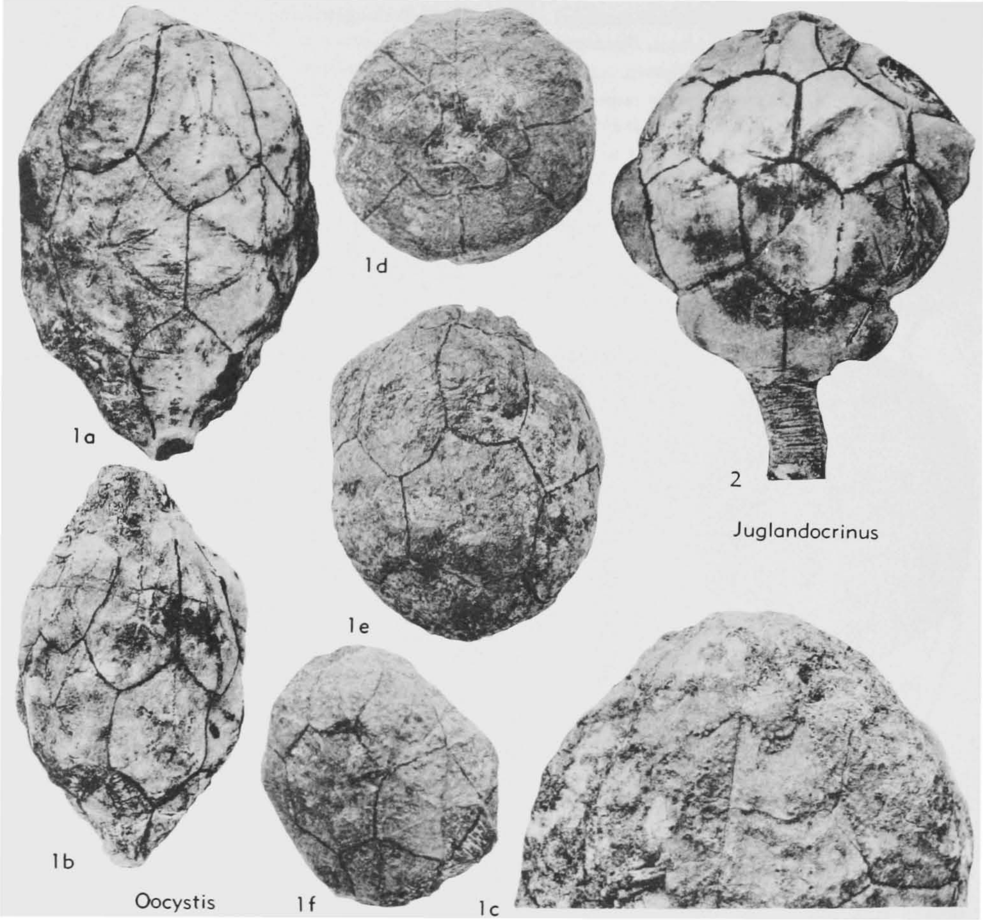


FIG. 123. Caryocrinitidae (p. S225).

base slightly tapered and oral surface rather gently convex. *BB* 4, 2 large and hexagonal and 2 small and pentagonal. *ILL* 6, large and polygonal, *IL* plate above junction of 2 hexagonal *BB* being hexagonal, whereas *2ILL* immediately above hexagonal *BB* are pentagonal; on each side, over junction of hexagonal and pentagonal *B, IL* plate is 7-sided, occupying so-called "interradial" position and directly supporting plate of *LL* series; above junction of 2 pentagonal *BB, IL* plate is subhexagonal. *LL* 8, presumably polygonal but with their adoral borders obscured in part by "tegmen" comprising plate cluster that covers ambulacral grooves and forms a vault over peristome, variously indented to accommodate small irregular plates in next circlet. Periproct relatively small, set high on theca within tegminal region, above *LL,* subcircular and containing anal pyramid. Brachiole facets at borders of "tegmen" and set upon adoral margins of *LL,* arranged in 3 general groups as result of subtegminal branching of 3 ambulacral grooves; number of brachiole facets related directly to ontogeny, small specimens having been observed with only 3 and very large specimens with 14 facets, most adults provided with 12 or 13. [As made known by FOERSTE (47), the type species is provided with pinnulate free arms, composed of biserial brachials and pinnulars; in the biserial nature of its pinnules, *Caryocrinites* differs from crinoids, in which pinnules have only a single row of pinnulars. JAEKEL (69) described internal structures of *Caryocrinites ornatus* in which traces of the alimentary canal can be seen within the theca, preserved by fortunate calcification of the gut-wall. Species vary in degree of radial ornamentation on the plates, number and distribution of pores, and proportions of the theca. The Middle Ordovician *Caryocrinites aurora* (BATHER) resembles *Hemicosmites* in having excavated brachiole facets and in exhibiting only a slight development of the "tegmen," whereas later species have a more pronounced "tegmen." This probably can be accepted as an indication of the phylogenetic derivation of the Caryocrinitidae. The close relationship of *Caryocrinites* and *Stribalocystites* is discussed under the latter genus.] *M.Ord-M.Sil.*, Asia (Burma)-Eu. (Sweden-Norway) - N. Am. (Ont.-N.Y.-Ky.-Ind.-Tenn.-Mo.-Iowa).——Fig. 121,*2a,b*. Plates diagrammed in comparison with crinoid; oral view of theca (10).——Fig. 121,*2c*. Plates diagrammed in comparison with Glyptocystitida (*ILL* with black borders, *RR* with dotted borders) (89).——Fig. 122,*1*. **C. ornatus*, *M.Sil.*(Niagaran), USA.; *1a,b*, lat. and aboral, adult; *1c-e*, lat., 3 thecae in various stages of growth; *1f*, plate diagram; *1g*, steinkern; *1h-j*, interior views of 3 plates (60); *1k,l*, oral and lat.; *1m-o*, lat., 3 thecae; *1p,q*, aboral, 2 specimens (31); all ×1. [See also Fig. 34,*3*].

Juglandocrinus Koenen, 1886, p. 249 [**J. crassus;* OD] [=*Inglandocrinus* Cuénot, 1953, p. 622 *(nom. null.)*.]. Theca rotund, ovate. Each row of plates exhibiting considerable range in size and variety of shapes; in particular, *LL* not arranged with discernible symmetry or equal spacing to fit above *ILL* sutures, as seen in *Caryocrinites* and *Oocystis;* "tegmen" much smaller than that of *Caryocrinites*, consisting of small hexagonal central plate and 3 similar adjoining ones set at nearly equal angles. Ambulacral grooves reaching exterior on 3 large plates underlying distal ends of 3 outer covering plates, former broad and pentagonal, separated by 3 narrow intervening plates also in *RR* tight circlet; one of narrow plates said to be thick and porous, apparently serving as hydropore. Periproct round, set high on theca near "tegmen." Column, in proximal part at least, composed of numerous, very short columnals (3 per mm.). Dreyfuss (39) showed rhombs only between *ILL* and *LL*. *U.Ord.*(Caradoc), Fr.——Fig. 121,*1a,b*. Plate diagram and oral region (*M* plate connecting with hydropore; *T*, tegminal plate) (10).——Fig. 123,*2*. **J. crassus;* lat., ×1.8 (*M* plate connecting with hydropore; *T*, tegminal plate) (39).

Oocystis Dreyfuss, 1939, p. 125 [**O. vulgaris* Dreyfuss, 1939, p. 127; SD Kesling, herein]. Theca with 3 cycles of principal plates, 4 *BB*, 6 *ILL*, and 8 *LL;* 2 adjacent *BB* (presumably *B3* and *B4*) hexagonal, other 2 pentagonal, *BB* indented for insertion of column, as in other cystoids of order; *ILL* 4, hexagonal, 2 of them with adoral indentations, their aboral apices directed between *BB*, and remaining 2 pentagonal, their bases atop *B3* and*B4; LL* symmetrical with respect to *BB* and *ILL*, each plate nearly or quite pentagonal, elongate, tapering adorally to very short side, 2 *LL* lying above *B1/B4* and *B2/B3* junctions (the so-called "interradial" positions) rather bluntly acuminate, set into slight indentations in *ILL* below, other 6 *LL* with their aboral apices in angles between *ILL*. Rows of pores radiating from centers of plates to angles, some simple and some double; some pores covered by more or less rugose layer, as in *Caryocystites* or *Heliocrinites*, some open at surface, presumably exposed by abrasion. Two "interradial" *ILL* with 7 double rows of pores (constituting 7 half-rhombs), 2 other hexagonal *ILL* with 4 double rows and reportedly with 2 vertical simple rows, 2 pentagonal *ILL* with 5 double rows; *LL* with rhombs between them and with rhombs shared with all adjacent *ILL*. Oral surface somewhat truncated, small; small plates present above *LL*, but their number and arrangement is unknown. Mouth triangular, with each corner directed toward large brachiole facet and with small brachiole facet along each side. Periproct unknown, so that position of genus in Hemicosmitidae or Caryocrinitidae cannot be definitely determined; affinities appear to be with *Caryocrinites* in plate arrangement. *U.Ord.*(Caradoc), Eu.(Fr.-Wales).——Fig. 121,*4;* 123,*1d,e*. *O. vulgaris subsphaeroidalis* Dreyfuss, Fr.; 121,*4a*, plate diagram; 121,*4b*, oral view showing 6 brachiole facets (*ILL* numbered clockwise); 123, *1d,e*, oral and lat., ×0.9 (39).——Fig. 123,*1a-c*. **O. vulgaris*, Fr.; *1a,b*, lat., 2 thecae, ×0.9; *1c*, lat., oral end, ×1.8 (39).——Fig. 123,*1f*. *O. rugata* (Forbes), Wales; lat., ×0.9 (39).

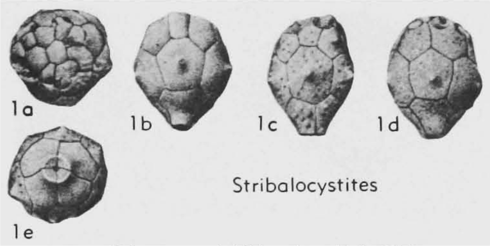


Fig. 124. Caryocrinitidae (p. *S225*-*S226*).

Ptychocosmites Jaekel, 1918, p. 97 [**P. sardinicus*]. Theca known only from isolated plates. Pore areas of plates in spaces between radial ridges, not arranged in rows. [Although Jaekel (71) compared plates of *Ptychocosmites* with those of *Hemicosmites* and placed his new genus in the Hemicosmitidae, the only illustrated plate was nearly equilaterally pentagonal, not elongate. This shape occurs in the *ILL* of *Caryocrinites* but not of *Hemicosmites*. Furthermore, some specimens of *Caryocrinites ornatus* have some of the pores of the general rhombic alignment, whereas such occurrences have not been noted in *Hemicosmites*.] *U.Ord.*, Sardinia.——Fig. 121,*3*. **P. sardinicus;* thecal plate (71).

Stribalocystites S. A. Miller, 1891, p. 20 [**S. tumida;* OD] [=*Stribalocystis* Bather, 1900, p. 67 *(nom. van.); Strybalocystis* Rowley, 1900, p. 71 *(nom. van.)*]. Theca with plates in similar arrangement to those of *Caryocrinites;* ridges on

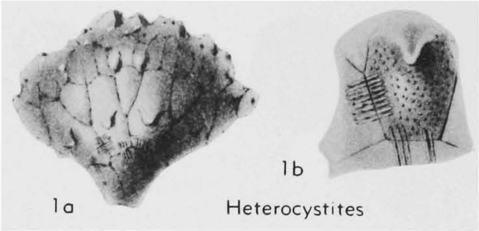


FIG. 125. Heterocystitidae (p. *S226-S227*).

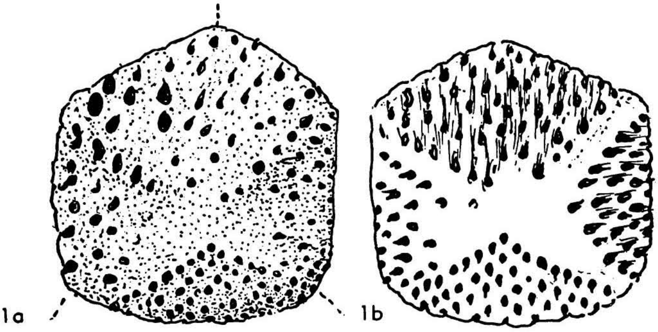
thecal plates absent or merged into general tumid shape. Pores may be obscure. Brachiole facets in some species not distinctly marked, perhaps due to small size of theca and strong development of "tegmen." [The status of this genus is open to question. JAEKEL (69) presented it with question and later (71) tentatively placed it in the Hemicosmitidae. BATHER (12), in a survey of *Caryocrinites,* divided the species into two groups, a "normal series" having ridges radiating from centers of thecal plates and bordered by pores (e.g., *C. ornatus*) and a "*Stribalocystis* series, as one may conveniently term it," lacking distinct ridges and "with pores often obscure." *Stribalocystites* was recognized as a separate genus by BASSLER (5) but not by BASSLER & MOODEY (7). The close resemblance to *Caryocrinites* is unmistakable, but until additional species are described it seems advisable to maintain *Stribalocystites*.] *M.Sil.-L.Dev.,* N. Am.(Ind.-Ky.-Tenn.-Mo.).——FIG. 124,*1*. *S. bulbulus* (MILLER & GURLEY), M.Sil.(Niagaran), USA (Tenn.); *1a-e,* oral, 3 lat., and aboral, ×1 (Springer, 1926).

Family HETEROCYSTITIDAE Jaekel, 1918

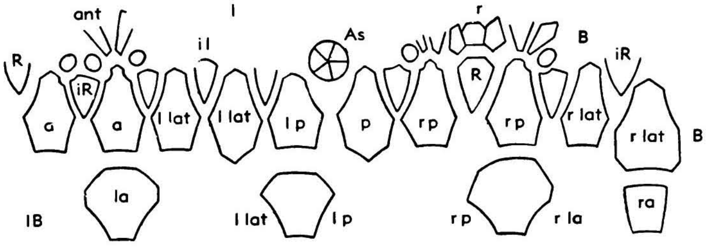
[*nom. correct.* KESLING, herein (*pro* Heterocystidae JAEKEL, 1918, p. 98)]

Circlet above *BB* containing 10 *ILL*; *LL* nine, subtriangular, their acuminate aboral ends inserted between *ILL. M.Sil.*

Heterocystites HALL, 1851, p. 229 [**H. armatus;* OD] [=*Heterocystis* BATHER, 1900, p. 67 *(nom. van.)*]. *BB* 4, different from those in other genera of Hemicosmitida, with 3 large 6- to 8-sided plates and 1 small subquadrate plate; *ILL* 10, subpentagonal, elongate, all in contact and forming complete circlet in their aboral thirds, their adoral two-thirds tapering to leave triangular spaces between adjacent plates; in one of these spaces lie plates of periproct and in other 9 acuminate aboral ends of *LL* are inserted. Ambulacra bifurcating, as in *Caryocrinites,* perhaps to a greater extent; oral region incomplete in only known specimen, but apparently consisting of a complex of tegminal plates. Thecal plates nodose. [BATHER (10) suggested the derivation of this genus from *Hemicosmites* by vertical bisection of 4 *ILL* and aboral displacement of the *LL.* The plate arrangement warrants the assignment to a special family, despite incomplete information on



Polycosmites



2

Heterocystites

FIG. 126. Polycosmitidae *(1)*; Heterocystitidae *(2)*. Plates and plate diagram (p. *S226-S227*).

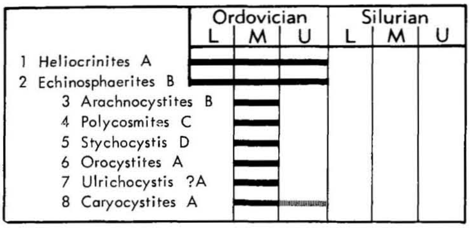


FIG. 127. Stratigraphic distribution of genera belonging to the superfamilies Polycosmitida and Caryocystitida. Classification of the genera in families is indicated by letter symbols: A—Caryocystitidae, B—Echinosphaeritidae, C—Polycosmitidae, D—Stichocystidae. The following alphabetical list of genera furnishes cross reference to the serially arranged numbers on the diagram (Kesling and Moore, n).

Generic Names of Polycosmitida and Caryocystitida and Index Numbers

Arachnocystites—3
Caryocystites—8
Echinosphaerites—2
Heliocrinites—1
Orocystites—6
Polycosmites—4
Stichocystis—5
Ulrichocystis—7

the oral field.] *M.Sil.*, USA(N.Y.).——FIG. 125, *1;* 126,*2.* **H. armatus;* 125,*1a*, lat., holotype (crushed), ×1; 125,*1b*, thecal plate, enl. (60); 126,*2*, plate diagram [*a, ant*, anterior; *As*, anus; *B*, basal; *IB*, infrabasal; *il*, interlateral; *iR*, interradial; *l*, left; *lat*, lateral; *p*, posterior; *R*, radial; *r*, right] (10).

Superfamily POLYCOSMITIDA Jaekel, 1918

[*nom. transl.* REGNÉLL, 1945, p. 107 (*ex* Polycosmitidae JAEKEL, 1918, p. 98)] [=suborder Polycosmites JAEKEL, 1918, p. 98]

Theca composed of numerous, irregularly arranged plates. Pore rhombs on all sides of thecal plates. Pores inclined, not connected by inside or outside calcified tubes. *M.Ord.*

As set forth by JAEKEL (1918), the family Polycosmitidae and suborder Polycosmites were intended to emphasize the pore structure, which is remarkably intermediate between that of the Hemicosmitida and that of the Caryocystitida. In the hemicosmitid *Caryocrinites* the holes through the plates and nearly attaining the exterior (covered only by a thin calcareous layer in the distal tubercles) are connected by inner pore canals or tubes; but in the caryocystitid *Echinosphaerites* the holes lead from the interior of the theca to tubes within the plates; and in the polycosmitid *Polycosmites* or *Stichocystis* the holes in the thecal plates lack calcified tubular connections of either kind.

The Polycosmitida is a superfamily based on JAEKEL's Polycosmitidae, not on his suborder Polycosmites, for the latter is not a family-group taxon; this is so even though the content of the superfamily and suborder is the same.

The stratigraphic distribution of polycosmitid genera is shown in Figure 127.

Family POLYCOSMITIDAE Jaekel, 1918

[Polycosmitidae JAEKEL, 1918, p. 98]

Thecal pores not arranged in long rows. Plates apparently disposed as in Hemicosmitida, but no complete theca known. *M.Ord.*

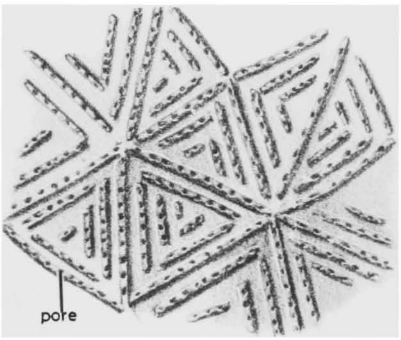
Polycosmites JAEKEL, 1918, p. 98 [**P. bohemicus;* OD]. Theca including at least some polygonal plates penetrated by simple pores distributed in rhombic sectors but not arranged in long rows. *M.Ord.*, Eu.(Boh.).——FIG. 126,*1.* **P. bohemicus; 1a,b,* thecal plate ext. and int. (71).

Family STICHOCYSTIDAE Jaekel, 1918

[Stichocystidae JAEKEL, 1918, p. 98]

Theca conspicuously ornamented by very straight ridges bearing rows of pores, linking centers of adjacent plates in triangles, with short, strictly parallel, additional ridges forming concentric pattern. *M.Ord.*

Stichocystis JAEKEL, 1899, p. 325 [**Caryocystis geometrica* ANGELIN, 1878, pl. 12, fig. 22-24; OD]. Theca composed of 50 to 60 plates, mainly hexagonal, sutures (in many specimens not generally recognizable) crossed at right angles by 1 to 5 ridges, rigorously parallel, each pierced by series of pores. Ambulacral area semilunar, apparently with 5 brachiole facets. Mouth a narrow slit. Periproct circular, above mid-height. Hydropore not definitely established and gonopore unknown. Column



1 Stichocystis

FIG. 128. Stichocystidae (p. S227-S228).

very small, to judge from cicatrix on theca. *M. Ord.*, Eu. (Sweden - Ger.) - Asia (China).——FIG. 128,*1*. **S. geometrica* (ANGELIN), Ger.(drift); exfoliated, ×3 (69).

Superfamily CARYOCYSTITIDA Jaekel, 1918

[*nom. transl. et correct.* REGNÉLL, 1945, p. 111 (*ex* Caryocystidae JAEKEL, 1918, p. 99)] [=suborder Caryocystites JAEKEL, 1918, p. 99]

Theca composed of numerous, irregularly arranged plates. Pore rhombs with tubes or pore canals within plates, with pore at each end reaching through plate into interior of theca; epitheca covering exterior of tubes, and where epitheca removed by weathering, tubes are exposed as sharply defined parallel grooves arranged in rhombic patterns between plates. Brachioles relatively few, erect. Ambulacra very short, unbranched, number variable in some species. *L.Ord.-U.Ord.*

The stratigraphic distribution of genera belonging to the Caryocystitida is shown in Figure 127.

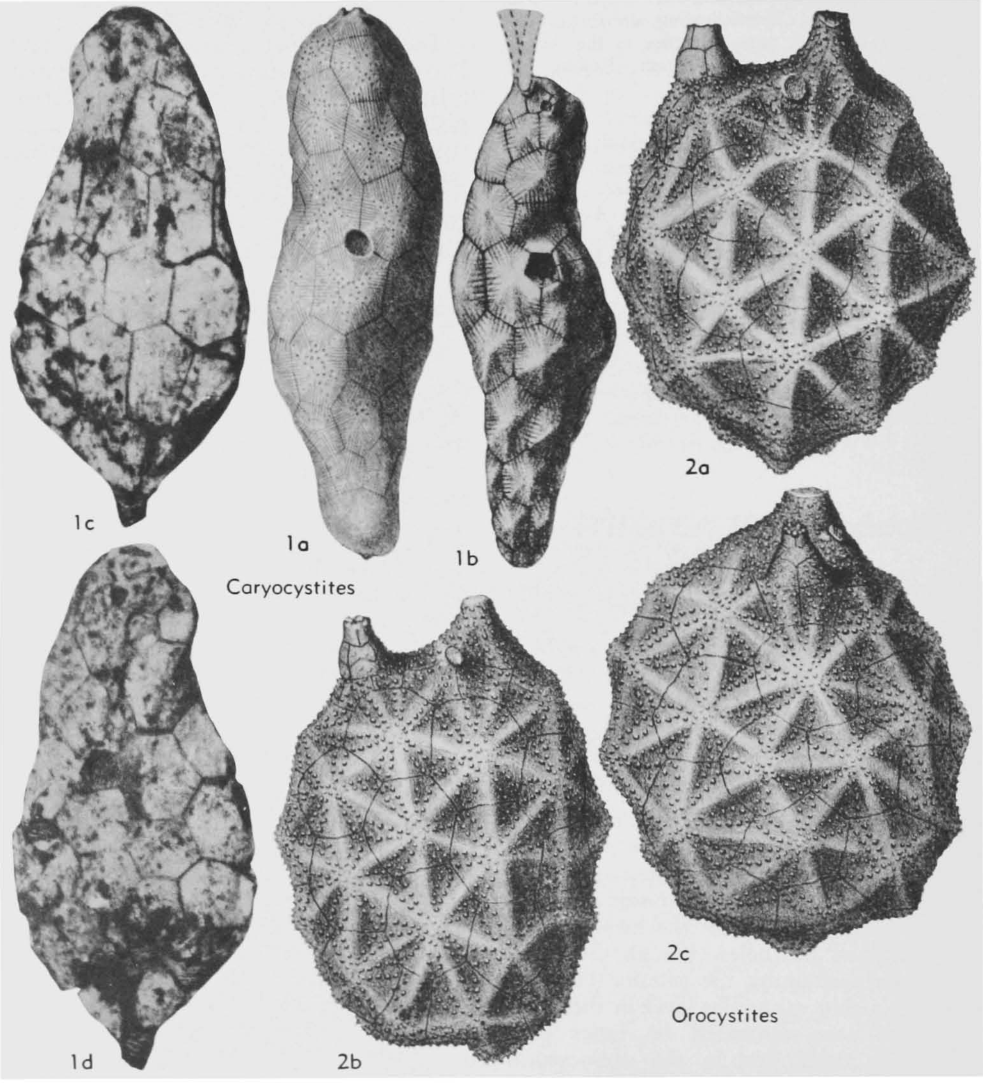


FIG. 129. Caryocystitidae (p. S229, S231).

Family CARYOCYSTITIDAE Jaekel, 1918

[*nom. correct.* REGNÉLL, 1945, p. 111 (*pro* Caryocystidae JAEKEL, 1918, p. 99)]

Theca ovate to elongate, containing 30 to 120 plates, polygonal, mostly hexagonal and alternating. Epitheca seldom preserved. Pore canals within plates, simple or compound. Brachioles few, facets bordering mouth. *L.Ord.-U.Ord.*

Key to Genera of Caryocystitidae

1. Theca subovate; peristome and periproct protuberant from opposing sides of top of theca, both directed upward .... *Orocystites*

   Theca elongate; periproct not protuberant, not on top of theca, and not directed upward 2

2. Theca claviform, tapering aborally to small stemlike base; periproct only one-fourth height from oral pole .... *Ulrichocystis*

   Theca not claviform, its greatest diameter near mid-height or below; periproct about one-third to one-half height from oral pole 3

3. Height of theca more than twice greatest diameter; theca tapering toward each end, with greatest diameter median; pore canals compound, several connecting each pair of pores; sculpturing of thecal plates not very prominent .... *Caryocystites*

   Height of theca scarcely exceeding twice greatest diameter, even in more attenuated specmens; theca pear-shaped, aborally more rotund and tapering adorally; pore canals simple, tangential, one canal connecting each pair of pores; sculpturing and ornamentation of plates by folds and ridges .... *Heliocrinites*

Caryocystites VON BUCH, 1846, p. 128 [**Caryocystis angelini* HAECKEL, 1896, p. 59 (=**Caryocystites testudinarius* VON BUCH, 1846, p. 19, OD, *nom. in errore pro "Sphaeronites testudinarius"* HISINGER, 1837, pl. 25, fig. 8d, *non* fig. 9d, *recte "S. citrus"* HISINGER; *non S. testudinarius* HISINGER, 1826, p. 115, =*Heliocrinites granatum* (WAHLENBERG); *non S. citrus* HISINGER, 1837, p. 91, =*Echinosphaerites aurantium* (GYLLENHAAL); *Amorphocystis buchi* JAEKEL, 1899, p. 339)] [=*Caryocistites* D'ORBIGNY, 1850, p. 23 *(nom. null.); Caryocystis* ANGELIN, 1878, p. 28 [*nom. van.*); *Amorphocystites* JAEKEL, 1896, p. 411 (type, *A. buchi* JAEKEL =*C. testudinarius* VON BUCH); *Amorphocystis* JAEKEL, 1899, p. 337 *(nom. van.)*]. Theca elongate, its greatest diameter near mid-height or below and less than half of height, tapering toward each end, containing about 30 to 80 plates, most of them hexagonal and tending to be disposed in tiers or circlets; plates not strongly sculptured. Pore canals within plates, compound, with several connecting each pair of pores. Periproct slightly above mid-height, filled by valvular anal pyramid. Column rather feebly developed. Mouth elongate in sagittal plane, with 2 terminal brachiole facets, or triangular, with 3 facets at corners. Opening covered by low pyramid between mouth and anal pyramid, slightly offset to right, interpreted as gonopore by REGNÉLL (99), who failed to find evidence for a hydropore as figured by ANGELIN (1). [The confusion regarding the type species was adequately resolved by BATHER in REED (12). *Heliocrinites* was founded by EICHWALD in 1840, using his 1829 species *Echinosphaerites balticus* as the type. In 1846 (31) (or variously reported as 1844 or 1845) VON BUCH introduced *Caryocystites* for two species, of which one, *Echinosphaera granata,* is congeneric with *Heliocrinites balticus.* If *E. granata* is regarded as the type species, then *Caryocystites* becomes a junior synonym of *Heliocrinites.* The second of VON BUCH's species was called *Caryocystites testudinarius,* in connection with which he referred to "*Sphaeronites testudinarius* HISINGER, Lethaea Suecica, taf. 25, figure 9*d*." Owing to a lithographer's lapse in placing the numbers, the figure should have been "8*d*," which was explained as *"Sphaeronites citrus"* but was actually distinct from that species (acknowledged as a synonym of *Echinosphaerites aurantium*). HAECKEL (58) proposed the name *Caryocystis Angelini* for figures 4-9 of ANGELIN's plate 13; "more by accident than design" (12), these figures represent HISINGER's specimen erroneously called *C. testudinarius.* However conceived, HAECKEL's *C. angelini* is valid and sufficient to substantiate *Caryocystites.* JAEKEL (69) overlooked HAECKEL's action and named the type species *Amorphocystis buchi;* by his interpretation, *Caryocystites* was *Amorphocystites* and *Heliocrinites* was *Caryocystites.*] *M.Ord., ?U.Ord.,* Asia(China)-Eu.(Sweden-Est.-?Wales) - ?N. Am. (USA).——FIG. 129,*1a,b.* **C. angelini* (HAECKEL), M.Ord. (*Chasmops* Beds), Sweden; *1a,* lat., ×1 (31); *1b, "Amorphocystis buchi"* of JAEKEL (69), lat., ×1 (69).——FIG. 129,*1c,d. C. lagenalis* REGNÉLL, M.Ord.(Kullsberg Ls.), Sweden; *1c, d,* opposite lat., ×0.75 (99).

Heliocrinites EICHWALD, 1840, p. 189 [**Echinosphaerites balticus* EICHWALD, 1829, p. 231; OD] [=*Heliocrinus* EICHWALD, 1859, p. 629 *(nom. van.); Heliocrinus* QUENSTEDT, 1876, p. 701 *(nom. null. pro Heliocrinus); Heliocystis* HAECKEL, 1896, p. 58 (type, *Heliocrinus radiatus* EICHWALD, 1840); *Heliocrinum* HAECKEL, 1896, p.58 (type, *Caryocystites granatum* VON BUCH) (*subgen. ad Heliocystis); Heliopirum* HAECKEL, 1896, p.59 (type, *Heliocrinus radiatus* EICHWALD, 1840)]. Theca ovoid to moderately elongate, its height scarcely more than twice greatest diameter even in attenuated specimens, more or less pyriform with greatest diameter in aboral half and tapering adorally, containing 50 to 120 plates, which are distinctively ornamented by pore-bearing ridges in concentric triangles or rhombs, more pronounced in some species than in others where they are partly superseded by similar pattern of axial folds. Pore canals simple and tangential, one canal connecting each

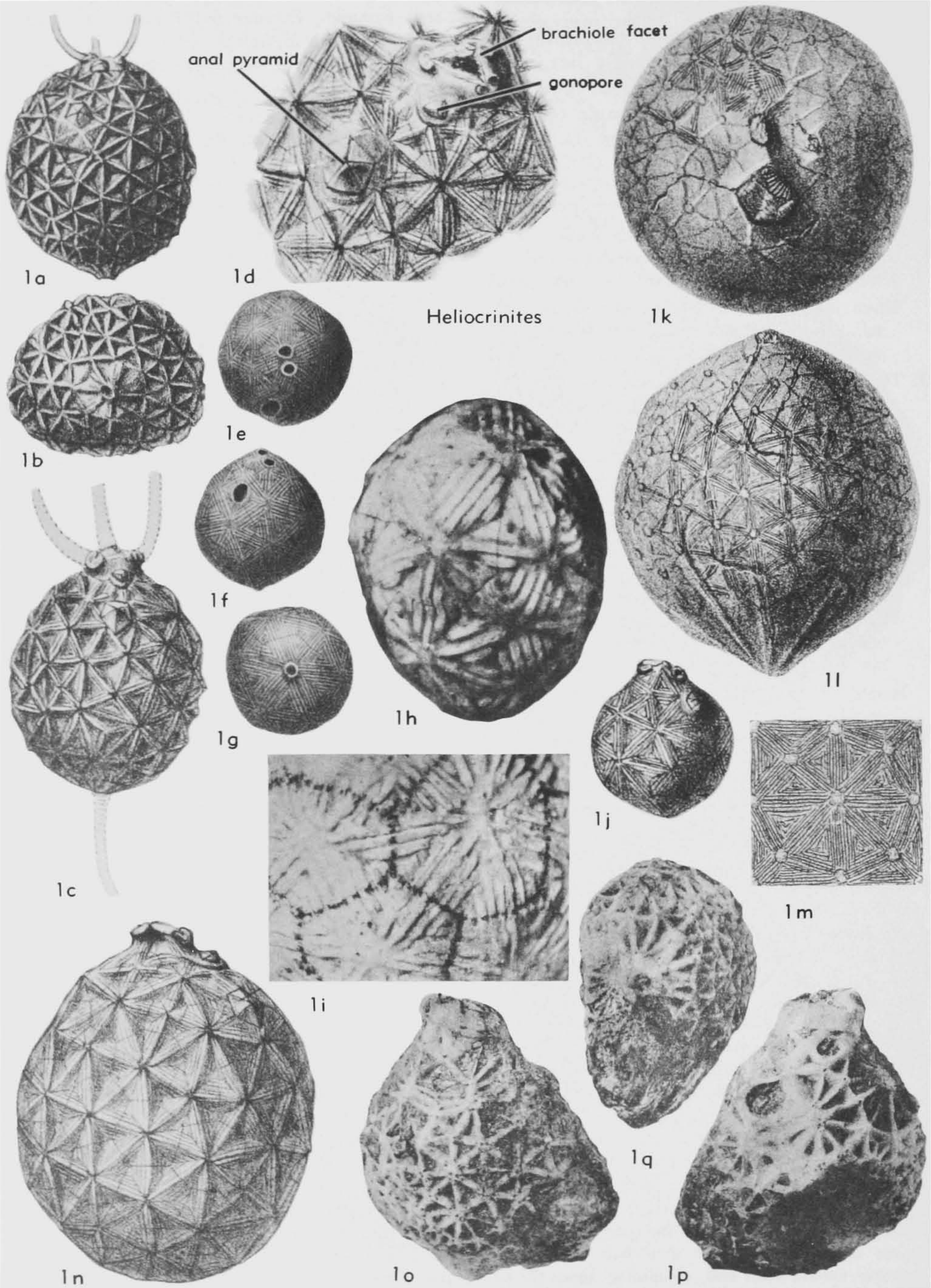


Fig. 130. Caryocystitidae (p. S229-S230).

pair of pores. Peristome may be elevated. Brachioles few, near the mouth. Periproct in adoral part of theca, not protuberant, not directed upward. Hydropore slightly offset from line between mouth and periproct, nearer to former. Column minute, pentagonal. [The taxonomic confusion of this genus and *Caryocystites* is discussed under the latter, explaining why JAEKEL (69) described *Heliocrinites* under the name *Caryocystites*.] *L. Ord.-U.Ord.*, Asia(Burma) Eu.(Est.-Sweden-Ger.-Czech.)-N.Afr.(Alg.).——FIG. 130,*1a-d*. **H. balticus* (EICHWALD), M.Ord., Est.;*1a,b*, lat. and aboral, ×1; *1c*, lat., ×1; *1d*, oral region, enl. (69).——FIG. 130,*1n*. *H. araneus* (VON SCHLOTHEIM), M.Ord., Est.; lat., ×1 (3).——FIG. 130, *1k-m*. *H. confortatus* (BARRANDE), M.Ord.(Dd_4), Boh.; *1k-m*, oral and lat., part of weathered surface, ×1 (3).——FIG. 130,*1e-j*. *H. granatum* (WAHLENBERG), M.Ord.(L.*Chasmops*), Sweden; *1e-g*, oral, lat., aboral, ×1 (31); *1h,i*, lat. (×1.5) and thecal plates (×2.25) (99); *1j*, lat., ×1 (69). ——FIG. 130,*1o-q*. *H. rouvillei* (VON KOENEN), M.Ord.(Caradoc), Fr.; *1o-q*, opposite lat. and aboral, ×1.8 (39). [See also Fig. 37,2.]

Orocystites BARRANDE, 1887, p. 168 [**O. helmhackeri;* OD] [=*Orocystis* BATHER, 1889, p. 209 *(nom. van.)*]. Theca ovoid, with notably protuberant peristome and periproct also protuberant as subconical projection at oral end, small hexagonal scar for attachment of column at opposite end. Plates relatively large, about 50 in theca, polygonal and mostly hexagonal, set in 5 or 6 irregular circles (exclusive of peristome and periproct), each plate with prominent ridges radiating from raised center to each side, dividing surface into as many kite-shaped cavities as there are sides; ridges from 3 adjacent plates outlining triangle, so that theca is covered by large network of ridges, junctions of which are at centers of plates. Pores arranged in "double" rows, whereby pores on side of one rhomb are close and parallel to those on adjacent side of next; thus, 2 rows of pores radiate from near center to each corner of plate. No pores in 1 or 2 circles of plates around opening presumed to be peristome, summit of which bears small pentagram or star with slightly enlarged tips, presumably points of attachment for tiny brachioles. Hydropore a distinct opening, oval, nearer to periproct than to peristome and offset to left, only slightly elevated. *M.Ord.*, Eu(Boh.-Port.-Ger.).——FIG. 129,*2*. **O. helmhackeri*, Dd_4, Boh.; *2a-c*, 3 lat., ×2 (3).

?**Ulrichocystis** BASSLER, 1950, p. 276 [**U. eximia;* OD]. Theca elongate, sub-pyriform or clavate, tapering from ovate oral region to small produced base, composed of polygonal (mostly hexagonal) plates, about 75 plates in only known specimen, said to be distributed as 3 elongate plates in basal circle, 5 in second, 6 circumoral, and 5 vertical rows of 6 plates, each between second circle and circumorals. Mouth an elliptical opening at oral pole, surrounded by raised rim. Periproct in adoral part of theca, about 5 mm. below top in 34 mm.-high theca. Each thecal plate with coarse parallel ridges filling each sector perpendicular to sides of plate, so that ridges form concentric triangles around junction of 3 plates. Grooves between ridges presumably simple tangential pore canals exposed by weathering off of epitheca, arranged in pore rhombs. [The author mentioned "only a trace of a recumbent arm with facets for the support of brachioles." Such a structure would indeed be foreign to cystoids of this general type, and, if present, would justify BASSLER's erection of the monogeneric family Ulrichocystidae.] *M.Ord.*, USA(Tenn.).——FIG. 131,*1*. **U. eximia;* lat., ×2 (6).

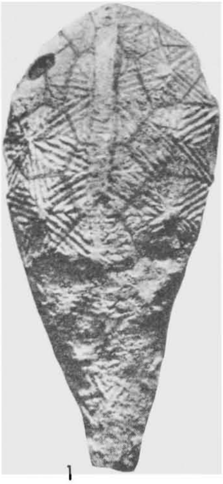


FIG. 131. Caryocystitidae (p. S231).

Family ECHINOSPHAERITIDAE
Neumayr, 1889

[Echinosphaeritidae NEUMAYR, 1889, p. 414]

Theca spheroidal to ovoid to pear-shaped, composed of 200 to more than 800 tiny, irregularly polygonal plates. Most tangential pore canals compound. Epitheca preserved in many specimens as smooth, concentrically marked laminae concealing pore canals. *L. Ord.-U.Ord.*

Key to Genera of Echinosphaeritidae

Theca typically subspheroidal, in few species pear-shaped, with aboral projection formed of one or two circlets of plates but not stemlike; one form with plates subequal, many hexagonal, and another

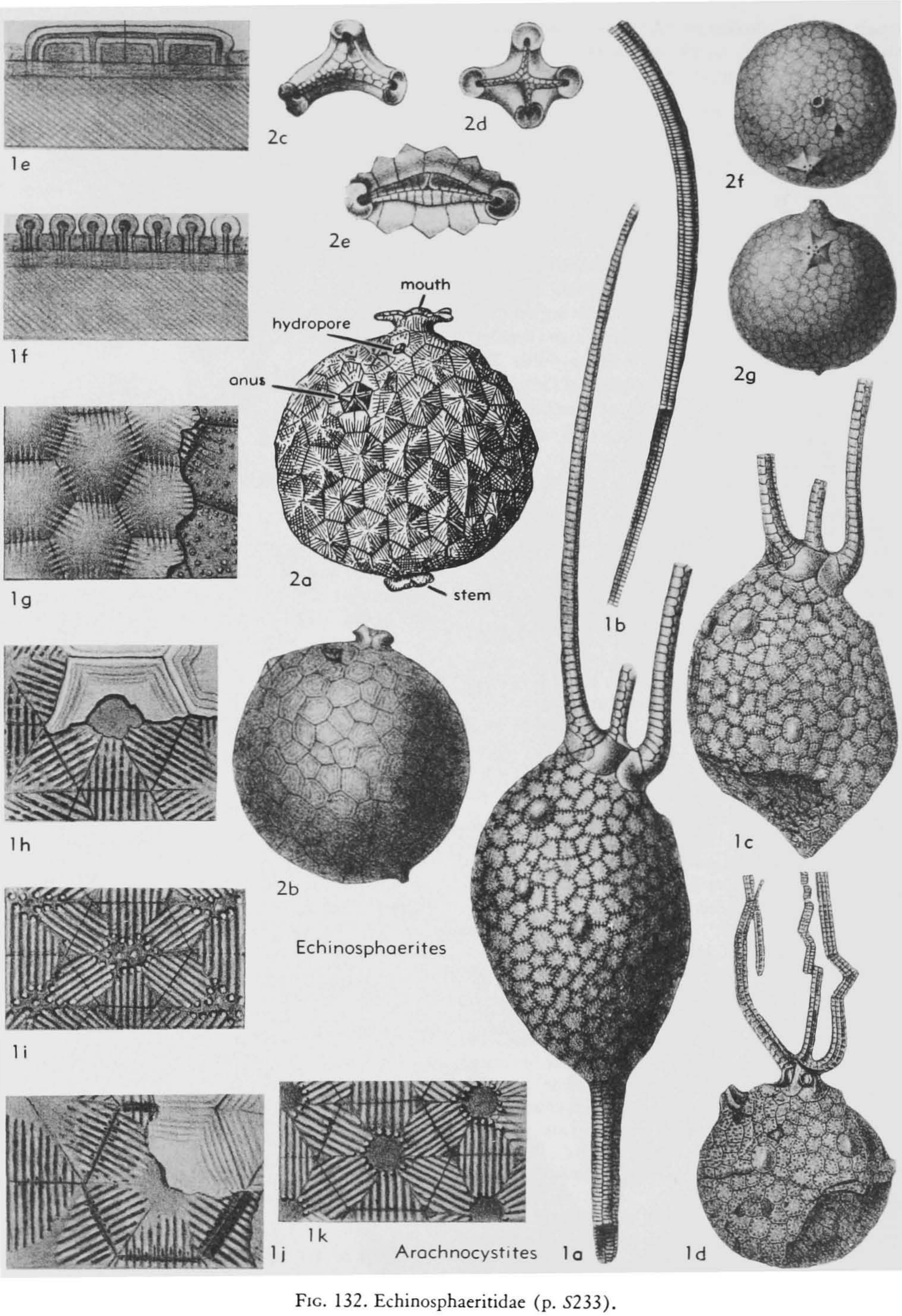


FIG. 132. Echinosphaeritidae (p. S233).

form with polymorphous plates; two to five ambulacra short but distinct, set upon oral projection .... *Echinosphaerites*

Theca pear-shaped, tapering to remarkably prolonged, thin, stemlike section of alternating rows of tiny hexagonal plates; most other plates small (200 to 800) but few larger plates interspersed, very few plates hexagonal; two or three brachioles springing more or less directly from oral projection with little or no development of intervening ambulacra ...... *Arachnocystites*

Echinosphaerites Wahlenberg, 1818, p. 44 [**Echinus aurantium* Gyllenhaal, 1772, p. 245 (=*Sphaeronites citrus* Hisinger, 1837, p. 91; *S. pomum* Hisinger, 1828, p. 196, *partim; Leucophthalmus strangwaysi* Koenig, 1825, pl. 1, fig. 1)] [=*Echinosphaera* Angelin, 1878, p. 28 *(nom. van.) non* Hertwig, 1879; *Echinosphora* Scudder, 1882, p. 118 *(nom. null.); Deutocystites* Barrande, 1887, p. 145 (type, *D. modestus*); *Deutocystis* Bather, 1889, p. 269 *(nom. van); Leucophthalmus* Koenig, 1825, pl. 1, fig. 1 (type, *L. strangwaysi*=*Echinus aurantium* Gyllenhaal); *Citrocystis* Haeckel, 1896, p. 68 (type, *Sphaeronites citrus* Hisinger=*Echinus aurantium* Gyllenhaal); *Crystallocystis* Haeckel, 1896, p. 66 (type, *Echinus aurantium* Gyllenhaal); *Trinemacystis* Haeckel, 1896, p. 65 (type, *Echinosphaera aurantium triactis*=*Echinosphaerites aurantium* var. Müller, 1854)]. Theca in type and many other species subsphaeroidal, for which reason these abundant cystoids have long been called "crystal apples"; in some (e.g., *E. pirum*) theca aborally produced to attain pear shape. Adults composed of 200 to several hundred polygonal plates; one form with many plates hexagonal and nearly all subequal, and another form with considerable variation in size, with plates having 3 to as many as 10 sides, both forms occurring within same species. Tangential pore canals exposed on weathered specimens as very regular, straight grooves distributed in rhombic areas, each rhomb formed by 2 triangular sectors of adjacent plates and nearly filled by several equally spaced, subparallel grooves. Each end of tangential pore canal joined to vertical pore canal, commonly called pore, leading to interior of theca, fillings or casts of vertical canals commonly appearing as granules or short pegs on steinkerns of thecae. Tangential canals compound as a rule, 2 to 4 of them extending between paired pores. Tangential pore canals covered in well-preserved specimens by generally smooth epitheca of several thin laminae, each somewhat distinctively ornamented with concentric lines, probably growth lines. Brachiole facets upon peristomial or oral projection, which in many forms is emphasized by slight constriction giving oral field appearance of small platform resting upon neck. Ambulacra commonly arranged in triradiate or tetraradiate pattern, although specimens have been figured and reported with only 2 brachioles attached to facets at each end of narrow peristomial-ambulacral series of plates; ambulacra short, facets distinct, rimmed concavities; number of brachioles not constant within a species. Anal pyramid in upper part of theca, closed by variable number of triangular plates. Gonopore rounded to triangular, about half diameter of anal pyramid, closed by few valvular plates in form of flat pyramid; gonopore offset to right from line connecting mouth and anal pyramid; relative spacing of mouth, anal pyramid, and gonopore fairly constant within a species. Remnants of feeble column known, most thecae without any column; few circlets of plates adjacent to base more regularly disposed than other plates. [The subequal- and unequal-plated forms within a species have been interpreted (99) as individuals that "have attained a certain degree of stability as to the increase of the skeleton" and others that are expanding by "abundant growth of new plates." The type species, *E. aurantium*, and closely allied forms have been recorded from many areas in Sweden, where they are exceedingly abundant in many strata, and from Yunnan, USSR, Estonia, Norway, Poland, northern Germany, Great Britain, and the United States (Pa., Va., Tenn.). *L.Ord.-U.Ord.*, Asia (Burma-China) - Eu.(USSR-Est.-Sweden-Norway-Pol.-Ger.-Belg.-Brit.-Boh.)-N.Am. (USA).——Fig. 132,*2*. **E. aurantium* (Gyllenhaal); *2a,* reconstr., ×1 (10); *2b,* reconstr., ×1 (69); *2c-e,* oral regions, 3 specimens, showing different numbers of brachiole facets, enl. (69); *2f,g,* oral and lat., ×1 (31). [See also Fig. 33,*1*; 37,*3*.]

Arachnocystites Neumayr, 1889, p. 403 [**Echinosphaerites infaustus* Barrande, 1887, p. 155] [=*Arachnocystis* Bather, 1889, p. 268 *(nom. van.)*]. Theca subpyriform, strongly inflated adorally and tapering to unique prolonged, thin, stemlike section of alternating rows of tiny hexagonal plates; most other plates small, so that theca contains 200 to 800, but few larger plates interspersed; very few plates in main part of theca hexagonal. Pore canals like those of *Echinosphaerites,* of which this genus was considered synonym by Jaekel (69) and Gekker (53). Periproct in upper half of theca, filled by anal pyramid. Gonopore somewhat offset from line connecting anal pyramid and mouth. Mouth in peristomal projection, with 2 or 3 brachioles springing more or less directly from it, with little or no development of ambulacra. *M.Ord.*, Eu.(Boh.).——Fig. 132,*1*. **A. infaustus* (Barrande); *1a,* lat., reconstr., ×1; *1b,* long section of column, ×1 (69); *1c,d,* lat., 2 specimens, ×1; *1e,f,* enlarged sections along and through pore canals; *1g-k,* enlarged parts of thecal plates in various stages of exfoliation (3).

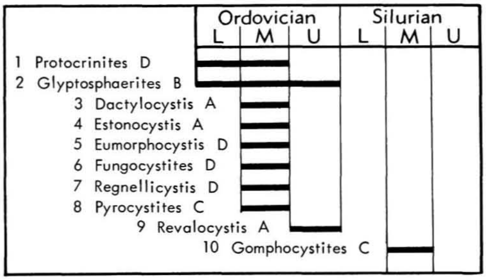


FIG. 133. Stratigraphic distribution of genera belonging to the superfamily Glyptosphaeritida. Classification of the genera in families is indicated by letter symbols: A—Dactylocystidae, B—Glyptosphaeritidae, C—Gomphocystitidae, D—Protocrinitidae. The following alphabetical list of genera furnishes cross reference to the serially arranged numbers on the diagram (Kesling and Moore, n).

Order DIPLOPORITA Müller, 1854

[*nom. correct.* BATHER, 1899, p. 920 (*pro* Diploporiten MÜLLER, 1854, p. 249)] [=Diploporitidées EICHWALD, 1860, p. 616; Gemellipora ANGELIN, 1878, p. 30]

Thecal pores developed as units mostly confined to single plates, typically in form of diplopores but in some present as haplopores. *L.Ord.-L.Dev.*

Thecal plates in the majority of these cystoids are irregularly arranged, but the Asteroblastida contain some genera with regularity approaching that of the Glyptocystitida in the Rhombifera.

The thecal pores tend to be confined to ambulacral plates in the Glyptosphaeritida and to special interambulacral plates in the Asteroblastida. Pores are small and very numerous in the Glyptosphaeritida and Sphaeronitida but relatively large and few in most of the Asteroblastida.

A column is never strongly developed. It is absent in adults of nearly all Sphaeronitida and some Glyptosphaeritida. It is small in the Asteroblastida.

Superfamily GLYPTOSPHAERITIDA Bernard, 1895

[*nom. transl. et correct.* KESLING, herein (*ex* Glyptosphaeridés BERNARD, 1895, p. 204)] [=order Seriolata JAEKEL, 1918, p. 101 (*nom. neg.*)]

Diplopore-bearing cystoids with globular, ovate, pear-shaped, or saclike thecae. Ambulacra radial, extending over theca, with alternating lateral branches (single or in groups) leading to brachiole facets; in many genera, ambulacra bordered by alternating "adambulacrals" on which facets are located. Diplopores invariably present on ambulacra-bearing plates, in some forms also in the interambulacral areas. Most with column, a few molting column as adults. *L.Ord.-M.Sil.*

The stratigraphic distribution of genera belonging to the Glyptosphaeritida is shown in Figure 133.

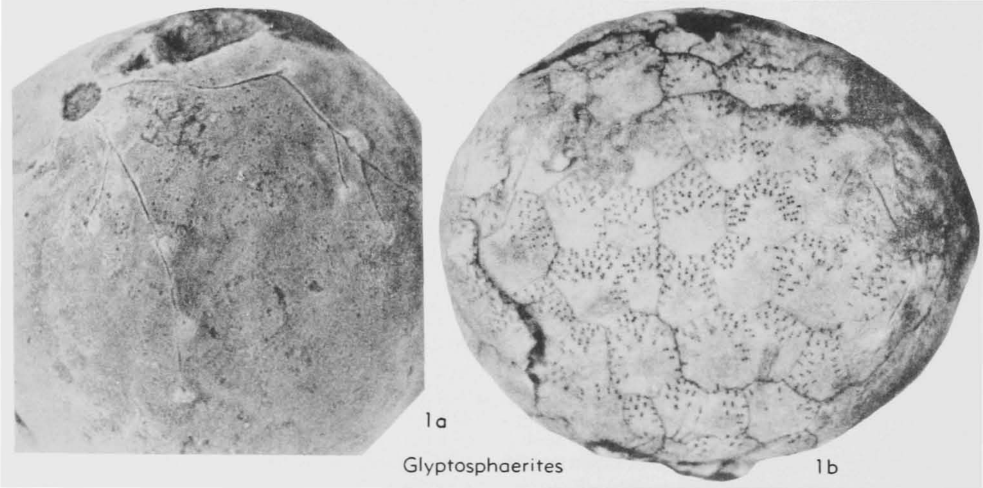


FIG. 134. Glyptosphaeritidae (p. S235).

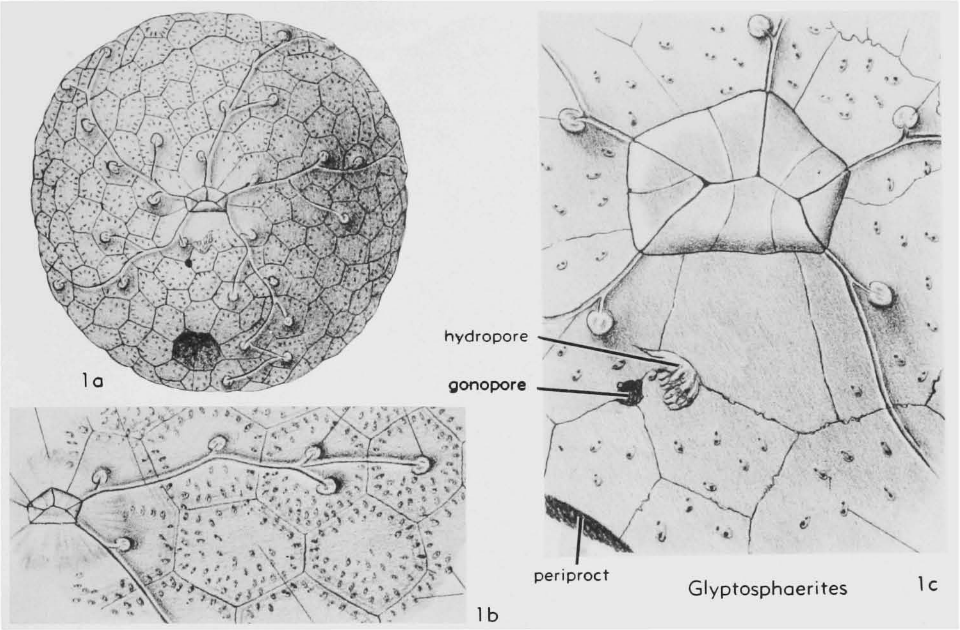


Fig. 135. Glyptosphaeritidae (p. *S*235).

Family GLYPTOSPHAERITIDAE Bernard, 1895

[*nom. correct.* Bassler, 1938, p. 12 (*pro* Glyptosphaeridés Bernard, 1895, p. 204)] [=Glyptosphaeridae Bather, 1899, p. 920]

Theca apple-shaped, thin-walled. Short column present. Oral region pentagonal, with peristomial covering plates displaying nearly perfect trimerous fivefold suture pattern, one suture aligned with each ambulacrum; other thecal plates irregularly polygonal, numerous. Diplopores distributed over theca except in oral region, some more or less radially oriented. Ambulacral grooves narrow, each branching to few irregularly alternating small brachiole facets. *L.Ord.-U.Ord.*

Glyptosphaerites Müller, 1854, p. 186 [**Sphaeronites leuchtenbergi* Volborth, 1846, p. 187] [=*Glyptosphaera* Angelin, 1878, p. 31 *(nom. van.)*; *Glyptosphora* Scudder, 1882, p. 145 *(nom. null. pro Glyptosphaera)*]. Theca large in some species, attaining size as well as shape of apple, with oral half hemispherical and aboral half indented at junction with column. Ambulacra normally slightly arcuate, groove very narrow and radiating over thecal plates without reference to plate boundaries; most ambulacra curved slightly clockwise, with first branch on left and other branches alternating, but pattern of branching somewhat irregular, particularly in distal part. Brachiole facets small, not strongly developed, only about 6 or 7 in each ambulacrum, rarely found on aboral half of theca. Periproct rather large, situated in posterior interambulacrum, provided with valvular pyramid. Diplopores in some forms concentrated in adoral parts of thecal plates, absent in oral region; each diplopore in simple elliptical depression. Hydropore 3-cornered, spongy and not solidly skeletonized, located between periproct and peristome; gonopore a small circular perforation to left and aboral to hydropore. *L.Ord.-U.Ord.*, Eu.(USSR-Sweden-N.Ger.-Boh.).——Fig. 134,*1*; 135,*1*. **G. leuchtenbergi* (Volborth), L.Ord.(*Platyurus* Ls.), Sweden (134,*1*); L.Ord., USSR (135,*1*); 134,*1a*, inclined oral, ×2.5; 134,*1b*, lat. showing distribution of diplopores, ×2.5 (99); 135,*1a*, oral, adult, ×1; 135,*1b*, peristome and ambulacrum, ×3; 135,*1c*, oral region of juvenile, ×6 (69). [See also Fig. 44,*1*.]

Family DACTYLOCYSTIDAE Jaekel, 1899

[Dactylocystidae Jaekel, 1899, p. 425] [=Estonocystidae Jaekel, 1918, p. 101]

Theca oviform to pear-shaped, thick-plated, with or without column. Ambulacra five, long, straight, pentamerally arranged, vertical; numerous brachioles, at ends of short, very regularly alternating branches, so that those on each side of an

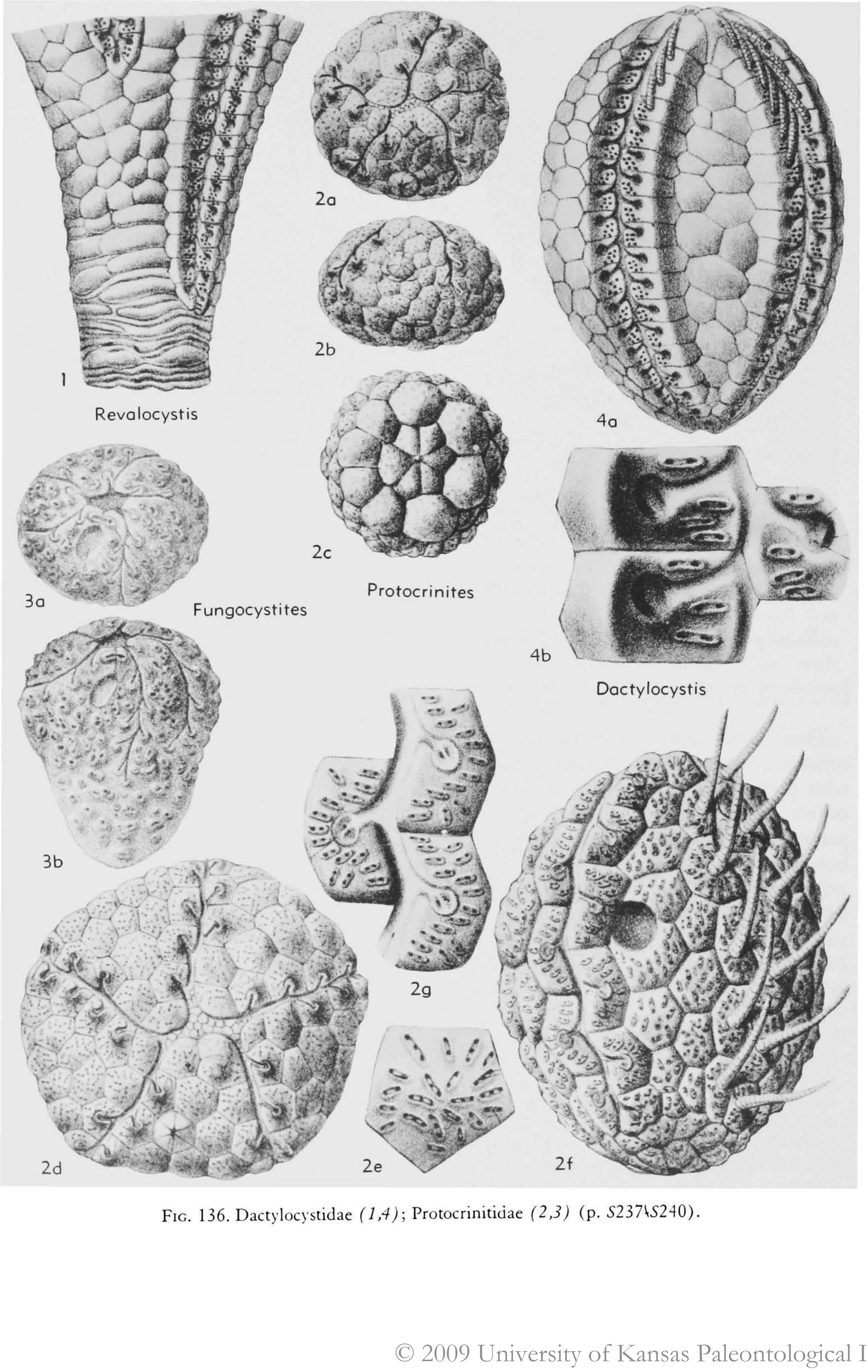


Fig. 136. Dactylocystidae *(1,4)*; Protocrinitidae *(2,3)* (p. S237-S240).

ambulacrum are aligned. Diplopores restricted to brachiole-bearing plates or "adambulacrals," which regularly alternate in paired vertical rows. Interambulacral plates irregularly arranged, without diplopores. Periproct large, circular, at mid-height. *M. Ord.-U.Ord.*

This family displays much higher regularity and symmetry than other families assigned to the superfamily Glyptosphaeritida. Its strong pentamerism might be compared with that in the Asteroblastida, but the ambulacra do not terminate on plates that can be classed as *RR,* the brachiole-bearing "adambulacrals" are not as highly developed, and the diplopores occur in the ambulacral areas rather than interambulacral. The restriction of diplopores to different areas of the theca may be regarded as evidence of extensive divergence.

Key to Genera of Dactylocystidae

1. Theca pear-shaped, gradually tapering to broad column; ambulacra of unequal length .... *Revalocystis*
   Theca ovate or ellipsoidal, distinctly set off from column; ambulacra of equal length 2
2. Each ambulacral area of two long, vertical rows of alternating large irregular-shaped plates, each of which has one large and several small brachiole facets with diplopores between ambulacral extensions; each interambulacral area with one vertical row of plates of irregular shape .... *Estonocystis*
   Each ambulacral area of two long, vertical rows of alternating small, transversely elongate plates, each of which has only one brachiole facet and bears diplopores; each interambulacral area filled with irregular plates, not arranged in vertical row and some larger than ambulacral plates, entire area depressed ....*Dactylocystis*

Dactylocystis Jaekel, 1899, p. 434 [**D. schmidti;* OD] [=*Proteroblastus* Jaekel, 1895, p. 116 *(nom. nud.)*]. Theca ovate to ellipsoidal, with strong pentameral symmetry, distinctly set off from thin column. Ambulacra of equal length, branching with precise regularity to alternating brachiole facets, one on each "adambulacral." Brachiole-bearing "adambulacrals" small, hexagonal, transversely elongate plates, elevated and distinct from interambulacral plates, set in 2 vertical rows, one on each side of straight ambulacrum; diplopores restricted to these plates. Each diplopore with 2 openings at opposite ends of narrow groove surrounded by thin rim, diplopores tending to be aligned horizontally and confined to area between brachiole facets. Interambulacral plates irregular, polygonal, some larger than "adambulacrals," set in elongate, lanceolate, depressed area. Brachioles small and short, their length not exceeding one-fourth diameter of theca. *M.Ord.,* Eu.(Est.).——Fig. 136,*4.* **D. schmidti; 4a,* lat., ×3; *4b,* part of ambulacrum enl. to show diplopore arrangement (69). [See also Fig. 33,*6*.]

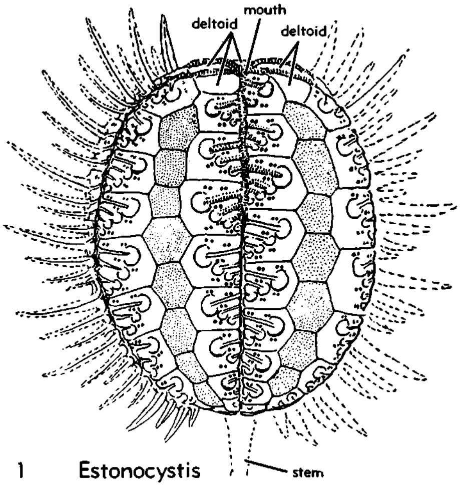


Fig. 137. Dactylocystidae (p. *S*237).

Estonocystis Jaekel, 1918, p. 101 [**E. antropoffi;* OD] [=*Esthonocystis* Chauvel, 1941, p. 122 *(nom. van.)*]. Theca ovate, distinct from narrow column. "Adambulacrals" large, with irregular borders against interambulacral plates but with horizontal, parallel upper and lower sides, alternating along sides of each long, straight, meridional ambulacrum. Each adambulacral containing one large and a few small brachiole facets, so that facets alternate by clusters, rather than individually. Diplopores confined to area between ambulacral extensions leading to brachiole facets. Interambulacral areas each with one vertical row of irregularly polygonal plates, many of which are hexagonal, none exceeding "adambulacrals" near middle of theca. *M.Ord.,* Eu.(Est.).——Fig. 137. **E. antropoffi,* Jewe F., lat., reconstr., ×3 (71).

Revalocystis Jaekel, 1918, p. 101 [**Dactylocystis mickwitzi* Jaekel, 1899, p. 436]. Theca pear-shaped, gradually tapering into the column. Adambulacra of unequal length. Ambulacra, "adambulacrals," and diplopores like those in *Dactylocystis. U.Ord.,* Eu.(Est.).——Fig. 136,*1.* **R. mickwitzi* (Jaekel); aboral end of theca, ×2 (69).

Family PROTOCRINITIDAE Bather, 1899

[*nom. correct.* BASSLER, 1938, p. 12 (*pro* Protocrinidae BATHER, 1899, p. 920)]

Theca saclike, bullet-shaped, subcylindrical, ovate or spherical, composed of numerous plates, mostly irregularly arranged. Diplopores on ambulacral and interambulacral plates alike. Ambulacra extending radially from peristome, with short branches to brachiole facets more or less alternating. Column in young specimens, may be lost in adults. Thecal plates bearing ambulacra rather regularly alternating, comprising so-called "adambulacrals." *L.Ord.-M.Ord.*

The Protocrinitidae can be distinguished from related Glyptosphaeritidae by their more numerous brachioles, which have facets set at ends of short, more or less alternating branches along each ambulacrum, rather than at ends of long, irregular branches. They can be differentiated readily from the Dactylocystidae by presence of diplopores on interambulacral, as well as ambulacral, plates. The shape of the theca alone serves to separate the Protocrinitidae from the pear-shaped, aborally produced Gomphocystidae.

BRANSON & PECK (26) created the family Eumorphocystidae for their genus *Eumorphocystis,* distinguishing it from the Protocrinitidae on the basis of shorter ambulacra, differentiated *BB, RR,* and *OO,* and more perfect symmetry. They stated, "An alternate procedure would be to emend the definition of the Protocrinitidae to include this genus." Until additional cystoids of the group are known, the alternative seems advisable.

The specimen described by BASSLER (6) as a new species, genus, and family, does not afford justification for his Regnellicystidae. *Regnellicystis* is more closely related to *Eumorphocystis* than to *Protocrinites.*

Key to Genera of Protocrinitidae

1. Theca composed of several hundred tiny plates; 4*BB* much larger than adjacent plates, imperforate, conspicuous; column present in adult 2

   Theca composed of less than 200 plates; no special *BB,* at least in adult specimens; column not developed or not retained in the adult 3

2. Theca elongate; ambulacra terminating on platforms of special flooring plates set upon large thecal plates possibly qualifying as *RR* .... *Eumorphocystis*

   Theca ovate, rotund; ambulacra not extending to raised structures, no thecal plates differentiated as *RR* .... *Regnellicystis*

3. Theca saclike; ambulacra zigzag; theca attached by broad base, typically concave; few diplopores, not more than four to a plate and mostly one or two to a plate .... *Fungocystites*

   Theca ovate to spherical; ambulacra nearly straight or slightly curved, not zigzag, with short lateral alternating branches to brachioles; theca attached by column when young, free when adult; numerous diplopores, several to each plate .. *Protocrinites*

Protocrinites EICHWALD, 1840, p. 185 [**P. oviformis;* OD] [=*Protocrinus* BRONN, 1848, p. 1047 *(nom. van.)*]. Theca ovate to spherical, composed of numerous subpolygonal tumid plates. Column present in young individuals, attached to blunt cone of 4 *BB*; adults free, *BB* modified, no longer differentiated from adjacent plates. Diplopores numerous, present on all plates, those on "adambulacrals" tending to be oriented normal to ambulacrum. Ambulacra 5, well developed, radiating, slightly curved, diverging from trimerous peristome as rather deeply embedded grooves from which short grooves alternate to brachiole facets; ambulacra extend between alternating thecal plates called "adambulacrals," each of which bears a brachiole facet. Periproct filled by low anal pyramid of 6 triangular pieces, located in posterior interambulacrum well away from mouth. [YAKOVLEV (146) reported that in the posterior oral region of *P. fragum* are 3 plates, 2 of which are large, situated 1 on each side, and meeting on their adoral sides at a short meridional suture; aboral to this suture, the 2 diverge to accommodate the apex of the third plate, considerably smaller; the hydropore is shared by the small plate and the large plate on the right, whereas the gonopore is shared by the small plate and the large plate on the left. The side-by-side arrangement of hydropore and gonopore in *Protocrinites* was considered by YAKOVLEV (146) strongly to resemble that of *Glyptosphaerites,* in contrast to that of the Rhombifera, in which the gonopore is aboral to the hydropore. Ambulacra tend to curve clockwise, as viewed orally, with 1 or 2 brachiole facets missing in the proximal region of the concave side of each ambulacrum.] *L.Ord.-M.Ord.,* Eu. (USSR-Est.-Scand.-Ger.)-Asia (Burma).——FIG. 136,*2f,g.* **P. oviformis,* Est.; 136,*2f,* lat. ×1; 136,*2g,* 3 adambulacrals and brachiole facets, enl. (69). [See also Fig. 47,*1-3.*]——FIG. 136,*2a-e. P. fragum* (EICHWALD), L.Ord.(*Vaginatum* Ls.), Est.; 136,*2a-c,* oral, lat., and aboral, small speci-

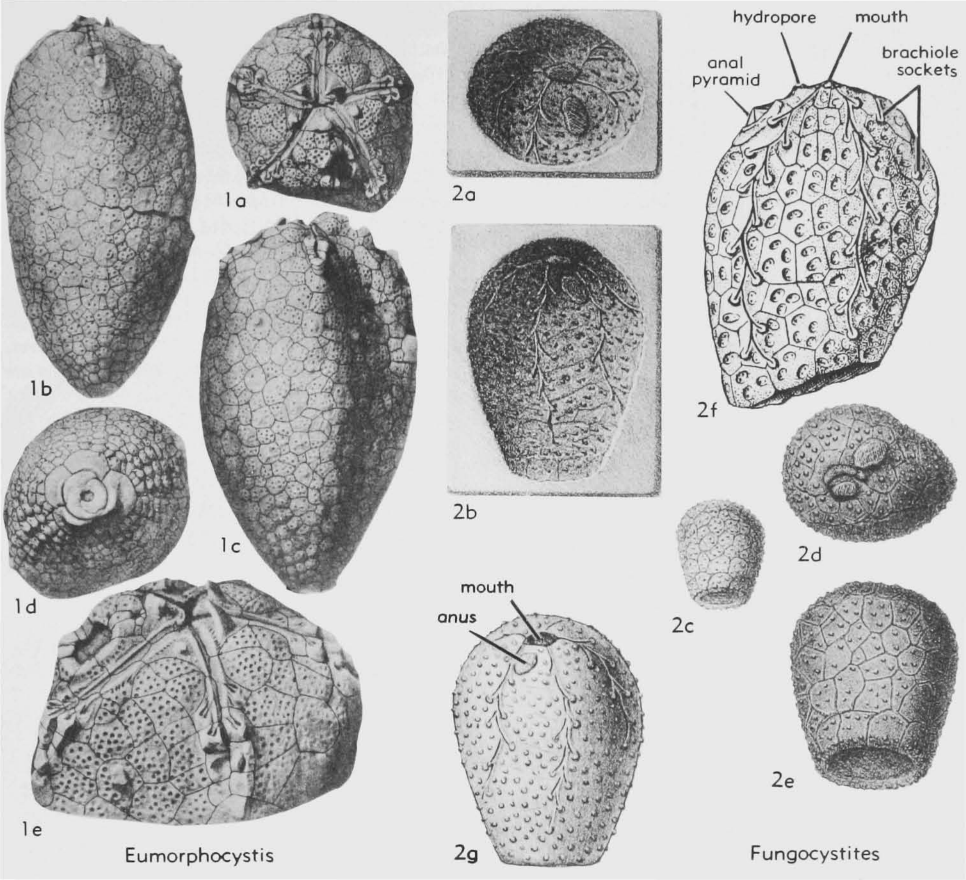


FIG. 138. Protocrinitidae (p. *S*239-*S*240).

men, ×1; 136,*2d,* oral, large specimen, ×1; 136,*2e,* thecal plates enl. to show diplopores (69). [See also Fig. 46.]

Eumorphocystis BRANSON & PECK, 1940, p. 89 [*E. *multiporata;* OD]. Theca elongate, subcylindrical, tapering to junction with column, composed of several hundred tiny plates. *BB* 4, much larger than adjacent plates, imperforate, indented to form facet for column; 5 large *OO,* imperforate, each a triangular sector of pentagon. Ambulacra equally spaced, nearly straight, confined to uppermost quarter of theca; each ambulacrum passing between alternating thecal plates called "adambulacrals" (not homologous with adambulacrals or other echinoderms), terminating on platform of small plates resting upon large thecal pore-bearing plates called *RR.* Other thecal plates irregular polygons, 1 to 3 mm. in diameter; all but smallest bearing diplopores, most with many (some with 15); scattered over the theca, but mostly in aboral third, are plates with few diplopores, some with only 1. Periproct between posterior ambulacra, set rather high on theca; small opening between periproct and mouth, probably hydropore. Six to 8 brachiole facets on each ambulacrum, more or less alternating, set at ends of very short ambulacral branches, facets starting well beyond *OO.* Mouth oblong, slightly curved around edge of *O1* (oral in posterior interambulacrum). *M. Ord.,* USA (Okla.).——FIG. 138,*1.* *E. *multiporata; 1a-d,* oral, 2 lat., and aboral; ×1; *1e,* oral region, ×2 (26).

Fungocystites BARRANDE, 1887, p. 157 [*F. *rarissimus;* OD] [=*Fungocystis* HAECKEL, 1896, p. 104 *(nom. van.)*]. Theca saclike, base broad and typically concave for attachment to some object. Thecal plates irregularly polygonal, each bearing few diplopores (mostly 1 or 2, never more than 4). Ambulacra zigzag, extending nearly to base, with branches extending from each angle in line with main groove, about 9 to 12 brachiole facets to each ambulacrum. Periproct closed by anal pyramid, set in adoral part of theca but well away from peristome; small circular hydropore between

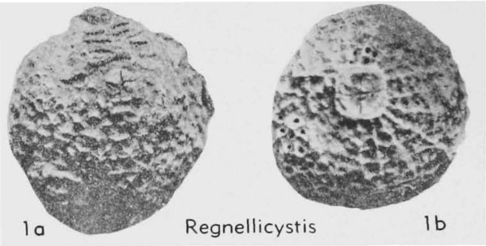


FIG. 139. Protocrinitidae (p. S240).

periproct and mouth. *M.Ord.*, Eu.(Boh.).——FIG. 136,*3*; 138,*2*. **F. rarissimus*; 136,*3a,b*, oral and lat., ×2 (69); 138,*2a,b*, oral and lat., ×2; 138,*2c*, lat., steinkern, ×1; 138,*2d,e*, oral and lat., steinkern, ×2 (3); 138,*2f*, lat., enl. (10); 138,*2g*, lat., reconstr. with surface of plates based on steinkerns and ambulacra superimposed (69).

Regnellicystis BASSLER, 1950, p. 276 [**R. typicalis*; OD]. Theca ovate to subglobular, with 4 distinct large *BB* and exceptionally small thecal plates more or less radially disposed, each divided into small compartments by sharp ridges, with single large diplopore in each compartment. Anal pyramid filling periproct near top. Peristome bearing 5 "simple food grooves extending to the lower level of the pyramid and lines with thin flat brachioles." *M.Ord.*, USA(Va.).——FIG. 139,*1*. **R. typicalis*, Blackriv.; *1a,b*, lat. and aboral, ×2 (6).

Family GOMPHOCYSTITIDAE Miller, 1889

[*nom. correct.* BASSLER, 1938, p. 12 (*pro* Gomphocystidae S. A. MILLER, 1889, p.215)]

Theca shaped like inverted pear, tapering aborally, no true column known. Ambulacra five, spiraled clockwise from oral apex and not extending below mid-height of globular portion of theca; branches, if present, only from left side of ambulacra. Diplopores in open oval pits. *M.Ord.-M.Sil.*

Key to Genera of Gomphocystitidae

Thecal plates along ambulacra regularly arranged in alternating pattern ("adambulacrals") .... *Gomphocystites*

Thecal plates along curved ambulacra irregular, without pattern .... *Pyrocystites*

Gomphocystites HALL, 1865, p. 309 [**G. glans* HALL, 1864, p. 6; OD] [=*Gomphocystis* ANGELIN, 1878, p. 31 (*nom. van.*)]. Theca bulb-shaped, pear-shaped, or pestle-shaped, according to proportions and relative sizes of globose oral and tapering aboral sections. Plates along spiral ambulacra alternating as "adambulacrals"; other thecal plates irregularly polygonal. Periproct and hydropore very near peristome. *M.Sil.*, Eu.(Sweden)-N. Am. (Wis.-Ill.-Ind.-Ohio-Ky.-N.Y.-Calif.).——FIG. 140,*1b*. **G. glans* (HALL), Racine Dol., USA (Ill.); lat., ×1 (69).——FIG. 140,*1e-h*. *G. bownockeri* FOERSTE, Cedarville Dol., USA(Ohio); *1e-h*, oral and 3 lat., ×0.8 (49).——FIG. 140,*1a*. *G. gotlandicus* ANGELIN, Sweden(Gotl.); oral, ×1 (69).——FIG. 140,*1i,j*. *G. indianensis* MILLER, Osgood F., USA(Ind.); *1i,j*, 2 inclined lat., ×1 (49).——FIG. 140,*1c,d*. *G. tenax* HALL, Lockport F., USA(N.Y.); *1c,d*, oral and lat., ×1 (10).

Pyrocystites BARRANDE, 1887, p. 170 [**P. pirum*; OD] [=*Pirocystis* BATHER, 1889, p. 269 (*nom. van.*); *Pyrocistis* CARPENTER, 1891, p. 26 (*nom. van.*)]. Theca pear-shaped, all plates irregularly arranged. Ambulacra spiraled around theca without reference to thecal plate disposition, branches extending to left of main groove. Diplopores limited to middle parts of plates, narrow diplopore grooves each rimmed by strong wall, more peripheral diplopores approximately radially disposed. *M. Ord.*, Eu.(Boh.).——FIG. 140,*2*. **P. pirum*, Dd₁; *2a*, lat., steinkern, ×1 (3); *2b*, lat., ×2; *2c*, diplopores, enl. (69).

Superfamily SPHAERONITIDA Neumayr, 1889

[*nom. transl.* REGNÉLL, 1945, p. 161 (*ex* Sphaeronitidae ZITTEL, 1900, p. 182, *nom. correct. pro* Sphaeronitiden NEUMAYR, 1889, p. 412)] [*non* order Sphaeronita JAEKEL, 1918, p. 103]

Ambulacra short, either branching directly from angles of mouth and not extending far beyond peristomial region, or extremely short, or absent, with two to five brachioles set close to corners of mouth. Most forms attached by base of theca. Pores irregularly distributed over theca. *L.Ord.-L.Dev.*

Of all superfamilies, the Sphaeronitida is in the least satisfactory condition. It shows little uniformity in pore structure, shape of theca, or minor structures. Generic boundaries are not sharply drawn; quite probably, the genera described here contain several synonyms. Until these genera are clearly defined and adequately known, however, it seems advisable to continue all created taxa that might possibly qualify. Of the two indicated families, the Aristocystitidae contains the greater number of problems, as discussed later; these include interpretation of the poorly preserved materials and criteria for differentiating genera.

The stratigraphic distribution of genera belonging to the Sphaeronitida is shown in Figure 141.

Family SPHAERONITIDAE Neumayr, 1889

[*nom. correct.* Zittel, 1900, p. 182 (*pro* Sphaeronitiden Neumayr, 1889, p. 412)]

Theca typically spherical to ovoid. Ambulacra short, commonly preserved as grooves in thecal plates of oral region, branching directly (fan-wise) from corners of mouth; several brachioles in each ambulacral group. Anal pyramid well developed. Column small or absent. *L.Ord.-L. Dev.*

Key to Genera of Sphaeronitidae

[Not necessarily indicative of phylogenetic relationships]

1. Anal pyramid set adjacent to orals (plates covering peristome) on summit of theca, modified so that one side fits against posterior oral plate; gonopore displaced to left of periproct-peristome junction .... *Sphaeronites*

Anal pyramid not adjacent to *OO*, although it may be high up on theca; gonopore, if present, directly between periproct and peristome or only slightly offset 2

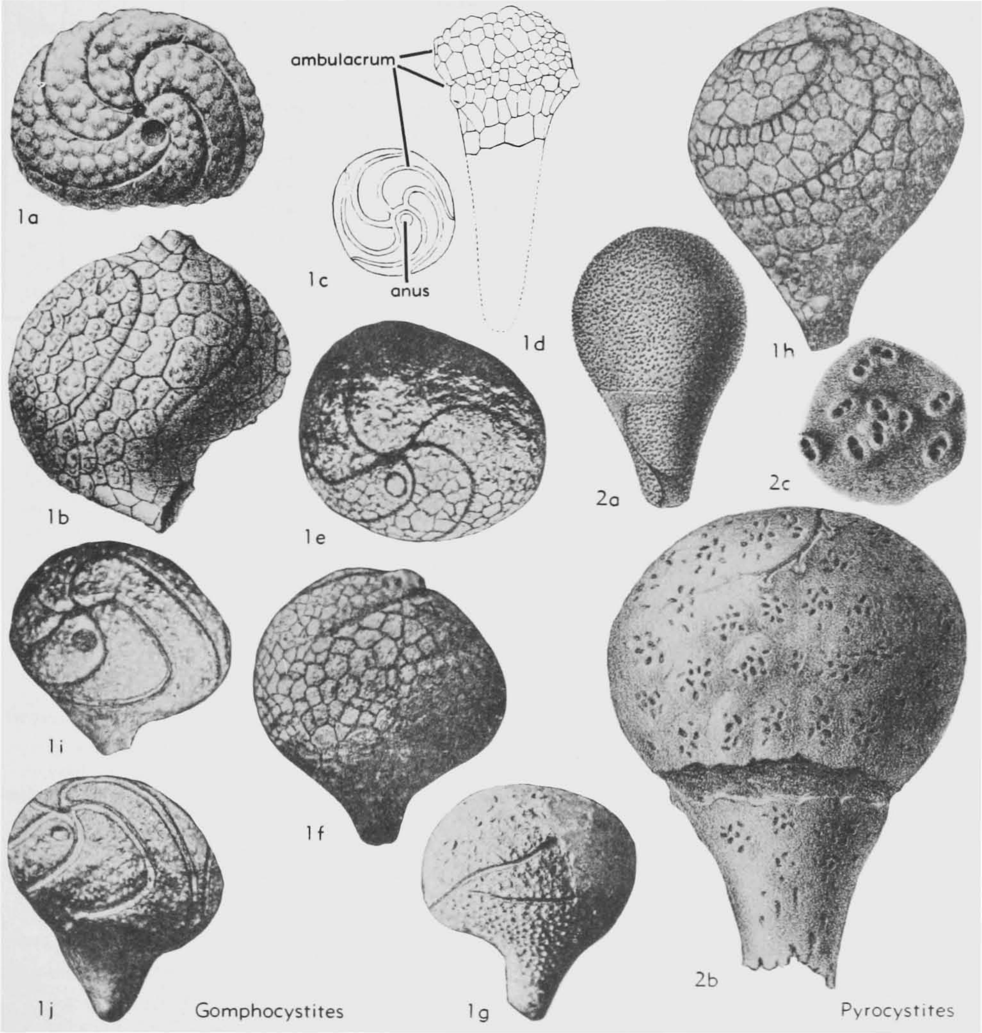


Fig. 140. Gomphocystitidae (p. S240).

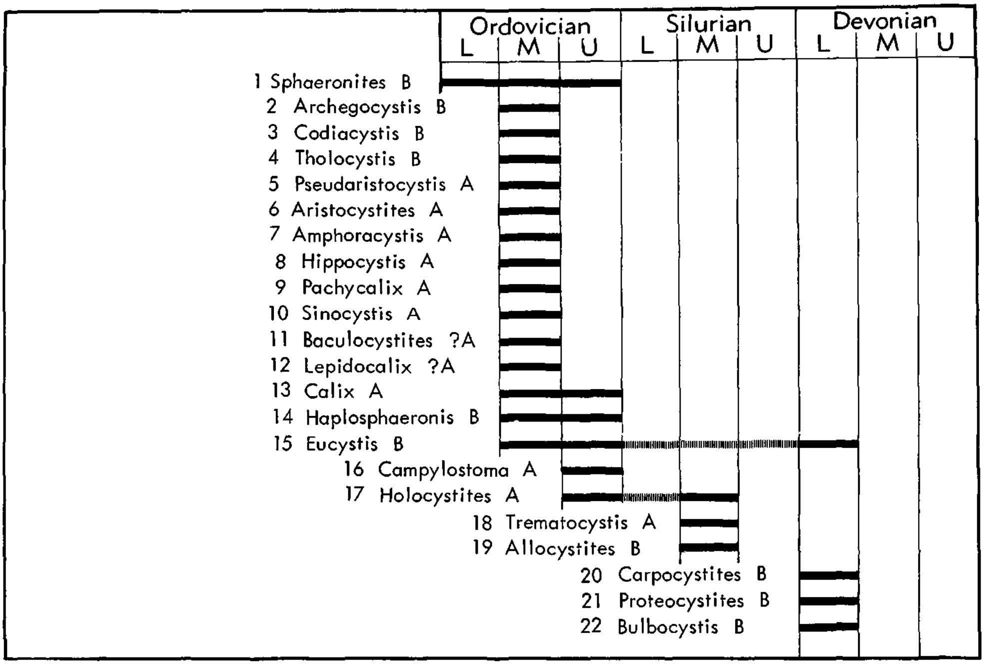


FIG. 141. Stratigraphic distribution of genera belonging to the superfamily Sphaeronitida. Classification of the genera in families is indicated by letter symbols: A—Aristocystitidae, B—Sphaeronitidae. The following alphabetical list of genera furnishes cross reference to the serially arranged numbers on the diagram (Kesling and Moore, n).

Generic Names of Sphaeronitida and Index Numbers

Allocystites—19
Amphoracystis—7
Archegocystis—2
Aristocystites—6
Baculocystites—11
Bulbocystis—22
Calix—13
Campylostoma—16
Carpocystites—20
Codiacystis—3
Eucystis—15
Haplosphaeronis—14
Hippocystis—8
Holocystites—17
Lepidocalix—12
Pachycalix—9
Proteocystites—21
Pseudaristocystis—5
Sinocystis—10
Sphaeronites—1
Tholocystis—4
Trematocystis—18

2. All or nearly all branches of each ambulacrum confined to single adoral plate (at most, one may extend beyond) 3
   Some branches of each ambulacrum extending beyond adoral plate 9
3. Relatively few thecal plates (less than 50 .. 4
   Numerous thecal plates (over 50, some with several hundred) 6
4. Theca tapering to small aboral area; plates highly irregular; peristome apparently raised above general level of theca *Allocystites*
   Theca typically conical with flat base, some dome-shaped; ring of plates forming base, conical oral part undivided; peristome elevated .... *Paleosphaeronites*
   Theca ovate to spherical; plates rather regular; peristome not elevated 5
5. Theca with three to five circles of plates; diplopores not very numerous, large, mostly limited to adoral half of theca *Eucystis*
   Theca with two circles of plates, lower one of seven plates and upper one of five; diplopores numerous, distributed over theca .... *Haplosphaeronis*
6. Thecal plates vermiculate, with diplopores in troughs; spherical theca said to have stem .... *Carpocystites*
   Thecal plates not highly ornamented, having only simple depressions for diplopores; stem unknown 7
7. Theca with shape of kettle, resting on its broad base; numerous brachioles at or near periphery of star formed by ambulacra .... *Tholocystis*
   Theca ovoid to saclike; brachioles connected to mouth by short ambulacral branches 8
8. Each ambulacrum primarily bifurcated with further divisions leading to seven or eight brachiole facets nearly in row and equally spaced from center of mouth; thecal plates thick .... *Codiacystis*

Each ambulacrum at end of straight suture between two of five peristomial covering plates, subdivided into five to seven short branches with clockwise curvature, brachiole facets not aligned in row; theca weakly calcified .... *Archegocystis*

9. Ambulacra somewhat irregular, not strongly developed; no definite number of brachioles .... *Proteocystites*

Ambulacra very regular, well developed; definite number of brachioles, five facets at corners of mouth and five others at periphery of adoral part of theca .. *Bulbocystis*

Sphaeronites Hisinger, 1828, p. 185 [**Echinus pomum* Gyllenhaal, 1772, p. 242; OD] [=*Sphaeronis* Angelin, 1878, p. 30 *(nom. van.)*; *?Pomonites* Haeckel, 1896, p. 96 (type, *P. pentactea, sp. hypoth.?)*]. Theca more or less round, attached by basal surface (many specimens preserving imprint of objects to which attached), or tapering aborally to form broad stemlike prolongation. Thecal plates numerous (as many as several hundreds), pierced by abundant diplopores within suboval to polygonal peripores with more or less raised margins; in some thecal plates bearing reticulation of low ridges with pair of pores within each polygon thus outlined. Periproct separated from mouth only by narrow bar made by extensions of 2 plates, one from each side; periproct and mouth so closely set that anal pyramid is tangent to orals or peristomial covering plates. Mouth pentagonal, with long posterior border, roofed by 5 orals, of which *O1* is largest. Ambulacra very short, brachiole facets set practically at angles of mouth, with 1 to 3 facets per ambulacrum. Major thecal opening through protuberance at left of anal pyramid and near mouth is interpreted as gonopore by Lovén (80) and Angelin (1), as hydropore by Bather (10, fig. 38), and as combined gonopore and hydropore by Bather (10, p. 72) and Regnéll (99); illustrated by Angelin (1) as having tiny pyramid of 3 pieces. Specimens of this genus so numerous in certain strata as to constitute major rock-forming deposits. *L.Ord.-U.Ord.*, Asia(China)-Eu.(USSR-Sweden-Norway-Eng.-Wales-Italy).——Fig. 142, *1a,b*. **S. pomum* (Gyllenhaal), M.Ord.(*Asaphus* Ls.), Sweden; *1a*, diagram of oral region, enl. (10); *1b*, thecal plates, ×2.5 (99).——Fig. 142, *1c-f*. *S. globulus* (Angelin), M.Ord.(L. *Chasmops* Beds), Sweden; *1c,d*, oral region in diagram (×5) and photograph (×7) (99); *1e*, lat., ×1 (10); *1f*, lat., small specimen, ×2.5 (99).

Allocystites S. A. Miller, 1889, p. 222 [**A. hammelli;* OD] [=*Allocystis* Bather, 1900, p. 72 *(nom. van.)*]. Theca ovate, slightly elongate aborally, there tapered to small area, probably site of attachment to narrow column. Thecal plates highly irregular and unequal, with no definite arrangement, forming approximately 6 series from base to peristome, all poriferous according to author. Flared, phialine oral projection on which thick circumoral plates make platform. Hydropore a long transverse slit between periproct and mouth. Brachiole facets and ambulacra unknown, casting doubt on taxonomic assignment; oral projection strongly resembling that in rhombiferan *Echinosphaerites*. *M.Sil.*, USA(Ind.).——Fig. 143, *4*. **A. hammelli; 4a,b*, oral and lat., ×1? (85).

Archegocystis Jaekel, 1899, p. 395 [**Pyrocystites? desideratus* Barrande, 1887, p. 172; OD]. Theca rounded adorally, composed of numerous small, weakly calcified plates, surface appearing leathery. From each of 5 corners of peristome, 5 to 7 short, subequal, curved (clockwise) branches spread fanwise with brachiole facet at end of each ("hydrophores palmées" of Barrande, 3); all brachiole facets within boundaries of circumoral circlet of plates. Anal pyramid apart from peristome, in adoral part of theca. Hydropore hatchet-shaped, at short distance from mouth; gonopore a small circular opening thereunder. Diplopores apparently without distinct depressions, surrounding ridges, or other markings to show their association, but 2 pores of each pair close-set. *M.Ord.*, Boh.——Fig. 142,*4*. **A. desiderata* (Barrande), Dd$_1$; *4a*, oral region, ×2.5 (3); *4b,c*, oral regions, 2 specimens (*I-V*, ambulacra corresponding to *D, E, A, B, C*, of Carpenter), ×2.5 (69).

?**Barbieria** Termier & Termier, 1950, p. 25 [**B. stitensis*; OD]. Theca known only from external mold of oral region. Peristome apparently pentagonal, composed of 5 sector-like plates arranged as in *Haplosphaeronis*; from each corner, few slightly curved, closely grouped ambulacral branches onto theca for distance about equal to width of peristome. Thecal plates small, numerous, said to imbricate, each provided with central tubercle. Hydropore, gonopore, and anal pyramid unknown. [Imbrication of thecal plates and presence of tubercles suggest possibility that this fossil may be primitive echinoid. The peristome is very different, however, from the periproct region of an echinoid, especially in presence of structures presumed to be ambulacral branches. From the mold of one fragment, close relationships impossible to determine, but probably this is a cystoid near *Proteocystites*, from which it differs in arrangement of ambulacral branches.] *M.Ord.*, N.Afr.(Alg.).——Fig. 144,*3*. **B. stitensis*; cast from external mold of oral region, ×2 (126).

Bulbocystis Růžička, 1939, p. 292 [**B. mirus*; OD]. Similar to *Proteocystites*, but ambulacra very regularly arranged, with 5 brachiole facets at angles of mouth and 5 others at periphery of adoral part of theca. *L.Dev.*, Boh.—Fig. 144,*4*. **B. mirus* Růžička; oral diagram, ×5 (95a).

Carpocystites Oehlert, 1887, p. 67 [**C. soyei;* OD] [=*Carpocystis* Bather, 1889, p. 73 *(nom. van.)*]. Theca spherical, attached to small column, containing many plates. Surface of theca ornamented

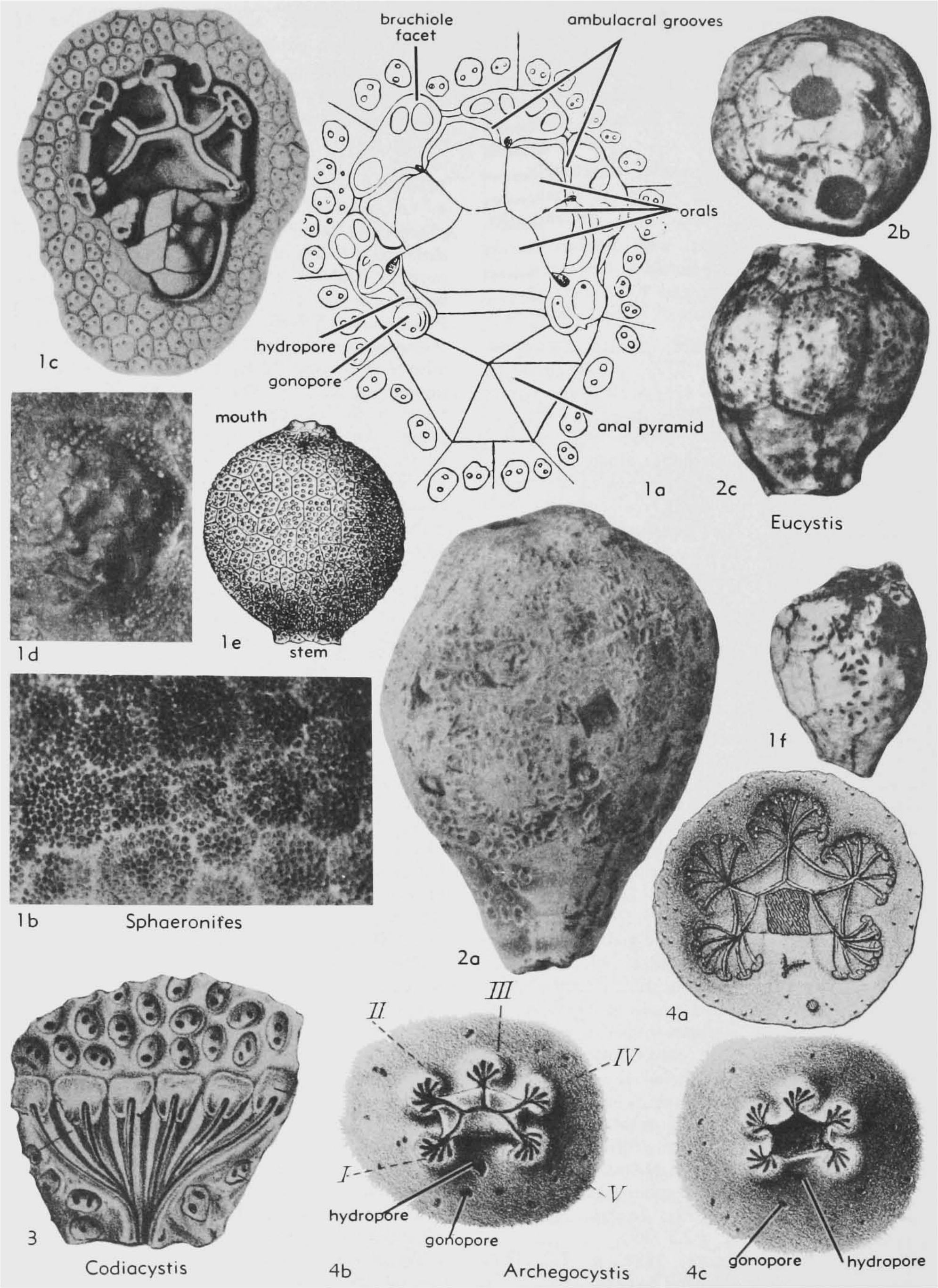


FIG. 142. Sphaeronitidae (p. S243, S245, S247).

with vermicular ridges separated by grooves or troughs wherein diplopores are found. *Carpocystites* and *Proteocystites* regarded by REGNÉLL (99) as junior synonyms of *Eucystis*. *L.Dev.*, Fr.

Codiacystis JAEKEL, 1899, p. 398 [*nom. subst. pro Craterina* BARRANDE, 1887 (*non* BORY, 1826; *nec* CURTIS, 1826, *nom. van. pro Crataerina* OLFERS, 1816; *nec* GRUBER, 1884)] [**Craterina bohemica*

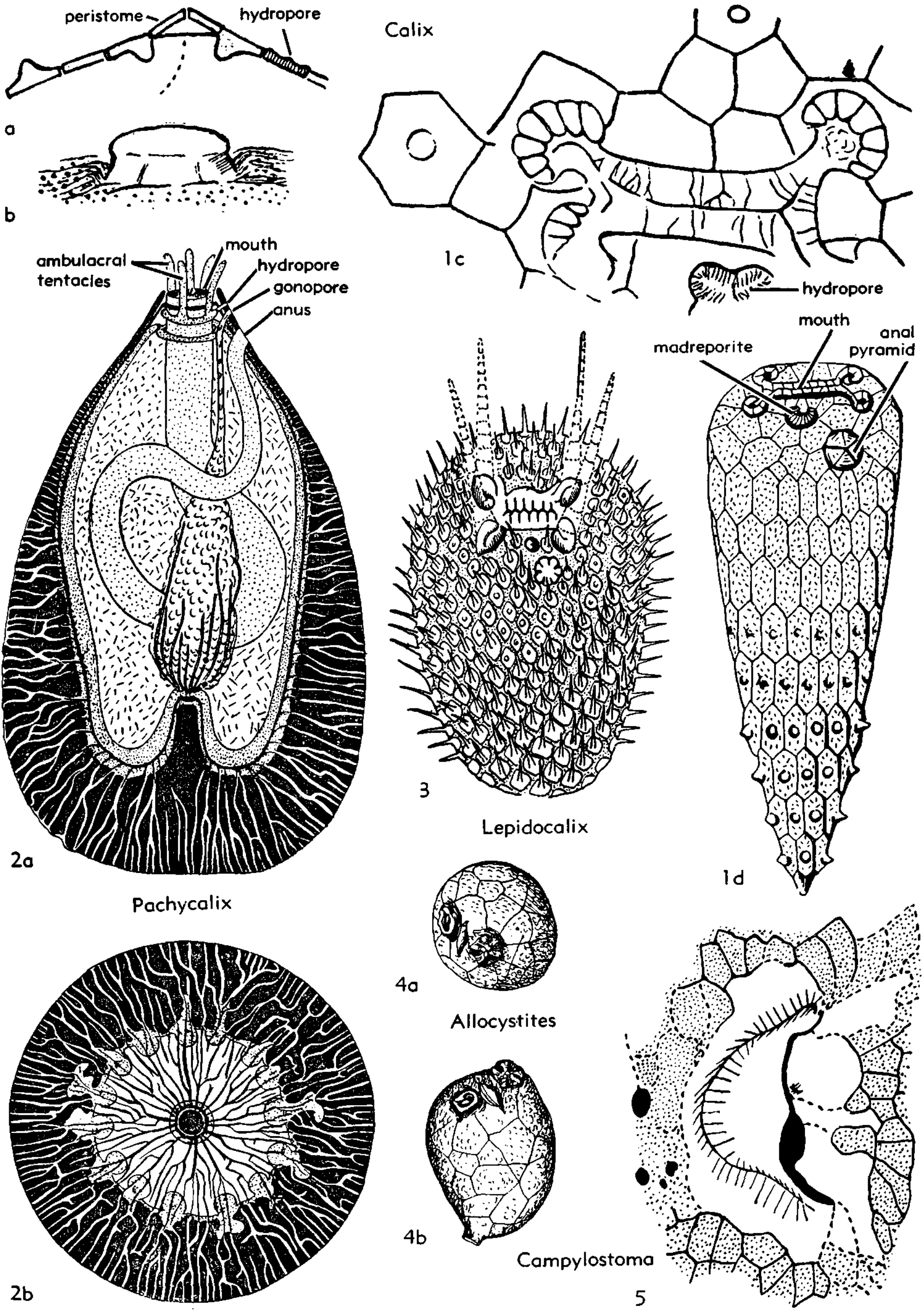


FIG. 143. Aristocystitidae *(1-3,5)*; Sphaeronitidae *(4)* (p. S243, S254-S256).

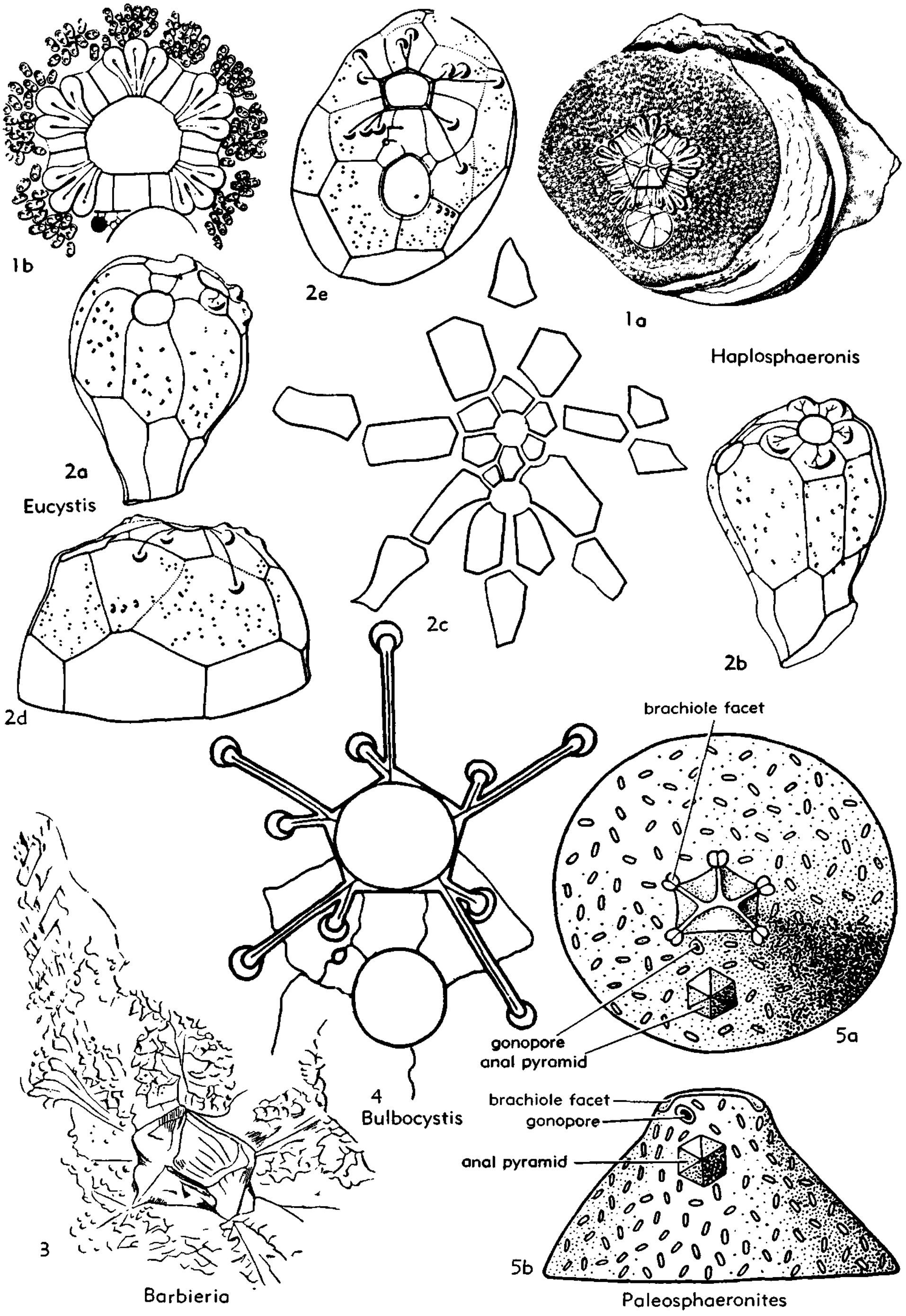


Fig. 144. Sphaeronitidae (p. *S*243, *S*247-*S*248).

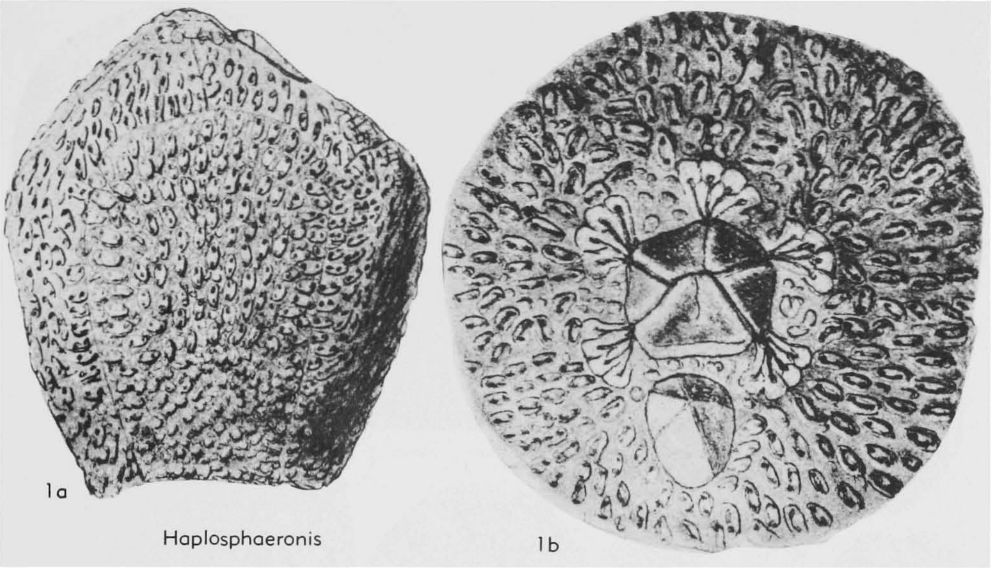


Fig. 145. Sphaeronitidae (p. *S*247-*S*248).

Barrande, 1887, p. 129; OD]. Theca ovoid or sac-shaped, composed of numerous thick plates. Aboral zone of steinkern invaginated in manner of base of wine bottle; no column known. Each ambulacrum with primary division into 2 parallel branches, with each branch further divided into about 3 branches (or "twigs") diverging gradually, each leading to subquadrate brachiole facet; 7 or 8 facets in each ambulacrum arranged in nearly straight line on one adoral plate. Diplopores with simple oval depressions, numerous, distributed over entire theca. Mouth, hydropore, and gonopore equally spaced. Plates in adoral half of theca rather loosely bound together, so that many specimens contain aboral half intact and adoral part disarticulated into jumble of plates; as result, periproct not observed among numerous specimens found. *M.Ord.*, Boh.——Fig. 142,*3*. **C. bohemica* (Barrande); ambulacrum, enl. (69). [See also Fig. 33,*5*.]

Eucystis Angelin, 1878, p. 31 [**E. raripunctata;* OD] [=*Palmacystis* Haeckel, 1896, p. 131 (type, *P. palmata*)]. Theca ovate to spherical, some specimens somewhat aborally extended to become pyriform, composed of moderate number of plates arranged in 3 to 5 circlets; plates polygonal, rather regular. Ambulacra 4 or 5, branching, longest grooves in some extending line into circlet of plates below adoral circlet but not in most; about 3 or 4 brachiole facets per ambulacrum. Periproct apart from peristome. Hydropore a small transverse slit and gonopore a small round opening below it, both lying on suture between circumoral plates in posterior interambulacrum. Diplopores not numerous, mostly limited to adoral half of theca; in thecae with only 3 circlets of plates, concentrated in middle one; in type species, diplopores sparse in lateroposterior region and rather abundant in lateroanterior. Base with short column or attached directly. [*Eucystis* was considered by Jaekel (69) and Regnéll (99) to be a senior synonym of *Proteocystites* Barrande (1887) and *Carpocystites* Oehlert (1887).] *M.Ord.-L. Dev.*, ?Asia(Yunnan)-Eu.(Brit.-Sweden-Ger.-Boh.-Fr.)-N.Afr.(Morocco).——Fig. 142,*2a;* 144,*2d,e*. **E. raripuncta,* M.Ord.(Boda Ls.), Sweden; 142, *2a,* lat., ×2.5; 144,*2d,e,* lat. and oral, both showing periproct, ×3 (99).——Fig. 142,*2b,c*; 144,*2a-c*. *E. angelini* (Lovén), U.Ord., Sweden; 142, *2b,c,* oral and lat., photogr. in alcohol, ×2.5; 144,*2a,b,* 2 lat., both showing periproct, ×2; *2c,* plate diagram (99).

Haplosphaeronis Jaekel, 1926, p. 19 [**H. ḳiaeri;* OD] [=*Pomocystis* Haeckel, 1895, p. 401 (type, *Sphaeronis uva* Angelin, 1878); *Pomosphaera* Haeckel, 1896, p. 99 (type, *Sphaeronis oblonga* Angelin, 1878)]. Theca ovoid to spherical, composed of few thick plates, attached directly by basal surface. Thecal plates in 2 circlets, lower of 7 rectangular to trapezoidal plates (called *LL*) and upper of 5 hexagonal to pentagonal plates (called *RR*) around peristome, which forms nearly regular pentagon, only very slightly elongate, covered over by 5 plates (called *OO*), *O1* largest and bearing slit that may possibly be hydropore. Base generally broad and flat, in some attached to other organisms. Diplopores very numerous all over surface of plates, in part radially arranged. Pores within elongate peripores, many of which are dumbbell-shaped and have raised margins.

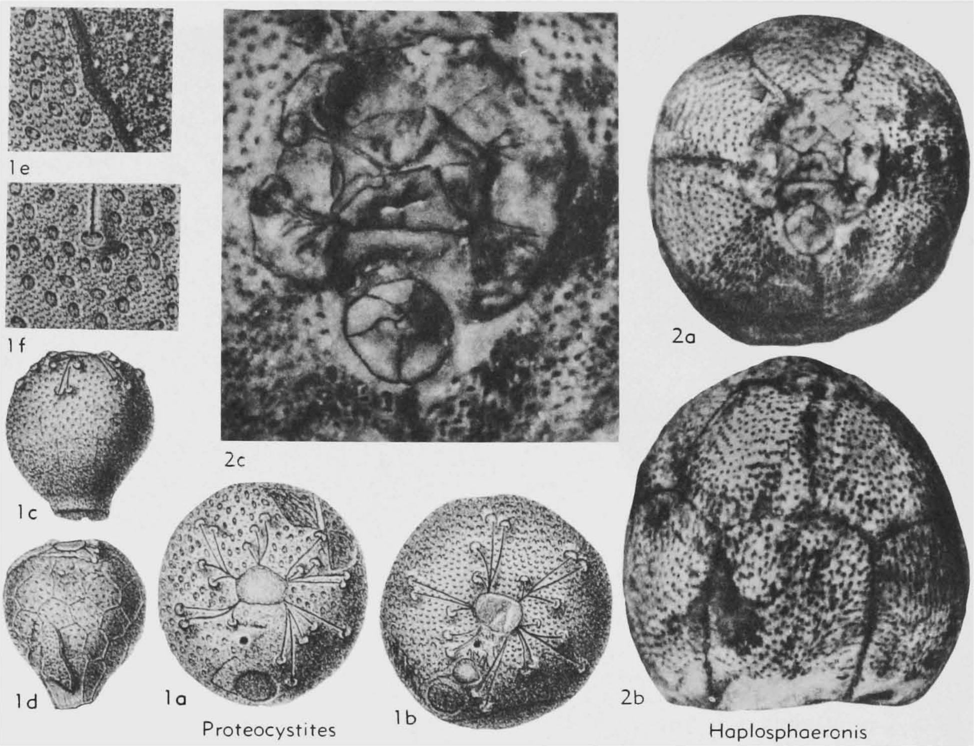


FIG. 146. Sphaeronitidae (p. S247-S249).

Ambulacral branches spread fan-wise from corners of pentagonal peristome, not curved, subequal; 3 or 4 branches of each ambulacrum crossing only 1 circumoral *(R)* plate to brachioles along its outer edge. Periproct subcircular, set close to circumoral circlet *(RR)*, filled by anal pyramid of 6 or 7 irregular pieces. Gonopore small, circular, set at adoral left side of anal pyramid. *M.Ord.-U.Ord.*, Eu.(Norway-Sweden-USSR-Belg.)——FIG. 144,*1;* 146,*2*. *H. oblonga* (ANGELIN), M.Ord(Kullsberg Ls.), Sweden; 144,*1a*, oral, ×3; 144,*1b*, oral region, ×9; 146,*2a,b*, oral and lat., ×2.5; 146.*2c*, oral region, ×4.5 (99).——FIG. 145,*1*. **H. kiaeri*, M.Ord., Norway; *1a*, lat., enl.; *1b*, oral, enl. (72).

Paleosphaeronites PROKOP, 1964, p. 9 [**Sphaeronites crateriformis* RŮŽIČKA, 1927, p. 12 (=*Sphaeronites batheri* RŮŽIČKA, 1927, p. 12, *partim*); OD]. Theca with flat base, typically conical, some dome-shaped to bell-shaped. Base containing 8 trapezoidal, radially arranged plates; large conical oral surface not divided into plates. Peristomial cover plates forming broad pentagon; 2 close-set oval brachiole facets very close to each corner of peristome. Anal pyramid hexagonal, containing 6 nearly equal plates, situated midway between peristome and border of oral surface; gonopore circular, in center of crater-like elevation, offset to left between largest peristomial plate and anal pyramid, closer to former. Diplopores large, scattered, each surrounded by large longitudinally elliptical depression. Surface of plates smooth to finely granulose. [Differs from *Sphaeronites* in having conical shape, smaller anal pyramid, distinct separation of peristome and anal pyramid, and larger, more elliptical diplopores. This genus resembles members of the Aristocystitidae in having brachiole facets practically at corners of the peristome, but it seems closer to the Sphaeronitidae in all other respects.] *L.Ord.*, Eu.(Boh.).——FIG. 144,*5*. **P. crateriformis* (RŮŽIČKA); *5a,b*, lat. and oral, ×4 (95a).

Proteocystites BARRANDE, 1887, p. 78 [**P. flavus;* OD] [=*Proteocystis* BATHER, 1889, p. 269 *(nom. van.)*]. Theca with broad attachment surface or short, thick columnar process. Ambulacra rather long, unequal, irregularly branched, not strongly developed. Several brachiole facets, unevenly spaced and distributed, in each ambulacrum. Diplopores numerous, apparently in elliptical peripores. Hydropore and gonopore between mouth and anal pyramid. [Genus considered by JAEKEL (69) and REGNÉLL (99) to be a junior synonym of *Eucystis*, but maintained by BATHER (10).] *L. Dev.*, Boh.——FIG. 146,*1*. **P. flavus*, F_2; *1a,b*, 2 oral, ×2; *1c*, lat., ×1; *1d*, lat., exfoliated, ×1; *1e*, surface of thecal plate at left, steinkern at

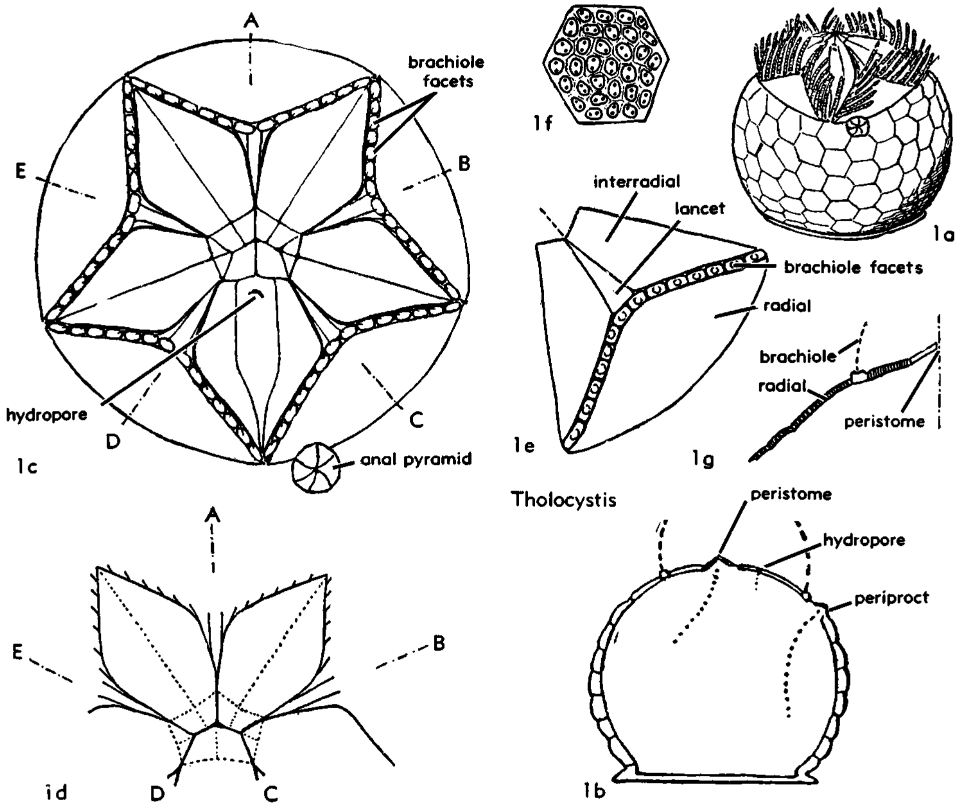


FIG. 147. Sphaeronitidae (p. S249-S250).——*1.* **Tholocystis kolihai* CHAUVEL, M.Ord., France; *1a,b,* posterior (*CD* interray) view of theca (reconstr.) and hypothetical cross section through peristome, ×2; *1c-e,* diagrammatic analyses of ambulacral field, ambulacral branching, and sector of ambulacral field, with ambulacral positions indicated as *A-E,* ×5; *1f,* plate from side of theca, showing diplopores, ×9; *1g,* section through peristome and attachment of brachiole, ×3 *(34).*

right, enl.; *1f,* surface of thecal plate showing diplopores and brachiole facet, enl. (3).

Tholocystis CHAUVEL, 1941, p. 88 [**T. kolihai;* OD]. Theca globose, shaped like kettle resting on its broad base, with large adoral area, corresponding to lid of kettle, consisting of *RR, OO,* and peristomial covering plates in very regular arrangement; remainder of theca composed of flat base with surrounding rim and globose walls of numerous polygonal plates, mostly hexagonal, bearing abundant diplopores in subpolygonal peripores. Periproct small, circular, filled with anal pyramid, located in posterior interambulacrum at junction of *RR* circlet and many-plated sides of theca. Numerous brachiole facets along the adoral margins of *RR,* forming star. *RR* 5, each an obtuse subspherical triangle, bearing diplopores. Five large *OO* forming star within brachiole facets, bearing diplopores, each pentagonal and meridionally elongate, posterior one tripartite, others apparently bipartite, with meridional suture dividing each into symmetrical halves; adjacent *OO* said to be separated by narrow wedgelike plate comparable to lancet-plate of blastoids. Ten covering plates of peristome forming broad pentagon, arranged in trimerous pentamerism with 2 plates in each interambulacrum, smooth, devoid of diplopores. Ambulacra represented by 2 main branches radiating from each angle of peristome, slightly diverging for half their length, then strongly diverging so that each main branch terminates at tip of oral plate, there meeting end of main branch from adjacent ambulacrum; from each main branch, short secondary branches lead aborally to brachiole facets; about 7 facets on each main branch, making 70 in all; apices of star formed by brachiole facets thus interradial and attaining circle that marks distal limit of oral field. Crescentic slit in posterior oral interpreted as hydropore. Each of wedgelike "lancet" plates extending from reentrant angle of star of brachiole-facets adorally to corner of peristome, supporting flooring plates of adoral sections of branches of ambulacra. Brachiole facets borne on quadrangular plates, thicker than other plates and analogous to adambulacrals in *Mesocystis*. [The exceptional symmetry developed in the oral region might be considered sufficient ground to erect a separate family for this unusual cystoid.] *M.Ord.*, Fr.——FIG. 147,*1*. **T. kolihai; 1a,b,* reconstr. of theca and hypothetical cross section through peristome, ×2; *1c-e,* diagrams of ambulacral field, ambulacral branching, and sector of ambulacral field, with ambulacral positions indicated as *A-E,* ×5; *1f,* plate from side of theca, showing diplopores, ×9; *1g,* section through peristome and attachment of brachiole, ×3 (34).

Family ARISTOCYSTITIDAE Neumayr, 1889

[*nom. correct.* BASSLER, 1938, p. 8 (*pro* Aristocystiden NEUMAYR, 1889, p. 413)]

Theca ovate to elongate, typically tapered or constricted at aboral end, containing numerous, irregularly arranged plates. Column small and degenerate where present, absent in most forms. Most pores confined to one plate, canals simple, irregularly branched, or regularly divided to form typical diplopores. Brachioles arising from facets adjacent to mouth; ambulacra very short and unbranched, scarcely developed in some. *L.Ord.-M.Sil.*

Of all families of cystoids, the Aristocystitidae contain the most diverse and heterogeneous assemblage of forms. The difficulty in precise definition and taxonomy is compounded by the fragmentary nature of specimens representing many genera. The thecal pores are not developed as classic diplopores in some of the genera, and may not branch at all in a few. The character of the thecal pores does not appear to be correlated with other features of the theca, so that certain genera rest solely upon their kind of pores. Thus, in a manner of speaking, *Pseudaristocystis* is an *Aristocystites* in which the pores are not developed as diplopores, and *Pachycalix* is a *Calix* in which the pore canals do not divide regularly. The general strong resemblances of the genera concerned are interpreted here as expressions of relationship rather than convergence. It may be worth mentioning, perhaps, that in *Hippocystis,* remarkable for the classic form of its diplopores, a few pores are not diplopores. At any rate, the concept of taxonomy should not be dominated by the name "Diploporita," but instead should be guided by consideration of the significant contrast between perforations which almost invariably pass from one plate to another and those which are predominantly confined to one plate.

For many years, the Aristocystitidae were assigned to the order Amphoridea of HAECKEL (58), along with genera properly referable to the Paracrinoidea, Eocrinoidea, and Carpoidea. BATHER (10-13) was a longtime champion of the Amphoridea, strongly defending exclusion of the Aristocystitidae from the Diploporita, until finally (15) he capitulated and dropped Amphoridea in his last summary of cystoids. As late as 1943, however, BASSLER & MOODEY (7) maintained the order Amphoridea, in which they placed, in addition to the Aristocystitidae, the families Eocystitidae (with seven eocrinoids and two paracrinoids), Anomalocystidae (with 18 "carpoids" and one eocrinoid), Dendrocystitidae (with two "carpoids" and an eocrinoid), Cothurnocystidae (with two "carpoids"), Malocystitidae (with four paracrinoids and one eocrinoid), and Comarocystitidae (with two paracrinoids). Such radically different kinds of pelmatozoans can scarcely be maintained as an order, whether or not they are assigned to the cystoids.

JAEKEL (69, 71) referred the Aristocystitidae to the Diploporita, placing them close to the Sphaeronitidae. REGNÉLL (99) summed up his discussion with "From this review it should have appeared, though there remains some doubt as to the position of a few genera, that the fam. Aristocystitidae has to be removed from the fatal Amphoridea and to be placed mainly in the Diploporita. By this procedure there is nothing to be left of the order Amphoridea in the sense of BASSLER 1938."

Key to Genera of Aristocystitidae

[Including only genera that appear to be well founded; key highly artificial and not intended to indicate phylogenetic relationships]

1. Theca very elongate conical, commonly more than 30 cm. high and attaining height of 40 cm.; provided with aboral terminal tubercle and composed of about 2,000 small plates, some ornamented .. *Calix*
   Theca not in form of very elongate cone, seldom exceeding height of eight cm.

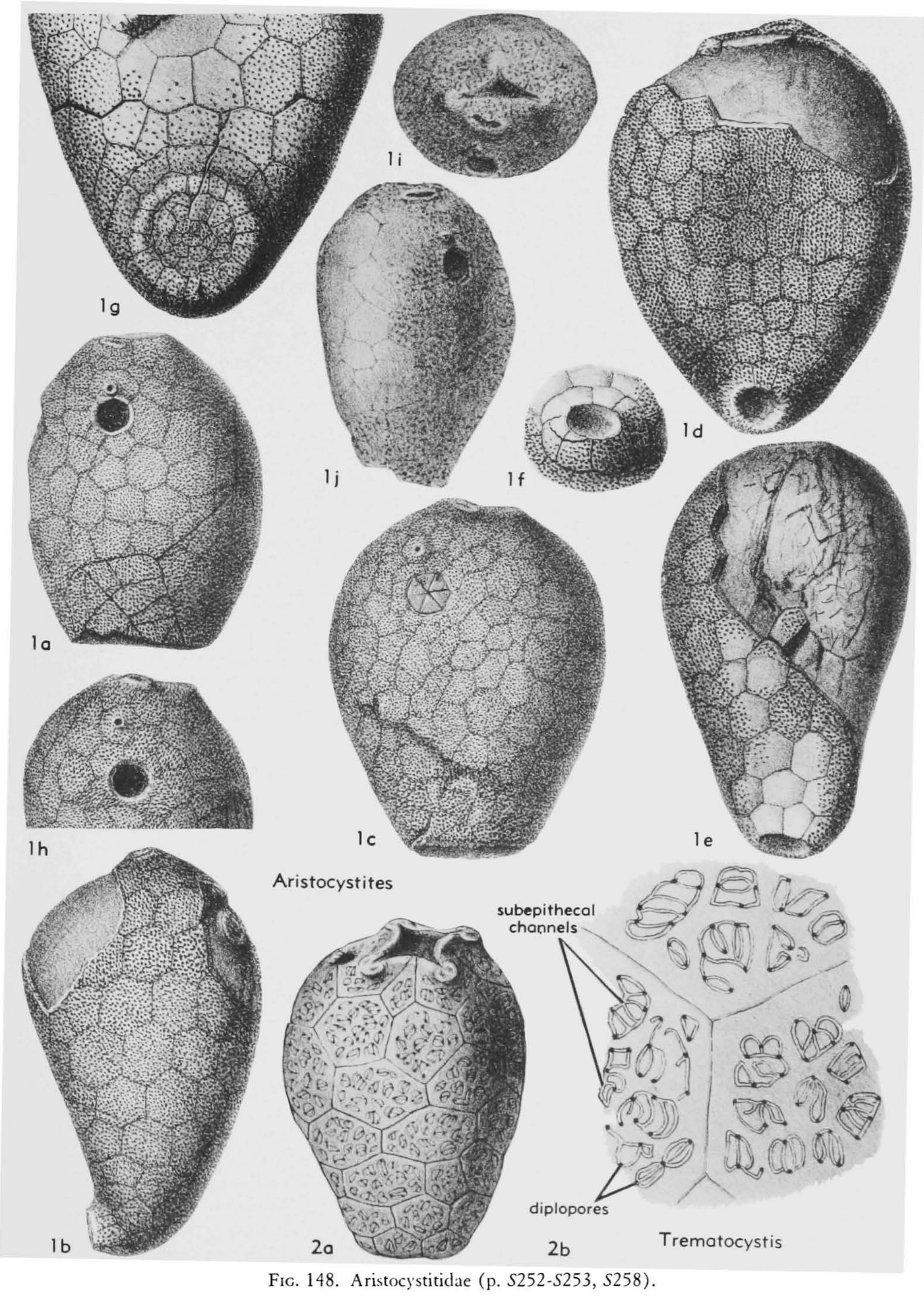


FIG. 148. Aristocystitidae (p. S252-S253, S258).

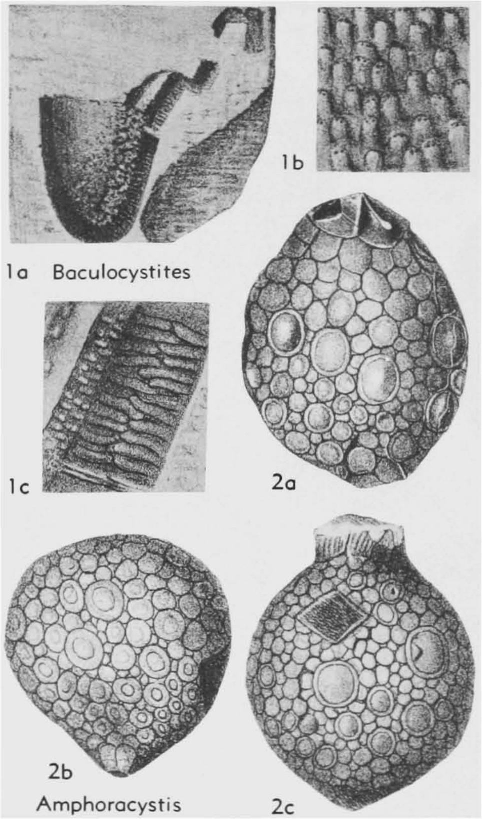


FIG. 149. Aristocystitidae (p. S253-S254).

and most forms smaller; no aboral tubercle, theca composed of only a few hundred plates, at most 2

2. Adult theca composed of plates of two drastically different sizes, large primary plates and small intercalated secondary or accessory plates 3
 Adult theca composed of subequal plates 4

3. Primary and secondary plates polygonal .... *Holocystites*
 Primary plates oval, secondary plates rounded or subpolygonal .... *Amphoracystis*

4. Mouth sinuous, bordered on one side by single large crescentic plate .... *Campylostoma*
 Mouth not sinuous, more than one plate on either side 5

5. Theca shaped like flared cone or bell, aboral part of theca exceptionally thick .... *Pachycalix*
 Theca more or less ovate, theca not exceptionally thick 6

6. Subepithecal channels connecting pores in shape of horseshoe .... *Hippocystis*
 Subepithecal channels, if present, not shaped like horseshoe 7

7. Normally two brachioles set at ends of elongate mouth, or oral slit, three known (?anomalous) .... *Aristocystites*
 Normally four brachioles 8

8. Thecal perforations large, not developed as diplopores, some continuing from one plate to another .... *Pseudaristocystis*
 Thecal perforations small, developed as diplopores, very few if any continuing from one plate to another 9

9. Mouth narrow and elongate, with short ambulacral grooves diverging from each end; brachiole facets set as at corners of oblong rectangle .... *Sinocystis*
 Mouth large and nearly square, with ambulacral grooves scarcely more than extensions of corners of mouth; brachiole facets set as at corners of square *Trematocystis*

Aristocystites BARRANDE, 1887, p. 95 [**A. bohemicus*; OD (=*A.? grandiscutum* BARRANDE, 1887, p. 109)] [=*Aristocystis* BATHER, 1889, p. 259 *(nom. van.)*]. Theca ovate to subpyriform or bulb-shaped, tapering aborally, base commonly truncate and shaped according to object to which attached. Young specimens may have possessed a column, but all traces of such attachment are absent in large forms. Thin epidermal layer, seldom preserved, smooth. Inner layer, composed of numerous polygonal plates, rather thin in oral region and becoming much thicker aborally, very thick at aboral pole; thickness also related to size (probably age) of individual. Pores numerous on most plates, shown on steinkerns as protuberances formed by casts (fillings) of inner portions of canals, on thick inner layer as openings connected by grooves or channels in groups of 2 to 6 (commonly 2). Mouth or peristomial opening elongate, more or less pointed at each end, set at right angles to plane through periproct and peristome; 2 brachiole facets normal, one specimen known with 3. Gonopore a small round opening between periproct and mouth, much closer to former. Hydropore an elongate slit near mouth and subparallel to it, in left posterior region. Periproct apparently filled by anal pyramid, hexagonal. [Some question remains of the nature of the pores. BATHER (12) stated, "The order Amphoridea, however much it be dismembered, still seems to find justification in the existence of genera, such as *Aristocystis,* which have neither diplopores (so far as I can observe) nor epithecal extensions of the subvective grooves. . . ." On the other hand, SUN (123) spoke of "double pores" in *Aristocystites* specimens from China. JAEKEL (69, 71) referred the family to the Diploporita, and other authors have followed his example.] *M. Ord.,* Eu.-Asia (China).——FIG. 148,*1*. **A.*

bohemicus, Dd_4, Boh.; *1a-d*, lat., 4 thecae, ×1; *1e,f*, lat. and part of aboral end of specimen, ×1; *1g*, aboral end, enl.; *1h*, oral end, ×1 (3); *1i,j*, oral and lat., specimen with 3 brachiole facets, ×1 (69). [See also Fig. 39.]

Amphoracystis HAECKEL, 1896, p. 52 [**Deutocyst-*

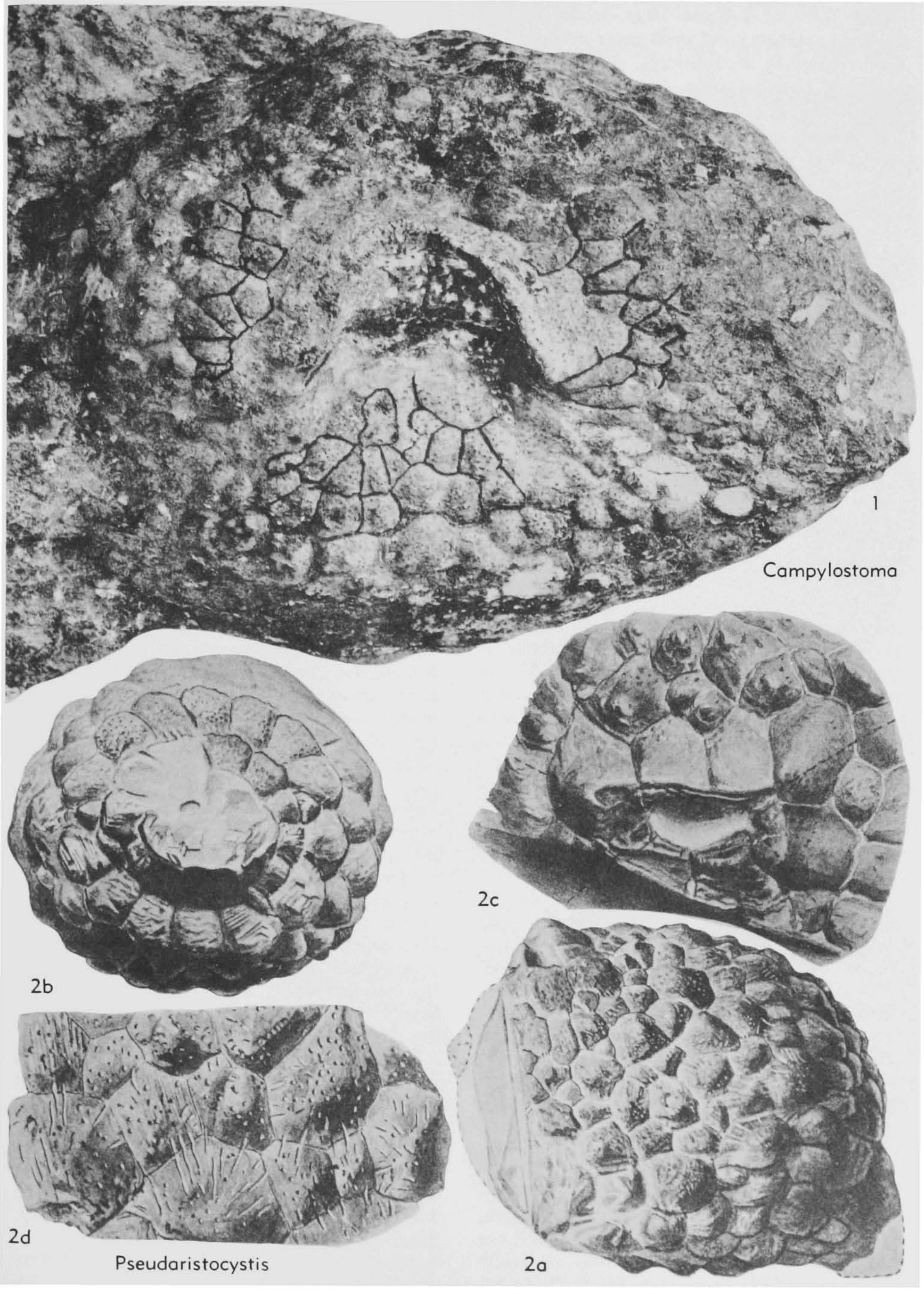


FIG. 150. Aristocystitidae (p. S254, S256-S257).

ites irregularis Barrande, 1887, p. 147; OD]. Theca small, ovoid, tapering slightly at base. Oral aperture elongate, probably produced (to judge from published figures). Periproct rhombic. Thecal plates of 2 types: large circular or oval (probably primary) and small more nearly polygonal (secondary or accessory). Pores unknown. *M.Ord.*(D_4), Boh.——Fig. 149,*2*. **A. irregularis* (Barrande); *2a-c*, 3 lat., ×2 (3).

?**Baculocystites** Barrande, 1887, p. 118 [**B. simplex;* OD]. Known only from fragment. Plates 3 to 4 mm. thick comprising conical base, externally smooth. Steinkern with fillings or casts of pores irregularly distributed and partly grouped, said to resemble features of *Codiacystis* more than *Aristocystites*. *M.Ord.*(D_4), Boh. —— Fig. 149,*1*. **B. simplex*; *1a*, fragment with thecal wall mostly dissolved, ×1; *1b,c*, int. mold and long. sec., enl. (3).

Calix Rouault, 1851, p. 358 [**C. sedgwicki;* OD] [=*Dorycystites* Kloucek, 1917, p. 3 (type, *D. purkynei*) (*fide* Chauvel, 1941, p. 82]. Theca cylindrical to conical or carrot-shaped, very elongate, bearing aboral terminal tubercle, very large, attaining height of 40 cm., making it largest known cystoid; theca composed of about 2,000 small plates in adult form, many with central tubercle or prominence. Mouth elongate, with brachiole facet at each end. Diplopores with simple oval or slightly curved pits covered over by epitheca, which seldom is preserved. Chauvel (33) differentiated 3 stages of development in type species: (1) aboral zone composed entirely of primary plates bearing tubercles, (2) appearance of secondary or supplementary plates between tuberculiferous plates (single circle of secondary between 2 circles of tuberculiferous primaries), and (3) appearance of secondary tubercles on primary plates, secondary plates, and possibly on plates of oral zone. Top of theca comprising corona of 8 to 12 plates without diplopores. Anal pyramid with 6 triangular plates. *M.Ord.-U.Ord.*, Eu.(Boh.-Fr.-Port.-Spain).——Fig. 143,*1*. **C. sedgwicki*, M.Ord., Fr.; *1a*, section through peristome and hydropore; *1b*, internal mold of peristome; *1c*, diagram of oral region (34); *1d*, reconstr., about ×0.2 (128). [See also Fig. 39,*2*.]

Campylostoma Dreyfuss, 1939, p. 118 [**C. grandis;* OD]. Theca apparently oviform, to judge from only specimen well preserved, with short height, composed of very numerous plates without orderly arrangement; plates thick, convex. Pores single or in groups of 2 or 3, irregularly distributed. Mouth or peristome sinuous, bordered on one side by large, unique, crescent-shaped plate and on other by 4 or 5 plates not convex and 2 or 3 times as large as other plates of theca; 4 depressions near crescentic plate, of which one may be gonopore and others probably are brachiole facets. *U.Ord.*, Fr.——Fig. 143,*5;* 150,*1*. **C. grandis;* 143,*5*, oral region; 150,*1*, oral, holotype, ×0.9 (39).

Hippocystis Bather, 1919, p. 72 [**Aristocystites bohemicus subcylindricus* Barrande, 1887, p. 114; OD]. Theca ovoid, composed of numerous polygonal plates, many of which are subhexagonal. General organization like that of *Aristocystites*, genus in which it was originally included. Diplopores distinctly defined as pairs of pores linked by horseshoe-shaped grooves, as exposed on weathered surfaces of plates. Diplopores obscured or covered in specimens in which smooth external layer is preserved. [This genus presents the classic example of diplopores.] *M.Ord.*, Boh.——Fig. 151,*2*. **H. subcylindrica* (Barrande), Dd_4; *2a-d*, 3 lat. and aboral, ×1; *2e*, aboral pole, enl.; *2f,g*, 2 plates, somewhat weathered, enl. (3).

Holocystites Hall, 1864, p. 7 [**Caryocystites cylindricum* Hall, 1861, p. 23; OD] [=*Holocystis* Carpenter, 1891, p. 47 *(nom. van.)* *(non* Lonsdale, 1849); *Megacystites* Hall, 1865, p. 380 *(nom. subst. in errore pro Holocystites* Hall, 1864, not preoccupied by *Holocystis* Lonsdale, 1849); *Megacystis* Angelin, 1878, p. 29 *(nom. van.)*]. Theca elongate subovate, aborally tapering; plates arranged in more or less alternating transverse or more or less alternating vertical rows, polygonal, in some predominantly hexagonal; large plates considered primary and small ones secondary or accessory, intercalation of smaller plates probably a feature of ontogeny, not a specific character. Mouth terminal, periproct nearby in oral part of theca, filled with anal pyramid of 5 or 6 triangular plates. [Difficulty in interpreting this genus arises from preservation of the type and related species as steinkerns, which reveal only traces of diplopores as internal casts or fillings and furnish no information on the brachioles, subepithecal connections of pores, ornamentation of plates, etc. Some, possibly most, of the cystoids ascribed to this genus by S. A. Miller (85) perhaps properly were separated as *Trematocystis* by Jaekel (69), although he mentioned only *T. subglobosus* (Miller), the type species, in particular. In cystoids which he assigned to *Holocystites*, Foerste (49) reported forms with 4 and with 5 grooves from the oral opening, presumably leading to brachiole facets.] *U.Ord.-M.Sil.*, Eu. (Sweden)-N. Am.(Wis.-Ill.-Ind.-Ohio-Tenn.)——Fig. 152,*1a-e*, *H. alternatus* (Hall), M.Sil.(Racine Dol.), Wis. *(1a-d)*, M.Sil.(Cedarville Dol.), Ohio *(1e)*; *1a*, lat., plates classed as primary indicated by letters A, B, C, D, in successive rings aborally, ×1 (Foerste, 1917); *1b-d*, lat., 3 thecae, ×0.8; *1e*, lat., ×0.8 (49).——Fig. 152,*1f-h*. *H. greenvillensis* Foerste, M.Sil.(Cedarville Dol.), Ohio; *1f-h*, lat., 3 thecae, ×1 (Foerste, 1917).——Fig. 152,*1i*. *H. gyrinus* Miller & Gurley, M.Sil. (Osgood Ls.), Ind.; oral region, ×1 (10).

?**Lepidocalix** Termier & Termier, 1950, p. 26 [**L. pulchrum;* OD). Theca known from plates, which show external perforation ending as pustule and 2 corresponding internal pores. Said by the authors to resemble *Calix* and *Pachycalix* but with spine-bearing and imbricating plates. As reconstructed its oral region resembles that of *Calix* or *Sinocystis*, with adjacent anal pyramid, and pore between them. [TERMIER & TERMIER (128) thought the pustule or perforated tubercle was articular, bearing a spine; if so, this would be drastically different from other cystoids, more nearly resembling a primitive echinoid.] *M.Ord.*, Algiers.——FIG. 143,*3*. **L. pulchrus*; reconstr. (128).

Pachycalix CHAUVEL, 1936, p. 3 [**Calix halli*

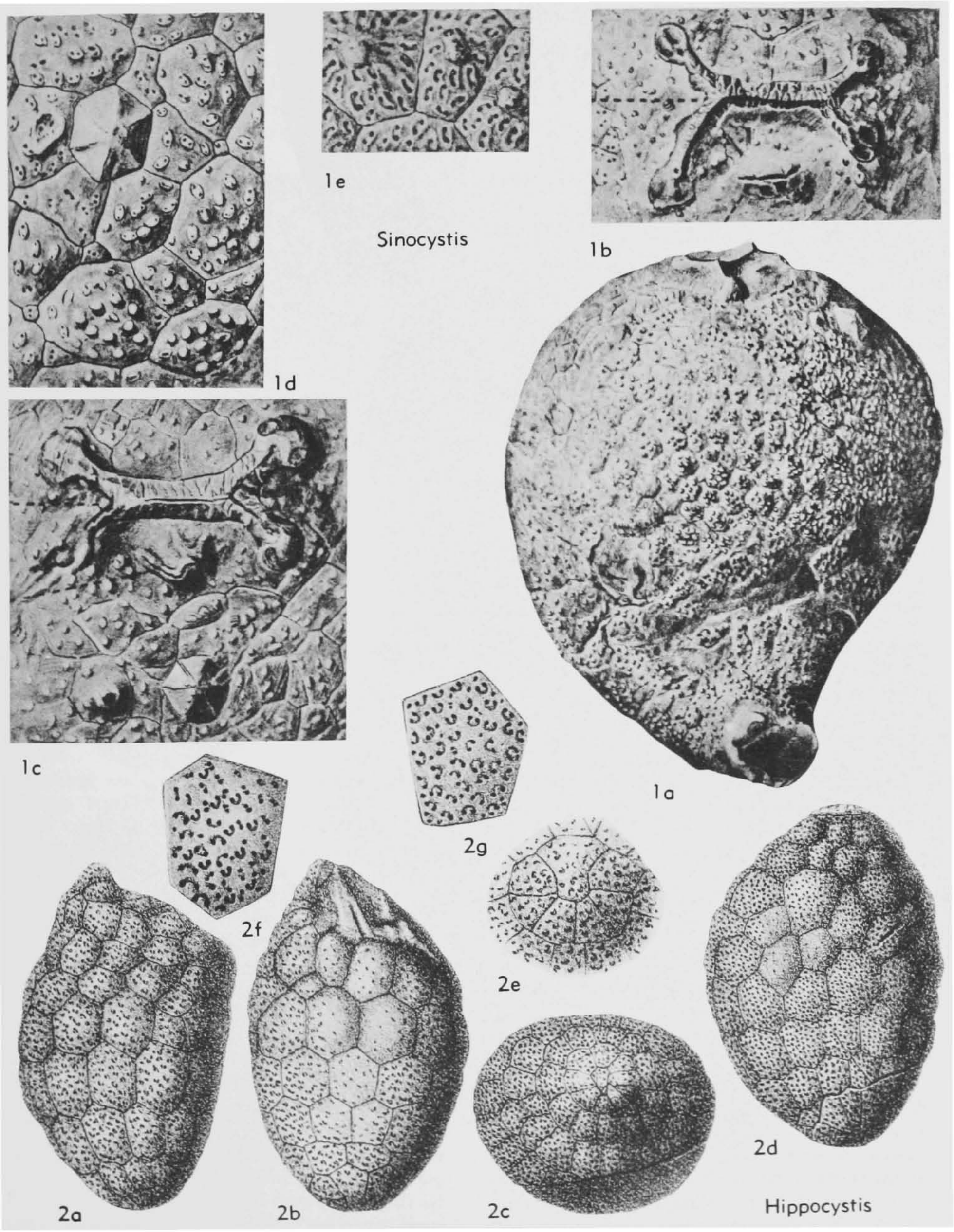


FIG. 151. Aristocystitidae (p. S254, S257-S258).

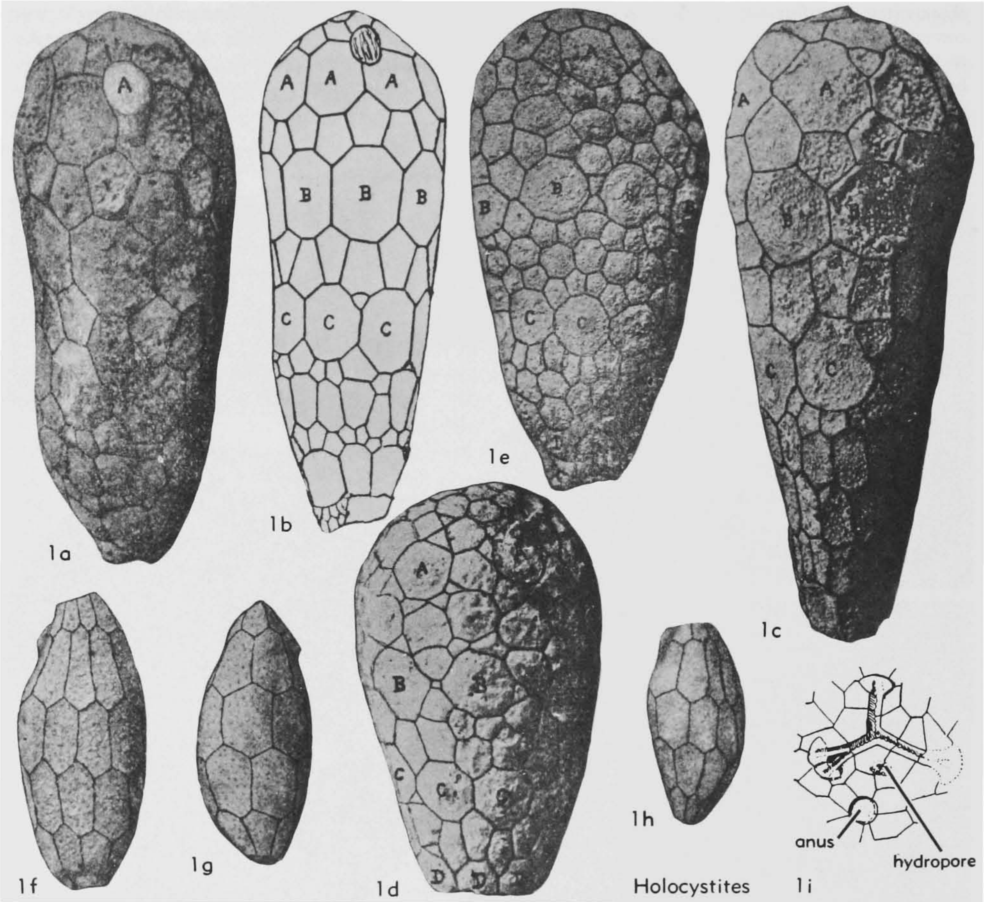


FIG. 152. Aristocystitidae (p. S254).

ROUAULT, 1851, p. 358; OD]. Theca with shape of flaring cone, devoid of tubercles, composed of very thick plates (8 to 12 mm.). Pores of large diameter (1 to 2 mm.), some ramified in form of Y, many sinuous, many in groups of 2 but not necessarily in typical diplopore form; by some authors referred to as haplopores. Between mouth and periproct is hydropore. *M.Ord.*, Eu.-N.Afr. ——FIG. 143,*2*. *P. pachythecus* TERMIER & TERMIER, Caradoc, Morocco; *2a,b,* long. and transv. secs. (reconstr.) (128). [See also Fig. 33,*3*.]

Pseudaristocystis SUN, 1936, p. 480 [**Aristocystis dagon* BATHER, 1906, p. 8; OD] [=*Dagoncystis* CHAUVEL, 1941, p. 52 *(obj.)*]. Theca ovoid, judged from incomplete holotype of only known species to have been pear-shaped and to have lived in prostrate position with narrower end bent downward for attachment to sea floor. Mouth elongate, surrounded by 7 plates with longer axes radiating from center, edges of plates beveled (presumably to accommodate peristomial covering plates); at each end of oral opening circumoral plates indented, forming facets for 2 brachioles; 4 facets arranged at corners of long trapezoid, with those on anterior side farther apart than those on posterior. Obscure opening near mouth in posterior area thought to be hydropore. Periproct not preserved. Thecal plates 150 to 200, irregularly arranged but tending to be disposed in rows, plates at aboral constriction in 2 circlets; 2 or 3 rows of plates around circumorals conspicuously smaller and quite irregular, considered by BATHER (12) to represent region of thecal growth; plates swollen, with rather rough irregular surface, stout. Large pore canals pierce plates of oral and aboral regions with irregular courses more or less at right angles to general surface, but in plates of side walls canals tend to be directed toward sutures between plates, and some pass across sutures although not disposed into rhombs; no differentiation of canals to form diplopores. [BATHER (12) regarded the pore canals as an incipient stage leading to pore rhombs.] *M.Ord.*, Burma.——FIG. 150,*2*. **P. dagon* (BATHER), Naungkangyi Beds; *2a,b*, lat. and aboral, ×1; *2c*, oral region, ×2; *2d*, weathered plates showing directions of pores, ×2 (12). [See also Fig. 33,*2*.]

Sinocystis REED, 1917, p. 3 [**S. loczyi*; SD BATHER, 1918, p. 51] [=*Ovocystis* REED, 1917, p. 7 (type, *O. mansuyi*)]. Theca variable in shape, roughly ovate pyriform, tapering to base which may be prolonged as short unspecialized stem, composed of 100 to 600 irregular polygonal plates bearing conspicuous diplopores, several to a plate. Peristome elongate, with 2 short ambulacra diverging from each end and terminating in large brachiole facets; 4 brachioles, therefore, set at corners of small oblong. Periproct in posterior region, about midway between peristome and periphery as viewed orally. Gonopore situated left of periproct; hydropore a curved slit between gonopore and peristome. Covering plates of ambulacra and peristome irregular, biserial. [In some species, the crowding of diplopores is made possible by elevations, called "turrets" by BATHER (12), each containing a few diplopores.] *M.Ord.*, China.——FIG. 151,*1a-d*. **S. loczyi*, Shih-tien, *1a*, lat., ×1; *1b,c*, 2 oral regions, ×2, ×2.5; *1d*, periproctal

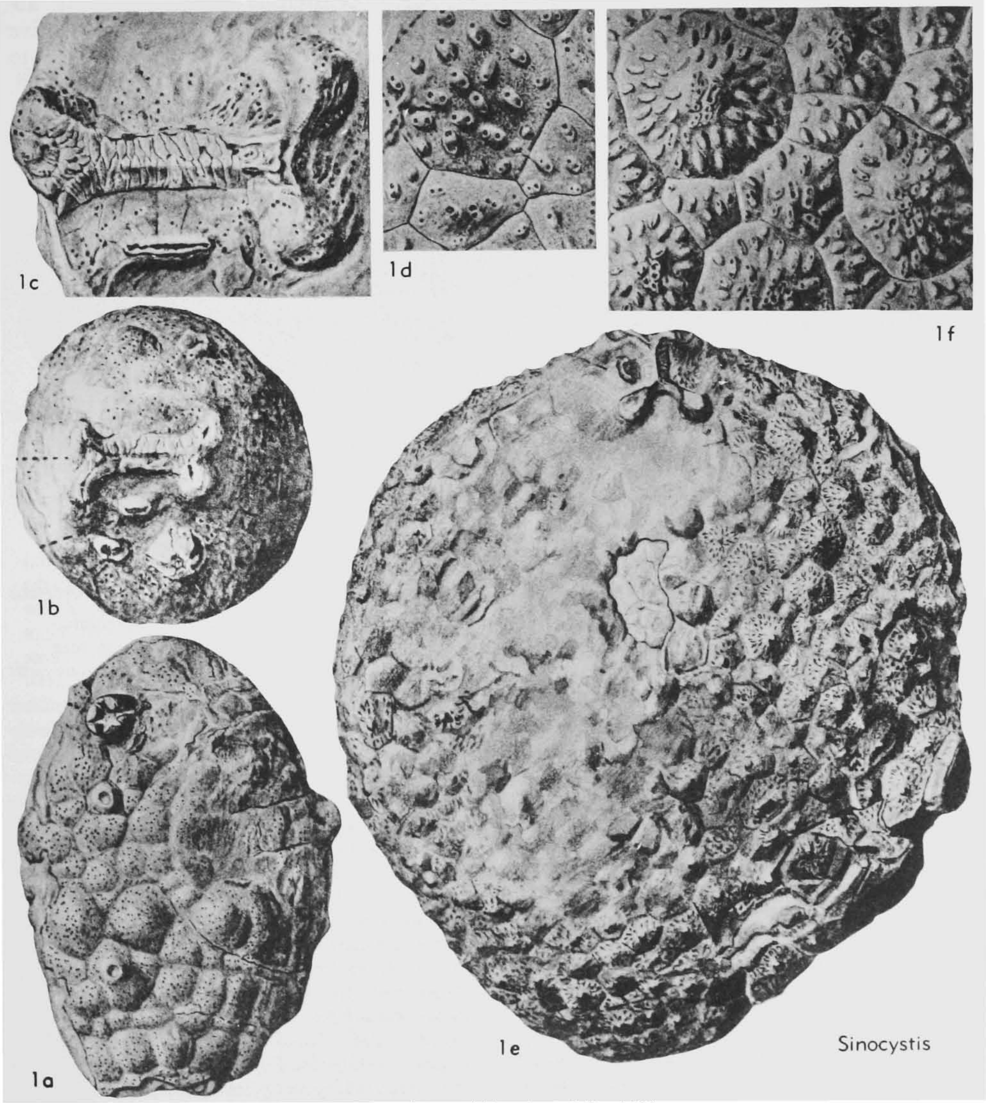


FIG. 153. Aristocystitidae (p. S257-S258).

region, ×3 (98).——FIG. 151,*1e;* 153,*1e,f*. *S. yunnanensis* REED, Shih-tien; 151,*1e*, weathered plates, ×5; 153,*1e*, lat., crushed specimen, ×1; 153,*1f*, plates, ×4 (98).——FIG. 153,*1a-d*. *S. mansuyi* (REED), Shih-tien; *1a*, lat., ×1; *1b*, oral, young specimen, ×2; *1c*, oral region, ×2.5; *1d*, thecal plates, ×4 (98).

Trematocystis JAEKEL, 1899, p. 414 [**Holocystites subglobosus* S. A. MILLER, 1889, p. 255; OD]. Theca subovate to subpyriform, tapering to rather blunt or truncated base. Mouth large, bordered by prominent rim, with corners leading to 4 brachiole facets, spaced at corners of square. Periproct in upper part of theca, near mouth. Subepithecal multiple, twisted or winding channels connecting diplopores. Pores small. Thecal plates apparently subequal, although this may only be a feature of youth in which accessory plates have not developed. [FOERSTE (49) predicted that *Trematocystis* would become eventually a junior synonym of *Holocystites*. Apparently, however, the mouth is much larger, the theca less elongate, and the plates more nearly equal in size.] *M.Sil.*, E.C. N.Am.——FIG. 148,*2*. **T. subglobosa* (MILLER); *2a*, lat., reconstr., ×1; *2b*, weathered surface, enl. (69).

Superfamily ASTEROBLASTIDA
Bather, 1900

[*nom. transl.* KESLING, herein (*ex* Asteroblastidae BATHER, 1900, p. 80)] [=order Asterocystida JAEKEL, 1918, p. 100]

Diplopore-bearing cystoids in which diplopores are restricted to interambulacral areas. Theca pentremite-, bud-, or bullet-shaped, with strong pentameral symmetry. Ambulacra five, straight, each bearing numerous brachioles, distally resting on *RR*. Specialized oral or deltoid plates, angular and close-fitting around small mouth opening, plate in posterior interradius divided. Column present. *L.Ord., ?M.Ord.*

Considerable interest has been stirred by the fossils assigned to this superfamily because of their resemblance in general form to the blastoids. As early as 1874, SCHMIDT (114) concluded that these Estonian cystoids were transitional forms leading to the blastoids. The lack of conclusive evidence, however, is exemplified in the 1953 volume of the *Traité de Zoologie*, in which CUÉNOT placed *Asteroblastus* in his chapter on cystoids and BERGOUNIOUX included it in his chapter on blastoids. WANNER (1951) became convinced that if the eublastoids were at all descended from cystoids, only the Asteroblastidae satisfied the prerequisites. It is worth consideration that the author of the family Asteroblastidae originally placed it in the Blastoidea; and BASSLER (5) assigned these genera to the Protoblastoidea. Unfortunately, much of the morphology of these interesting pelmatozoans is known only in gross aspect, and especially the internal structures need additional study.

Family ASTEROBLASTIDAE
Bather, 1900

[Asteroblastidae BATHER, 1900, p. 80] [=Asterocystidae JAEKEL, 1918, p. 101]

Theca pentremite or bud-shaped; aborally conically globose; orally with five broad, flat, distally tapering, linguloid to spatulate ambulacra sloping from small, truncate oral area to join aboral half of theca, interambulacral spaces being filled with various plates. Column present, rather thin. *L.Ord., ?M.Ord.*

Key to Genera of Asteroblastidae

1. In each interambulacrum diplopore-bearing area composed of one large, sub-rhombic suboral plate (so-called "subdeltoid"); four plates in vertical row in each interambulacrum except that with periproct, here called *O*, suboral, *L*, and *IL* .... *Asteroblastus*
   In each interambulacrum diplopore-bearing area composed of several small plates, not single large suboral plate 2
2. On aboral side of theca, each interambulacrum (except that having periproct) composed of *IL* and *L*, with few small accessory plates .... *Asterocystis*
   On aboral side of theca, each interambulacrum composed of small plates in four to six rows .... *Metasterocystis*

Asteroblastus EICHWALD, 1862, p. 62 [**A. stellatus* EICHWALD, 1862 (=**Protocrinites foveolatus* EICHWALD, 1860, p. 623; OD]. Theca composed of relatively few definitely arranged plates comparable with those in Rhombifera. *BB* 4, small, 2 hexagonal, one on each side of posterior interambulacrum, other 2 pentagonal, occurring together on opposite side. Above circlet of *BB* is circlet of 6 plates, distributed 2 in posterior interambulacrum and 1 in each other interambulacrum, apparently representing 5 *ILL* and 1 anal, or *X;* from latter, a series of polygonal plates leads adorally to periproct. In addition, each interambulacrum contains vertically elongate hexagonal plate *(L)*, subpentagonal plate bearing numerous diplopores (suboral or pore-plate), and crescentic elongate plate *(O)* bordering small pentagonal mouth opening; plates in these *LL*,

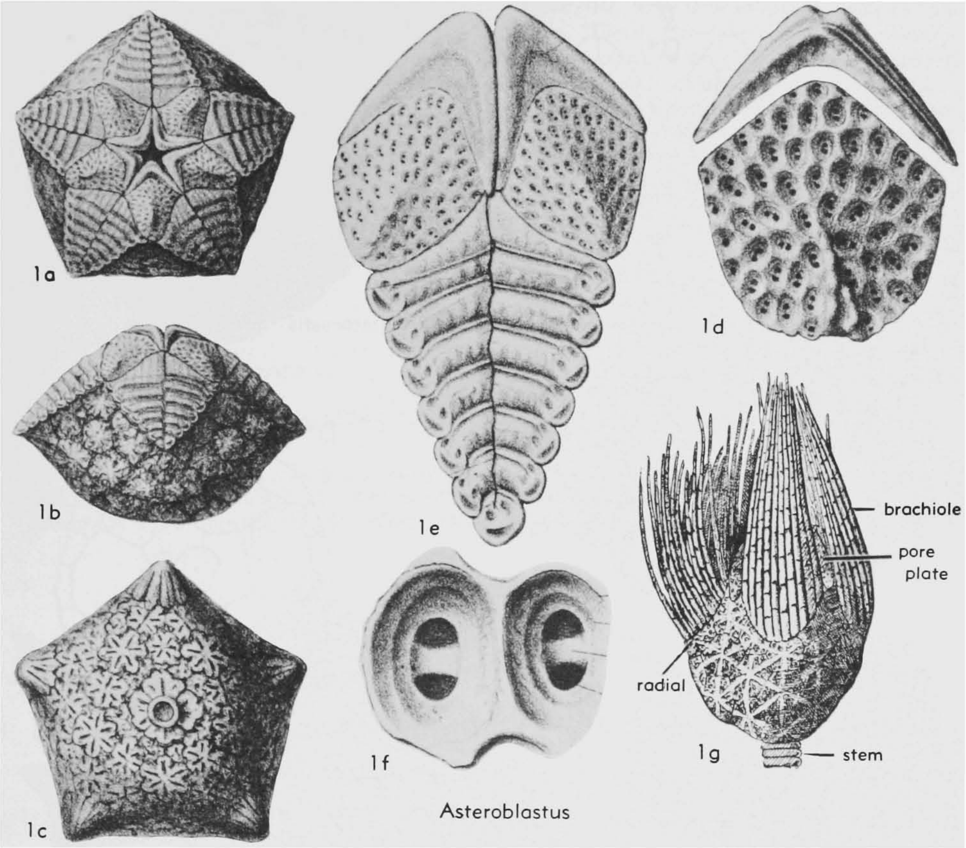


FIG. 154. Asteroblastidae (p. *S258-S259*).

suboral, and *OO* series separated from those in adjacent interambulacra by ambulacra and *RR* on which their aboral ends rest. *O1* plate in posterior region divided in 2 equal parts, periproct a small circular opening below pore-plate. Ambulacra 5, broad, petaloid, composed of horizontally elongate, alternating, elevated plates starting from distal points of *OO*, bearing brachioles in specialized facets along their outer borders. Diplopores concentrated in suboral plates, but a few may occur in underlying *LL*. Column thin. [Considerable question relates to the type species. *Protocrinites foveolatus* was founded by EICHWALD (44) on a pore-bearing plate of an *Asteroblastus*. Later (1862) he erected the genus *Asteroblastus* with *A. stellatus* as the type species by monotypy. JAEKEL (69) considered the 2 species synonymous. BASSLER & MOODEY (7) classed the 2 as synonymous but, for some reason, chose to recognize the junior *Asteroblastus stellatus*. *L.Ord.*, *?M.Ord.*, Eu.(USSR)-?N.Afr.(Morocco).——FIG. 154,*1a-f*. **A. foveolatus*, L.Ord., USSR; *1a-c*, oral, lat., and aboral, sl. enl.; *1d*, pore-plate; *1e*, 2 pore-plates and ambulacrum; *1f*, 2 diplopores, enl. (69).——FIG. 154,*1g*. *A. volborthi* SCHMIDT; lat., reconstr., somewhat enl. (10).——FIG. 155,*2*. *A. regularis* JAEKEL, *Vaginatum* Ls., USSR(Leningrad); *2a*, plate diagram; *2b*, lat. [*I-V* as used here by JAEKEL for rays correspond to *E,A,B,C,D*, Carpenter symbols] (71). [See also Fig. 33,*4*.]

Asterocystis HAECKEL, 1896, p. 116 [**Asteroblastus tuberculatus* SCHMIDT, 1874, p. 33; OD]. Theca with same basic organization as that in *Asteroblastus*, but with numerous small plates in place of large suborals or pore-plates and with a few accessory small plates inserted here and there above second circlet of thecal plates *(ILL)*. Most diplopores in the adoral part of theca below *OO*, all interambulacral. *L.Ord.*, Eu.(USSR-Est.).——FIG. 155,*1*. *A. globula* JAEKEL, Est.; *1a*, plate diagram; *1b*, aboral, ×4 [*I-V* as used here by JAEKEL for rays correspond to *E,A,B,C,D* Carpenter symbols] (71).

Metasterocystis JAEKEL, 1918, p. 101 [**M. micropelta*; OD]. Theca with general shape like that of *Asteroblastus* and *Asterocystis*, but with different arrangement of plates. Several small plates instead of large pore-plate in each suboral area; thus,

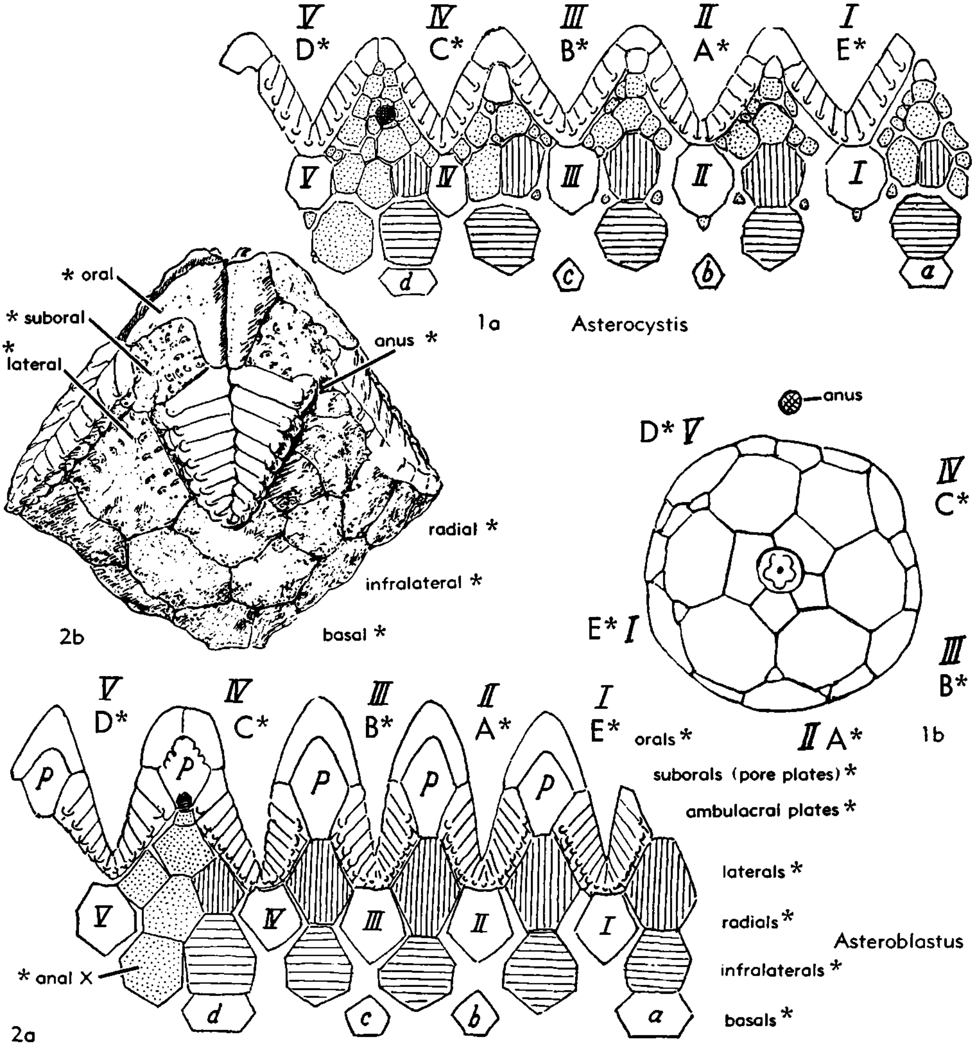


FIG. 155. Designations of plates and rays in Asteroblastidae, given by JAEKEL and identifications of them (marked by asterisks) judged by KESLING to be appropriate (Kesling, n).

orally theca resembles that of *Asterocystis.* On aboral side, however, each interambulacrum composed of small plates in 4 to 6 rows or circlets. *L.Ord.,* Eu.(USSR).——FIG. 156,*1.* **M. micropelta,* L.Ord.(Kunda,B$_3$), Leningrad; incl. lat., ×2 (69).

Family MESOCYSTIDAE Bather, 1899

[Mesocystidae BATHER, 1899, p. 920]

Theca bullet-shaped, inflated, rounded subpentagonal in cross section, its base indented at junction with thin column. Ambulacra long, straight, extremely thin, grooves and miniature brachiole facets distinctly inscribed in substantial elevated flooring plates crossing theca. *RR* very small, interambulacral plates very numerous, small, covered with diplopores. *L.Ord.*

Mesocystis BATHER, 1899, p. 102 [*nom. subst. pro Mesites* HOFFMAN, 1866, p. 2 (*non* SCHOENHERR, 1838; *nec* GEOFFREY, 1838; *nec* JENYNS, 1842; *nec* LUDWIG, 1893)] [**Mesites pusirefskii* HOFFMAN, 1866, p. 4; OD (=*Agelacrinus pusyrewskii* SCHMIDT, 1874, p. 34; *Mesocystis pusirefski* BATHER, 1900, p. 76; *Mesocystis pusirewskii* WANNER, 1933, p. 491; *Mesocystis pusireffskyi*

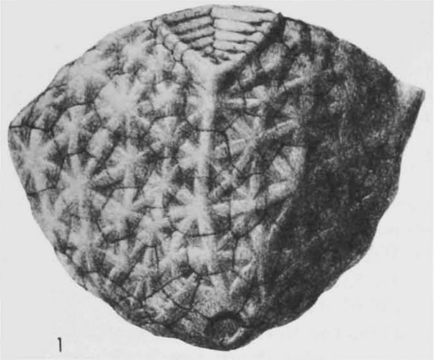


FIG. 156. Asteroblastidae (p. S259-S260).

YAKOVLEV, 1937, p. 35)]. Theca with small oral field atop globose adoral half, in which mouth is surrounded by 5 interambulacrally placed crescentic *OO*, with thin ambulacra radiating therefrom. Thecal plates very thin and numerous, flooring plates of ambulacra more substantial and serving as struts to give rigidity to theca. [In the type species, JAEKEL (69) distinguished approximately 1,000 ambulacrals, 2,000 interambulacrals, 1,000 brachioles (each with 50 dorsal and 100 ventral platelets bordering the groove, a total of 150,000) and 10,000 small covering plates along the ambulacral grooves. The tiny brachiole facets are set on lateral platforms of the flooring plates, so that the ambulacral edges are finely scalloped.] Periproct lateral, with valvular pyramid. Diplopores restricted to interambulacral plates. Structures in posterior oral *(O1)* probably represent hydropore and gonopore. *L.Ord.*, Eu.(USSR).—FIG. 157,*1*. **M. pusirefskii* (HOFFMAN); *1a*, aboral, basal part, ×1; *1b*, lat. (part reconstr.), specimen lacking aboral end (this fig. copied and used as basis for belief that base was flat), ×0.5; *1c*, oral region, enl. (69); *1d*, sec. through ambulacrum, enl. (10).

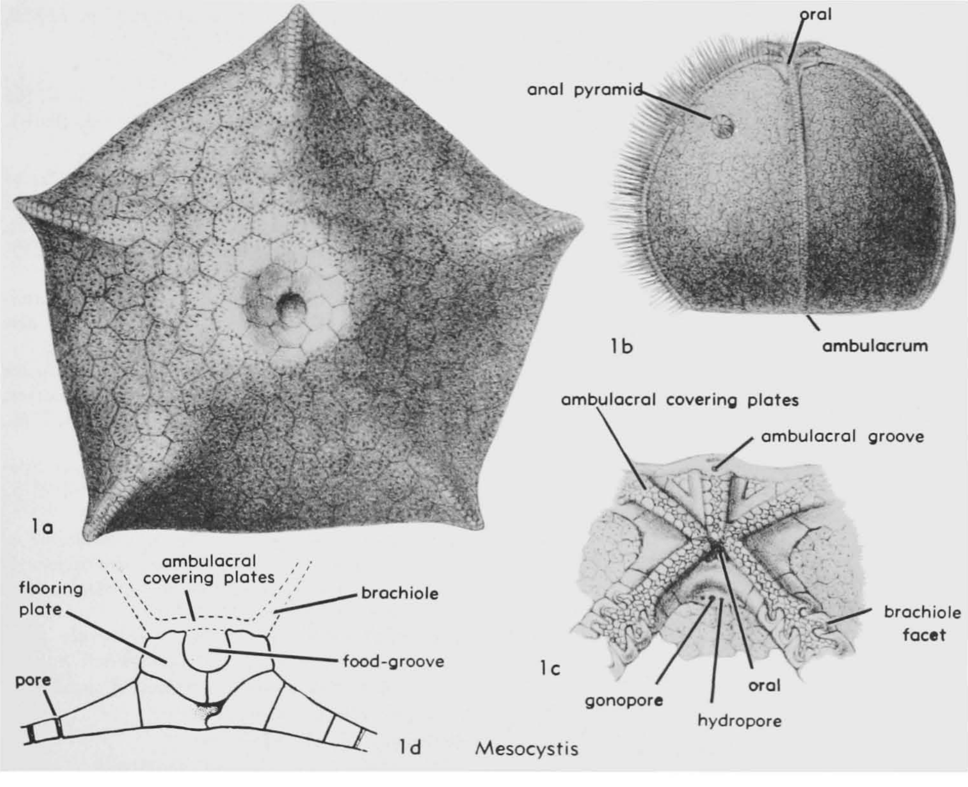


FIG. 157. Mesocystidae (p. S260-S261).

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PARACRINOIDS

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INTRODUCTION

Paracrinoids are extinct pelmatozoan echinoderms. Insofar as the paleontological record is known, they developed suddenly, flourished briefly, and became extinct, all in the span of Middle Ordovician time. Because the record is fragmentary, it seems quite reasonable to suspect that the paracrinoids made their appearance before this epoch, and that some lingered after it; at any rate, paleontologists should not confine their search to Middle Ordovician rocks in looking for Paracrinoidea.

Although they are locally abundant, the paracrinoids never achieved world-wide distribution, nor did they evolve enough diversity of form to require complicated taxonomy. As compared with other groups of echinoderms, the paracrinoids are a small, fairly homogeneous taxon. Needless to say, they are not considered as guide fossils.

Paracrinoids bear morphological similarities to other pelmatozoans (Fig. 158). They have a theca like that of the cystoids, pinnuliferous arms like those of the crinoids, and a column like that of the blastoids. At least some forms have a hydropore and gonopore like those of the cystoids. The thecal pores extend from the interior into the plates but terminate beneath the epitheca; thus, they have the same general plan as that present in the superfamily Caryocystitida of the cystoids.

Yet distinct differences set the Paracrinoidea apart as a class. They can be distinguished from cystoids and eocrinoids by the uniserial nature of their ambulacral structures, as well as by the presence of pinnules. They differ from crinoids in having the body covering arranged as a continuous theca, not divided into a calyx and a tegmen. They are separated from the blastoids by irregularity of plate arrangement and by form of the pore system. Therefore, a well-preserved specimen of the paracrinoids can be identified as such without difficulty.

Diagnostic features of many paracrinoids, however, are seriously affected by fossilization. In particular, the pinnules and arms are lost from many specimens. Details of hydropore, gonopore, anal pyramid, column, and surface ornamentation may not be preserved. Some of the genera are incompletely known.

Paracrinoids seem to have lived in much the same manner as many of their contemporary cystoid relatives. The animals were anchored to holdfasts by a flexible column. There is no conclusive evidence on whether adults were immovably fixed at one site, or whether they could release their hold and perhaps drift to a more desirable location. The paracrinoids possessed what appears to have been an effective strainer mechanism for gathering nutrition, consisting of pinnuliferous arms. Presumably the supply of microscopic food was an important, even limiting, ecological factor.

As with other classes of pelmatozoan echinoderms, the paleoecology of the Paracrinoidea needs more data, the morphology needs better-preserved specimens, and the classification needs discoveries to fill the gaps which we can reasonably infer between known taxa. Knowledge of these fossils has progressed slowly and sporadically. Although species have been known for more than a century, it was not until 1945 that the class was formally distinguished by Regnéll (99). Much of the classification is the work of Billings (18, 20). Articles by Foerste (47, 49, 148) added to understanding of morphology. From time to time, other writers described a new form or two, grouped genera into families, or noted additional occurrences, but their contributions were minor.

From this log of accomplishment, it is obvious that new advances will be made at such time, and only at such time, as new finds of paracrinoids come to light.

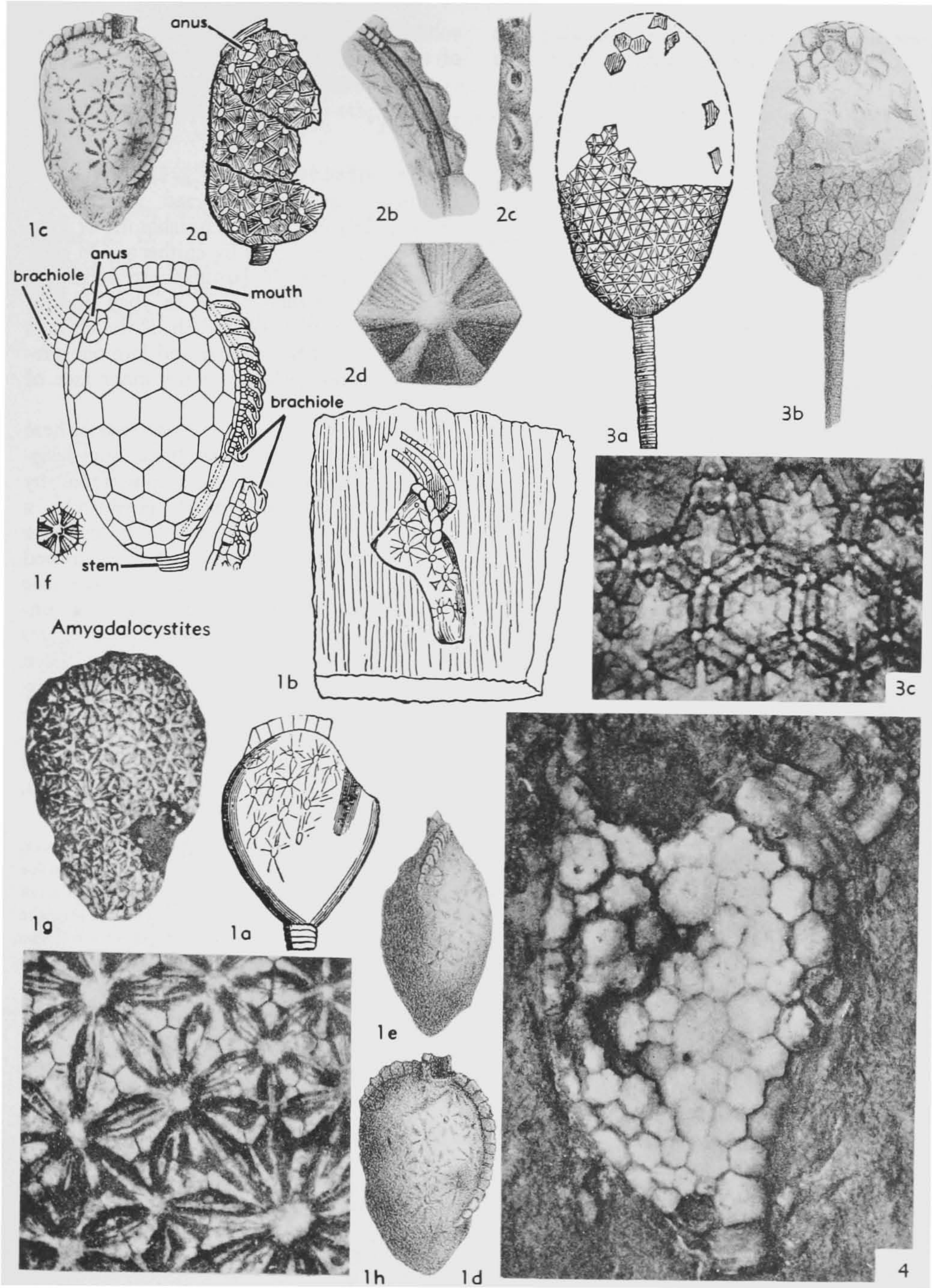


FIG. 158. Morphological features of Paracrinoidea illustrated by *Amygdalocystites,* all Middle Ordovician from Ontario; *1,* **A. florealis* BILLINGS; *2, A. tenuistriatus* BILLINGS; *3, A. radiatus* BILLINGS; *4, A. laevis* W. R. BILLINGS.

The treatment here must be considered as a summary of current concepts, not as a substantial addition to our understanding of the class.

MORPHOLOGY

PORE STRUCTURES

No pore structure is visible externally on any unweathered paracrinoid that has been investigated. The epitheca is unperforated, so that whatever pore structures are present lie in the stereotheca.

Only in certain species of *Comarocystites, Amygdalocystites* (Fig. 158), and *Canadocystis* has a concerted study of pore structures been made. This is unfortunate. In the closely related Cystoidea, the nature of pore structures is the basis for separation of the two orders. Possibly, it may prove to have greater taxonomic significance in the Paracrinoidea when more observations have been made.

COMAROCYSTITES

The thecal plates of this genus are so unusual that Billings (18-20) mentioned the external features in early descriptions. Each plate has a deep central concavity and a raised border or margin. Billings (20) said:

> In certain states of preservation the sutures are marked by minute thickly set square or oblong rough punctuations, which do not however appear to penetrate through to the interior. . . . The greater portion of the area of the plate is marked with deep fissure-like striae at right angles to the suture, and with thin erect lamellae or partitions between them. These are sometimes crossed by other lamellae parallel with the edges of the plates the effect of which is to produce a pecularly rough surface. Sometimes none of these are visible, and the surfaces of the plates are then uniformly smooth and solid. These variations are the results both of weathering and of structure.

The inner surface of thecal plates was studied in greater detail by Foerste (47). The junction where three plates meet is marked on the interior by a deep triangular pit, so that the plates are very thin at the corners. The **stereotheca** of each plate contains vertical laminae distributed in triangular areas, one area along each side; the laminae are perpendicular to the side (suture) and continuous with the laminae of the adjacent plate (Fig. 159,*1i*). The laminae thus are restricted to rhombic areas, much like the pectinirhombs of cystoids, but covered over by **epitheca**. On each plate, the areas of laminae are separated by grooves, which taper as they radiate from the center toward each of the corners of the plate. The grooves and laminae produce a stellate pattern on the inner face of the theca.

Near the interface of the two layers, here called epitheca and stereotheca, but designated as epistereom and mesostereom by Foerste (47), are paired pores. On a weathered surface from which the epitheca has been removed, each pore is expressed as a lunate groove, with its concave side facing the other pore of the pair. On unweathered surfaces, the position of pores may be marked by short lunate ridges. Each pore extends down into the plate as a circular to oblong tube leading to an interlamellar space; the two pores of a pair invariably connect with different interlamellar spaces, being separated by one lamella. According to Foerste (47),

> The right hand pore of one pair, however, usually is connected with the same inter-lamellar space as the left hand pore of the nearest adjacent pair, proximally or distally, i.e., either nearer the center of the thecal plate or nearer the suture line. In this manner, three or four pores belonging to different pairs may be connected to the same inter-lamellar space. . . . The pores penetrating the outer continuous sheet of the mesostereom are directed perpendicularly toward the suture lines between the plates, but incline more or less obliquely downward. They apparently widen in a direction parallel to the inter-lamellar spaces in passing through the outer sheet of the mesostereom, since, in strongly weathered specimens showing the inter-lamellar spaces, the latter frequently appear interrupted by transverse partitions a short distance below the outer continuous sheet of the mesostereom.

In comparison with the pore system of cystoids, therefore, *Comarocystites* may be said to have an inner set of laminae like the pectinirhombs of the Glyptocystitida, an outer epitheca concealing the pore structure like that of the Caryocystitida, paired pores like the Diploporita, an external expression of subepithecal pores like the Hemicosmitida. Such a combination of characters is unknown in any other echinoderm.

AMYGDALOCYSTITES

The inner structure of plates in this genus, as well as *Comarocystites,* was described by Foerste (47). The inner surface of each thecal plate is marked by radial ridges, in some specimens sufficiently developed to be called short plates (Fig. 158,*1h*). One ridge extends to each corner, and some paracrinoids have additional ridges to the mid-point of each side. Certain specimens have pores along the sutures, with half of each pore on one of the adjacent plates. Possibly these pores are covered over by epitheca in unweathered specimens. Either one pore occurs at the middle of each side, or two pores are on each side close to the radial ridges leading to the corners.

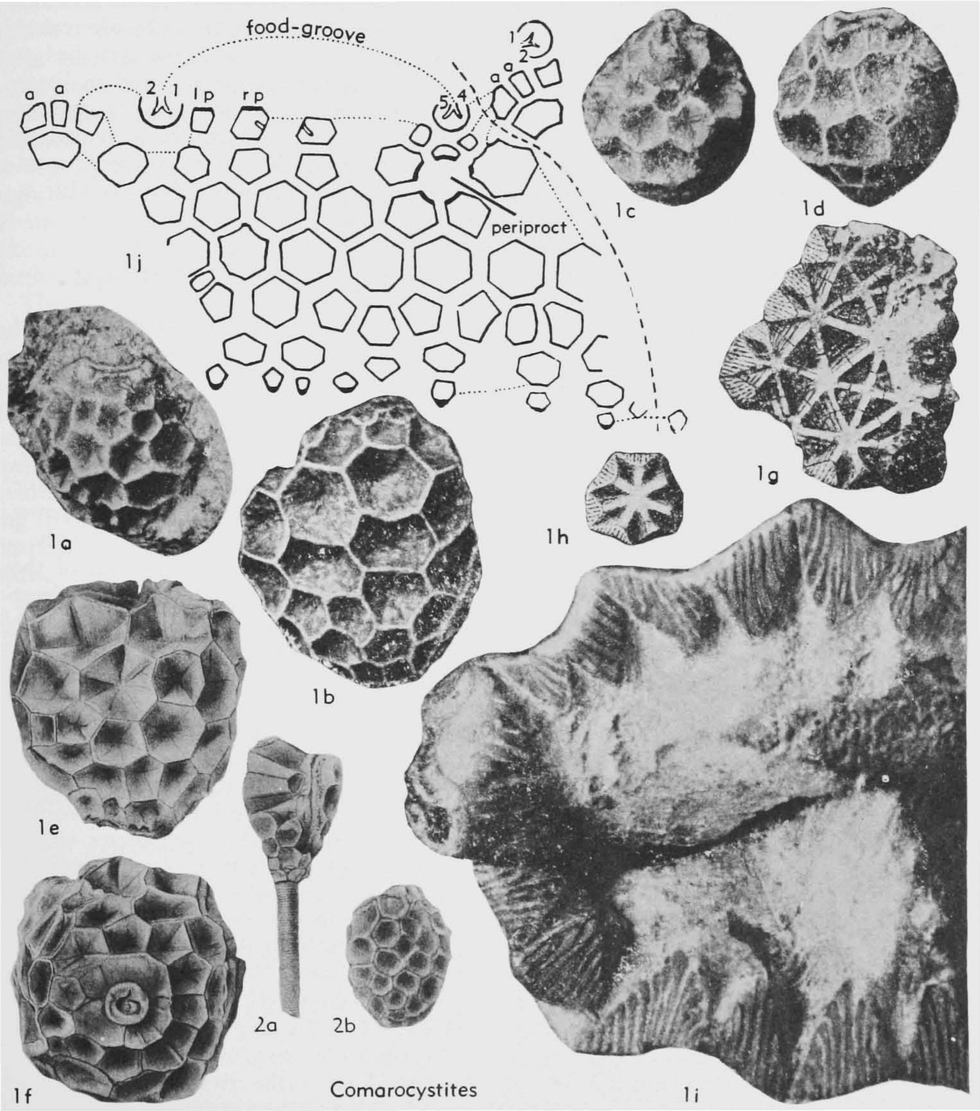


Fig. 159. Morphological features of Paracrinoidea illustrated by *Comarocystites,* all Middle Ordovician of Missouri; *1, C. shumardi* Meek & Worthen; *2, C. obconicus* Meek & Worthen.

CANADOCYSTIS

Despite the close resemblance of the theca and arms of *Canadocystis* to those of *Amygdalocystites,* the former has no radiate ridges or sutural pores on its thecal plates. Further, *Canadocystis* lacks internal lamellae, such as occur in *Comarocystites.* It apparently had no pore structure in the thecal plates, at least not in the preserved stereotheca.

The absence of any kind of pore structure in a genus that otherwise seems related to genera in which they are well developed raises a serious question as to the function and significance of such structures. We have no answer at this time.

THECA

The thecae of paracrinoids do not vary drastically. None are strongly compressed and most are somewhat globular. The periproct is not far removed from the peristome in any species. None are known to have pores visible on the exterior. Hence, a certain degree of homogeneity is present.

Thecae do exhibit variations in number of plates, ornamentation, and relationship to the arms. *Malocystites* may have as few as 30 thecal plates, and *Billingsocystis* as many as 175. *Comarocystites,* unquestionably a paracrinoid, has about 150 plates.

The ornamentation of plates can be classed in three major types: 1) plates concave, 2) plates radially ridged, and 3) plates with minor features of ornamentation. Concave plates occur in *Comarocystites* and *Sinclairocystis,* the former with free arms and the latter with attached arms. Radially ridged plates, in which ribs or ridges extend from the center to the corners of each plate, are found in *Amygdalocystites* and *Billingsocystis;* the former has attached arms and the latter, insofar as indicated in the account of Bassler (6), seems to have had free arms. Plates with smooth or slightly tuberculate surfaces occur in *Canadocystis* and probably in *Malocystites* and *Schuchertocystis.*

It appears from these data that arms (brachioles) and ornamentation have little correlation. If both kinds of arms occur with each of the three kinds of ornamentation of plates, then classification must be determined by only one character—in the *Treatise* and in previously adopted systems, the nature of the arms was the selected character.

In one group of paracrinoids, the arms rise free from the region of the mouth, being attached only by their proximal ends at facets; in the other group, the arms are attached along one edge, in somewhat the same manner as long ambulacra in certain glyptocystitidan cystoids. The attachment of plates of the ambulacral system to the thecal plates involves both kinds of plates. The integument which secreted one must have joined and fused with the integument which secreted the other. The arms that are recumbent on the theca are firmly attached to thecal plates. Insofar as reported in literature, the character of the arms is constant within a species and within a genus; no species has been discovered with some specimens having free arms and some with attached arms.

AMBULACRAL SYSTEM

No paracrinoid has more than four arms **(brachioles)** and none has pentameral symmetry of any kind. The mouth is a relatively small circular or slightly elliptical hole; it lies in the bottom of a trough which could be regarded as a peristomial groove, roofed over by biserial plates. The basic structure common to all arms is this narrow extension on opposite sides of the mouth.

The free arms rise near the end of the peristomial groove. In all forms that have been described, the groove divides at each end into short, equal, diverging ambulacral grooves leading to the arms facets. In specimens which do not have the arms preserved, the facets are seen to lie as two pairs, one pair at each end of the elongate narrow peristome. The symmetry in this group of paracrinoids is more or less bilateral, with a plane of symmetry along the center of the peristome and also with a plane across the middle of the peristome.

Paracrinoids with attached arms also possess a long narrow **peristome,** and assume their characteristic shape according to the manner in which the arms grow onto the theca from the ends of the peristome. In *Malocystites* the arms branch several times. In *Canadocystis* the two arms are about equal in size and curvature. In *Sinclairo-*

cystis the two are curved in the same direction but with sharp differences in length and degree of curvature. In *Wellerocystis* one arm divides and the other curves sharply around the periproct. In *Amygdalocystites* the arms are long and unbranched, slightly curved, with the anus (periproct) on the convex side of the nearer arm (Fig. 158,*1f*).

Except in *Malocystites,* which has nearly straight branches of the arms, the attached arms of paracrinoids are curved clockwise as viewed orally. Thus, in *Canadocystis* the whole of the attached part has the form of a large letter S. In the almond-shaped *Amygdalocystites,* the curvature is less pronounced and follows the slightly skewed edges of the biconvex theca. In *Sinclairocystis* and *Wellerocystis,* one arm is short and curved tightly in the oral region, whereas the other (branched in *Wellerocystis*) is curved more like an arm of *Amygdalocystites* and extends farther aborally.

There is a tendency among paracrinoids, much stronger than among cystoids, for the periproct to lie opposite to the attachment of the column and for the peristome to be offset onto the side of the theca. This is particularly well exemplified by numerous specimens of *Canadocystis* and *Malocystites.* No evidence is seen that such asymmetry resulting from the offset peristome-columnar axis bears any relation to differences in the two arms.

All arms are uniserial, whether attached or free. Insofar as known, each brachial gives rise to a uniserial pinnule. FOERSTE (47) reported that some pinnules did not bear extensions of the ambulacral system; that is, some lacked a groove covered by tiny plates. Pinnules are rarely found, especially in a good state of preservation, so that no general conclusion about the ambulacral extent can be drawn.

In attached arms, the pinnules issue from the convex side of the curve; thus, they join onto the left side of the arm, as viewed orally. Concerning paracrinoids with free arms FOERSTE (47) stated, "Analogy with *Amygdalocystites* and *Canadocystites* [*sic*] suggests that the pinnules of all four arms of *Comarocystites* were attached to the right side of the arms, the aboral side of each arm facing the observer, and the distal end being directed upward."

The length of free arms was estimated to be about half again the greatest diameter of the theca in *Comarocystites.* The greatest length of attached arms is about equal to the height of the theca; the arms are curved, but do not extend to the columnar facet.

HYDROPORE AND GONOPORE

The hydropore appears as a narrow, sinuous ridge with a slitlike opening along its crest. It is located near the mouth, as in Cystoidea. Nearby minute pits have been reported in some specimens but not found in others; the presence of a gonopore is not established. Nor has a hydropore been observed in *Amygdalocystites.* Additional specimens are needed to study these structures.

COLUMN

The column observed by FOERSTE (47) in *Comarocystites shumardi* seems to be complete, extending from the theca to a structure interpreted as a holdfast. Unlike the column in cystoids, this structure is of nearly constant diameter throughout its length. The columnals are very thin, alternating in thickness.

GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO PARACRINOIDEA

Relative importance of terms is indicated by the type in which they appear: first rank by boldface capital letters, second rank by boldface small letters, and third rank (including obsolete terms, terms having cross reference, and synonyms) by italic small letters.

abactinal. See aboral.

aboral. Located away from mouth; used in a general way to indicate position of column, although mouth and column are not directly opposite in most paracrinoids.

actinal. See oral.

adoral. Located toward mouth.

ambulacral. Referring to food-gathering system.

ambulacral covering plates. Small plates arranged biserially and covering over ambulacral grooves in arms and pinnules.

ambulacral groove. Groove through which food was conveyed from pinnules through arms to mouth, a trough covered by movable ambulacral covering plates.

ANAL PYRAMID. Valvular structure of triangular plates in periproct, serving to close anus.

anterior. Located on side of theca opposite hydropore or gonopore, or both.

anus. Exit of alimentary canal or gut.

ARM. Main branch of ambulacral system, composed of uniserial brachials and bearing pinnules; in some paracrinoids arms are free, attached to theca only at their proximal ends; but in others, arms are attached, one edge being fastened to thecal plates.

attached arm. Arm fastened to thecal plates by one edge, with pinnules extending from opposite edge; such arm lies on thecal surface much as ambulacrum of a cystoid.

basal. Part of theca near base.

base. Aboral part of theca, that to which column is attached.

BRACHIAL. One of uniserial plates in arm.

COLUMN. Stemlike structure attached to aboral end of theca, used for anchorage of paracrinoid; distal end in some modified into disc-shaped holdfast.

columnal. Unit composing column.

columnar facet. Indentation in basal plates to accommodate proximal end of column.

covering plate. See ambulacral covering plate *and* peristomial covering plate.

epistereom. See epitheca.

EPITHECA. Thin, nonporous layer on outside of thecal plates.

exothecal. Outside of theca; secreted by integument not secreting thecal plates, especially applied to arms and pinnules.

food groove. See ambulacral groove.

free arm. Arm attached to theca only by its proximal end.

genital pore. See gonopore.

GONOPORE. Small opening or aperture in posterior region, close to mouth, penetrating thecal plates; presence of a gonopore has not been established in all paracrinoids.

holdfast. Disclike structure at distal end of column in some paracrinoids, presumably for attachment; no evidence on permanence of such attachment has been offered.

HYDROPORE. Opening or openings through thecal plates in posterior part of theca near mouth; presence of a hydropore not established for all paracrinoids.

integument. Supposed exterior layer of tissue in paracrinoids which secreted thecal and other plates, similar to layer known in living echinoderms.

lamina. Vertical plate of stereotheca, developed in some paracrinoids.

lateral. Located on side of theca.

madrepore. See hydropore.

mesostereom. See stereotheca.

MOUTH. Aperture at oral pole through which food entered body from ambulacral system; small circular opening in peristomial structure, lying in bottom of trough-shaped ambulacral groove, roofed over by covering plates.

oral. Associated with mouth.

oral pole. End of theca containing mouth.

ornamentation. Surficial features of thecal plates.

PERIPROCT. Major thecal opening containing anal pyramid.

PERISTOME. Major structures associated with mouth; used by Foerste (1916) to include the "transverse apical food-groove," troughlike part of ambulacral system extending on either side of mouth and continuous with arms; peristome is covered by peristomial covering plates.

peristomial covering plate. Any of small plates covering mouth and continuous with ambulacral covering plates of arms; peristomial covering plates may have been immovable.

pinnular. Any uniserial plate composing pinnule.

PINNULE. Terminal structure of ambulacral system, attached to arm, composed of uniserial pinnulars and biserial covering plates.

plate. Any calcareous secretion forming structural unit in paracrinoid.

pore. Perforation in thecal plate but not reaching exterior; pores present in some paracrinoids, not in others.

posterior. Part of theca containing hydropore; sector of paracrinoid in which hydropore is located.

recumbent. See attached arm.

skeleton. All carcareous parts of paracrinoid.

stem. See column.

STEREOTHECA. Inner layer of thecal plate, in some composed of vertical laminae; stereotheca houses all of pore structure present in paracrinoids.

subvective appendage. See arm.

subvective groove. See ambulacral groove.

suture. Contact between two plates; boundary line marking junction of two plates.

THECA. Plated structure housing body of paracrinoid.

THECAL PLATE. One of skeletal units comprising theca.

water pore. See hydropore.

CLASSIFICATION

Taxonomy of the Paracrinoidea is not yet satisfactory. The treatment of the class here merely summarizes the classification that has been developed to date.

The paracrinoids that were described by Billings(18) in 1854 later were simply assigned by him to the "Cystideae" along with such cystoids as *Glyptocystites* and *Pleurocystites.* For nearly half a century, the paracrinoids were not differentiated from other pelmatozoans. Then Bather (9) created the families Comarocystitidae and Malocystitidae, which he placed in the order Rhombifera of the class "Cystidea." He defined the two families as follows:

> Fam. Comarocystidae. Thecal plates numerous, indefinite, with strong radial structure of stereom, but no pore-rhombs. Brachioles branched; columnals uniserial.
>
> Fam. Malocystidae. Thecal plates numerous, indefinite, radiately folded, no rhombs. Food grooves on exothecal processes pass over theca and bear brachioles.

It will be noted that the arms are called by Bather the "brachioles" in the Comarocystitidae and the "exothecal processes" in the Malocystitidae. According to this classification, the two families have in common numerous thecal plates of irregular arrangement and both lack pore rhombs; they differ in ambulacral arrangement.

In defining the Carpoidea, Jaekel (70) separated out one order, named Eustelea, to contain the paracrinoids. He distinguished those with attached arms as the suborder Varicata and those with free arms as the suborder Brachiata. This system is retained here as the best that has been proposed to date. In addition, Jaekel (70) distinguished the family Amygdalocystitidae, which he differentiated from the Malocystitidae by the presence of unbranched arms.

Foerste (47) was the first to study intensively the morphology of paracrinoids. He examined *Comarocystites* in particular, and compared its pore structure with that of *Amygdalocystites* and *Canadocystis.* Despite his contributions to morphology, Foerste offered little on taxonomy except to state that *Comarocystites* and its allies, because of their arm structure, were not normal cystoids.

In 1918, in his revision of the classification of pelmatozoan echinoderms, Jaekel (71) assigned *Malocystites* to the questioned order Deviata of the subclass Eocrinoidea of the class Crinoidea. As related forms, he mentioned *Amygdalocystites* and *Comarocystites.* Under the latter, he expressed doubt about position, and suggested that the uniserial condition of the ambulacral system, if established, might open possibilities of relationship to the "higher" Crinoidea, rather than Eocrinoidea. Evidently Jaekel was unaware of Foerste's work published two years previously; this would not be surprising, for the time was during World War I.

Bassler (5) and Bassler & Moodey (7) reverted to certain of Bather's (9-12) concepts of pelmatozoan classification. The class Cystoidea was maintained as a greatly expanded taxon. In the order Amphoridea were placed the families Malocystitidae and Comarocystitidae. *Amygdalocystites* was relegated to the Malocystitidae. Hence, no notice was taken of either Jaekel's (70) separation of these forms from the cystoids or his creation of the family Amygdalocystitidae. The taxonomy was not discussed in the two publications.

Regnéll (99) introduced the class Paracrinoidea, to which he assigned with certainty only *Comarocystites, Amygdalocystites,* and *Canadocystis,* defining the new class as follows:

> A class of Pelmatozoa, the plate-system of which is not affected by polymeric symmetry and shows no differentiation into a calycinal and a tegminal portion; the exothecal subvective skeletal appendages are developed as uniserial brachia (free or recumbent) bearing uniserial pinnulae; a subepithekal pore-system is present in typical forms.

Bassler (6) described numerous pelmatozoans, including paracrinoids. Unfortunately, his diagnoses tend to be cryptic and his illustrations leave details to be desired. Many of the characteristics described in the fossils are insignificant and many diagnostic features are omitted. Restudy is needed.

Characteristics of paracrinoid genera are listed in Table 1, in which genera are listed in order of geologic appearance. As shown in figures in the Systematic Descriptions, remarkable resemblances exist between the thecal plates of *Comarocystites* and Bassler's *Sinclairocystis.* They suggest that ornamentation (or external form) of thecal plates may have suprageneric value. In Table 2, therefore, genera are grouped according to plate ornamentation.

The classification adopted in the *Treatise* is based on Jaekel's (71) concept of the importance of the manner in which arms are attached. In Table 3, the grouping of genera follows the taxonomy and offers a simple key for practical identification. It will doubtless be modified when paracrinoids are better understood.

TABLE 1. *Characters of Paracrinoid Genera.*

Genera	Shape of Theca	*No. Plates	Arms	Branching	Pore System	Plate Surface	Age
Malocystites	globular	30	attached	both	?	smooth	Chazy.
Canadocystis	globular	30	attached	none	none	smooth	Chazy.
Wellerocystis	ovate	40	attached	one	?	smooth	Blackriv.
Schuchertocystis	ovate	35	free	?	lamellae?	smooth	Blackriv.
Sinclairocystis	globular	30	attached	none	?	concave	Blackriv.
Comarocystites	ovate	150	free	?	lamellae in rhombs	concave	Blackriv.
Amygdalocystites	biconvex	90	attached	none	rad. ridges, marg. pores	ridged	Trenton.
Billingsocystis	globular?	175	free	?	?	ridged	Trenton.

* Typical or average number of plates.

TABLE 2. *Grouping of Paracrinoids According to Plate Ornamentation.*

Concave; centers smooth, the margins elevated as flat rims bearing quadrate pits or punctae	Arms attached		*Sinclairocystis*
	Arms free		*Comarocystites*
Convex; central boss or umbo from which ridges radiate to the corners	Arms attached		*Amygdalocystites*
	Arms free		*Billingsocystis*
Convex; smooth, papillose, or tuberculate, no radial elements	Arms free		*Schuchertocystis**
	Arms attached	Both arms branched	*Malocystites*
		One arm branched	*Wellerocystis*
		Neither arm branched	*Canadocystis*

* Some doubt persists as to the original surface of thecal plates; holotype (only specimen known) may be weathered, to judge from BASSLER's (6) description and figures.

TABLE 3. *Grouping of Paracrinoids According to Character of Arms.*

Order VARICATA: arms attached	Family Malocystitidae: arms branched	Both branched		*Malocystites*
		One branched		*Wellerocystis*
	Family Amygdalocystitidae: arms unbranched	Theca compressed		*Amygdalocystites*
		Theca globular	Plates convex	*Canadocystis*
			Plates concave	*Sinclairocystis*
Order BRACHIATA, Family Comarocystitidae: arms free	Thecal plates few			*Schuchertocystis*
	Thecal plates numerous	Plates concave		*Comarocystites*
		Plates radiate		*Billingsocystis*

SYSTEMATIC DESCRIPTIONS

Class PARACRINOIDEA Regnéll, 1945

[Paracrinoidea Regnéll, 1945, p. 37] [=Eustelea Jaekel, 1900, p. 673; Deviata Jaekel, 1918, p. 27]

Calcareous plates encasing body constituting a theca, not differentiated into dorsal calyx and ventral tegmen; thecal plates variable in number, irregularly arranged, those of some species provided with pore structures in inner layer; theca invariably anchored by column of thin uniserial disc-shaped columnals. Ambulacral system made up of uniserial arms bearing uniserial pinnules. Arms may be free or attached on thecal surface, not more than four arms known in any species, although one or more arms may branch; ambulacral grooves covered by tiny plates, may not extend to ends of all pinnules. Hydropore present in some forms, not found in others; gonopore reported in some, not definitely established. Many forms with periproct opposite columnar facet and peristome offset to one side; periproct provided with anal pyramid. *M. Ord.*

Regnéll (99) first set these echinoderms apart as a distinct class, although the taxon was essentially constructed by Jaekel (70) when he placed the genera in his order Eustelea of the class Carpoidea. It seems preferable to use the name proposed by Regnéll.

The late erection of the class may be attributed to the poor state of knowledge concerning these pelmatozoans. Contrasts with other groups were not sufficiently clear to suggest that paracrinoids would be better fitted into the taxonomic pattern as a new class. Even now, essential information on many genera is not available.

The paracrinoids differ from crinoids in having a theca of irregular plates, from cystoids in having uniserial appendages, from blastoids in lacking symmetry and hydrospires, and from "carpoids" in having a uniserial column and less strongly compressed theca. The taxon is not very well known or understood. It suffers the disadvantage of inheriting all the problem genera of pelmatozoans after the cystoids, blastoids, crinoids, "carpoids," edrioasteroids, and eocrinoids were removed. The array of known forms emphasizes the paucity of the record. The ancestors of the paracrinoids are unknown, the diversity and evolutionary trends are incompletely founded, and morphology has not been studied at all in most species. The taxonomic divisions presented here are subject to revision whenever and as soon as new, reliable information is set forth.

Key to Orders and Families of Paracrinoidea

1. Arms attached to thecal surface (Order Varicata) 2
   Arms free (Order Brachiata) .... Family Comarocystitidae
2. Arms branched, spread out over theca .... Family Malocystitidae
   Arms unbranched, two simple curved rays, together forming a sort of S .... Family Amygdalocystitidae

The key stresses the fact that taxonomic divisions adopted here are based on the nature of the arms. Of greater significance, one would expect, is nature of the pore system. Unfortunately, this has not been studied in the majority of paracrinoids. When it is established, however, there can be little doubt that it will provide a substantially different taxonomic grouping of the genera. Still other divisions could be made by considering first the number of thecal plates; in *Amygdalocystites,* some species have few and other species have many plates, so that the number does not seem to have much taxonomic value, at least in this genus.

Order VARICATA Jaekel, 1900

[Varicata Jaekel, 1900, p. 674]

Arms recumbent, attached to theca. *M. Ord.*

Family MALOCYSTITIDAE Bather, 1899

[*nom. correct.* Bassler, 1938, p. 9 (*pro* Malocystidae Bather, 1899, p. 920)]

Arms branched, spread out over theca. *M.Ord.*

Key to Genera of Malocystitidae

Both arms branched, branches spreading over theca without regular curvature .. *Malocystites*

Only one arm branched, with all branches curved toward right; unbranched arm coiled about periproct .... *Wellerocystis*

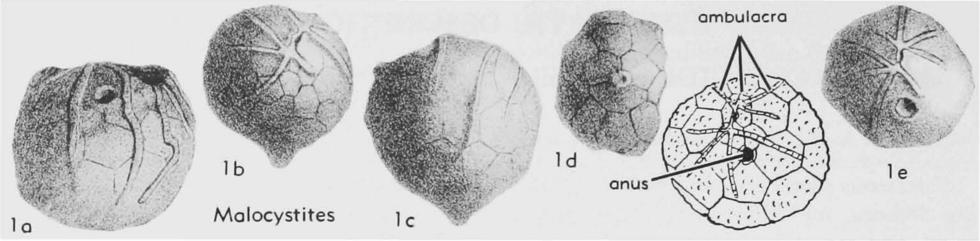


FIG. 160. Varicata (Malocystitidae) (p. S278).

Malocystites BILLINGS, 1857, p. 302 [**M. murchisoni;* OD] [=*Malocystis* CARPENTER, 1891, p. 27 *(nom. van.)*]. Theca globular, composed of about 30 irregularly distributed polygonal plates. Peristome consisting of transverse trough roofed by small plates, from each end of which 2 recumbent arms branch quickly, several long branches of each extending over theca without discernible pattern of curvature, arms uniserial, but distribution and nature of pinnules unknown; peristome not directly opposite columnar attachment or facet in known specimens; instead, peristome offset and periproct more nearly diametrically opposite column; thecal plates more or less smooth. [HUDSON (1916) stated, "Most specimens of *Malocystites* when rolled on a table come to rest with the food-collecting field uppermost."] *M.Ord.*, N.Am. (Que.-N.Y.).——FIG. 160,*1*. **M. murchisoni,* Aylmer F., Que.; *1a-e,* 3 lat., aboral, and oral, ×1 (Billings, 1858); *1f,* incl. oral, ×1 (70).

Wellerocystis FOERSTE, 1920, p. 36 [**W. kimmswickensis;* OD]. Theca ovoid, not compressed in any way, composed of about 40 polygonal plates of various sizes and shapes. Basals 3; other plates tending to be disposed in oblique rows parallel to direction of distal ends of arms; surface of plates relatively smooth, without radiate folds. Arms 2, one which remains undivided encircling periproct, other bifurcating almost immediately beyond peristome, so that the genus may be conveniently said to have 3 arms. In comparison with *Canadocystis,* this genus has added arm on left side of that opposite periproct and it has periproct on concave side of nearby arm instead of its convex side. As in *Amygdalocystites* and *Canadocystis,* curvature of arms is clockwise in oral view, and facets for pinnules are invariably on convex side of curved ambulacral grooves. Arm encircling periproct has about 5 facets; on opposite arm, left branch has about 10 and right branch about 8. Pinnules not known. Mouth elongate in direction of peristome connecting opposite arms, about 0.25 mm. wide and 1 mm. long in theca 20 mm. high. Periproct diametrically opposed to columnar facet. Hydropore and gonopore not known. *M.Ord.*, USA(Mo.).——FIG. 161,*1*. **W. kimmswickensis*; *1a,b,* lat. and oral, ×1; *1c,* plate diagram (148).

Family AMYGDALOCYSTITIDAE Jaekel, 1900

[*nom. correct.* KESLING, herein (*pro* Amygdalocystidae JAEKEL, 1900, p. 675)]

Recumbent arms on theca unbranched. *M.Ord.*

Key to Genera of Amygdalocystitidae

1. Theca almond-shaped, compressed; numerous (more than 80) plates in some species; thecal plates ornamented by central boss or umbo from which ridges radiate to corners .... *Amygdalocystites*
   Theca globular or slightly compressed, never almond-shaped with angular edge; plates few (seldom exceeding 50); plates not radially ridged 2
2. Plates convex; the surface smooth, slightly papillose, or tuberculate .... *Canadocystis*
   Plates concave; centers smooth, margins adjacent to sutures elevated as flat rim bearing quadrate pits or deep punctae (not perforating full thickness of plate) .... *Sinclairocystis*

Amygdalocystites E. BILLINGS, 1854, p. 270 [**A. florealis;* OD] [=*Amygdalocystis* CARPENTER, 1891, p. 27 *(nom. van.); Ottawacystites* WILSON, 1946, p. 14 (type, *Amygdalocystites florealis laevis* W. R. BILLINGS, 1883)]. Theca almond-shaped (hence generic name), compressed, with sharp boundary or edge where 2 sides join. About 90-180 thecal plates, each ornamented by radial ridges extending from center to each corner; on inner surface also, plates bear radial ridges, one to each corner and, in some specimens, another to middle of each side. [FOERSTE (1916) reported that "in some specimens pores exist along the sutures between the plates, either a single pore at the middle of each side, or two pores along each side, close to the radial ridges extending to the angles of the plate. Half of each pore occurs on half of each of the adjoining plates." These pores were probably originally concealed by epitheca. The two arms extend more or less along the sharp edges of the theca and are slightly curved clockwise in oral view; therefore, the theca is not

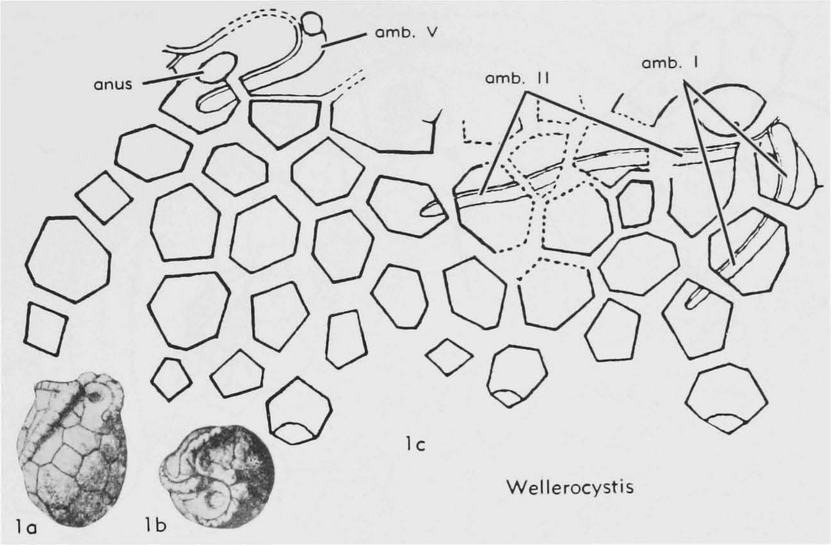


Fig. 161. Varicata (Malocystitidae) (p. *S*278).

simply biconvex but is twisted or skewed by several degrees. From each of the uniserial arms, uniserial pinnules are attached to facets on the convex side. The ambulacral extension lies facing the mouth on one of the narrower sides of the compressed pinnule. The facets supporting the pinnules are indented on the side where the branch from the main ambulacral groove passed on the base of the attached pinnule.] Periproct on convex side of nearest arm. Hydropore and gonopore not known. *M.Ord.*, N.Am.(Ont.-Que.-Ky.).——Fig. 158,*1a-h*. **A. florealis*, Hull Ls., Ont.; *1a,b*, lat., theca and fragment with pinnules, ×1 (18); *1c-e*, 3 lat., × (20); *1f*, theca with detail of plate (left) and arm (right), sl. enl. (10); *1g,h*, theca, ×1, and detail of plates, ×4 (141).——Fig. 158,*2*. *A. tenuistriatus* Billings, Hull Ls., Can.(Ont.); *2a*, lat., ×1 (18); *2b,c*, 2 views of arm, enl.; *2d*, thecal plate, enl. (20).——Fig. 158, *3*. *A. radiatus* Billings, Hull Ls., Can.(Ont.); *3a*, lat., ×1 (18); *3b*, lat., ×1 (20); *3c*, detail of plates, ×4 (141).——Fig. 158,*4*. *A. laevis* W. R. Billings, Hull Ls., Can.(Que); lat., ×4 (141).

Canadocystis Jaekel, 1900, p. 675 [**Malocystites barrandi* Billings, 1858, p. 67 (=*M. barrandei*, *nom. correct.* Kesling, herein); OD] [=*Sigmacystis* Hudson, 1911, p. 254 (type, *Malocystites emmonsi* Hudson, 1905)]. Theca globose or ovoid to subpyriform, basal part somewhat produced. Theca composed of about 30 to 40 polygonal plates of variable sizes, shapes, and arrangement, many thecae containing a few small diamond or triangular plates, most other plates irregularly pentagonal, hexagonal, or septagonal; basal plates 3, of which 1 is conspicuously smaller than other 2; theca variously ornamented by few scattered umbos on larger plates with connecting ridges and by granulations on all plates; large umbo between periproct and base in *C. emmonsi*. Finer radiating ridges may branch and cross sutures to form very fine reticulations. Inner surface of thecal plates relatively smooth, lacking pores or lamellae of any kind. Mouth not directly opposite columnar attachment; in *C. emmonsi*, periproct, opposite column and mouth strongly offset to one side; in *C. barrandei*, eccentric position of mouth not as strongly emphasized. Peristome slightly elevated in *C. barrandei*, set upon neck in *C. emmonsi*. The 2 arms and peristome combined forming an S, called by Hudson (149) the "sigma." Oral region of theca made up of 4 main plates or orals: 2 small plates in posterior and anterior positions (normally slightly offset clockwise around mouth), and 2 large semicircular plates filling each side of peristomial region, each bearing one arm. Arms uniserial, plates decreasing in size distally; each plate with its outer border convex, so that arm has scalloped edge. From each C-shaped ambulacral groove, short extensions on outer side of curve lead to facets for attachment of pinnules, which are unknown. Periproct rather small, set high on theca, bordered by 4 or 5 plates. Hydropore probably small roughened mound at junction of 3 plates: small posterior oral, large arm-supporting oral to right, and plate of circlet of 6 supporting the orals (one which curves aborally to the periproct). Gonopore reported to be small perforation through posterior oral, not said or shown to lie along a suture, as does the gonopore of cystoids. Column very small; column of *C. emmonsi*, at least, bent rather abruptly backward next to theca. [According to

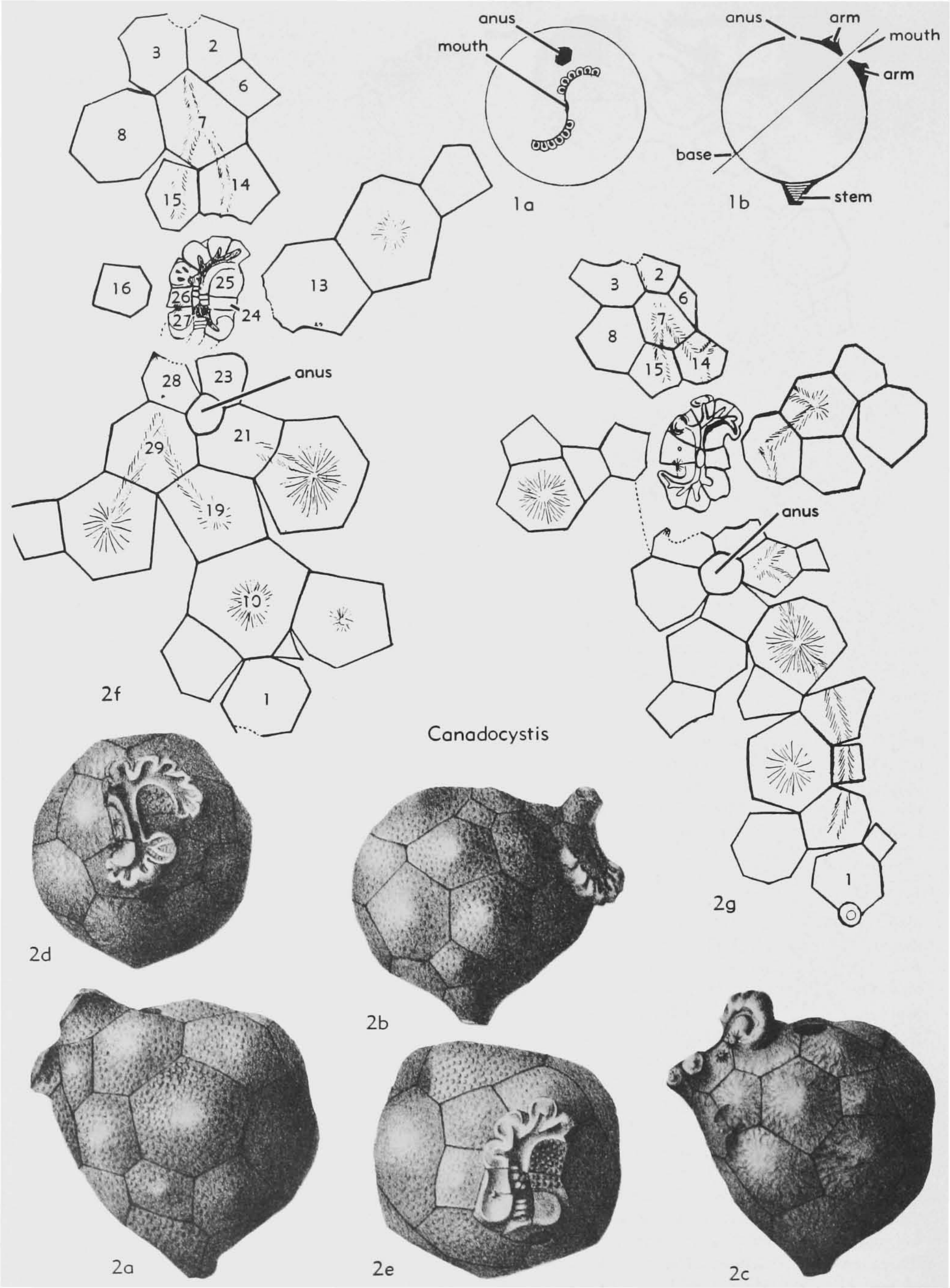


FIG. 162. Varicata (Amygdalocystitidae) (p. *S*279, *S*281).

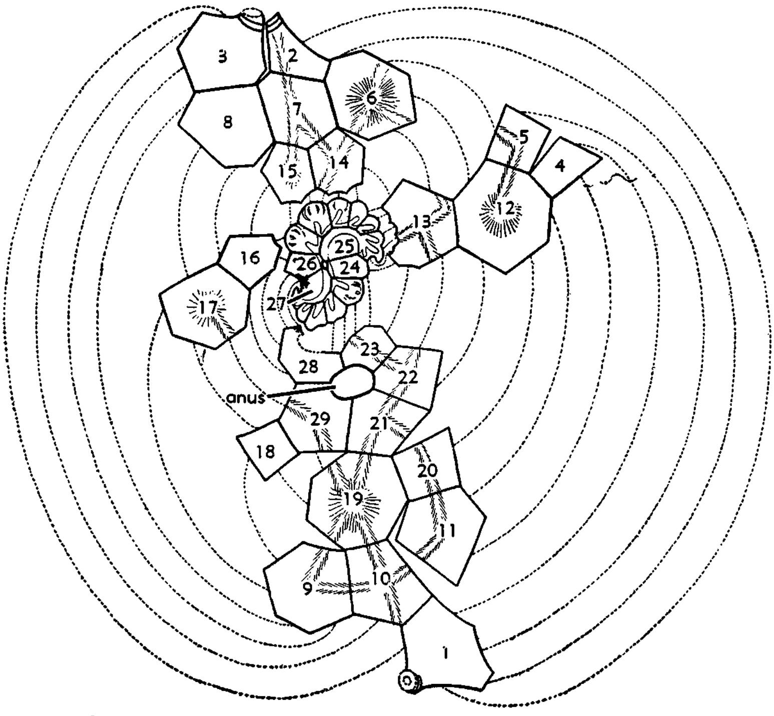


Fig. 163. Varicata (Amygdalocystitidae) (p. *S*279, *S*281).

Hudson (149), "The stem appears to have been short and used perhaps as an anchor but not for complete support"; he also suggested that the ancestors of these paracrinoids "were once supported by the stem alone and had their arms in a normal position, but that descendants with weak stems often found themselves let down to the ocean floor and had to make shift to live under adverse conditions. Increased growth of the posterior plates or decreased growth of the anterior plates would have brought the arms again uppermost and given rise to a form like that shown here."] In proximal section of column, lumen is round and about half diameter of columnals. Species of this genus are marked by strong individual variations in plate arrangement, number of plates, plate shapes, ornamentation, and other features. *M.Ord.*, N.Am.(Que.-N.Y.).——Fig. 162,*1*. **C. barrandei* (Billings), Aylmer F., Que.; *1a,b,* oral diagram and vert. sec. (20).——Fig. 162,*2*; 163,*1*. *C. emmonsi* (Hudson), Chazyan, N.Y.; 162,*2a-e,* 3 lat. and 2 oral, X4 (149); 162,*2f,g,* 2 plate diagrams (149); 163,*1*, plate diagram with dotted lines connecting adjacent edges (149).

Sinclairocystis Bassler, 1950, p. 276 [**S. praedicta*; OD]. Theca irregularly ovoid, composed of about 30 to 60 plates according to species, 3 basals and 4 plates bordering periproct in all specimens described; plates concave, with edges raised in rim or margin which contains very numerous rectangular deep pits (*S. praedicta, S. angulata*) or fewer circular pits *(S. sulphurensis)*, which may not penetrate into "body cavity," as suggested by Strimple (1952), but instead may constitute well-developed ornamentation (evidently true for *Comarocystites*); interior of thecal plates unknown. Two arms, both attached to theca, differently developed, one arm passing close along left side of periproct, looping clockwise (as seen orally), and in some species terminating high on theca; other arm longer, nearly vertical, extending in opposite direction from first, and nearly or quite reaching column in some species; each arm composed of relatively thick brachials, with pinnule attached to each brachial. Peristome not as strongly protuberant as arms, more or less expressed as saddle. Hydropore apparently a small pustule set very close to peristome. Gonopore unknown. Periproct filled by anal pyramid, set nearly diametrically opposite column. [In *S. sulphurensis,* the anterior side has fewer and much larger thecal plates than the posterior, with only 2 or 3 plates between the basals and

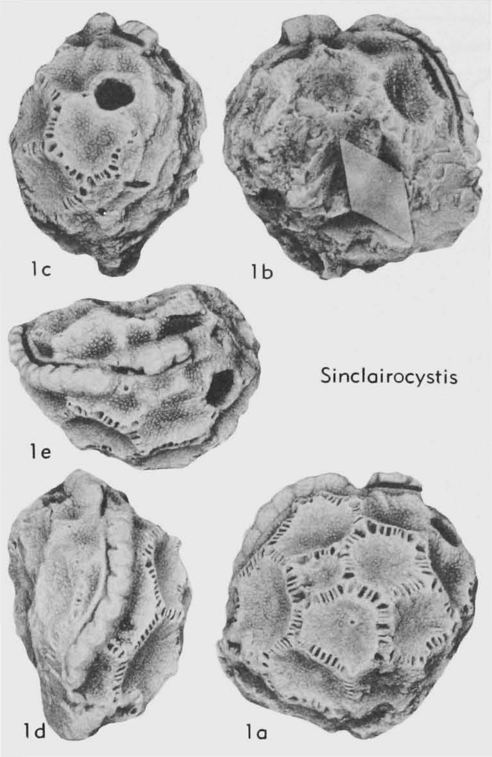


FIG. 164. Varicata (Amygdalocystitidae) (p. S281-S282).

circumperiproctal plates]. *M.Ord.*, USA(Okla.).——FIG. 164,*1*. **S. praedicta*, Bromide F.; *1a,b,* side with hydropore and opposite side; *1c,* side with anus showing partly exfoliated arm at right; *1d,* side showing longer arm; *1e,* oral view showing arms and small hydropore; all ×2 (Kesling, n).——FIG. 165,*1*. *S. sulphurensis* STRIMPLE, Bromide F.; *1a-d,* lat. views, ×4 (152).——FIG. 165,*2*. *S. angulatus* STRIMPLE, Bromide F.; *2a-d,* lat. views, ×2.5; *2e,* oral view, ×2.5 (152).

Order BRACHIATA Jaekel, 1900

[Brachiata JAEKEL, 1900, p. 276]

Arms free above their proximal attachment to theca. *M.Ord.*

Family COMAROCYSTITIDAE Bather, 1899

[*nom. correct.* BASSLER, 1938, p. 9 (*pro* Comarocystidae BATHER, 1899, p. 920)]

Characters of order. *M.Ord.*

At present the order Brachiata is undivided. Until the basis for paracrinoid classification is more firmly decided, it is not advisable to introduce more families.

Key to Genera of Comarocystitidae

1. Thecal plates few (about 30 to 40) .... *Schuchertocystis*
   Thecal plates numerous (more than 70) 2
2. Thecal plates deeply concave, their margins punctate (at least in worn specimens) .... *Comarocystites*
   Thecal plates highly irregular polygons, with radiating ridges to corners .... *Billingsocystis*

Comarocystites BILLINGS, 1854, p. 268 [**C. punctatus*; OD] [=*Comarocystis* CARPENTER, 1891, p. 27 (*nom. van.*)]. Theca obovate, some attaining length of 75 mm., composed of about 150 plates (in type species) to about 65 (in *C. shumardi*); as many as 15 plates in the basal circlet, number and shape of plates variable, only those around peristome and periproct exhibiting considerable degree of fixity in number, position, and general outline. [According to FOERSTE (47), in the type species "certain tendencies may be observed even among these other thecal plates. For instance, the plate directly below the middle of the anal pyramid, but not in contact with the latter, is pentagonal in form, and has its upper angle inserted between the two plates forming the lower border of the pyramid. Directly beneath this pentagonal plate is a series of hexagonal plates which, instead of forming a strictly vertical row, are arranged along a line which curves moderately toward the front on approaching the base of the theca. Parallel to this series of plates, on its anterior side, are similar series of hexagonal plates, causing the anterior side of the theca to present the appearance of diagonally intersecting rows, with the angles of the thecal plates directed toward the top of the specimen. On the posterior side of the theca, a similar tendency toward the arrangement of plates in rows causes one of the sides of the hexagonal plates, rather than one of its angles, to face the top of the specimen."] Plates bordering peristome (in *C. punctatus*) include 2 on anterior side, about equal in size, their common suture located about midway on side of peristome and perpendicular to it, right anterior plate more or less obliquely hexagonal, and left posterior plate pentagonal; posterior edge of peristome also bordered by 2 plates, that at right hexagonal, occupying about 0.7 of border, much larger than small, quadrangular plate at left, right plate containing part of the hydropore. Periproct bordered by 5 thecal plates, 2 on aboral side, 2 lateral, and 1 inserted between periproct and nodular facets for right pair of arms; plate on right side invariably largest. Exterior surface of plates deeply concave, inner surface more or less stellately convex, cross sections perpendicular to mid-points of sutures showing that inner surface presents almost straight line from center of one plate to center of next, but toward angles where 3 plates meet, inner surface curves outward so strongly that deep triangular pits mark these junctions on interior; epithecal layer of plates thin and nonporous; greater part of stereotheca forming vertical lamellae which are not radial but perpendicular to sutures, lamellae in each sector of given plate being thus parallel and filling triangular space; they are continuous with lamellae of adjacent plates, forming rhombs on interior of theca; where epitheca is weathered away, short lunate pores are revealed in outermost part of stereotheca, extending parallel to epitheca and just beneath it, expressed on weathered stereotheca as short lunate grooves, of which concave sides of each pair face each other; presence of these pores may be indicated on exterior of epitheca by short lunate ridges; 3 or 4 series of pores may occur between center and sides of plate, the pairs of different series alternating in position, each lunate pore connected near its distal end with circular pore or tube leading to an interlamellar space; pores of pair invariably connecting with different spaces, being separated by one lamella. Peristome con-

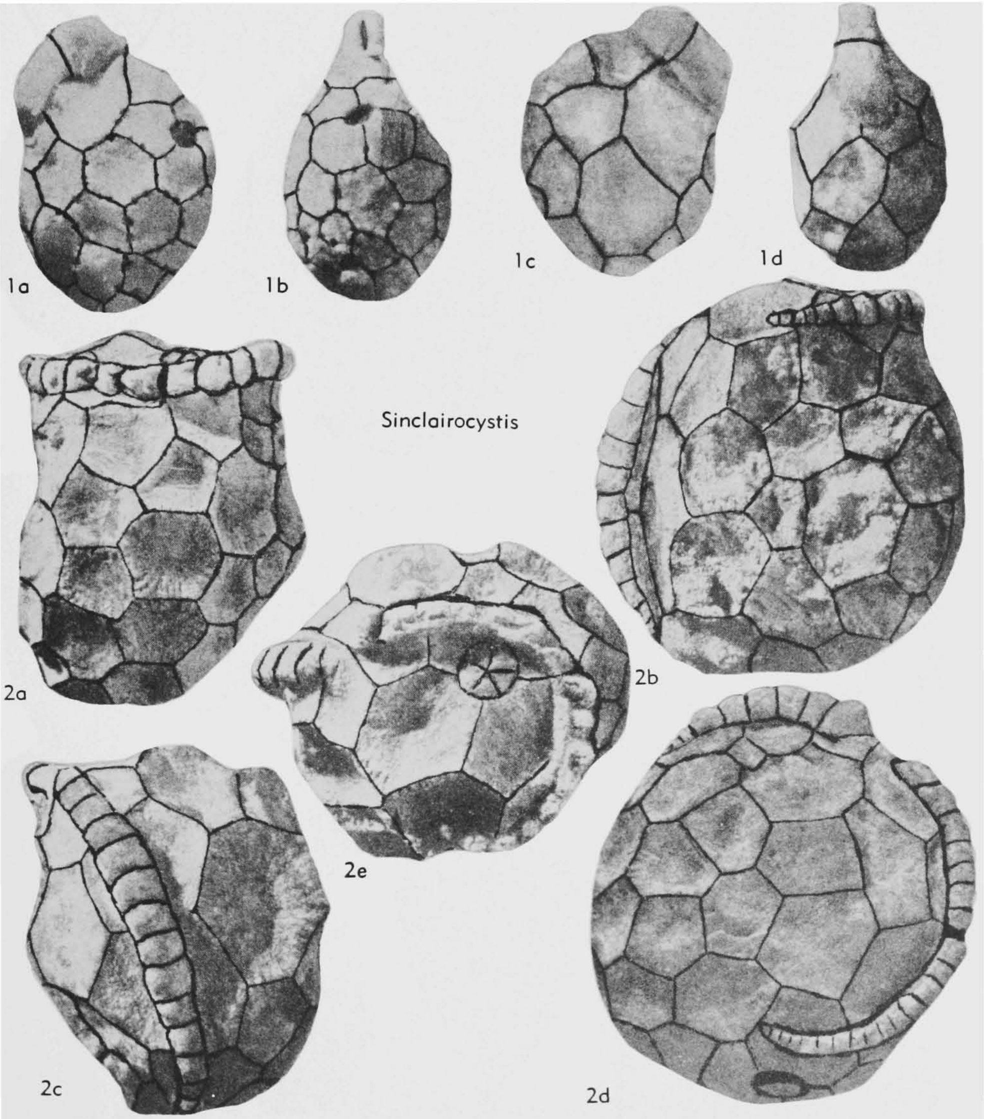


FIG. 165. Varicata (Amygdalocystitidae) (p. S281-S282).

stituting a “transverse apical food-groove” (Foerste, 1916), covered by biserial covering plates meeting along center line to form acute ridge. Mouth a small circular or oval opening

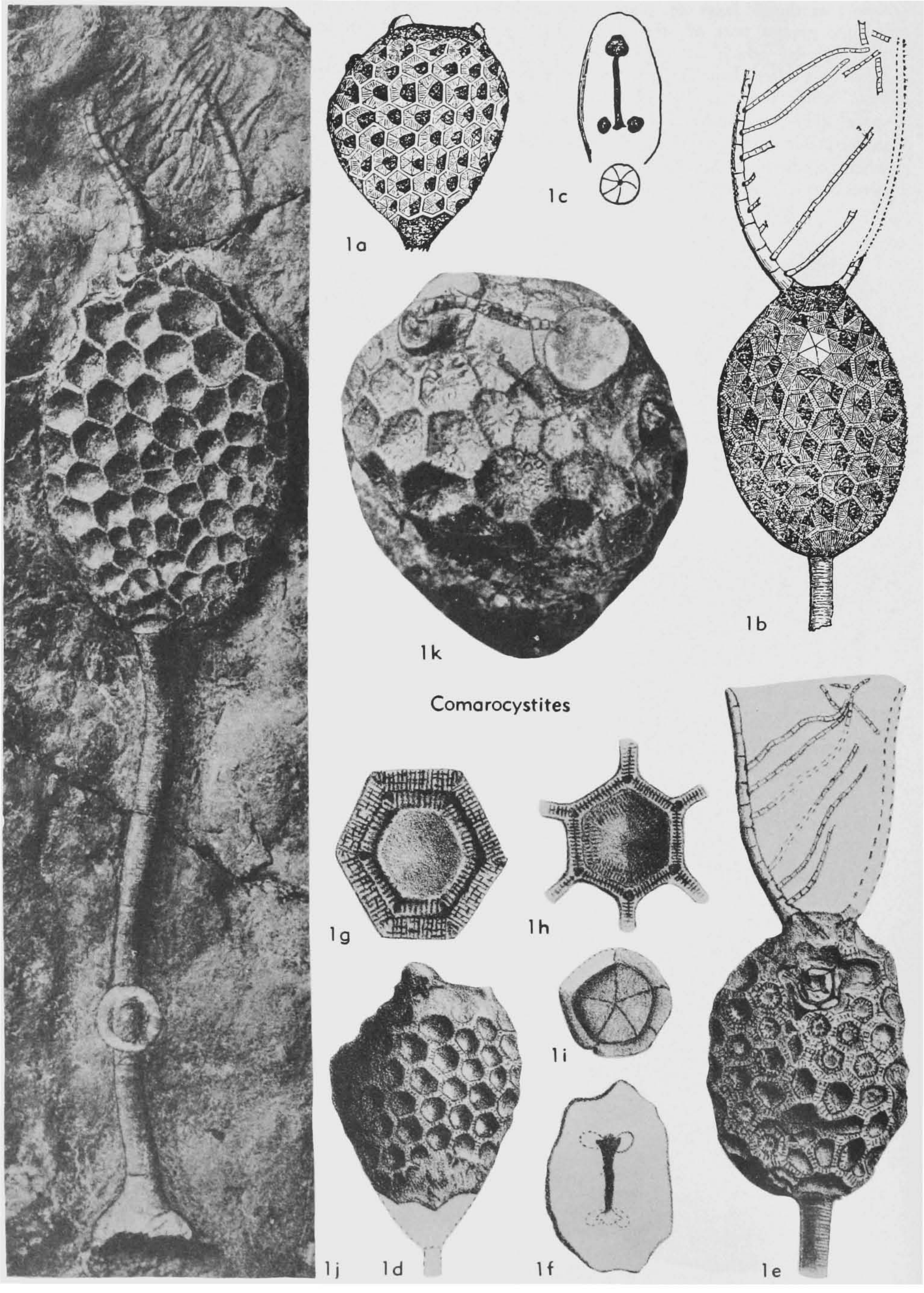


Fig. 166. Brachiata (Comarocystitidae) (p. *S*282-*S*287).

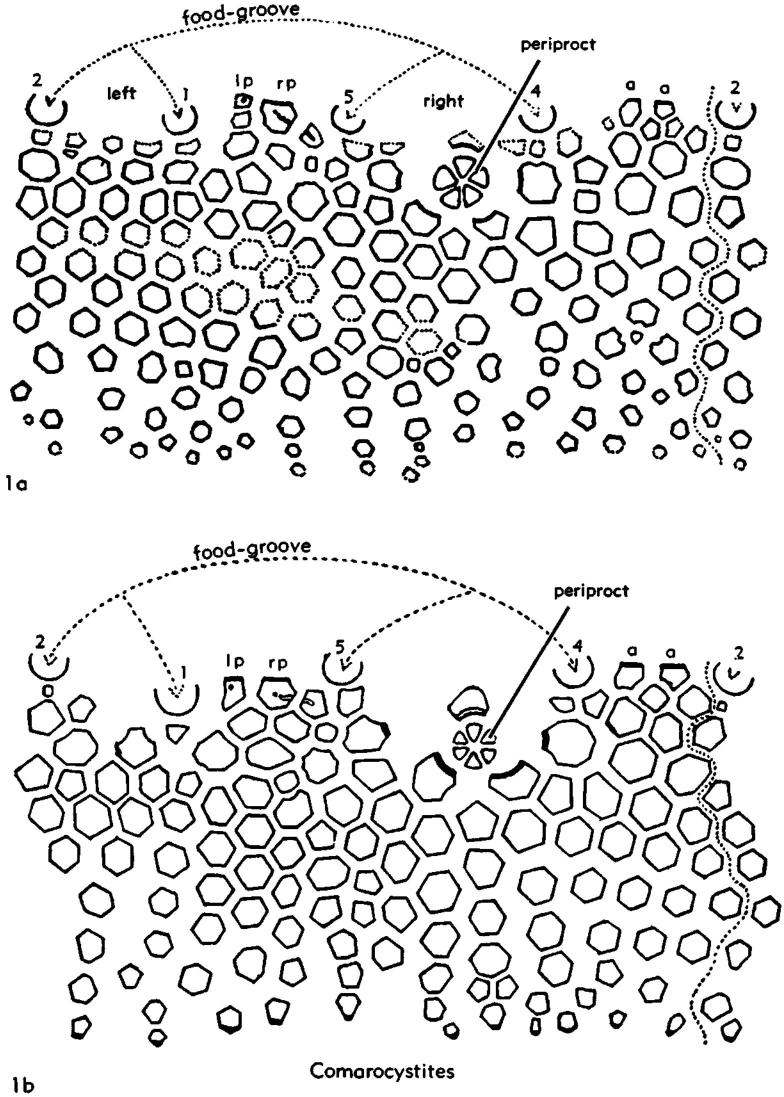


FIG. 167. Brachiata (Comarocystitidae; two plate diagrams) (p. S282-S287).

in bottom of groove at middle of peristome, ambulacral grooves at either side bifurcating in short branches that extend to 2 pairs of arm facets, each pair of facets constituting a single protuberance at one end of peristome, bilobed, with ambulacral groove rising from point of bifurcation onto the facet. Arms 4, uniserial, tapering gradually, estimated to have been 1.5 times height of theca, arm composed of at least 12 brachials, each of which bears single pinnule on its left side (as viewed orally); all brachials above first slightly compressed from front to back, length of each brachial about 1.5 times its lateral diameter. Facets for pinnules concave, margins distinctly raised, set slightly above middle of brachial. Pinnules uniserial, some attaining length nearly equal to half of theca height; pinnulars nearly equal in size, all except initial 2 or 3 in each pinnule strongly flattened transversely; covering plates on pinnules small, quadrangular. [The right posterior arm of one specimen exhibits an ambulacral groove only on the proximal part of the first brachial; not enough arms are preserved to venture an opinion on whether this is normal or abnormal.] No trace of ambulacral grooves observed on pinnules, and no indentation in pinnular facet to indicate its extension onto basal pinnular. [This is not decisive on specimens studied; a well-developed ambulacral system may have extended onto the pinnules without conspicuous grooves.] Periproct filled by anal pyramid of 5 or 6 triangular plates, which have general subglobose form with flattened apex. Hydropore expressed as faint narrow groove apparently representing aperture of thin slitlike stone canal, located on crest of narrow, sinuous ridge extending from center of larger posterior oral plate to center of adjacent plate on its aboral right border, some specimens with minute but distinct pit just beyond left end of hydropore-bearing ridge, but since most

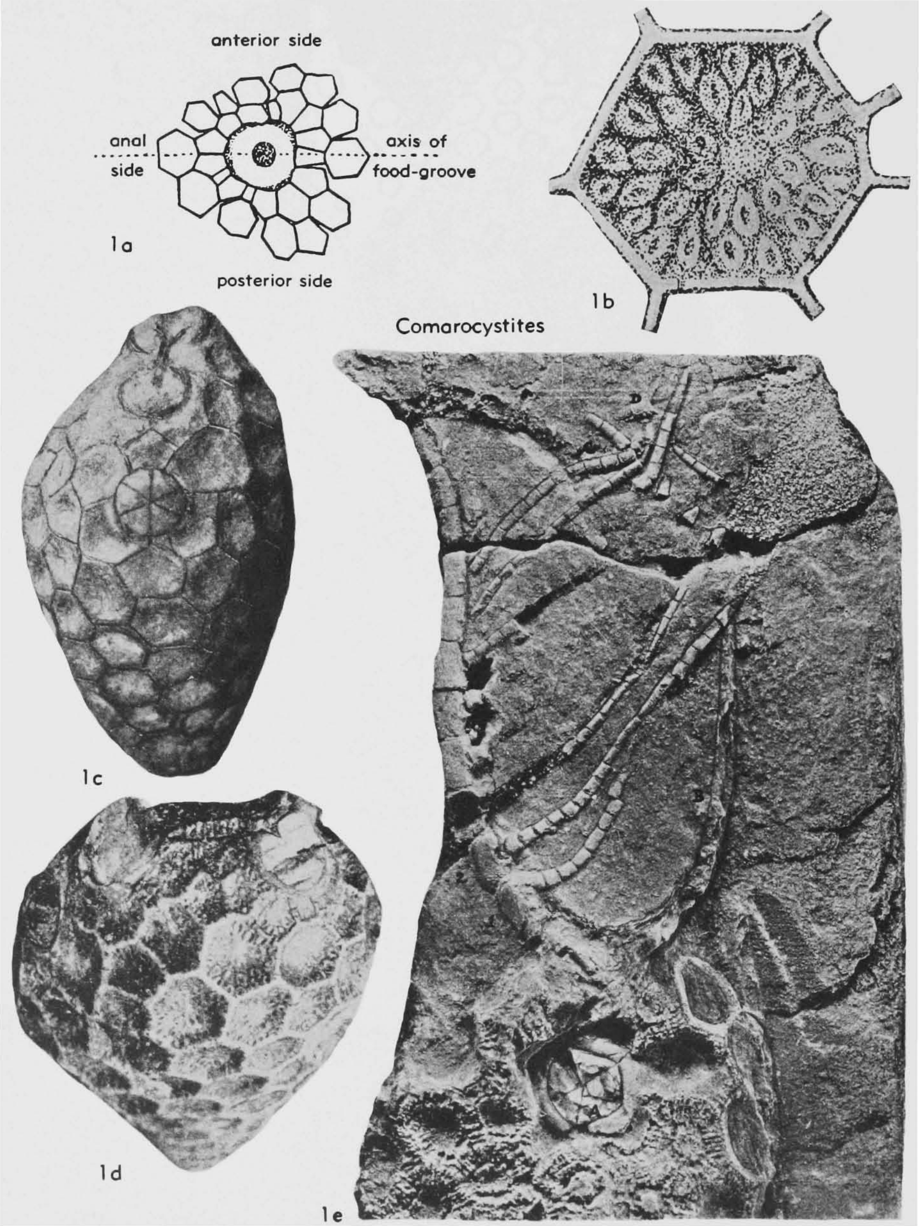


FIG. 168. Brachiata (Comarocystitidae) (p. S282-S287).

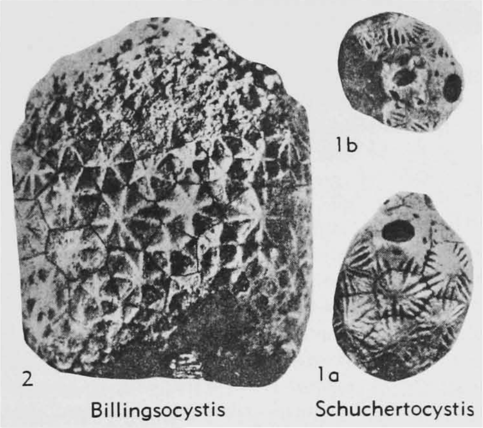


FIG. 169. Brachiata (Comarocystitidae) (p. *S*287-*S*288).

specimens lack this structure, interpretation of it as a gonopore is doubtful. The column shown by complete specimen of type species 108 mm. long (attached theca 65 mm. high) and about 5 mm. in diameter near middle, base expanded to form circular attachment disc or holdfast about 17 mm. in diameter; columnals very thin, circular, with lumen about 0.25 of diameter and with flat surface radially striate; exterior of column ornamented by minute granules arranged quincuncially in diagonally intersecting rows. *M.Ord.*, N.Am. (Ont.-Mo.).——FIG. 159,*1*. *C. shumardi* MEEK & WORTHEN, Kimmswick Ls., USA(Mo.); *1a-d*, 4 lat. sl. incl., ×1 (47); *1e,f*, lat. and aboral, ×1 (151); *1g,h*, weathered specimen and isolated plate, ×1 (148); *1i*, weathered surface showing internal structures, enl. (47); *1j*, plate diagram (47).——FIG. 159,*2*. *C. obconicus* MEEK & WORTHEN, Kimmswick Ls., USA(Mo.); *2a,b*, lat. views, ×1 (151).——FIG. 166,*1*; 167,*1*; 168,*1*. **C. punctatus*, Hull Ls., Can.(Ont.); 166,*1a-c*, 2 lat. and oral, ×1 (18); 166,*1d-f*, 2 lat. and oral, ×1 (20); 166,*1g-i*, 2 plates and anal pyramid, enl. (20); 166,*1j*, nearly complete specimen, ×0.8 (47); 166,*1k*, incl. lat., ×3 (47); 167,*1a,b*, 2 plate diagrams (47); 168,*1a*, diagram of plates in aboral region; 168,*1b*, thecal plate, ×8; 168, *1c,d*, 2 lat., ×2.4 and ×3; 168,*1e*, part of theca with attached arms, ×2 (47).

Billingsocystis BASSLER, 1950, p. 274 [**B. invaginata*; OD]. Theca ovoid to oblong, base invaginated, sides somewhat compressed in only specimen described, composed of about 175 small polygonal plates disposed in 8 or 9 irregular circlets. Ambulacral system very imperfectly known, described by BASSLER (1950) as: "Food-groove system confined to a single short, transverse, relatively deep, semilunate groove. No branches of this groove and no facets for the attachment of arms are present." [Inasmuch as attached arms of paracrinoids are either preserved or leave distinct marks on the thecal plates, it is presumed here that the arms of this genus are free.] Strong ridges radiating from center of each thecal plate to its corners, number of rays in each star thus formed equal to number of sides of plate on which it occurs; inner surface of thecal plates unknown. Periproct small, situated near peristome. Column composed of thin columnals. *M.Ord.*, USA(Ky.).——FIG. 169,*2*. **B. invaginata*; lat., ×2 (6).

Schuchertocystis BASSLER, 1950, p. 274 [**S. radiata*; OD]. Original description stated: "Theca resembling a small *Amygdalocystites* but lacking recumbent arms. The base consists of three plates, two on the antanal and one on the anal side. Plate sutures crossed at right angles by long slits in the mesostereom that shorten at their passage through the hypostereom into elliptically elongate pores." [The similarity to the theca of *Amygdalocystites* is difficult to envisage. *Schuchertocystis* has only slight lateral compression of the theca with exposure of a few coarse parallel grooves perpendicular to each suture extending from one plate to another, the arms appearing to have been free. In contrast, *Amygdalocystites* has strong lateral compression with a sharp edge between the 2 halves; plates marked by radial ridges; and arms attached. Each genus has about 30 thecal plates. *Schuchertocystis* resembles *Canadocystis* and some other paracrinoids in location of the periproct, rather than peristome, nearly opposite the columnal attachment. The main problem of interpretation is the nature of the thecal plates. If the deep sets of grooves are indeed in the stereotheca, then all epitheca is destroyed and the nature of the ornamentation cannot be determined.

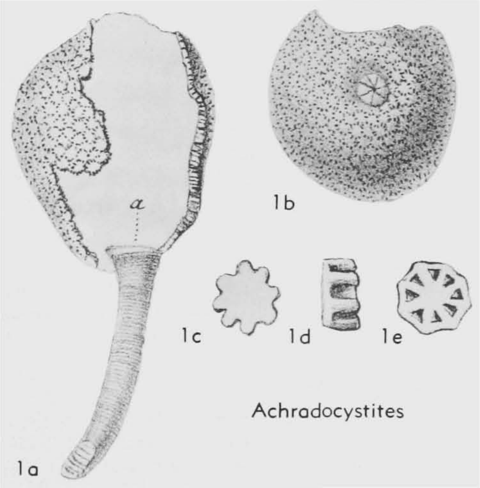
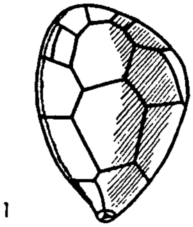


FIG. 170. Class, Order, and Family Uncertain (p. *S*288).



Platycystites

FIG. 171. Class, Order, and Family Uncertain (p. S288).

The illustrations show nothing of the "elliptically elongate pores" mentioned by BASSLER.] *M.Ord.*, USA(Tenn.).——FIG. 169,*1*. **S. radiata*; *1a,b*, lat. and oral, ×2 (6).

Order and Family UNCERTAIN

Achradocystites VON VOLBORTH, 1870, p. 9 [**A. grewingkii*; OD] [=*Achradocystis* HAECKEL, 1896, p. 56 *(nom. van.)*]. Theca composed of very numerous small plates of various sizes, each strongly marked by radial ridges to its corners and (if one may credit certain figures) by a marginal rim; edges of plates scalloped, perhaps by pores inward reaching along sutures, scalloped edges more apparent on inner surface than exterior. [VON VOLBORTH (1870) reported that on the inner surface the plates lay with "tooth against tooth," and "canal against canal," which is interpreted to mean that there were pores along the sutures.] Theca (as preserved) incomplete, but apparently pear-shaped, with smaller end attached to column; periproct filled by anal pyramid, composed of 7 triangular plates; peristome unknown. Column round, consisting of numerous thin columnals, not much flared at junction with theca. No traces of arms discerned in preserved portion, indicating that perhaps arms were free (inasmuch as some traces of attached arms could be expected). *U.Ord.*, Eu.(Est.).——FIG. 170,*1*. **A. grewingkii*; *1a,b*, lat. and anal, ×1; *1c-e*, int., side, and ext., thecal plate, ×4 (137).

Platycystites MILLER, 1889, p. 272 [**P. faberi*; OD] [=*Platycystis* BATHER, 1900, p. 51 *(nom. van.)*]. Theca, if such it be, subpyriform, tapering to scar of attachment as for a column; form somewhat compressed, compared originally to a peach seed with "a narrow rim on the border," specimen reported to be worn, with no traces of openings; 3 plates adjoining attachment scar, others large and irregularly polygonal, each said to be filled with minute pores. [The age of this fossil is doubtful, since MILLER (1885) reported that "it was received by Charles Faber among a lot of fossils from the Kaskaskia Group in the southern part of West Virginia, but as no cystideans have ever been found above the Lower Devonian, and as the specimen is worn as if it had been drifted, the probability is that it belongs to the Silurian rocks." BATHER (1900) tentatively classified the specimen as "a worn Anomalocystid of indeterminable affinities," but later (1913) suggested that it could be columnar appendage of *Rhipidocystis* (L.Ord.-M.Ord.). BASSLER & MOODEY (1943), without question, recorded *P. faberi* as occurring in the Heiskell Shale, of Chazyan(M.Ord.) age. The curious lack of thecal openings in a completely plated form suggests that BATHER's interpretation of it as a columnar appendage of some pelmatozoan may be correct.] *?M.Ord.*, USA(Va.).——FIG. 171,*1*. **P. faberi*; lat., ×1 (12).

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EDRIOBLASTOIDS

By Robert O. Fay
[Oklahoma Geological Survey]

INTRODUCTION

Primitive attached echinoderms which different authors have variously associated with blastoids, cystoids, and edrioasteroids now are considered to belong in a class of their own, named Edrioblastoidea (Fay, 1962). The fossils occur in the Middle Ordovician of Canada, and except for the importance of their known morphological features might be relegated to an *incertae sedis* pigeonhole on the ground of extreme rarity. Only two specimens have been collected and one of them subsequently has been lost. The type specimen, which belongs to the Geological Survey of Canada, is well preserved and reasonably complete, satisfactorily showing all essential external features at least. The theca is modest in size, measuring 21 mm. in height and 19 mm. in width. It displays regular pentameral symmetry and a blastoid-like form, with evenly conical aboral side and strongly rounded oral side.

MORPHOLOGY

The theca is composed of 20 main plates arranged in four circlets, from the stem attachment upward consisting of five basals, five radials, five deltoids, and five orals (Fig. 172). Elements of each circlet alternate in position with those of adjoining ones. In addition, numerous small plates occur. These include variously shaped and somewhat unevenly disposed infradeltoid plates located interradially and a host of regular, nearly even-sized ambulacral plates in double rows within each ambulacrum. The infradeltoids are interposed between the radial limbs and deltoids, supplemented on the anal side by many small plates (up to 30) surrounding the anal orifice (Fig. 173,*2*). The ambulacral cover plates are parallel-sided elongate ossicles which extend obliquely in adoral inward direction from outer margins of the subpetaloid ambulacral tracts, those of opposed rows meeting in a zigzag line along the longitudinal axis of the ambulacrum.

All of the main plates, and to some extent the infradeltoids also, are characterized by relatively broad and deep infolds which tend to cross plate sutures at right angles (Fig. 172, 174). They are somewhat irregular and a majority have short branched extensions laterally and terminally. Some of the infolds coincide with sutures, running along them in part of their course. These inflections of thecal stereom are not associated with slits or pores leading to the interior of the theca and seem

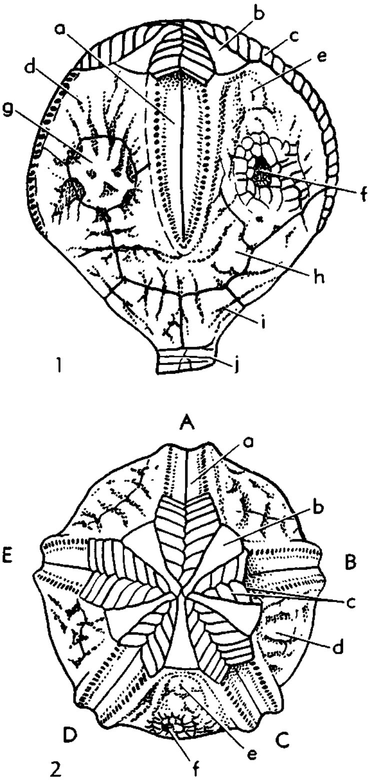

Fig. 172. Morphological features of edrioblastoids—oral (*1*) and *D*-ray (*2*) views of theca of **Astrocystites ottawaensis*, ×2 (reconstr.) (1). [Explanation: *a*, part of ambulacrum with cover plates removed, showing marginal rows of pores in floor plates; *b*, oral plate; *c*, cover plates; *d*, deltoid; *e*, ?hydropore; *f*, anal orifice; *g*, infradeltoid; *h*, radial; *i*, basal; *j*, column.]

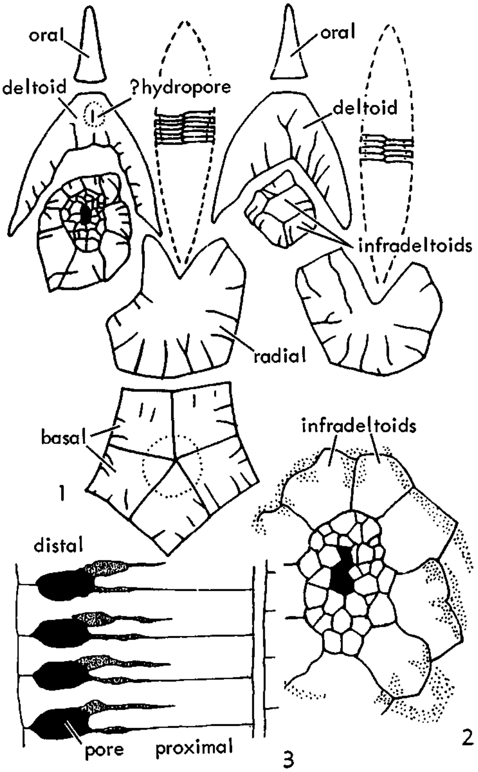

FIG. 173. Morphological features of edrioblastoids—**Astrocystites ottawaensis.*——*1.* Partial plate layout, ×2.5 (based on HUDSON, 4).——*2.* Plates surrounding anal orifice, ×5 (based on HUDSON, 4).——*3.* Part of ambulacral floor showing marginal pores with depressions on plates extending toward perradial groove, ×20 (2).

to be entirely unrelated to the pore rhombs of cystoids or hydrospires of blastoids. The grooves provide a distinctive pattern of surface ornament and may have served as skin gills, but possible functions otherwise are unknown.

The margins of each ambulacrum are marked by evenly distributed, closely spaced pores, a single row occurring along any one margin (Fig. 173,*3*). They are placed next to outer edges of the ambulacral plates and are not associated with any sign of brachiolar facets. Accordingly, as stated confidently by BATHER (1900, p. 209; 1914, p. 202), these echinoderms differed from blastoids and cystoids in lacking brachioles, and BATHER was first to point out morphological resemblance to edrioasteroids.

A hydropore appears to have been located either within the anal deltoid or in a separate plate aborally placed next to its adoral extremity (Fig. 172,*2*).

The surface of most thecal plates bears closely spaced minute pore or pits that seem not to penetrate far into the plates. The pits may constitute features of ornament.

A stem is represented by columnals, each of which is composed of five or more curved polygonal small plates, together forming a circular disc. Although only the topmost part of this attachment stalk is known, it tapers somewhat distally.

Class EDRIOBLASTOIDEA Fay, 1962

[Edrioblastoidea FAY, 1962, p. 201]

Theca blastoid-like in shape and symmetry, composed of five mutually similar basals, five radials, five deltoids, and five orals, supplemented by a moderately large number of small interradially disposed plates called infradeltoids and around the anal orifice numerous still smaller plates; ambulacra subpetaloid, long, in that they reach below mid-height of the theca, their margins converging aborally and each bearing single row of close-spaced pores, elongate cover plates extending from margins to mid-line of ambulacra, double rows of these plates in each ambulacrum meeting in zigzag line; inferred hydropore between anal orifice and summit of theca. Main thecal plates marked by pattern of relatively broad and deep grooves representing inflections of stereom, not associated with openings to interior of theca. Stem composed of small polygonal plates grouped to form circular columnals. *M.Ord.*

The single known species placed in this class is *Astrocystites ottawaensis* WHITEAVES (1897), from the Cobourg Limestone (Trentonian) in Ottawa, Ontario, Canada. Although it was originally interpreted as a cystoid, virtually none of the attributes of this class, such as possession of brachioles, perforation of thecal plates by paired pores (as in the Diploporita) or pore rhombs (as in the Rhombifera), and prevailing lack of clearly marked pentameral symmetry, is found in *Astrocystites.*

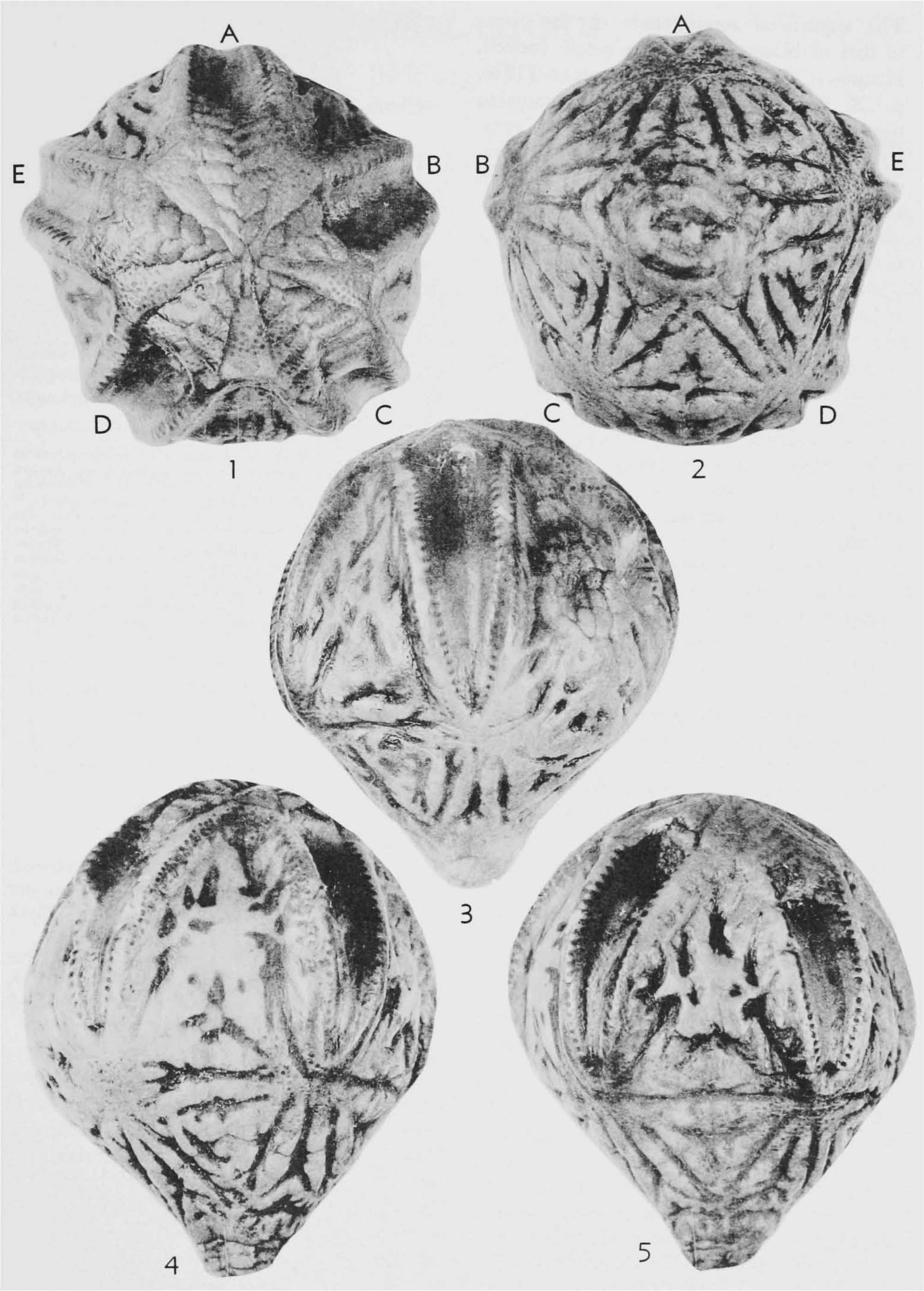

FIG. 174. Astrocystitidae (**Astrocystites ottawaensis*) (p. S292).

The superficial resemblance of the theca to that of blastoids has been noted. Indeed, HUDSON (1927, p. 97) and BASSLER (1936, p. 23; 1938, p. 13) assigned the genus to the Blastoidea. Taking account of the presence of the numerous small plates (infradeltoids) irregularly intercalated between the radials and deltoids of *Astrocystites,* closer similarity of the type form of the edrioblastoids to that of the parablastoids represented by *Blastoidocrinus* than to true blastoids is seen. Both blastoids and parablastoids have numerous brachioles arising from margins of the ambulacra, however. It is mainly on account of the lack of brachioles in *Astrocystites* that this genus was transferred by BATHER (1900) and others (SPRINGER in ZITTEL, 1913, p. 160; BASSLER & MOODEY, 1943, p. 8; CUÉNOT, 1948, p. 29; PIVETEAU, 1953, p. 655) to the Edrioasteroidea.

It is possible that the Blastoidea descended from the Edrioblastoidea, with the Fissiculata and Spiraculata perhaps arising independently as derivatives of the class, or the Fissiculata alone, with the Spiraculata developed later from fissiculate progenitors. These suggested phylogenetic relationships are speculative, but it is reasonable to presume that the ambulacral pores of the edrioblastoids differed in function from those of the blastoids, in the former serving as passageways for tube feet instead of inlets for movement of water to the hydrospires, as in the latter. With atrophy of the postulated edrioblastoid tube feet, gaps would be left between outer extremities of the ambulacral cover plates (corresponding to blastoid side plates). If thecal infolds along ambulacral margins of the radial and deltoid plates of edrioblastoids became aligned with these margins, they may readily have evolved to become hydrospires. The gaps along the ambulacral margins would become hydrospire pores. The secretion of stereom around the median ambulacral canal to protect it could explain the origin of lancet plates, which are a unique skeletal element of the Blastoidea. The brachioles of blastoids probably developed by the formation of tiny biserially arranged rows of plates around fleshy food-gathering outgrowths produced from edges of the ambulacra.

Order PENTACYSTIDA Jaekel, 1918

[Pentacystida JAEKEL, 1918, p. 99]

Characters of class. *M.Ord.*

Family ASTROCYSTITIDAE Bassler, 1938

[Astrocystitidae BASSLER, 1938, p. 13] [=Steganoblastidae BATHER, 1900, p. 209]

Characters of order. *M.Ord.*

Astrocystites WHITEAVES, 1897, p. 287 [**A. ottawaensis*; OD, M] [=*Steganoblastus* WHITEAVES, 1898, p. 395]. Characters of family. *M.Ord.,* N. Am.(Can.).——FIG. 174,*1-5*. **A. ottawaensis,* Cobourg Ls., Ottawa, Ont.; *1-5,* oral, aboral, *D*-ray, *BC*-interray, *AB*-interray views of holotype, ×3.3 (3).

[Publication of the name *Steganoblastus* by WHITEAVES as replacement for *Astrocystites* was suggested by BATHER (1914, p. 193), who erroneously thought that *Asterocystis* HAECKEL, 1896, is a senior homonym of *Astrocystites.* It is not. Although the family name Steganoblastidae has long priority over Astrocystitidae and has been used by several authors, including CUÉNOT (1948, p. 11, as Stéganoblastinés) and PIVETEAU (1953, p. 655), it must yield to the junior name, since the Code (1961, Art. 11,c) provides that "A family-group name must, when first published, be based on the name then valid for a contained genus. . . ." *Steganoblastus* does not qualify as a family name-giver.]

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PARABLASTOIDS

By Robert O. Fay
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INTRODUCTION

Parablastoids are pelmatozoan echinoderms that were attached to the sea bottom by a cylindrical stalk composed of thin discoid columnals resembling those of many blastoids and crinoids. The theca has a general blastoid-like form, with strongly developed pentameral symmetry and stellate appearance in oral or aboral views. Only two genera, each represented by a single species, have been described. They consist of a poorly known form which has not been illustrated, reported from the upper part of the Lower Ordovician of the Leningrad region, USSR, and a comparatively well-known form from the lower part (Chazyan) of the Middle Ordovician of New York and Quebec. Many specimens of the American parablastoid, known as *Blastoidocrinus,* have been collected and they serve to demonstrate the morphological distinctness of the group. The parablastoids are judged to be not closely related to either edrioblastoids or true blastoids.

MORPHOLOGY

The theca is composed of rather numerous plates, so arranged that the oral and aboral portions are well differentiated. The aboral (or dorsal) region is formed by three or more circlets of plates, the lowermost of which consists of small basals placed deeply within the basal concavity and largely or entirely concealed by the proximal stem segment. Seemingly, they are five in number. Next above the basals and alternating with them are five moderately large radials, which are narrow below and widen upward to slightly beyond their mid-length and then narrow to a point (Fig. 175,*2*). Plates of the radial circlet are widely in contact with each other all around. In line with the radials are five pairs of elongate plates named bibrachials with long perradial sutures between them (Fig. 175,*2,4,5*). A group of approximately 13 interbrachials, arranged in one or more transverse rows, occurs between each two pairs of bibrachials.

The oral (or ventral) side of the theca is formed by numerous plates belonging to the five radially placed subpetaloid ambulacra and five large interradial plates identified as deltoids (Fig. 175,*1,4,5*). No lancet plate is present in an ambulacrum but biserially alternating sets of adambulacrals support the food groove. Relatively large cover plates alternate with the adambulacrals, occurring above them with 3 wing plates above the cover plates. Each adambulacral plate bears a long brachiole with biserially arranged tiny ossicles attached to its admedial side (Fig. 175,*3*). The brachioles rise parallel to one another packed closely together along sides of wing plates in the middle of each ambulacrum. They extend to the upper edge of the wing plates. The oral opening is tightly covered by a thick pentalobate apical plate, which has a large crescentic orifice on the inner surface of its anal side, perhaps opening outward laterally but not upward at the summit. The apical plate fits closely against the distal wing plates of the five ambulacra (Fig. 175,*1,4,5*).

Five large triangular deltoids are present between the ambulacra. They are shallowly concave transversely and moderately convex longitudinally along their mid-lines, which slope upward rather steeply in convergent manner to their tips. Each deltoid has many sets of parallel infolds, termed cataspires. They extend to pores along the ambulacral margins and reach aborally to pores along the aboral margin of the deltoid. The cataspires are not interconnected laterally, but those joined to pores along the ambulacral margins are seemingly connected to the aborally directed set of cataspires, so that water entering the ambulacral pores could pass along cataspires to outlets along the aboral margin of the deltoids. Evidently, the cataspires were not outwardly open slits, for they are covered by stereom which produces small parallel ridges on the surface of the deltoids.

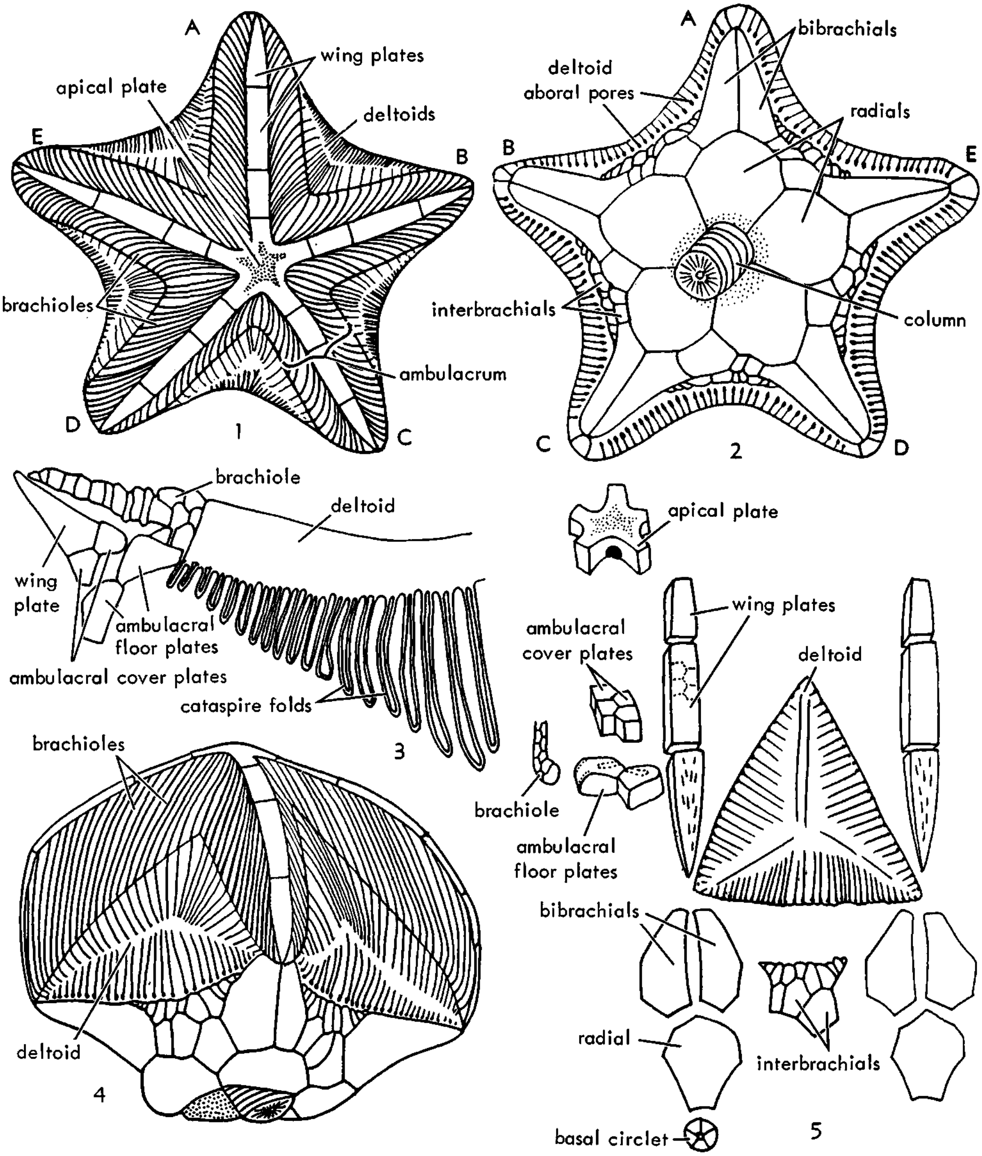

FIG. 175. Morphological features of parablastoids.——**Blastoidocrinus carchariaedens* (all Fay, n).——*1,2*. Oral and aboral view of theca, ×2.4.——*3*. Cross section of part of deltoid and ambulacrum showing cataspires, ×8.——*4*. *D*-ray view of theca, ×2.4.——*5*. Partial layout of plates, ×2.4.

Class PARABLASTOIDEA Hudson, 1907

[Parablastoidea HUDSON, 1907, p. 97]

Stem-bearing pelmatozoan echinoderms with blastoid-like theca formed by three or more circlets of plates on aboral side, and by ambulacral wing plates and biserial cover plates covering numerous adambulacrals along five radii, apical plate at summit, and five large triangular deltoids; radial plates surmounted by pairs of bibrachials; rows of small interradials between bibrachial pairs; adambulacrals bearing parallel rows of moderately elongate biserial brachioles;

pores along ambulacral margins connected with cataspire infolds of deltoids, which include aborally directed sets joined to pores on aboral margins of each deltoid. Stem composed of discoid columnals. *L.Ord.-M.Ord.*

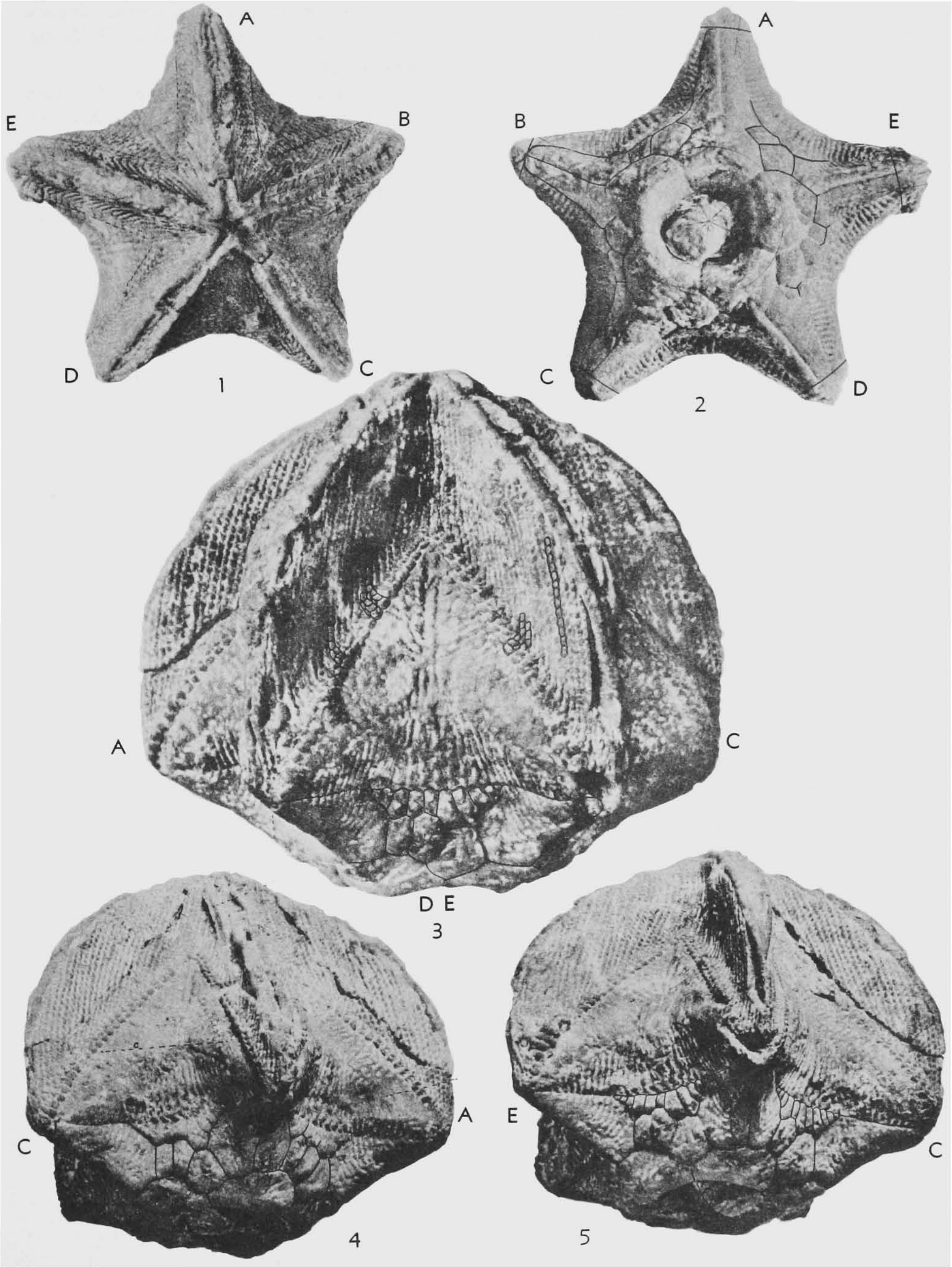

FIG. 176. Blastocystidae (**Blastoidocrinus carchariaedens*) (p. S296).

Family BLASTOCYSTIDAE Jaekel, 1918

[Blastocystidae JAEKEL, 1918, p. 107]

Characters of class. *L.Ord.-M.Ord.*

Blastocystis JAEKEL, 1918, p. 107 [**B. rossica*; OD, M]. Large interradials below triangular deltoids. [Not figured or well understood. Type specimen probably lost. Even so, valid name-giver for family.] *Up.L.Ord.* (Kunda Formation, B_3), near Leningrad, USSR.

Blastoidocrinus BILLINGS, 1859, p. 18 [**B. carchariaedens*; OD, M]. Characters of class; pentamerous symmetry strongly defined; theca composed of approximately 90 somewhat regularly arranged plates. [Seemingly unlike *Blastocystis* in having rows of small interradials. The best available description of the genus is that published by HUDSON (1907).] *Low.M.Ord.(Chazy.)*, N. Am. (Que.-N.Y.).——FIG. 176,*1-5*. **B. carchariaedens,* USA(N.Y.); *1,2,4,5,* oral, aboral, *B*-ray, *D*-ray views of typical specimen, ×2.2 (2); *3, DE*-interray view of same specimen, ×3 (2).

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Part S
ECHINODERMATA 1

By H. H. BEAVER, K. E. CASTER, J. W. DURHAM, R. O. FAY, H. B. FELL, R. V. KESLING, D. B. MACURDA, JR., R. C. MOORE, GEORGES UBAGHS, and †JOHANNES WANNER

VOLUME 2

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PART S

ECHINODERMATA 1

GENERAL CHARACTERS

HOMALOZOA—CRINOZOA (EXCEPT CRINOIDEA)

By H. H. Beaver, K. E. Caster, J. W. Durham, R. O. Fay, H. B. Fell, R. V. Kesling, D. B. Macurda, Jr., R. C. Moore, Georges Ubaghs, and †Johannes Wanner

VOLUME 2

BLASTOIDS

By Harold H. Beaver,[1] Robert O. Fay,[2] Donald B. Macurda, Jr.,[3] Raymond C. Moore,[4] and Johannes Wanner[5]

CONTENTS

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INTRODUCTION

By Robert O. Fay

Blastoids are moderately small stemmed echinoderms having a calyx that mostly measures less than 25 mm. in diameter or height. They are restricted to marine Paleozoic rocks ranging from Silurian to Permian, attaining greatest abundance and variety in Lower Carboniferous (Mississippian) deposits.

The **stem** which attached blastoids to the sea bottom is rarely preserved in position joined to the theca, but a sufficient number of specimens makes clear that it was very slender and comparatively short, with probable maximum length amounting to little more than 25 cm. It was composed of thin discoid ossicles (Fig. 177).

The main part of the animal, at the top of the stem, consisted of a globular to pyriform body armored by regularly arranged calcareous plates (**calyx** or **theca**). This relatively thin-plated theca enclosed the viscera, of unknown nature, and along the borders of five linear or petaloid tracts termed **ambulacra,** disposed in regular radial positions extending downward from the summit of the theca, very numerous threadlike armlets **(brachioles)** projected upward as food-gathering appendages. The whole structure borne by the stem was a fringed budlike form termed **anthus** (Greek, blossom) or crown (Fig. 177).

The **mouth** of blastoids is centrally located at the summit of the theca and median grooves in each ambulacrum connect with it, for they were the main passageways on the surface of the theca for transportation of food particles brought to them by the brachioles by way of lateral grooves on the ambulacra (Fig. 178). The outlet of the digestive system is an orifice on the posterior side of the theca known as the **anus,** or it may be located in the summit area as part of the vent termed **anispiracle** (Fig. 178,*1*). It is invariably interambulacral in position and located not far below the mouth. Other openings in the theca are rounded or slitlike vents which functioned as outlets (**spiracles, hydrospire slits**) of the respiratory system and with these belong numerous diminutive openings (**hydrospire pores**) which served as water inlets. The hydrospires are internal thin-walled folds of calcareous tissue which are characteristic of the blastoids and which are described in some detail in the section on Morphology. Possibly the hydrospire structures served reproductive functions, as well as respiration.

As a rule, the theca of blastoids is composed of 18 to 21 main plates and myriad diminutive ones. The main plates are regularly arranged in definite cycles or circlets, in upward succession from the stem consisting of (1) **basals,** (2) **radials,** (3) **lancets**

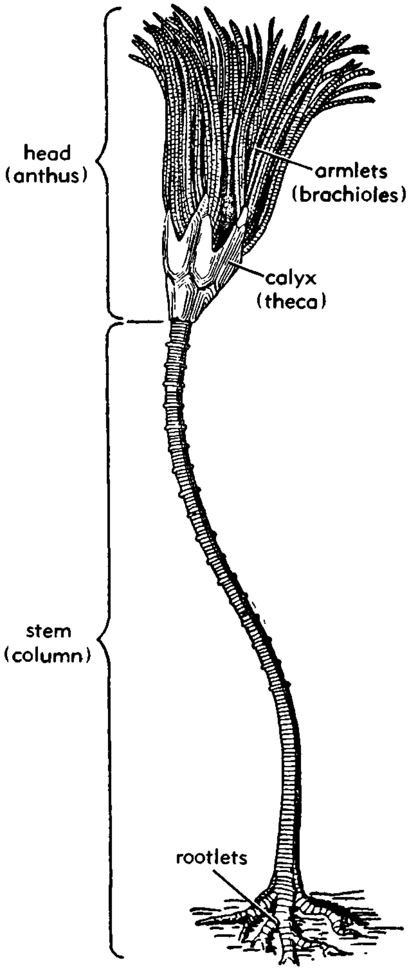

Fig. 177. Reconstruction of entire blastoid (*Orophocrinus,* Miss., N.Am.), showing principal parts (Bather).

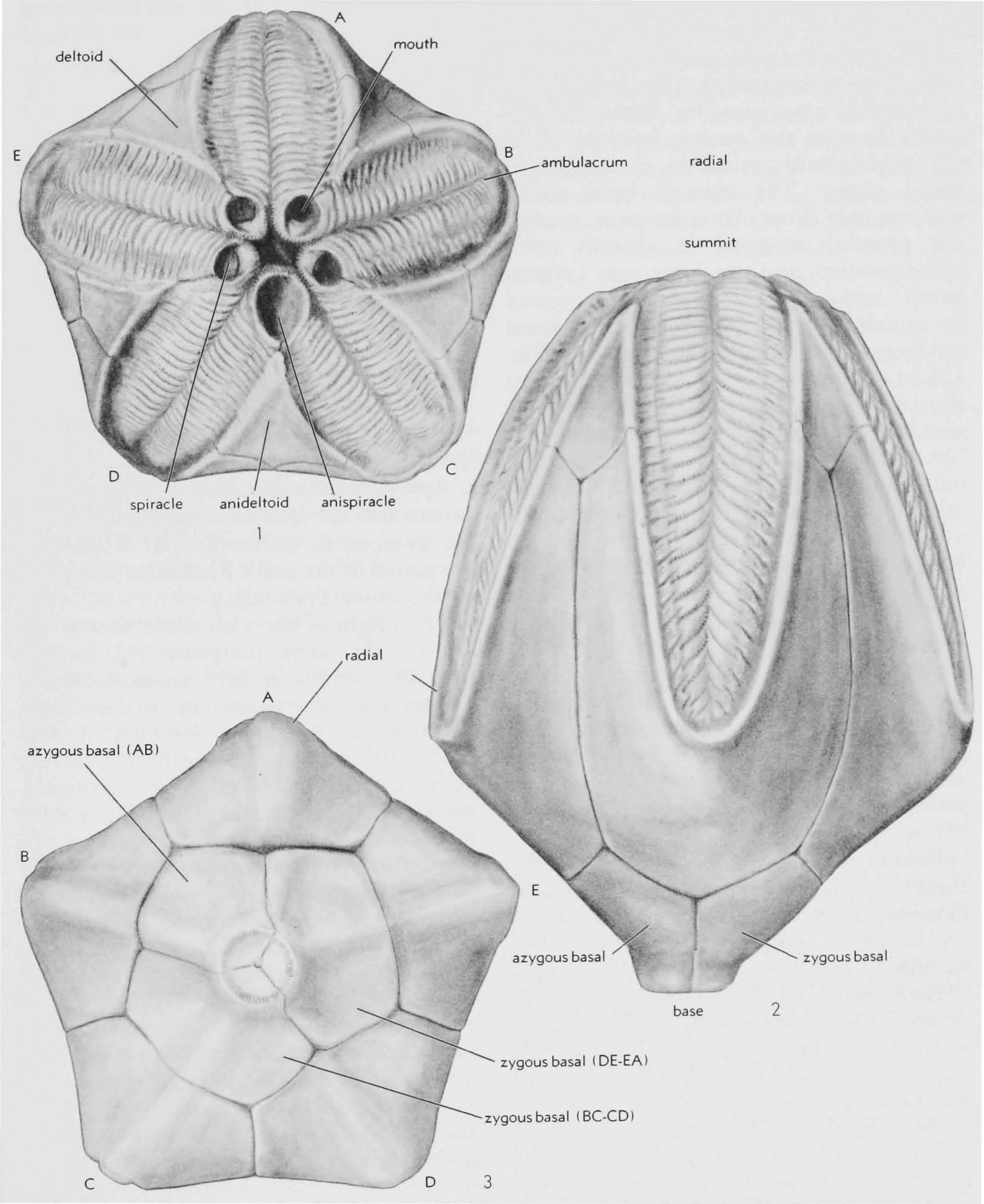

FIG. 178. Calyx of typical blastoid, *Pentremites symmetricus* HALL, U.Miss.(Chesteran), USA(Ill.), showing externally visible parts of theca, ×4.5 (drawings by Roger B. Williams; Beaver, n).——*1*. Summit (oral) view, mouth opening at center surrounded by 4 spiracles (relatively small rounded orifices in interambulacral position) and large anispiracle in posterior interambulacrum (below mouth), also showing petaloid ambulacra (*A* at top, followed in clockwise direction by *B, C, D,* and *E* ambulacra) deltoid plates next to summit between ambulacra.——*2*. Lateral view of calyx from the anterior (*A*-ray) side, especially showing deeply sulcate form of radial plates embracing aboral parts of ambulacra.——*3*. Basal (aboral) view showing the stem impression borne by the basal circlet consisting of 2 large (zygous) plates and 1 small (azygous) plate.

and (4) **deltoids.** Plates in position of the five ambulacra and radials are defined as radial and plates in position alternating with them as interradial. The basal plates of blastoids are classed as interradial elements because the sutures between them all coincide with mid-lines of contiguous radial plates. The blastoid basal circlet contains only three plates, however, a small one (termed **azygous**) in obvious interradial position, and two large ones (**zygous** basals) which occur directly below two of the radials because each represents the fused product of two interradial elements (Fig. 178,*2,3*). The radial plates are more or less elongate U- or V-shaped skeletal elements which enclose the ambulacra between their lateral extension, known as **limbs.** Interradially disposed plates at or near the summit of the theca are rhomboid to subtriangular (delta-shaped) elements termed **deltoids.** The **lancets** are elongate spear-shaped plates inserted between the deltoids and hence radial in position; actually they extend aborally well beyond the aboral limits of the deltoids, occupying most of the spaces (sinuses) between the radial limbs and underlying very numerous small plates of the ambulacra. These latter consist of so-called **side plates** and **outer side plates.** The **brachioles** are attached to these plates.

Deltoid plates on the posterior side of the theca are collectively designated as **anal deltoids.** They include special types which are differently named, as described subsequently.

Each plate of the blastoid theca consists of crystalline calcite having its own optical orientation. The plates expand laterally and in thickness during growth from juvenile to adult stages.

Blastoids commonly occur in limestones, calcareous shales, and in some light-colored clayey shales; they are rarely found in black shales and are virtually unknown in sandstones. Some Mississippian (especially Chesteran) shaly limestones are locally so crowded with specimens of *Pentremites* that these strata became known to early geologists as the Pentremital Beds. Blastoids are also very abundant in parts of the Permian in Timor (East Indies). The known stratigraphic range of the class is Silurian to Permian, with maximum dispersion in Devonian, Lower Carboniferous (Mississippian), and locally in Permian deposits. They have been reported from all continents except Antarctica, but largest collections have been made in North America, Europe, and the island of Timor.

Approximately 78 presently distinguished genera and 350 described species of blastoids are grouped in 12 families, of which five are placed in the order Fissiculata and seven in the order Spiraculata.

The origin of the class Blastoidea is unknown. In some morphological features striking resemblance between blastoids and various rhombiferan cystoids is discernible, but this has not been acceptably demonstrated to have genetic significance. In my opinion, the Middle Ordovician Edrioblastoidea possess characters which are judged most likely to belong to ancestors of the blastoids, even though only a single edrioblastoid genus now is known.

A blastoid consists primarily of two connected parts, a **stem (column)** which was anchored to the sea bottom by branching rootlets, and a "head" **(anthus)** composed of a central budlike body and numerous attached armlets termed **brachioles** (Fig. 177). The budlike body is covered by skeletal plates, collectively forming the **theca (calyx),** and internally there are thin-walled folded structures, named **hydrospires.**

MORPHOLOGY

By Harold H. Beaver
[Esso Production Research Company]

COLUMN

Although the stem attachment of a blastoid, known as the **column,** was first described approximately 140 years ago (Say, 1820), little has been added subsequently to our knowledge of this structure. Virtually all skeletal parts of blastoids are more commonly preserved than the stem, at least in its attached position to the theca. Most unattached segments of blastoid stems have not yet been discriminated definitely from columnal fragments of crinoids and cystoids. According to Etheridge & Carpenter (1886, p. 9), the column of a specimen of *Pentremites* in the collections of Wachsmuth ends below in a branching root. The column measures 5 to 8 inches in length. Galloway & Kaska (1957, p. 8) have reported a length of 1 to 3 inches for length of the column in *Pentremites*. All available information indicates that the stems of blastoids generally were quite short, much shorter than most crinoid columns, although seemingly similar in structure and appearance. At present no trustworthy criteria for distinction of discrete segments of blastoid and crinoid columns other than absence of nodal and internodal columnals and absence of cirri in blastoids have been reported. Further, no blastoid stems with pentagonal, elliptical, or crescentic transverse section are known, whereas these are found in some crinoid genera.

The stems of blastoids consist of many small circular segments called **columnals,** each with a tiny round central opening **(lumen)** which is inferred to have functioned as a neurovascular canal. This axial canal opened into the central cavity of the theca. The margins of top and bottom surfaces of each columnal have alternating fine ridges **(culmina)** and grooves **(crenellae)** which interlock with similar markings on adjoining columnals, so that a moderately firm articulation results. With exception of a specimen of *Pentremites conoideus* in the collection of Galloway & Kaska (1957, pl. 13, fig. 8) which has small spines on the exterior of the column, nothing is known of columnal ornamentation. Some blastoid genera (e.g., *Astrocrinus, Eleutherocrinus, Notoblastus*) seem to have lacked a column, at least in the adult stage (Etheridge & Carpenter, 1886, p. 9; Fay, 1961, p. 9). A distinct stem facet is seen in adult specimens of *Timoroblastus.*

CALYX

The term **calyx** (Greek, bud of flower) is an appropriate designation for the bud-shaped skeletal structure borne at top of the stem (column) of the echinoderms known as blastoids (Greek, *blastos*, bud). It comprises the complete head **(anthus)** of these echinoderms, minus the threadlike brachiolar appendages borne by the ambulacra (Fig. 177). This portion of the hard parts is also properly named **theca** (in Greek signifying sheath or case). The principal plates of the calyx (theca) are basals, radials, deltoids, and those of the ambulacra (Fig. 178). The **basals** compose the lower portion of the calyx and articulate with the stem. Overlying and alternating or in series with the basals are **radials,** each of which is partially divided by a **sinus** for reception of the aboral portion of an ambulacrum. Above the radials and alternating with them are interambulacral plates designated as **deltoids.**

SHAPE AND SIZE

Blastoids exhibit many variations in shape of the calyx. These differences are seen in genera from all geologic systems in which blastoids occur, but are most pronounced in forms of Permian age. Representatives of the various genera can be separated into four broad groups (Fig. 179).

Group 1, characterized by a pyriform outline, includes both spiraculate and fissiculate blastoids (defined later). The typical form (e.g., *Pleuroschisma*, Fig. 179,*4*) has ambulacra that nearly equal half the height of the theca. At one extreme are steeply conical types with short ambulacra largely confined to the summit (e.g., *Ceratoblastus,* Fig. 179,*8*), whereas the other extreme is marked by genera with expanded summits and relatively long ambulacra (e.g., *Orophocrinus,* Fig. 179,*1*).

Group 2 is distinguished by blastoids having a globose shape. Two subgroups are readily recognized, the first having short ambulacra confined to the summit (*Paracodaster, Agmoblastus,* Fig. 179,*9,10*), and the second with ambulacra nearly equal in length to height of the theca (*Poroblastus, Nymphaeoblastus, Granatocrinus, Auloblastus,* Fig. 179,*11-14*). Studies of many specimens of *Globoblastus,* a globose type belonging to the second subgroup, show that individuals commonly change shape with age. Young specimens are generally elongate globose, whereas old ones are depressed globose.

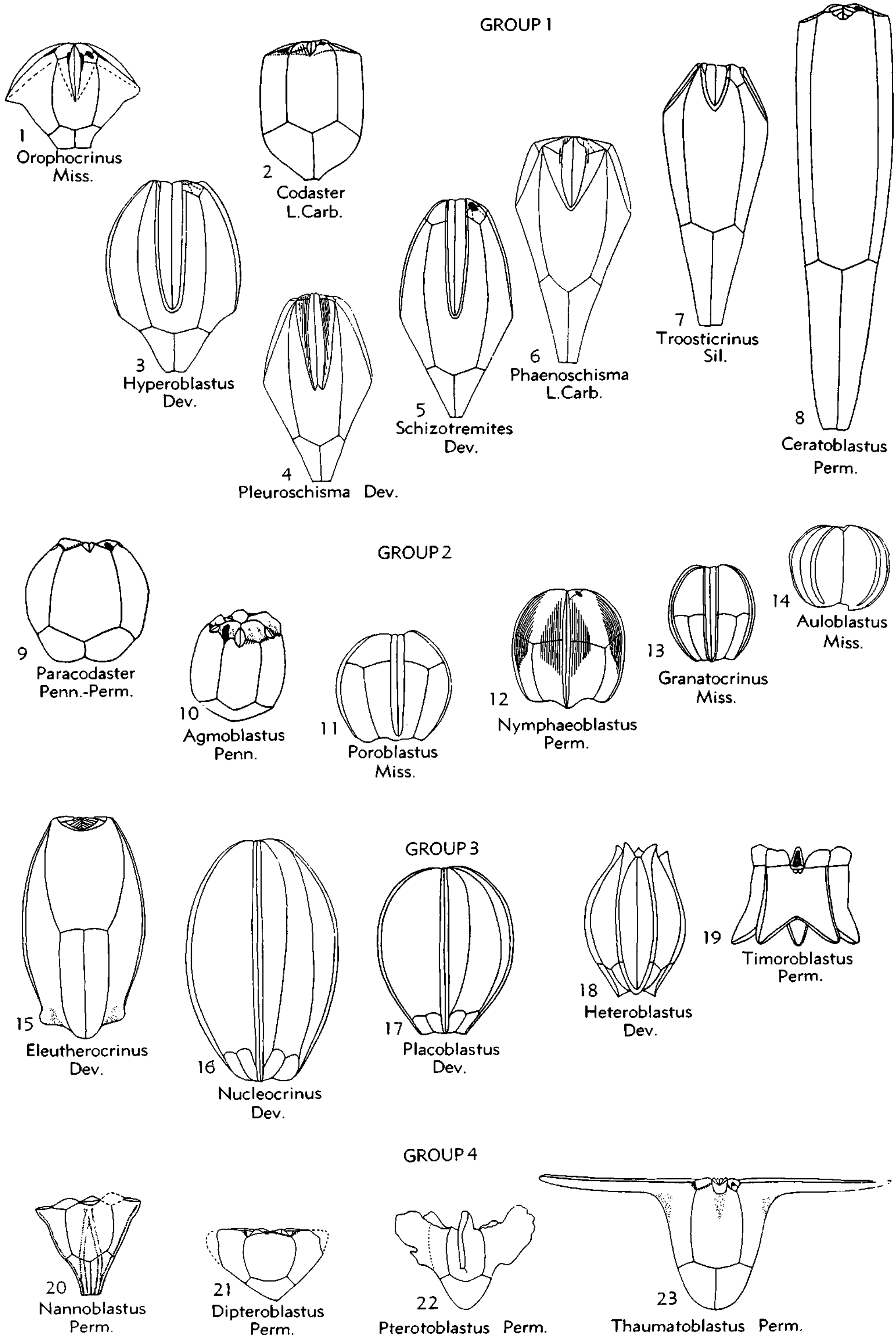

Fig. 179. Shapes of blastoid calyces, shown in lateral views. Groupings are not inferred to delineate phylogenetic assemblages (drawings from Fay, n).

Group 3 includes types which in adult growth stages are elongate globose (e.g., *Eleutherocrinus, Nucleocrinus, Placoblastus, Heteroblastus,* Fig. 179,*15-18*) or are highly irregular in shape but have height and width of the calyx nearly equal (e.g., *Timoroblastus,* Fig. 179,*19*). Some genera have pointed protruding deltoid tips (e.g., *Heteroblastus*), whereas others may have projecting radials and deltoids (e.g., *Timoroblastus*).

Group 4 is composed of vase-shaped blastoids (e.g., *Nannoblastus, Dipteroblastus,* Fig. 179,*20,21*) and similar genera with extended radials and accompanying long ambulacra (e.g., *Pterotoblastus, Thaumatoblastus,* Fig. 179,*22,23*).

Variations in shape commonly are significant at specific levels and, in conjunction with other morphological features such as patterns of the hydrospires, may aid in determining phylogenetic trends. Detailed examinations of species belonging to *Pentremites* have established phylogenetic lineages within this genus (Fig. 180). The oldest known representative, *P. elongatus* (Fig. 180,*A*) of Osagian age, is elongate globose, with an essentially flat base and ambulacra nearly equal to height of the theca. It is succeeded in the Meramecian by *P. conoideus* (Fig. 180,*B*) with similar characteristics. In the later Meramecian, however, two types diverged from *P. conoideus,* one characterized by a nearly flat base (Fig. 180, *D,F,H,I,K,L*) and the other by a pyriform or inverted-pear shape (Fig. 180, *C,E,G,J*). Offshoots of the flat-based group, mainly species closely related to *P. sulcatus* (Fig. 180,*I*), developed in the middle and late Chesteran. Thecal variations include a marked increase in size (up to twice or more common pentremite size), the development of protruding deltoids, nodose thecal exteriors, or serrated ambulacral rims.

Blastoid calyces differ greatly in thecal length from one genus to another and also may show considerable variation within a given genus. In addition, no consistent change in size of calyx is apparent in blastoids as a class from their earliest occurrence in the Silurian to their last-known appearance in the Permian.

Specimens of *Placoblastus obovatus,* some species of *Pentremites* (e.g., *P. sulcatus, P. obesus, P. maccalliei*), and *Tricoelocrinus woodmani* are representative of very large blastoid species, commonly having a height of 2 inches or more. Seemingly adult specimens of *Diploblastus glaber, Mesoblastus crenulatus, Monadoblastus granulosus,* and a few species of *Pentremites* (e.g., *P. princetonensis, P. pulchellus*) are typically small blastoids, generally having a height of about 0.25 inch.

Silurian genera (e.g., *Troosticrinus, Polydeltoideus, Decaschisma*) commonly are represented by specimens having a height slightly less than one inch. Devonian genera exhibit greater range in height, some forms being very large (e.g., *Placoblastus*), whereas representatives of other genera are relatively small (e.g., *Heteroschisma*). Mississippian blastoids vary greatly in size, some being very small (e.g., *Diploblastus, Mesoblastus*), others intermediate (e.g., *Globoblastus, Schizoblastus, Orbitremites, Codaster*), and a few very large (e.g., *Tricoelocrinus,* some species of *Pentremites*). Penn-

[*See* pages S304-S305]

FIG. 180. Calyx shape correlated with accompanying structural modifications, including character of internal features, in succession of Mississippian blastoids belonging to the genus *Pentremites,* interpreted to show phylogenetic trends. Letters refer to photographs (X1) and drawings based on thin sections on opposite page (position of section indicated by pairs of arrows).——*A. P. elongatus* SHUMARD, L.Miss. (Burlington Ls.), near Springfield, USA (Mo.).——*B. P. conoideus* HALL, U.Miss.(Salem Ls.), Spergen Hill, USA (Ind.).——*C. P. princetonensis* ULRICH, U.Miss.(Ste. Genevieve Ls.), Cedar Bluff, USA (Ky.).——*D. P. pulchellus* ULRICH, U.Miss. (Ste. Genevieve Ls.), Cedar Bluff, USA (Ky.).——*E. P. symmetricus* HALL, U.Miss.(Paint Creek F.), near Floraville, USA(Ill.).——*F. P. godoni* (DEFRANCE), U.Miss.(Paint Creek F.), near Floraville, USA (Ill.).——*G. P. pyriformis* SAY, U.Miss.(Golconda F.), near Vienna, USA (Ill.).——*H. P. tulipaformis* HAMBACH, U.Miss.(Bangor Ls.), near Rockwood, USA (Ala.).——*I. P. sulcatus* (ROEMER), U.Miss.(Glen Dean Ls.), near Vienna, USA (Ill.).——*J. P. girtyi* ULRICH, U.Miss.(Menard Ls.), near Chester, USA (Ill).——*K. P. halli* GALLOWAY & KASKA, U.Miss.(Kinkaid Ls.), SE of Chester, USA(Ill.).——*L. P. rusticus* HAMBACH, L.Penn.(Bloyd Sh.), near Fort Gibson. USA (Okla.).

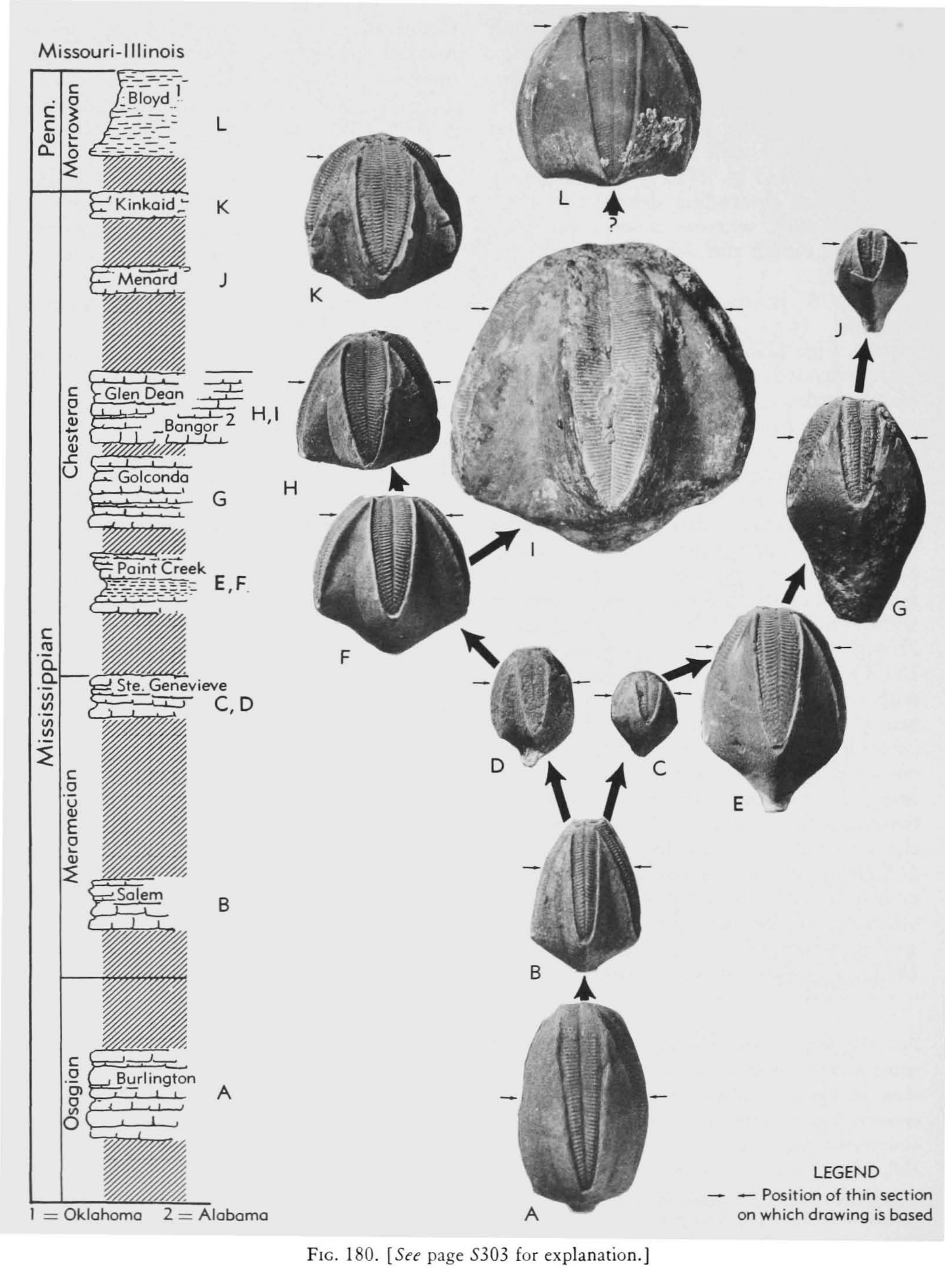

FIG. 180. [*See* page S303 for explanation.]

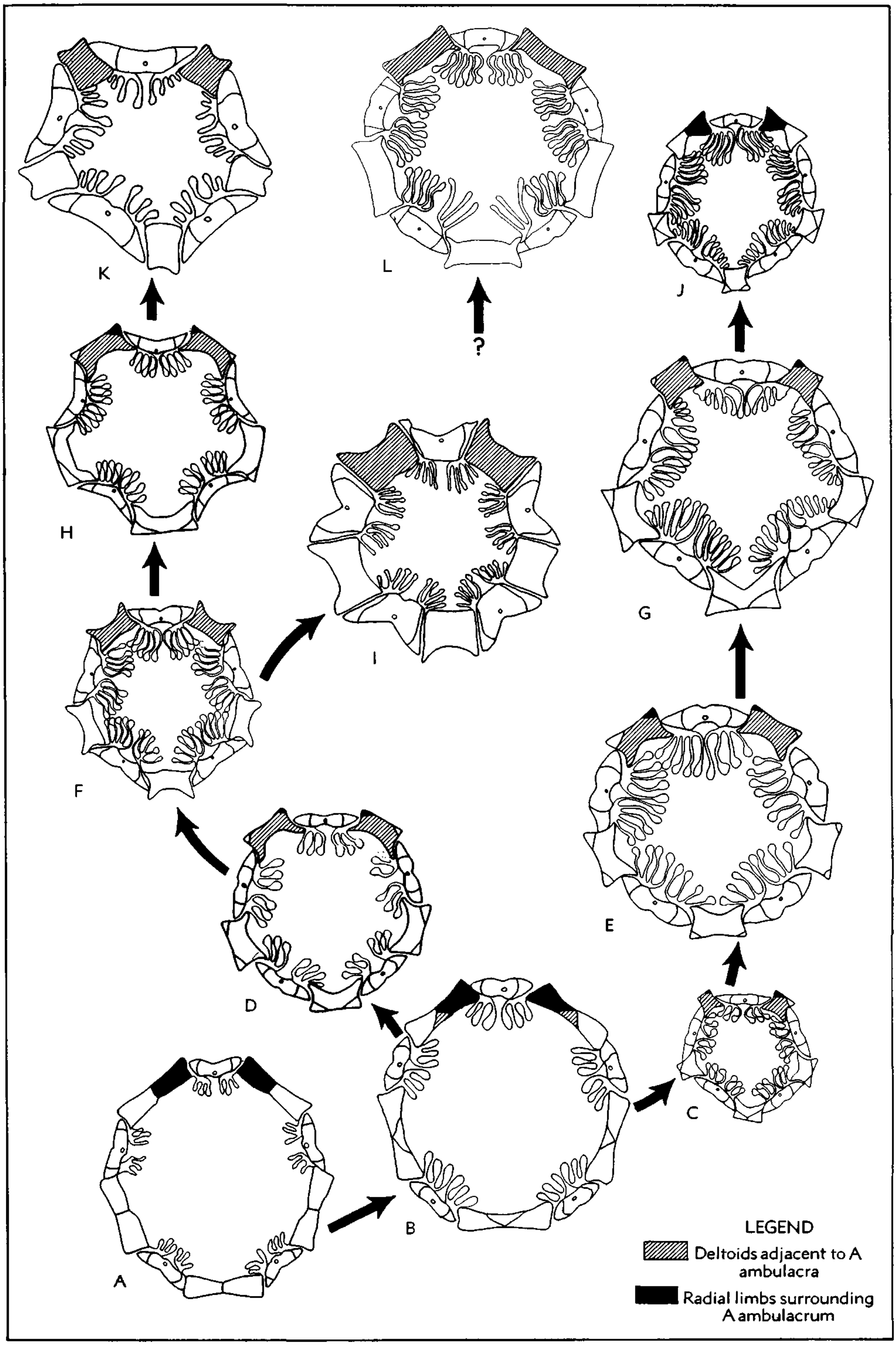

FIG. 180. *(Continued).*

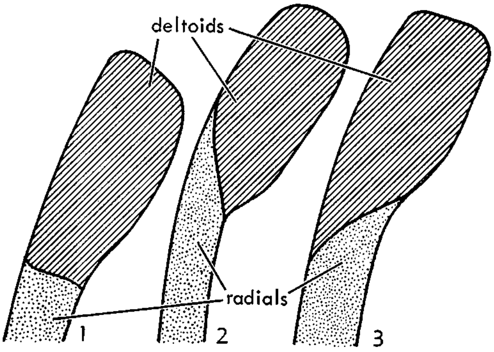

FIG. 181. Radial-deltoid relationships illustrated by diagrammatic sections; *1,* normal abutment; *2,* radial overlap; *3,* deltoid overlap (radials stippled, deltoids oblique ruled, exterior of calyx toward left).

sylvanian blastoids, represented by few species, and Permian forms, consisting of many species and genera, show about the same range in the size of specimens as do Mississippian and older blastoids.

STRUCTURAL FEATURES

Although the blastoid calyx normally consists of a constant number of plates, their range in shape and structure is great enough to aid in generic distinctions. Features commonly used in classification include shape, respective size of the plates, and position of other structures in relation to the thecal plates (e.g., relationships of spiracles to deltoids). One useful observation, mostly unmentioned in the literature, is the nature of sutural contacts between radials and deltoids.

In various genera three different conditions are found, even though gradation of one to another introduces some intermediate types which reduce sharpness of distinction. The contacts may be illustrated by sections cut approximately at right angles to the radial-deltoid suture (Fig. 181). A simplest condition (type 1) is marked by the sutural (contact) surface disposed perpendicularly to the outer and inner surfaces of the plates; then abutment of radial against deltoid is **normal** (e.g., *Codaster*). In other conditions the abutment may be more or less strongly oblique. If the sutural surface is inclined outward adorally or adlaterally (type 2), the radial margin overlies an edge portion of the deltoid and this is designated as **radial overlap** (e.g., *Globoblastus*). If the sutural surface is inclined inward, adorally or adlaterally (type 3), the deltoid margin overlies an edge portion of the radial and this is designated as **deltoid overlap** (e.g., *Schizoblastus*).

The calyx is pierced by numerous openings, some of which are illustrated here (Fig. 178,*1*) and some later. A central opening at the summit **(mouth)** served as an inlet to the digestive tract of the living animal. The **anus** is a relatively large orifice (anal opening) located in the posterior *(CD)* interray. It functioned as the excurrent opening of the digestive tract. Small, generally rounded apertures **(spiracles)** penetrate the deltoids or occur adjacent to them in some (spiraculate) blastoids. Typically in such blastoids tiny openings parallel the sides of ambulacra and connect internally with the hydrospires. These openings, called **hydrospire pores,** are located between the margin of the ambulacrum and the adjacent radial and deltoid plates, or they may be excavated in the radial and deltoid plates. In other (fissiculate) blastoids, the hydrospire pores may be replaced by long, very narrow **hydrospire clefts,** which open directly into the hydrospires. Generally, these clefts are excavated in the radial and deltoid plates and transect the radial-deltoid suture. In a few blastoids the spiracles are lengthened into long slits **(spiracular slits)** along the sides of an ambulacrum.

In well-preserved specimens, thecal openings in the vicinity of the summit (mouth, anus, spiracles) are covered by tiny skeletal plates, collectively termed **summit plates.** These plates, however, are commonly highly specialized and differ in number, shape, and size from one genus to another.

ORNAMENT

The exterior surface of blastoid calyces may be quite smooth, or it may bear various sorts of sculpture. Ornamentation of the theca, where present, commonly consists of growth lines and ridges or rows of nodes distributed over the surface. Generally, growth lines of the basals are parallel to the plate margins, such lines being crowded together next to the column, less closely

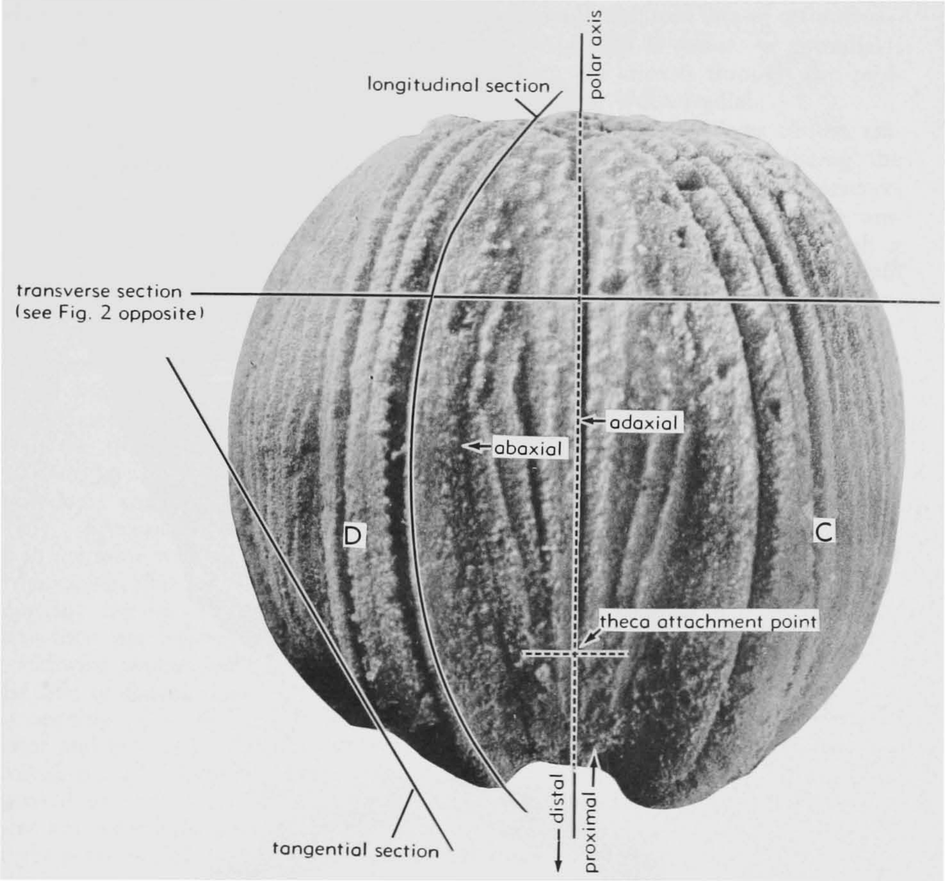

FIG. 182. Terminology related to orientation of blastoid theca illustrated on side view of *Globoblastus norwoodi* (OWEN & SHUMARD), L.Miss.(Burlington Ls.), Burlington, USA (Iowa) (Beaver, n).

spaced adjacent to the interbasal sutures, and farthest apart near the radial-basal sutures (FAY, 1961, p. 10). This arrangement reflects differential expansion of the plates during ontogeny, growth distally and laterally being greater than proximally. The growth lines of the radials are parallel to the margins of the plates, indicating that accretion occurred along edges next to basals, deltoids, and contiguous radials. On deltoids the growth lines usually are most widely spaced parallel to the radial-deltoid sutures, for the adoral tips of the deltoids were secreted first and growth occurred around sides of the plates, particularly in an aboral direction.

ORIENTATION

For purposes of description and comparison of blastoid calyces, standards of orientation and designations of corresponding parts must be agreed on. Mostly, these matters offer little difficulty, since the mouth, at the summit of the calyx, furnishes reference for defining adoral and aboral directions and differentiation of the rays may be decided according to a simple, practicable system. The treatment of blastoids from these viewpoints and nomenclature for descriptive purposes are explained in this section.

An imaginary line extending from the mouth of a blastoid to the center of its column is called the **polar axis** (Fig. 182). Any section in a plane coinciding with this axis or parallel and close to it is termed a **longitudinal section** and any section perpendicular to it is a **transverse section.** A section tangent to the outer surface of the theca and relatively near it is called a **tangential section.** Any direction toward the polar

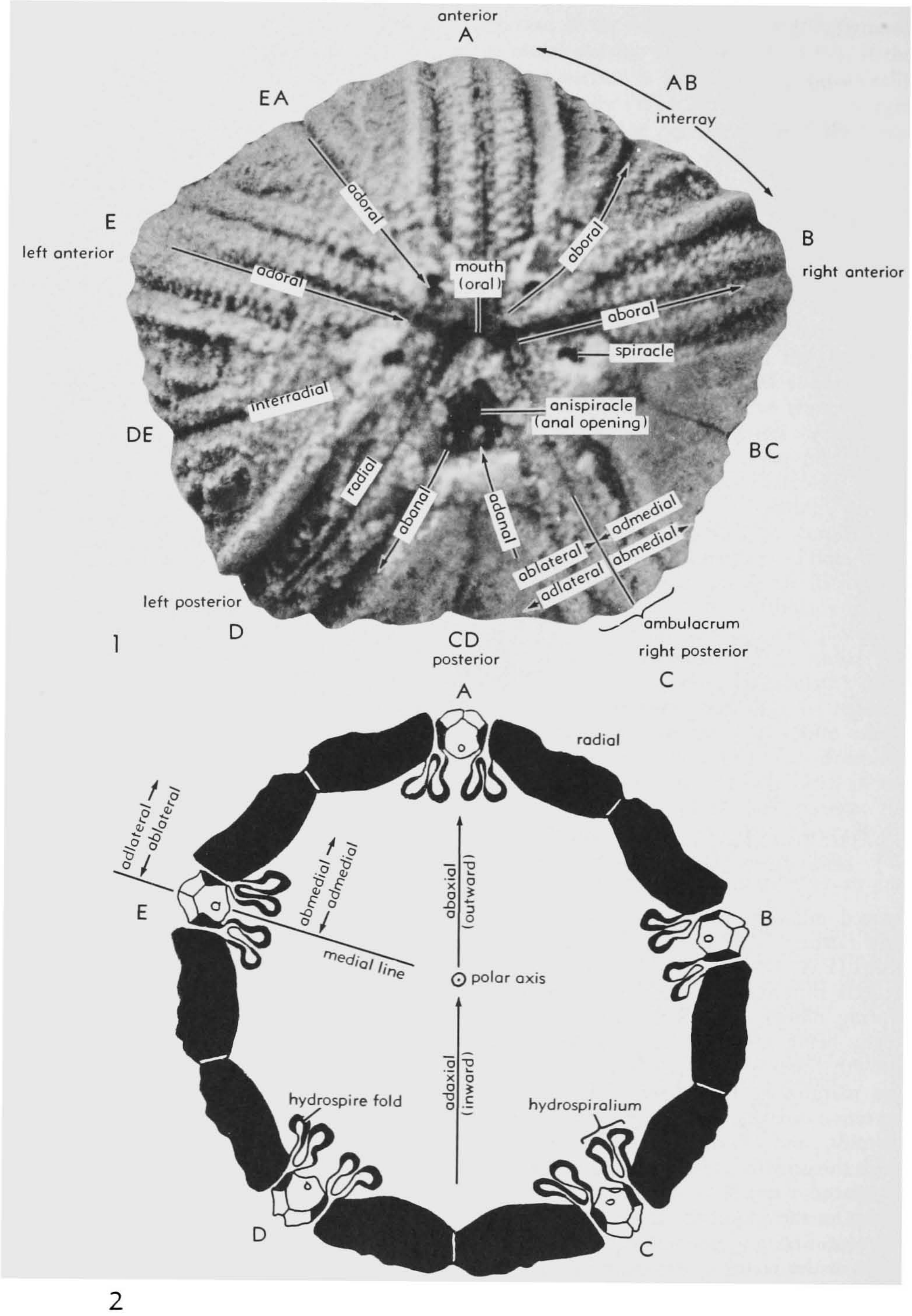

FIG. 183. Terminology related to orientation of blastoid theca illustrated by oral view *(1)* and transverse section *(2)* of *Globoblastus norwoodi* (scale same as in Fig. 193) (Beaver, n).

axis and approximately perpendicular to it is **adaxial** and any away from it is **abaxial.** Directions toward the geometric center of the theca are **inward** and those away from it are **outward.** The area surrounding the mouth is termed **oral.** Any direction toward the mouth is **adoral** and any away from it is **aboral.** A direction toward the point of attachment of column and theca is defined as **proximal**; a direction away from this point is **distal.**

According to nomenclature introduced by Carpenter (1878) and adopted herein, when a blastoid specimen is viewed from the oral side with the anal opening directed toward the viewer, the ambulacrum on the far side of the theca is designated by the letter *A*; then, in a clockwise direction the other ambulacra are lettered *B* through *E* (Fig. 183). Specimens viewed aborally, oriented in the same way with the anal side toward the viewer, also have the *A* ambulacrum opposite the viewer, but the other ambulacra then are lettered *B* to *E* in a counterclockwise manner. A direction toward the side of the theca which contains the anal opening (*CD* interray) is classed as posterior and that away from it (toward the *A* ambulacrum) is anterior. Areas may be designated similarly. The *B,C,D,* and *E* ambulacra are sometimes termed right anterior, right posterior, left posterior, and left anterior, respectively. A line from the mouth through the mid-line of an ambulacrum is designated as **radial** (or **perradial**); a line from the mouth through the mid-line of a deltoid is **interradial.**

Directions relative to plates of the ambulacrum may be made by utilizing the mid-line of an ambulacrum as a reference. A direction toward the mid-line of an ambulacrum thus is **admedial** or **ablateral**; a direction away from the mid-line is **abmedial** or **adlateral** (Fig. 183,*1*).

BASALS

The basal circlet of blastoid calyces consists of three plates, two major ones of approximately equal size and shape, termed **zygous basals,** and a minor one that is smallest and quite different in shape from the others; this last-mentioned plate is termed **azygous basal** (Fig. 178,*3*), a name signifying unyoked (unfused) in contrast to the major zygous basals, each of which evidently is the product of fusion together of two pre-existing plates comparable in size and shape to the azygous basal. Aborally, the basals are attached to the column; adorally, they are overlain by the radials. Normally, the azygous basal lies in the position of the *AB* interray. Rarely, the basals seem to be fused into a single plate (e.g., *Acentrotremites*).

[*See* pages S310-S311]

Fig. 184. Morphological features shown by disarticulated parts of blastoid theca, illustrated by fragments of *Pentremites godoni* (Defrance), U.Miss.(Chester), near Floraville, Ill., all ×7 except *1* (×3.5), *7* (×8) and *8b* (×8) (Beaver, n).——*1.* Basal circlets; *1a-e,* interior views showing median excavation in C-ray zygous basal; *1f,* exterior view showing thickened area around stem impression.——*2.* Deltoids; *2a,* exterior of deltoid body with beveled aboral tips which project beneath adoral extremities of radial limbs (illustrating radial overlap) (cf. *4a,b*); *2b,* exterior surface of deltoid body with lateral lips covered by attached side plates of ambulacra; *2c,* side view showing hydrospire canal and admedial surface of side plates.——*3.* Lancets; *3a,* exterior surface with well-preserved median and lateral food grooves; *3b,* interior surface showing 2 longitudinal ridges which carry attachments of admedial ends of hydrospire folds.——*4.* Radials; *4a,* exterior surface showing sloping sides of radial sinus and admedial abaxial surfaces of adjacent hydrospiralia (not underlancet plate); *4b,* interior surface showing beveled adoral extremities of limbs which overlap borders of deltoids (radial overlap) and partly preserved hydrospires in radial sinus.——*5.* Basals; *5a,* interior surface showing elongate depression (aligned with *C* ambulacrum) on *C* zygous basal; *5b,* exterior surface of circlet showing central moundlike elevation (consisting of secondary calcite) which bears stem attachment.——*6.* Lancet plate; *6a,* exterior surface showing side plates attached along margins; *6b,* interior surface showing hydrospire pores and their relation to side plates and outer side plates.——*7.* Deltoid; interior surface of specimen shown in Fig. *2b,* showing position of hydrospire canals and their relation to deltoid septum.——*8.* Summit part of theca composed of deltoid and adjoining ambulacra; *8a,* oblique view of outer surface showing spiracle at tip of deltoid; *8b,* interior surface showing deltoid septum which connects deltoid body and lip, lancet plates at left and right.

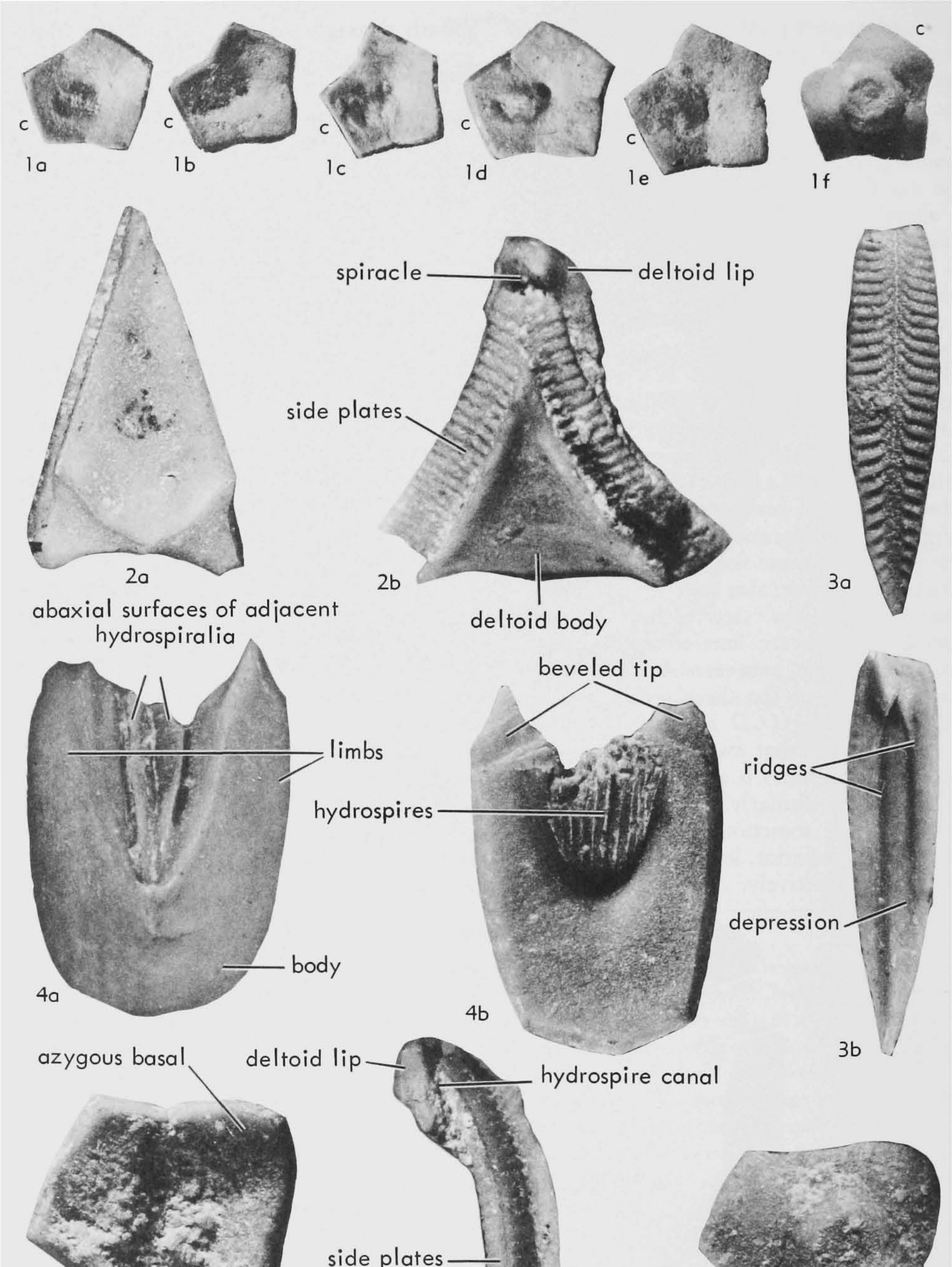

FIG. 184. [*See* page S309 for explanation.]

Lyons (1857, p. 469) described what he presumed to be a circlet of plates in some blastoids below the basals. Although this interpretation was supported by Billings (1869, p. 83), subsequent evidence has shown that these presumed extra plates consist merely of thickened calcite adjacent to the stem impression (Fig. 184,*1f,5b*) (Etheridge & Carpenter, 1886, p. 21).

DIMENSIONS

The basals may be relatively large, forming most of the proximal part of the theca, or they may be very small and difficult to

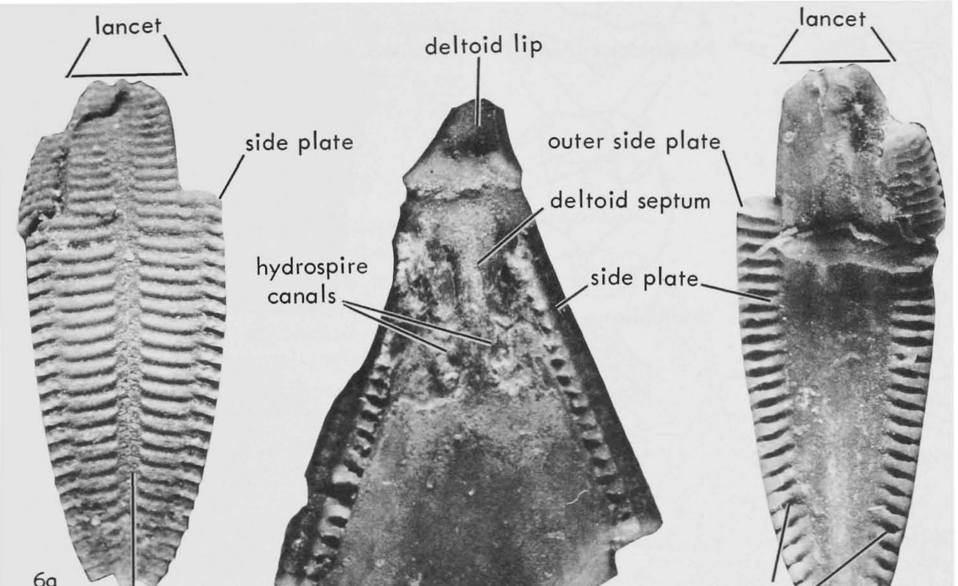

Fig. 184. *(Continued.)*

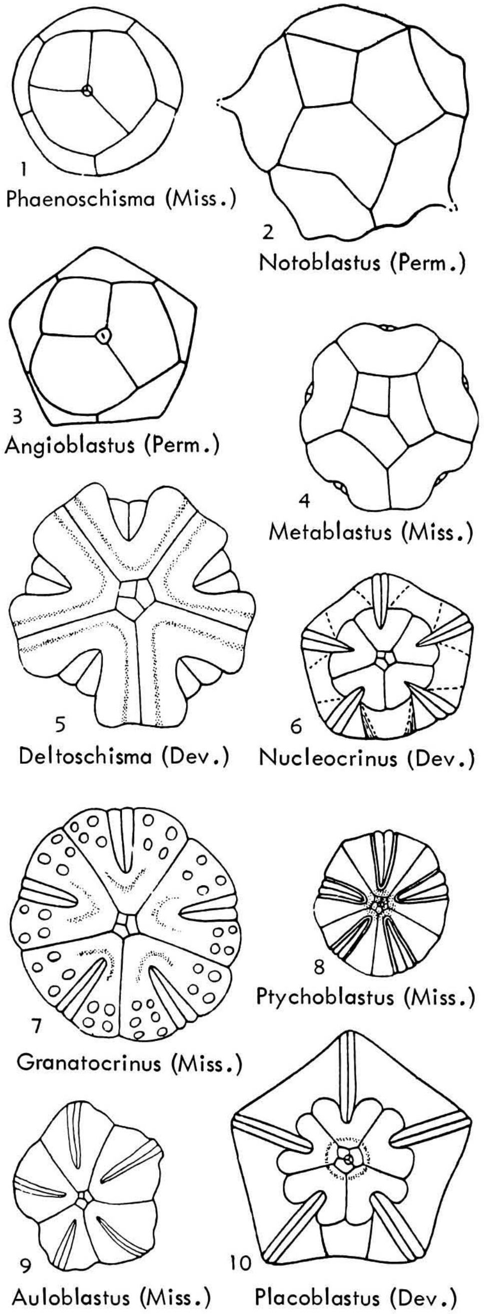

FIG. 185. Aboral views of blastoid calyces showing variation in relationships of basal circlet to adjacent plates of theca; *1-4,* basal circlet relatively large; *5-10,* basal circlet diminutive (not to scale) (Fay, n).

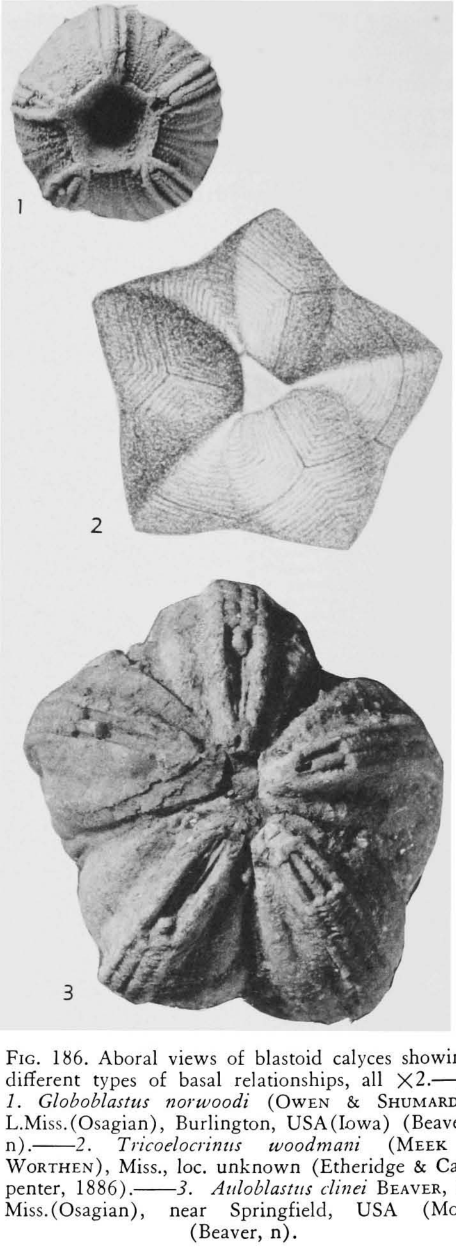

FIG. 186. Aboral views of blastoid calyces showing different types of basal relationships, all ×2.——*1. Globoblastus norwoodi* (Owen & Shumard), L.Miss.(Osagian), Burlington, USA(Iowa) (Beaver, n).——*2. Tricoelocrinus woodmani* (Meek & Worthen), Miss., loc. unknown (Etheridge & Carpenter, 1886).——*3. Auloblastus clinei* Beaver, L. Miss.(Osagian), near Springfield, USA (Mo.) (Beaver, n).

observe (Fig. 185). They make up much of the basal view in most genera with moderate to short ambulacra (e.g., *Tricoelocrinus,* Fig. 186,*3*). In examples with ambulacra that nearly equal height of the theca, the basals are generally small and occupy very little of the basal view (e.g., *Globoblastus,*

Fig. 186,*1*). Some blastoids exhibit unusual basals because of asymmetrical thecas or poorly known basal relationships (Fig. 187). For example, *Astrocrinus* has a small quadrangular plate in the position of the azygous basal (*AB* interray), suggesting that the two other basals were resorbed (Fig. 187,*3*) (Fay, 1961, p. 10). In many genera with extended ambulacra the basals may be partially hidden in a shallow-basal depression (e.g., *Auloblastus,* Fig. 186,*3*), or in a deep cavity (e.g., *Globoblastus,* Fig. 186,*1*).

EXTERNAL FEATURES

Swellings and ridges are developed on the basals of some genera. Many specimens of *Pentremites* exhibit a swollen area on each basal, the largest one located on the azygous basal in an interradial position. The swellings on the large zygous basals are developed beneath ambulacra *C* and *E,* appearing as enlargements of ridges that extend from the aboral tip of each ambulacrum to the point of column attachment.

Prominent ridges are developed on the basals of *Tricoelocrinus* (Fig. 186,*2*). The azygous basal is trisected by two ridges which extend from the point of column attachment to the lower tip of ambulacra *A* and *B*. Each of the zygous basals is transected by a strong ridge projecting from the point of attachment to the lower tip of ambulacra *C* and *E,* respectively. More weakly developed ridges follow a curved path from the point of column attachment to the ambulacra located at right and left of the ambulacrum to which the strong ridge leads.

INTERNAL FEATURES

Little attention has been devoted to the internal nature of blastoid basals. Carpenter (1884, p. 413) speculated that the median canals of the lancets connected with the axial canal of the column by way of passageways within the basals and radials. Sections of the lancets near their aboral extremities indicate that the median canals of the lancet progressively decrease in size and seem to disappear. Careful examination of sections through the basals has failed to establish the presence of canals in the basals. A passageway connects the axial canal of the column with the central cavity of the theca.

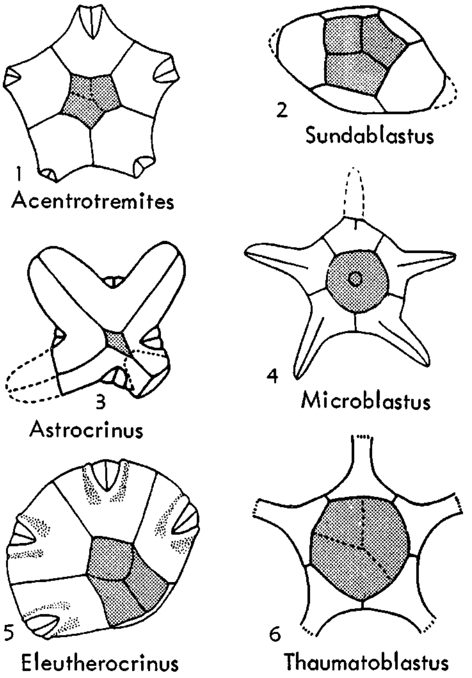

Fig. 187. Aboral views of blastoid calyces showing unusual features or relationships of basal circlets (shaded) (Fay, n).

Disarticulated basal plates permit study of internal surfaces and possible structures. An interesting feature of uncertain significance is an elongate depression on the inner surface of the *BD* zygous basal of *Pentremites* (Fig. 184,*1a-e*). This shallow trough is in the position of the *C* ambulacrum and aligned with it.

RADIALS

Radial plates of the blastoid calyx overlie and alternate with the basals. The upper portion of each radial is divided by a deep sinus which is occupied by an ambulacrum (Fig. 178,*2*). The lower, undivided part of the plate is the **radial body**; the portions of the radial separated by the ambulacrum are the **radial limbs.** Each of the five radials is the same except in asymmetrical blastoids (e.g., *Eleutherocrinus,* Fig. 179,*15*).

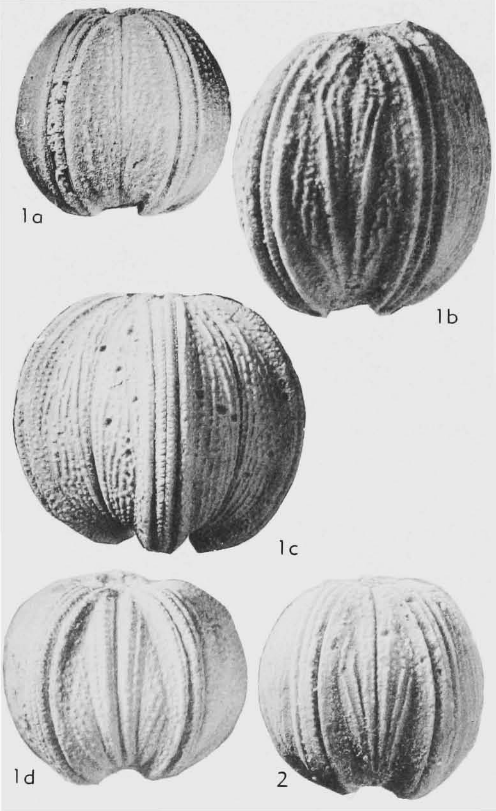

FIG. 188. Variation in ornament of radial plates of *Globoblastus norwoodi* (OWEN & SHUMARD), L. Miss.(Osagian), all ×2; *1a,c,d, 2,* specimens from Burlington Ls., at Burlington, Iowa; *1b,* specimen from Burlington Ls., near Springfield, Mo. (Beaver, n).

SIZE AND SHAPE

The size and shape of radials vary greatly. Generally they equal half to two-thirds of the height of the theca (e.g., *Troosticrinus,* Fig. 179,*7*). In some elongate-globose forms the radials are very small and make up little of the theca (e.g., *Nucleocrinus,* Fig. 179,*16*). The shape of the radials may be governed largely by length of the ambulacra in blastoids where the ambulacra are confined to the summit. The radials may be only slightly notched if the ambulacra are short (e.g., *Agmoblastus,* Fig. 179,*10*) or wing-shaped if the ambulacra are long (e.g., *Thaumatoblastus,* Fig. 179,*23*).

PORES OR SLITS

The radials are perforated by pores or slits only where these lead adaxially to the hydrospires. In some genera a row of tiny pores **(hydrospire pores)** connect the hydrospires with the exterior. In such genera the pores occur in a row parallel to an ambulacrum (Fig. 184,*6b*). The portion of each radial between the row of hydrospire pores and this ambulacrum is sometimes called the **hydrospire plate.** In other blastoids the radials (and deltoids) may be pierced by extended slits **(hydrospire clefts** or **spiracular slits)** that parallel the ambulacra and lead to the hydrospires. Generally two or more such clefts occur on either side of an ambulacrum.

ORNAMENT

Surface sculpture of radials commonly ranges widely between genera. Many genera have radials which are nearly smooth except for the slight ridges indicating growth stages. Others, however, are strongly ornamented with nodes arranged in a random pattern or with rows of nodes in a symmetrical arrangement. Variations of ornament exist, not only between genera but between individuals of the same genus and species. For example, individuals of *Globoblastus norwoodi* show considerable difference in arrangement of nodes on the radials (Fig. 188).

DELTOIDS

The deltoids are a circlet of interradially placed subtriangular plates which abut adoral edges of the radials (Fig. 178,*1,2*). Their sides normally are bounded by the ambulacra. The adoral portion of each deltoid bordering the mouth is called the **deltoid lip** (Fig. 184,*2b,7,8b*). Aborally, the deltoid lip is connected with the main portion of the deltoid, termed **deltoid body** (Fig. 184,*2a,b, 8b*), by a narrow internal connecting septum, termed **deltoid septum** (Fig. 184,*7, 8b*). In some genera, an external ridge called the **deltoid crest** longitudinally divides the deltoid (e.g., *Codaster*).

VARIATIONS

The length of the deltoids is variable in different genera and, to a limited degree, within a given genus. The deltoids may be very large, exceptionally nearly equal to the total height of the theca (e.g., *Nucleo-*

crinus, Fig. 179,*16*), or oppositely, they may be so small as to be barely visible (e.g., *Troosticrinus,* Fig. 179,*7*). In *Pentremites,* slight differences of deltoid length are observed, but no definite trend during some portion of geologic time is recognized (Fig. 180). In the past, species having widely different deltoid lengths but apparently similar morphology otherwise have been grouped together in a single genus. Additional research on such species has shown that commonly they are characterized by important structural differences in addition to dissimilarity of the deltoids.

ANAL DELTOIDS

[Section on anal deltoids by H. H. Beaver, R. O. Fay, and R. C. Moore]

Posterior interradial elements (in *CD* interray) of the blastoid theca are collectively termed **anal deltoids,** because they are associated in various ways with the anal opening. This orifice may or may not be confluent with spiracles of the posterior interray. Clearly, the anal deltoids are important morphological features.

NOMENCLATURE

During the past 50 years various names have been introduced for different anal deltoids. The more important of these are **hypodeltoid** and **epideltoid** (Wanner, 1924), **subdeltoid** and **superdeltoid** (Cline & Heuer, 1950), **cryptodeltoids** (Beaver, 1961), and **paradeltoids** (Reimann & Fay, 1961). Usage of these and other terms has varied a good deal when applied to genera of differing age and morphology. It seems evident that precision in morphological descriptions and systematic diagnoses will be enhanced by agreement on terminology, accompanied by consistent use of appropriate names for the different kinds of anal deltoids.

Generally, plates classed as anal deltoids are clearly visible on the exterior surface of the blastoid calyx, or at least a major part of each such plate can be seen. Marginal features, however, are likely to be concealed and some anal-deltoid elements are largely or entirely hidden beneath the surface. Removal of skeletal material to expose the concealed plate or plates may be effected by weathering, by etching with an acid, and by grinding. Correct understanding of morphological relationships and nomenclature of features dependent on this call for thorough investigation of concealed characters, along with observation of surface features.

Anideltoid.—The name anideltoid is employed for an externally visible anal deltoid which is proved or not known to be accompanied by any others and which lies almost wholly on the aboral side of the anal opening *(Acentrotremites)* or anispiracle *(Pentremites, Ambolostoma)* (Fig. 189, *1a,b*). In genera with an anispiracle, this orifice seems to be located beyond the adoral extremity of the anideltoid, separating this plate from the mouth. Actually, a very small part of this undivided anal deltoid is visible externally between the anispiracle and the mouth. It is connected internally with the main part of the anideltoid by a slender, extremely fragile bar (deltoid septum) which extends beneath the anal opening and in nearly all specimens is concealed by matrix (Fig. 189,*1a*). Anideltoids and other deltoids of this type are termed **disjunct.**

Hypodeltoid.—Many blastoids have a single unpaired anal deltoid bordering the anal orifice on its aboral side. This plate is named hypodeltoid (Greek, *hypo-,* below, beneath) (Fig. 189,*2a-c, 3-5*). Hypodeltoids range in size from diminutive to very large, in some genera (e.g., *Granatocrinus,* Fig. 189,*4c*) comprising most of the posterior interray. Typically, the hypodeltoid overlaps adjacent anal deltoid plates and may form a hood over the anal opening. Oppositely, it may be concealed by bordering parts of the *C* and *D* radial limbs and in various genera judged to have possessed a small hypodeltoid, specimens fail to reveal its presence, owing to concealment and lack of detection by grinding, or possibly by separation and loss of the plate, or perhaps because of atrophy during ontogeny.

Epideltoid. An unpaired anal deltoid bordering the anal orifice on its adoral side is named epideltoid (Greek, *epi-*, above, upon) (Fig. 189,*1c, 2a-c*). An epideltoid may extend along the left and right sides of the anal opening but not the aboral side. Normally, epideltoids are associated with hypodeltoids, but in at least six genera *(Agmoblastus, Codaster, Microblastus, Para-*

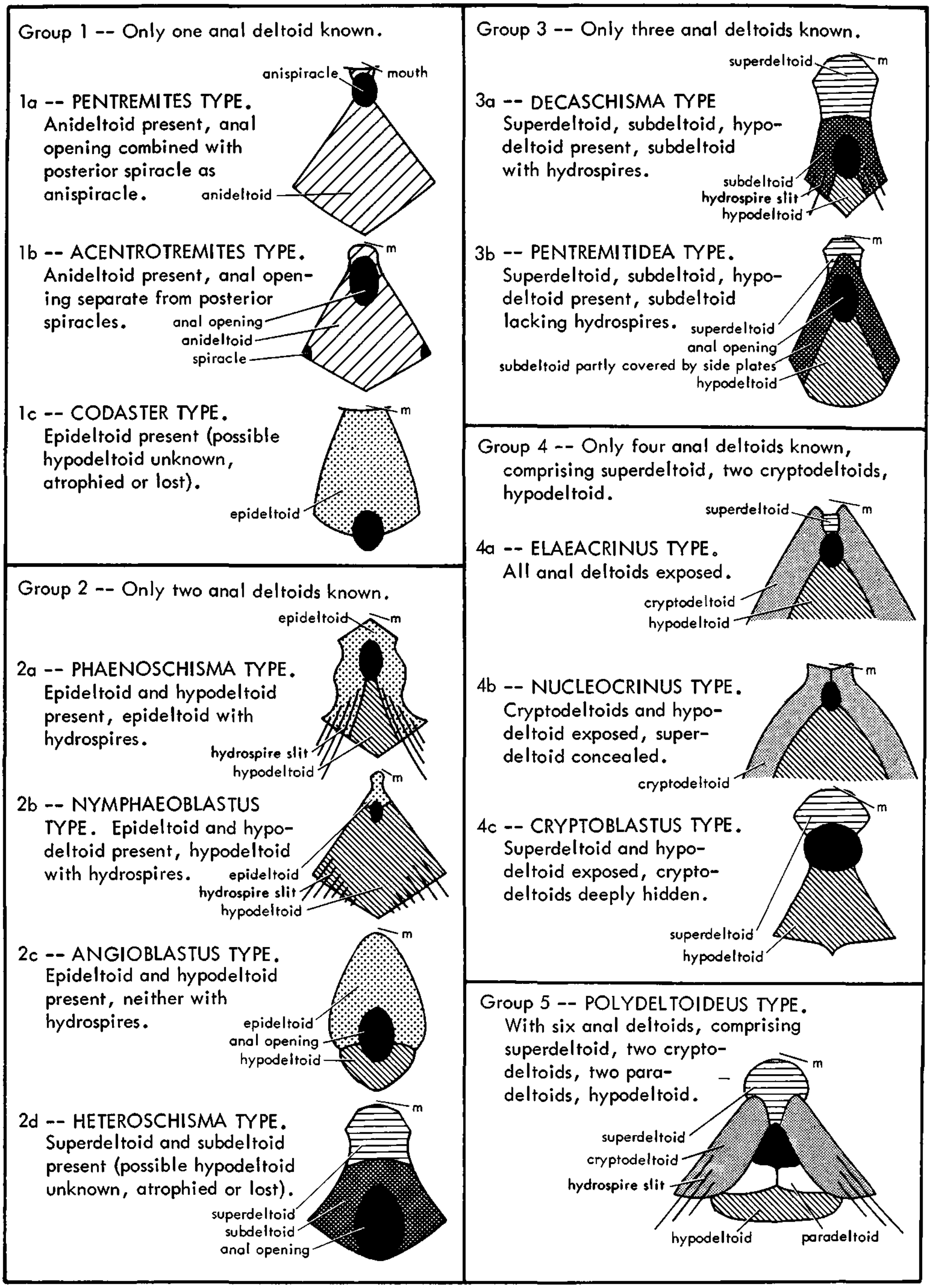

FIG. 189. Types of anal-deltoid relationships in blastoids (see Table 1 for distribution among genera) (Beaver, Fay, & Moore, n).

codaster, Pterotoblastus, Sagittoblastus) a hypodeltoid is missing or its presence is unproved (Fig. 189, *1c*). The unpaired well-exposed anal deltoid in these genera is identified as an epideltoid (rather than anideltoid) because it lies above the anal opening in manner exactly corresponding to undoubted epideltoids. Normally, epideltoid plates border the mouth, as well as the anal opening. Internally, the lateral portions of epideltoids may be infolded into hydrospires or conversely, epideltoid plates are not known to bear hydrospires. Table 1 records 32 genera having epideltoids with hydrospires and 12 genera having epideltoids without associated hydrospires.

Subdeltoid. A subdeltoid is defined as a small to moderately large, inverted U-shaped plate of the posterior interray in a few blastoids, located on the adoral and lateral margins of the anal orifice and abutting the aboral edge of a plate called superdeltoid (Fig. 189,*2d, 3*). As previously noted, subdeltoid and superdeltoid are terms introduced by Cline & Heuer (1950) and, although considered to be undesirable on etymological grounds, they are adopted because of their morphological significance. Subdeltoids now are recognized in five genera *(Decaschisma, Brachyschisma, Pentremoblastus, Heteroschisma, Pentremitidea)* among which this plate in the first three listed contains hydrospires, whereas no hydrospires have been observed in anal deltoids of the others. In Moore's opinion, comparison of subdeltoids with the paired plates called cryptodeltoids in several genera (e.g., *Polydeltoideus,* Fig. 189,*5*) strongly suggest homology because fusion of the adoral extremities of the cryptodeltoids would produce a plate exactly like the narrow-limbed inverted U-shaped subdeltoid seen in *Decaschisma,* for example. Conversely, a separation of the subdeltoid limbs would yield a pair of cryptodeltoids.

Superdeltoid.—A fourth kind of unpaired anal deltoid (counting anideltoid, hypodeltoid, and epideltoid as others) has been termed superdeltoid. Such a plate invariably is located at the summit of the posterior interray, adjoining the mouth, and is distinguished from epideltoid, which also may border the mouth, by lack of any contact with the anal opening in genera which possess a subdeltoid (Fig. 189, *2d,3*) and in other genera by association with cryptodeltoids (Fig. 189,*4-5*). If the cryptodeltoids do not meet each other on the adoral side of the anus the superdeltoid may border both oral and anal orifices (as shown in numerous diagrams illustrating adoral parts of subdeltoid- and cryptodeltoid-bearing blastoids which accompany systematic descriptions in the *Treatise*). As a "rule of thumb" we may say that all blastoids with a subdeltoid or pair of cryptodeltoids have a superdeltoid and no epideltoid. All blastoids lacking a subdeltoid or cryptodeltoids have an epideltoid, or the single anal deltoid is an anideltoid.

Cryptodeltoids.—Anal deltoids located on opposite lateral margins of the anal opening and invariably paired are termed cryptodeltoids (Greek, *crypto-,* hidden) because generally they are only partly visible externally and in some genera they are entirely concealed by other plates of the theca. They may be short and small (e.g., *Troosticrinus*) or relatively long and large (e.g., *Elaeacrinus, Nucleocrinus,* Fig. 189,*4a,b*); they may be entirely separated from one another (e.g., *Elaeacrinus,* Fig. 189,*4a,c,5*) or may meet adorally (e.g., *Nucleocrinus,* Fig. 189,*4b*) in manner cutting off contact of a superdeltoid from the anal opening. Substance of the cryptodeltoids may be infolded in the form of hydrospires. In at least a dozen genera, all with two externally visible anal deltoids, the presence of cryptodeltoids can be demonstrated by grinding or by cutting properly oriented thin sections (Table 1). Such preparations show that the cryptodeltoids mostly are slender elongate plates which are overlapped on their aboral parts by the hypodeltoid, invariably present in blastoids provided with cryptodeltoids. The cryptodeltoids may form internal walls between spiracular and anal passageways of an anispiracle and adorally they may be confluent with superdeltoid extensions (septa). Exceptionally, cryptodeltoids are very large, almost completely exposed plates which are prominent components of the theca (e.g., *Nucleocrinus, Elaeacrinus, Placoblastus,* Fig. 189,*4a,b*).

Paradeltoids.—Small paired plates termed paradeltoids (Greek, *para-*, associated) are distinguished in a single genus (*Polydeltoid-*

TABLE 1.--Distribution of Anal-deltoid Types among Blastoid Genera

[Explanation.--Numbered anal-deltoid types correspond to those described in accompanying text. Each kind of anal-deltoid plate is indicated by letter designation, as follows: A = anideltoid, C = cryptodeltoids, E = epideltoid, H = hypodeltoid, S = subdeltoid, SS = superdeltoid. Symbols for hydrospire slits or infolds: + indicates present, o indicates absent.]

Anal-deltoid Types					Suprageneric and Generic Taxa	Anal-deltoid Plates						Age
1	2	3	4	5		A	C	H	E	S	SS	
					FISSICULATA							
					PHAENOSCHISMATIDAE							
?1d	-	-	-	-	Microblastus	-	-	?H	E +	-	-	Perm.
-	2a	-	-	-	Phaenoschisma	-	-	H o	E +	-	-	Miss.
-	2a	-	-	-	Hadroblastus	-	-	H o	E +	-	-	Miss.
-	2a	-	-	-	Phaenoblastus	-	-	H o	E +	-	-	L.Carb.
-	2a	-	-	-	Dipteroblastus	-	-	H o	E +	-	-	Perm.
-	2a	-	-	-	Neoschisma	-	-	H o	E +	-	-	Perm.
-	2a	-	-	-	Notoblastus	-	-	H o	E +	-	-	Perm.
-	2a	-	-	-	Sphaeroschisma	-	-	H o	E +	-	-	Perm.
-	2a	-	-	-	Sundablastus	-	-	H o	E +	-	-	Perm.
-	2a	-	-	-	Thaumatoblastus	-	-	H o	E +	-	-	Perm.
-	2a	-	-	-	Timoroblastus	-	-	H o	E +	-	-	Perm.
-	2b	-	-	-	Nymphaeoblastus	-	-	H +	E o	-	-	Miss.
-	-	3a	-	-	Decaschisma	-	-	H o	-	S +	SS	Sil.
-	-	-	4a	-	Deltoschisma	-	C +	H o	-	-	SS	Dev.
-	-	-	4a	-	Pleuroschisma	-	C +	H o	-	-	SS	Dev.
-	-	-	4c	-	Hyperoblastus	-	C +	H o	-	-	SS	Dev.
-	-	-	-	5	Polydeltoideus	-	C +	H o	-	-	SS	Sil.
					BRACHYSCHISMATIDAE							
-	-	3a	-	-	Brachyschisma	-	-	H o	-	S +	SS	Dev.
					CODASTERIDAE							
1c	-	-	-	-	Codaster	-	-	?H	E o	-	-	Miss.
1c	-	-	-	-	Agmoblastus	-	-	?H	E o	-	-	Penn.
1c	-	-	-	-	Paracodaster	-	-	?H	E o	-	-	Perm.
1c	-	-	-	-	Pterotoblastus	-	-	?H	E o	-	-	Perm.
1c	-	-	-	-	Sagittoblastus	-	-	?H	E o	-	-	Perm.
-	2c	-	-	-	Angioblastus	-	-	H o	E o	-	-	Perm.
-	2c	-	-	-	Indoblastus	-	-	H o	E o	-	-	Perm.
-	2c	-	-	-	Nannoblastus	-	-	H o	E o	-	-	Perm.
-	2d	-	-	-	Heteroschisma	-	-	?H	-	S o	SS	Dev.
					OROPHOCRINIDAE							
-	2a	-	-	-	Orophocrinus	-	-	H o	E +	-	-	Miss.
-	2a	-	-	-	Pentablastus	-	-	H o	E +	-	-	Penn.
-	2a	-	-	-	Anthoblastus	-	-	H o	E +	-	-	Perm.
					ASTROCRINIDAE							
?1a	-	-	-	-	?Pentephyllum	?A	-	-	-	-	-	L.Carb.
-	2c	-	-	-	Cryptoschisma	-	-	H o	E o	-	-	Dev.
-	2c	-	-	-	Astrocrinus	-	-	H o	E o	-	-	L.Carb.
-	2c	-	-	-	Ceratoblastus	-	-	H o	E o	-	-	Perm.
-	-	?3b	-	-	Pentremitidea	-	-	H o	-	S o	SS	Dev.

TABLE 1 (continued)

Anal-deltoid Types					Suprageneric and Generic Taxa	Anal-deltoid Plates						Age
1	2	3	4	5		A	C	H	E	S	SS	
					SPIRACULATA							
					TROOSTICRINIDAE							
-	-	-	4a	-	Troosticrinus	-	C +	H o	-	-	SS	Sil.
-	-	-	4a	-	Schizotremites	-	C +	H o	-	-	SS	Dev.
-	-	-	4a	-	Metablastus	-	C +	H o	-	-	SS	Miss.
-	-	-	4a	-	Tricoelocrinus	-	C +	H o	-	-	SS	Miss.
					DIPLOBLASTIDAE							
-	2a	-	-	-	Nodoblastus	-	-	H o	E +	-	-	Miss.
-	-	-	4c	-	Diploblastus	-	C +	H o	-	-	SS	Miss.
					GRANATOCRINIDAE							
-	2a	-	-	-	Granatocrinus	-	-	H o	E +	-	-	Miss.
-	2a	-	-	-	Carpenteroblastus	-	-	H o	E +	-	-	Miss.
-	2a	-	-	-	Cribroblastus	-	-	H o	E +	-	-	Miss.
-	2a	-	-	-	Dentiblastus	-	-	H o	E +	-	-	Miss.
-	2a	-	-	-	Heteroblastus	-	-	H o	E +	-	-	Miss.
-	2a	-	-	-	Monadoblastus	-	-	H o	E +	-	-	Miss.
-	2a	-	-	-	Monoschizoblastus	-	-	H o	E +	-	-	Miss.
-	2a	-	-	-	Poroblastus	-	-	H o	E +	-	-	Miss.
-	2a	-	-	-	Ptychoblastus	-	-	H o	E +	-	-	Miss.
-	-	-	4a	-	Pyramiblastus	-	C +	H o	-	-	SS	Miss.
-	-	-	4c	-	Cryptoblastus	-	C +	H o	-	-	SS	Miss.
-	-	-	4c	-	Mesoblastus	-	C +	H o	-	-	SS	Miss.
-	-	-	4c	-	Tanaoblastus	-	C +	H o	-	-	SS	Miss.
					SCHIZOBLASTIDAE							
1b	-	-	-	-	Acentrotremites	?A+	-	-	-	-	-	L.Carb.
-	2a	-	-	-	Strongyloblastus	-	-	H o	E +	-	-	Dev.
-	2a	-	-	-	Deltoblastus	-	-	H o	E +	-	-	Miss.
-	2a	-	-	-	Lophoblastus	-	-	H o	E +	-	-	Miss.
-	2a	-	-	-	Orbiblastus	-	-	H o	E +	-	-	Miss.
-	2a	-	-	-	Schizoblastus	-	-	H o	E +	-	-	Miss.
-	-	-	4c	-	Auloblastus	-	C +	H o	-	-	SS	Miss.
					NUCLEOCRINIDAE							
-	-	-	4a	-	Elaeacrinus	-	C +	H o	-	-	SS	Dev.
-	-	-	4a	-	Placoblastus	-	C +	H o	-	-	SS	Dev.
-	-	-	4b	-	Nucleocrinus	-	C +	H o	-	-	SS	Dev.
					PENTREMITIDAE							
1a	-	-	-	-	Pentremites	A +	-	-	-	-	-	Miss.-Penn.
1a	-	-	-	-	Ambolostoma	A +	-	-	-	-	-	Miss.
-	?2a	-	-	-	Belocrinus	-	-	H o	?E +	-	-	Dev.
-	2a	-	-	-	Petaloblastus	-	-	H o	E +	-	-	Miss.
-	2a	-	-	-	Calycoblastus	-	-	H o	E +	-	-	Perm.
-	-	3a	-	-	Pentremoblastus	-	-	H o	-	S +	SS	Miss.
-	-	-	4a	-	Eleutherocrinus	-	C +	H o	-	-	SS	Dev.
-	-	-	4a	-	Rhopaloblastus	-	C +	H o	-	-	SS	Perm.
-	-	-	4c	-	Cordyloblastus	-	C +	H o	-	-	SS	Dev.
-	-	-	4c	-	Devonoblastus	-	C +	H o	-	-	SS	Dev.
					ORBITREMITIDAE							
-	-	-	4c	-	Orbitremites	-	C +	H o	-	-	SS	Miss.
-	-	-	?4c	-	Doryblastus	-	?C +	H o	-	-	SS	Miss.
-	-	-	4c	-	Ellipticoblastus	-	C +	H o	-	-	SS	Miss.
-	-	-	4c	-	Globoblastus	-	C +	H o	-	-	SS	Miss.

eus, Fig. 189,*5*), which has externally visible cryptodeltoids, a hypodeltoid, and a superdeltoid. The paradeltoids adjoin aboral parts of the cryptodeltoids and rest on the adoral margin of the hypodeltoid.

RELATION OF HYDROSPIRES TO ANAL DELTOIDS

Information is yet far from sufficient for full appraisal of the infolding of anal deltoid plate substance into hydrospires or of septal extensions of such plates adjoining hydrospires. Also, the extent to which hydrospire relationships may bear on discrimination of different kinds of anal deltoids is now incompletely determined. An objective in preparing Table 1, given on later pages, has been to record what may be considered as reasonably known, bearing in mind that present lack of observations on hydrospire characters by no means established their nonexistence.

TYPES OF BLASTOIDS BASED ON ANAL-DELTOID CHARACTERS

Blastoids are classifiable in groups defined by the kinds, numbers, and arrangements of anal deltoids. These are described briefly in following paragraphs with designations of included types and the distribution of genera among the types as indicated in Table 1. Inasmuch as assemblages differentiated on the basis of anal-deltoid characters may include representatives of two or more families belonging either to the Fissiculata, or Spiraculata, or both, it is evident that the placement of blastoid genera in one anal-deltoid type or another is unrelated to systematic classification.

Group 1

Genera in which only one anal deltoid is known are placed in Group 1, and these are divisible into three types, as follows.

Type 1a—Pentremites Type.—In this type the single anal deltoid recognized consists of an anideltoid, in which the anal opening is combined with the posterior spiracle to form an anispiracle located near the adoral extremity of the plate (Fig. 189,*1a*). The anideltoid is disjunct. Only the comparatively uncommon *Ambolostoma* is joined with myriads of *Pentremites* individuals assigned to numerous species in Type 1a.

Type 1b—Acentrotremites Type.—An anideltoid is present in Type 1b, as in 1a, but distinguished by separateness of the anal opening from a pair of posterior spiracles and by the location of all of these near the aboral margin of the anideltoid, which is described as conjunct (Fig. 189,*1b*). *Acentrotremites* is the sole known representative of the type. The possible occurrence of an additional anal deltoid or deltoids, as reported by Joysey & Breimer (1963, p. 483), is very uncertain.

Type 1c—Codaster Type.—In this type the single observed anal deltoid is identified as an epideltoid, with the anal opening medially placed on its aboral margin (Fig. 189,*1c*). A hypodeltoid, which is unknown, may be atrophied or lost in all specimens studied. Type 1c includes *Agmoblastus, Codaster, Microblastus, Paracodaster, Pterotoblastus,* and *Sagittoblastus,* all of which belong to Fissiculata.

Group 2

Group 2 is characterized by the presence of only two known anal deltoids. It is by far the largest of the differentiated anal-deltoid groups, for its 39 contained genera are approximately one-half of all known blastoid forms. Among four types that are discriminated, two are represented only by their single name-giving genus, whereas the others contain 31 and six genera, respectively.

Type 2a—Phaenoschisma Type.—The two anal-deltoid plates of Type 2a are an epideltoid and hypodeltoid, the epideltoid bearing hydrospires (Fig. 189,*2a*). Counting one questionably assigned spiraculate genus, the Spiraculata outnumber the Fissiculata in the ratio of 19 to 12. The spiraculates are distributed among four families and the fissiculates among three families (Table 1). Listed alphabetically (with spiraculates distinguished by an asterisk), the genera of Type 2a are as follows: *Anthoblastus, ?*Belocrinus, *Calycoblastus, *Carpenteroblastus, *Cribroblastus, *Deltoblastus, *Dentiblastus, Dipteroblastus, *Granatocrinus, Hadroblastus, *Heteroblastus, *Lophoblastus, *Monadoblastus, *Monoschizoblastus, Neoschisma, *Nodoblastus, Notoblastus, *Orbiblastus, Orophocrinus, *Pentablastus, *Petaloblastus, Phaenoblastus, Phaenoschisma, *Poroblastus, *Ptychoblastus, *Schizoblastus, Sphaeroschisma, *Strongyloblastus,* *Sundablastus, Thaumatoblastus, Timoroblastus.*

Type 2b—Nymphaeoblastus Type.—As in Type 2a, the two anal deltoids are epideltoid and hypodeltoid, distinction of Type 2b resting on the occurrence of hydrospires in the hypodeltoid of *Nymphaeoblastus* (Fig. 189,*2b*).

Type 2c—Angioblastus Type.—The two anal deltoids are an epideltoid and a hypodeltoid, neither of which bears hydrospires, on this basis being assigned to a separate type (Fig. 189,*2c*). Six fissiculate genera are included in Type 2c, three belonging to the Codasteridae and three to the Astrocrinidae (Table 1). They are as follows: *Angioblastus, Astrocrinus, Ceratoblastus, Cryptoschisma, Indoblastus,* and *Nannoblastus.*

Type 2d—Heteroschisma Type.—This type differs from the others of Group 2 in that the two anal deltoids are distinguished as a superdeltoid and a subdeltoid. A postulated possible hypodeltoid is unknown, perhaps atrophied or lost (Fig. 189,*2d*). Only *Heteroschisma,* among blastoids now known, belongs to Type 2d.

Group 3

Blastoids having three, but only three, known anal deltoids comprise Group 3, within which two types are distinguished.

Type 3a—Decaschisma Type.—The three anal deltoids consist of a superdeltoid, a subdeltoid, and a hypodeltoid, the subdeltoid bearing hydrospires (Fig. 189,*3a*). The type includes two fissiculate genera *(Brachyschisma, Decaschisma)* and a single spiraculate genus *(Pentremoblastus).*

Type 3b—Pentremitidea Type.—This type corresponds to Type 3a in having superdeltoid, subdeltoid, and hypodeltoid plates but is distinguished by lack of hydrospires in the subdeltoid (Fig. 189,*3b*). Only *Pentremitidea* appears to belong here.

Group 4

Blastoids characterized by the possession of four anal deltoids, but no more than four, are placed together in Group 4. The four anal-deltoid plates comprise a superdeltoid, two cryptodeltoids, and a hypodeltoid, all of which may be at least partly visible externally or some concealed.

Type 4a—Elaeacrinus Type.—In blastoids of Type 4a all anal deltoids are entirely or at least partially exposed (Fig. 189,*4a*). The type includes two fissiculate genera—*Pleuroschisma, Deltoschisma*—and nine spiraculate genera—*Elaeacrinus, Eleutherocrinus, Metablastus, Placoblastus, Pyramiblastus, Rhopaloblastus, Schizotremites, Tricoelocrinus,* and *Troosticrinus* (Table 1).

Type 4b—Nucleocrinus Type.—In the *Nucleocrinus* Type, which includes only this genus, the cryptodeltoids and hypodeltoid are large, fully exposed anal deltoids but the superdeltoid is a small concealed plate (Fig. 189,*4b*).

Type 4c — Cryptoblastus Type. — Anal-deltoid Type 4c is characterized by external visibility of the superdeltoid and hypodeltoid, combined with complete concealment of the cryptodeltoids, which in some genera are deeply hidden (Fig. 189,*4c*). The type includes one fissiculate genus, *Hyperoblastus,* and 11 spiraculates: *Auloblastus, Cordyloblastus, Cryptoblastus, Devonoblastus, Diploblastus, ?Doryblastus, Ellipticoblastus, Globoblastus, Mesoblastus, Orbitremites, Tanaoblastus.*

Group 5

No blastoid has only five anal-deltoids but one form with six such plates is known. It is assigned to Group 5 and Type 5.

Type 5—Polydeltoideus Type.—The anal deltoids of *Polydeltoideus,* which is the only presently known representative of Type 5, consist of a superdeltoid, two cryptodeltoids, two paradeltoids, and a hypodeltoid, all more or less exposed (Fig. 189,5).

Not definitely placed in any anal-deltoid type is the problematical genus *Pentephyllum,* described from a fossil that evidently is a steinkern (internal mold) and presently available for study only from artificial replicas. Efforts by Macurda (personal communication) and others to locate the type specimen have been fruitless. On this account and because of anomalous features shown by the replicas, in the view of Macurda, Beaver, and Moore, this nominal genus should be disposed of as "Unrecognizable" or at least "Classification Uncertain." Fay, however, considers it assignable to the Astrocrinidae, and thinks that its anal deltoid, without known anal orifice, is a doubtful sort of anideltoid. To place *Pentephyllum* as questionable representative

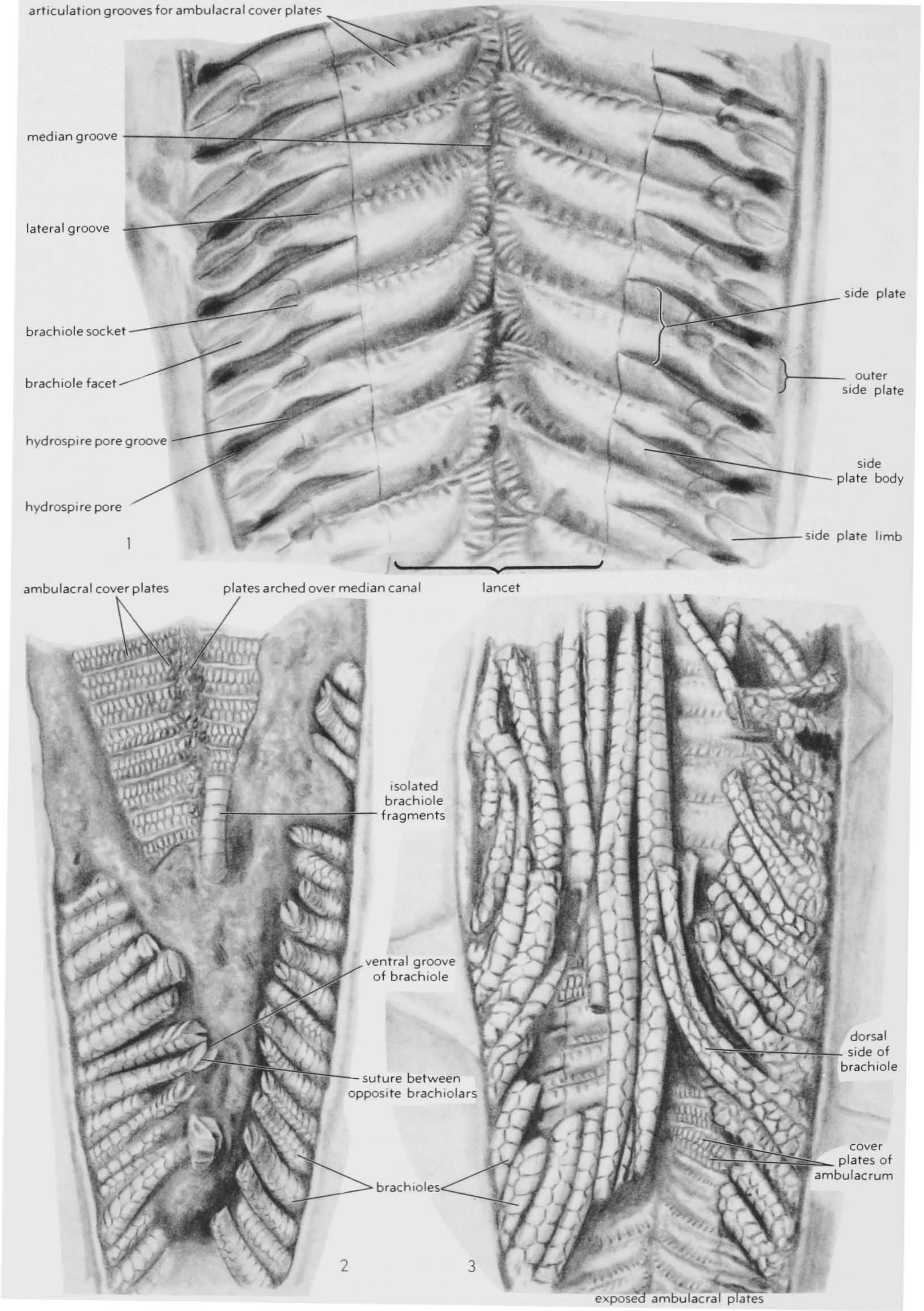

FIG. 190. [*Explanation on facing page.*]

of anal-deltoid Type 1b, associated with *Acentrotremites,* as proposed by FAY, or alternatively, to introduce a separate type for it (say Type 1d) are equally undesirable.

AMBULACRA AND AMBULACRAL PLATES

The ambulacra normally consist of five petaloid to narrowly linear areas which radiate from the vicinity of the mouth (Fig. 178,*1*). The length of the ambulacra may be short, as in *Codaster,* or very long, with ambulacra equal to length of the theca, as in *Globoblastus* (Fig. 188). In profile, the exposed abaxial surfaces of the ambulacra may be convex, flat, or concave. For example, in *Orbitremites* and *Cryptoblastus,* genera with side plates lying on the lancet, the ambulacra are convex, but in *Pentremites* with side plates abutting against the lancet, the ambulacra may be convex, flat, or concave (Fig. 180). The principal structures of the ambulacra concerned with food gathering are the median groove, lateral grooves, brachiole sockets, and ambulacral cover plates; the hydrospire pores, commonly considered structures of the ambulacra, are part of the water-vascular system (Fig. 190).

MEDIAN AND LATERAL GROOVES

The **median groove** is a shallow V-shaped groove that notches the mid-line of an ambulacrum longitudinally (Fig. 191). The groove passes under the summit into the mouth adorally; termination of the groove occurs at the aboral end of the lancet. The sides of the groove are marked by tiny indentations (crenulations); the covering plates of the ambulacrum are seated in these indentations.

Lateral grooves, located at intervals equal to the width of the side plates, lead from the brachiole sockets to the median groove (Fig. 191,*1*). Small indentations similar in design and function to those of the median groove occur on either side of each lateral groove. Transverse ridges lie parallel to and alternate with the lateral grooves, sides of the ridges sloping into the grooves.

The median groove is entirely located on the side plates in many pre-Mississippian genera. Among Mississippian blastoids (e.g., *Cryptoblastus, Orbitremites, Globoblastus*), in which the side plates rest on the lancet, the adoral portion of the median groove is located on the lancet, whereas the aboral part of the groove rests on the side plates. In *Pentremites,* the median groove and the admedial part of the lateral grooves are excavated in the lancet.

LANCET

A relatively narrow linear thecal element in the longitudinal middle part of each ambulacrum is known as the **lancet plate** (Fig. 184,*3a,b, 6a,b,*). In many genera (e.g., *Orbitremites*) the lancet nearly fills the radial sinus, and the side and outer side plates rest upon it. In *Pentremites,* however, the side plates abut against the lancet, rather than lie on it, and the lancet fills only about half the width of an ambulacral area (Fig. 184,*2b,c, 6a,b*).

The internal (adaxial) surface of the lancet is smooth except for two longitudinal adaxial ridges which nearly equal the length of the lancet (Fig. 184,*3b*). A shallow medial depression occurs between these ridges.

TRANSVERSE SHAPE

The transverse shape of the lancet may be nearly flat, concave, or convex. Within the limits of a species, however, and at a given transverse level, the shape and struc-

[*See facing page*]

FIG. 190. Morphological features of blastoid ambulacra illustrated by *Pentremites symmetricus* HALL, U. Miss.(Chester), USA(Ill.).——*1*. Part of ambulacrum lacking brachioles, ×9.——*2*. Part of ambulacrum with proximal portions of numerous brachioles in position of attachment, biserial arrangement of brachiolars clearly shown on their dorsal (external) side and broken terminations demonstrating presence of deep V-shaped ventral food groove; biserially arranged small cover plates over lateral grooves of ambulacrum shown in upper part of figure, but along median groove they fail to show any systematic arrangement, ×4.2.——*3*. Brachioles resting on ambulacrum in position of their articulation, exposing dorsal or side portions, with biserial arrangement of brachiolars clearly evident, ×4.2 (Beaver, n).

ture of this plate are fairly constant. For example, thin sections of typical specimens of *Globoblastus* cut at the radial-deltoid suture show the adaxial surface of the lancet to be nearly flat (Fig. 191,6); in sections made distally from the mid-length of

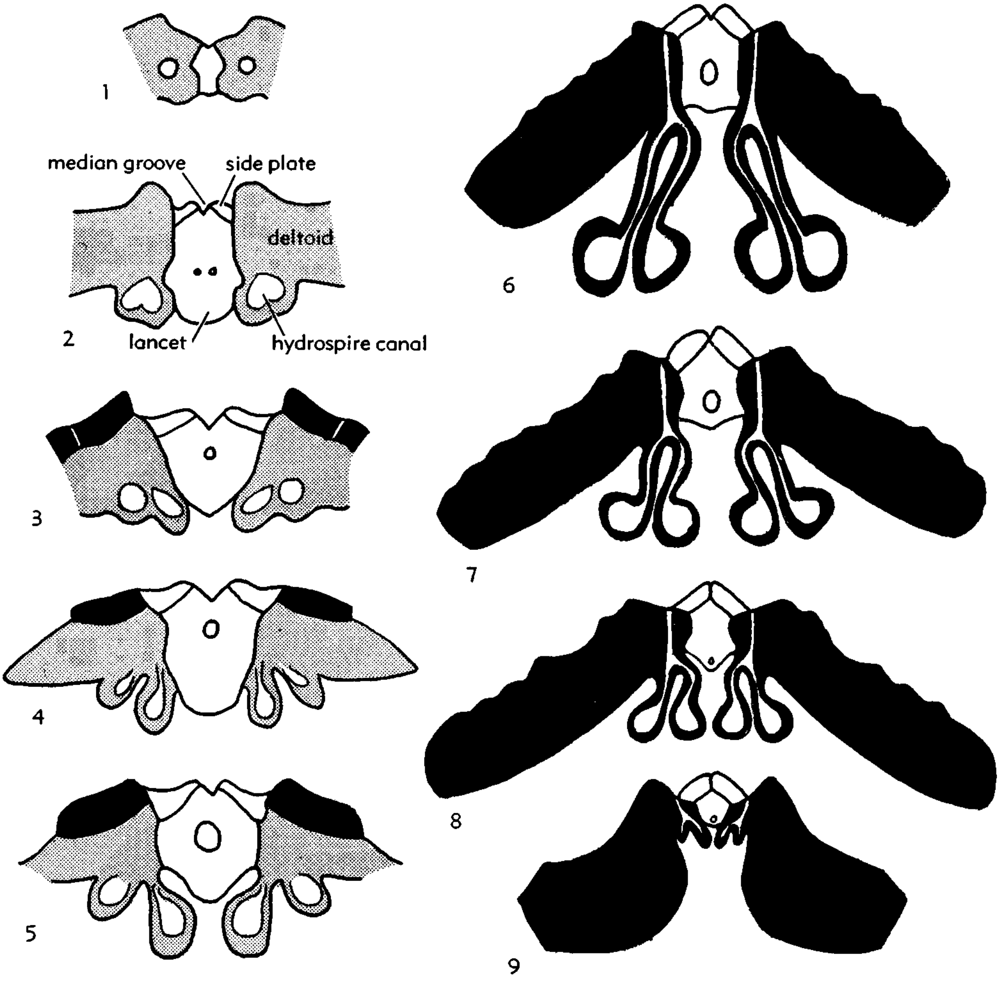

FIG. 191. Lancet and hydrospire structures of *Globoblastus,* L.Miss.(Osag.), USA(Mo.); drawings of thin sections of *G. norwoodi* cut perpendicular to an ambulacrum showing development of hydrospires; (lancet and side plates unshaded, deltoids shaded, radials black), ×8 (Beaver, 1961).——*1*. Section at adoral end of ambulacrum showing one of divided hydrospire canals on each side of lancet.——*2*. Section slightly below *1,* division of hydrospire canals produced by infolding of deltoidal material; longitudinal canal of lancet divided here into two canals which separate farther and farther and leave lancet on their respective sides to form oral ring canal.——*3*. Section just below radio-deltoid suture, radials resting on deltoids. The division of the hydrospire canals within the deltoids has been completed.——*4*. Section below *3,* showing hydrospire folds beginning to form.——*5*. Section below *4,* hydrospire development still in deltoid material.——*6*. Section short distance below radio-deltoid suture showing fully developed hydrospires composed entirely of radial material.——*7*. Section about 0.3 length of ambulacrum below summit of calyx.——*8*. Section just below half length of ambulacrum showing hydrospires noticeably shortened and longitudinal canal of lancet adaxially migrated.——*9*. Section near lower end of ambulacrum showing adaxial parts of radials about to envelop tiny hydrospires.

the ambulacrum, the lancet protrudes adaxially toward the interior of the calyx (Fig. 191,*8,9*). Specimens that deviate widely from the lancet structure observable in typical specimens of a species should be examined for other morphological differences, indicating that they may belong to other species or genera.

CANALS

Three longitudinal passageways (median canal and two lateral canals) are excavated partially or entirely in the lancet. The **median canal** is a small longitudinal internal canal that extends from the distal end of the lancet to the vicinity of the summit, where it divides to form part of the oral ring canal. For example, in *Globoblastus* (Fig. 191), from the vicinity of the summit aborally, this canal decreases in size and changes position from the center of the lancet to its median adaxial margin. The **lateral canals** are two small passageways lying on either side and obliquely adaxial to the median groove; they are excavated in lancet and side plate material along the suture between the lancet and side plates. The lateral canals parallel the median groove from its aboral extremity to beyond the radial-deltoid suture. The course of the lateral canals in the vicinity of the summit is unknown. They have been recognized in *Auloblastus* and WANNER indicated their presence in *Thaumatoblastus*.

"UNDERLANCET"

The so-called "underlancet" or "sublancet" plate was first illustrated (WACHSMUTH & SPRINGER, 1879, p. 387, pl. 17) in a cross-sectional drawing of *Pentremites* which showed a triangular-shaped plate lying beneath the lancet. The "underlancet" was shown to be perforated by a longitudinal canal, whereas the lancet was indicated to be imperforate. An examination of several hundred thin sections of *Pentremites* under binocular and petrographic microscopes has failed to show this "underlancet." The observed structure apparently is either a deposit of secondary calcite beneath the lancet, a thickening of the inner walls of the hydrospires, or a filling of fine clay in the area bounded by the inner surface of the lancet and upper walls of the hydrospires. Similar "underlancet" structures have been reported in *Orophocrinus, Pentablastus,* and *Calycoblastus,* in which this element is recognized to consist of two adjacent hydrospire plates joined beneath the lancet, or formed by thickening of the inner walls of hydrospires beneath the lancet (FAY, 1961, p. 15). JOYSEY & BREIMER (1963, p. 479-481) have recently described in considerable detail the so-called "underlancet" plate of *Pentablastus.* Their description agrees essentially with that of FAY, for they state that the "two halves of the underlancet are continuous with a pair of hydrospire plates" (Fig. 192). The name "fused hydrospire plate" is undoubtedly a more suitable term than "underlancet," but even the name hydrospire plate is not desirable, because it refers only to the portion of the radial and deltoid occurring between the hydrospire pores or slits, and the ambulacral margin (lancet and side plates). In reality, therefore, when the terms "fused hydrospire plate" or "underlancet" are used, they refer to the juncture of radial or deltoid material beneath a lancet.

SIDE PLATES AND OUTER SIDE PLATES

The **side plates** of ambulacra consist of numerous small skeletal elements which either rest on the lancet (Fig. 193,*2*), or lie between the walls of the radial sinus and the lancet (Fig. 190,*1*). The abmedial, adoral portion of each side plate is excavated for the reception of an outer side plate. The wider, admedial portion of the side plate is called the **side-plate body**; the narrower, abmedial area is the **side-plate limb.**

SIDE PLATES RESTING ON LANCET

Globoblastus is representative of blastoids in which the side plates rest on the lancet. Approximately 50 to 60 side plates are arranged along either side of each ambulacrum. At the aboral end and along the mid-line of an ambulacrum, the admedial ends of the side plates are in contact with each other and the median groove is developed on these side plates. The abmedial ends of the side plates rest with a slanted surface against the portion of the radials which is sometimes called the hydrospire plate.

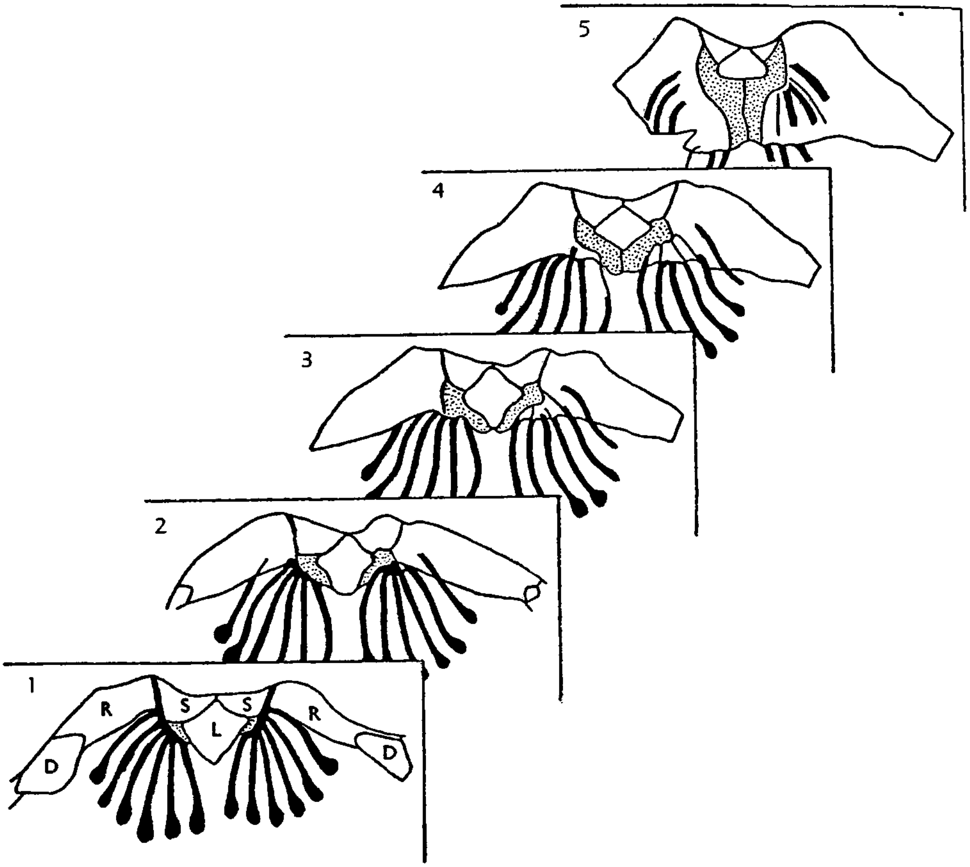

FIG. 192. Serial sections of *Pentablastus supracarbonicus* Sieverts-Doreck, U.Carb., Spain, showing hydrospire plates (stippled) coming together admedially beneath lancet to develop so-called "underlancet" in aboral to spiracular slits; section *1* is at level of spiracular slits, whereas section *5* is at aboral extremity of ambulacrum, ×5. [Deltoid (D), lancet (L), radial (R), side plates (S).] (Joysey & Breimer, 1963.)

SIDE PLATES ABUTTING LANCET

In *Pentremites* the side plates are located between the walls of the radial sinus and the lancet. The surface of contact between the lancet and the side plates commonly is curved, the abmedial convex surface of the

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[*See facing page*]

FIG. 193. Ambulacral structures especially in relation to hydrospires (lancet and side plates shaded, deltoids oblique-ruled, radials black) (Beaver, n).——*1. Orbitremites derbiensis* (Sowerby), L.Carb. (Middle Ls.), Eng.(Yorks.); ×10.——*2. Globoblastus norwoodi* (Owen & Shumard), L.Miss.(Burlington Ls.), near Springfield, Mo.; ×4.5.——*3. Placoblastus obovatus* (Barris), M.Dev.(Thunder Bay Ls.), near Alpena, Mich.; ×4.4 (from Fay, 1961, fig. 194).——*4. Mesoblastus crenulatus* (Roemer), L.Carb. (Tournais.), Belg.; ×5.8 (from Fay, 1961, fig. 153).——*5. Troosticrinus reinwardti* (Troost), Sil. (Niagara Gr.), Decatur Co., Tenn.; ×9.1 (from Fay, 1961, fig. 220).——*6. Auloblastus clinei* Beaver, L.Miss.(Burlington Ls.), near Springfield, Mo.; ×5.8.——*7. Pentremites godoni* (Defrance), U.Miss. (Paint Creek F.), near Floraville, Ill.; ×7.——*8. Orophocrinus stelliformis* (Owen & Shumard), L.Miss. (Burlington Ls.), near Hannibal, Mo.; ×9.5.——*9. Eleutherocrinus cassedayi* Shumard & Yandell, M. Dev.(Hungry Hollow F.), Thedford, Ont.; ×7.5 (from Fay, 1961, fig. 134).——*10. Pentremites rusticus* Hambach, L. Penn.(Bloyd Sh.), near Fort Gibson, Okla.; ×5.2.——*11. Hyperoblastus filosus* (Whiteaves), M.Dev.(Hungry Hollow F.), near Thedford and Arkona, Ont.; ×15.4 (from Fay, 1961, fig. 31).

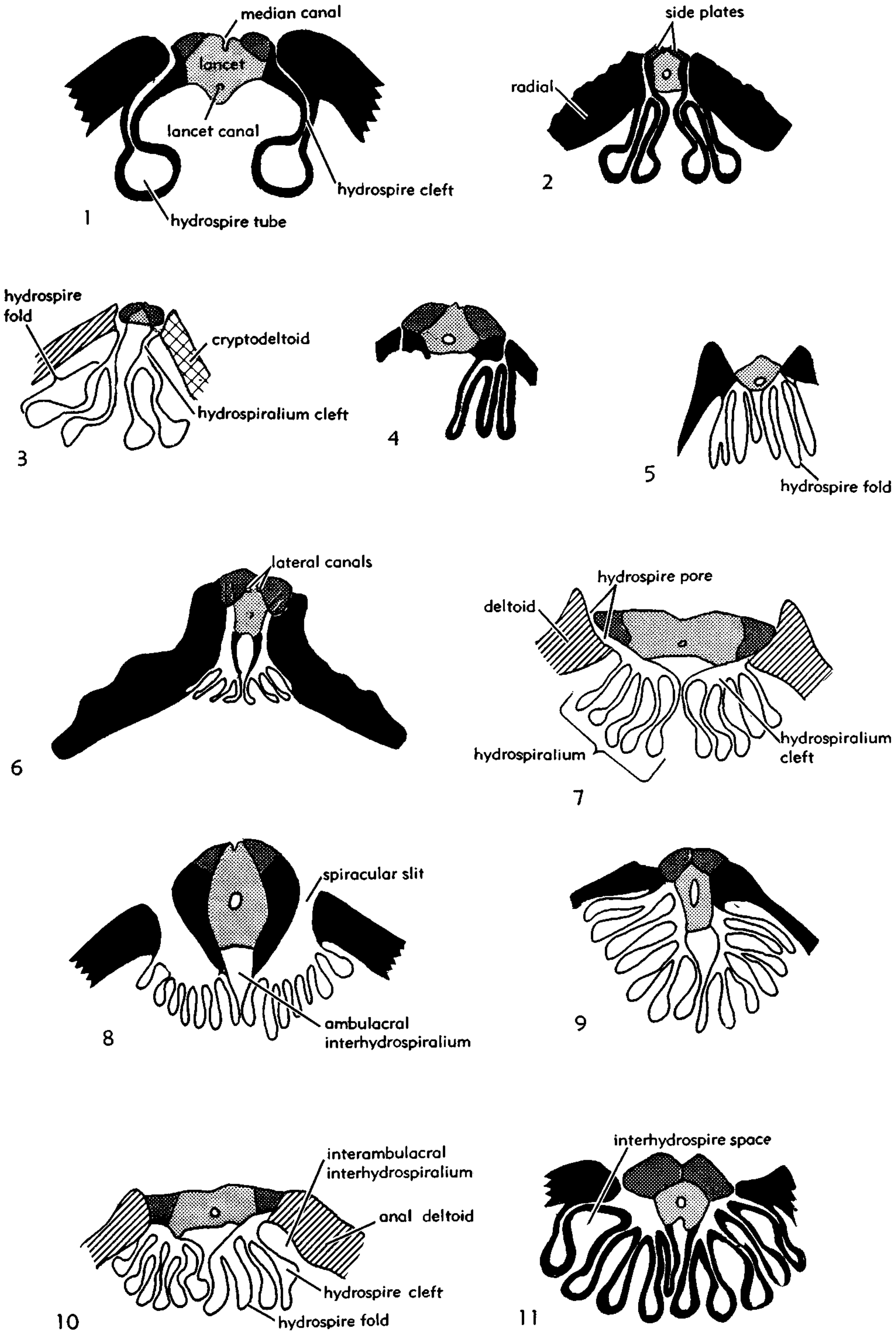

FIG. 193. [*Explanation on facing page.*]

lancet fitting snugly into the abmedial concave surface of the side plates (Fig. 184, *2b,c*; 193,*7*). The adoral and aboral sutures between side plates of *Pentremites* do not coincide with the lateral grooves as in some genera, but alternate with them. The lateral groove of the lancet extends onto the side-plate body and leads to the **brachiolar socket** (place of attachment of a brachiole), located on the admedial portion of the side-plate limb. A deep pore groove or pore furrow located on the suture between the side and outer plate leads to the hydrospire pore.

OUTER SIDE PLATES

The outer side plates, for example in *Pentremites,* are located adorally from the side-plate limb and aborally from a hydrospire pore groove. The aboral portion of the outer side plate forms half of the brachiolar socket and includes one of the brachiolar facets or articulation depressions (Fig. 190,*1*; 194,*1*).

In *Globoblastus* the outer side plates are relatively large, their length being approximately two-thirds the length of the side plates. The width of the outer side plate increases abmedially from the admedial contact of each outer plate with the side plate to the margin of the radial sinus, the width of the outer side plate equaling that of the side plate. One outer side plate adjoins each side plate.

BRACHIOLAR SOCKETS

A brachiolar socket is a pit centrally placed on a prominent round mound or knob located at the adlateral end of a lateral groove, generally near the margin of an ambulacrum (Fig. 190,*1*). In genera with side plates lying on the lancet (e.g., *Globoblastus*), the socket is located on the admedial, adoral portion of each side plate; each socket has tiny ridges and grooves extending down and away from the summit of its mound or knob. The ridges and grooves aid in articulation of the brachioles and ambulacral covering plates. In *Pentremites,* each brachiolar socket is located on the admedial portion of a side-plate limb, similar to its position in *Globoblastus.* Between the brachiolar socket and margin of the radial sinus, two gently depressed surfaces, the brachiolar facets, occur. The aboral facet is located on the side-plate limb; the adoral facet is developed on the outer side plate. The presence of a suture between the facets may have provided flexibility to the biserially arranged brachiole.

AMBULACRAL COVER PLATES

The **ambulacral cover plates** are tiny polygonal plates which roof over the lateral and median grooves to provide a series of passageways from the brachiolar sockets to the vicinity of the mouth (Fig. 194,*1*). The plates covering the lateral grooves are seated in tiny depressions, termed **cover plate sockets,** which alternate on either side of the lateral grooves (Fig. 190,*1*). In general, the tips of the plates are arranged in a biserial pattern; this system is not always perfect, however, and commonly the upper ends of the plates merely abut. The plates

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[*See facing page*]

FIG. 194. Ambulacral and summit structures of calyx illustrated by *Pentremites godoni* (DEFRANCE), U.Miss. (Chester.), U.S.A.(Ill.), ×12 (drawings by Roger B. Williams; Beaver, n).——*1*. Ambulacrum showing well-preserved cover plates in position over lateral and median grooves, part of single small brachiole preserved on right side of ambulacrum; cover plates biserially arranged over lateral grooves but lacking orderly pattern over median groove. The cover plates are inferred to have roofed over the grooves in manner forming conduits for passage of fluids from brachioles to the mouth.——*2*. Oral pyramid viewed from anal *(CD)* interray, mouth concealed by solid triangular slightly curved elongate plates which appear to be seated in regularly spaced sockets around mouth, anal opening covered by smaller spinose plates arranged in alternating rows, and spiracles also concealed by relatively broad plates disposed in imbricating manner. Movements of the plates which would facilitate flow of fluids through these orifices are inferred to have been possible.——*3*. Specimen shown in Fig. *2* rotated slightly toward right, providing nearly direct view of plates covering *DE* spiracle, ×12. Although relationships of the median groove (with its cover plates) to the oral pyramid is not clear, owing to imperfect preservation, the passageway along the median groove is interpreted to enter the mouth beneath the oral pyramid, but no evidence of an external opening appears at the point of entry.

which roof over the median groove are arranged in a much less symmetrical manner than those of the lateral grooves and the "roof" is higher.

In well-preserved specimens of *Pentremites godoni,* 11 or 12 cover plates occur along each side of a lateral groove. Allowing about 22 plates for each lateral groove

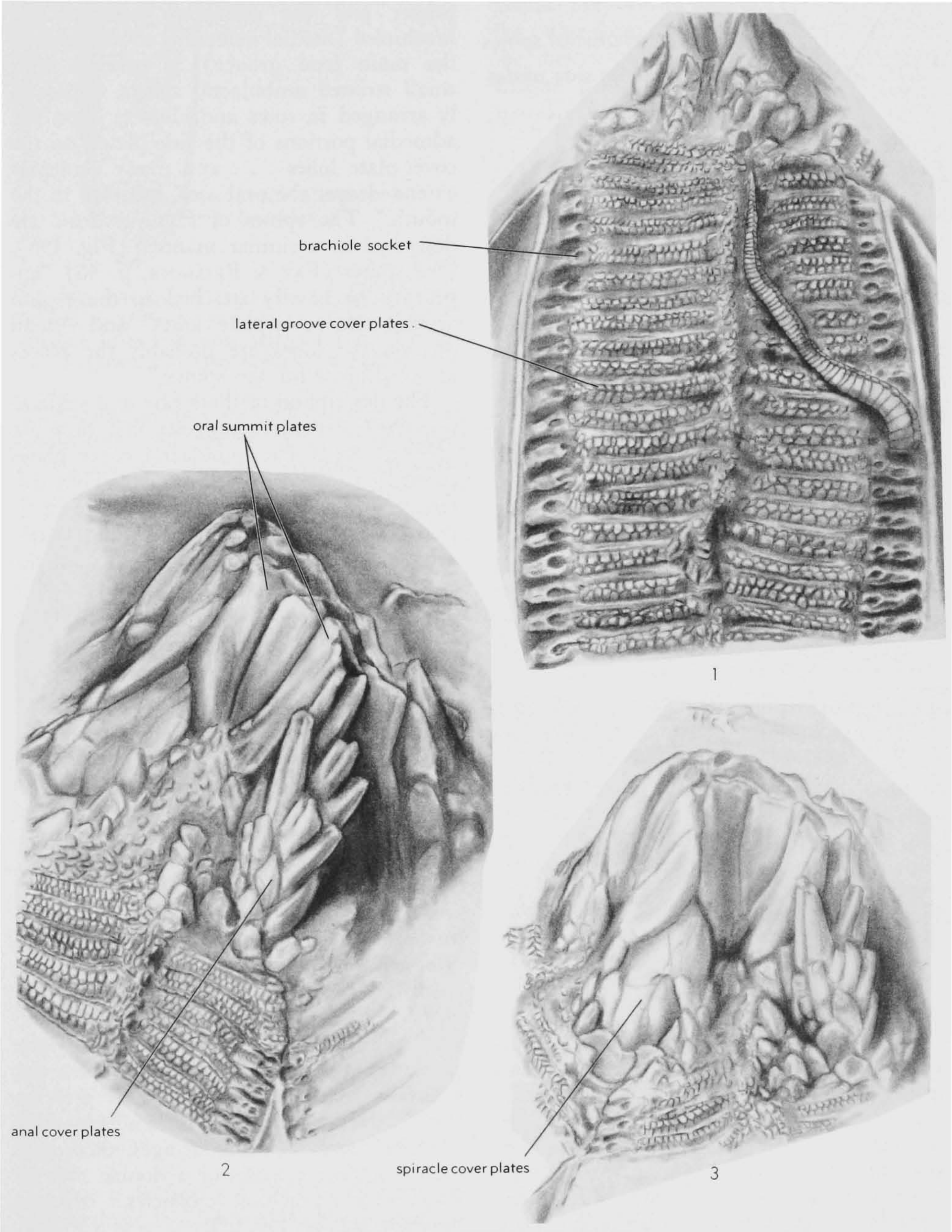

FIG. 194. [*Explanation on facing page.*]

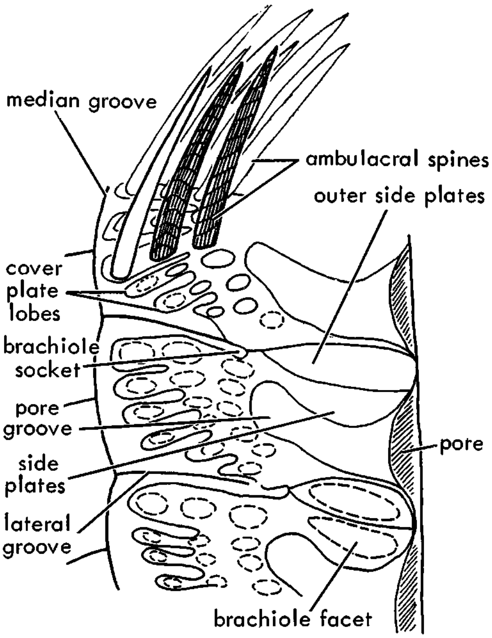

FIG. 195. Composite diagrammatic drawing of side plates in *Hyperoblastus nuciformis* (REIMANN), M. Dev.(Hungry Hollow F., Widder beds), near Thedford, Ontario; showing probable position of ambulacral spines, ×75 (Fay & Reimann, 1962).

and approximately 100 grooves for each of the five ambulacra, an adult individual of *P. godoni* must have had some 10,000 or more cover plates for the lateral grooves, not including the hundreds that covered the median grooves of the five ambulacra. In the area of the summit the covered median groove seems to pass between the plates of the anal pyramid so as to lead to the mouth (Fig. 194,*2,3*).

AMBULACRAL SPINES

Small needle-like curved plates (**ambulacral spines**) attached to the side plates and arranged in rows along sides of the ambulacral median groove have recently been described by FAY & REIMANN (1962). Each of the spines is about 1 mm. long and 0.1 mm. wide and has spiral striations. The spines have been recognized in *Placoblastus, Devonoblastus,* and *Hyperoblastus.* In *Placoblastus* they are attached to the side plates and seem to be restricted to the area adjacent to the median groove. Concerning *Devonoblastus* FAY & REIMANN (p. 35, 36) stated, "The region adjacent to the thecal main food groove, between the food grooves proper and the admedial walls of the brachioles (medial referring to the line of the main food groove), is covered with small striated ambulacral spines, apparently arranged in rows and clusters upon the admedial portions of the side plates, on the cover-plate lobes . . . and many evidently extended over the oral area, adjacent to the mouth." The spines of *Hyperoblastus* are described in a similar manner (Fig. 195). The spines (FAY & REIMANN, p. 48) "appear to be basally attached to the region around the cover-plate lobes" and "small pits on the lobes are probably the places of attachment for the spines."

The description of these rare and seldom-preserved structures suggests that they are different from the ambulacral cover plates so well preserved in *Pentremites.* They differ in being more spinelike and in their location away from the median and lateral grooves proper. The occurrence of ambulacral spines in the summit area indicates that some Devonian genera (e.g., *Hyperoblastus*) probably had an oral pyramid similar to that of *Pentremites.*

BRACHIOLES

Brachioles are armlet appendages which articulate with the brachiolar facets of the side plates and outer side plates, and rise from the margin of each ambulacrum, adoral ones extending well above the summit of the theca. They have been described from a number of genera, including *Devonoblastus, Diploblastus, Eleutherocrinus, Globoblastus, Hyperoblastus, Pentremites, Pleuroschisma, Pyramiblastus, Troosticrinus, Orophocrinus,* and *Placoblastus.* Examination of many almost complete specimens of *Pentremites* from Chesteran rocks of southwestern Illinois, as well as excellently preserved individuals belonging to other genera of different ages, show that each brachiole consists of a double row of alternating brachiole ossicles, termed **brachiolars** (Fig. 190,*2,3*).

In *Pentremites* each brachiolar is slightly longer than wide and is longitudinally grooved by approximately 12 striations.

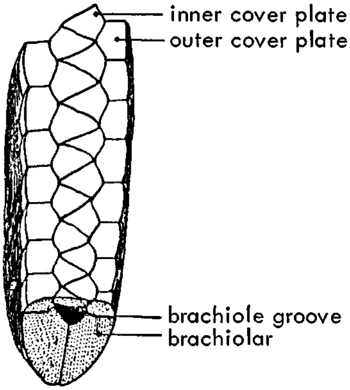

FIG. 196. Diagram of brachiolar fragment *Hyperoblastus nuciformis* (REIMANN), M.Dev., Ontario, showing inner and outer series of brachiole cover plates, ×35 (Fay & Reimann, 1962).

The upper surface of each joint is heavily crenulated and serves as an articulating surface in the same manner that columnals of the stem articulate with each other. The brachiolars are smallest where they articulate with the brachiolar facets; they become progressively longer for a short distance, and then attain a uniform length. The average length of each brachiolar is approximately 0.5 mm. The ventral or admedial side of each brachiole bears a V-shaped groove **(brachiolar groove),** formed by two rows of adjacent and alternating joints (Fig. 190,2); the groove extends over the brachiolar socket (Fig. 194,*1*). Although cover plates have not been observed to enclose ventral grooves of brachioles, such plates probably existed. The length of the brachioles ranges from 1 to 2 times the height of the theca. Seldom, even in excellently preserved specimens, are all brachioles preserved and consequently, the very large number of brachioles borne by a complete individual is not commonly realized. A count of the brachiolar sockets shows that average-sized specimens of *Pentremites godoni* had approximately 500 brachioles; larger specimens possessed nearly 600, but young individuals only about 200.

FAY & REIMANN (1962, p. 48) have described the brachiole cover plates of *Hyperoblastus nuciformis.* The brachiole groove is covered by an inner and outer series of alternating cover plates (Fig. 196). The outer series (called outer cover plates) occurs along either side of the ventral brachiole surface as alternating plates; each brachiolar carries about four outer cover plates. The brachiole groove is bounded by the outer cover plates and is roofed over by the biserially arranged small triangular-shaped inner cover plates, which correspond in number to the outer cover plates.

SUMMIT PLATES

For a century or more, controversy has existed over the presence or absence of summit plates in blastoids. If their presence was admitted, details of their appearance, arrangement, and function have been disputed (OWEN & SHUMARD, 1850, p. 65; SHUMARD, 1858, p. 244; WHITE, 1863, p. 482; HAMBACH, 1884, p. 541; ETHERIDGE & CARPENTER, 1886, p. 70; WACHSMUTH & SPRINGER, 1887; FAY & REIMANN, 1962). The principal reason for disagreements and differing descriptions is that various blastoid genera apparently have different types of summit structures and that in the overwhelming number of blastoids collected, summit plates are lacking, or poorly preserved.

At least three different types of summit structures are known to occur. A first type characterized by many small polygonal plates which cover the general vicinity of the mouth is designated as the *Globoblastus* type. A second type distinguished by the presence of approximately six relatively large many-sided oral plates is designated as the *Placoblastus* type. A third type having a pyramid-like structure of numerous plates over the mouth is defined as the *Pentremites* type.

GLOBOBLASTUS TYPE

The summit of *Globoblastus norwoodi* is covered by numerous very tiny plates which completely cover the peristome (Fig. 197,*3b*) and seem to extend down each ambulacrum where they become the ambulacral cover plates (WHITE, 1863, p. 483). Nothing is known of plates that may cover the spiracles and anus, but by analogy with other genera, it is assumed they also were present.

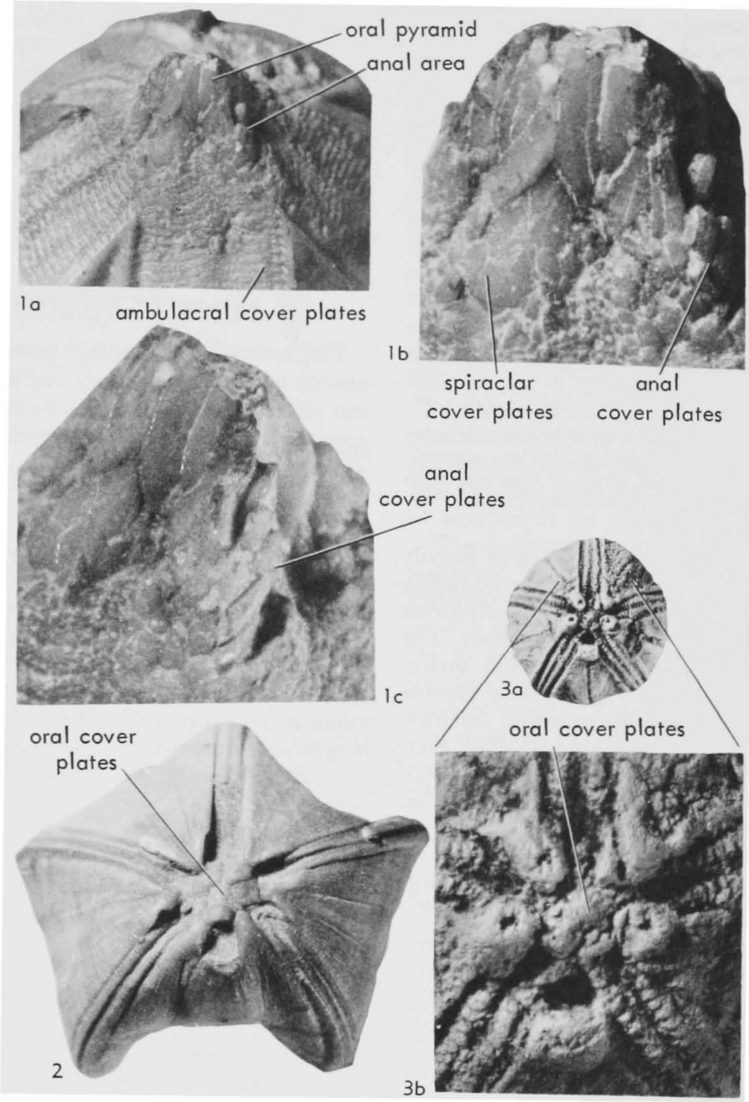

FIG. 197. Types of blastoid summit plates (Beaver, n).——*1. Pentremites godoni* (DEFRANCE), U.Miss. (Chester.), USA(Ill.); *1a,* summit view showing pyramid-like structure over mouth area and ambulacral cover plates, ×6; *1b,* oral pyramid and plates covering spiracle and anal opening, ×15; *1c,* anal cover plates, ×15.——*2. Placoblastus obovatus* (BARRIS), M.Dev., USA(Mich.); oral cover plates, ×3.——*3. Globoblastus norwoodi* (OWEN & SHUMARD), L.Miss.(Osag.), USA(Iowa); *3a,* summit view showing tiny oral plates, ×2; *3b,* oral cover plates, ×7.

PLACOBLASTUS TYPE

Placoblastus is representative of blastoids having approximately six oral plates which completely roof over the summit area between the deltoid tips (Fig. 197,*2*). The plates are irregular in outline, with five or six ill-defined sides. Several of them seem to be located at adoral tips of the deltoids, but two of the plates are adoral of ambulacra *D* and *E*.

PENTREMITES TYPE

Pentremites represents a blastoid group distinguished by having a pyramid-like structure, termed **oral pyramid,** developed over the mouth area (Fig. 194,*2*,*3*; 197,*1*). The pyramid is composed of numerous solid, slightly curved, toothlike plates which arch over the summit so that the mouth, spiracles, and anal openings are completely covered by them.

The lower ends of the plates covering the mouth articulate with the theca along adoral extremities of the deltoids. The deltoid lips, adjacent to the mouth, have alternating ridges and grooves, the toothlike plates being seated in the latter.

The plates covering the spiracles, which are broader and shorter than those above the mouth and seemingly immovable, pass adorally between and beneath the plates over the mouth (Fig. 194,*3*; 197,*1b*).

Plates covering the anus are short toothlike spines which become gradually larger near the plates covering the mouth. They are arranged biserially along both sides of the opening (Fig. 194,*2*; 197,*1c*).

The lower ends of the plates covering the spiracles and anus are attached to the theca along inner margins of the spiracles and anal opening. The toothlike plates above the anus and plates concealing the mouth appear to be more flexible than those covering the spiracles and probably were able to open and close.

HYDROSPIRES

Distinctive internal structures of blastoids are known as **hydrospires.** Each such structure is a calcareous thin-walled linear infold extending adaxially beneath either side of an ambulacrum. Hydrospires may occur singly (e.g., *Orbitremites,* Fig. 193,*1*), or as a group of associated hydrospires (**hydrospiralium,** Fig. 193,*7*). The hydrospiralium (or alternatively, a single hydrospire) connects abaxially with hydrospire pores or slits which penetrate various thecal plates (radials, deltoids, and anal deltoids), or occur beneath them and an ambulacrum. It leads adorally to a simple hydrospire canal which opens into a spiracle or has its external outlet in a single spiracular slit or in a number of subparallel hydrospire slits. The thin calcareous wall surrounding a hydrospire is termed a **hydrospire fold** (Fig. 193,*3*), and the space enclosed by the fold is a **hydrospire cleft** (Fig. 193,*1*). Commonly, the adaxial portion of a hydrospire is expanded to develop a **hydrospire tube** (Fig. 193,*1*). Space within a hydrospiralium exclusive of the hydrospire clefts is the **hydrospiralium cleft** (Fig. 193,*3*). The area between adjacent hydrospires of the same hydrospiralium is an **interhydrospire space** (Fig. 193,*11*). Space between adjacent hydrospiralia is termed an **interhydrospiralium.** It may refer to an area adaxial to the lancet, and thus be ambulacral (Fig. 193,*8*), or may concern a space adaxial to the deltoids or adjacent radial limbs, and be interambulacral (Fig. 193,*10*).

DEVELOPMENT OF HYDROSPIRES

Hydrospires develop through infolding of deltoid and radial material adaxially adjacent to the lancet. The most admedial hydrospire of blastoids develops first and then other folds are formed successively in an abmedial direction. From maximum size near the radial-deltoid suture, the hydrospires diminish in size and finally disappear at the aboral end of an ambulacrum.

Hydrospire development in *Globoblastus* is representative of that observed in many other blastoid genera. Development, as shown by serial sections cut normal to an ambulacrum, begins when the single external spiracle opening divides initially into two hydrospire canals. Each of the canals leads into a hydrospiralium developed beneath the nearest sides of adjacent ambulacra. Formation of two canals, one on either side of a lancet, into the hydrospires within adjacent deltoids is illustrated in Figure 191,*1-5*. Each of the canals subdivides into two hydrospires by infolding of the deltoid material (Fig. 191,*2-5*). At this position, with the hydrospires completely formed, transition from deltoid to radial material occurs.

The hydrospires attain greatest size just below the deltoids, and from this area they progressively decrease in size aborally (Fig. 191,*6-9*). Hydrospire size and greatest thecal diameter do not correspond longitudinally; maximum hydrospire size occurs substantially adoral to the greatest thecal diameter.

STRUCTURE OF HYDROSPIRES

Some workers (e.g., WACHSMUTH & SPRINGER, 1879) have supposed that the hydrospire folds of blastoids expanded and contracted during life. Serial sections of numerous specimens representing several genera, however, indicate a remarkable constancy of hydrospire shape at various levels of the theca and in different hydrospiralia. Minor differences may occur in parts of any given hydrospiralium (Fig. 191,*4-9*), but these are introduced gradually between its adoral and aboral extremities. Also the hydrospiralia of any given specimen or species may display minor differences when one is compared to another. In a few species (e.g., *Pentremites rusticus,* Fig. 180,*L*; 194,*10*) the hydrospire folds of the anal hydrospiralia differ markedly in configuration from others. All of these features suggest that the hydrospire folds were relatively inflexible.

Petrographic examination shows that the walls of hydrospires are composed of very small calcite crystals. Whether the folds were permeable in life is not determinable, but it seems reasonable to suppose that they were.

NUMBER OF HYDROSPIRE FOLDS

The number of hydrospire folds in blastoids of any given species and constancy of this number in different individuals of the species differ from species to species and from genus to genus. For example, *Orbitremites* (Fig. 193,*1*) and *Monoschizoblastus* have a single hydrospire fold on each side of an ambulacrum, whereas *Schizoblastus* and *Globoblastus* (Fig. 193,*2*) have two folds in each hydrospiralium, and various species of *Pentremites* (Fig. 180) have three to seven or more folds in each hydrospiralium. *Orophocrinus* may have as many as 11 folds in each hydrospiralium. Constancy in the number of hydrospire folds belonging to individual hydrospiralia in Silurian and Devonian genera is poorly known but examination of many thin sections of Mississippian blastoids (e.g., *Orbitremites, Cryptoblastus, Globoblastus, Schizoblastus*) show that the number of folds in each of the hydrospire groups is very constant.

Species of *Pentremites,* particularly geologically younger ones, show less consistency in the number of hydrospire folds belonging to a hydrospiralium. For example, *P. princetonensis* (Fig. 180,*C*) and *P. pulchellus* (Fig. 180,*D*), both from the Ste. Genevieve Limestone of Meramecian age, typically have three folds in each of the ten hydrospiralia, although one specimen of the latter species has been found to possess a fourth fold in one hydrospiralium. *P. godoni* (Fig. 180,*F*) and *P. symmetricus* (Fig. 180,*E*), from the Paint Creek Formation of early Chesteran age, normally have four or five folds in each hydrospiralium, but a specimen of *P. symmetricus* has been observed which shows four folds in some hydrospiralia and five folds in others. *P. halli* (Fig. 180,*K*), from the Kinkaid Limestone of late Chesteran age, has three or four folds in each hydrospiralium, some showing three folds in each hydrospiralium, others four folds in each, and a few four folds in certain hydrospiralia and three folds in remaining ones.

Early Pennsylvanian *Pentremites,* from the Morrowan of Oklahoma, exhibit greater variability in the number and shape of the hydrospires, particularly in the hydrospiralia adjacent to the anal interradius, than any older species of the genus among those studied. *P. rusticus* (Fig. 180,*L*), which belongs to this group, commonly has five to seven folds in hydrospiralia not adjacent to the anal *(CD)* interradius, whereas hydrospiralia next to the anal interradius contain only three or four folds and these are markedly different from the others in shape (the entire fold being expanded, rather than just the adaxial portion). Although the number of folds is constant in each of the two types of hydrospiralia, serial sections near the summit show differences in shape of the hydrospire folds, both in the hydrospiralia adjacent to the anal interradius and in the remaining eight hydrospiralia adjoining other interradii. Hydrospire folds in *P. rusticus* are generally much thicker than those of pre-Pennsylvanian *Pentremites.*

THECAL OPENINGS

Openings in the blastoid theca are related primarily to the digestive system (mouth, anus) and respiratory system (spiracles, spiracular slits, hydrospire pores, hydrospire slits). The mouth is centrally placed at the summit of the theca and the anus is generally located between posterior deltoid elements (anal deltoids) or excavated in deltoid material slightly below and behind the mouth. The spiracles and spiracular slits, inferred to have served as excurrent openings of the respiratory system, generally are observed in the vicinity of the summit. The hydrospire pores and slits, which open into the hydrospires, occur along margins of the ambulacra.

MOUTH

The mouth is the inlet to the digestive tract of the living animal. In blastoids the oral orifice is a small opening, commonly pentagonal in outline, at the apex of the summit (Fig. 178,*1*). The shape and size of the mouth opening in the theca are determined by the gap between the adoral tips of the five deltoids. In general, the mouth is smaller than the anus but approximately equal in size to one of the spiracles. Weathering of the summit may make the mouth aperture appear to be abnormally large. The connection of the mouth and digestive tract and the path of this tract aborally have not been recognized positively, although questionable traces of the digestive tract immediately below the mouth have been observed. As already described, the mouth in well-preserved fossils is covered by a complex arrangement of summit plates.

ANUS

The anus, which is the exit of the digestive system, may be excavated in a single posterior deltoid plate (e.g., *Pentremites*), surrounded by various posterior deltoid plates (e.g., *Globoblastus*), or located along the sutures between posterior deltoids and adjacent limbs of the radials (e.g., *Heteroschisma*). The anus may be confluent with the posterior spiracles, so as to form a single opening termed **anispiracle** (e.g., *Pentremites, Cryptoblastus*), or it may be separate from them (e.g., *Schizoblastus*). In size, the anus is invariably larger than the spiracles and generally bigger than the mouth. The rim of the plates surrounding the anus generally conforms to the surface of the surrounding thecal plates, but in some genera (e.g., *Lophoblastus*), the opening is partially sheltered aborally by a hoodlike projection of the hypodeltoid. The passageway connecting the anus with the digestive tract is not well known, but traces of it have been seen in *Globoblastus* and its influence in modifying adjacent structures is apparent in Early Pennsylvanian specimens of *Pentremites,* for example in pushing the posterior hydrospiralia apart and in affecting the shape and number of posterior hydrospire folds. Analogous effects of the anus on the respiratory system are the absence (e.g., *Heteroschisma*) or reduction in number (e.g., *Thaumatoblastus*) of hydrospire slits on the posterior side. The plates that cover the anus are poorly known in many blastoid genera, but are observed to differ from those over the spiracles and mouth in some genera (e.g., *Pentremites*).

SPIRACLES

Five to ten generally rounded openings adjacent to the mouth are called **spiracles** (Fig. 178,*1*). Blastoids with spiracles and hydrospire pores are said to be spiraculate. Spiraculate genera can be divided into three main types based on the number of spiracular openings and their relationship with the anus. They are named from selected representative genera as (1) *Elaeacrinus* type, (2) *Tanaoblastus* type, and (3) *Pentremites* type.

ELAEACRINUS TYPE

Blastoids of *Elaeacrinus* type are characterized by having ten spiracles located round the mouth (Fig. 198). The anus is separate from spiracles in the posterior interray. Generally each spiracle lies in an excavation along either side of a deltoid; a lancet and side plates bound the opening laterally. In most genera, the spiracles occur near the adoral tips of the deltoids, but in some (e.g., *Acentrotremites,* Fig. 198,*4*) they are located near the aboral margin of the deltoids.

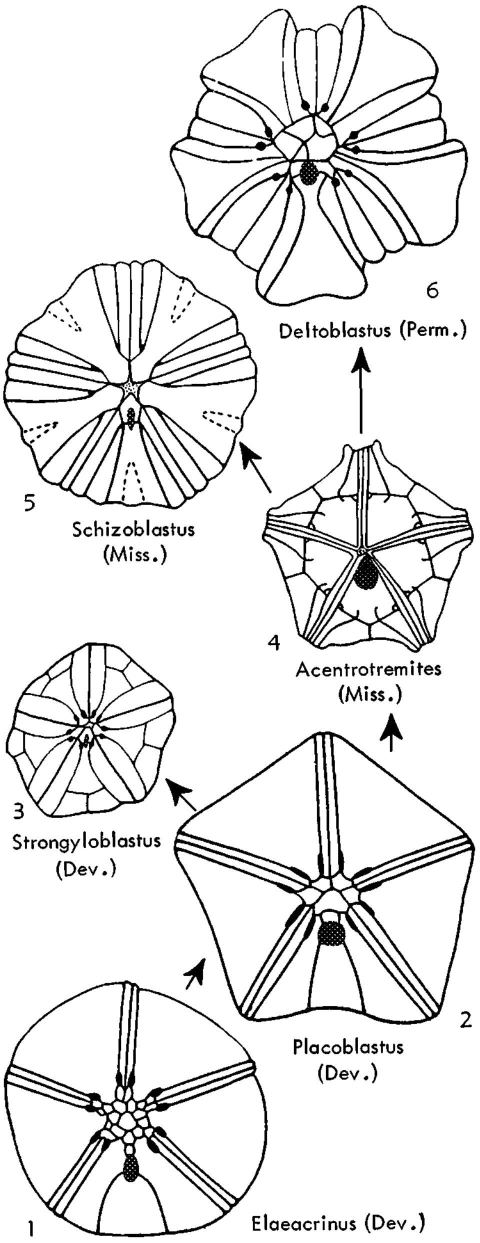

FIG. 198. Variations in spiracles of *Elaeacrinus* type, characterized by 10 spiracles surrounding mouth and separate anus, genetic lineages not implied (drawings from Fay).

TANAOBLASTUS TYPE

The *Tanaoblastus* type is distinguished from the *Elaeacrinus* type in that the posterior spiracles are confluent with the anus forming an **anispiracle.** Thus, eight spiracles and an anispiracle are present (Fig. 199). The spiracles are very small and are located along the adoral margins of the deltoids.

PENTREMITES TYPE

Blastoids like *Pentremites* with four single external spiracles and an anispiracle and genera such as *Doryblastus* and *Nodo-*

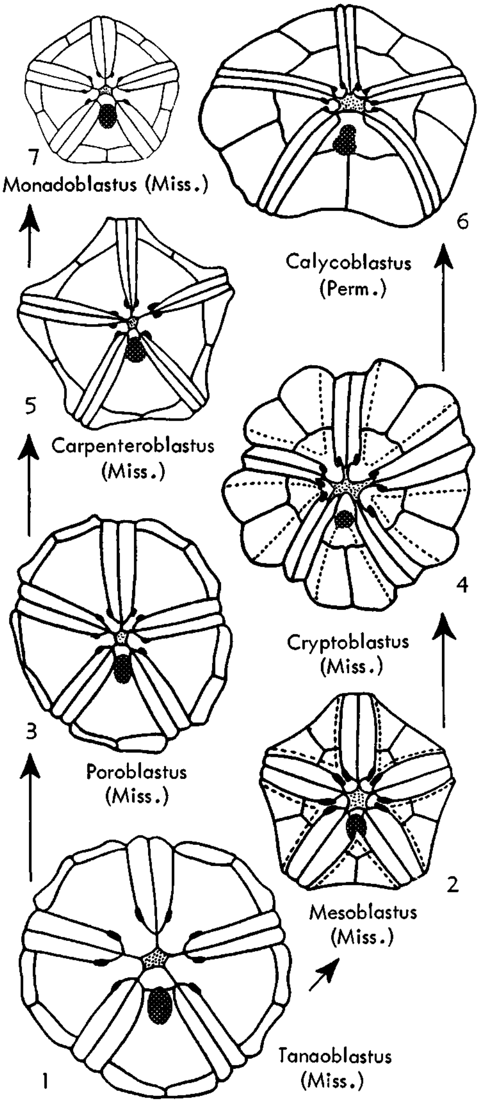

FIG. 199. Variations in spiracles of *Tanaoblastus* type, distinguished by 8 spiracles around mouth and posterior spiracles confluent with anus forming anispiracle, genetic lineages not implied (drawings from Fay).

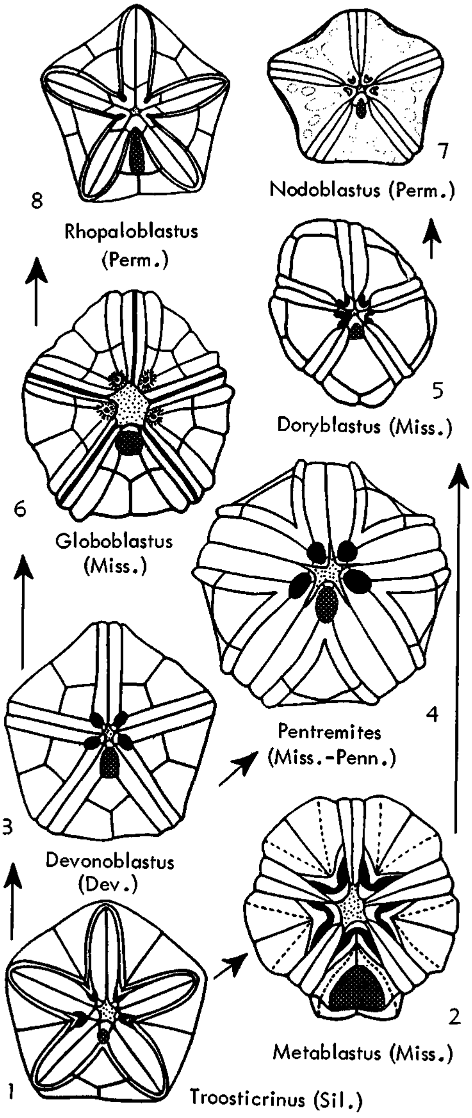

Fig. 200. Variations in spiracles of *Pentremites* type, having four spiracles or four paired spiracles and anispiracle surrounding mouth area, genetic lineages not implied (drawings from Fay).

blastus in which an anispiracle is accompanied by four external spiracles nearly divided by a strongly developed deltoid septum (called **paired spiracles**) are designated as spiraculate forms of *Pentremites* type (Fig. 200). The size of the spiracle openings in forms with four external spiracles is generally greater than in genera having eight or ten spiracles.

SPIRACULAR SLITS

In many genera an elongated spiracle, termed **spiracular slit,** may be seen on each side of an ambulacrum (Fig. 201,*1*). Typically, the spiracular slits are excavated in marginal parts of deltoids and radials and they run parallel to the ambulacra. The thin body of skeletal substance between slit and ambulacrum commonly is referred to as the **hydrospire plate** (Fig. 193,*8*). Blastoids with exposed spiracular slits and hydrospire slits are termed fissiculate. Those with spiracular slits may be grouped on the basis of relationship of the slits to the anus.

OROPHOCRINUS TYPE

In the *Orophocrinus* type, distinguished by the presence of two distinct slits in each interray, ten in all, the slits may be very short or relatively long and generally they transect the deltoid-radial suture (Fig. 201, *1-3*). Also, the slits may be located adjacent to the mouth area or at a considerable distance from it.

SAGITTOBLASTUS TYPE

In the *Sagittoblastus* type only eight distinct slits occur, for those belonging in the posterior *(CD)* interray are coalesced with the anus to form an anispiracle (Fig. 201, *4-7*).

HYDROSPIRE SLITS

Longitudinal openings excavated in plate substance of the deltoids and radials and disposed parallel to adjacent ambulacral margins are defined as **hydrospire slits.** They lead inward to **hydrospire clefts** (Fig. 193,*11*; 202).

As many as 18 of these slits may be found on either side of an ambulacrum. Three groups of blastoids bearing hydrospire slits, respectively designated by the names of representative genera, can be discriminated on the basis of relationship of the slits in the posterior interray to the anus.

POLYDELTOIDEUS TYPE

The *Polydeltoideus* type, illustrated by *Polydeltoideus, Pleuroschisma, Hadroblastus,* and *Neoschisma,* is characterized by the presence of slits in all interrays, those

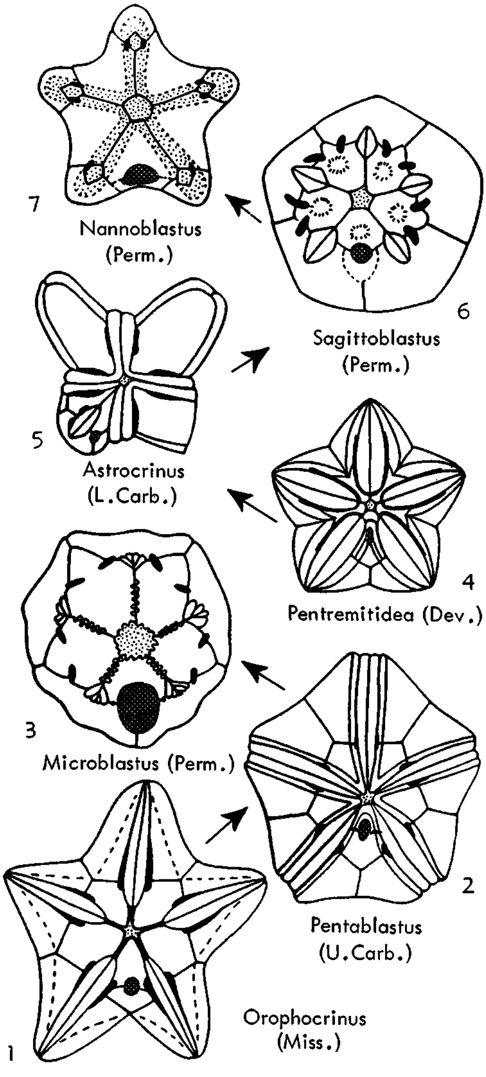

FIG. 201. Variations in spiracular slits. The *Orophocrinus* type is characterized by having 10 slits around mouth and separate anus. The *Sagittoblastus* type differs in that posterior slits are confluent with the anus, resulting in 8 slits and an anispiracle, genetic lineages not implied (drawings from Fay).

of the posterior interray being entirely separate from the anus (Fig. 202,*1-4*). The fully or partly exposed slits of the calyx are arranged in ten fields. Commonly, however, the number of slits in the posterior interray is markedly reduced (e.g., five slits in each posterior field of *Neoschisma,* in contrast to 18 slits in normal fields as observed in this genus).

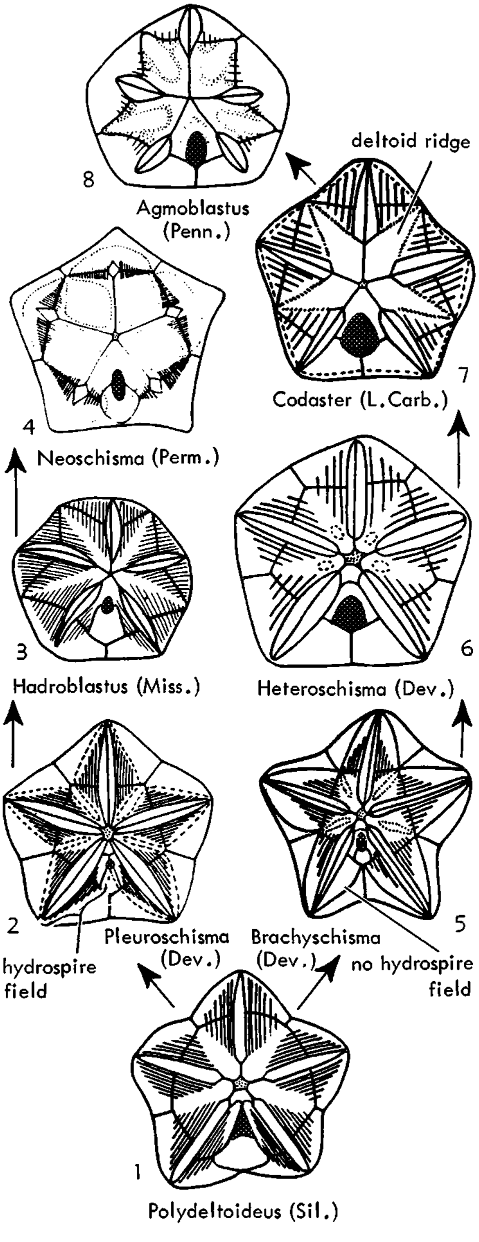

FIG. 202. Variations in hydrospire slits. *1-4,* genera of *Polydeltoideus* type, with slits exposed or partially exposed in 10 fields and separate anus. *5. Brachyschisma,* sole representative of *Brachyschisma* type, with nine exposed hydrospire fields and separate anus, slits lacking on left side of anus. *6-8.* Genera of *Codaster* type, differing from others in entire lack of slits in posterior interray (drawings from Fay).

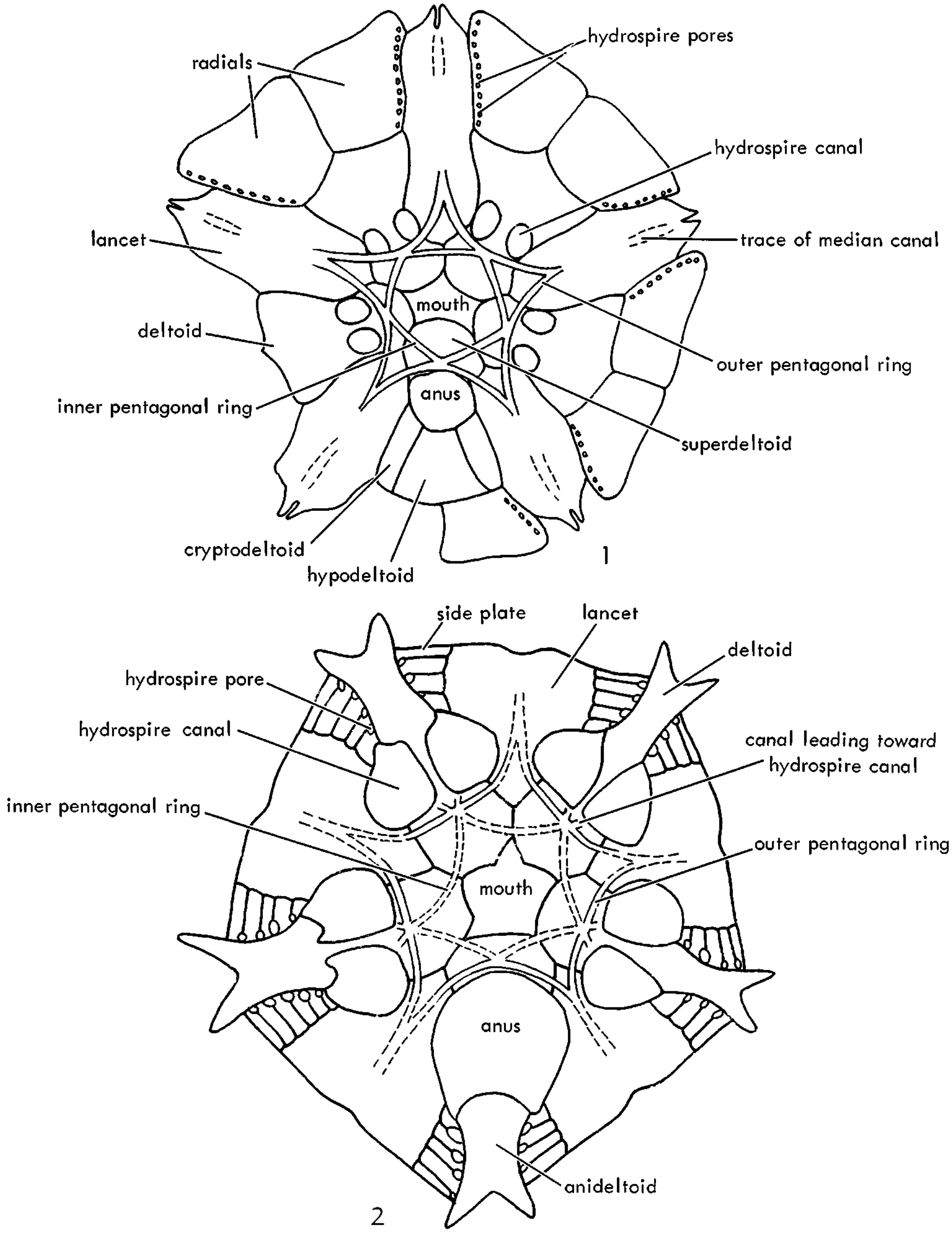

FIG. 203. Drawings based on thin sections of oral ring canal.——*1. Globoblastus norwoodi* (OWEN & SHUMARD), L.Miss.(Burlington Ls.), near Springfield, Missouri; inner and outer pentagonal ring canals, each branch of outer ring connecting aborally with median canal of lancet.——*2. Pentremites godoni* (DEFRANCE), U.Miss.(Paint Creek F.), near Floraville, Ill.; oral ring canal with short canals that lead from interradial mid-point of outer pentagonal ring toward each hydrospire canal, connection of small canals with outer ring canal clearly shown but opposite connection of short canals with hydrospire canals indistinct.

BRACHYSCHISMA TYPE

The *Brachyschisma* type differs from the first in having a single hydrospire field in the posterior interray, located on the right side of the anal opening. Thus, the calyx has a total of nine fields. *Brachyschisma* (Fig. 202,*5*) is the sole known representative.

CODASTER TYPE

In the *Codaster* type no hydrospire slits are found in the posterior interray, and accordingly the calyx shows eight fields distributed around the summit, two in each interray other than the posterior. Representative genera are *Heteroschisma, Codaster,* and *Agmoblastus* (Fig. 202,*6-8*).

HYDROSPIRE PORES

Hydrospire pores are minute openings arranged in a row next to each ambulacral margin. They lead to the hydrospires and occur mainly in spiraculate blastoids. Two groups are readily differentiated, designated as *Globoblastus* and *Pentremites* types, respectively.

GLOBOBLASTUS TYPE

The *Globoblastus* type includes genera in which the pores are larger and less closely spaced near the summit than in aboral parts of the ambulacra where many more pores in a unit distance are observed (Fig. 194,*1,2*). The number and distribution of pores in each row are independent of such ambulacral elements as side plates and outer side plates, which are constant in width throughout the ambulacra. In one subtype the pores are restricted to borders of the radials (e.g., *Globoblastus*) and in another some of the pores pierce both radial and deltoid plate margins (e.g., *Orbitremites*).

PENTREMITES TYPE

The *Pentremites* type is characterized by hydrospire pores distributed along the entire length of ambulacra on each of their sides, each pore being bounded by a side plate and outer side plate (Fig. 193,*6,7*). Thus, the number of pores is directly proportional to that of the side plates and outer side plates. Representative examples are *Pentremites, Auloblastus,* and *Schizoblastus.*

THECAL CANALS

The existence in blastoids of ring canals surrounding the mouth and uniting with the longitudinal canals of the lancet plates has been known for nearly 80 years. The ring canals are termed **circumesophageal rings.** Etheridge & Carpenter (1882, p. 217-219) observed their presence in *Pentremites, Globoblastus, Schizoblastus, Phaenoschisma, Orophocrinus,* and *Codaster.* The structure probably is best known in *G. norwoodi.*

The longitudinal canal of each lancet plate in *Globoblastus* divides near the summit of the theca, giving rise to branches which pass through the deltoid under the paired spiracles and adoral to them. The branches then join with others given off from the longitudinal canals of adjacent lancets so as to form a pentagonal ring (Fig. 203,*1*). A smaller pentagonal ring inclosed by this one joins with it at lengthwise mid-points of inner parts of the deltoids in positions just adoral to the divided spiracles. On the anal side, the circumesophageal rings pass through the superdeltoid. Angles of the outer pentagonal ring are interradial, whereas those of the inner ring are radial in position.

The circumesophageal rings of *Pentremites* are similar to those of *Globoblastus* except that traces of a canal can be seen leading from the interradial mid-points of the outer ring toward each hydrospire canal (Fig. 203,*2*). Canals of this type have been observed to penetrate each of the deltoids other than the anideltoid. The open connections of the small canals with circumesophageal rings are quite distinct but exact relationships of opposite extremities of the diverging canals to the hydrospires are obscure. They appear to open into the spiracles.

PHYSIOLOGICAL FEATURES

FOOD-CARRYING SYSTEM

The food-carrying system of blastoids is complex, being supported externally by the brachioles and structures of the ambulacra and internally by unknown structures of the alimentary tract which doubtless existed. The number of plates directly related to the extrathecal food-carrying sys-

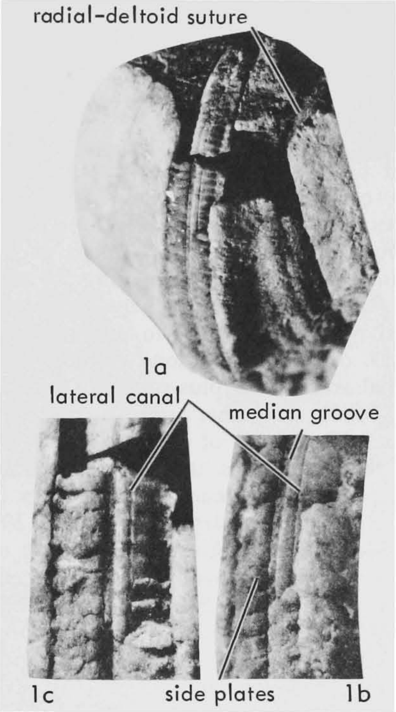

FIG. 204. Lateral canals in *Auloblastus clinei* BEAVER, Miss.(Osag.), near Springfield, Mo.; *A*, ×4; *B,C*, ×10 (*A*, Beaver, n; *B,C*, Beaver, 1961).

tem is tremendously greater than the number involved in the water-vascular or other systems. The total number of plates in a representative genus (e.g., *Pentremites*), including brachiole and ambulacra cover plates, certainly amounts to tens of thousands and possibly to hundreds of thousands.

By analogy with modern crinoids and other echinoderms, food is inferred to have entered the food-carrying system along the brachiole median grooves and to have moved along these grooves to the brachiole sockets, located on the ambulacral margins. From these points of brachiole attachment the food moved admedially along the lateral grooves to the ambulacral median groove and then was transported adorally to the mouth at the summit of the calyx. It seems reasonable to suppose that the brachiole cover plates were movable and that cover plates of the lateral grooves also may have been able to move. The general lack of symmetry in the arrangement of cover plates of the ambulacral median groove suggests that these plates may not have been movable. The small elongate plates covering the anus (e.g., *Pentremites*) were probably capable of movement, and thus could have disposed of waste products.

Virtually nothing is known of the digestive tract within the central cavity of the animal.

WATER-VASCULAR SYSTEM

The water-vascular system of blastoids includes the hydrospires and associated thecal openings and canals. In spiraculate blastoids sea water is inferred to have entered the hydrospires through the hydrospire pores and to have moved adorally through the hydrospire canals to the spiracles. Fluids from the spiracles are interpreted to have entered the area beneath the summit plates of the mouth, and to have emerged from the theca through them, or possibly between the plates covering the spiracles, if these were movable. In fissiculate genera without hydrospire pores, but with spiracles, sea water apparently entered the hydrospires through hydrospire slits and emerged from the theca through the summit plates or possibly through the spiracles. Where neither pores nor spiracles are present, hydrospire slits must have served both as an entrance and exit to water entering the hydrospires.

The large surface area represented by the hydrospire folds, inferred to have been semipermeable, permitted sea water within the hydrospires to aerate the fluids of the body cavity. Little is known about trends involving an increase or decrease in hydrospire surface area through geologic time in selected blastoid lineages. Factors affecting hydrospire surface area include length of ambulacra, number and shape of hydrospire folds in each hydrospiralium, and adaxial extension of the hydrospire folds. Variation in hydrospire wall thickness is an undetermined feature in evaluating the effectiveness of the water-vascular system.

NERVOUS SYSTEM

The circumesophageal rings and their lateral branches in the lancets (median canals) are inferred to represent the nervous system in blastoids. This system of canals encircles the mouth area and seemingly ends at the aboral extremities of the lancets. An apparent connection between the circumesophageal rings and the spiracles has been recognized in *Pentremites* (Fig. 203, *2*). The median canals are entirely embedded in the lancets and do not open into other systems (i.e., hydrospiralia). The lateral canals which lie on either side and obliquely adaxial to the median canal in *Auloblastus* possibly may be a part of the nervous system (Fig. 204). Lack of knowledge of their adoral and aboral extent and relationships to other structures limits an interpretation of their function.

ABNORMALITIES

Blastoids with malformed structural elements are fairly common in various species represented by abundant specimens.

Wanner (1932) distinguished 133 abnormal specimens of *Deltoblastus* from the Permian of Timor in a large collection of more than 24,000 specimens, or a proportion of one abnormal specimen to every 182 examples. While a thorough examination has not been conducted on the proportion of malformed *Pentremites* from the Upper Mississippian of the Ohio River area, the above ratio probably is not far out of line. Deformed specimens of numerous other genera have been reported in the literature, but generally the number of abnormal individuals is small and prevents generalization.

Abnormalities may occur in any of the blastoid structural elements, including the column and brachioles. Doubtless owing to the rarity of preserved intact columns and brachioles, however, known examples are confined to structures of the theca. Wanner (1932) recognized three principal groups of malformed specimens of *Deltoblastus*. One group, composing 3.6 percent of total abnormal specimens, is characterized by thecae with 2 to 4 normal radial areas, combined with one or more stunted radial areas, or surplus plates, or both (Fig. 205,*1,2,4*). Another group, representing about 13 percent of all malformed *Deltoblastus* individuals, includes normal thecae except for the presence of extra plates (Fig. 205,*3*), or with enlarged plates (Fig. 205,*5*). A third group, making up 83 percent of all deformed specimens, is distinguished by some combination of too few structural elements. These include near-obliteration of interradial elements which gives rise to seemingly double ambulacra (Fig. 205,*6*), lack of ambulacra (Fig. 205,*7,9,11*), and abnormally shortened ambulacra (Fig. 205, *8,10*). Defects observed in *Pentremites* (Fig. 206,*8*) are similar in many respects to those of *Deltoblastus*. The deformities described by Wanner and some of those recognized in *Pentremites* and *Globoblastus*

[*See opposite page*]

Fig. 205. Abnormal specimens of *Deltoblastus* from the Permian of Timor, all *D. permicus* (Wanner), except *7*, which is *D. batheri* (Wanner).——1. Lateral and basal views of theca with three normal radials and ambulacra; *1a*, radial *(A)* shortened, with no evidence of sinus; *1b*, one ambulacrum *(E)* with surplus plates; ×2.5.——*2*. Basal and lateral views of calyx with 3 normal radials and ambulacra; one abnormal radial and deltoid indented with trace of a radial sinus *(A)*; double ambulacra in position of *E* ambulacrum; ×2.5.——*3*. Normal specimen except for protruding lower half of a deltoid (*CD* interray); ×2.——*4*. Calyx with 4 normal radials and ambulacra, sinus for abnormal ambulacrum *(B)* reduced to notch; 2 extra plates present, ×2.——*5*. Normal theca except for extra plate between 2 radials and slightly shortened and modified overlying deltoid (*AB* interray); ×2.——*6*. Calyx with radial limbs and deltoid lying between 2 ambulacra nearly obliterated so as to give appearance of double ambulacra (*AB* interray); ×3.——*7*. Theca with 3 normal radials and ambulacra, positions of missing ambulacra *(C,D)* indicated by poorly developed radial sinuses and abnormal rays slightly shorter than normal rays, ×2.5.——*8*. Calyx with one ambulacrum greatly shortened and apparently without facets for covering plates and brachioles, associated radial much smaller than normal; basals in contact with only 4 radials, laterally adjacent ambulacra somewhat shortened, ×2.5.——*9*. Calyx with 3 normal radials and ambulacra, 2 rays entirely missing, 3-sided in basal view, ×2.5.——*10*. Normal theca except for shortened ambulacrum *(A)* and adjacent deltoid (*AB* interray) which is stunted at its upper end, ×2.5.——*11*. Theca with one abnormal ray *(E)*, ambulacrum entirely missing but radial sinus partially preserved, abnormal radial greatly shortened and malformed, ×2.5 (Wanner, 1932).

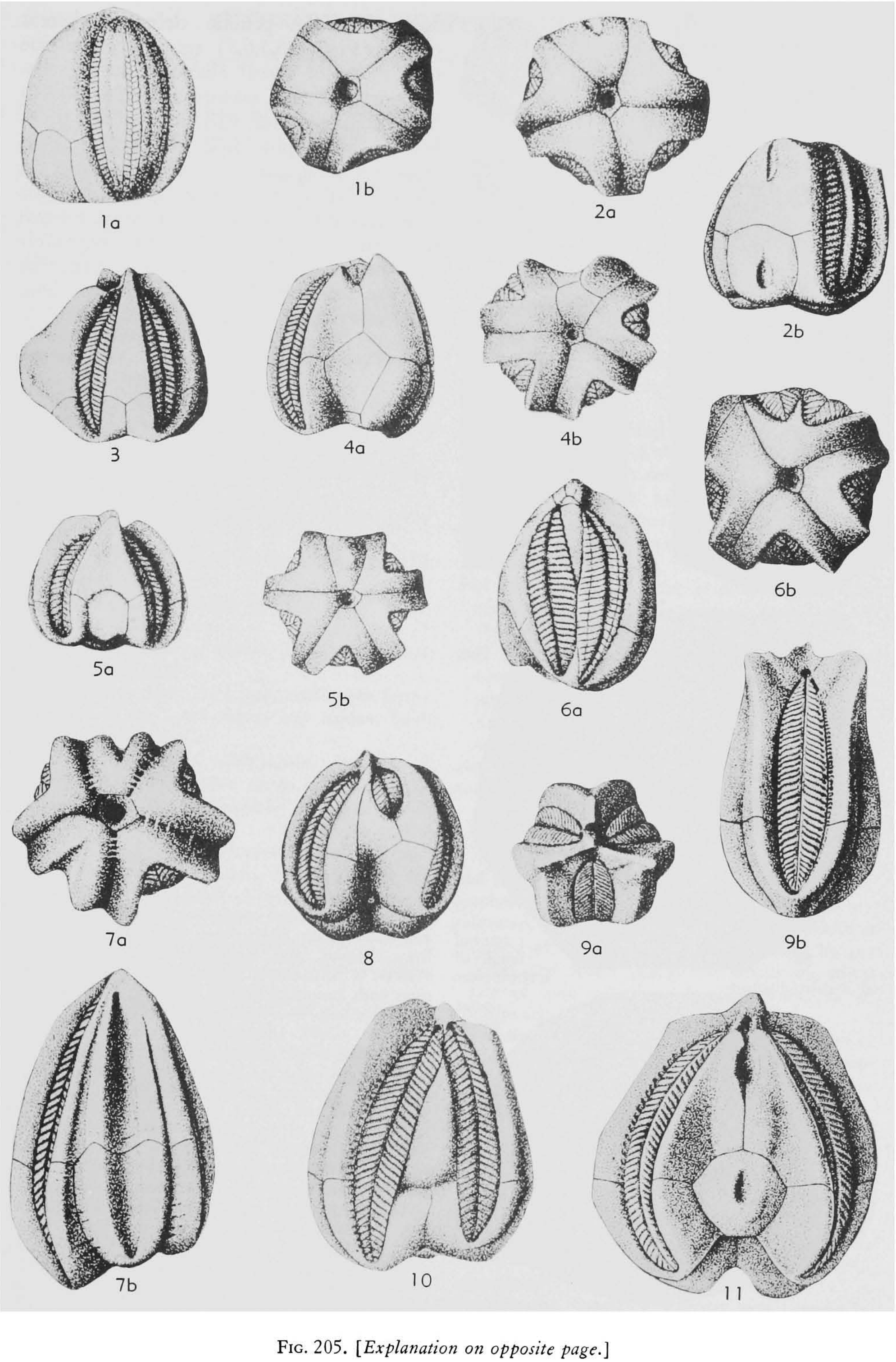

Fig. 205. [*Explanation on opposite page.*]

apparently are genetic defects, whereas others (Fig. 206,*5,6,8*) seemingly are due to damage of thecal elements during life.

Etheridge & Carpenter (1886, p. 41) have suggested that variations in the number of hydrospire folds in hydrospiralia represent irregularities and inequalities of growth. Although this may be true, it seems more likely that such variations are normal in some species. Hydrospires commonly may be broken or lacking, but generally one can ascertain that they have been damaged after death of the individual.

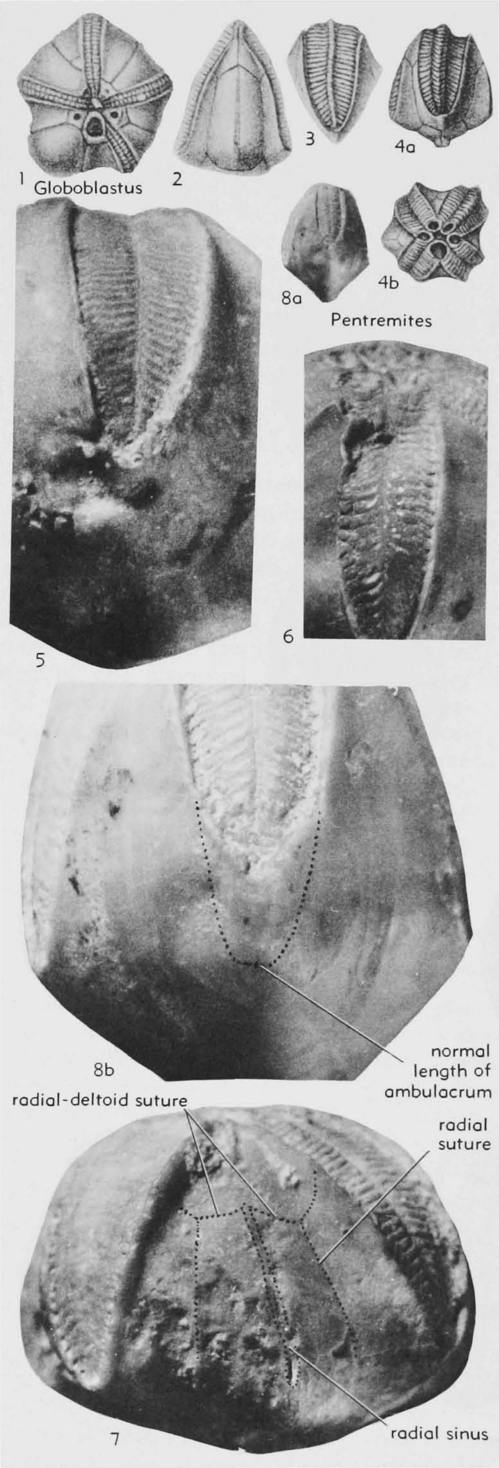

Fig. 206. Abnormal specimens of *Globoblastus (1)* and *Pentremites (2-8)* from Mississippian rocks of Iowa, Illinois, and Alabama.——*1. G. norwoodi* (Owen & Shumard), Iowa; adoral view of specimen with abnormal radials, ambulacrum lacking in *D* ray, ×1.3.——*2-7. P. godoni* (Defrance) from Alabama *(2-4)* and Illinois *(5-7)*; *2,* specimen with radial sinus reduced to narrow slit without ambulacrum, ×1.3; *3,* specimen showing ridge instead of median groove in ambulacrum, ×2.2; *4a,b,* lateral and adoral views of specimen having only 4 radials, *A* and *B* rays with abnormal combined ambulacrum, ×1.3; *5,* specimen with damaged radial body and aboral part of ambulacrum, ×4.5; *6,* specimen with deformed *A* ambulacrum, ×4.5; *7,* specimen with extra radial in *AE* interray, its sinus reduced to narrow slit (sutures and sinus marked by dotted lines), ×4.5.——*8. P. symmetricus* Hall; *8a,b,* lateral views of specimen with one considerably shortened ambulacrum, normal outline indicated by dotted line in *8b.* ×1, ×4.5 (*1-4,* Etheridge & Carpenter, 1886; *5-8,* Beaver, n).

GLOSSARY OF MORPHOLOGICAL TERMS

By Harold H. Beaver, Robert O. Fay, and Raymond C. Moore

A ray, radial and ambulacrum. Distinguished by location opposite interradially placed anal opening or anispiracle; also termed anterior.

abanal. Direction away from anus (in plane of theca near anus).

abaxial. Direction perpendicularly away from polar axis.

ablateral. Direction away from margin of ambulacrum toward its mid-line.

abmedial. Direction away from mid-line of ambulacrum toward either margin.

aboral. Direction away from mouth (in plane of theca or along polar axis).

accessory oral plate. One of many small plates of peristome surrounding 5 main oral plates, adoral to side plates and meeting cover plates.

adanal. Direction toward anus (in plane of theca near it).

adaxial. Direction perpendicularly toward polar axis.

adlateral. Direction toward one or other margin of ambulacrum.

admedial. Direction toward mid-line (main food-groove) of ambulacrum.

adoral. Direction toward mouth (in plane of theca or along polar axis).

ambulacral cover plate. Tiny polygonal ossicle forming part of roof over lateral and median food grooves of ambulacrum.

ambulacral field. Entire ambulacrum exclusive of brachioles, including side plates and associated structures, in addition to exposed portion of lancet plate.

ambulacral flange. Clifflike enclosure of ambulacrum produced by abruptly elevated edges of deltoids and radial sinus above general level of ambulacrum.

ambulacral groove. *See* main food-groove.

ambulacral half-field. One-half of ambulacral field, on either side of main food-groove.

ambulacral ratio. Maximum length of ambulacrum divided by its maximum width.

ambulacral rim. Entire margin of ambulacrum from deltoid tips to bottom of radial sinus; may be flush with surface of theca or accented by ambulacral flange.

ambulacral spine. Small needle-like curved spine attached to the side plate body, arranged in rows along sides of main food-groove; each is approximately 1 mm. long by 0.1 mm. wide, with spirally arranged striations.

ambulacrum. Radially disposed area extending aborally from mouth, with narrow depression (main food-groove) running longitudinally along its center, with side food-grooves joined to this groove, and with side plates and associated structures, including brachioles; exposed portion of lancet plate may be included as part of ambulacrum. Viewing specimen from oral side, with anal opening toward observer, ambulacrum opposite anal opening is lettered *A* and considered to be anterior. Proceeding clockwise, other ambulacra are designated *B* (right anterior), *C* (right posterior), *D* (left posterior), and *E* (left anterior).

anal area. Region near anal opening.

anal cover plate. One of many small polygonal plates which may extend over and conceal anal opening in theca, bordered marginally by anal deltoid or deltoids.

anal deltoid. Undivided interradial plate on posterior *(CD)* part of theca below circlet of orals or mouth opening; collectively, anal deltoids include all differently named kinds of such plates of the posterior interray (anideltoid, cryptodeltoid, epideltoid, hypodeltoid, paradeltoid, subdeltoid, superdeltoid).

anal opening. Large orifice in theca marking position of anus in living animal, located in *CD* (posterior) interradius.

anal plate. One of many small polygonal plates covering immediate anal opening, bordered marginally by anal deltoid, epideltoid, hypodeltoid, superdeltoid, subdeltoid, cryptodeltoids, or paradeltoids.

anal pore. *See* anispiracle.

anal pyramid. Cone-shaped anal structure composed of elongate, imbricate anal plates, above smaller polygonal plates, arranged in several rows; may include anal oral plates also.

anal sac. *See* anal pyramid.

anephebic. Mature but smaller than normal.

anideltoid. Externally visible anal deltoid which is proved or not known to be accompanied by any others and which lies almost wholly on aboral side of anal opening *(Acentrotremites)* or of anispiracle *(Pentremites, Ambolostoma)*.

anispiracle. Enlarged opening in summit portion of posterior interray, formed by union of anal opening and posterior spiracle (or spiracles), also termed anal pore (see paired anispiracle).

anterior ambulacrum. *See A* ambulacrum.

anthus. Complete blastoid calyx and brachioles borne by it; entire skeleton of blastoid exclusive of stem (Greek, *anthus*, flower or blossom).

anus. Excurrent opening of digestive tract in living animal, located in summit part of *CD* interray, generally indenting anal deltoids and possibly may border posterior radial or oral plates.

anus separate. Condition whereby anal opening is separate from adjacent spiracles.

apex. Highest distal point on theca.

axis. *See* polar axis.

azygous basal plate. Smallest of 3 plates of basalia (name signifying unyoked or unfused), normally located in anteroright *(AB)* interray but may be posteroleft *(DE)*.

B ray, radial and B ambulacrum. *See* ambulacrum.

basal angle. *See* pelvic angle.

basal circlet. *See* basalia.

basal periphery. Outline of calyx seen from base.

basal plate. Component of proximal circlet of theca adjoining stem, or rarely adjoining subbasal plates, almost invariably consisting of 2 subequal large zygous plates (*BD*, right posterior and *DA*, left anterior) and a small azygous basal plate (*AB*, anteroright); in a few forms the small (azygous) basal plate may be in *DE* (posteroleft) in position. The basals may be reduced to a single plate by atrophy, resorption, or coalescence, and in some forms the basals may be irregular in position.

basalia. Basal circlet of plates in blastoid theca, normally consisting of 2 large (zygous) and 1 small (azygous) plates but may include 1 large basal plate formed from coalesced basals or 1 small basal where others have atrophied or have been resorbed.

base. *See* pelvis.

brachiolar facet. Large elliptical scarlike area on side plate limb and outer side plate, adlateral to brachiolar pit or side food-groove, being bifascicular, with aboral portion on side plate limb and adoral portion on outer side plate; also termed brachiolar socket or brachiole facet.

brachiolar groove. Depression running along ventral surface of brachiole, vaulted over by series of cover plates, serving for transport of food particles to lateral and median grooves of ambulacrum.

brachiolar pit. Small round depression at adlateral termination of side food-groove.

brachiolar plate. One of biserially arranged plates of brachiole, semielliptical in cross section and subquadrangular in side view, with basal pair attached at brachiolar facet.

brachiolar socket. Centrally placed pit on rounded knob located at adlateral extremity of lateral groove on ambulacrum, providing for articulation of brachiole; also termed brachiole socket.

brachiole. Slender food-gathering appendage attached to border of ambulacrum, composed of numerous, short, biserially arranged ossicles (brachiolars), with subvective system and covering plates on ventral surface; brachioles on one side of ambulacrum alternate in position with those on opposite side, and where reclined, they form an imbricate pattern (also termed pinnule).

C ray, radial and ambulacrum. Elements next clockwise from *B* ray in oral view of theca, also, termed right posterior (*see* ambulacrum).

calyx. Skeletal cover (theca) of blastoid including internal structures (hydrospires, etc.) but excluding appendages (brachioles) and stem (calyx literally signifies cup; *see* anthus).

central canal. *See* median canal.

circumesophageal ring. Double pentagonal ring of canals around esophagus, with corners of outer ring meeting meeting median canals of lancet plates, and corners of inner ring joining sides of outer ring beneath spiracles at adoral ends of deltoids. Although previously thought to be part of water-vascular system, recent opinions indicate that this structure is part of the nervous system.

column. *See* stem.

columnal. Individual segment of blastoid stem.

conjunct deltoid process. Ventrally raised portion of adoral tips of deltoids and adjacent radial limbs.

cover plate. One of tiny polygonal plates arranged in double alternating series over side and main grooves; quadruple alternating series placed on brachioles, inner double set termed inner cover plates and outer set termed outer cover plates; also, *see* anal cover plate.

cover plate lobe or ridge. Small rounded elongate raised area along edges of side and main food-grooves extending to lancet stipes and deltoid lips; presumably sutures between adjacent cover plates are along median lines of each lobe.

cover plate socket. Depression between adjacent cover plate lobes, presumably place of attachment for cover plate.

crenella (pl., **crenellae**). Small radially disposed groove on stem impression at base of theca and on distal and proximal surfaces of columnals, commonly extending less than one-third of distance from perimeter toward center; *see* culmen.

cross section. Section normal to polar axis, also termed transverse section.

crown. *See* anthus.

cryptodeltoid plate. One of 2 plates on either side of anal opening, generally overlapped aborally by hypodeltoid and adjacent radial limbs, abutting against superdeltoid plate adorally, bordering lancet plate laterally, and infolded into hydrospire folds on inner side. By adoral extension and fusion together above anal opening, cryptodeltoids may form horseshoe-shaped subdeltoid developed in some genera, such plate being adjoined on adoral side by superdeltoid.

culmen (pl., **culmina**). Ridge between crenellae on articular surface of columnal.

D ray, radial and ambulacrum. Elements next clockwise from *C* ray in oral view of theca, also termed left posterior ambulacrum (*see* ambulacrum).

deltoid body. Main portion of deltoid plate, seen externally, comprising median and aboral regions, term applicable also to anideltoid but not to other anal deltoids.

deltoid crest. Raised ridge, seen externally, connecting deltoid body with deltoid lip, with depressions on either side (termed oral crest by some authors); same as raised deltoid septum.

deltoid head. Adoral part of externally visible deltoid plate (including anideltoid) set off from deltoid body by lateral indentations produced by paired spiracles or entirely separated surficially by interruption due to spiracle (or anispiracle).

deltoid lip. Adoral margin of deltoid contiguous to mouth opening.

deltoid plate. Interradial subtriangular plate near summit of theca but aboral to oral plates, between adjacent ambulacra and above radial plates, internally infolded into hydrospire folds, with spiracles excavated at adoral end; on anal side 1 to 6 deltoid plates may be present, each specially named, but only single deltoid is present in each of other 4 interradial positions.

deltoid septum. Thin internal portion of deltoid plate between adjacent hydrospire canals, connecting deltoid lip to deltoid body; on anal side are 2 septa formed by variously named plates.

deltolancet suture. Common line or division between deltoid and lancet plates.

disjunct deltoid. Deltoid with lip externally separated from body by spiracle or anispiracle.

distal. Direction away from point of stem attachment with theca (compare ventral). [Bather, Cline, and Wanner ill-advisedly used this term in describing hydrospires and ambulacra to mean away from the mouth, but otherwise they followed definition here given.]

dorsal. Direction toward point of attachment of stem with theca (compare proximal).

dorsal pole. Center of dorsal surface of theca.

dorsal region. *See* pelvis.

double spiracle. *See* paired spiracle.

E ray, radial and ambulacrum. Elements next clockwise from *D* ray in oral view of theca, also termed left anterior ambulacrum; (*see* ambulacrum).

ephebic stage. Mature or adult growth stage.

epideltoid. Anal deltoid bordering adoral side of anal opening and adjoining mouth opening, with or without hydrospires; differs from superdeltoid in lacking association with cryptodeltoids.

equator. Circumference about theca at one-half height of theca.

esophogeal ring. *See* circumesophageal ring.

fissiculate. Having exposed or partly exposed hydrospire slits or spiracular slits.

food-groove. *See* main food-groove.

fused basal plate. Large single basal plate seen in some blastoids, formed by fusion of entire basal circlet.

fused hydrospire plate. Elongate thickened projection of radial and deltoid plates beneath lancet plate, generally accompanied by lateral displacement of pores and slits away from ambulacral margins (formerly termed sublancet or underlancet plate). If projection is thin, each side is termed a hydrospire plate.

gerontic stage. Old-age growth stage.

granulostriations. Ornamentation of some brachiolars with microstriations parallel to brachiolar food-groove and small ridges at right angles to groove.

hydrospiralium. Group of two or more (to 18) conjoined hydrospires located along border of ambulacrum.

hydrospiralium cleft. Space within hydrospiralium exclusive of hydrospire clefts.

hydrospire. Infolded thin-walled calcareous linear structure on either side of ambulacrum, excavated in radial and deltoid plates, approximately parallel to ambulacral margin; on anal side, this may be excavated in cryptodeltoids, epideltoid, subdeltoid, and (in *Nymphaeoblastus*) in hypodeltoid.

hydrospire canal. Adorally directed tubular passageway in adambulacral part of deltoid leading from hydrospire, hydrospiralium, or confluent hydrospiralia to spiracle (or anispiracle).

hydrospire cleft. Space inclosed by hydrospire fold.

hydrospire field. Area of theca underlain by single group of hydrospires (hydrospiralium).

hydrospire fold. Thin calcareous wall surrounding hydrospire.

hydrospire pore. Minute rounded opening between side plates or outer side plates near margin of ambulacrum, leading into hydrospire.

hydrospire slit. Longitudinal opening of hydrospire fold excavated in substance of deltoids and radials parallel to ambulacral margins on either side.

hydrospire tube. Expanded adaxial portion of hydrospire fold.

hypodeltoid. Interradial plate on anal side adjacent to posterior radial limbs, forming aboral part of anal opening; internal portions may rest upon cryptodeltoids, subdeltoid, and septal projections of epideltoid, in addition to parts of hydrospire plate and fused hydrospire plate.

inner cover plate. One of series of biserial kite-shaped small plates over brachiolar food-groove, alternating with set of pentagonal outer cover plates on margins.

inner side plate. Small triangular plate between side plates at admedial corners near main food-groove, present in some genera (*see* side plate, outer side plate).

interambulacral. *See* interradial.

interdeltoid suture. Common line or suture between adjacent deltoid plates.

interhydrospiralium. Space between adjacent hydrospiralia.

internal. Toward inside of theca, same as inward.

interradial. Position of line extending from mouth halfway between adjoining radii or ambulacra, through mid-line of any deltoid plate. Orals, deltoids, and azygous basal are interradial in position. If 5 deltoids are present, they are termed *AB* (anteroright), and *BC* (posteroright), *CD* (posterior), *DE* (posteroleft), *AE* (anteroleft); same as interambulacral.

interradial suture. Common line or division between adjacent radial plates.

inward. Direction toward geometric center of calyx or polar axis of theca or stem, or toward inside of brachiole; same as internal.

lancet plate. Elongate spear-shaped plate extending from aboral tip of ambulacrum to oral opening, located along mid-line of ambulacrum, with elongate central canal (median canal) that connects with circumesophageal ring adorally. Adoral end, termed lancet stipe, adjoins adjacent spiracles laterally and internally rests on adjacent deltoid plates. In primitive blastoids, lancet is covered by side plates, but in advanced forms it supports main and side food-grooves also. In some forms, lateral canals are excavated in its outer surface beneath side plates, parallel to main food-groove.

lancet-side plate suture. Common line or division between lancet plate and side plate.

lancet stipe. Restricted adoral extension of lancet plate, resting internally on truncated ventral surface of adjacent deltoid lips, but adjoining oral orifice externally and generally bordering adjacent spiracles laterally; small cover plate lobes and sockets may be present.

lateral. Direction toward margin of ambulacrum or brachiole.

lateral canal. One of 2 small longitudinal canals on outer surface of lancet plate, beneath side plates, parallel to and on either side of main food-groove.

lateral food-groove. *See* side food-groove.

left anterior ambulacrum (E). *See* ambulacrum.

left posterior ambulacrum (D). *See* ambulacrum.

length. Vertical distance between apex and base of theca.

length-width ratio. Length of theca divided by width of theca.

limb. Adoral portion of radial plate along side of ambulacrum; *see* radial limb.

longitudinal section. Section parallel to polar axis.

lumen. Small round opening in center of stem columnals, which may or may not be continuous with body cavity above basal plates of theca; also termed stem cavity.

main food-groove. Longitudinal depression extending length of middle line of ambulacrum, excavated in side plates or lancet plate, bordered by cover plate lobes and sockets; also termed median groove, food-groove, and ambulacral groove.

medial. Line or direction of main food-groove.

median canal. Internal central opening of lancet plate, extending longitudinally to circumesophageal ring; also termed radial canal and central canal.

median groove. *See* main food-groove.

median pit. External depression in middle of side plate body.

median ridge. Small, regularly curved ridge around median pit on side plate body, curving adlaterally around brachiolar pit, joining ridge on adjacent side plate, parallel to adoral, admedial, and aboral edges of side plate body.

metaphebic. Mature and normal in size.

mouth. Central opening at summit of theca leading to digestive tract.

neanic stage. Youthful or immature growth stage.

nepionic stage. Growth stage between embryonic and neanic stages.

oral. Region about mouth; of or pertaining to mouth; *see* peristome and summit.

oral crest. *See* deltoid crest.

oral groove. Medial groove of lancet stipe and adjacent deltoid lips, adjacent to oral opening.

oral hood. *See* oral pyramid.

oral opening. Pentagonal opening at summit of theca, marking position of mouth in living animal.

oral plate. One of 5 main interambulacrally located polygonal plates covering mouth, but may include other summit plates where 5 main plates are lacking; *see* accessory oral plate, posterior oral plate, peristome, oral pyramid, oral spine, cover plate, and summit plate.

oral pyramid. Conical structure about oral opening, which comprises specialized elongate oral and accessory oral plates (termed oral spines) or oral cover plates, basally adjacent to many small polygonal accessory orals that cover spiracles (spiracular plates); also termed oral hood.

oral ring canal. *See* circumesophageal ring.

oral spine. Elongate conical oral or accessory oral or specialized anal plate around oral opening, forming part of anal and oral pyramids.

outer cover plate. One of polygonal cover plates along ventral margins of brachiole, single set on one side alternating in position with that on opposite side, brachiolar food-groove between these plates, roofed over by biserial set of inner cover plates that fit tightly against outer cover plates in zigzag pattern and alternate with them.

outer side plate. Small semielliptical to subtriangular plate that generally rests upon adlateral margin of side plate, bearing part of brachiole; in some specimens position may be more admedial; same as secondary side plate (*see* side plate, inner side plate).

outward. Direction away from geometric center of theca or polar axis of stem, or away from inside of brachiole.

paired spiracle. Spiracle with deltoid septum almost at surface externally so that V-shaped spiracle is formed, giving appearance of 2 connected spiracles with actually single opening; also termed double spiracle.

paradeltoid plate. One of 2 small subtriangular plates resting upon beveled adoral margin of hypodeltoid, on aboral side of anal opening, resting upon cryptodeltoids and not infolded into hydrospire folds.

parephebic. Mature but larger than normal in size.

pelvic angle. In side view, angle measured from dorsal pole (as center) to aboral tips of ambulacra farthest apart, with one radial position toward observer; same as basal angle.

pelvis. Portion of theca from aboral tips of ambulacra to dorsal pole; also termed base and dorsal region.

periphery. Circumference of theca at its widest part.

peristome. Area of oral and accessory oral plates around oral opening, located at summit of theca.

pinnules. *See* brachioles (not same as crinoid pinnules).

polar axis. Line extending from oral center to center of stem.

pore. *See* hydrospire pore.

pore furrow. Elongate depression on side plate handle extending abmedially from side plate body to hydrospire pore, between adjacent brachioles.

posterior oral plate. One of 5 main oral plates, larger than others and located in anal *(CD)* interradius.

primary side plate. *See* side plate.

primary side plate suture. *See* side plate suture.

profile. Outline of theca in side view.

proximal. Direction toward point of attachment of stem and calyx (compare dorsal). [According to Bather, Cline, and Wanner with respect to ambulacra, direction toward center of the mouth is proximal, but they used the definition first given for thecal orientation.]

pyriform. Pear-shaped.

radalia. Radial plates of theca.

radial. Position of line extending from centrally placed mouth to aboral end of any ambulacrum; lancets, radials, and ambulacra are radial in position.

radial body. Portion of radial plate below or aborally away from aboral tip of ambulacrum; same as trunk.

radial canal. *See* median canal.

radial circlet. *See* radalia.

radial limb. Adoral portion of radial plate along side of ambulacrum; sometimes termed limb.

radial lip. Thickened portion of radial plate at aboral tip of radial sinus.

radial plate. One of 5 cleft plates above basalia, radial in position, that receives aboral extremity of ambulacrum.

radial sinus. V-shaped indentation in adoral part of radial plate which receives ambulacrum.

radiodeltoid suture. Line or division between deltoid plate and adjacent radial limbs.

right anterior ambulacrum (B). *See* ambulacrum.

right posterior ambulacrum (C). *See* ambulacrum.

root. Presumably expanded, branching, treelike extension at distal end of stem.

secondary side plate. *See* outer side plate.

side food-groove. One of many short transverse depressions on ambulacrum, subparallel to each other, adorally directed at oblique angle to and emptying into main food-groove from base of brachiole, alternating in position on either side of main food-groove, and commonly bordered by cover plate lobes and sockets.

side plate. One of many small subquadrangular plates of ambulacrum, partly superposed on lancet plate or on its adlateral margin, arranged alternately on either side of main food-groove and between side food-grooves, bearing outer side plate and brachiole; also termed primary side plate (*see* inner side plate, outer side plate).

side plate body. Admedial portion of side plate, admedial to outer side plate.

side plate limb. Abmedial portion of side plate, normally aboral to outer side plate; sometimes termed side plate handle.

side plate suture. Line or division between adjacent side plates along line of lateral food-groove.

sinus. V-shaped indentation of ambulacrum along deltoid and radial margins.

sinus edge. Margins of radial and deltoids bounding ambulacrum; also termed ambulacral rim.

sinus flange. Clifflike enclosure of ambulacrum produced by abruptly elevated margins of radial and deltoids above general level of ambulacrum; same as ambulacral flange.

spiracle. Opening, generally rounded, near adoral tip of deltoid and excavated within it, bounded adorally by deltoid lip and aborally by deltoid body, and generally adjoined laterally by lancet stipe and side plates; *see* paired spiracle. Where deltoid septum is exposed externally, 2 spiracles are formed in deltoid.

spiracular cover plate. One of series of small polygonal plates that cover spiracles, extending adorally into oral spines; these may be part of series of accessory oral plates that are highly specialized; *see* oral pyramid.

spiracular slit. Elongate spiracle at side of ambulacrum, excavated in adjoining radial and deltoid plates, with fused hydrospire plate forming admedial wall and one or more hydrospire folds opening into hydrospire canal.

spiraculate. Having spiracles, in some genera including anispiracle.

stem. Cylindrical column beneath theca that may have served as means of support, composed of numerous discoid, button-shaped columnals, with central lumen, supposedly attached to root distally. The axial canal represented by the lumens of columnals connects with the body cavity. The stem also is termed column. Some forms probably lacked a stem.

stem cavity. *See* lumen.

stereome. Calcareous tissue in the mesodermal endoskeleton of the living echinoderm. This, together with the stroma, where both are replaced by calcium carbonate, forms the material of blastoid plates.

stroma. Organic tissue in mesodermal endoskeleton of living echinoderm.

subbasal plate. Small plate, or one of 3 plates, secreted between basal plates and top of the stem; also termed supplementary basal plate.

subdeltoid. Small to moderately large anal deltoid, typically inverted U-shaped, located on adoral and lateral margins of anal opening and on aboral border of superdeltoid; *see* epideltoid.

sublancet plate. *See* fused hydrospire plate (=underlancet).

subradial plate. *See* fused hydrospire plate.

summit. Distal extremity of theca.

summit plates. Oral and accessory oral plates.

superdeltoid. Anal deltoid on border of mouth opening, associated either with subdeltoid or pair of cryptodeltoids abutting its aboral margin and in some genera bordering anal opening.

supplementary basal plate. *See* subbasal plate.

suture. Plane of junction between adjacent plates.

tangential section. Section tangent to outer surface of theca.

theca. Main skeleton enclosing body of blastoid, including ambulacra but excluding stem and brachioles (equivalent to "calyx").

transverse section. Section perpendicular to longitudinal section.

trunk. *See* radial body.

underlancet. *See* sublancet plate.

vault. Portion of theca above pelvis; also termed ventral region.

vault-pelvis ratio. Height of vault divided by height of pelvis, measured parallel to polar axis.

ventral. Side of theca containing mouth or direction toward it (compare distal).

ventral pole. Geometric center of oral opening.

ventral region. *See* vault.

width. Maximum width of theca, measured at right angles to polar axis.

zygous basal. Large plate of basal circlet in *BD* (right posterior) or *DA* (left anterior) position, formed by fusion (*zygos*, yoked) of pair of antecedent small basals comparable to azygous basal in *AB* (anteroright) interray.

TECHNIQUES

By Harold H. Beaver

Many techniques have been used over the years in studying blastoids. Those particularly well suited to solving problems of blastoid morphology are discussed briefly here.

WEATHERED, REPLACED, AND DISARTICULATED SPECIMENS

Morphological features probably can be studied best on deeply weathered specimens and those consisting of disarticulated remains. Surfaces of internal structural elements, many complexly sculptured, may be well preserved and easily photographed in this condition. Exquisitely preserved specimens may be collected in large numbers along weathered joint surfaces (e.g., Burlington Ls., Mississippian). Disarticulated plates may be abundant in washed samples from shales rich in blastoids (e.g., Paint Creek F., Chesteran). Silicified thecas commonly are excellent for external study but provide little information on internal structures because obliteration of sutures prevents examination of plate relationships. Replacement of thecal elements by iron oxides, however, may be advantageous for morphological study. Hydrospires, for example, may be especially accentuated.

GROUND SURFACES

Ground surfaces may be prepared readily to show internal relationships of blastoid skeletal parts. The various plates reflect light differently so that plate boundaries may be seen easily. Joysey & Breimer (1963, p. 472) accentuated the effect by increasing contrast during photography. A camera lucida is commonly used to produce drawings.

ACETATE PEELS

Acetate peels can be made rapidly, cheaply, and they can be enlarged photographically. If serial sections are desired, the fossil surface may be ground to any number of desired levels and peels prepared. Peel quality is dependent on the nature of the calcite of the theca and the enclosed matrix material. Peels are well suited for many purposes, but are generally less desirable

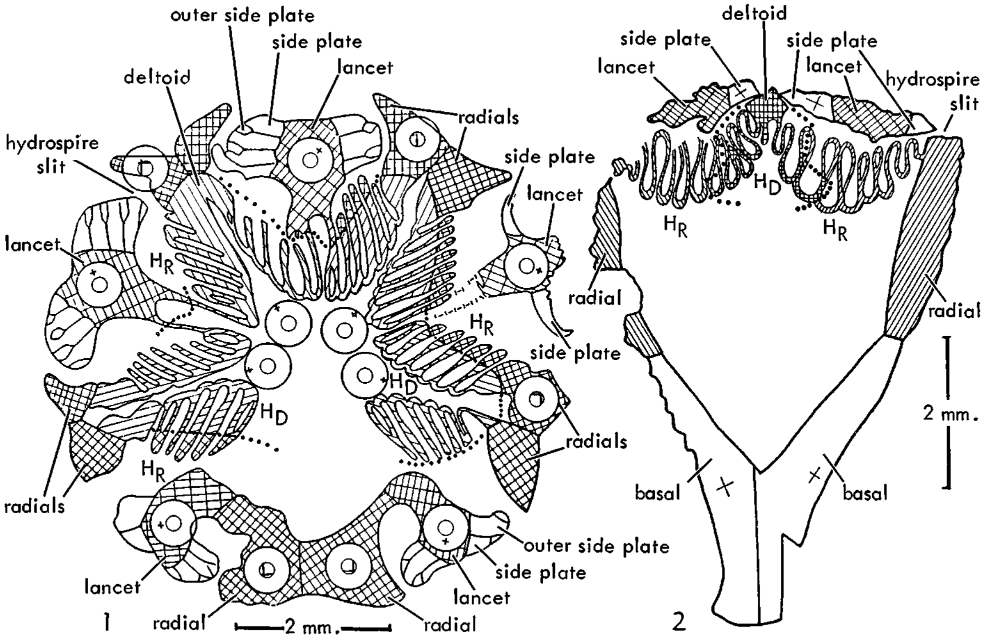

FIG. 207. Optical properties of *Cryptoschisma schultzii* (D'ARCHIAC & DE VERNEUIL).——*1.* Drawing of transverse section in summit area (Lucas, 1953).——*2.* Drawing of slightly inclined longitudinal section through an interray. [H_R, part of hydrospires interpreted to have formed from the radials; H_D, part of hydrospires interpreted to have formed from the deltoids. Circles indicate position of crystallographic axes of calcite for each thecal plate; in inner circles the interference figure in convergent polarized light is shown where the calcite optic axis is nearly vertical; in outer circles the positions of the crystallographic axes are shown as they would appear plotted in stereographic projection. The ruled lines are parallel to the vibration directions of the ordinary and extraordinary ways in the calcite crystals, rectangles (square, if the section were perpendicular to the crystallographic axis) being more elongate as the crystallographic axis is increasingly inclined with respect to the polar axis of the blastoid.]

than thin sections for detailed morphological investigations.

THIN SECTIONS

Thin sections are advantageous for studying internal structural elements of blastoids such as hydrospires, concealed anal deltoids, and canals such as the oral ring canal and its aboral extensions. Very thin sections are best for studies involving polarized light, whereas thicker sections are superior for distinguishing plate relationships and sutures. Furthermore, relatively thick sections provide better photographs than excessively thin sections.

Serial thin sections are particularly useful for determining progressive changes in structural elements (e.g., development of hydrospires). The main problems in preparing serial thin sections are the impossibility of obtaining closely spaced sections and the tendency of specimens to shatter during sawing. Recently, JOYSEY & BREIMER (1963, p. 473) have described a new saw which apparently is capable of ameliorating these problems.

STAINS

Stains may be useful in emphasizing certain plates and thus in making plate relationships more apparent. The stains commonly are used on ground surfaces and for working with acetate peels and thin sections.

OPTICAL CHARACTERISTICS OF PLATES

For many years optical properties have been utilized to determine plate relationships in echinoderm skeletons. As reviewed by RAUP (1959, p. 661), each of the structural elements of echinoderms behaves as a single calcite crystal. Thus, the various plates of a blastoid theca become extinguished in different positions when viewed in thin section with a polarizing microscope. The technique is most often used to observe the boundaries and relationships of thecal plates and to differentiate between plate sutures and adventitious cracks in the theca. LUCAS (1953, p. 635-637) used this method in attempting to determine which thecal plates of *Cryptoschisma schultzii* contributed to the development of the hydrospires. He concluded that the lancets, radials, and deltoids all shared in their formation (Fig. 207). More recently JOYSEY & BREIMER (1963, p. 472-473), in studying *Pentablastus*, used the technique in distinguishing plate relationships but found that "both optical continuities and discontinuities can be the product of secondary recrystallization."

Examination of thin sections of *Pentremites* and *Globoblastus* under polarized light aids in distinguishing plate relationships, sutures, and cracks in the theca, but is not useful in determining the identity of thecal plates which contribute to the hydrospires. The hydrospire folds are composed of very small calcite crystals, so tiny that at magnifications up to ×450 it is not possible to recognize when the crystals are extinguished. Mostly, the thecal interior is filled with large calcite crystals which generally are in optical continuity with the nearest thecal plates.

ONTOGENY

By HAROLD H. BEAVER

Numerous publications, particularly in recent years, have been concerned with blastoid ontogeny. Principal in importance are papers by ETHERIDGE & CARPENTER (1886), HAMBACH (1903), SMITH (1906), ULRICH (1918), WELLER (1920), BATHER (1922), CRONEIS & GEIS (1940), MOORE (1940), BURMA (1948), WANNER (1951), JOYSEY (1953, 1959), GALLOWAY & KASKA (1957), and REGNÉLL (1960). Growth series have been described for a number of genera, including *Codaster*, *?Diploblastus*, *Globoblastus*, *Orbitremites*, *Orophocrinus*, and *Pentremites*. Published growth series of various species of *Pentremites* are particularly numerous because of the relative abundance of collected specimens. Nearly complete series have been illustrated for *P. conoideus* (SMITH, 1906, pl. 46), *P. girtyi*, and *P. okawensis* (GALLOWAY & KASKA, 1957, pl. 11).

LARVAL AND JUVENILE STAGES

Almost nothing is known about the earliest growth stages of blastoids. CRONEIS & GEIS (1940) described some extremely tiny forms (length or diameter as small as 0.1 mm.) which they identified as *Mesoblastus* [*Diploblastus*] *glaber* and *Pentremites princetonensis*. Very much doubt remains, however, as to whether the specimens studied by them actually are blastoids. They have not been reported on further or made available for examination by other workers. Also, efforts to duplicate collections used by CRONEIS & GEIS have been unsuccessful.

The smallest specimens of *Pentremites* yet found in the Salem and Harrodsburg Limestones (Meramecian) of Indiana are reported by SMITH (1906) to be approximately 0.8 mm. in length. These specimens had three basals and five radials, but the plates in the oral region were not preserved.

In general, young blastoid individuals tend to be elongate. This appears to be true not only in genera with species which may be flat-based or pyriform as adults (e.g., *Pentremites*), but also in typically globular types. As previously mentioned, the young of *Globoblastus* are typically elongate globular, whereas adult specimens are nearly globular. It is presumed that the same is true of many other blastoids.

ADULT AND GERONTIC STAGES

Large collections of blastoids, such as are obtainable at many places, especially in outcrop areas of fossiliferous Upper Mississippian (Chesteran) strata, consist predominantly of specimens having approximately the same size and all relatively large. They obviously represent a mature growth stage and may be classed as adults, though no sharp boundary separates them from slightly undersized and distinctly smaller-than-average specimens. The small individuals, comprising a minority, grade downward to the smallest, interpreted as juveniles.

Old-age blastoids generally have a tendency to become obese. Globular types in old age are commonly depressed globular (e.g., *Globoblastus*). Flat-based *Pentremites* tend to increase width of the theca relative to thecal length, with a resultant increase in the ambulacral length.

GROWTH SERIES OF PENTREMITES

Examination of fine fractions of shale, rich in *Pentremites* from the Paint Creek (Chesteran) Formation, near Floraville, Illinois, shows that the smallest specimens are about 2 mm. in height. They are clearly recognizable as belonging to *Pentremites.* Because blastoids change shape and because some structures are modified during growth, it is commonly difficult to distinguish youthful individuals on the specific level if two or more specimens occur together. For example, abundant specimens generally identified as *P. godoni, P. gemmiformis, P. pyramidatus,* and *P. symmetricus,* may be collected from this same formation and locality. Many thousands—in all probability many tens of thousands—of *Pentremites* have been taken from two adjacent exposures at the Floraville locality. In adult or near-adult stages, *P. symmetricus* may be identified by shape of the calyx and length of the ambulacra. Progressively smaller specimens of this and other species are increasingly difficult to distinguish because all representatives of *Pentremites* are steeply conical when young, with ambulacral aras largely confined to the summit of the theca. Close examination of ambulacral features indicates that minor differences in characters of the side plates, transverse ridges, and hydrospire pore grooves may aid in recognizing species of different types. Two major types are distinguished, the first (Type 1) consisting of calyces with a nearly flat base in the adult stage *(P. godoni)* (Fig. 208), and the second (Type 2) characterized by calyces with a pyriform outline in the adult stage (Fig. 209). This type includes *P. gemmiformis, P. pyramidatus,* and *P. symmetricus.*

The relatively flat-based Type 1, represented solely by *Pentremites godoni,* includes specimens ranging from about 2 mm. to more than 20 mm. in height. The very small specimens (Fig. 208,*1-3*) are steeply conical, the ambulacra are short and the basals make up a considerable part of the theca. The ambulacra are extremely short and nearly confined to the summit in the tiniest specimens (Fig. 208,*1*). Only seven or eight side plates occur along either margin of an ambulacrum. Much of the summit is occupied by the spiracles, anal opening, and mouth. With increase in size, the ambulacra lengthen progressively. In larger specimens, three trends in shape are distinguishable, the first (Subtype 1a) including individuals with nearly equidimensional calyces, with height of theca approximately the same as width (Fig. 208,*4-9*), another (Subtype 1b) represented by specimens having calyces which become increasingly slender, with height greater than width (Fig. 208,*10-14*), and a third (Subtype 1c) characterized by calyces which are wider than high (Fig. 208,*15-19*). All three subtypes may be presumed to develop from juveniles which in most diminutive examples show steep-sided conical form (Fig. 208,*1-3*).

Species of *Pentremites* with pyriform adult calyces, grouped in Type 2, include *P. symmetricus, P. pyramidatus,* and *P. gemmiformis.* Very small individuals presumed to represent the same species are essentially similar in shape and size to representatives of Type 1. The pyriform thecal shape of the diminutive calyces persists, however, in larger specimens, among which three different trends are discernible. In one group (Subtype 2a) the theca becomes more slender and the ambulacra ex-

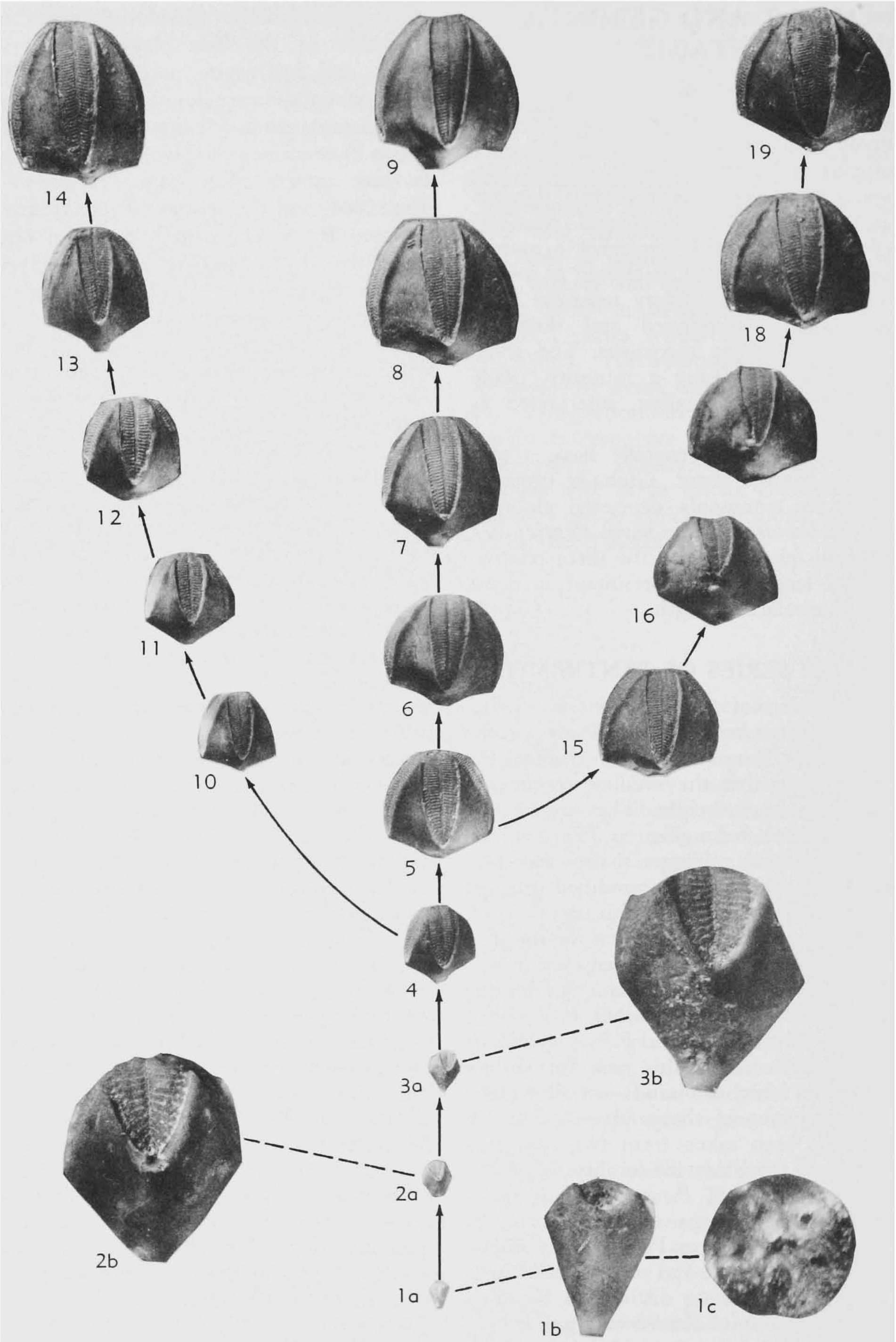

FIG. 208. Growth series of relatively flat-based *Pentremites* calyces (Type 1) represented by *P. godoni* (DEFRANCE), Paint Creek F. (Chester.), near Floraville, Illinois; Subtype 1a, equidimensional, *1-9*; Subtype 1b, slender, *10-14*; Subtype 1c, broad, *15-19*; all figures ×1 except as indicated (Beaver, n).

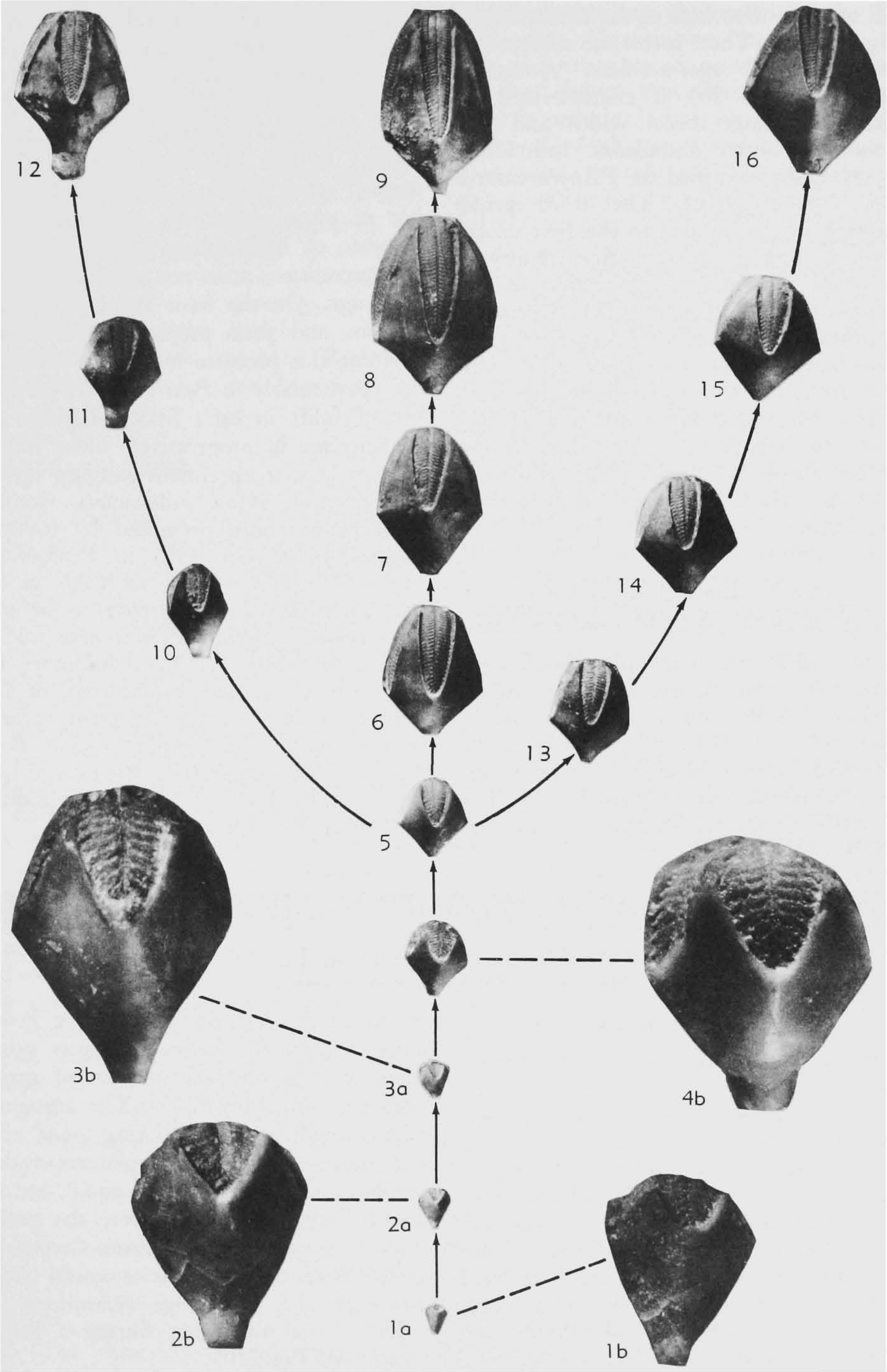

Fig. 209. Growth series of pyriform *Pentremites* calyces (Type 2), all from Paint Creek F. (Chester), near Floraville, Illinois; Subtype 2a, *P. symmetricus* Hall, *6-9*; Subtype 2b, *P. gemmiformis* Hambach, *10-12*; Subtype 2c, *P. pyramidatus* Ulrich, *?13,14-16*; all figures ×1 except as indicated (Beaver, n).

tend to more than half of the thecal height (Fig. 209,*6-9*). These forms are customarily identified as *P. symmetricus.* A second group (Subtype 2b) is characterized by somewhat greater thecal width and proportionally shorter ambulacra. Individuals are generally identified as *P. pyramidatus* (Fig. 209,*?13, 14-16*). The third group (Subtype 2c) is similar to the first except for thickening of the aboral extremity of the theca, seemingly by accretion of secondary calcite (Fig. 209,*10-12*). Specimens with these characteristics are assigned to *P. gemmiformis.* The possibility that adult pyriform calyces of Type 2, generally interpreted to represent these different species, actually belong to a single species having variable shape and ambulacral length or thickened aboral extremity needs further investigation.

CHANGES IN THECAL ELEMENTS WITH GROWTH

It is well known that with growth some thecal and brachiole elements increase in number, whereas other elements simply become larger. Major plates, such as the basals, radials, and deltoids, increase in size with age, as indicated by growth lines. The ambulacra, however, increase in size by adding side and outer side plates at the aboral tips of the ambulacra. These plates are accompanied, of course, by additional brachioles and auxiliary elements such as ambulacral and brachiole cover plates. Additions to the ambulacral system during growth result in the extremely large number of plates previously mentioned. The number of hydrospires, contrary to some interpretations, does not seem to increase with age. On the basis of numerous thin sections and peels prepared specifically to examine this problem in a number of genera (particularly in *Pentremites*), the number of folds in each hydrospiralium does not increase in progressively older individuals, at least in specimens ranging upward in size from a few millimeters. Contrary evidence has been presented by Joysey & Breimer (1963, p. 481) in *Pentablastus,* where a specimen with six folds in each hydrospiralium is interpreted to be older than another individual with five folds in each hydrospiralium. This difference may be due to unlike age, as inferred, or alternatively, it may merely represent variation in the number of hydrospires in *Pentablastus.* The examination of a large number of individuals of all ages is required to answer this question.

DEVELOPMENT AND HYDRODYNAMICS OF BLASTOIDS

By Donald B. Macurda, Jr.
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DEVELOPMENT

The skeleton of living echinoderms is an endoskeleton, secreted by mesodermal tissue. The microstructure of this skeleton was likened to the open girderwork of a modern skyscraper by Nichols (1962, p. 93). By analogy with Recent echinoderms, the calcite of the blastoid skeleton was also formed by the mesoderm. Growth lines are commonly preserved on outer surfaces of the principal calyx plates (Fig. 210). Growth was accretionary and episodic, occurring in a lateral direction, although occasional secondary deposits are found covering the origins of the plates.

The tissue which secreted the calcite lay between opposing plate edges. The width of the calcite laid down during a growth increment on the plate edge was usually small, with a multiple number of growth lines per mm. (Fig. 210). The amount of calcite deposited on opposing plate edges within the same series of plates (as along the interradial suture) was equal, but differential rates of growth were the general rule along radiodeltoid sutures. Commonly, several times as much calcite would be laid down on one plate edge (commonly the radial) as on the other during a growth increment (Fig. 210).

The microstructure of the calcite in blastoid plates is usually destroyed by recrystallization, but plates belonging to *Rhopaloblastus* from the Permian of Western

Australia have a reticulate pattern (Fig. 210) suggestive of the calcite latticework of modern echinoderms. The calcite of the external surface has a fenestrate appearance, with the long axes or ribs very closely spaced and arrayed perpendicular to edges of the plates along which growth occurred. A very sharp divergence of the long axes is observed at the intersection of adjacent growth fronts. The cross bars connecting long axes are as wide as the axes; the fenestrules or openings are approximately rectangular and are not as wide as the ribs of the crossbars. They are evenly spaced. Internal and lateral edges have a very fenestrate appearance. Secondary calcite has filled in the open spaces in the lattice and appears as clear blebs of calcite.

Growth lines are preserved only on the external surface. Nissen (1963) has presented data suggesting that the calcite of an echinoid plate is a composite of tiny crystal units, with the c-axes oriented in the same direction. Each individual plate of a blastoid behaves optically as one crystallographic unit. The maximum size for one plate may be several tens of millimeters, a large size for an individual crystal. The latticework of the blastoid skeleton may have consisted of many individual fibers similar to those found in echinoids, which were added onto the lattice during each growth increment, and then subsequently recrystallized to form an individual crystal. It is unclear why growth lines are only reflected externally.

The growth lines preserved on the external surfaces of the plates record the complete postmetamorphic development of the blastoid. The principal plate of the calyx is the radial, which usually has six edges. The growth lines converge toward the origin of the radial which is at the aboral end of the ambulacrum. The radial has grown outward in three primary directions perpendicular to the sutures along which calcite was added (growth fronts) (Fig. 211). Each axis and front has a complement on the opposite side of the radial. The direction of growth toward the radiodeltoid suture is designated the *RD* axis, that toward the interradial suture the *RR* axis, and that toward the radial basal suture, the *RB* axis (Fig. 211). Growth fronts are designated as the *RD* front, etc. Quantitative analysis of the rates and amounts of growth along these axes has shown that development of the radial is orderly, indicating a close genetic control. Growth curves can be constructed by plotting growth axes against one another to show the ontogenetic development of the plate (Fig. 212,*2*). Most growth curves are isometric, there being little change in rates relative to one another. When the amount of growth along an axis is plotted against the width of the growth front for an ontogenetic series, a well-ordered pattern is found (Fig. 212,*1*). An ontogenetic study of *Orophocrinus* (Macurda, 1965, 107; 1966, 109) showed that quantitative measurements of growth axes and fronts were useful and discriminatory taxonomic characters and permitted greater insight into blastoid development, morphology, and physiology.

Quantitative analysis of the development of the radial in genera other than *Orophocrinus* has shown that the development is almost always isometric as well. The amount of calcite added along a growth front during one increment is almost constant throughout the entire ontogenetic history of the individual from a neanic to a gerontic stage. The development was thus under close genetic control. The length of a growth axis provides a time character by which the relative level of development of different individuals can be compared. The *RR* axis was used in the study of *Orophocrinus* previously cited (Macurda, 1965, 107; 1966, 109); study of other genera suggests that the sum of the *RD, RR,* and *RB* axes for an individual is a better time character.

Analysis to date has treated the growth axes as two-dimensional parameters, i.e., as though they were all arrayed in one plane. The radial plates of blastoids have many different shapes as a result of growth along the sutures (Fig. 213,*1-3,7*). It will be necessary to array the axes in a three-dimensional matrix to realize the full potential of ontogenetic analysis and specific differentiation. The lengths of the axes of two plates may be very similar, but the directions of growth of these in a third dimension may result in a globular form such as *Orbitremites* or *Globoblastus,* or

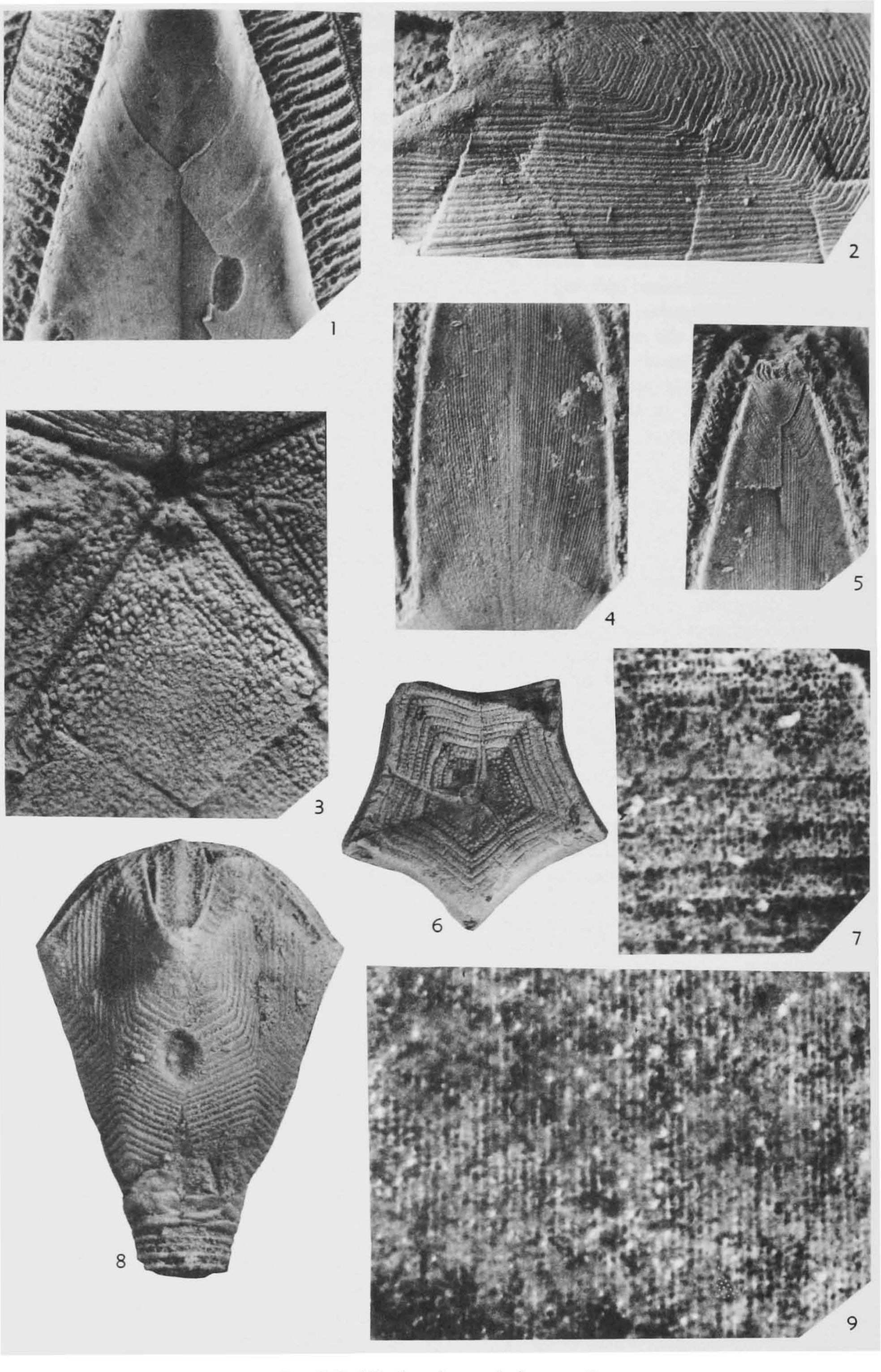

FIG. 210. [*Explanation on facing page.*]

produce a very angular form, as *Hadroblastus* or *Codaster.*

The origin of the radial is commonly obscured by secondary deposits of calcite (Fig. 213,*5-6*). These secondary deposits may result from the more intensive physiological activity which took place at the aboral end of the ambulacrum where new side plates were formed. Some blastoids utilized the ability to secrete this extra calcite to form a prong on the radial (Fig. 213,*4*), by which the length of the ambulacrum could be extended and the food-gathering capacity multiplied without effecting a change in the shape of the calyx. This evolutionary experiment occurred several times, as in the Mississippian genus *Dentiblastus* and the Permian *Thaumatoblastus.*

The basals of a blastoid are usually small in relation to the radials. Most show two primary directions of growth, toward the radial-basal (*BR* axis) and interbasal sutures (*BB* axis) (Fig. 214,*11*). The rate of growth along the *BR* axis is usually several times that of the *BB* axis; the origin of the basal is located near the distal end .of the plate.

The rate of growth of the *BR* axis of the basal is usually about equal to the *RB* axis of the radial, one half of the pelvis being formed by the basals, one half by the radials (Fig. 214,*1*). In a few genera with a narrow, conical pelvis, the area available for basal growth is unconfined, not being restricted by the radials in globose genera such as *Mesoblastus* or *Cryptoblastus,* and the rate of growth on *BR* may be several times that of *RB* as in *Belocrinus* (Fig. 214,*11*).

The stem was attached to the distal ends of the three basals. The mass and volume of the calyx increased throughout the ontogenetic development of the organism. If the original growth pattern of the basals was maintained without any modification, the attachment of the calyx to the stem would be highly unstable. It would consist of three points resting on a cylinder (Fig. 212,*3*). Therefore, the configuration of the plate had to be modified. In most genera this was accomplished by the secretion of a secondary deposit over the origin of the basal, thus modifying the three points to a cylinder (Fig. 212,*4*; 214,*3-4,7,9*). The secondary deposits increased during development. An alternative mechanism was adopted by some genera, as *Phaenoschisma* and *Rhopaloblastus,* with long, narrow basals. There is a third growth axis (the *BA* axis), directed toward the stem attachment area, which maintained the flat circular attachment area at the base of the calyx (Fig. 214,*10*).

The entire calyx and thus the weight of the blastoid were supported by a cylindrical, jointed stem in its aqueous environment. As the surface area of the plates increased, the weight of the organism would multiply at an increasingly accelerating rate, since it is a function of the volume (V^3). The cross-sectional area of the stem attachment in ephebic individuals was apparently insufficient for support of neanic or gerontic individuals, for the diameter of the crenellar ring (Fig. 214,7) and thus the effective cross-sectional area of the stem-calyx joint increased throughout ontogenetic development of the individual. In

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[*See facing page*]

FIG. 210. Plate growth in blastoids.

1. Growth lines of radials and deltoid in interambulacral area of *Pentremites godoni* DEFRANCE, U.Miss., USA(Ill.), ×7.5 (Macurda, n).

2. Growth lines in interradial and radial-basal sectors of radial of *Rhopaloblastus belfordi* (CROCKFORD & BROWN), Perm., Australia, ×7.5 (Macurda, n).

3. Growth lines of deltoid, paralleling radial-deltoid and interdeltoid sutures in *Indoblastus granulatus* WANNER, Perm., Timor, ×6 (Macurda, n).

4. Growth lines in interambulacral area of *Hyperoblastus filosus* (WHITEAVES), reflecting accelerated growth along radial-deltoid axis, Dev., Can.(Ont.), ×7.5 (Macurda, n).

5. Opposing growth lines of radial and deltoid reflecting faster growth on radial, in *Hyperoblastus filosus* (WHITEAVES), Dev., Can.(Ont.), ×7.5 (Macurda, n).

6. Growth lines of basals in *Timoroblastus coronatus* WANNER, Perm., Timor, ×2 (Macurda, n).

7. Fenestrate structure of calcite in interradial sector (7) and radial-basal sector (9) of radial of *Rhopaloblastus belfordi* (CROCKFORD & BROWN), plate edge toward bottom of figure, Perm., Australia, ×38 (Macurda, n).

8. Opposing growth lines of radials and basals in *Orophocrinus conicus* (WACHSMUTH & SPRINGER), L.Miss., USA(Iowa), ×6 (107).

Fig. 211. Growth axes and fronts of radial plate in *Belocrinus cottaldi* (Munier-Chalmas), Dev., Fr., ×8 (Macurda, n).

Orophocrinus, new stem plates apparently were added at the junction of the calyx and stem, starting to form initially in a small depression of the basals, then being moved into position and completed. Once formed, the size of the plate was apparently fixed, for the height of stem plates is constant throughout the stem and if the diameter was to be increased, it would involve resorption of the crenellar ring which is part of an interlocking projection and depression between plates in *Orophocrinus* (Fig. 214,*5-6*). The diameter of stem plates decreases gradually down the column. By increasing the cross-sectional area of the stem-attachment area, greater stability would be provided against fluctuations in wave or current energy in the environment. A similar pattern can be found in other stemmed echinoderms, as the crinoid *Neoplatycrinus* and the cystoid *Strobilocystites,* as the area to which the stem was attached increased during ontogeny. Some genera (e.g., *Globoblastus, Orbiblastus, Deltoblastus*) developed a concave base (Fig. 214,*8*), which would shield the stem-attachment area and buffer it against energy fluctuations. Other genera (e.g., *Eleutherocrinus, Dipteroblastus*) completely lost their stem and adopted a free-living life mode (Fig. 214,*2*). The growth pattern of the basals and radials has been altered by adoption of a bilateral symmetry characteristic of organisms with a nonattached mode of life.

The deltoids which surrounded the mouth had complex growth patterns because of the bordering peristome, entrances to hydrospires, presence of food grooves, and the hydrospires themselves (Fig. 215, *2-3*). The adoralmost edge of the deltoid borders the peristome. The adoral lateral edges bear the adoral ends of the main food grooves. The aboral lateral edges are usually bordered by ambulacra; an entrance to the hydrospires is usually present on the median lateral edge of most spiraculate genera. The aboral edge of the plate abuts against the adoral edges of two adjacent radial limbs. When first formed, the adoral portion of the plate is quite large in relation to the aboral part (Fig. 212,*5*). After metamorphosis, the space around the peristome had to be filled by five plates. This meant rapid development of the adoral portion of the plate. After an individual has reached 3 to 4 mm. in length and width, most development is directed in an aboral direction (the *DR* axis). Calcite is secreted along the radiodeltoid suture; the rate of growth of the *DR* axis is usually several times less than that of the opposing *RD* axis. Each deltoid normally bears the adoral ends of two groups of hydrospires, which hang as pendant-like folds into the visceral cavity. The two groups of hydrospires are normally separated at their adoral ends (Fig. 215,*1*). This separation may reflect the initial size of the plate or reflect the formation of hydrospires when the deltoid reached a particular size. When calcite was added to the radials and deltoids along the radiodeltoid suture, it was also added to the hydrospires; their length increased throughout the ontogenetic development of the individual. Their greatest height is at the radiodeltoid suture (Fig. 215,*5*); this increases with age. The radiodeltoid suture can be traced across the hydrospires. Once formed, the number of hydrospires per group was usually constant throughout the ontogenetic development of the individual. However, in some fissiculate genera, the hydrospires occupy the entire width of the *RD* and *DR* growth fronts, each hydrospire exiting individually to the exterior (Fig. 215). As the blastoid grew, the number of hydrospires in these genera (e.g., *Codaster, Hadroblastus, Notoblastus*) increased, to a maximum number of 60 on one edge of a radial of *Hadroblastus.*

In spiraculate genera there are pores along the margins of the ambulacra. In some genera (e.g., *Cryptoblastus, Globoblastus, Mesoblastus*) the pores pierce the solid calcite of the radials (Fig. 216,*3-4*). New pores were formed when new calcite was added along the radiodeltoid suture. In other genera (e.g., *Cordyloblastus, Lophoblastus, Pentremites, Rhopaloblastus, Schizoblastus*), the pores are formed as a gap between the edges of the side plates and adjacent radials and deltoids (Fig. 217,*4-5*). These pores were formed at the same time that new ambulacral plates were added at the aboral end of the ambulacrum. In *Cordyloblastus* and *Rhopaloblastus,* new calcite was eventually added which filled in the adoral or earliest-formed pores; they are thus absent along part or all of the

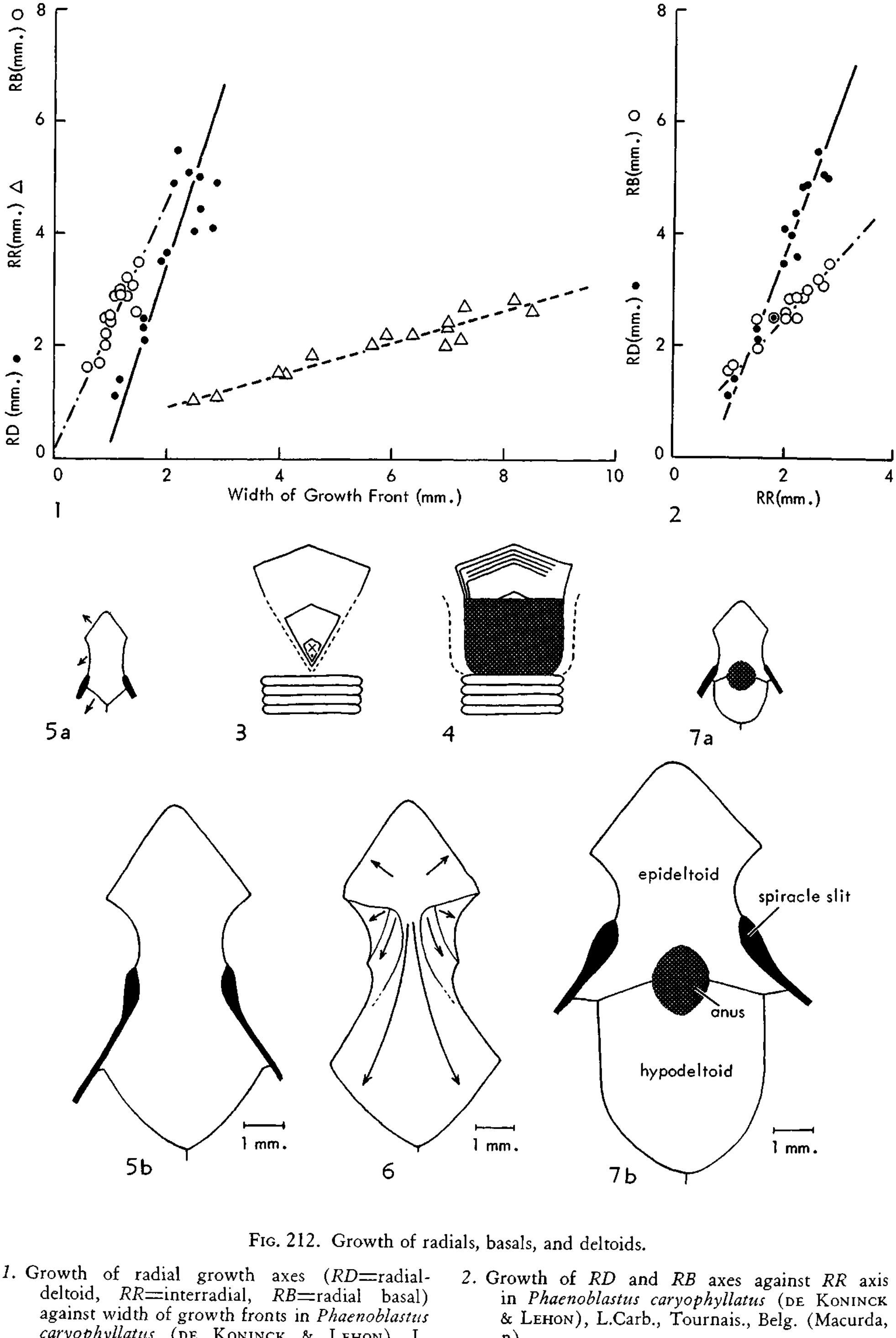

Fig. 212. Growth of radials, basals, and deltoids.

1. Growth of radial growth axes (*RD*=radial-deltoid, *RR*=interradial, *RB*=radial basal) against width of growth fronts in *Phaenoblastus caryophyllatus* (de Koninck & Lehon), L. Carb., Tournais., Belg. (Macurda, n).

2. Growth of *RD* and *RB* axes against *RR* axis in *Phaenoblastus caryophyllatus* (de Koninck & Lehon), L.Carb., Tournais., Belg. (Macurda, n).

deltoid. In large specimens of *Schizoblastus,* the pores in the middle of the ambulacra were eventually sealed off.

New calcite was also added along the adoral edges of the deltoid in some genera (*DD* axis) (Fig. 212,*6*). As a consequence,

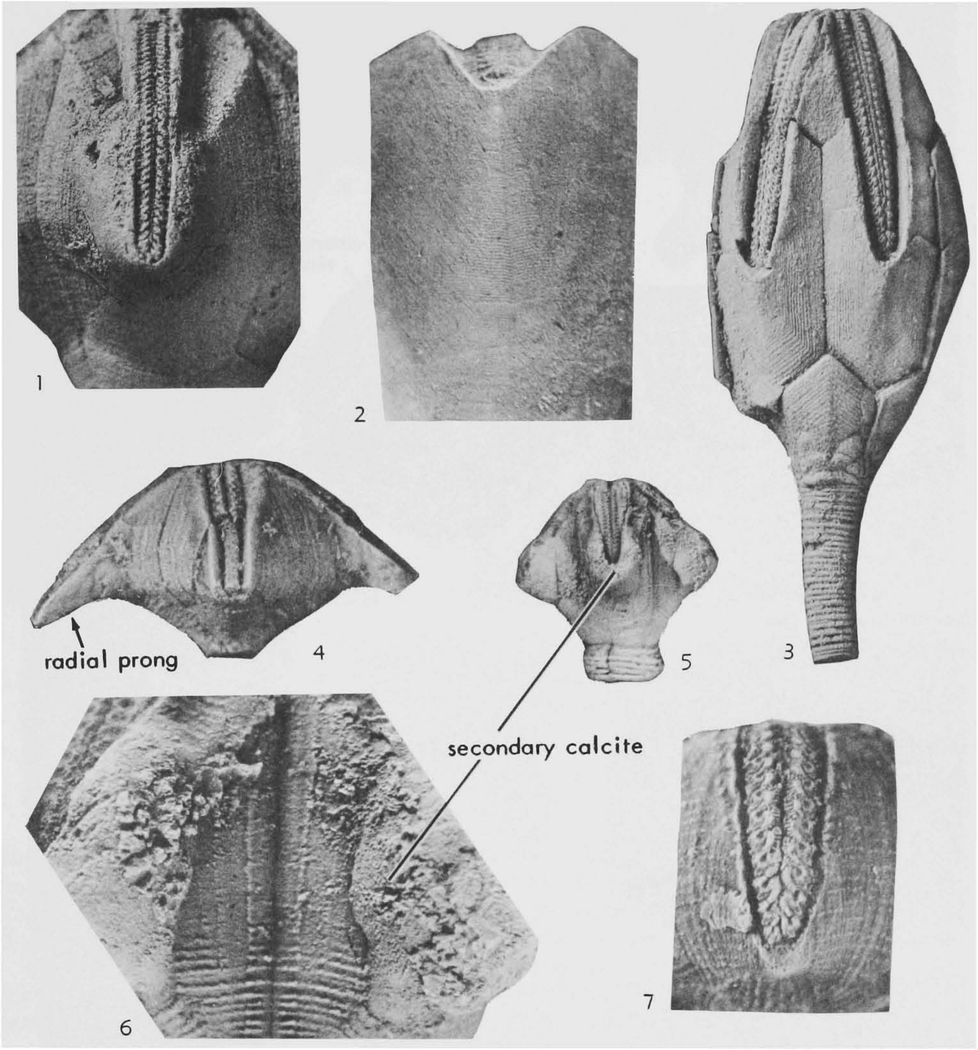

FIG. 213. Growth patterns of radials and secondary calcite deposits.

1. Orophocrinus stelliformis (OWEN & SHUMARD), L.Miss., USA(Iowa), ×3 (108).

2. Heteroschisma canadense (BILLINGS), Dev., Can. (Ont.), ×7.5 (Macurda, n).

3. Pyramiblastus fusiformis (WACHSMUTH & SPRINGER), L.Miss., USA(Iowa), ×3 (104).

4. Dentiblastus sirius (WHITE), L.Miss., USA(Mo.), ×6 (102).

5-6. Orophocrinus stelliformis (OWEN & SHUMARD), L.Miss., USA(Mo.), *5,* ×2 (109), *6,* ×7.5 (Macurda, n).

7. Monadoblastus crenulatus (ROEMER), L.Carb., Tournais., Belg., ×7.5 (Macurda, n).

FIG. 212. *(Continued.)*

3-4. Growth of basals of *Orophocrinus stelliformis* (OWEN & SHUMARD) and secondary overgrowth (x marks origin) (109).

5-7. Growth of deltoids of *Orophocrinus stelliformis* (OWEN & SHUMARD) showing growth of small plate to maturity and growth axes of plate (109) (*5a, 7a,* youthful phases).

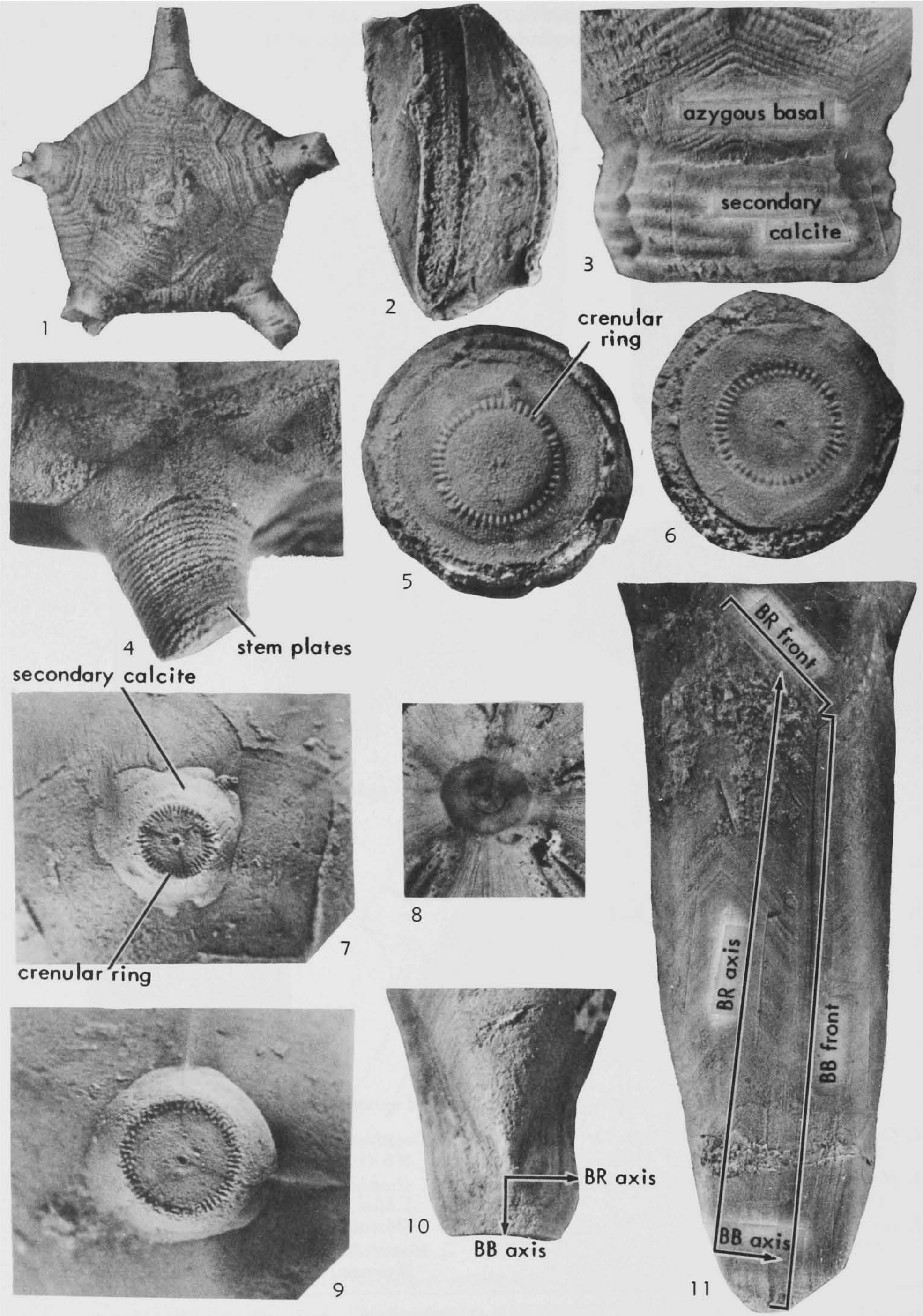

FIG. 214. Growth of basal and stem plates. *(Continued on facing page.)*

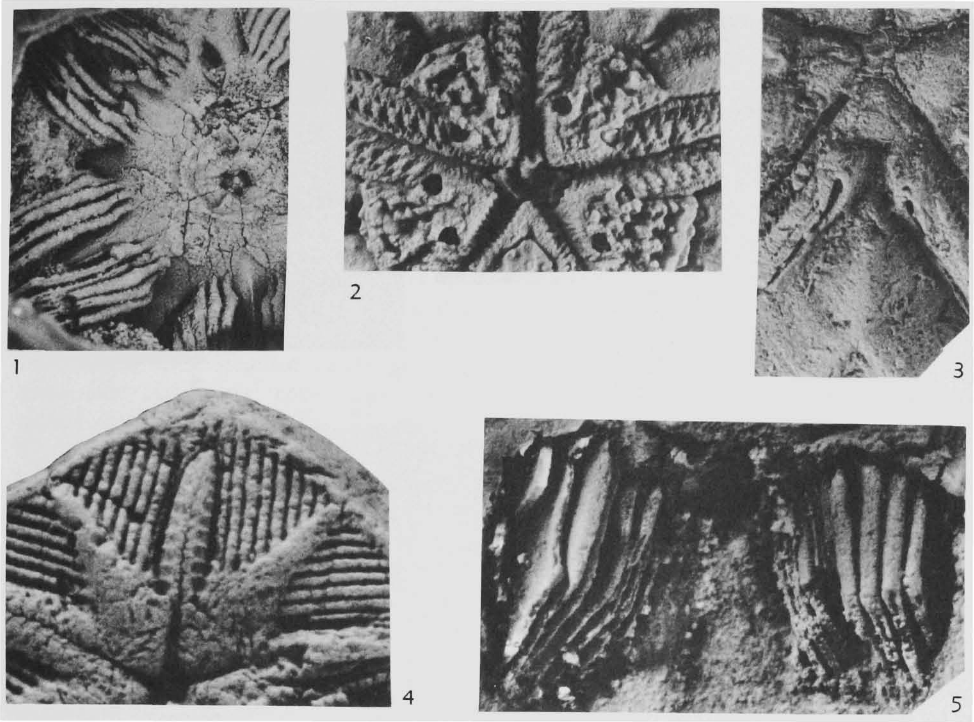

FIG. 215. Deltoids and hydrospires.

1. Internal view of hydrospires of *Orophocrinus stelliformis* (OWEN & SHUMARD), L.Miss., USA (Iowa), ×2 (109).

2. Deltoids of *Cryptoblastus melo* (OWEN & SHUMARD), L.Miss., USA(Ill.), ×7.5 (Macurda, n).

3. Deltoid of *Orophocrinus stelliformis* (OWEN & SHUMARD), L.Miss., USA(Iowa), ×4 (109).

4. Hydrospire slits of *Codaster acutus* M'COY, L. Carb., Eng., ×6.5 (Macurda, n).

5. Hydrospires of *Orophocrinus stelliformis* (OWEN & SHUMARD), L.Miss., USA(Iowa), ×7.5 (109).

the food groove was constantly being reformed. If no calcite was added on the free edge bordering the peristome, then the latter's area increased with age.

The adoral openings to the hydrospires, either as spiracles, or spiracle slits, may undergo little ontogenetic modification or may migrate, as in *Orophocrinus* (Fig. 212,*6*; 217,*6*). Spiracles of *Globoblastus* are single openings which pierce the calcite of the deltoid (see Fig. 219). They increased in diameter with age, which implies resorption.

The development of the anal deltoids

[*Continued from facing page*]

1. *Dentiblastus sirius* (WHITE), L.Miss., USA(Mo.), ×6 (102).

2. *Eleutherocrinus cassedayi* SHUMARD & YANDELL, Dev., Can.(Ont.), ×3 (Macurda, n).

3. *Orophocrinus stelliformis* (OWEN & SHUMARD), L.Miss., USA(Mo.), ×7.5 (Macurda, n).

4. *Pentremites* sp., U.Miss., USA(Tenn.), ×7.5 (Macurda, n).

5-6. Stem plates of *Orophocrinus stelliformis* (OWEN & SHUMARD), L.Miss., USA(Ill.), ×7.5 (109).

7-9. *Pentremites godoni* DEFRANCE, U.Miss., USA (Ill.), ×7.5 (Macurda, n).

8. *Orbiblastus hoskynae* MACURDA, L.Miss., USA (Ark.), ×2 (106).

10. *Rhopaloblastus belfordi* (CROCKFORD & BROWN), Perm., Australia, ×7.5(Macurda, n). [For BR read BB, and for BB read BA.]

11. *Belocrinus cottaldi* (MUNIER-CHALMAS), Dev., Fr., ×4 (Macurda, n).

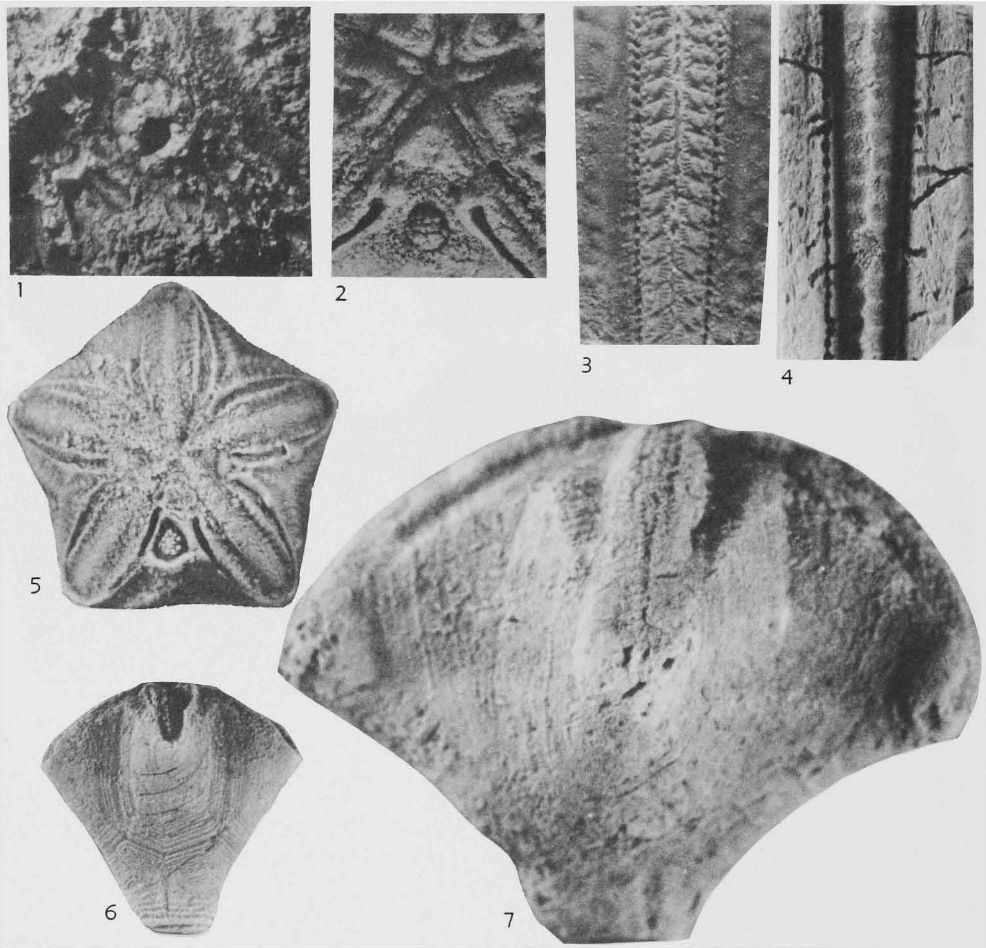

Fig. 216. Cover plates, hydrospire pores, and ontogenetic change in calyx shape.

1. Anal pyramid of *Orophocrinus stelliformis* (Owen & Shumard), L.Miss., USA(Mo.), ×7.5 (109).

2. Oral and anal cover plates of *O. stelliformis* (Owen & Shumard), L.Miss., USA(Iowa), ×6 (109).

3. Hydrospire pores of *Cryptoblastus melo* (Owen & Shumard), L.Miss., USA(Ill.), ×7.5 (Macurda, n).

4. Hydrospire pores of *Globoblastus norwoodi* (Owen & Shumard), L.Miss., USA(Mo.), ×7.5 (Macurda, n).

5. Oral, ambulacral, and anal cover plates of *Orophocrinus conicus* Wachsmuth & Springer, L.Miss., USA(Iowa), ×6 (107).

6-7. Ontogenetic change in calyx shape of *Orophocrinus stelliformis* (Owen & Shumard), L. Miss., USA(Mo.), ×3 (Macurda, n).

parallels that of the regular deltoids. The presence of multiple anal deltoids allowed the size of the anal opening to increase with growth. The development of the adoral part of an epideltoid is identical to a regular deltoid; if hydrospires were present, their length increased by the addition of calcite along the epiradial suture. The anus embays the aboral edge of the epideltoid in *Orophocrinus*; it migrated aborally as the epideltoid increased in size (Fig. 212,*7*). The hypodeltoid also migrated aborally from the mouth, increasing in size by the addition of calcite along the edges, the rate being faster along the hyporadial suture. Secondary calcite was deposited on the hypodeltoid of *Orophocrinus* to form a ramp to guide the anus when it was extended (Fig. 217,*10*). Little is known about the ontogenetic development of other types of anal deltoids. Cryptodeltoids apparently increased in length by the addition of calcite along the cryptoradial suture.

The ambulacra are composed of a central lancet plate which extends the full length of the ambulacrum, side and outer side plates which rest upon the lancet and in many genera completely conceal it, brachioles which were attached to the side and outer side plates, and cover plates which roofed the food grooves (Fig. 216,*2,5*; 217,*8*). Commonly an ambulacrum is partially or completely surrounded by a radial and two deltoids. The only way it could increase in length was by growth along the margins of the principal calyx plates; this created free space into which the ambulacrum could then grow. New additions of side plates and outer side plates occurred at the aboral end of the ambulacrum. Shortly after its formation, the size of a side plate and the outer side plate were stabilized. The brachiolar facet thus had a constant dimension. No new calcite was added between side plates insofar as is known, but calcite may have been added on the admedial edges of side plates, as in *Orophocrinus* (Fig. 217,*3*). Side plates shifted adorally with respect to topographic points on the radial during development.

The growth of the lancet is not fully understood, apparently varying somewhat between genera. New calcite was added at the aboral end in all genera, increasing the length. In some genera (e.g., *Orophocrinus*), the main food groove is initially borne by the admedial edges of the side plates but as development proceeded, the main food groove migrated to the lancet (Fig. 217,*9*). The lancet thus also grew upward and side plates were shifted laterally. The main food groove on the side plates was apparently filled in but the admedial edge of these plates did not expand. In *Orophocrinus* the lancet also increased in width. The cross section is rhombic and new calcite was apparently added to the rhombic faces. In other genera (e.g., *Pentremites*) the main food groove is borne by the lancet from the offset. The plate is more rectangular in cross-section. No new calcite was added to the upper surface but lateral growth did occur, resulting in the side plates being laterally displaced; the side food grooves thus increased in length (Fig. 217,*5*). In still other genera where the lancet is completely concealed by the side plates, as in *Pentremitidea,* the lancet must increase in length but further detail is unknown. Further investigation of the patterns of development of this plate are needed.

The side and main food grooves are roofed by a series of ambulacral cover plates (Fig. 216,*5*; 217,*2*). These are seldom preserved. In *Orophocrinus,* polygonal plates covering the peristome are the largest cover plates (Fig. 217,*7*). When a peristome increased in size, the cover plates would also have to increase. The length of the main food groove borne by the deltoids increased in length during the ontogenetic development of *Orophocrinus.* In small specimens, there are usually four cover plates which roof over the width of the food groove. As the groove increased in length, the plates were reorganized; this proceeded aborally. They increased in size and only a pair ultimately covered the food groove. Thus, by increasing the cover plates in size and shifting them aborally, the increasing length of the groove was accommodated without forming new plates. New cover plates on the ambulacrum proper were formed at the same time as new side plates and brachioles were added at the aboral end of the ambulacrum. There was no shifting of these relative to the side plates in *Orophocrinus.* Since the length of the side food grooves increased in *Pentremites,* the cover plates of these grooves would either have to undergo reorganization or growth (or both) or new ones would have been added.

The growth of brachioles is poorly understood. The largest plates are located at or near the bottom and they decrease in size upward, as in *Pyramiblastus* (Fig. 217,*8*). The size of the lower plates was stabilized very shortly after the addition of the brachiole to the ambulacra. This may imply very rapid initial growth with a constant length thereafter. Since the brachioles are biserial and the centers are offset, one edge

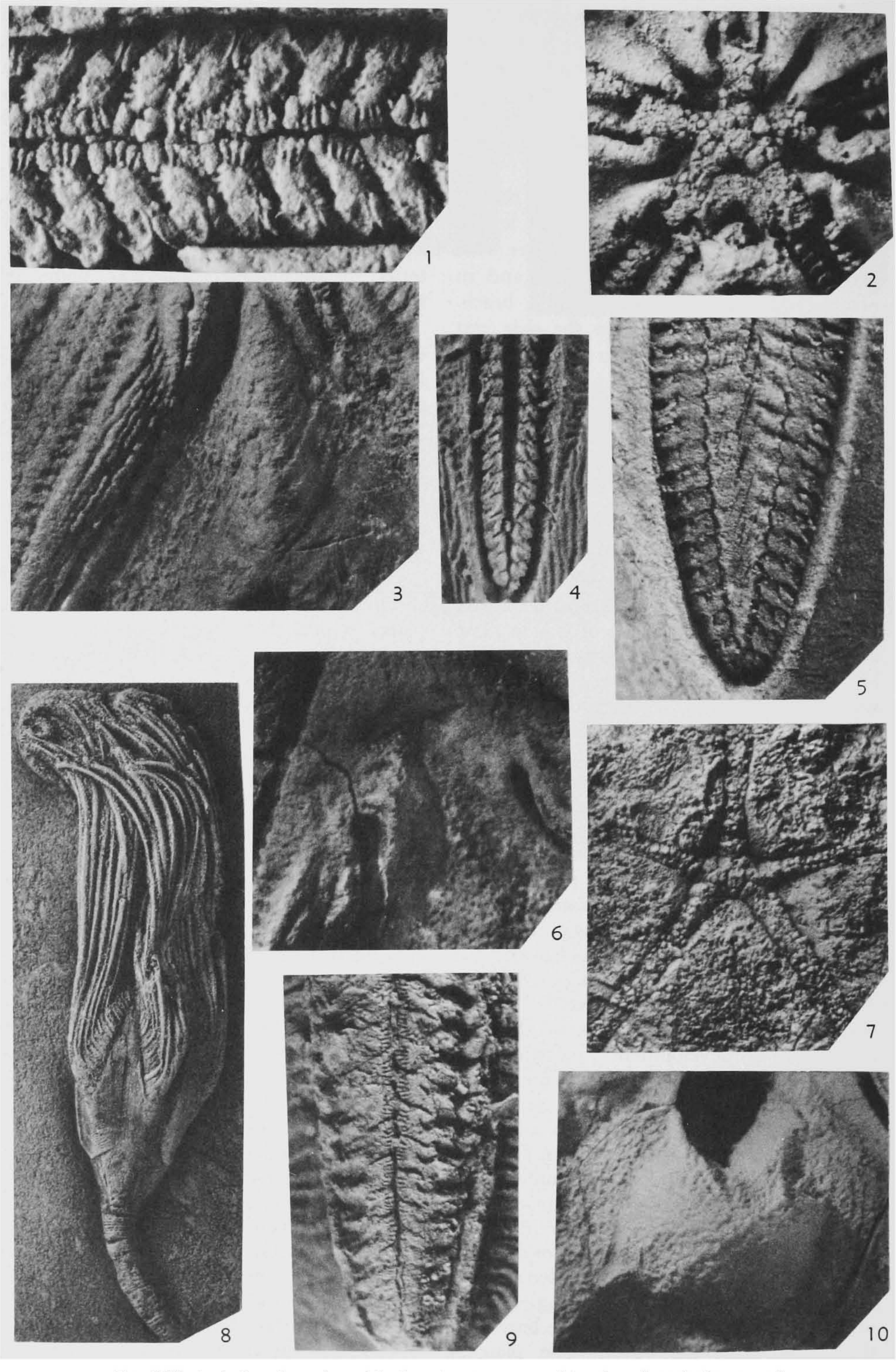

FIG. 217. Ambulacral, anal, and hydrospire structures. *(Continued on facing page.)*

of the brachiolar facet was set lower than the other to permit their attachment to the side and outer side plates (Fig. 217,*1*).

The curves of most growth axes are linear. Only a few instances of nonlinear development are known, as in *Orophocrinus stelliformis* (Fig. 218). In this species, the *RB* axis slowed down with growth and the *RD* accelerated. As a result, the space available for ambulacral development increased (and thus the food-gathering capacity) at an increasingly faster rate. This change is reflected in the change of shape of the calyx with development (Fig. 216, *6-7*).

HYDRODYNAMICS

The visceral mass of a blastoid was completely isolated and protected from the outside environment by the calcareous endoskeleton. Blastoids were passive feeders and some kind of propulsive mechanism was necessary to convey food particles captured by the brachioles through the tunnels of the ambulacral system to the peristome. In Recent echinoderms this is accomplished by ciliary action. The hydrospires of blastoids are apparently rigid structures, as their shape is constant from specimen to specimen in the same species. Their only means of communication with the exterior is through a series of pores, slits, or spiracles. The function of hydrospires is not clear, but a respiratory or reproductive function, or both, are those commonly suggested. If they served a respiratory or reproductive function, it would be necessary to move a water mass through the hydrospires. Ciliary action might provide a mechanism for doing so. Since both the hydrospires and food-gathering-ambulacral-alimentary canal-anal system involve water transport through enclosed passages, the laws of hydrodynamics are involved. Functionally, a blastoid would probably be better adapted to its environment if various structures evolved to an optimum hydrodynamic configuration.

In spiraculate blastoids, the circulation system in the hydrospires was a two-way affair. Spiracles provided one entrance or exit, ambulacral pores the other. The flow pattern was apparently in through the pores and out through the spiracles (Fig. 219,*7*). Evidence for this is twofold: pore furrows and spiracle and anispiracle cover plates. In most spiraculate blastoids, a pore furrow (Fig. 219,*2*) leads to the entrance of each pore. The function of this structure is not clear but its troughlike nature, even though usually vertical in a living animal, is suggestive of a guide for currents. In some spiraculate blastoids the anal spiracles are combined with the anus to form an anispiracle. If water currents entered the hydrospires through an anispiracle, there would have been a danger of fecal material fouling the hydrospires. With water entering the hydrospires through the pores and exiting from the anispiracle, fecal matter would be carried away from the calyx. In *Pentremites,* the spiracles were closed by a series of toothlike plates (Fig. 219,*3*). This is the only genus known with spiracle cover plates. They may have been present in other genera but not preserved. In some specimens of *Globoblastus,* the adoral edge of the spiracle was formed by oral cover plates, whereas usually it is formed completely by deltoid material

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[*Explanation of Fig. 217, continued*]

1. Brachiolar facets and food grooves, *Rhopaloblastus belfordi* (Crockford & Brown), Perm., Australia, ×5 (Macurda, n).

2. Oral cover plates of *Schizoblastus sayi* (Shumard), L.Miss., USA(Ill.), ×7.5 (Macurda, n).

3. Growth lines, admedial edge of side plates and deltoid in *Orophocrinus stelliformis* (Owen & Shumard), L.Miss., USA(Mo.), ×7.5 (109).

4. Pore furrows and hydrospire pores in *Lophoblastus neglectus* (Meek & Worthen), L.Miss., USA(Mo.), ×7.5 (Macurda, n).

5. Lancet and hydrospire pores of *Pentremites* sp., U.Miss., USA(Ill.), ×7.5 (Macurda, n).

6. Growth lines bordering spiracle slits in *Orophocrinus stelliformis* (Owen & Shumard), L. Miss., USA(Ill.), ×7.5 (Macurda, n).

7. Oral cover plates in *O. stelliformis* (Owen & Shumard), L.Miss., USA(Mo.), ×7.5 (109).

8. Brachioles in *Pyramiblastus fusiformis* (Wachsmuth & Springer), L.Miss., USA(Iowa), ×3 (105).

9. Lancet and side plates in *Orophocrinus catactus* (Rowley), L.Miss., USA(N.Mex.), ×7.5 (Macurda, n).

10. Secondary secretion and trough for extension of anus, *Orophocrinus stelliformis* (Owen & Shumard), L.Miss., USA(Iowa), ×7.5 (109).

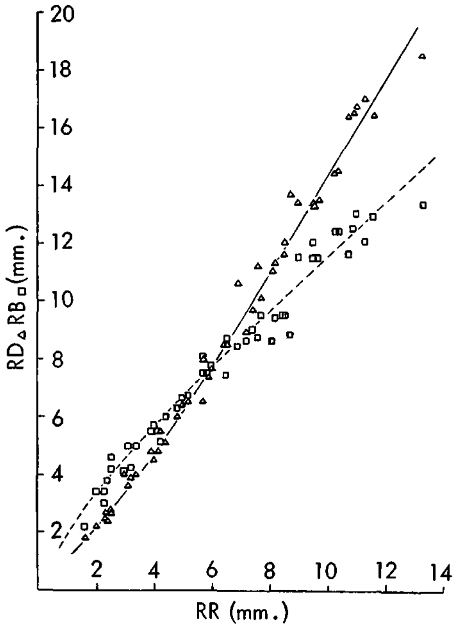

Fig. 218. Growth of *RD* (radial-deltoid) and *RB* (radial-basal) axes of *Orophocrinus stelliformis* (Owen & Shumard) plotted against growth of *RR* (interradial) axis, L.Miss., USA(Iowa-Mo.) (109).

(Fig. 219,*6-7*). Cover plates of the anispiracle are different from spiracle cover plates in *Pentremites,* consisting of rod-shaped elements (Fig. 219,*10*). This probably provided greater ease for anal opening and closing to get rid of fecal wastes.

The circulation in the ambulacral system was fairly complex. Some genera preserve brachiolar cover plates. If these plates were movable, then the brachiolar food groove could be exposed to capture food particles. If they were immobile, an additional brachiolar protoplasmic extension would be required. Once entrapped, food particles would be carried downward to the ambulacrum. The entrance to the side food groove is very small, thus limiting the maximum size of food particles. These particles would then be conducted laterally to the main food groove. The side food grooves are offset from one another and inclined at approximately 45 degrees to the main food groove (Fig. 219,*1*). With this offset, there is a gradual buildup in the volume of water entering the main food groove tunnel, rather than a sudden jump. By having the side food grooves inclined to the main food groove, rather than at right angles, the passage of water from the side to the main food groove was facilitated. If it was at a right angle, there would have been a sharp drop in water velocity where it had to enter the main food groove. Less energy was expended in an inclined configuration. Similar orientations are found in some cystoids, as *Lipsanocystis* and *Strobilocystites.* Once the food entered the main food groove, convection was against the force of gravity in most genera, the ambulacra lying topographically below the peristome which is at the top of the calyx (Fig. 219,*7*). In *Pterotoblastus,* however, the ambulacra are elevated above the mouth (Fig. 219,*5*). In *Orophocrinus,* there are apparently points of attachment for the alimentary canal located on the underside of the deltoids (Fig. 219,*8*). The flow of water through the alimentary canal could have been facilitated by muscular expansions and contractions of the canal. The exit for water in the canal was the anus, which was closed by a series of small polygonal plates and roofed by a small dome (Fig. 216,*1-2*), of rodlike plates (Fig. 219,*10*), or elongated in the form of an anal tube as in *Schizoblastus* (Fig. 219,*4*). Indentations of plates appar-

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[*Explanation of Fig. 219, facing page*]

1. Ambulacrum of *Timoroblastus granulatus* Wanner, Perm., Timor, ×7.5 (Macurda, n).

2. Brachiolar facets, *Pentremites* sp., U.Miss., USA (Ill.), ×7.5 (Macurda, n).

3. Spiracle cover plates of *Pentremites* sp., U.Miss., USA(Tenn.), ×7.5 (Macurda, n).

4. Anal tube of *Schizoblastus sayi* (Shumard), Miss., USA(Mo.), ×7.5 (Macurda, n).

5. *Pterotoblastus gracilis* Wanner, Perm., Timor, ×3 (Macurda, n).

6. Oral cover plates and spiracles of *Globoblastus norwoodi* (Owen & Shumard), Miss., USA (Iowa), ×5.9 (108).

7. Spiracles, *G. norwoodi* (Owen & Shumard), Miss., USA(Iowa), ×6.2.

8. Depressions on undersurface of deltoids around peristome (attachment for alimentary canal?), *Orophocrinus stelliformis* (Owen & Shumard), L.Miss., USA(Iowa), ×6 (107).

9. Facets of anal tube of *Deltoblastus* sp., Perm., Timor, ×7.5 (Macurda, n).

10. Anal and spiracle cover plates of *Pentremites* sp., U.Miss., USA(Tenn.), ×7.5 (Macurda, n).

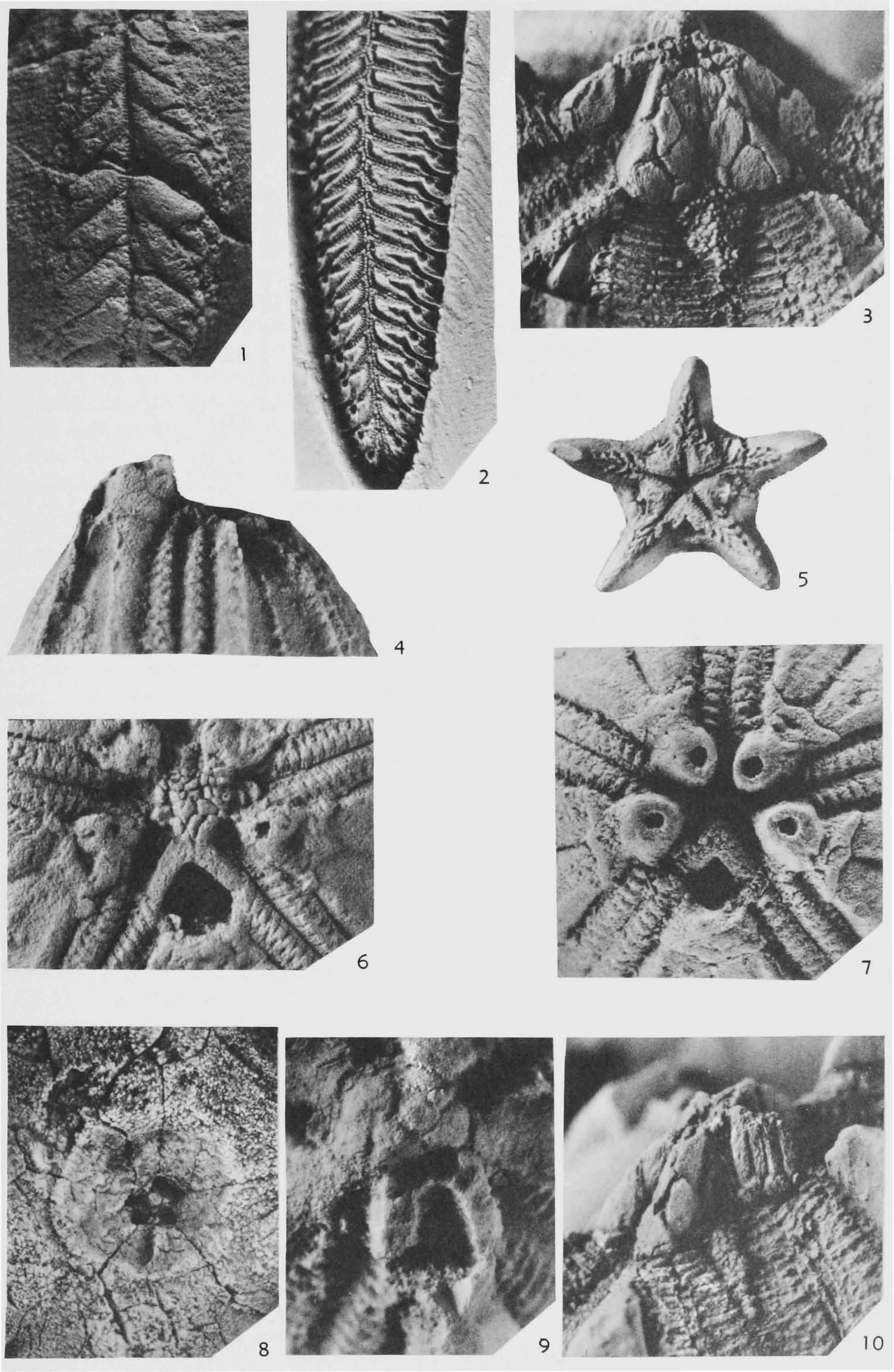

FIG. 219. Ambulacral, oral cover plates, anal, and alimentary canal structures.

ently forming an anal tube are preserved in *Deltoblastus* (Fig 219,9). The presence of an anal tube would further reduce fouling of the brachioles and indicates that the anus was a muscular organ capable of extension and retraction. The cover plates

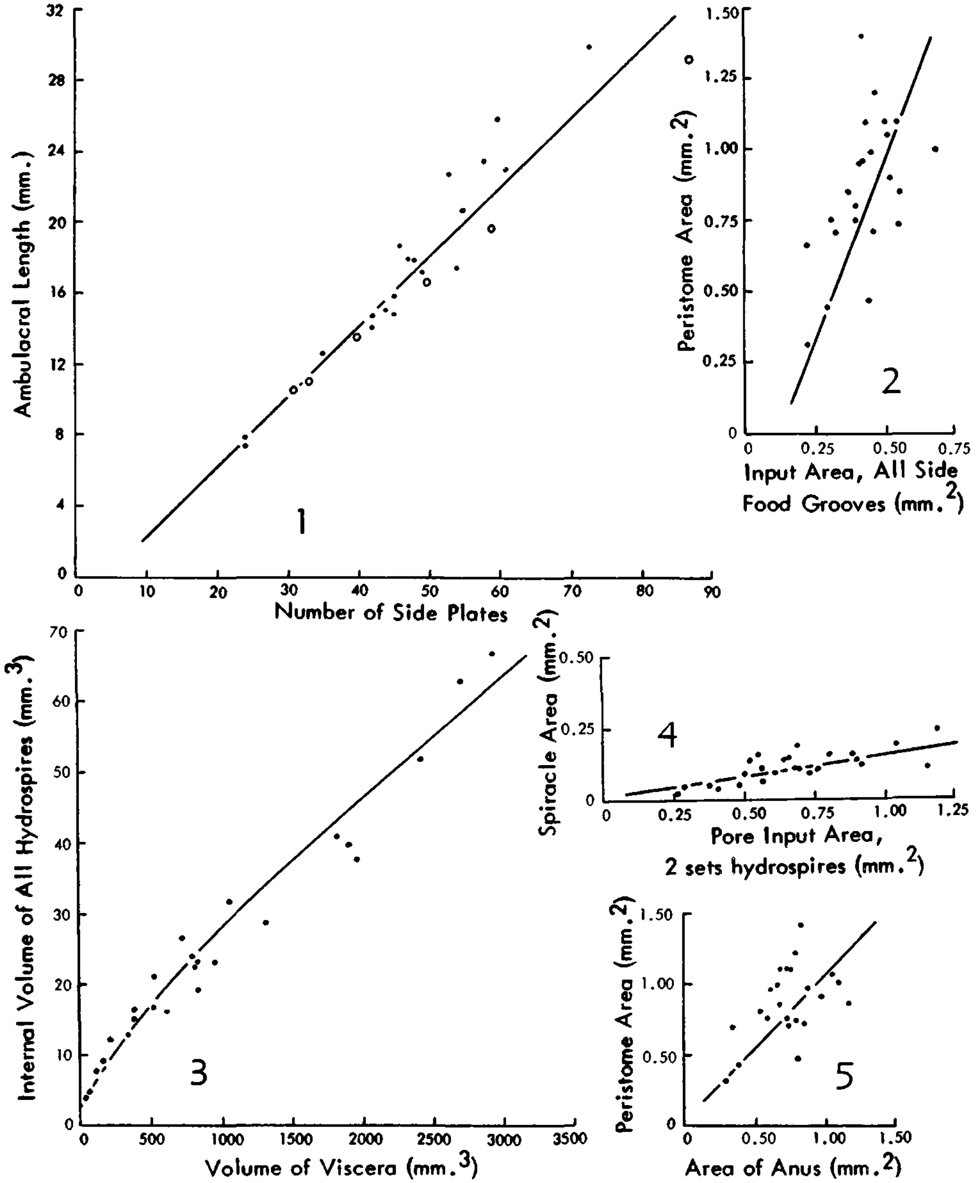

FIG. 220. Hydrodynamics of *Globoblastus norwoodi* (OWEN & SHUMARD), L.Miss., USA(Iowa), throughout an ontogenetic series (108).

1. Ambulacral length plotted against number of side plates on side of ambulacrum.

2. Area of peristome plotted against cross-sectional input area of side food grooves on all ambulacra.

3. Total internal volume of all hydrospires plotted against volume of viscera.

4. Area of one spiracle plotted against input area of pores associated with two sets of hydrospires with which former connects.

5. Area of peristome plotted against cross-sectional area of anus.

in *Orophocrinus* would apparently be carried outward when the anus was extended.

Various quantitative parameters reflect the conditions of flow in the hydrospire and ambulacral sytems, and indirectly the physiology of the animal. These characters are best studied throughout an ontogenetic series, as their configuration at any one time is determined by ontogenetic development and probably reflects the needs of the animal. The number of pores, volume of the hydrospires, area of the peristome, number of arms (and thus food-gathering capacity), etc., all changed during development. The only genus on which a complete hydrodynamic analysis has been made is *Globoblastus* (Macurda, 1965, 108).

The input area of the hydrospire system in *Globoblastus* is reflected by the cross-sectional area of the pores, while the output area is that of the spiracle openings throughout an ontogenetic series (Fig. 220,*4*). Since input area is six times output area, the outgoing current could have had a maximum velocity of six times the input current. In *Rhopaloblastus belfordi,* however, the ratio is 1:1. The volume of the hydrospires in *Globoblastus* increased sharply (Fig. 221); the increase in entrance and exit dimensions apparently facilitated change of the water mass in the hydrospires. Assuming an arbitrary input velocity of 0.1 mm./sec., the entire water mass in the hydrospires could be changed in 40 seconds in a small specimen and 100 seconds in a large specimen. The internal volume of the hydrospires compared to the volume of the viscera is rather large (Fig. 220,*3*), varying from 1:20 in small specimens to 1:45 in large ones. The surface area of the hydrospires is also large in relation to the visceral volume (Fig. 221). These data reinforce the interpretation of the hydrospires having a respiratory function, since the capacity for water replacement and the surface area for CO_2/O_2 exchange are large in relation to the volume of tissue in the viscera. The gases would have had to diffuse through the hydrospire wall. The microstructure of this wall is poorly known but the calcite is thinner than that of the calyx wall and may have a filamentous appearance.

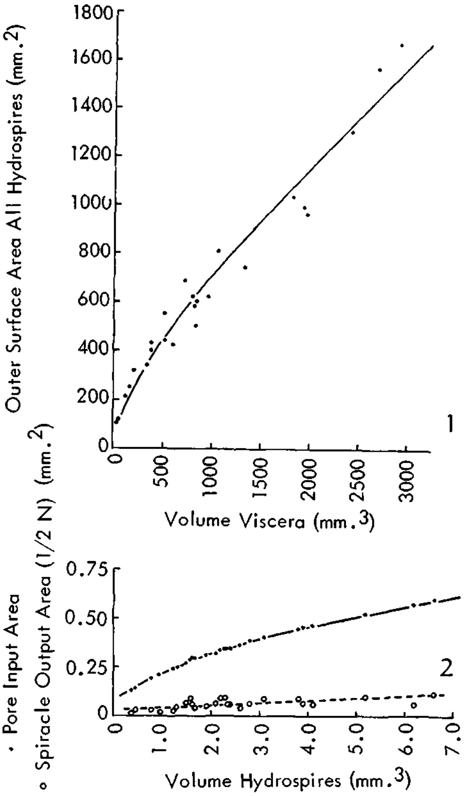

Fig. 221. Hydrodynamics of *Globoblastus norwoodi* (Owen & Shumard), L.Miss., USA(Iowa), throughout ontogenetic series (108).

1. Total outer surface area of all hydrospires plotted against volume of viscera.

2. Input area of pores along one side of ambulacrum and output area for one set of hydrospires (one-half spiracle area) plotted against internal volume of one group of hydrospires.

The hydrodynamics of circulation in fissiculate blastoids has not been determined. In forms with exposed hydrospire slits, each hydrospire would have been an individual circulation cell, with water entering one part and exiting from the other. This may have been less efficient than the two-way system of spiraculate genera. In the same ecological situation, the number of hydrospires in a fissiculate genus and thus the surface area available for respiration may be much greater than in a spiraculate, as in the occurrence of *Codaster* (fissiculate—number of hydrospires increases during ontogeny) and *Orbitremites* (spira-

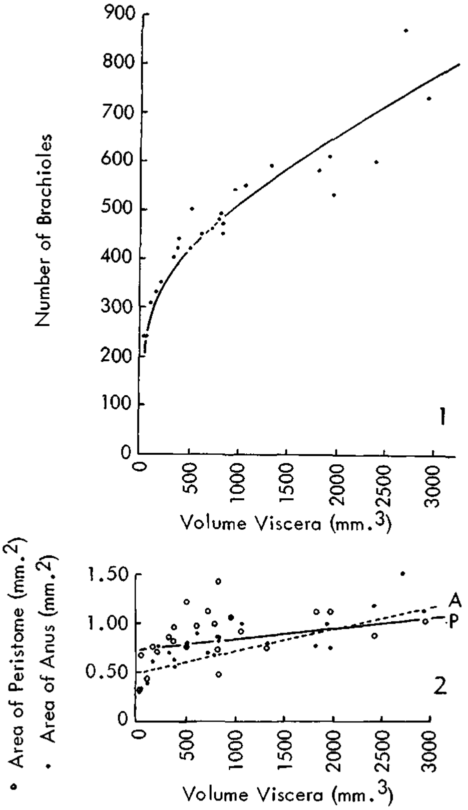

FIG. 222. Hydrodynamics of *Globoblastus norwoodi* (OWEN & SHUMARD), L.Miss., USA(Iowa), throughout ontogenetic series (108).

1. Number of brachioles plotted against volume of viscera.

2. Area of peristome and anus plotted against volume of viscera.

culate, number constant throughout growth, one hydrospire per group) in the Lower Carboniferous of England near Grassington, Yorkshire. If circulation of an individual exposed hydrospire slit was less efficient, a greater number would be needed to provide a respiratory capacity equal to that of the spiraculate form. This may explain the presence of almost 600 hydrospires in a large specimen of *Hadroblastus* (MACURDA, 1965, 106).

As a blastoid grew, the number of arms and thus the food-gathering capacity, constantly increased (Fig. 220,*1*). In *Globoblastus,* most of the growth of the radials was along the *RD* axis which facilitated a rapid increase in ambulacral length. An increasing food-gathering capacity was necessary to support the increasing volume of tissue in the viscera (Fig. 222). In some Permian genera (e.g., *Timoroblastus*) the ambulacral area and thus number of arms were extremely small in relation to volume of viscera (see Fig. 226). The volume of water entering the main food groove from the more numerous side food grooves in *Globoblastus* increased during development; the area of the peristome increased to accommodate the increased water flow (Fig. 220,*2*). Area of the anus increased at the same rate as the peristome to provide easier egress for greater volumes of water (Fig. 220,*5*). Areas of the peristome and anus increased linearly in relation to the expanding volume of the viscera (Fig. 222).

The use of hydrodynamic studies in blastoids provides a dynamic interpretation of the organism and should find increasing utilization in taxonomy, and interpretations of functional morphology, physiology, and ecology.

[*Explanation of Figure 223*]

1-2. Polydeltoideus enodatus REIMANN & FAY, Sil., USA(Okla.), ×2 (Macurda, n).

3. Cryptoschisma schultzii (D'ARCHIAC & DE VERNEUIL), Dev., Spain, ×3 (Macurda, n).

4. Hyperoblastus filosus (WHITEAVES), Dev., Can. (Ont.), ×2.5 (Macurda, n).

5. Brachyschisma subcrassum REIMANN, Dev., USA (N.Y.), ×3 (Macurda, n).

6-7. Heteroschisma canadense (BILLINGS), Dev., Can.(Ont.), ×3 (Macurda, n).

8. Belocrinus cottaldi (MUNIER-CHALMAS), Dev., France, ×2 (110).

9. Devonoblastus leda (HALL), Dev., USA(N.Y.), ×3 (Macurda, n).

10. Placoblastus ehlersi FAY & REIMANN, Dev., USA(Mich.), ×2 (Macurda, n).

11. Phaenoschisma laeviculum (ROWLEY), Miss., USA(Mo.), ×4.5 (104).

12. Cryptoblastus melo (OWEN & SHUMARD), Miss., USA(Ill.), ×3 (Macurda, n).

13. Radial of *Pentablastus supracarbonicus* SIEVERTS-DORECK, L.Carb., Spain, ×3 (Macurda, n).

14. Pentremites elongatus SHUMARD, L.Miss., USA (Iowa), ×2 (Macurda, n).

15. Codaster acutus M'COY, L.Carb., Eng., ×3 (Macurda, n).

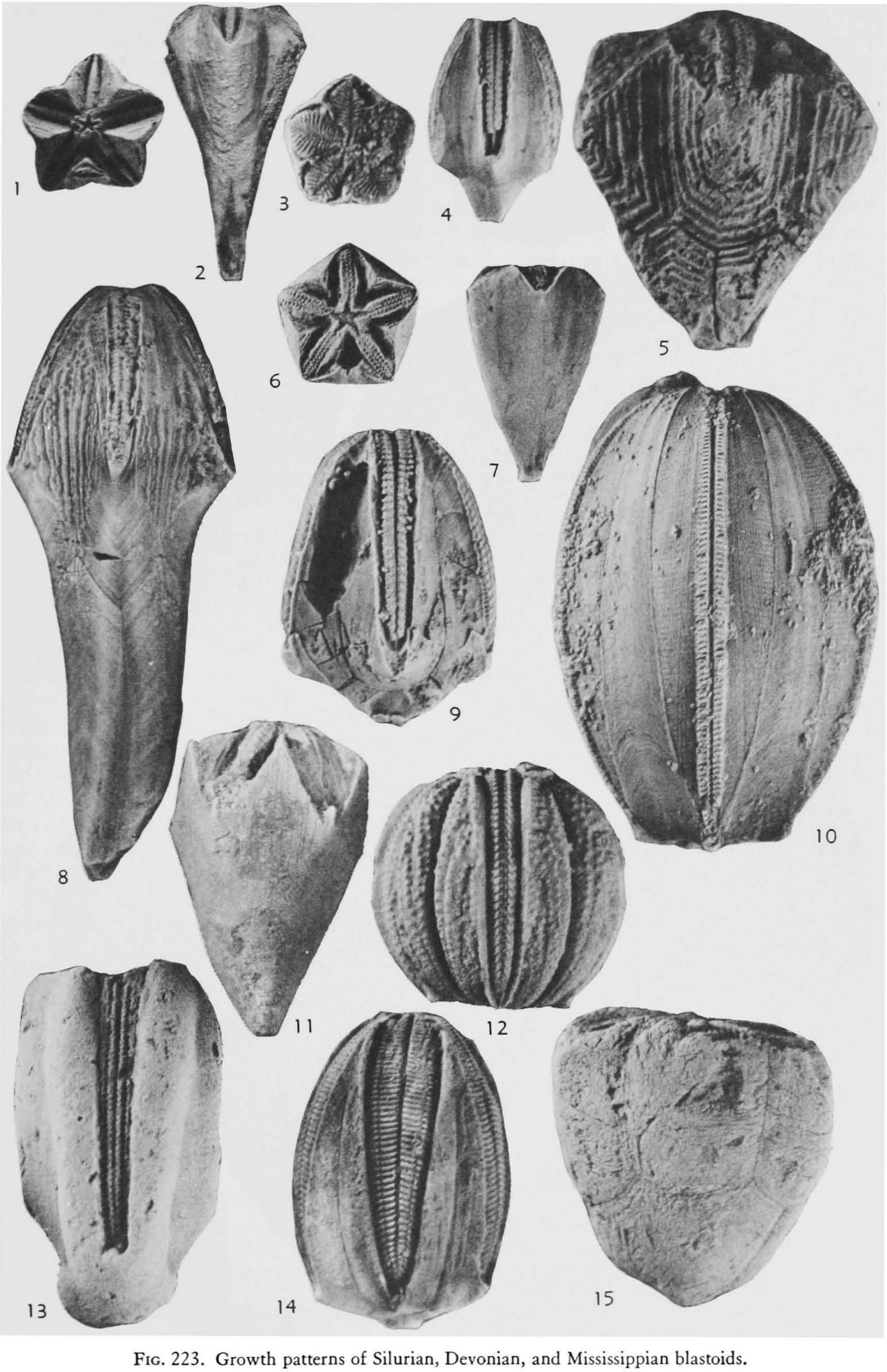

FIG. 223. Growth patterns of Silurian, Devonian, and Mississippian blastoids.

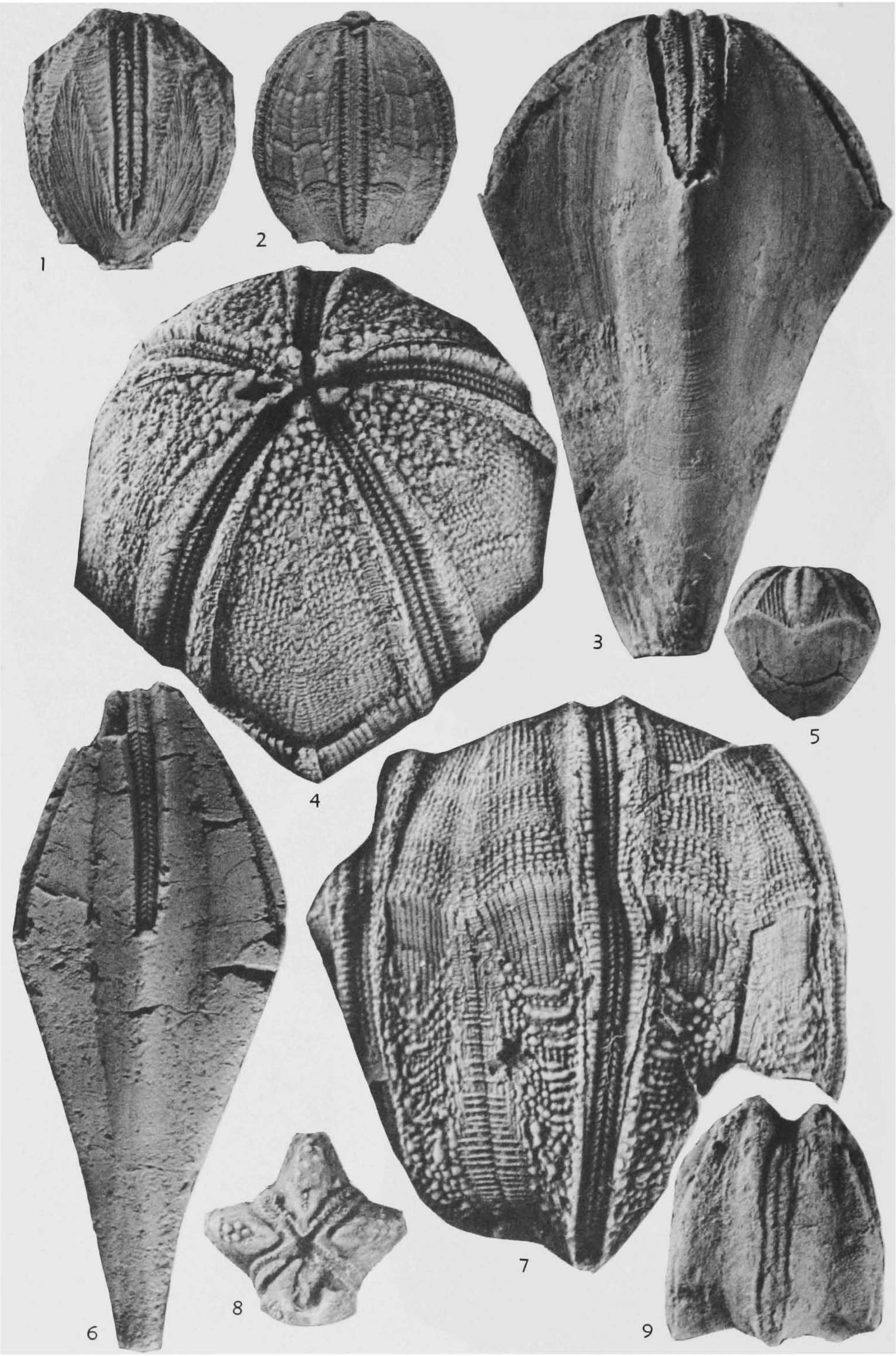

Fig. 224. Growth patterns of Mississippian blastoids. (Continued on facing page.)

TEMPORAL DISTRIBUTION OF GROWTH PATTERNS IN BLASTOIDS

The first blastoids, as the class is now understood, appeared in the Middle Silurian. The number of principal plates and their basic mode of growth (lateral accretionary addition) was stable until blastoids became extinct in the Permian. Growth patterns are important in any discussion of the derivation of evolutionary record of blastoids. If calyx shape changed from pyramidal to globose through time, then visceral shape, points of origin of the plates relative to the viscera, and rates of growth along plate-growth axes must be modified to produce this change.

The three or four known Silurian fissiculate and spiraculate blastoid genera have an obconical calyx, with a long pelvis and a short vault (e.g., *Polydeltoideus,* Fig. 223). Thus the basals had a high rate of growth, as did the *RB* axis of the radials. Growth rates of the *RR* and *RD* axes and the deltoid were small and the aboral growth of the deltoid was confined to the ambulacral sinus, since no radiodeltoid growth occurs outside the sinus (Fig. 223,*2*). Reflexed growth lines are lacking by the ambulacral sinus, and the aboral portion of the deltoid is a sharp crest. The ambulacra are short and confined to the uppermost part of the calyx. This basic growth pattern may have been present in the ancestor of Silurian blastoids.

The growth pattern of Silurian forms carries on into the Devonian, particularly in the fissiculate genera. It is found in *Deltoschisma, Heteroschisma* (Fig. 223), *Pentremitidea,* and *Pleuroschisma. Cryptoschisma* is similar but has expanded the ambulacral field; it is one of the few early blastoids in which the lancet is exposed (Fig. 223,*3*). *Hyperoblastus* has modified growth rates of the radial so that the *RD* axis is dominant and the ambulacra are much longer but still narrow, producing a club-shaped theca. The base is conical. The deltoid still does not grow outside the radial sinus (Fig. 223,*4*). The only Devonian fissiculate blastoid in which an external growth sector is found on the deltoid is *Brachyschisma.* The growth of the *RB* and *BR* axes is still about equal, producing a conical pelvis, but the rates and directions of *RD* and *RR* have been modified to produce a parachute-shaped calyx (Fig. 223,*5*).

Much more experimentation is found in the Devonian spiraculates. Most species of *Cordyloblastus* are suggestive of the basic Silurian growth pattern. *Belocrinus* is somewhat similar (Fig. 223). However, *Schizotremites* and *Devonoblastus* (Fig. 223) (particularly the latter) modified the growth of the radials and deltoids so that the *RD* axis became the dominant radial growth axis, permitting an increase in ambulacral length; the deltoid also grew outside the ambulacral sinus. The calyx shape became biconvex to subovoid; the pelvis of each, however, is still conical. *Strongyloblastus* is similar to these genera but has more petaloid ambulacra, exposing the lancet. The most radical change in growth patterns is found in the closely related genera *Elaeacrinus—Nucleocrinus—Placoblastus* and *Eleutherocrinus.* In the former group (Fig. 223,*10*), rate of growth of the basals has become quite reduced and they are confined to a basal concavity. The growth rates of the radials are also quite modified, being reduced; they are confined to the base of the calyx. The rate of growth of the deltoids has become extremely high, *DR* being several times *RD,* and the deltoids extend almost to the base of the globose calyx. The ambulacra are still narrow, however. *Eleutherocrinus* (Fig.

[*Explanation of Figure 224, continued*]

1. Lophoblastus neglectus (Meek & Worthen), L.Miss., USA(Mo.), ×3 (Macurda, n).

2. Schizoblastus sayi (Shumard), L.Miss., USA (Iowa), ×3 (Macurda, n).

3. Orophocrinus praelongus Bailey, L.Carb., Ire., ×2 (Macurda, n).

4,7. Nymphaeoblastus bancroftensis McKellar, L. Carb., Australia, ×3 (Macurda, n).

5. Hadroblastus conicus Fay, L.Miss., USA(N. Mex.), ×3 (Macurda, n).

6. Metablastus lineatus (Shumard), Miss., USA (Iowa), ×2 (Macurda, n).

8. Astrocrinus benniei (Etheridge), L.Carb., Scot., ×8.3 (Macurda, n).

9. Nodoblastus librovitchi (Yakovlev), L.Carb., USSR, ×3 (Macurda, n).

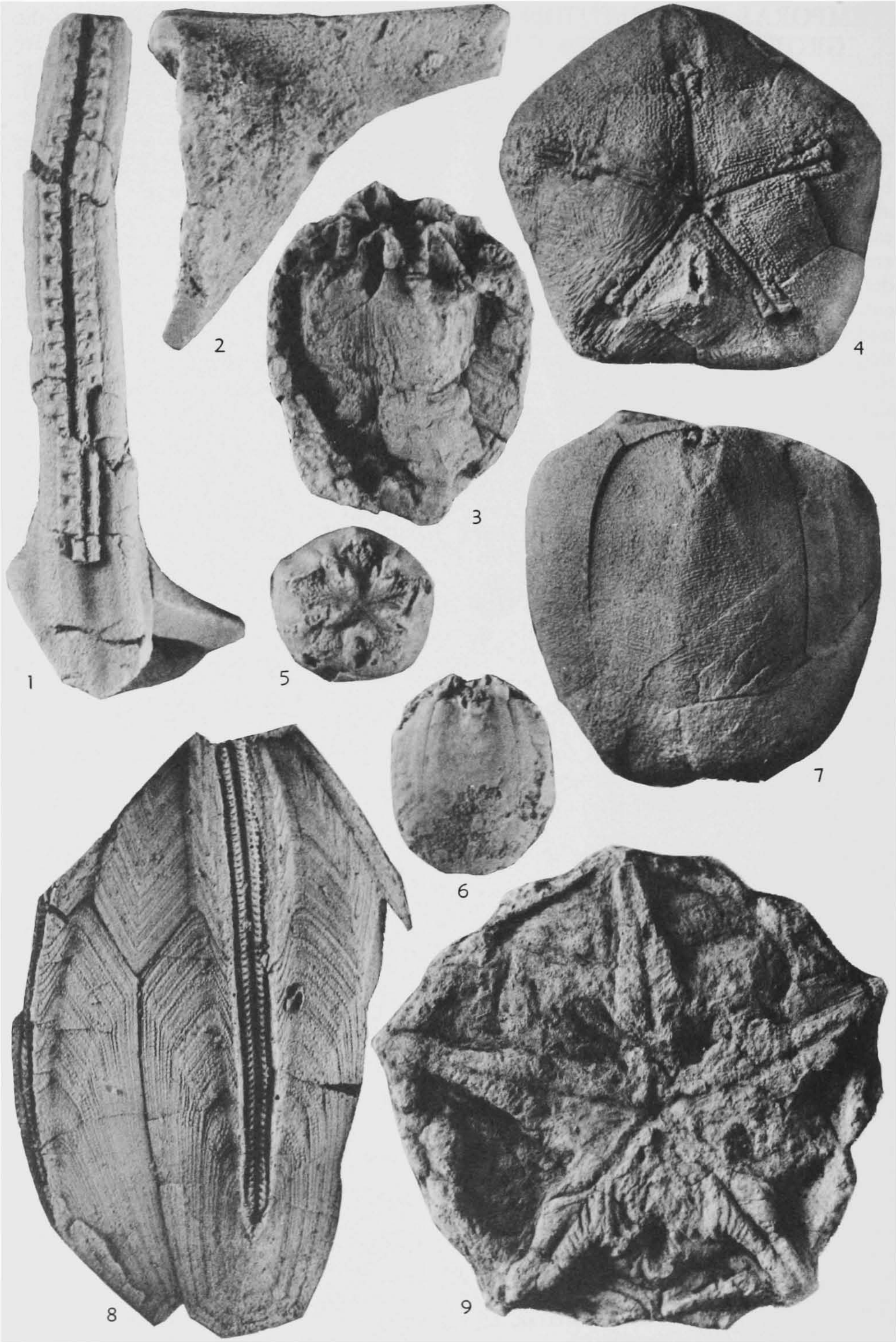

FIG. 225. Growth patterns of Pennsylvanian and Permian blastoids (*See* facing page.)

214) represents the most radical departure. The *RD* axis has become dominant, allowing the ambulacra to expand almost to the base of the calyx. The deltoids also grew outside the radial sinus. The most extreme feature is the adoption of an eleutherozoic habit. One ambulacrum *(D)* became quite shortened so as to allow the animal to lie free on the ocean floor. The basals lying in this radius grew halfway up the calyx.

The Lower and Middle Mississippian saw a great proliferation of globose genera in which the deltoids are relatively short, their growth being confined to the top portion of the calyx. The *RD* axis of the radial was dominant and the arcuate ambulacra extend almost to or to the base of the calyx, and the basals are small, being confined to the very base of the calyx (Fig. 223,*12*) (genera *Auloblastus, Carpenteroblastus, Cribroblastus, Cryptoblastus, Diploblastus, Doryblastus, Globoblastus, Mesoblastus, Monadoblastus,* and *Tanaoblastus*). In a few of these globose blastoids (*Ambolostoma, Ellipticoblastus, Granatocrinus, Lophoblastus, Orbiblastus, Poroblastus,* and *Ptychoblastus*), the deltoid grew at a faster rate, extending one-third the length of the calyx (Fig. 224,*1*) and in a few (*Heteroblastus, Monoschizoblastus, Orbitremites,* and *Schizoblastus*), it grew much faster, reaching almost to the base (Fig. 224,*2*). However, the basic form and extent of the ambulacra are the same. A few of these globose genera developed slight or deep basal concavities (Fig. 214,*8*) to which the basals were confined (*Cribroblastus, Doryblastus, Globoblastus, Granatocrinus, Monoschizoblastus, Orbiblastus, Poroblastus,* and *Ptychoblastus*). A few of the Mississippian spiraculate genera (*Metablastus, Pyramiblastus,* and *Tricoelocrinus*) have an obconical or biconical calyx with relatively short ambulacra (Fig. 224,6), reminiscent of growth patterns in *Troosticrinus* and *Schizotremites.* Other genera (*Pentremites, Pentremoblastus,* and *Petaloblastus*) developed an obconical or club-shaped theca with a large exposed lancet and relatively large ambulacral areas (Fig. 223,*14*). *Pentremites* underwent a great deal of evolutionary experimentation, persisting into the Lower Pennsylvanian. *Acentrotremites* and *Nodoblastus* (Fig. 224) developed dome-shaped calyces, pentagonal in outline with flat bases and relatively long ambulacra. One new evolutionary experiment was attempted in *Dentiblastus,* in which the ambulacra extended out beyond the discoidal theca on prongs (Fig. 213,*4*).

The growth patterns in some Mississippian fissiculate genera are little changed from those of the Devonian. *Phaenoblastus* and *Phaenoschisma* (Fig. 223) have club-shaped or obconical thecas with conical pelvises; growth of the deltoid was confined to the ambulacral sinus. In *Codaster* (Fig. 223), *Hadroblastus* (Fig. 224), and *Pentephyllum*(?) the theca is still conical, or biconical, but the deltoid grew outside of the ambulacral sinus and there was a proliferation of the number of hydrospire slits. *Orophocrinus* (Fig. 224) retained a conical pelvis but underwent a great deal of experimentation in growth rates in the radials, producing thecas ranging from narrow, conical to flaring, parachute-shaped (Fig. 216,*7*). *Nymphaeoblastus* (Fig. 224) is highly unusual, as it is a globose form with exposed hydrospire slits; the rate of growth of the deltoid was high. *Pentablastus* is unique among the blastoids. The shape of the calyx (ovoid) with relatively long ambulacra and a rather flat base is conventional, but the radial is split into a number of separate plates (Fig. 223). *Astrocrinus* is another peculiar eleutherozoic form, the basic growth patterns having been modified to produce a tetragonal outline with one shortened ambulacrum (Fig. 224). As in *Eleutherocrinus,* the *D* ambulacrum was the modified one.

[*Explanation of Figure 225, continued*]

1-2. Ambulacral prong and radial of *Thaumatoblastus longiramus* Wanner, Perm., Timor, ×3 (Macurda, n).

3. Agmoblastus dotti (Moore & Strimple), Penn., Okla., ×3 (Macurda, n).

4,7. Indoblastus granulatus Wanner, Perm., Timor, ×2.5 (Macurda, n).

5-6. Sagittoblastus wanneri (Yakovlev), Perm., USSR, ×3 (Macurda, n).

8. Undescribed blastoid, U.Carb., Australia, ×2 (Macurda, n).

9. Notoblastus brevispinus Brown, Perm., Australia, ×2.5 (Macurda, n).

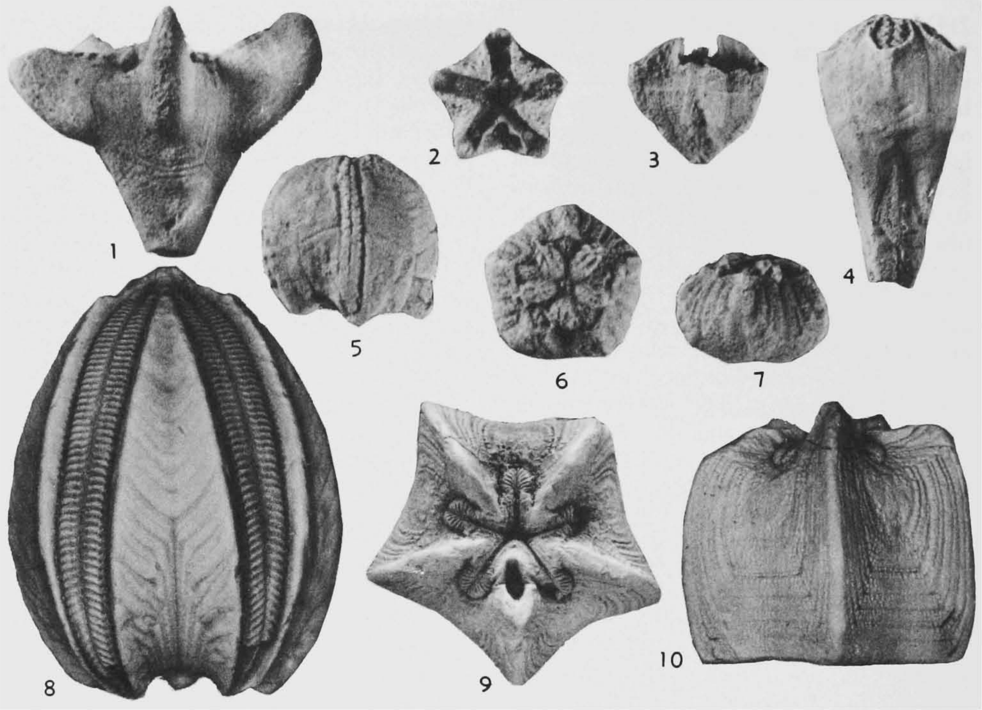

FIG. 226. Growth patterns of Permian blastoids.

1. *Pterotoblastus gracilis* WANNER, Perm., Timor, ×3 (Macurda, n).
2-3. *Nannoblastus pyramidatus* WANNER, Perm., Timor, ×3 (Macurda, n).
4. *Rhopaloblastus timoricus* WANNER, Perm., Timor, ×3 (Macurda, n).
5. *Orbitremites malaianus* WANNER, Perm, Timor, ×3 (Macurda, n).
6-7. *Angioblastus variabilis* WANNER, Perm., Timor, ×3 (Macurda, n).
8. *Deltoblastus* sp., Perm., Timor, ×2 (Macurda, n).
9-10. *Timoroblastus coronatus* WANNER, Perm., Timor, ×3 (Macurda, n).

The known record of Pennsylvanian blastoids is very sketchy. *Pentremites* extended into the lowermost Pennsylvanian. The growth pattern of a new Pennsylvanian spiraculate genus (Fig. 225,*8*) from Queensland does not depart extensively from those found in the Mississippian. The calyx is elongate ovoid, with large deltoids; the *RD* axis is dominant on the radial and probably slightly greater in rate of growth than *DR*, and the pelvis is conical. The only known Pennsylvanian fissiculate genus, *Agmoblastus* (Fig. 225), appears to be transitional in its form between *Codaster* and some of the Permian forms. The calyx is subcylindrical, the basals being relatively large in their development, producing a broad base. *RB* is the dominant growth axis of the radial. The ambulacra are short and confined to the summit. The deltoids and *RD* fronts have exposed hydrospire slits; the deltoids begin to develop elevated processes.

The pattern of development of some Permian fissiculate genera (*Angioblastus,* Fig. 226; *Microblastus, Paracodaster, Sagittoblastus,* Fig. 225; and *Sundablastus*) is similar to that of *Agmoblastus*; the calyx is subcylindrical to flattened discoidal. The ambulacra are quite small in relation to the calyx and lanceolate. The basals are relatively large, the deltoids small. One can expand the basals of *Timoroblastus* (Fig. 226) or draw out the peculiar winged radials of *Pterotoblastus* (Fig. 226) from this basic plan, but these two genera are peculiar in their development. The development of a few Permian genera (*Neo-*

schisma, Notoblastus, Fig. 225) resembles that of the discoidal, open fissiculate *Hadroblastus. Indoblastus* (Fig. 225) has the same general calyx shape as *Codaster* but lacks any exposed hydrospire slits. The ovoid, flattened form of *Dipteroblastus* with its two elongate and three shortened ambulacra represents another eleutherozoic experiment. *Thaumatoblastus* (Fig. 225), with its elongate, needle-like radial spines which bore the ambulacra attempted to extend the food-gathering area, in contrast to some of the other genera. The ovoid form of *Sphaeroschisma* is unusual among the usually conical fissiculates. Some forms (*Anthoblastus, Ceratoblastus,* and *Nannoblastus,* Fig. 226) are highly peculiar and specialized.

Developmental patterns among the few Permian spiraculate genera are much more conventional by comparison. The only globose form, *Deltoblastus* (Fig. 226), has long ambulacra with high rates of growth on the *DR* and *RD* axes. The basals are indented in the deepest basal concavity of any genus. The biconvex, ovoid form of *Calycoblastus* with its long ambulacra and greater rate of growth of *RD* resembles a Mississippian developmental plan. *Rhopaloblastus* (Fig. 226), a conical form with much more restricted ambulacra, resembles some of the early spiraculates in its general form. The species of *Orbitremites* (Fig. 226) are apparently congeneric with *Orbitremites* from the Mississippian.

The earliest and presumably primitive developmental pattern in blastoids resulted in an obconical calyx with a long pelvis. The *RB* axis of the radials had the greatest rate of growth in the radials, the deltoids grew only in the ambulacral sinus, the ambulacra were narrow, and the lancet was concealed. This pattern carried over into most of the Devonian fissiculate genera, was partially modified by some spiraculate forms, and extensively modified by others. The basic developmental pattern of Mississippian spiraculate genera produced globular calices with long ambulacra; the deltoid was usually short but in some forms extended well down on the calyx. A few genera had an obconical or biconical calyx. Some Mississippian fissiculate genera had developmental patterns similar to those of Silurian and Devonian blastoids; others modified this and faintly suggest things to come. Knowledge of Pennsylvanian developmental patterns is limited. Spiraculate forms in the Permian are not very far removed from their precursors but fissiculates have many new and different plans of development, with the addition of extensive basal, radial, or deltoid processes, restricted ambulacra, and new calyx shapes.

PALEOECOLOGY

By Harold H. Beaver

Available published information on the paleoecology of blastoids is largely limited to three recent articles (Allen & Lester, 1953; Joysey, 1955; Cline & Beaver, 1957).

Allen & Lester compared the occurrence of large species of *Pentremites* in argillaceous limestones of Mississippian (Chesteran) age in Georgia with *Pentremites* of smaller size in underlying and overlying relatively pure crystalline or oölitic limestones. They interpreted the difference in size as related to availability of food and inferred that *Pentremites* living under silty conditions of deposition found it necessary to sieve larger amounts of water for food than those living in clear water. Conceivably, forms living in turbid water needed enlargement of the food-gathering system and a resultant relatively large theca. Galloway & Kaska (1957, p. 70) doubted that the large size of the species was due to a change from clear water to a silty depositional environment. Collections of *Pentremites* from rocks of the same age in other areas (e.g., southern Illinois) show that large calyces similar in size and shape to the robust specimens found in Georgia occur in both pure and impure limestones in Illinois.

Joysey (1955, p. 209-220) described the distribution of Lower Carboniferous blastoids in the vicinity of Grassington, Yorkshire, England. In this area three depositional environments, classed as shelf, shelf margin, and basin, have been described. Shelf-limestone deposition occurred on a relatively stable platform located north of an area of fault movements in the Craven fault belt; south of this belt, sandstone and shale accumulated in a rapidly subsiding basin. In the latter part of Early Carboniferous time the shelf-basin boundary shifted northward, and transitional beds of the shelf margin (Middle Limestone) are found to be intermediate between the underlying shelf facies and the overlying basin facies.

Blastoids occur in two facies of the shelf margin designated as shell banks (called reef knolls by Bond, 1950) and crinoid banks. The "shell banks" are discrete unbedded limestone mounds which developed to heights of several feet above the sea floor; bryozoans and crinoid remains are an important part of the fauna contained in this unbedded limestone. The mounds were subsequently buried by the crinoidal debris of the "crinoid banks," which were located shoreward of the shell banks. The blastoid *Orbitremites* is associated with the crinoid remains, occurring sparsely in the upper part of the shell banks, but it is more abundant in the overlying crinoidal debris. In some parts of the area the blastoids of the crinoid banks (*Orbitremites, Codaster*) are confined to thin rock layers a few to several inches in thickness; in other places, they are distributed in random manner through strata ranging from 10 to 30 feet in thickness. Where the blastoids occur in thin layers, the boundary between barren and blastoid-bearing layers is sharp. The blastoid calyces are buried in unsorted crinoidal debris. Bryozoan remains may be common, but invariably are subordinate to the crinoidal detritus. Basinward the limestone beds containing blastoids grade into deposits characterized by an abundant fauna of small brachiopods and the coral *Lonsdaleia*.

After an attempt to compile an annotated bibliography of the paleoecology of blastoids, which was unsuccessful owing to the absence of significant published investigations, Cline & Beaver (1957) summarized their own observations and inferences pertinent to the subject. Since blastoids are associated typically with rugose corals, brachiopods, fenestellid bryozoans, and crinoids, they concluded that blastoids lived in a normal marine environment which was characterized by at least some agitated water. The nature of their food-gathering system requires some current action and possibly a sea bottom with a substratum of skeletal debris that was most satisfactory for attachment. Evidence supporting these inferences is found at outcrops of the Paint Creek Formation (Chesteran), northeast of Waterloo, Illinois, where strata above red clay at the base of the formation comprise a sequence of beds in which specimens of *Pentremites* are alternately abundant and entirely absent. The succession of deposits

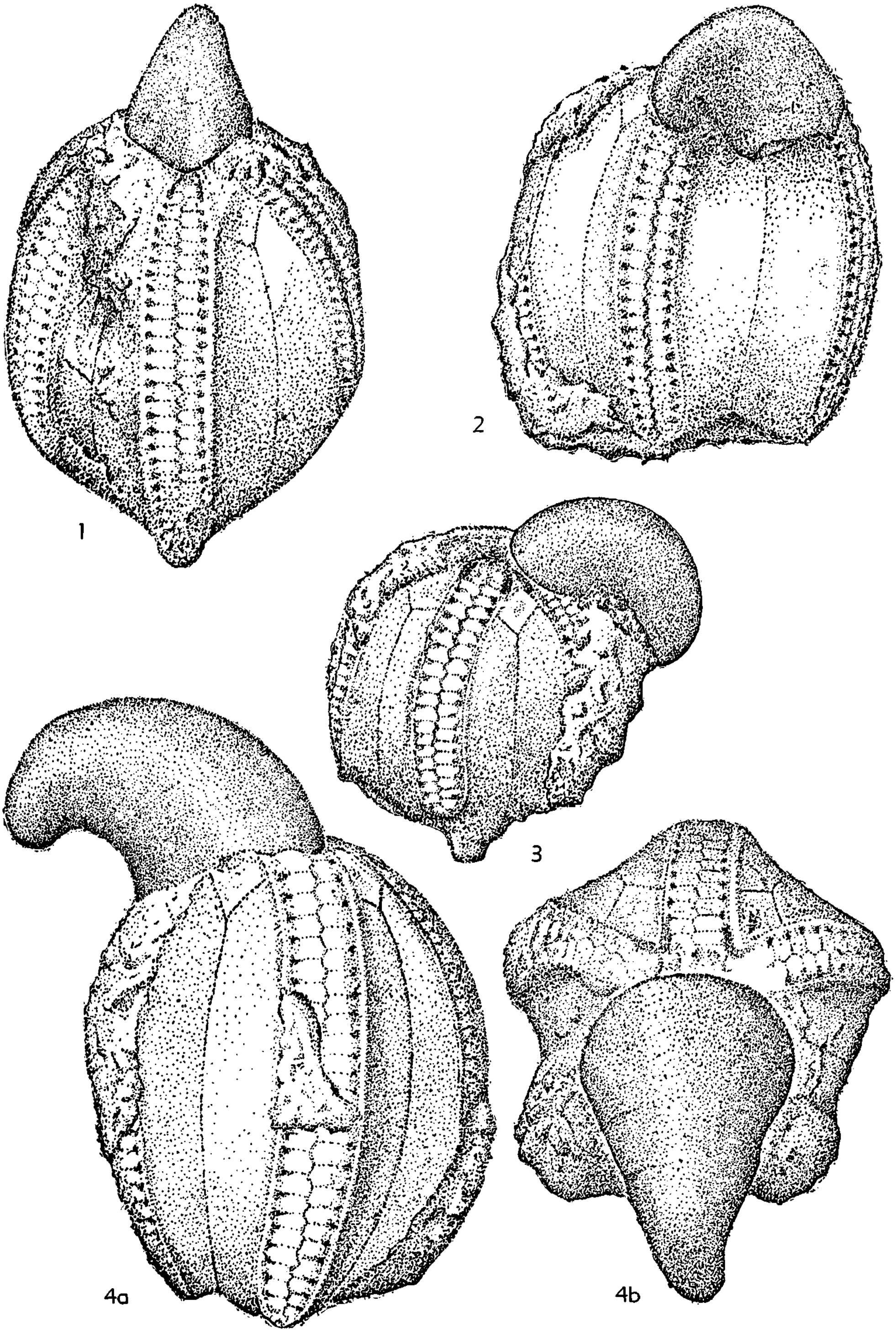

Fig. 227. Symbiotic association of blastoids, *Diploblastus kirkwoodensis* (Shumard), with coprophagous gastropods, *Platyceras (Platyceras)* sp., Miss. (Meramec., St. Louis Ls.), near St. Louis, Mo.; *1, A*-ray lateral view of specimen D; *2, D*-ray view of specimen C; *3, E*-ray view of specimen B; *4a,b, B*-ray and adoral views of specimen A; all ×9.5 (Levin & Fay, 1964).

is cyclic, a typical cycle consisting of a 0.5- to 1-inch layer of uncemented echinoderm remains overlain by nearly unfossiliferous, thinly bedded clay layers, 1 or 2 inches thick. *Pentremites,* brachiopods, and crinoid remains are common to abundant in the lower layer and are found in various states of preservation. Specimens of *Pentremites* with part of the column, brachioles, ambulacral covering plates, and summit plates are commonly preserved in the lower layer of echinoderm debris. Some specimens are abraded, however, and indicate agitated debris. The overlying clay layer has virtually no fossil remains, except for bryozoan fronds found locally. Apparently fine mud spread over the sea floor and smothered individual organisms living at the time. Cycles of this sort are repeated again and again.

The preservation of the upper Burlington (Osagian) blastoid fauna in the Ashgrove quarries several miles south of Springfield, Missouri, indicates that these specimens accumulated in shallow agitated water, probably near the zone of surf action. The blastoid calyces and the associated crinoid and brachiopod remains are broken, much abraded, and worn; preservation of internal features is poor. The interior of the calyces of *Pentremites elongatus* are filled with clear calcite crystals and practically none of the hydrospire folds are preserved.

The type of food on which blastoids lived can only be guessed at. Because food was taken from the water by ciliated furrows lining the brachioles and was transported along food grooves to the mouth, it is reasonable to assume that blastoids fed on planktonic organisms (CLINE & BEAVER, 1957, p. 959). Living comatulid crinoids, some of the nearest living relatives of the blastoids, live primarily on unicellular green algae (CLARK, 1915, p. 144).

The gregarious nature of many echinoderms frequently has been recorded. In rock strata their fossil remains may occur in a particular bed for long distances, or they may be abundant locally but laterally absent. As noted previously, sparse occurrences of blastoids have been recorded from the upper portion of some English "shell banks" termed reef knolls by some workers. Specimens are most common in the beds of crinoidal debris overlying the shell banks. Examination of a large blastoid collection made by LAUDON and BOWSHER from the Lake Valley Formation (Mississippian) of New Mexico showed that all the specimens had been collected from a nonreef facies (CLINE & BEAVER, 1957).

A previously unknown symbiotic relationship of blastoids and coprophagous gastropods has been discovered recently by LEVIN & FAY (1964), who report nearly a dozen individuals of *Diploblastus kirkwoodensis* (SHUMARD) with specimens of *Platyceras (Platyceras)* attached to the calyx (Fig. 227). The gastropods, which are small, with smooth apertural lip and constant angle of expansion, are found perched in various positions over the anal opening of the blastoids. Apparently they are mature individuals that fed on fecal pellets of their host and benefited by the association. The blastoids seem to have been neither harmed nor benefited by their molluscan "fellow travelers." Coprophagous gastropods attached to crinoid calyces are better known, several examples of them having been described by BOWSHER (1955). The *Platyceras*-bearing specimens of *Diploblastus* occur in shaly layers of the St. Louis Limestone (Meramecian) near St. Louis, Missouri; they are associated with many more blastoids which lack adherent gastropods, suggesting that the association is uncommon.

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION

By DONALD B. MACURDA, JR.

The earliest known blastoids are found in the Silurian. From the United States, 3 or 4 genera are represented by species found in Illinois, Ohio, Indiana, Kentucky, Tennessee, and Oklahoma (Fig. 228). One occurrence has been reported from the Silurian of Bohemia. It is identified as being congeneric with the Oklahoma genus, but the anal structure is unknown and the generic identification must be considered provisional.

The blastoids had become world-wide in their distribution by the Devonian (Fig. 228). Most forms are known from the Middle Devonian of the United States and Lower and Middle Devonian of western Europe. Some 11 genera have been described from the United States and range geographically from the Appalachians westward to Iowa (West Virginia, New York, Ontario, Ohio, Michigan, Indiana, Illinois, Wisconsin, Iowa, Kentucky, Tennessee, Missouri). There are also records from the Devonian of Oklahoma and New Mexico. In Europe, five or six genera have been reported from Spain, France, Great Britain, Belgium, and Germany. They also have been reported from Manchuria in China, Victoria in Australia[1], northwestern Africa, and fragments are known from South Africa and Bolivia in South America. These last-mentioned occurrences are poorly known taxonomically and may represent new genera. Individual Devonian genera do not appear to have a intercontinental distribution. There may be one that occurs in both the United States and Spain, and *Devonoblastus,* a New York genus, has been reported from China. Some genera have a fairly wide geographic range, as *Cordyloblastus* is found in France, Spain, and Germany; and *Nucleocrinus* ranges

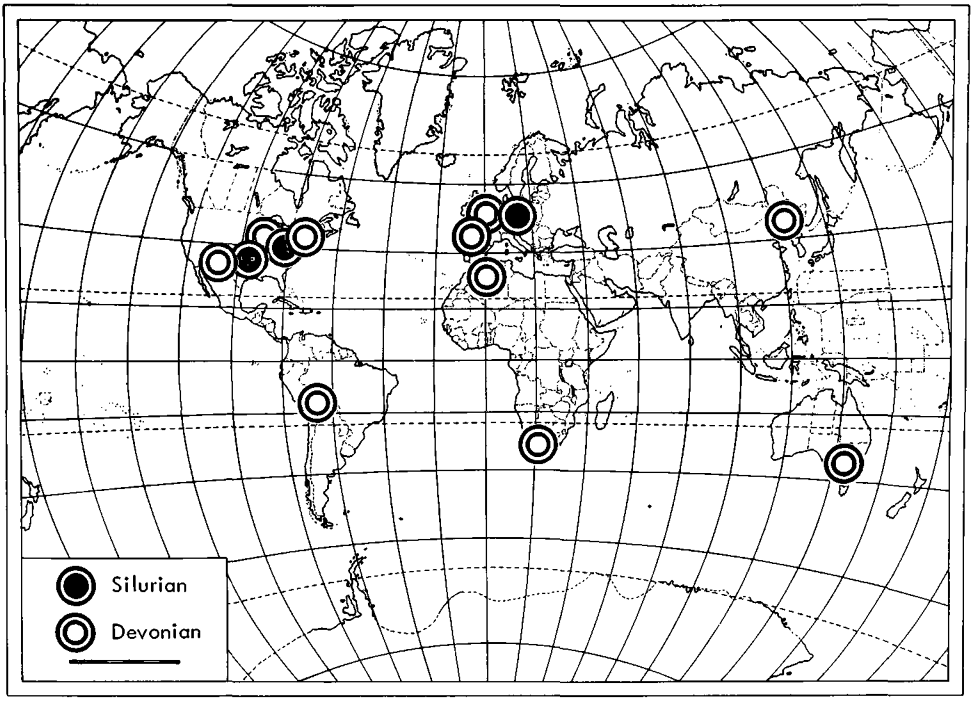

FIG. 228. Geographic distribution of Silurian and Devonian blastoids (Macurda, n).

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[1] Australian "blastoids" now are judged to be inadunate crinoids (J. SPRINKLE, personal communication).

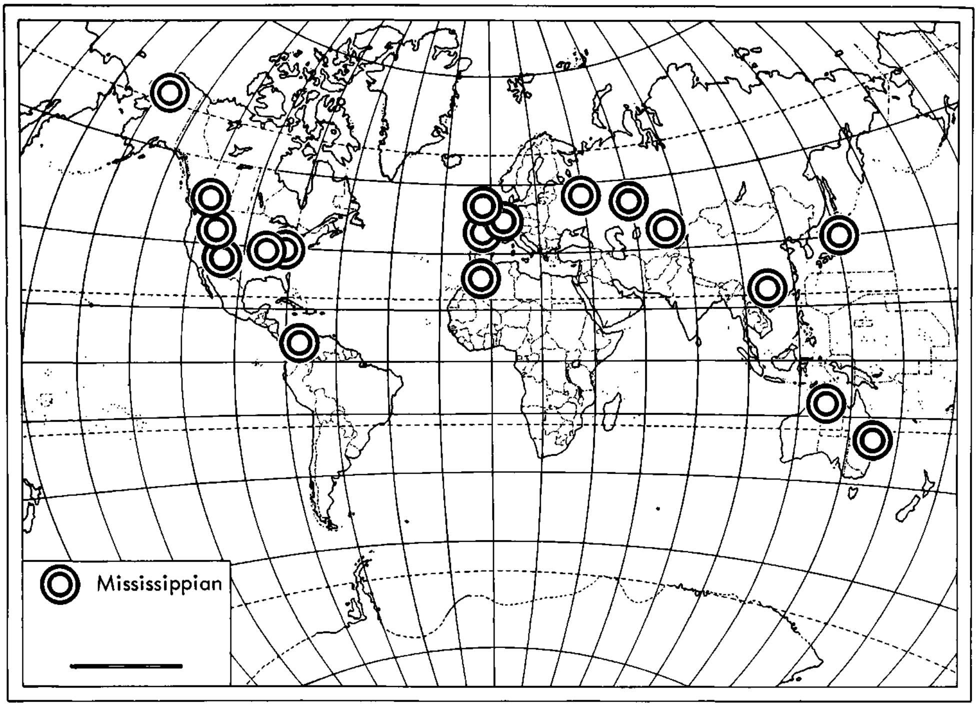

FIG. 229. Geographic distribution of Mississippian blastoids (Macurda, n).

from New York to Iowa and Missouri. A few of the known occurrences are Lower Devonian; most are Middle Devonian. Almost no Upper Devonian blastoids have been discovered.

The Mississippian represents the maximum known development of the blastoids (Fig. 229). About 45 genera (some undescribed) have been found in rocks of this period. About 25 of these have been collected from Mississippian deposits in states bordering the Mississippi River, all but a few from the Kinderhookian and Lower Valmeyeran. The Burlington Limestone has a greater diversity than any other formation. In the eastern and central United States, blastoids have been found in Alabama, Georgia, Mississippi, Kentucky, Tennessee, Virginia, West Virginia, Ohio, Indiana, Illinois, Iowa, Missouri, Arkansas, and Oklahoma. Most of the easternmost occurrences are Upper Mississippian; blastoids range throughout the Mississippian in the other states. Knowledge of blastoid distribution in the western United States is poorer because less attention has been given to search for them but they are known from New Mexico, Arizona, Nevada, Utah, Idaho, Wyoming, and Montana. Preliminary field work suggests that a large and varied blastoid fauna is present. Blastoids are also known from the Canadian Rockies and Brooks Range in Alaska; their description is in progress. The greatest diversity of blastoids occurs in the Lower Mississippian; the number of genera becomes sharply restricted after the Lower Valmeyeran.

Blastoids are also common in the Lower Carboniferous (Mississippian equivalents) of western Europe, some 14 genera being described from Eire, North Ireland, England, Scotland, Germany, Belgium, and Spain. Most of these occurrences are Tournaisian and Visean. They are also known from the Lower Carboniferous of the USSR, China, Japan, Australia, northwestern Africa, and South America (Colombia). Some Mississippian forms are cosmopolitan in distribution, *Pentremites*

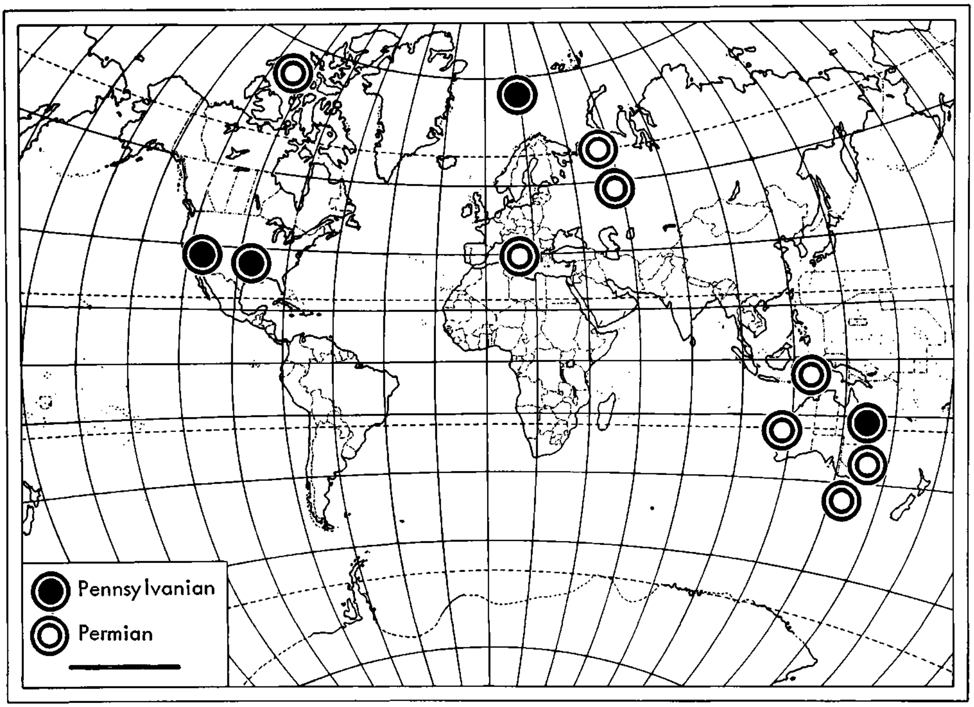

FIG. 230. Geographic distribution of Pennsylvanian and Permian blastoids (Macurda, n).

ranging from Alaska to Colombia, *Orophocrinus* from Arizona to Belgium, *Phaenoschisma* from New Mexico to England, *Cryptoblastus* from Missouri to Arizona, Alaska, and possibly to the central USSR, and *Nymphaeoblastus* from the USSR to Japan and Australia. All occurrences other than those in the eastern United States and western Europe are known only on a reconnaissance basis.

The record of the blastoids in the Pennsylvanian is very sparse (Fig. 230), only three or four genera being known from a period approximately in length to the Mississippian. Whether the paucity of Pennsylvanian blastoids represents an evolutionary crisis or nonpreservation in the geologic record is speculative. *Pentremites* lingered into the Pennsylvanian in Arkansas, Oklahoma, Utah, and Nevada. Other than this genus the only other known occurrences are in the mid-Pennsylvanian of Oklahoma, the Westphalian of Queensland, Australia, and the Upper Carboniferous of Spitzbergen.

During the Permian, most blastoids apparently were found in the eastern hemisphere (Fig. 230). The island of Timor in Indonesia is the most prolific locality, for 16 genera have been found there. Three or four genera are known from Australia (Western Australia, New South Wales, Tasmania). Some of these are congeneric with the Indonesian forms. Two or three genera are known from the USSR, one of which is congeneric with an Indonesian genus. A fragmentary blastoid has been reported from Sicily. Recently, the first Permian blastoid in the Western Hemisphere has been found on Melville Island in the Canadian Arctic.

Existing knowledge of the stratigraphic distribution and paleogeography of blastoids is incomplete. The occurrences described above show an obvious relationship to centers of research; with further exploration, it may change considerably. At least ten new genera from fairly well-known areas currently await description.

CLASSIFICATION

By R. O. Fay

PREVIOUS INVESTIGATIONS

The first descriptions and illustrations of a blastoid known to me were published by S. L. Mitchill (1808) and J. Parkinson (1808), who referred to an "Asterite" or "asterial fossil" from Kentucky and illustrated specimens of the species subsequently named *Pentremites godoni*. The specimens obtained by Dr. Samuel Brown in 1805 (Fay, 1961, 55) evidently were collected from beds now known as the Paint Creek Formation (U.Miss,. Chester.) of the Mammoth Cave or Bowling Green region of central Kentucky. In 1819, J. L. M. Defrance named this fossil *encrina Godonii,* thus applying the first binomial zoological designation for a blastoid species. In 1825, Thomas Say proposed the "family" Blastoidea as a separate group of the Echinodermata, the name referring to the predominant budlike form of the theca.

In 1851, the first morphologic study of blastoids was published by C. F. Roemer, who reported the discovery of ambulacral pores and internal folds that terminate near the mouth. These folds were termed hydrospires by Elkanah Billings in 1869. Roemer divided the blastoids into four groups, named Floreales (conical theca, petaloid ambulacra), Elliptici (globular theca), Truncati (flat summit), and Clavati (conical theca, linear ambulacra). Although these groupings were arbitrary, it is true that globular and conical blastoids may be separated into natural lineages.

In 1886, Robert Etheridge & P. H. Carpenter published a comprehensive study of the blastoids, based on seven years of intensive study by them on specimens in the British Museum (Natural History) and others obtained by loan. This work has served as basic reference material for all subsequent textbooks and treatises concerned with blastoids. Most pre-Permian genera were illustrated, and the first record was made of the double circumesophageal ring, hydrospire plates, and the occurrence of the abnormal specimens. Etheridge & Carpenter divided the Blastoidea into two orders called Regulares (five normal ambulacra) and Irregulares (four normal ambulacra and one short ambulacrum). The Regulares included five families termed Pentremitidae (pyriform, five spiracles); Troostoblastidae (conical, ten spiracles); Nucleoblastidae (globular, ten spiracles); Granatoblastidae (globular, five spiracles); and Codasteridae (without hydrospire pores). The Irregulares comprised one family, Astrocrinidae, with three genera *(Astrocrinus, Pentephyllum, Eleutherocrinus).* The classification given by Etheridge & Carpenter is unnatural but nevertheless important, because emphasis was placed upon profiles and spiracles, in addition to the presence or absence of pores as fundamental taxonomic features. The illustrations are works of art which illustrate excellently the shapes, sizes, and general plate relationships of numerous blastoids, even though they are somewhat inaccurate in showing details of the anal deltoids and relative exposure of the lancet plates. Many internal features were not reported, and no mention was made of the relative overlap of deltoids on radials or of radials on deltoids. As a result, it will be necessary to restudy almost all of the blastoid specimens in the British Museum and those in other collections before attempting to make a trustworthy classification of the blastoids.

In 1896, Charles Wachsmuth, who wrote the blastoid chapter in the first English edition of Zittel's *Textbook of Palaeontology,* followed Etheridge & Carpenter in almost every detail. In 1899, F. A. Bather in a short paper gave a new classification which is as follows.

Classification of Blastoidea by Bather (1899)

- Grade Protoblastoidea
  - Family Asteroblastidae [now classed with diplopore cystoids]
  - Family Blastoidocrinidae [now classed as parablastoids]
- Grade Eublastoidea [same as Blastoidea]
  - Series A. Codonoblastida
    - Family Codasteridae (hydrospire slits exposed)
    - Family Pentremitidae (hydrospire slits covered)
  - Series B. Troostoblastida

Family Troostocrinidae (conical forms, with hydrospire pores)
Family Eleutherocrinidae (one ambulacrum shorter than others)
Series C. Granatoblastida
Family Nucleocrinidae (lacking hydrospire plate)
Family Orbitremitidae (hydrospire plate present)
Family Pentephyllidae (stemless, large subpentagonal theca)
Family Zygocrinidae (stemless, small depressed theca)

BATHER expressed the belief that blastoids were derived from diplopore cystoids through a form like *Asteroblastus*, but intermediate forms are lacking to prove this concept. His classification is a mixture of unnatural units and the "Series" designated by him were never defined. The most important item suggested by BATHER's classification is that the Codasteridae and Pentremitidae may be more closely interrelated than the Orbitremitidae and Pentremitidae. Evidently BATHER did not believe that the presence or absence of hydrospire pores was fundamental.

In 1908, BATHER reported the occurrence of Permian blastoids on Timor Island in the Dutch East Indies, and subsequently similar Permian fossils were found in Russia, Sicily, and Australia (New South Wales). Only two or three genera were named up to 1918 and these finds did not affect previous classifications.

In 1918, OTTO JAEKEL defined the Blastoidea as a subclass of the Cystoidea, linking the two by means of *Cystoblastus*, and he thus derived the blastoids from pore-rhomb cystoids. BILLINGS (1869) and MOORE (1954) have expressed similar views, but all attempts to find intermediate forms to trace lineages connecting cystoids with blastoids have failed. JAEKEL's classification is as follows.

Classification of Blastoidea by Jaekel (1918)

Class Cystoidea
Subclass Blastoidea
  Order Parablastida (large number of thecal plates) (Blastocystidae)
  Order Radiolata [now termed Blastoidea proper]
    Suborder Spiraculata (hydrospire slits hidden, pores present)
      Families Troostoblastidae, Pentremitidae, Nucleoblastidae, Granatoblastidae (as defined by Etheridge & Carpenter, 1886)
    Suborder Fissiculata (hydrospire slits exposed)
      Family Orophocrinidae (spiracular slits present)
      Family Codasteridae (hydrospire slits exposed)
  Order Coronata [now transferred to the Crinoidea] (plates like those of blastoids, but lacking hydrospires, pores, slits, side plates, and brachioles)

The important contribution of JAEKEL is partition of the blastoids into groups designated as Fissiculata and Spiraculata, and the separation of fissiculate blastoids into those having spiracular slits from those with exposed hydrospire fields. The Parablastida are here set apart as the Class Parablastoidea, probably not related to the Blastoidea. The order Coronata is classed under the Crinoidea because the fossils in this group have crinoid-type arms, lack hydrospires and pores, and lack brachioles (FAY, 44, 57, 66). BATHER's and JAEKEL's studies indicate that the Blastoidea and Cystoidea are not closely related.

In 1924, J. WANNER described many new genera and species of Permian blastoids from Timor. Subsequently, H. MATSUMOTO (1929) modified BATHER's classification by dividing the class Blastoidea into three orders: Protoblastida, Mesoblastida (Fissiculata plus *Astrocrinus*), and Eublastida (Spiraculata minus *Astrocrinus*), thus arriving at a classification almost identical with that of JAEKEL. The Eublastida were divided into three "series," termed Troostoblastida, Pentremitida, and Granatoblastida.

In the 1930's, L. M. CLINE published on some Devonian and Mississippian blastoids of North America, and since 1935, I. G. REIMANN has described various Devonian blastoids. New morphological features, such as ambulacral spines and anal-deltoid plates, were investigated by these authors and questions began to be raised about generic relationships of known blastoid genera.

In 1940, WANNER described new Permian genera and species from Timor, in addition to those of his previous publications (1931, 1932). In all, he described 48 new species belonging to 16 new genera and provided morphological information which called for a revised classification of the blastoids. The most important part of WANNER's taxonomic changes was removal of the parablastoids, protoblastoids, and coronates from the Blastoidea, which thus were left with only two orders (Fissiculata, Spiraculata), and he concluded that the Fissiculata were in need of extensive subdivision. WANNER's classification is indicated in the following outline.

Classification of Blastoidea by Wanner (1940)

Class Blastoidea SAY, 1825
Order Fissiculata JAEKEL, 1918
  Family Codasteridae ETHERIDGE & CARPENTER, 1886 (eight hydrospire groups, anal deltoid present)
  Family Dipteroblastidae WANNER, n. fam. (ten hydrospire groups, epideltoid and hypodeltoid present, plates irregular)
  Family Zygocrinidae BATHER, 1899 (eight hydrospire groups, plates irregular)
  Family Angioblastidae WANNER, n. fam. (eight hydrospire groups, one to three slits in each, epideltoid and hypodeltoid present)
  Family Phaenoschismidae ETHERIDGE & CARPENTER, 1886 (*recte* Phaenoschismatidae) (ten hydrospire groups, many slits, plates irregular, base pyriform)
  Family Nymphaeoblastidae WANNER, n. fam. (ten hydrospire groups, many slits, plates regular, base flat to concave)
  Family Anthoblastidae WANNER, n. fam. (ten hydrospire groups, one slit in each, plates regular)
  Family Neoschismidae WANNER, n. fam. (*recte* Neoschismatidae) (ten hydrospire groups, interradial areas prolonged)
  Incertae sedis, *Thaumatoblastus* WANNER, 1924
Order Spiraculata JAEKEL, 1918
Suborder Troostoblastida BATHER, 1899
  Family Troostocrinidae BATHER, 1899 (*recte* Troosticrinidae)
  Family Eleutherocrinidae BATHER, 1899
Suborder Granatoblastida BATHER, 1899
  Family Nucleocrinidae BATHER, 1899
  Family Orbitremitidae BATHER, 1899
  Family Pentephyllidae BATHER, 1899
Suborder Pentremitida MATSUMOTO, 1929
  Family Pentremitidae D'ORBIGNY, 1851

Several difficulties are inherent in the above classification. The Eleutherocrinidae should belong with the Pentremitidae, the Pentephyllidae probably belong under the Fissiculata, and the Orbitremitidae may include diverse groups of globular blastoids, of unrelated origin. Several genera (e.g., *Brachyschisma, Thaumatoblastus*) had no place in the classification, and questions on morphology of old genera arose, especially in connection with anal structures. WANNER's works were a great step forward because he began to realize the importance of anal, oral, and internal structures, and their bearing on classification. By 1951 it was apparent that we would have to restudy all previous blastoid species.

In 1943, R. S. BASSLER & M. W. MOODEY prepared a bibliographic index to genera and species, recognizing approximately 50 genera and 350 species. They recognized the Protoblastoidea and Eublastoidea as orders, the latter being the Blastoidea of most authors. The protoblastoids included the Asteroblastidae (now removed to the diplopore cystoids) and the Blastoidocrinidae (relegated to the Parablastoidea). The eublastoids were divided according to WANNER's classification, rather than as was done by BASSLER in the *Fossilium Catalogus* (1938). There is present need for a comprehensive bibliography, objective index, and stratigraphic and geographic cross-index to the Blastoidea. One important contribution of BASSLER & MOODEY was transfer of the Coronata to the crinoids.

In 1945, GERHARD REGNÉLL transferred the blastoids to the cystoids on the ground that pores pierce the theca and biserial brachioles are common to both groups. His classification is as follows.

Classification of Blastoidea by Regnéll (1945)

Class Cystoidea VON BUCH, 1846
Subclass Hydrophoridea VON ZITTEL, 1903
Subclass Blastoidea SAY, 1825 [now a separate class]
  Order Coronata JAEKEL, 1918 [now transferred to Crinoidea]
  Order Parablastoidea HUDSON, 1907 [now segregated as separate class]
  Order Eublastoidea BATHER, 1899 [now same as Class Blastoidea]

The Parablastoidea have a type of hydrospires unknown in blastoids and contain many more thecal plates. It would be difficult to place this group with any known class of echinoderms and therefore it is best to raise them to the rank of a class. One important contribution of REGNÉLL's is that he removed the diplopore cystoids (e.g., *Asteroblastus*) from the Protoblastoidea, thus wiping out a separate group known as protoblastoids.

In 1953, F. M. BERGOUNIOUX followed the classification of BASSLER & MOODEY (1943) for the French *Traité de Paléontologie*. In this work, the genus *Asteroblastus* was

FISSICULATA	Sil.	Dev.	Miss.	Penn.	Perm.
1 Polydeltoideus (P)	--				
2 Decaschisma (P)	· · · --				
3 Deltoschisma (P)	· · ·	--			
4 Pentremitidea (A)	· ·	----			
5 Cryptoschisma (A)	· ·	----			
6 Pleuroschisma (P)	· ·	· --			
7 Hyperoblastus (P)	· ·	· --			
8 Brachyschisma (B)	· ·	· --			
9 Heteroschisma (C)	· ·	· --			
10 ?Pentephyllum (A)	· ·	· · ·	----		
11 Phaenoschisma (P)	· ·	· · ·	----		
12 Phaenoblastus (P)	· ·	· · ·	----		
13 Hadroblastus (P)	· · ·	· · · ·	--		
14 Nymphaeoblastus (P)	·	· · · ·	--		
15 Orophocrinus (O)	· ·	· · · ·	--		
16 Codaster (C)	· · · ·	· · · ·	--		
17 Astrocrinus (A)	· · ·	· · · ·	--		
18 Agmoblastus (C)	· · ·	· · · ·	· · ·	--	
19 Pentablastus (O)	· · ·	· · · ·	· · ·	--	
20 Dipteroblastus (P)	· ·	· · · ·	· · ·	· · · ·	----
21 Neoschisma (P)	· · ·	· · · ·	· · ·	· · · ·	----
22 Notoblastus (P)	· · ·	· · · ·	· · ·	· · · ·	----
23 Thaumatoblastus (P)	·	· · · ·	· · ·	· · · ·	----
24 Ceratoblastus (A)	· ·	· · · ·	· · ·	· · · ·	----
25 Nannoblastus (C)	· ·	· · · ·	· · ·	· · · ·	----
26 Angioblastus (C)	· · ·	· · · ·	· · ·	· · · ·	----
27 Paracodaster (C)	· · ·	· · · ·	· · ·	· · · ·	----
28 Pterotoblastus (C)	· ·	· · · ·	· · ·	· · · ·	----
29 Sagittoblastus (C)	· ·	· · · ·	· · ·	· · · ·	----
30 Anthoblastus (O)	· ·	· · · ·	· · ·	· · · ·	----
31 Indoblastus (C)	· · ·	· · · ·	· · ·	· · · ·	----
32 Microblastus (P)	· · ·	· · · ·	· · ·	· · · ·	----
33 Sphaeroschisma (P)	· ·	· · · ·	· · ·	· · · ·	----
34 Sundablastus (P)	· · ·	· · · ·	· · ·	· · · ·	----
35 Timoroblastus (P)	· · ·	· · · ·	· · ·	· · · ·	----
FAMILIES					
A Astrocrinidae		------	------	------	----
B Brachyschismatidae		--			
C Codasteridae		----	------	------	----
O Orophocrinidae			----	------	----
P Phaenoschismatidae	--	------	------	------	----

SPIRACULATA	Sil.	Dev.	Miss.	Penn.	Perm.
36 Troosticrinus (T)	--				
37 Belocrinus (P')	· · ·	--			
38 Schizotremites (T)	· ·	----			
39 Elaeacrinus (N)	· · ·	· --			
40 Nucleocrinus (N)	· ·	· --			
41 Placoblastus (N)	· · ·	· --			
42 Cordyloblastus (P')	· ·	· --			
43 Devonoblastus (P')	· ·	· --			
44 Eleutherocrinus (P')	·	· --			
45 Strongyloblastus (S)	·	· --			
46 Pentremoblastus (P')	·	· · · ·	--		
47 Pyramiblastus (G)	· ·	· · · ·	--		
48 Petaloblastus (P')	· ·	· · · ·	--		
49 Tanaoblastus (G)	· ·	· · · ·	----		
50 Carpenteroblastus (G)		· · · ·	· --		
51 Cribroblastus (G)	· ·	· · · ·	· --		
52 Cryptoblastus (G)	· ·	· · · ·	· --		
53 Dentiblastus (G)	· · ·	· · · ·	· --		
54 Granatocrinus (G)	· ·	· · · ·	· --		
55 Heteroblastus (G)	· ·	· · · ·	· --		
56 Lophoblastus (S)	· · ·	· · · ·	· --		
57 Mesoblastus (G)	· · ·	· · · ·	· --		
58 Monadoblastus (G)	· ·	· · · ·	· --		
59 Monoschizoblastus (G)		· · · ·	· --		
60 Orbiblastus (S)	· · ·	· · · ·	· --		
61 Poroblastus (G)	· · ·	· · · ·	· --		
62 Ptychoblastus (G)	· ·	· · · ·	· --		
63 Acentrotremites (S)	·	· · · ·	· --		
64 Auloblastus (S)	· · ·	· · · ·	· --		
65 Schizoblastus (S)	· ·	· · · ·	· --		
66 Doryblastus (O')	· · ·	· · · ·	· --		
67 Ellipticoblastus (O')	·	· · · ·	· --		
68 Globoblastus (O')	· ·	· · · ·	--		
69 Orbitremites (O')	· ·	· · · ·	· --		
70 Ambolostoma (P')	· ·	· · · ·	· --		
71 Metablastus (T)	· · ·	· · · ·	· --		
72 Tricoelocrinus (T)	· ·	· · · ·	· --		
73 Diploblastus (D)	· · ·	· · · ·	· ----		
74 Pentremites (P')	· · ·	· · · ·	· ----	--	
75 Nodoblastus (D)	· · ·	· · · ·	· · --		
76 Calycoblastus (P')	· ·	· · · ·	· · ·	· · ·	----
77 Deltoblastus (S)	· · ·	· · · ·	· · ·	· · ·	----
78 Rhopaloblastus (P')	·	· · · ·	· · ·	· · ·	----
FAMILIES					
D Diploblastidae	· · ·	· · · ·	· ----		
G Granatocrinidae	· ·	· · · ·	----		
N Nucleocrinidae	· · ·	· --			
O' Orbitremitidae	· · ·	· · · ·	· --		
P' Pentremitidae	· · ·	· ----	------	--	
S Schizoblastidae	· · ·	· ----	------	------	----
T Troosticrinidae	· · --	------	----		

FIG. 231. Stratigraphic distribution of blastoid genera. The letter symbols after the generic names refer to the families in which they are classified, with familial names listed at bottom of chart (Moore & Fay, n).

treated as a protoblastoid and in another section as a diplopore cystoid.

In 1961, FAY published a comprehensive study on pre-Permian blastoids, with revision of many genera and species. The work was incomplete and approximately 30 short papers were written from 1960 to 1962 as supplements to it. A new classification of the Blastoidea was presented, and sections were written on morphology, taxonomy, phylogeny, and bibliography, with the conclusion that a great amount of work is needed before we may begin to understand the features of blastoids that now exist in various museums. After these specimens are studied, we may have a better system of classification. The classification followed in the *Treatise* is essentially that of FAY

(1961, 60), and should be considered as tentative.

Currently several persons working on blastoids include J. A. Arendt (Moscow, USSR), H. H. Beaver (Houston, Texas), Albert Breimer (Amsterdam, Netherlands), R. O. Fay (Norman, Oklahoma), Alan Horowitz (Bloomington, Indiana), K. A. Joysey (Cambridge, England), R. G. McKellar (Brisbane, Australia); D. B. Macurda, Jr. (Ann Arbor, Michigan), I. G. Reimann (Ann Arbor, Michigan), and J. S. Sprinkle (Cambridge, Massachusetts). Much of their work has been on statistics, morphology, and taxonomy, with little emphasis on bibliographic compilations.

TREATISE CLASSIFICATION

In our present state of knowledge of the Blastoidea it is premature to present a definitive arrangement of these fossils. The primary basis for classification of Blastoidea, as now understood, is a combination of characters, especially of deltoid plates on the anal side. These features include (1) presence, absence, or reduction of hydrospires on the anal side, (2) number, type, and arrangement of the anal deltoids, (3) relative exposure of the deltoids, (4) relative closure of the radial sinuses, (5) number, type, and arrangement of the spiracles, (6) number, type, and arrangement of the hydrospires, (7) number, type, and arrangement of the hydrospire pores, (8) relative overlap of radials and deltoids along the radiodeltoid sutures, (9) number, type, and arrangement of the oral plates, (10) shape of the theca, and (11) relative exposure of the lancet plates to the exterior and position of the lancet stipe.

Separation of the orders Fissiculata and Spiraculata is based essentially on relative exposure of the hydrospire slits and the development of hydrospire pores and spiracles.

Families of the Fissiculata are separated by features that include formation of spiracular slits or reduction of hydrospire fields (hydrospiralia) on the anal side or both of these, combined with retention of exposed hydrospire slits, associated with atrophy of them on the anal side. The families of the Spiraculata are distinguished by type and arrangement of the spiracles and the conical to globular shape of the theca.

Genera of the Blastoidea are differentiated by the above-cited features in a variety of combinations. Ornamentation, shape, and statistical measurements are used to define species.

DISTRIBUTION

Many geographic and stratigraphic gaps exist in our knowledge of the class. For instance, a few nominal genera of blastoids have been recorded from Africa, South America, China, Japan, and the North Polar regions, whereas only three genera are recorded from Pennsylvanian rocks of the world. Only three Silurian genera are recorded, all from the United States and one of them also in Czechoslovakia. Of 78 described genera, it is possible to group a few in natural families or related categories, but almost impossible to trace direct lineages. It is quite possible that the families here outlined are polyphyletic and that in the future these may be raised to suborders or otherwise changed. There must be two to three times as many undescribed genera as now known and until these are described, it seems best to retain a simple classification of the Blastoidea. The stratigraphic distribution of blastoid genera is given in Figure 231.

PHYLOGENY AND EVOLUTION

By Robert O. Fay

The origin of the Blastoidea is unknown. It has been postulated by Jaekel (1918) and Moore (1954) that this group of echinoderms may have been derived from pore-rhomb cystoids by development of hydrospires through atrophy of the pore-rhombs although this type of atrophy has never been demonstrated. Regnéll (1945) classed the Blastoidea as a subdivision of the Cystoidea, because both groups possess biserial brachioles and pores that pierce the theca. Cline (1944) made no attempt to compare pore-rhombs with hydrospires and was of the opinion that the hydrospires represent successive infolds along ambulacral margins. WANNER (1940) declined to accept homology of pore-rhombs and hydrospires. At present I would agree with WANNER and CLINE, and further, would relate the Blastoidea to the class Edrioblastoidea (FAY, 1961) and suggest that the blastoids were derived from this class. BATHER (1900) presented the concept that the Blastoidea were derived from diplopore cystoids and that each hydrospire fold represents a pore-pair that has become elongated along the ambulacral margins and that hydrospire pores are specialized pore pairs. At the same time, however, BATHER thought that poreless blastoids (Fissiculata) gave rise to pore-bearing blastoids (Spiraculata), thus opposing his own postulate.

The class Edrioblastoidea seems to be the logical group from which the Blastoidea could have developed. The separate orders (in part) of the Blastoidea could have been derived independently from this class, or the order Fissiculata may have descended directly and the order Spiraculata indirectly by development from the Fissiculata. These suggestions are based upon judgment of inferred phylogenetic trends within the Blastoidea, as now understood. A most primitive blastoid is presumed to be similar to *Polydeltoideus,* in which the form of the calyx is conical, with six anal deltoids, ten exposed hydrospire fields (hydrospiralia), and a moderately long lancet plate covered by side plates. An advanced form is one similar to *Pentremites,* in which the calyx is rounded-conical, with a single anideltoid, the sinuses closed to form pores and spiracles, and the lancet plate displaced outward, pushing aside the side plates. If *Pentremites* came from a form ultimately like *Polydeltoideus,* and if one projects this trend backward, he may postulate the type of echinoderm best suited to represent the ancestral stock of the Blastoidea. This echinoderm should have at least six anal deltoids and otherwise possess regular plate symmetry, with random infolds in the thecal plates, a deep lancet (or better, no lancet, since the lancet is interpreted to be a plate secreted around the median canal, having little useful function of protection where deep—hence probably not secreted in a primitive form), five regular, straight ambulacra covered by an alternating biserial set of ambulacral plates, a primitive stem, and possibly primitive brachioles.

The class Edrioblastoidea has these features, except for primitive brachioles, but it is reasonable to postulate that brachioles could have arisen independently when tube-feet became atrophied, and further, that the brachioles of cystoids probably were derived in a similar manner from another class of Echinodermata. One may logically argue that the Edrioblastoidea have a hydropore and that the Blastoidea do not, but it is here interpreted that the hydropore has migrated internally on the anal side in the Blastoidea, and it is quite possible that it was atrophied. FAY (1960) has shown that the radial canal system of blastoids, ending adorally in the circumesophageal ring, is adjacent to the hydrospire canals, and thus it is possible that water entered the radial canal system by diffusion from the hydrospire canals. If this is true, there would have been little need for a hydropore. The canal system is now interpreted to be the main nervous system (because it is a double ring as in Recent echinoderms); so there may not have been a radial canal or water-vascular system in blastoids.

Therefore, the Blastoidea are considered to be a separate class of Echinodermata, closely related to the Edrioblastoidea, and independent of the Parablastoidea. The coronatids have been shown by FAY (1960, 44; 1961, 57; 1962, 66) to belong to the Crinoidea. Blastoid-like forms with pore-rhombs (e.g., *Cystoblastus*) or with diplopores (e.g., *Asteroblastus*) are judged to belong with the Cystoidea, and therefore the groups formerly classed as Protoblastoidea and Asteroblastidae by BATHER (1900), followed by BASSLER & MOODEY (1943), are not recognized as valid categories of the Blastoidea.

The Phaenoschismatidae are considered as the most primitive group of blastoids, from which most others could have been derived (Fig. 232). The ten exposed hydro-

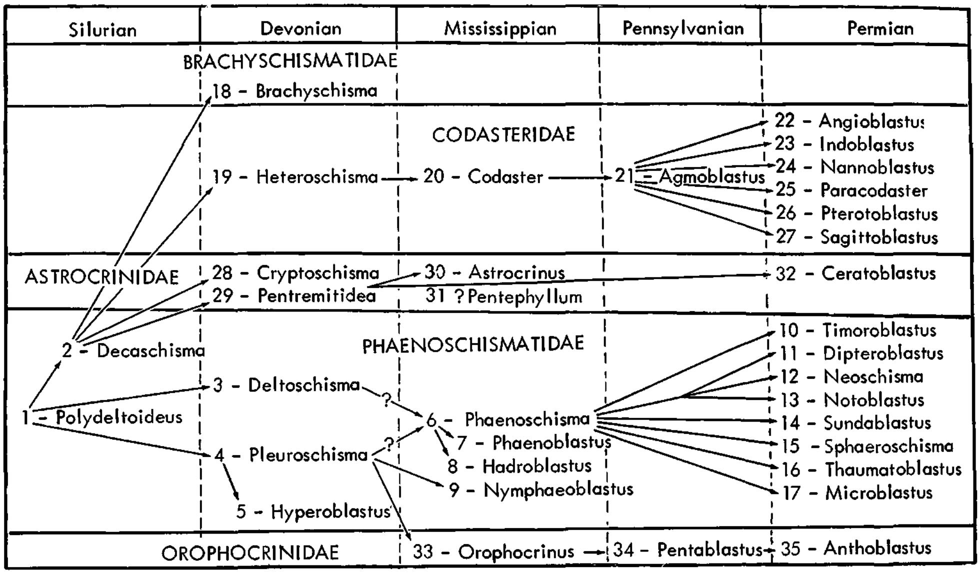

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FIG. 232. Phylogenetic diagram showing possible or inferred relationships of blastoid genera and families of the order Fissiculata (Fay, n).

spire fields could readily have been reduced to nine, thus forming blastoids classed as genera of the Brachyschismatidae, or to eight hydrospire fields, as observed in the Codasteridae. Another trend is toward closure of the sinuses to form ten spiracular slits (as in the Orophocrinidae), or atrophy of the hydrospire fields on the anal side, with formation of eight spiracular slits (e.g., Astrocrinidae).

The Pentremitidae may be descendants of the Phaenoschismatidae produced by complete closure of the sinuses and formation of gaps (hydrospire pores) between side plates (Fig. 233). This mode of developing hydrospire pores is thought to be probable, and accordingly it seems logical to derive *Devonoblastus* from *Hyperoblastus* and *Pentremites* from *Devonoblastus*. If this is correct, the Troosticrinidae are possible derivatives of the Phaenoschismatidae, though intermediate forms are lacking to prove this; alternatively, the Troosticrinidae may have developed independently from the same stock that gave rise to the Phaenoschismatidae. The Granatocrinidae could have been derived from the Troosticrinidae by outward migration of the deltoid septa, except on the anal side, where the deltoid septa migrated inward. The Schizoblastidae also may have descended from the Troosticrinidae, with outward migration of the deltoid septa, including those of the anal side. The Nucleocrinidae, likewise, are possible derivatives of the Troosticrinidae by outward migration of the deltoid septa and outward-downward migration of the large cryptodeltoids. The Pentremitidae may have come from the Troosticrinidae by internal migration of deltoid septa.

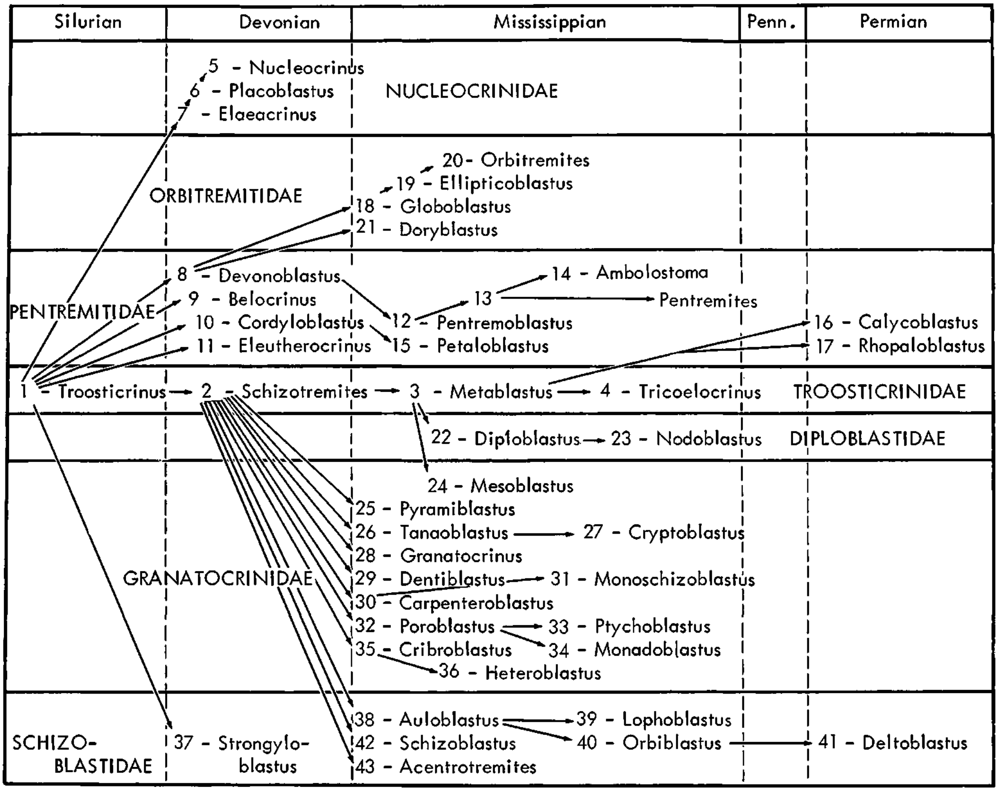

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FIG. 233. Phylogenetic diagram showing possible or inferred relationships ot blastoid genera and families of the order Spiraculata (Fay, n).

Within each family it is possible to trace certain lineages involving specific morphological parts. These trends appear to be similar in diverse families and therefore are here grouped. For instance, the lancet plate is covered by side plates in primitive forms and the side plates support the main food groove. In advanced forms, the lancet is exposed to the outside and supports the main food groove, or in extremely advanced forms, supports the side food grooves in addition. Thus, linear ambulacra are identified as primitive and petaloid ambulacra as advanced characters. The lancet stipe is adjacent to the mouth in a primitive blastoid and has migrated away from the mouth in an advanced form. There are four or six anal deltoids in a primitive form, and one may trace lineages whereby fusion must have taken place between the two cryptodeltoids to form a subdeltoid and between a subdeltoid and superdeltoid to form a single epideltoid, with consequent atrophy or suppression of the hypodeltoid.

The hydrospire fields (hydrospiralia) become atrophied or the number of hydrospire slits are reduced on the anal side. In the Spiraculata, which possess hydrospires in all ambulacra, certain trends are apparent; the number of hydrospires on each side of an ambulacrum apparently becomes reduced in number by atrophy, from five, to four, to three, to two, and to one in different genera, and the hydrospires on the anal side may differ in number from those of the other ambulacral areas within a single genus. With exception of *Pentremites,* the number of hydrospire folds on each side of an ambulacrum, if less than four, is apparently a stable criterion for differentiation of genera.

Another stable feature is the overlap of radials and deltoids along the radiodeltoid suture, which is constant for each genus and species. A primitive blastoid has short deltoids, overlapped by the radials; an advanced form is one having long deltoids, overlapping the radials. The pelvis is conical in a primitive blastoid, whereas it is rounded or with a concave base in an advanced form.

A blastoid with paired spiracles is considered to be primitive, and owing to migration outward or inward of certain deltoid septa it is possible to have forms with five, nine, or 11 openings around the mouth. Thus, the family Pentremitidae may be polyphyletic, possibly derived from the Phaenoschismatidae and Troosticrinidae.

The blastoid stem could have been derived from fused plates of the base of some Edrioblastoidea, and through time, the stem could have atrophied though disuse in a form like *Eleutherocrinus,* with consequent formation of bilateral symmetry and possible adaptation to swimming habits.

The pores, if formed as simple gaps between side plates, are primitive where one pore occurs between adjacent side plates along the deltoid and radial margins. In advanced forms, the pores evidently migrated laterally into margins of the deltoid and radial plates, and these plates folded along each pore to form multiple pores corresponding to each side plate. In some forms, the pores became atrophied along the deltoid margins and were lost, or the simple pores remained along the deltoid margins, but multiple pores formed along the radial margins (e.g., *Poroblastus*).

The cited features tend to show that although Permian blastoids of Timor and adjacent areas are fissiculate forms, they are highly specialized, advanced forms. Thus, they are not considered to be products of retrogressive evolution. The evolutionary theme in blastoids apparently is one of atrophy through disuse.

The problem of extinction of the Blastoidea is apparently one apart from morphological considerations because blastoids of the Permian possess features that warranted their survival into the Triassic and beyond. Thus, some major external physical change of a radical nature was the probable cause for extinction of the class.

SYSTEMATIC DESCRIPTIONS

By Robert O. Fay[1] and Johannes Wanner[2]

[[1]Oklahoma Geological Survey; [2]deceased, formerly University of Bonn]

The present classification is that adopted by Fay, but many ideas expressed on relationships and descriptions of Permian blastoids and most of the Permian tone illustrations are taken from materials submitted by Wanner. Various families, as here defined, would be raised to suborders by Wanner on the basis of greater emphasis given by him to anal and spiracular structures. Many specimens in museums probably belong to new genera, but circumstances have prevented new study of them. Until these specimens are correctly illustrated and described, it is best to retain a rather simple classification of the Blastoidea. The relationships among different genera of many recently recognized structures (e.g., inner side plates, paradeltoid plates, ambulacral spines, double brachiolar cover plates, accessory oral plates, lateral canals, anal cover plates) are not well understood. It is hoped that paleontologists will re-examine specimens in their collections, prepare polished thin sections of them, and publish detailed descriptions, supplemented by photographs and line drawings at ade-

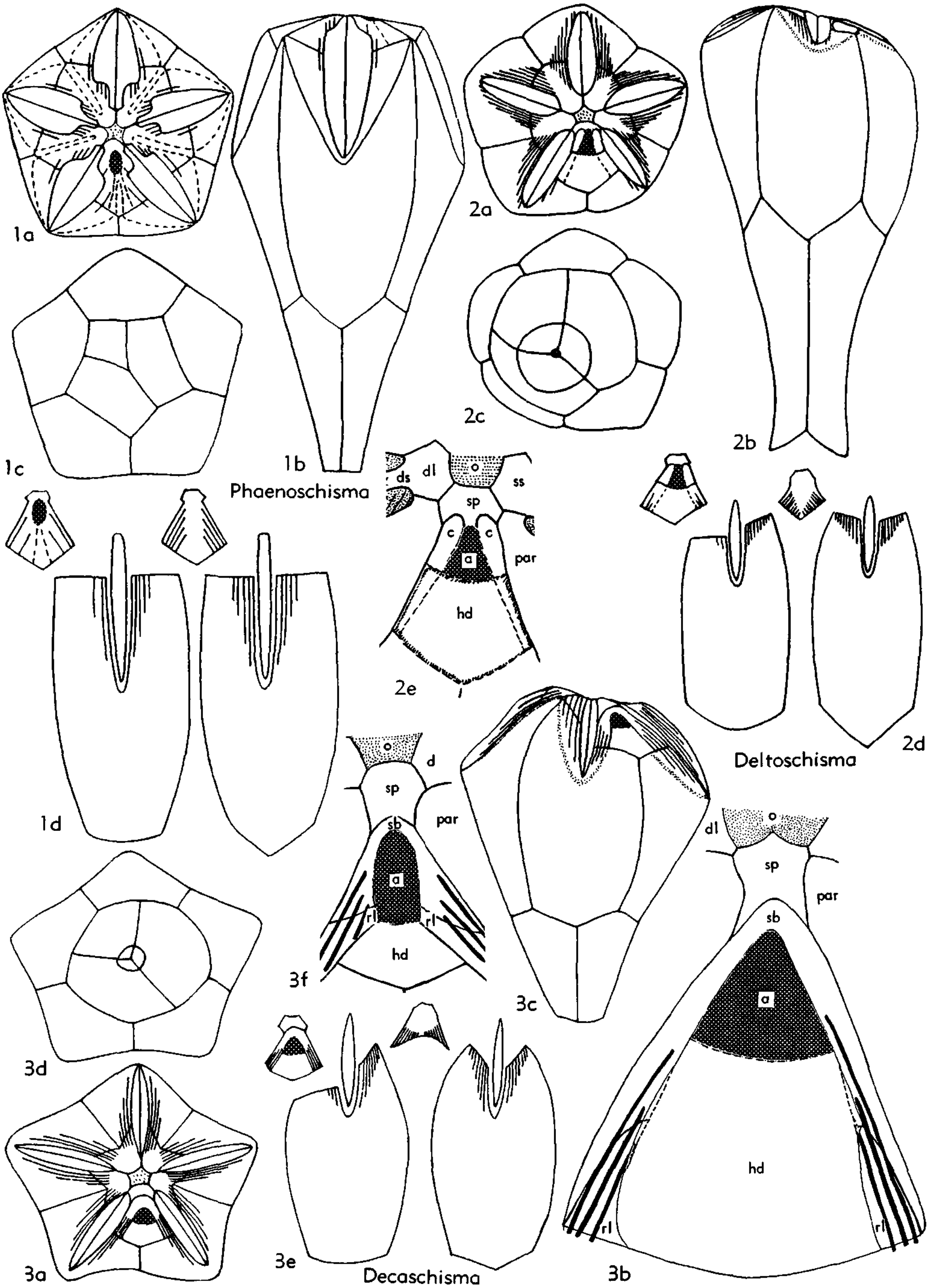

FIG. 234. Phaenoschismatidae (p. S400). [Explanation: *a*, anal opening, *c*, cryptodeltoid plate; *d*, deltoid plate; *dl*, deltoid lip; *ds*, deltoid septum; *hd*, hypodeltoid; *o*, oral opening; *par*, posterior ambulacrum (right); *rl*, radial limb; *sb*, subdeltoid plate; *sp*, superdeltoid plate.]

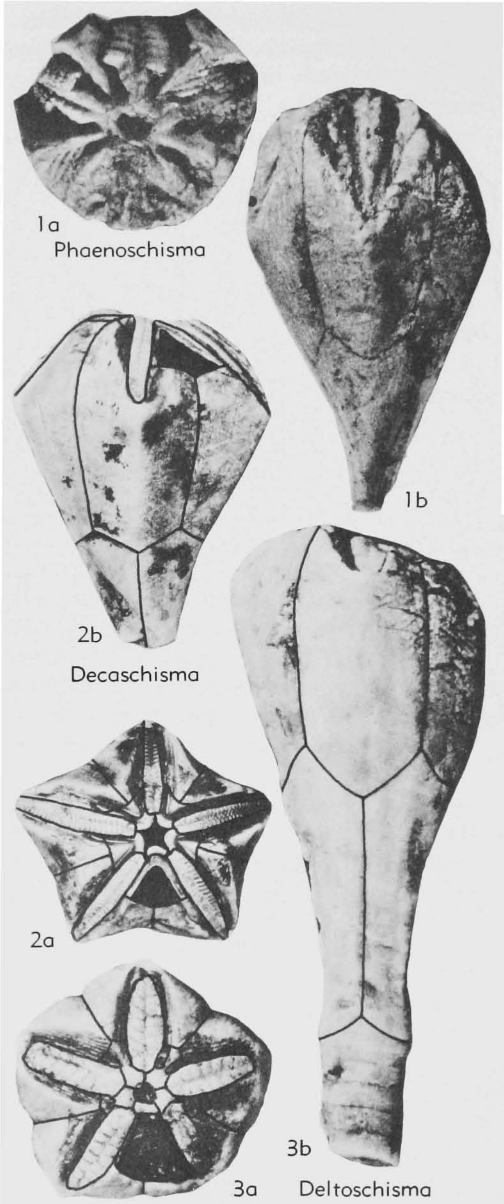

FIG. 235. Phaenoschismatidae (p. S400).

quately large scale. In this manner we may be able to fill in morphologic, stratigraphic, and geographic gaps in knowledge. A somewhat detailed account of previous classifications given in the introduction is not repeated here.

Class BLASTOIDEA Say, 1825

[Blastoidea SAY, 1825, p. 313 (type, *Pentremites* SAY, 1820, designated by FAY, herein)] [=Eublastoidea BATHER, 1899, p. 920 (type, *Pentremites* SAY, 1820, designated by FAY, herein)]

Hydrospire-bearing, stemmed echinoderms; theca composed of 18 to 21 major plates, which comprise three basals, surmounted by five radials, above which and alternating with them are five deltoids, in addition to five lancet plates in radial position located within radial sinuses; anal side may contain one, two, three, four, or six anal deltoids; hydrospires external or internal; pores and spiracles present mainly in forms with internal hydrospires. Ambulacra bear numerous biserially constructed brachioles. *Sil.-Perm.*

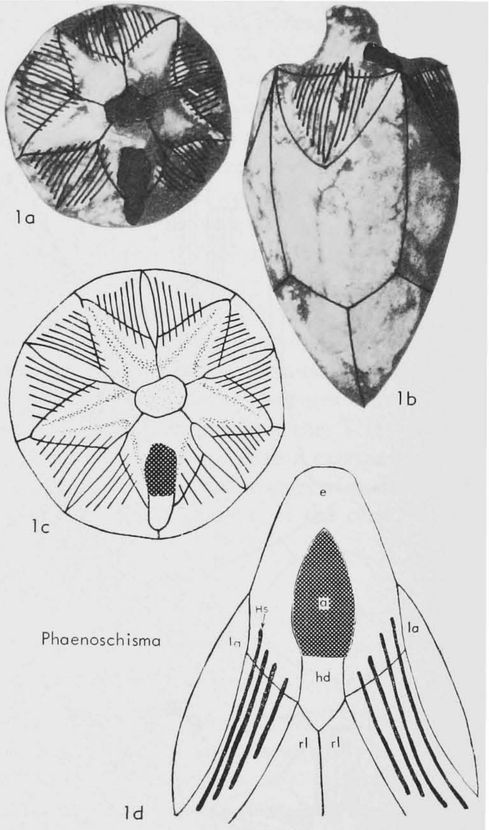

FIG. 236. Phaenoschismatidae (p. S400). [Explanation: *a*, anal opening; *e*, epideltoid plate; *hd*, hypodeltoid; *hs*, hydrospire slit; *la*, lancet plate; *rl*, radial limb.]

Order FISSICULATA Jaekel, 1918

[Fissiculata Jaekel, 1918, p. 108 (type, *Phaenoschisma* Etheridge & Carpenter, 1882, designated by Fay, herein)] [=Mesoblastida Matsumoto, 1929, p. 28 (type, *Phaenoschisma* Etheridge & Carpenter, 1882, designated by Fay, herein)]

Theca with exposed hydrospire slits or spiracular slits. *Sil.-Perm.*

Family PHAENOSCHISMATIDAE Etheridge & Carpenter, 1886

[*nom. correct.* Fay, 1961 (60), p. 19 (*pro* Phaenoschismidae Etheridge & Carpenter, 1886, p. 258)] [=Dipteroblastidae Wanner, 1940, p. 234; Neoschismidae (*recte* Neoschismatidae) Wanner, 1940, p. 238; Nymphaeoblastidae Wanner, 1940, p. 237]

Theca with ten exposed or partially exposed hydrospire fields. *Sil.-Perm.*

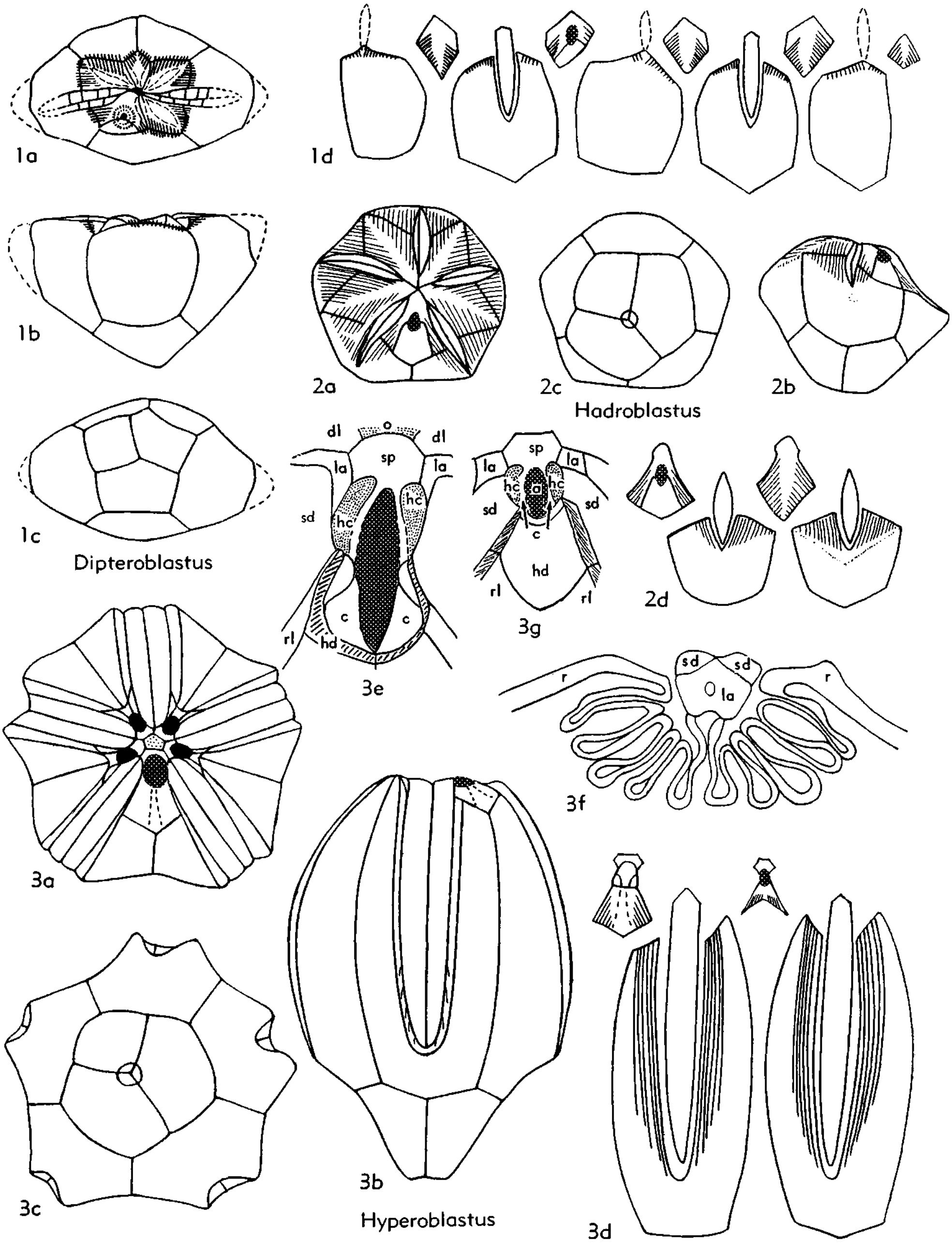

Fig. 237. Phaenoschismatidae (p. S400-S401). [Explanation: *a*, anal opening; *c*, cryptodeltoid plate; *dl*, deltoid lip; *hc*, hydrospire canal; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening; *r*, radial plate; *rl*, radial limb; *sd*, side plate; *sp*, superdeltoid plate.]

Phaenoschisma ETHERIDGE & CARPENTER, 1882, p. 226 [*emend.* MACURDA, 1964 (104), p. 719] [**Pentatrematites acuta* SOWERBY, 1834, p. 456; SD ETHERIDGE & CARPENTER, 1886, p. 270] [=*Conoschisma* FAY, 1961 (60), p. 23 (type, *Codaster laeviusculus* ROWLEY, 1900, p. 65)]. Theca biconical with hydrospire fields mostly hidden, but exposed along aboral ends or along outer ambulacral margins; number of hydrospire slits reduced on anal side; anus between epideltoid and hypodeltoid; lancet exposed along median 0.5 of its width; side plates touching deltoid crests, forming 5 teardrop-shaped spiracle-like openings at adoral end. *L.Carb.(Miss.)*, Eu.-N.Am.——FIG. 234,*1*; 235,*1*. **P. acutum* (SOWERBY), Eng.; 234, *1a,b,* oral and *D*-ray views, ×4.5 (41); 234,*1c,d,* aboral view and plate layout, ×4.5 (162); 235, *1a,b,* oral and *C*-ray views, ×4, ×4.7 (104).——FIG. 236,*1*. *P. laeviusculum* ROWLEY, L.Miss. (Burlington Ls.), USA(Mo.); type species of *Conoschisma, 1a,b,* oral and *D*-ray views, ×4.4 (60); *1c,* oral view, ×5.3 (60); *1d,* plates adjacent to anal opening, ×9 (60).

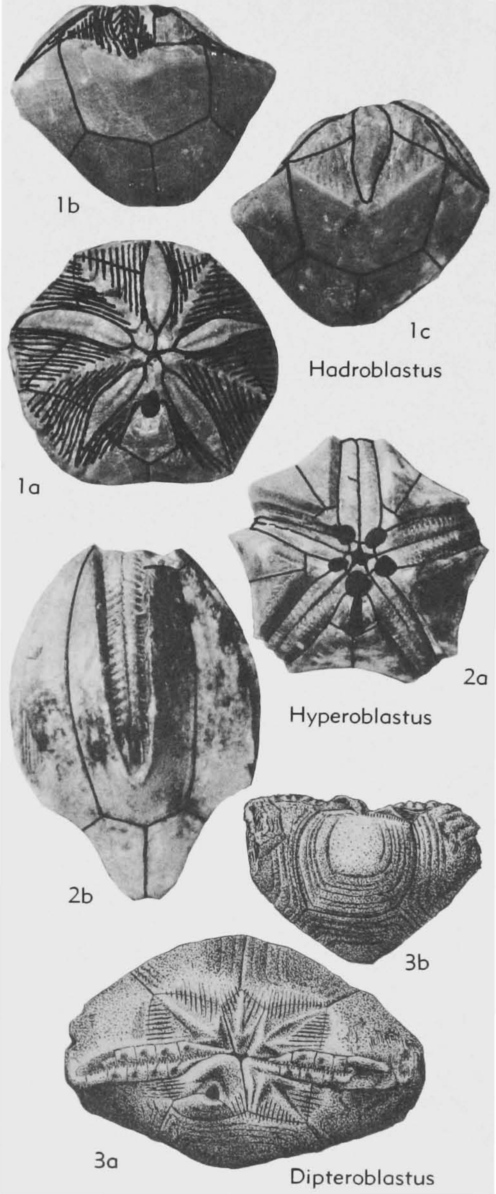

FIG. 238. Phaenoschismatidae (p. S400-S401).

Decaschisma FAY, 1961 (60), p. 27 [**Codaster pentalobus* HALL, 1879, p. 13; OD]. Theca obconical, with well-exposed hydrospire fields; superdeltoid, subdeltoid, and hypodeltoid present; lancet covered by side plates. *Sil.*, USA(Ind.).——FIG. 234,*3a-e*; 235,*2*. **D. pentalobus* (HALL), Niagaran; 234,*3a,* oral view, ×2.6; 234,*3b, CD* interray, ×10.1; 234,*3c, D*-ray view, ×2.6; 234, *3d,e,* aboral view and plate layout, ×2.7 (all 60); 235,*2a,b,* oral and *D*-ray views, ×2.5 (60).——FIG. 234,*3f*. *D. pulchellum* (MILLER & DYER), Niagaran; plates around anal opening, ×10 (60).

Deltoschisma FAY, 1961 (60), p. 29 [**Phaenoschisma archiaci* ETHERIDGE & CARPENTER, 1882, p. 229; OD]. Theca conical, with exposed hydrospire fields; strongly pentalobate in top view; with superdeltoid, 2 cryptodeltoids, and hypodeltoid, cryptodeltoids partly visible externally, partly hidden by hypodeltoid; number of slits reduced on anal side; lancet covered by large side plates. *Dev.*, Spain.——FIG. 234,*2*; 235,*3*. **D. archiaci* (ETHERIDGE & CARPENTER); 234,*2a-d,* oral, *D*-ray, aboral views, and plate layout, ×4.4; 234,*2e,* anal area, ×9.9; 235,*3a,b,* oral and *D*-ray views, ×4.7 (all 60).

Dipteroblastus WANNER, 1940, p. 249 [*emend.* BREIMER & MACURDA, 1965, p. 212] [**D. permicus*; OD]. Theca cup-shaped, with well-exposed hydrospire fields, with 8 to 13 hydrospire slits on *AB, BC,* and *DE* deltoids, but 3 to 6 on epideltoid, and 5 on *EA* deltoid; anus separate, between large epideltoid and large hypodeltoid; with 3 short *A, C,* and *E* ambulacra and 2 elongate *B* and *D* ambulacra confined to summit; lancet exposed along food groove. *Perm.*, E.Indies(Timor).——FIG. 237,*1*; 238,*3*. **D. permicus*; 237,*1a-d,* oral, *D*-ray, aboral views, and plate layout, ×1.7 (178); 238,*3a,b,* oral and C-ray views, ×2.7, ×1.7 (178).

Hadroblastus FAY, 1962 (72), p. 189 [**H. convexus*; OD]. Theca discoidal with rounded summit and base; hydrospire fields each with 11 slits except on anal side where 4 slits occur in each field; anal opening between large epideltoid and equally large hypodeltoid; lancet exposed along middle 0.3 of its width, raised well above broad flat sinus areas and hydrospire fields; ambulacra moderately long, linear, with lancet stipes moderately separated from oral opening; vault

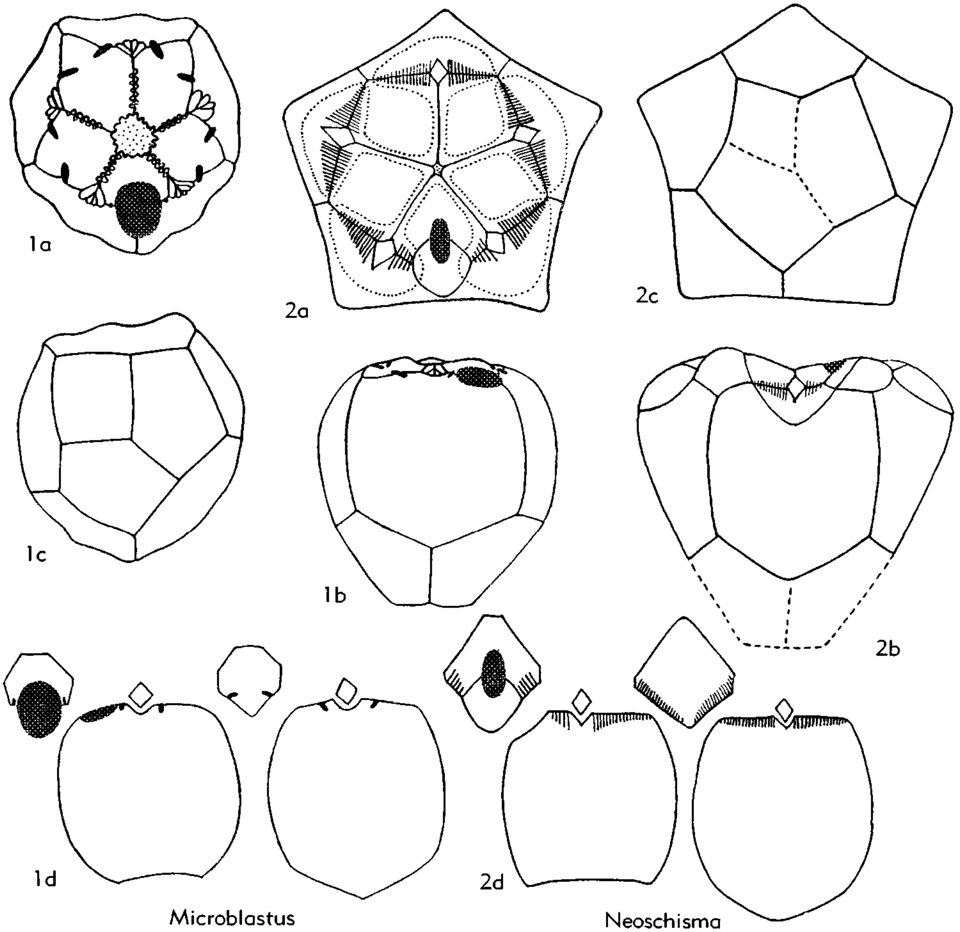

Fig. 239. Phaenoschismatidae (p. S401-S402).

almost equal to pelvic height; basalia large, composed of 3 basals. *L.Miss.*, USA(N.Mex.-Ark.-Okla.).——Fig. 237,*2*; 238,*1*. *H. convexus*, Osag., N.Mex.; 237,*2a-d*, oral, *D*-ray, aboral views, and plate layout, ×2 (72); 238,*1a-c*, oral, *D*-ray, and *B*-ray views, ×2.7 (72).

Hyperoblastus Fay, 1961 (60), p. 30 [*Pentremitidea preciosa* Reimann, 1945, p. 39; OD]. Theca club-shaped, with aboral ends of outermost hydrospire slits exposed; with pores formed as gaps between side plates; spiracles 5, developed between deltoid lip, deltoid septum, lancet, and side plates on each interambulacrum (including anispiracle on anal side); with superdeltoid, 2 cryptodeltoids, and hypodeltoid; lancet covered by side plates. *Dev.*, N.Am.——Fig. 237,*3a-e*; 238,*2*. *H. preciosus* (Reimann), Can.(Ont.); 237,*3a-d*, oral, *D*-ray, aboral views, and plate layout, ×3.5; 237,*3e*, anal area, ×10; 238,*2a,b*, oral and *D*-ray views, ×2.9 (all 60).——Fig. 237,*3f,g*. *H. filosus* (Whiteaves), Can.(Ont.); *3f*, cross sec. of ambulacrum, ×8.8; *3g*, anal area, ×10.2 (all 60).

Microblastus Eykeren, 1942, p. 283 [*M. pocilloformis*; OD]. Theca small, cup-shaped, with small restricted hydrospire slits confined to summit; anal opening separate from slits, between large, wide epideltoid and radial limbs, possibly with small ?hypodeltoid on aboral border; ambulacra short, wide, small, well away from mouth, with total of 2 or 3 side plates on each side. *Perm.*, E.Indies (Timor).——Fig. 239,*1*; 240,*1*. *M. pocilloformis*; 239,*1a-d*, oral, *D*-ray, aboral views, and plate layout, ×8.8 (42); 240,*1a,b*, oral and *CD*-interray views, ×6 (42).

Neoschisma Wanner, 1924 (173), p. 6 [*N. verrucosum*; OD]. Theca cup-shaped, with widely exposed hydrospire fields, each with 5 to 18 slits except on anal side where 1 to 5 slits occur on each side of anal opening; anal opening between

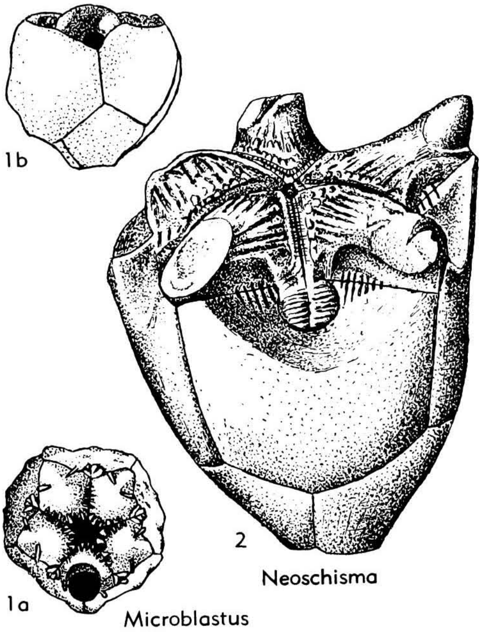

FIG. 240. Phaenoschismatidae (p. *S*401-*S*402).

large epideltoid and moderately large hypodeltoid; ambulacra short, wide, small, well away from mouth, confined to summit. *Perm.*, E.Indies (Timor).——FIG. 239,*2*. **N. verrucosum*; *2a-d*, oral, *D*-ray, aboral views, and plate layout, ×2.4 (173).——FIG. 240,*2*. *N. timorense* WANNER, Perm., Timor; *B*-ray view, ×3.3 (178).

Notoblastus BROWN, 1941, p. 98 [**N. brevispinus*; OD]. Theca discoidal, with widely exposed hydrospire fields, each with 12 to 14 hydrospire slits except on anal side, where slits are few; small anus separate, between large epideltoid and smaller hypodeltoid; ambulacra moderately short, longer than wide, with lancet stipe well away from mouth; radials prolonged into small, short, winglike processes; stem seemingly absent. *Perm.*, E.Australia.——FIG. 241,*4*; 242,*3*. **N. brevispinus*; 241,*4a,b*, oral and *C*-ray views, ×1.3; 242,*3a-d*, oral, *D*-ray, aboral views, and plate layout, ×1.3 (20, 179).

Nymphaeoblastus VON PEETZ, 1907, p. 15 [**N. miljukovi*; OD]. Theca ellipsoidal, with widely exposed hydrospire fields, each containing 10 to 15 slits which extend well down sides of theca; anal opening between small epideltoid and elongate hypodeltoid; lancet apparently covered by side plates; ambulacra long, linear, recurved below; base concave; deltoids almost as long as radials. *L.Carb.*, Eu.(USSR)-Asia(Japan).——FIG. 241,*1*. *N. anossofi* YAKOVLEV, Tournais., Japan; *1a,b*, oral and E-ray views, ×1.3 (52).——FIG. 242,*1*. **N. miljukovi*, USSR; *1a-d*, oral, *D*-ray, aboral views, and plate layout, ×0.8 (131, 190).

Phaenoblastus FAY, 1961 (60), p. 40 [*emend.* MACURDA, 1964 (104), p. 723] [**Pentremites*

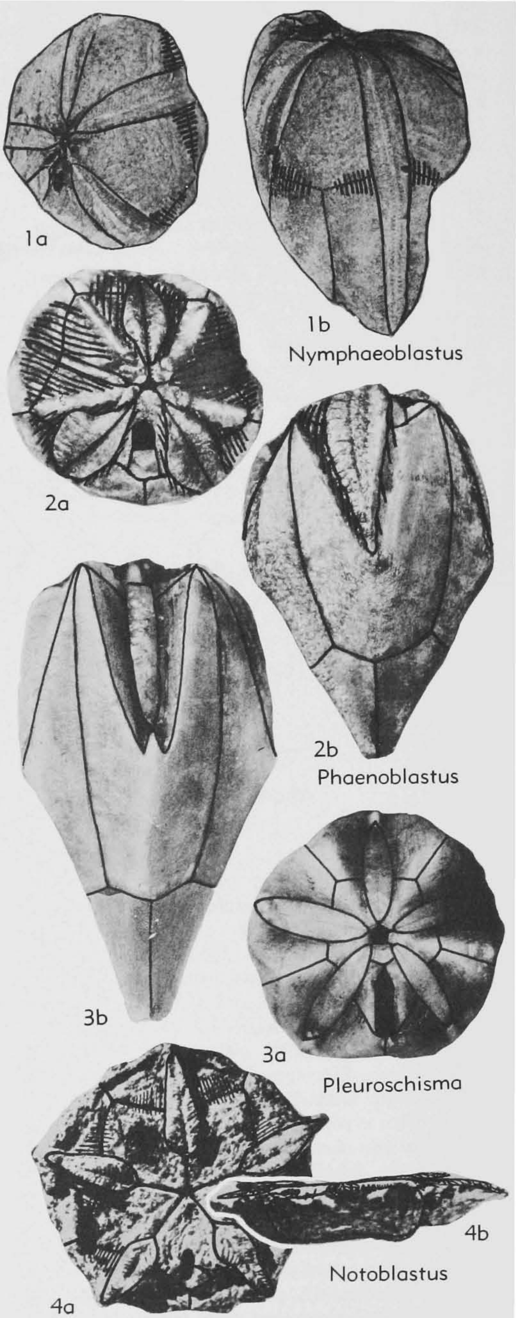

FIG. 241. Phaenoschismatidae (p. *S*402-*S*405).

caryophyllatus DEKONINCK & LEHON, 1854, p. 197; OD]. Theca club-shaped with ventral coronal processes; hydrospire fields wide, deeply indented, mostly hidden, each with 7 or 8 slits except on anal side where 4 occur; anal opening between large U-shaped epideltoid and small hypodeltoid; lancet widely exposed throughout its full width, deeply excavated in sinus; side plates large, covering most of slits, adorally forming 4 paired spiracle-like openings and false anispiracle with deltoid crests; ambulacra moderately long, petaloid; vault almost equal to pelvic height; basalia moderately large, composed of 3 basals; radials overlapping deltoids. *L.Carb.*, Eu.——FIG. 241,*2*; 242,*2*. **P. caryophyllatus* (DEKONINCK & LEHON), Tournais., Belg.; 241,*2a,b*, oral, *D*-ray views,

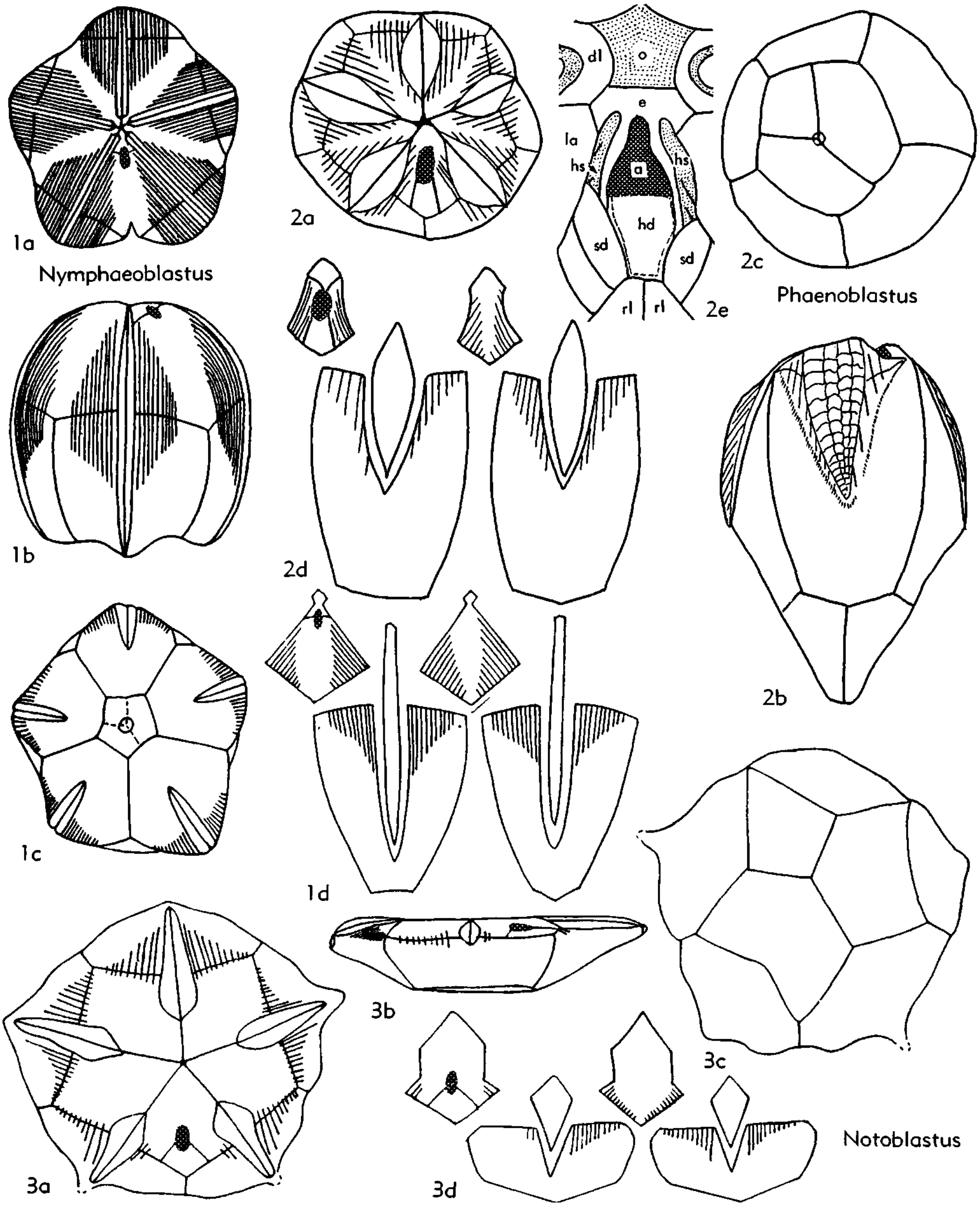

FIG. 242. Phaenoschismatidae (p. *S*402-*S*404). [Explanation: *a*, anal opening; *dl*, deltoid lip; *e*, epideltoid plate; *hd*, hypodeltoid; *hs*, hydrospire slit; *la*, lancet plate; *o*, oral opening; *rl*, radial limb; *sd*, side plate.]

×4; 242,*2a-d,* oral, *D*-ray, aboral views, plate layout, ×4; 242,*2e,* anal view, ×10 (60).

Pleuroschisma Reimann, 1945, p. 24 [**Pentremites lycorias* Hall, 1862, p. 151; OD]. Theca club-shaped, with exposed hydrospire fields; superdeltoid, 2 exposed cryptodeltoids, and hypodeltoid present; ambulacra extending downward along theca; lancet completely covered by side plates. *Dev.,* USA(N.Y.)-Can.(Ont.).——Fig. 241,*3*; 243,*1e*. *P. ontario* Reimann, M.Dev., Can.(Ont.); 241,*3a,b,* oral, *D*-ray views, ×6.2; 243,*1e,* anal area, ×10.2 (60).——Fig. 243,*1a-d*. **P. lycorias*

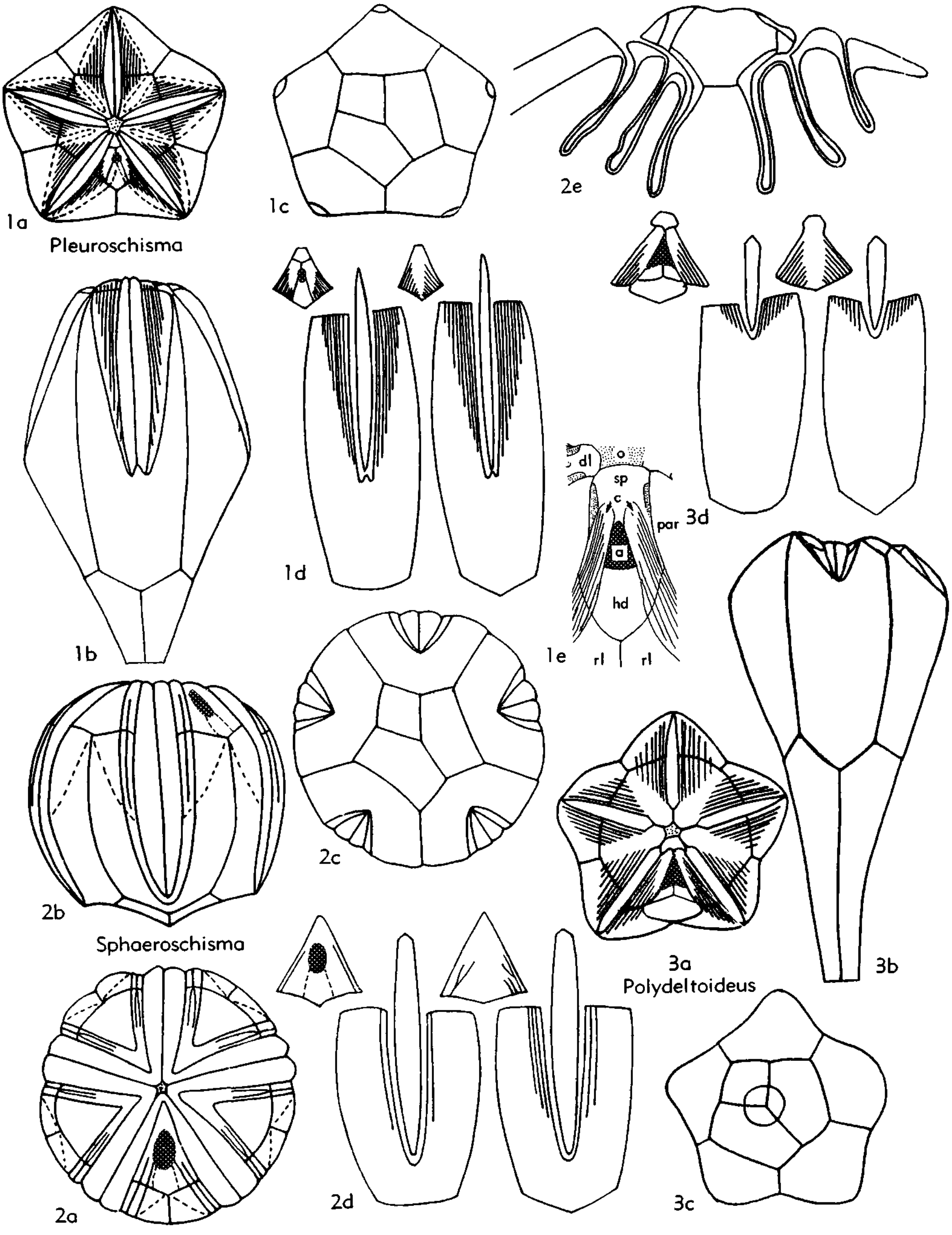

Fig. 243. Phaenoschismatidae (p. *S*404-*S*405). [Explanation: *a,* anal opening; *c,* cryptodeltoid plate; *dl,* deltoid lip; *hd,* hypodeltoid; *o,* oral opening or oral plate; *par,* posterior ambulacrum (right); *rl,* radial limb; *sp,* superdeltoid plate.]

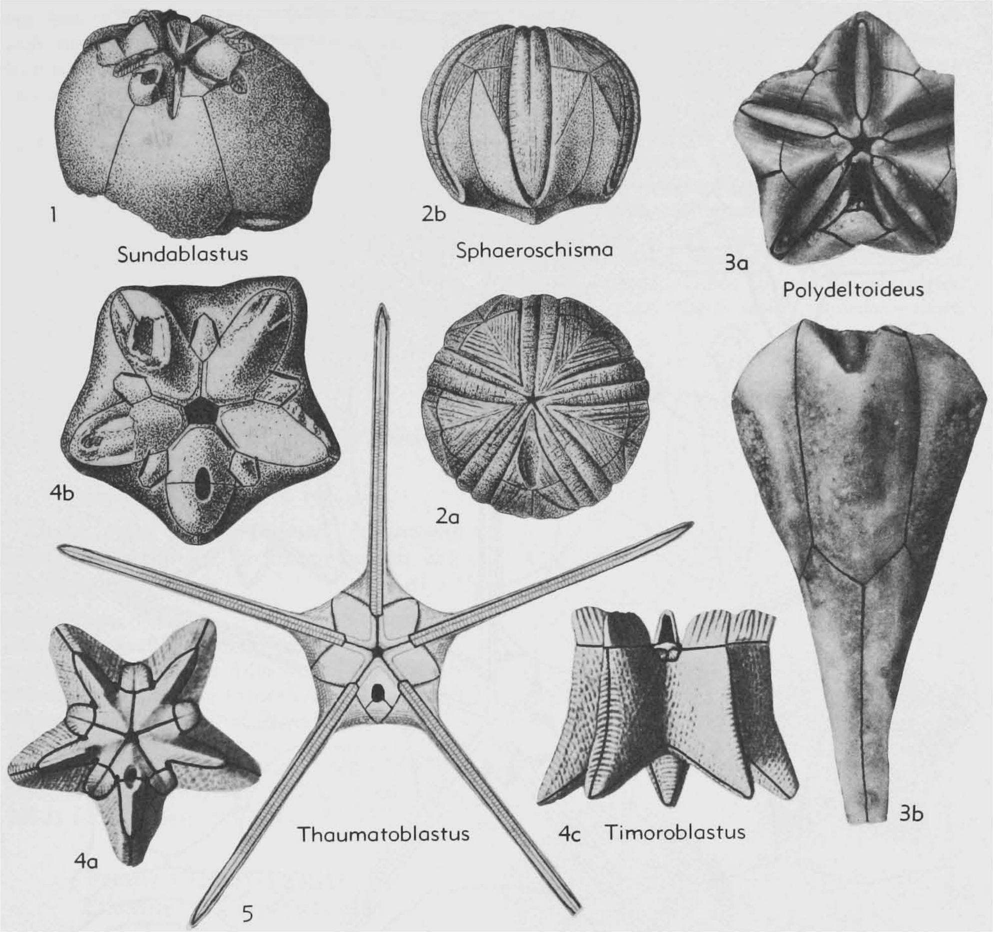

FIG. 244. Phaenoschismatidae (p. *S*405-*S*407).

(HALL), M.Dev., USA(N.Y.); *1a-d,* oral, *D*-ray, aboral views, and plate layout, ×4.4 (83, 139).

Polydeltoideus REIMANN & FAY, 1961, p. 86 [**Polydeltoideus enodatus*; OD]. Conical theca with exposed hydrospire fields; superdeltoid, 2 cryptodeltoids, 2 paradeltoids, and hypodeltoid present; ambulacra short, projected laterally, with broad sinuses; lancet covered by side plates; anal opening between superdeltoid, 2 cryptodeltoids, and 2 paradeltoids. *Sil.,* USA(Okla.)-?Czech.——FIG. 243,*3*; 244,*3*. **P. enodatus,* Sil., Okla.; 243,*3a-d,* oral, *D*-ray, aboral views, and plate layout, ×3 (143); 244,*3a,b,* oral, *D*-ray views, ×3 (143).

Sphaeroschisma WANNER, 1924 (174), p. 195 [*emend.* BREIMER & MACURDA, 1965, p. 212] [**S. somoholense*; OD]. Theca subglobular, fissiculate with 10 partially exposed hydrospire fields, with 1 to 3 folds per field, partially formed into spiracular slits; one fold is on both sides of *C* ambulacrum and on posterior side of *D* ambulacrum; 2 folds are on left side of *A* ambulacrum and anterior side of *B* ambulacrum, each opening into a spiracular slit; all other hydrospire fields have 3 folds, opening into single spiracular slit on radial limb and into 2 slits on deltoid; anal opening between epideltoid and ?hypodeltoid; deltoids overlap radials; deltoids and slits visible in side view; lancet exposed; ambulacra long, recurved below. *Perm.,* E.Indies(Timor).——FIG. 243,*2*; 244,*2*. **S. somoholense*; 243,*2a-d,* oral, *D*-ray, aboral views, and plate layout, ×3.6; 243,*2e,* cross sec. of *E* ambulacrum, ×13; 244, *2a,b,* oral, *A*-ray views, ×2.7 (174).

Sundablastus WANNER, 1924 (173), p. 32 [**S. weberi*; OD]. Theca subglobular, with small restricted hydrospire fields confined to summit; anal opening between large epideltoid and large hypodeltoid; ambulacra short, confined to summit, adjacent to mouth; lancet longer than wide, short, apparently covered by side plates; basals

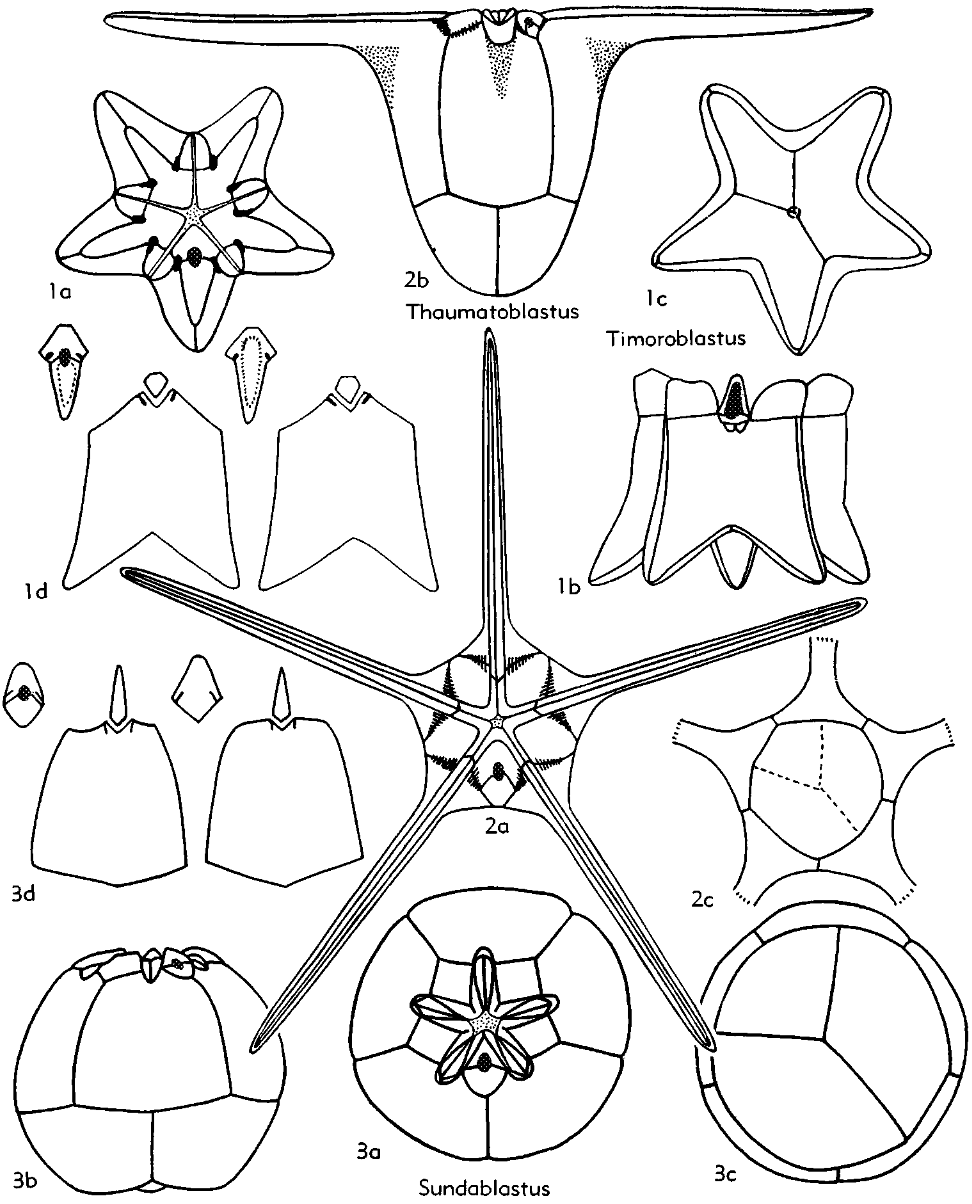

FIG. 245. Phaenoschismatidae (p. S405-S407).

almost equal in size to radials. *Perm.*, E.Indies (Timor).——FIG. 244,*1*; 245,*3*. **S. weberi*; 244,*1*, oblique *C*-ray view, ×1.3; 245,*3a-d*, oral, *D*-ray, aboral views, and plate layout, ×1.18 (173).

Thaumatoblastus WANNER, 1924 (174), p. 201 [**T. longiramus*; OD]. Theca cup-shaped, with widely exposed hydrospire fields; anal opening between large epideltoid and large hypodeltoid; slits reduced in number on anal side, but 7 or 8 slits occur in each field of other interambulacra; lancet plates long, extending into winglike extensions of radials; lancets almost completely covered by side plates; base round, summit flat. *Perm.*, E.Indies (Timor).——FIG. 244,*5*; 245,*2*. **T. longiramus*; 244,*5*, oral view, ×0.4; 245,*2a-c*, oral, *D*-ray, aboral views, ×0.44 (174).

Timoroblastus WANNER, 1924 (173), p. 14 [**T. coronatus typus*; OD]. Theca star-shaped, with small constricted hydrospire fields confined to summit, each with 1 to 3 hydrospire slits opening into it; one hydrospire slit on each side of anal opening; anus between wide epideltoid and long hypodeltoid; ambulacra short, wide, rounded aborally, well away from mouth; lancet covered by side plates; deltoids and radial limbs flaring outwardly into bluntly rounded winglike processes, with ambulacra in depressed areas between; deltoids projected ventrally into coronal processes; radials projected dorsally into alate processes; base concave. *Perm.*, E.Indies(Timor).——Fig. 244, *4a,c*; 245,*1*. **T. coronatus typus*; 244,*4a,c*, oral, *A*-ray views, ×1.7; 245,*1a-d*, oral, *D*-ray, aboral views, plate layout, ×1.7 (173).——Fig. 244, *4b*. *T. coronatus tesselatus* Wanner, Perm., Timor; oral view, ×2 (173).

Family BRACHYSCHISMATIDAE Fay, 1961

[Brachyschismatidae Fay, 1961 (60), p. 19]

Theca with nine exposed hydrospire fields; slits atrophied or absent on left side of anal opening. *Dev.*

Brachyschisma Reimann, 1945, p. 22 [**Codaster corrugatus* Reimann, 1935, p. 25; OD]. Theca conical, with hydrospire fields well exposed; superdeltoid, subdeltoid, and hypodeltoid present; lancet covered by side plates. *M.Dev.*, USA(N.Y.).——Fig. 246,*1*. **B. corrugatum* (Reimann); *1a-c*, plate layout, aboral, *D*-ray views, ×2.3; *1d*, oral view, ×2.2; *1e*, *C*-ray view, ×2.5; *1f*, oral view, ×2.3; *1g*, anal view, ×8.7 (60, 137, 139).

Family CODASTERIDAE Etheridge & Carpenter, 1886

[Codasteridae Etheridge & Carpenter, 1886, p. 257]
[=Angioblastidae Wanner, 1940, p. 235]

Theca with eight exposed or constricted hydrospire fields; hydrospire slits lacking on anal side. *Dev.-Perm.*

Codaster M'Coy, 1849, p. 250 [**C. acutus*; OD]. Theca conical, with flat summit and rounded base; hydrospire fields well exposed; epideltoid and ?hypodeltoid present; lancet stipe away from mouth; lancet covered by side plates; radials overlapping deltoids. *L.Carb.*, Eu.(Eng.).——Fig. 247,*3*; 248,*1*. **C. acutus*; 247,*3a-d*, oral, *D*-ray, aboral views, plate layout, ×2.2; 248,*1a,b*, oral, *D*-ray views, ×2.1 (10, 41, 60, 100).

Agmoblastus Fay, 1961 (59), p. 278 [**Paracodaster dotti* Moore & Strimple, 1942, p. 90; OD]. Form subcylindrical; hydrospire fields moderately exposed, each with 4 to 8 slits excavated in radials and deltoids, slits absent on anal side; anal opening between large U-shaped epideltoid and adjacent radial limbs, or possibly with small hypodeltoid on aboral side (atrophied or ?washed away); deltoids high, wide, arrow-shaped; ambulacra short, well away from oral opening; basals 3, large; lancet covered by side plates. *Penn.*, N.Am.——Fig. 247,*1*; 248,*2*. **A. dotti* (Moore & Strimple), USA(Okla.); 247,*1a-d*, oral, *C*-ray, aboral views, plate layout, ×3.7; 248,*2a,b*, oral, *C*-ray views, ×4.2 (59).

Angioblastus Wanner, 1931, p. 53 [**A. variabilis*; OD]. Theca subglobular, with small restricted hydrospire fields confined to summit, with 1 to 4 hydrospire slits in each field; anal opening separate from slits, located between long epideltoid and short hypodeltoid; lancet covered by side plates, with lancet stipe close to mouth; ambulacra short,

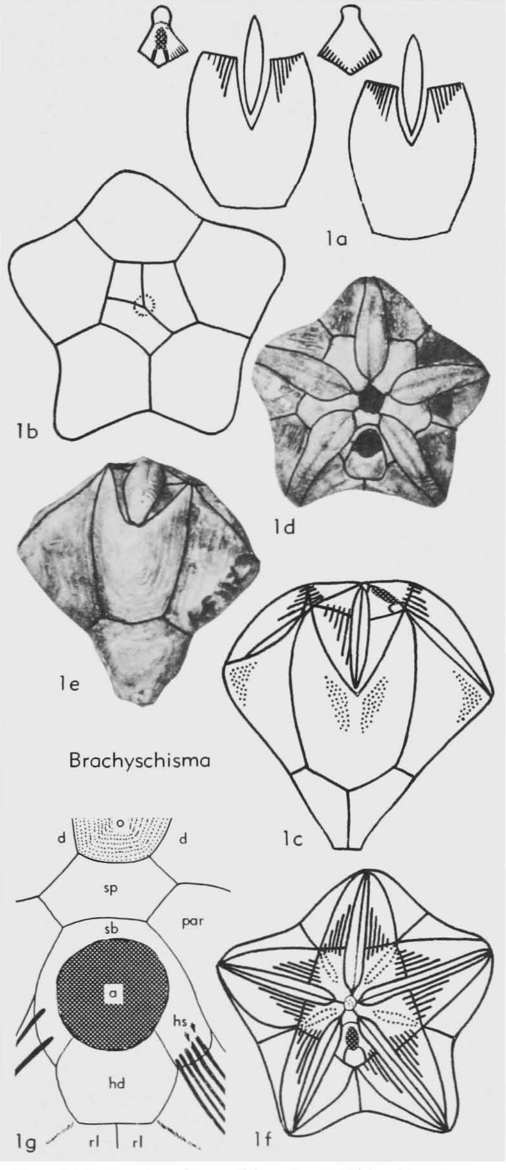

Fig. 246. Brachyschismatidae (p. S407). [Explanation: *a*, anal opening; *d*, deltoid plate; *hd*, hypodeltoid; *hs*, hydrospire slit; *o*, oral opening; *par*, posterior ambulacrum (right); *rl*, radial limb; *sb*, subdeltoid plate; *sp*, superdeltoid plate.]

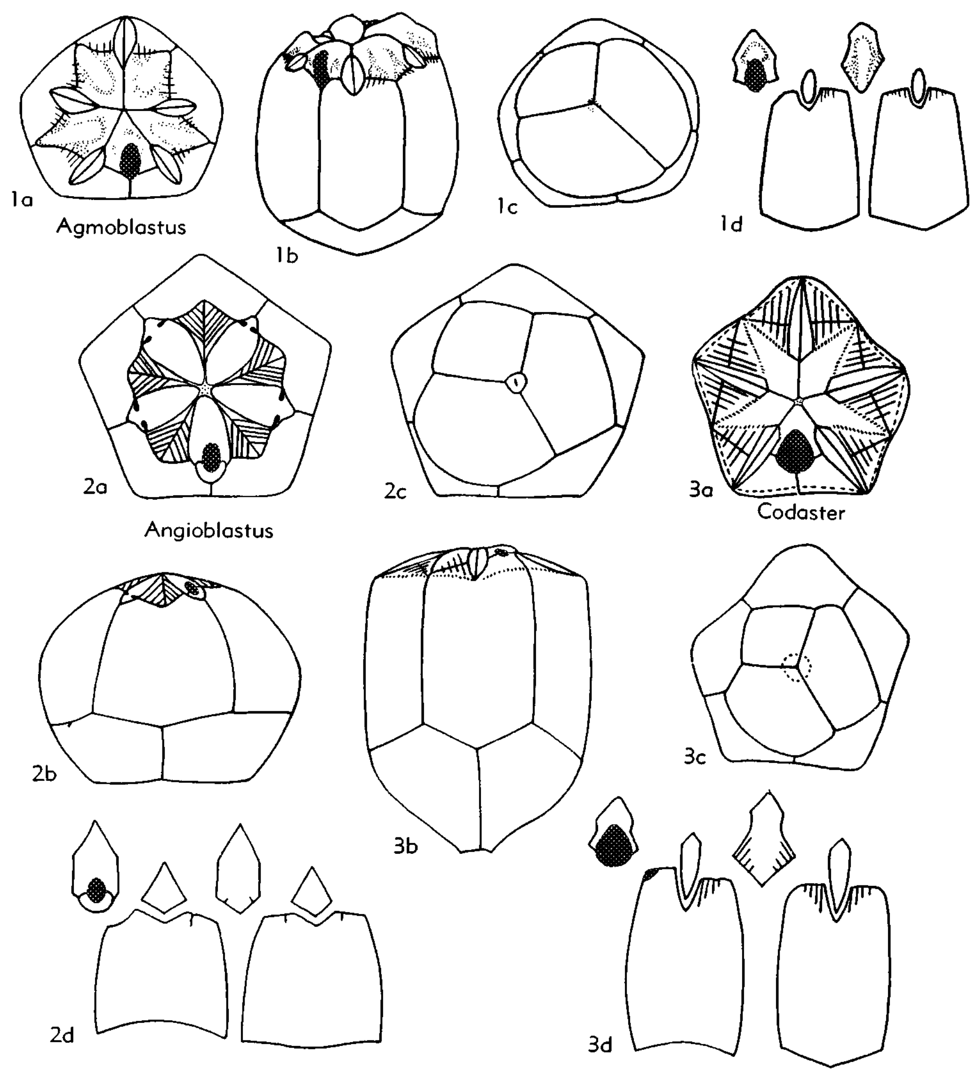

Fig. 247. Codasteridae (p. S407-S408).

wide, confined to summit; deltoids elongate, narrow. *Perm.*, E.Indies(Timor).——Fig. 247,*2*; 249, *6*. _*A. variabilis_; 247,*2a-d*, oral, *D*-ray, aboral views, plate layout, ×3.6; 249,*6a,b*, oral, *CD*-interray views, ×4 (175).

Heteroschisma Wachsmuth, 1883, p. 352 [_*H. gracile_; OD] [=*Trionoblastus* Fay, 1961 (60), p. 45 (type, *Pentremites subtruncatus* Hall, 1858, p. 485)]. Theca obconical with hydrospire fields well exposed; superdeltoid, subdeltoid, and presumably small ?hypodeltoid on anal side; hydrospire slits absent on anal side; lancet covered by side plates. *Dev.*, N.Am.——Fig. 248,*3a,b*; 250, *1h*. _*H. gracile,_ M.Dev., USA(Mich.); 248,*3a,b*, *D*-ray view, oral view, ×3.5; 250,*1h*, anal area, ×9.7 (60).——Fig. 250,*1a-e*. *H. subtruncatus* (Hall), USA(Iowa); *1a-d*, oral, *D*-ray, aboral views, plate layout, ×4.4; *1e*, anal view, ×9.7 (60).——Fig. 250,*1f*. *H. pyramidatus* (Shumard), M.Dev., USA(Ohio); anal area, ×7.3 (60).——Fig. 250,*1g*. *H. canadense* (Billings); M.Dev., Can.(Ont.); anal area, ×9.7 (60).

Indoblastus Wanner, 1924 (174), p. 28 [*emend.* Breimer & Macurda, 1965, p. 212] [_*I. granulatus_; OD]. Theca pear- to cup-shaped, with small restricted hydrospire fields confined to summit; anal opening between large epideltoid and equally large raised hypodeltoid; ambulacra moderately long, mostly confined to summit; lancet covered by side plates, with lancet stipe well away from mouth. *Perm.*, E.Indies(Timor).——Fig. 249,*2*; 250,*2*. _*I. granulatus_; 249,*2a,b*, oral, *D*-ray views, ×2,

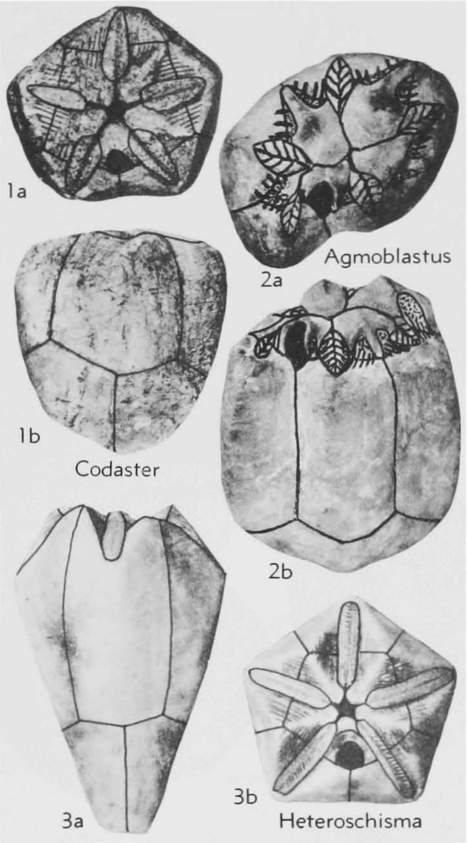

FIG. 248. Codasteridae (p. S407-S408).

×1; 250,*2a-d*, oral, *D*-ray, aboral views, plate layout, ×1.18 (173, 178).

Nannoblastus WANNER, 1924 (173), p. 24 [**N. pyramidatus*; OD]. Theca widely conical to cup-shaped, with small, short, restricted hydrospire fields confined to flat summit, appearing as 8 small slits; anus separate from slits, located between large epideltoid and small hypodeltoid; lancet covered by 2 or 3 side plates, short, wide, well away from mouth, confined to summit; with small, rounded radial wings. *Perm.*, E.Indies (Timor).——FIG. 249,*1*; 250,*3*. **N. pyramidatus*; 249,*1a-c*, oral view, ×6, oral, *CD*-interray views, ×3.1; 250,*3a-d*, oral, *D*-ray, aboral views, plate layout, ×5.9 (174, 175).

Paracodaster YAKOVLEV, 1940, p. 887 [**P. miloradovitschi*; OD]. Theca subglobular, with moderately exposed hydrospire fields confined to deltoids proper; hydrospire slits absent in anal area; anal opening between large epideltoid and radial limbs, with possible small ?hypodeltoid present; slits and ambulacra short, confined to summit; lancet stipes well away from mouth. *L.Perm.*, Eu. (USSR). —— FIG. 249,*4*; 251,*3*. **P. miloradovitschi*; 249,4, oral view, ×2; 251,*3a-d*, oral, *D*-ray, aboral views, plate layout, ×1.75 (186, 190).

Pterotoblastus WANNER, 1924 (173), p. 9 [**P. gracilis*; OD]. Theca cup-shaped, with moderately exposed to restricted hydrospire fields, each with 2 or 3 wide hydrospire slits; large epideltoid with small anal opening between it and radial limbs, possibly with small ?hypodeltoid; ambulacra moderately short, extended on long winglike projections of radials; lancet well away from oral opening, covered by few large side plates; with 3 basal plates. *Perm.*, E.Indies(Timor).——FIG. 249,*3*; 251,*2*. **P. gracilis*; 249,*3a*, oral view, ×8.2; 249, *3b*, *CD*-interray, ×2.5; 251,*2a-d*, oral, *D*-ray, aboral views, plate layout, ×1.1 (173, 175).

Sagittoblastus YAKOVLEV, 1937, p. 10 [**Timoroblastus wanneri* YAKOVLEV, 1926, p. 54; OD]. Theca globular, with small, deep, restricted hydrospire fields on summit, each with 2 or 3 hydrospire slits; deltoids arrow-shaped, wide; large epideltoid, with small anal opening between it and radial limbs, possibly with small ?hypodeltoid (missing) on aboral side of anal opening; with extremely short lancet covered by side plates; lancet well away from mouth. *Perm.*, Eu. (USSR).——FIG. 249,*5*; 251,*1*. **S. wanneri* (YAKOVLEV); 249,*5*, oral view, ×3.5; 251,*1a-d*, oral, *D*-ray, aboral views, plate layout, ×3.5 (184, 185, 190); 251,*1e*, anal view, ×10 (60).

Family OROPHOCRINIDAE Jaekel, 1918

[Orophocrinidae JAEKEL, 1918, p. 109] [=Anthoblastidae WANNER, 1940, p. 237] [=Pentablastidae SIEVERTS-DORECK, 1951, p. 113]

Theca with ten elongate spiracular slits bordering ambulacra. *Miss.-Perm.*

Orophocrinus VON SEEBACH, 1864, p. 110 [*emend.* MACURDA, 1965 (106), p. 1053] [**Pentremites stelliformis* OWEN & SHUMARD, 1850, p. 67; OD] [=*Codonites* MEEK & WORTHEN, 1869, p. 84 (*nec* AUDOUIN, 1826) (type, *Pentremites stelliformis* OWEN & SHUMARD); *Mitra* CUMBERLAND, 1826, *partim*, p. 31 (*non* MARTYN, 1784; *nec* BOLTEN, 1798; LAMARCK, 1798; LESSON, 1837; ALBERS, 1850) (type, *Mitra vera* CUMBERLAND, 1826)]. Theca conical to club-shaped, with 4 to 11 hydrospire slits opening into each spiracular slit; anal opening separate from slits, between epideltoid and hypodeltoid; lancet exposed along main food groove, with lenticular outer side plates between primary side plates, rarely touching abmedial ambulacral margins; thickened radials and deltoids beneath lancet on admedial side of spiracular slits, being termed sublancet or fused hydrospire plate (actually not a separate plate); radials overlap deltoids. *L.Carb.(Miss.)*, Eu.-N. Am.——FIG. 252,*2*; 253,*2*. **O. stelliformis* (OWEN & SHUMARD), L.Miss., Iowa; 252,*2a,b*, oral, *D*-ray views, ×1.68 (60); 253,*2a-d*, oral, *D*-ray,

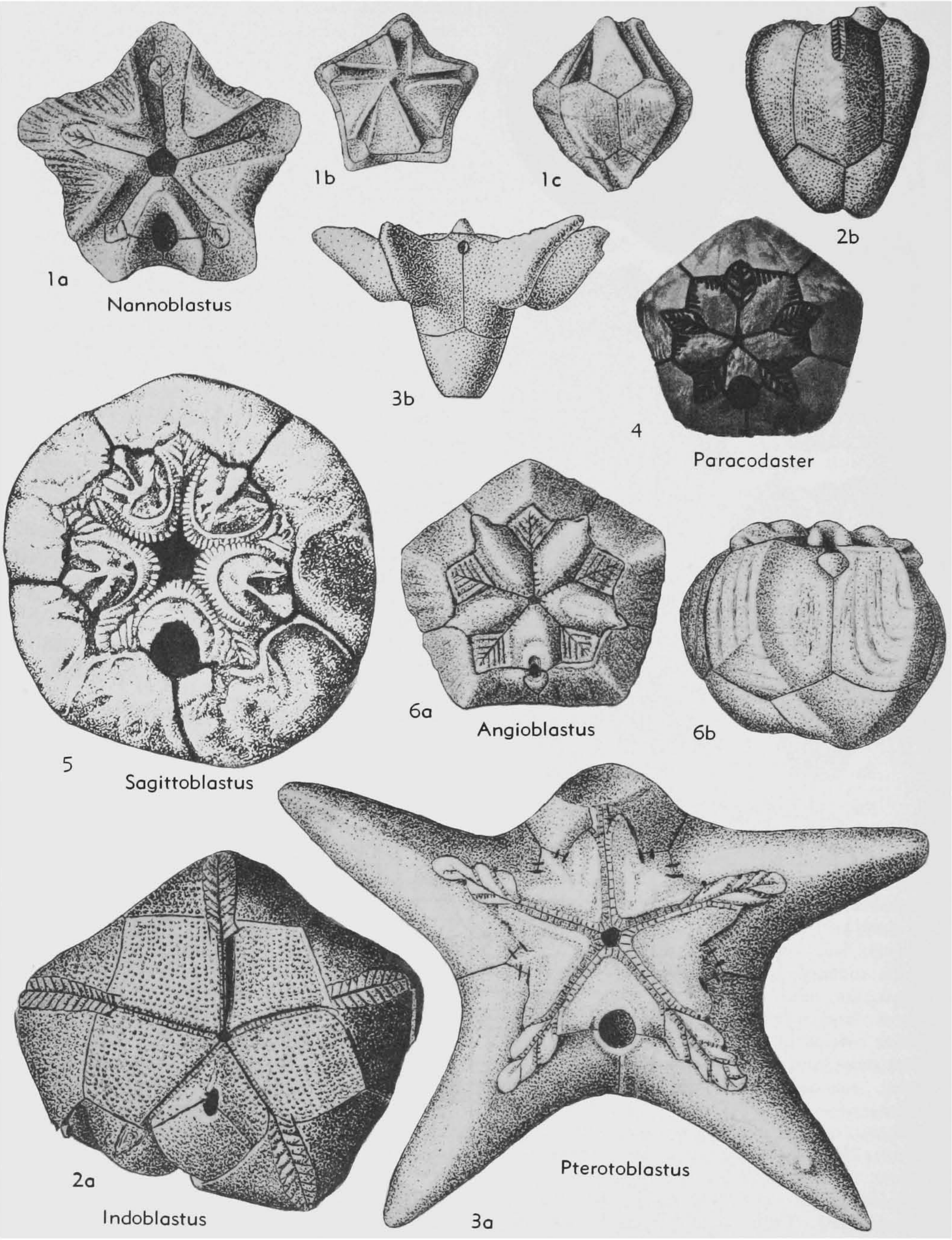

FIG. 249. Codasteridae (p. S407-S409).

aboral, plate layout, ×1.3; 253,*2e*, cross sec. of ambulacrum, ×8.8 (41, 60, 128, 153); 253,*2f*, anal view, ×27 (60).

Anthoblastus WANNER, 1924 (174), p. 205 [**A. brouweri*; OD]. Theca conical to club-shaped, with spiracular slits confined to summit; anal opening separate from slits, between small epideltoid and elongate hypodeltoid; deltoids with coronal processes; lancet exposed widely, forming petaloid ambulacra, which extend downward along theca. *Perm.*, E.Indies(Timor).——FIG. 252, *1*; 253,*1*. **A. brouweri*; 252,*1a,b*, oral, *CD*-interray views, ×1.68; 253,*1a-d*, oral, *D*-ray, aboral views, plate layout, ×2.4 (174).

Pentablastus SIEVERTS-DORECK, 1951, p. 113 [**P. supracarbonicus*; OD]. Theca subglobular, with short spiracular slits confined to summit; anal opening separate from slits, which appear to

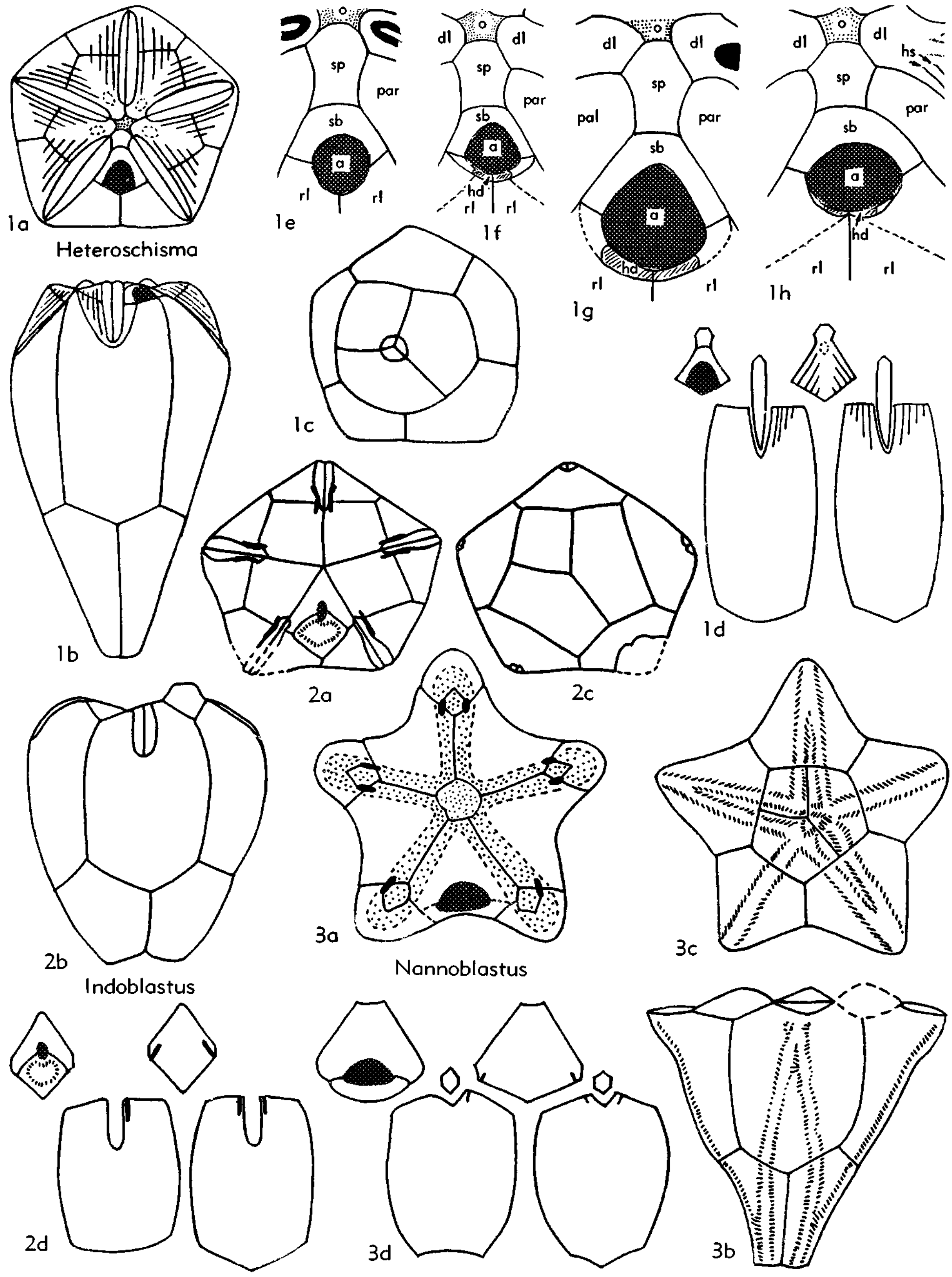

FIG. 250. Codasteridae (p. *S*408-*S*409). [Explanation: *a*, anal opening; *dl*, deltoid lip; *hd*, hypodeltoid; *hs*, hydrospire slit; *o*, oral opening; *pal*, posterior ambulacrum (left); *par*, posterior ambulacrum (right); *rl*, radial limb; *sb*, subdeltoid plate; *sp*, superdeltoid plate.]

terminate in hypodeltoid; anal opening between short epideltoid and long hypodeltoid; hydrospire folds 5 or 6 on each side of an ambulacrum; lancet covered by side plates, linear, slightly recurved below; lancet stipe near mouth; deltoids short, confined to summit; base concave. *U.Carb.*, Spain. ——FIG. 252,*3*; 253,*3*. **P. supracarbonicus*; 252, *3a,b*, oral, *C*-ray views, ×1.14; 253,*3a-d*, oral,

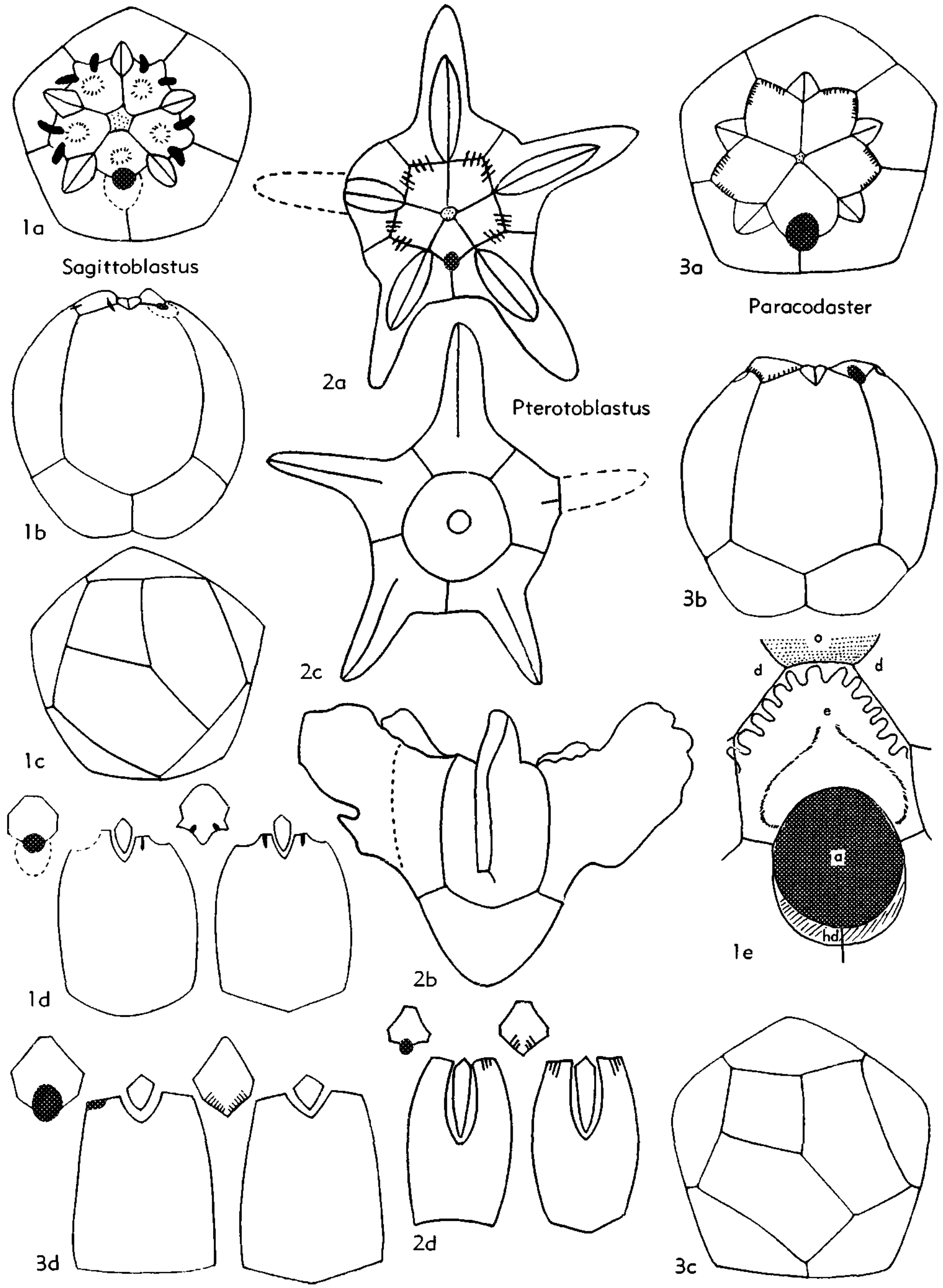

FIG. 251. Codasteridae (p. *S*409). [Explanation: *a*, anal opening; *d*, deltoid plate; *e*, epideltoid plate; *hd*, hypodeltoid; *o*, oral opening.]

D-ray, aboral views, and plate layout, ×1.3; 253,*3e*, cross sec. of ambulacrum, ×4.4 (159).

Family ASTROCRINIDAE
Austin & Austin, 1843

[*nom. correct.* Etheridge & Carpenter, 1886, p. 297 (*pro* Astracrinidae Austin & Austin, 1843, p. 205)] [=Pentephyllidae, Zygocrinidae Bather, 1899, p. 920]

Theca with eight spiracular slits along margins of ambulacra; anal side lacking slits. *Dev.-Perm.*

Astrocrinus Morris, 1843, p. 49 [**A. tetragonus* Morris, 1843, p. 42 (=*Astrocrinites tetragonus* Austin & Austin, 1843, p. 206, *nom. nud.*); OD] [=*Astracrinites* Austin & Austin, 1842, p. 110 (*nom. nud.*); *Astracrinites* Austin & Austin, 1843, p. 205 (invalid original spelling); *Astrocrinites* Austin & Austin, 1843, p. 206 (*non* Conrad, 1841, *nec* Mather, 1843, *nec* de Koninck, 1854); *Zygocrinus* Bronn, 1848, p. 1381 (type, *Astracrinites tetragonus*)]. Theca flattened star-shaped, small; epideltoid present, with possible hypodeltoid; ambulacrum *D* short, wide; lancet covered by side plates; single basal plate; theca spinose. *L.Carb.*, Eu.(Eng.-Scot.).——Fig. 254,*3*. **A. tetragonus*, Eng.; *3a-d*, oral, *D*-ray, aboral views, and plate layout, ×5.3 (41).——Fig. 255,*1*. *A. benniei* (Etheridge), L.Carb., Scot.; *1a*, oral view, ×13.8; *1b*, *D*-ray view, ×14.3; *1c*, aboral view, ×14.5 (177).

Ceratoblastus Wanner, 1940, p. 245 [*emend.* Breimer & Macurda, 1965, p. 214] [**C. nanus*; OD]. Theca steeply conical, with apparently small spiracular slits confined to summit along ambulacral margins; anal opening separate, between a large epideltoid and small ?hypodeltoid; ambulacra short, wide; lancet covered by side plates, with lancet stipe close to mouth. *Perm.*, E.Indies (Timor).——Fig. 254,*1*; 255,*2*. **C. nanus*; 254, *1a-d*, oral, *D*-ray, aboral views, plate layout, ×13.1; 255,*2a*, oral view, ×7.2; 255, *2b*, *DE* interambulacral view, ×2.25 (178).

Cryptoschisma Etheridge & Carpenter, 1886, p. 280 [**Pentremites schultzii* de Verneuil & d'Archiac, 1845, p. 479; OD]. Theca conical with elongate spiracular slits along ambulacral margins, with 9 hydrospire folds opening into each slit; epideltoid and hypodeltoid present; lancet completely exposed, forming petaloid ambulacra. *Dev.*, Spain.——Fig. 254,*2*; 256,*1*. **C. schultzii* (de Verneuil & d'Archiac); 254,*2a-d*, oral, *D*-ray, aboral views, and plate layout, ×3.6 (15, 41, 60); 254, *2e,f*, anal views, ×10 (60); 256,*1a*, oral view, ×4.8; 256,*1b*, *D*-ray view, ×3.5 (60).

?Pentephyllum Haughton, 1859, p. 512 [**P. adarense*; OD]. Theca large, cup-shaped or pentalobate, doubtfully fissiculate, perhaps with 8 elongate spiracular slits along ambulacral margins with short ambulacrum (*D?*), and 4 long, linear ambulacra; thecal plates somewhat irregular, but with 3 large, normally disposed basals, 5 large radials, and 5 short deltoids; anal structures unknown [position uncertain; characters based on interpretations of single cast]. *L.Carb.*, Eire.——Fig. 256,*3*; 257,*2*. **P. adarense*; 256,*3a,b*, oral, *AB?* interambulacral views, ×0.87; 257,*2a-d*, oral, *D*-ray, aboral views, plate layout, ×0.87 (41, 87).

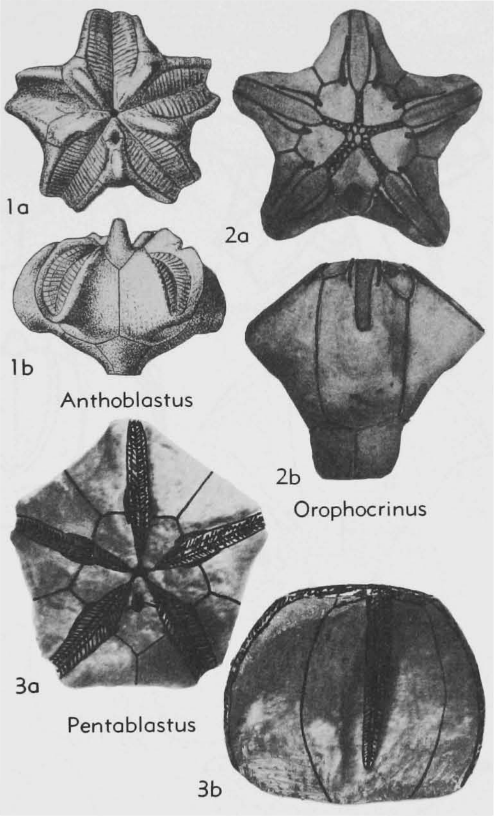

Fig. 252. Orophocrinidae (p. *S*409-*S*412).

Pentremitidea d'Orbigny, 1850, p. 102 [**Pentremites pailletti* de Verneuil, 1844, p. 213] [=*Pentetrematites* Steininger, 1849, p. 19 (*nom. van.*); *Pentremitidia* Quenstedt, 1876, p. 718 (*nom. van.*)]. Theca conical, with elongate spiracular slits, each having approximately 8 hydrospire folds; superdeltoids, subdeltoid, and hypodeltoid present; sinuses deep; lancet covered by side plates, with possible inner side plate present. *Dev.*, Spain-?N.Afr.——Fig. 256,*2*; 257,*1*. **P. pailletti* (de Verneuil); 256,*2a*, oral view, ×3.2; 256,*2b*, *D*-ray view, ×3.5 (60); 257,*1a-d*, oral, *D*-ray, aboral views, plate layout, ×3.6 (60, 167, 168); 257,*1e,f*, cross sec. of ambulacrum, anal area, ×10 (60).

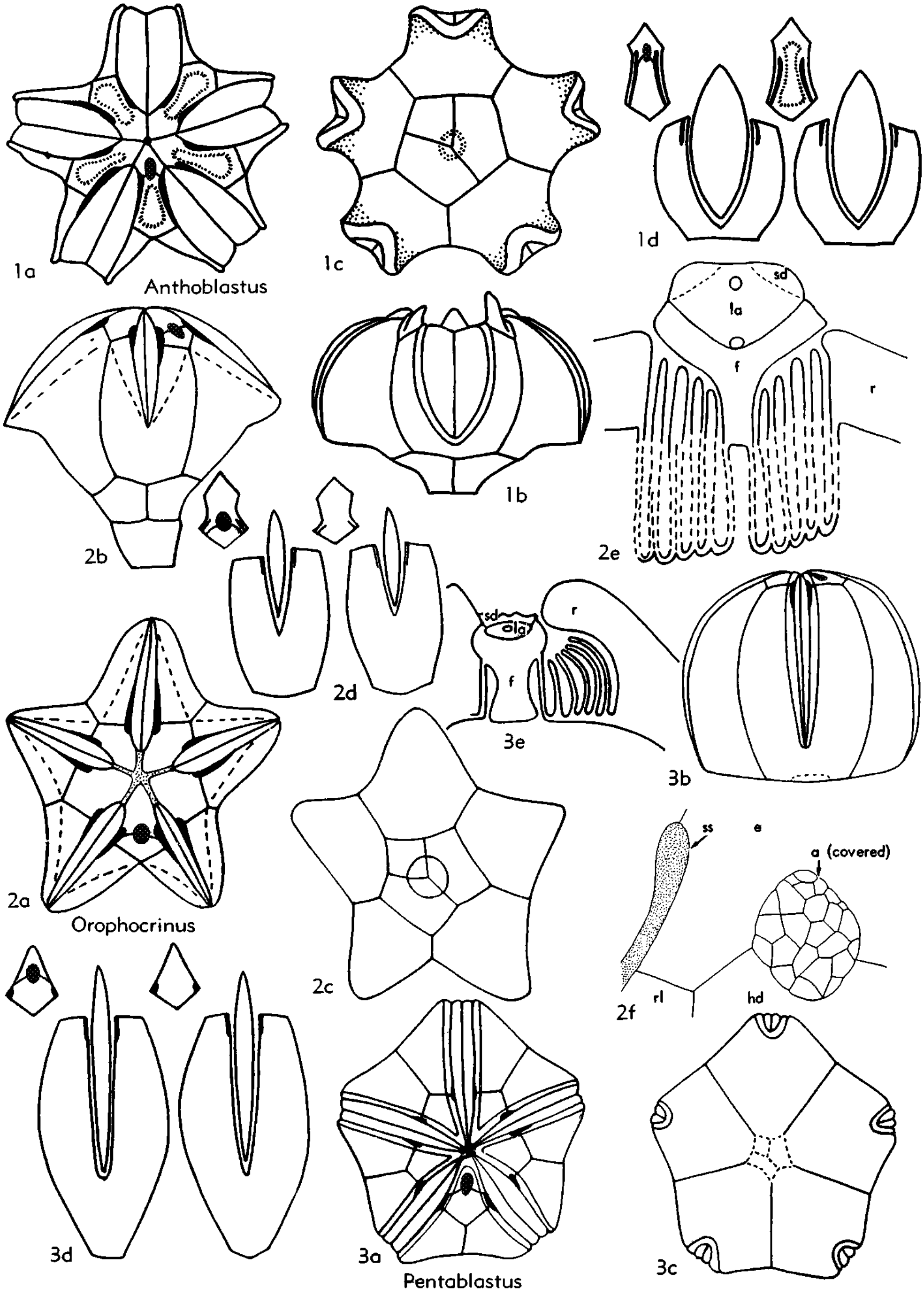

FIG. 253. Orophocrinidae (p. *S*409-*S*412). [Explanation: *a,* anal opening; *e,* epideltoid plate; *f,* fused hydrospire plate; *hd,* hypodeltoid; *la,* lancet plate; *r,* radial plate; *rl,* radial limb; *sd,* side plate; *ss,* spiracular slit.]

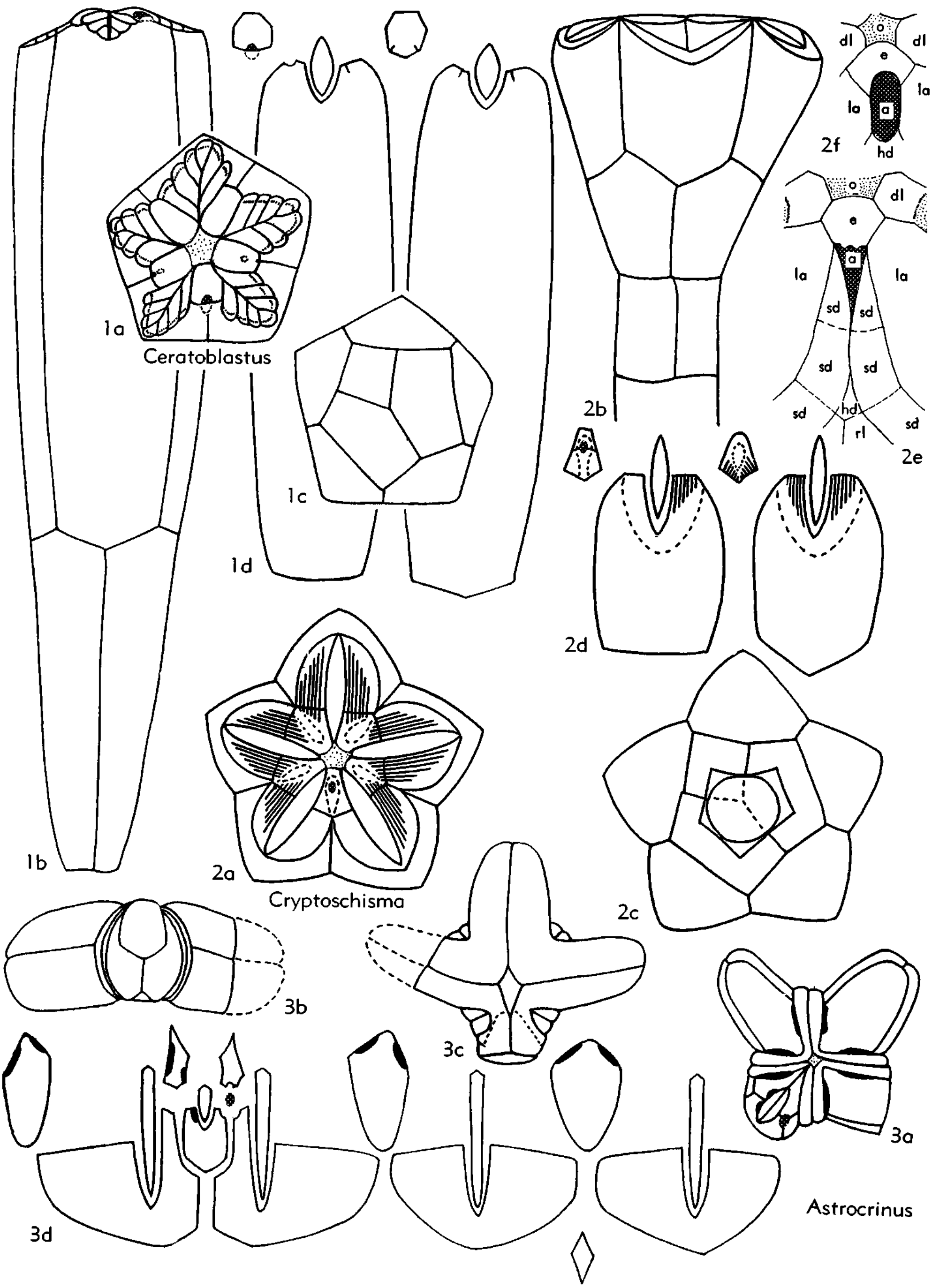

Fig. 254. Astrocrinidae (p. S413). [Explanation: *a*, anal opening; *e*, epideltoid plate; *dl*, deltoid lip; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening; *rl*, radial limb; *sd*, side plate.]

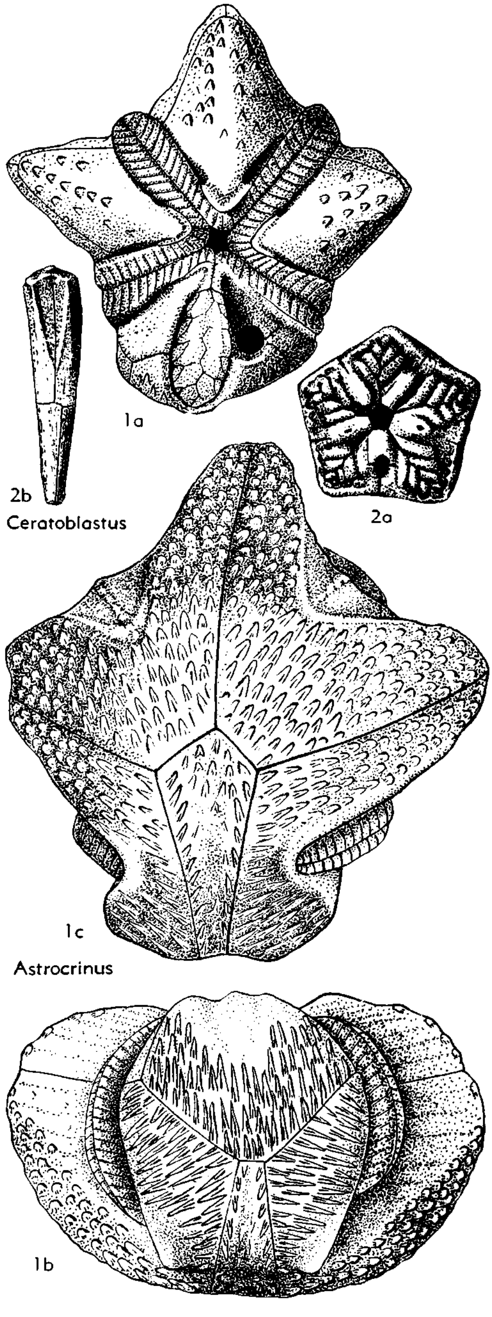

FIG. 255. Astrocrinidae (p. S413).

Order SPIRACULATA Jaekel, 1918

[Spiraculata JAEKEL, 1918, p. 107] [=Eublastida MATSUMOTO, 1929, p. 28 (type, *Troosticrinus* SHUMARD, 1866, p. 385, designated by FAY, herein)]

Theca with hidden hydrospire slits that open into hydrospire canals, with definite spiracles and hydrospire pores. *Sil.-Perm.*

Family TROOSTICRINIDAE Bather, 1899

[*nom. correct.* BASSLER, 1938, p. 14 (*pro* Troostocrinidae BATHER, 1899, p. 920)] [=Troostoblastidae ETHERIDGE & CARPENTER, 1886, p. 190]

Theca elongate conical or obconical with five paired spiracles around mouth. *Sil.-Miss.*

Troosticrinus SHUMARD, 1866, p. 385 [**Pentremites reinwardti* TROOST, 1835, p. 224; SD ETHERIDGE & CARPENTER, 1882, p. 247] [=*Troostocrinus* MEEK & WORTHEN, 1868, p. 356 (*nom. van.*); *Clavaeblastus* HAMBACH, 1903, p. 44 (obj.)]. Theca obconical, with superdeltoid, 2 cryptodeltoids, and hypodeltoid; edges of cryptodeltoids slightly exposed; lancet covered by side plates; one pore between adjacent side plates along ambulacral margins; radials overlapping deltoids; ambulacra short, directed outward and slightly downward; 3 to 5 hydrospire folds on each side of ambulacrum, with thin thecal plates; pelvis long; deltoids not visible in side view, but hypodeltoid visible in side view. *Sil.*, N.Am.——FIG. 258,*1*; 259,*1*. **T. reinwardti* (TROOST), Niagaran, USA(Tenn.); 258,*1a*, oral view, ×4; 258,*1b*, *D*-ray view, ×2.3; 259,*1a-d*, oral, *D*-ray, aboral views, plate layout, ×5.3; 259,*1e,f*, anal views, ×15, ×13 (60, 165).

Metablastus ETHERIDGE & CARPENTER, 1886, p. 196 [**Pentremites lineatus* SHUMARD, 1858, p. 241; OD]. Theca conical, with superdeltoid, 2 cryptodeltoids, and hypodeltoid; lancet covered by side plates; one pore between adjacent side plates along radial and deltoid margins; radials overlapping deltoids; 4 to 5 hydrospire folds on each side of an ambulacrum; radial plates thin; pelvis long; ambulacra extended downward aborally; deltoids not visible in side view, but large hypodeltoid visible in side view. *Miss.*, N.Am.(Ill.-Iowa-Ind.-Mo.-Ky.).——FIG. 258,*2a*; 259,*2a-f*. **M. lineatus* (SHUMARD), M.Miss., Ill.; 258,*2a*, *CD* interambulacral view, ×1.5; 259,*2a-d*, oral, *D*-ray, aboral views, plate layout, ×3.6; 259,*2e*, cross sec. of ambulacrum, ×7; 259,*2f*, anal view, ×5 (41, 60, 155).——FIG. 258,*2b,c*. *M. wachsmuthi* (GURLEY), M.Miss., Ind.; *2b,c*, oral, *D*-ray views, ×1.9, ×1.8 (60).——FIG. 259,*2g*. *M. wortheni* (HALL), M.Miss., Mo.; anal view, ×10 (60).

Schizotremites REIMANN, 1945, p. 25 [**S. kopfi*;

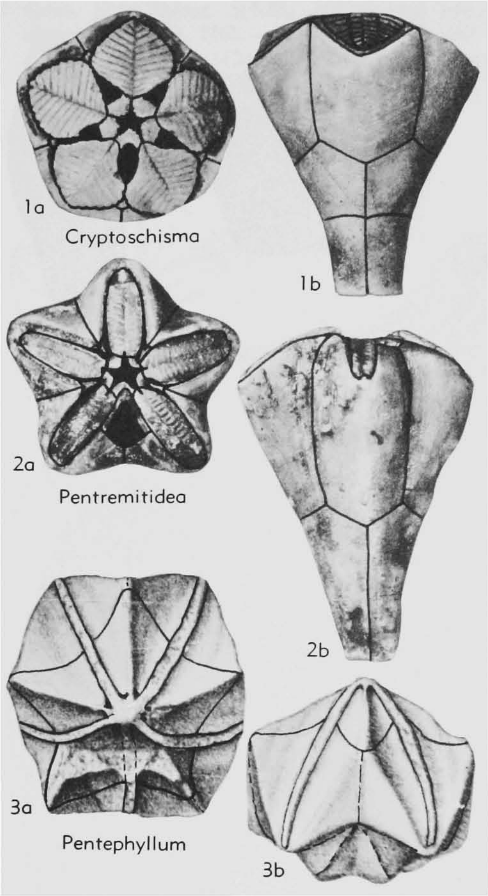

FIG. 256. Astrocrinidae (p. *S*413).

OD] [=?*Pentremitella* LEHMANN, 1949, p. 190 (type, *Pentremitella osoleae*; OD)]. Theca conical, with paired anispiracle located between long hypodeltoid and short superdeltoid, with 2 hidden cryptodeltoids; deltoids moderately long, seen in side view; lancet covered by side plates except near adoral end; one pore between side plates along deltoid and radial margins; 4 to 6 hydrospires on each side of an ambulacrum; radials overlapping deltoids. *Dev.*, N.Am.-?Ger.——FIG. 258,*3*; 260,*2*. **S. kopfi*, M.Dev., USA(N.Y.); 258,*3a,b*, oral, *D*-ray views, ×3.7; 260,*2a-d*, oral, *D*-ray, aboral views, plate layout, ×4.4; 260,*2e*, cross sec. of ambulacrum, ×15 (62, 139).

Tricoelocrinus MEEK & WORTHEN, 1868, p. 356 [**Pentremites (Troostocrinus?) woodmani* MEEK & WORTHEN, 1868, p. 356] [=*Saccoblastus* HAM-

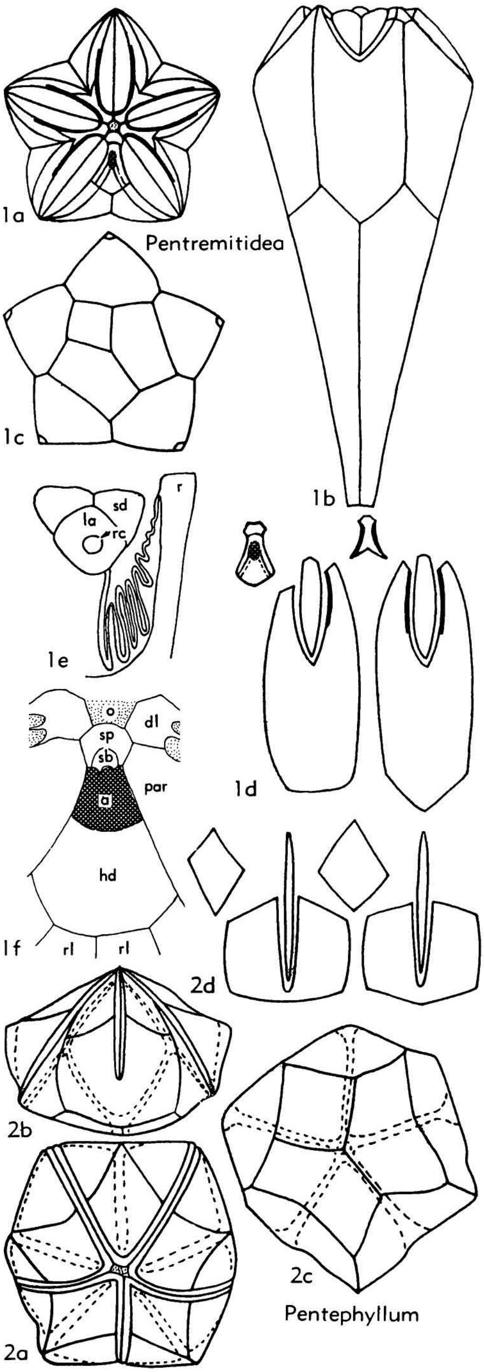

FIG. 257. Astrocrinidae (p. *S*413). [Explanation: *a*, anal opening; *dl*, deltoid lip; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening; *par*, posterior ambulacrum (right); *r*, radial plate; *rc*, radial canal; *rl*, radial limb; *sb*, subdeltoid plate; *sd*, side plate; *sp*, superdeltoid plate.]

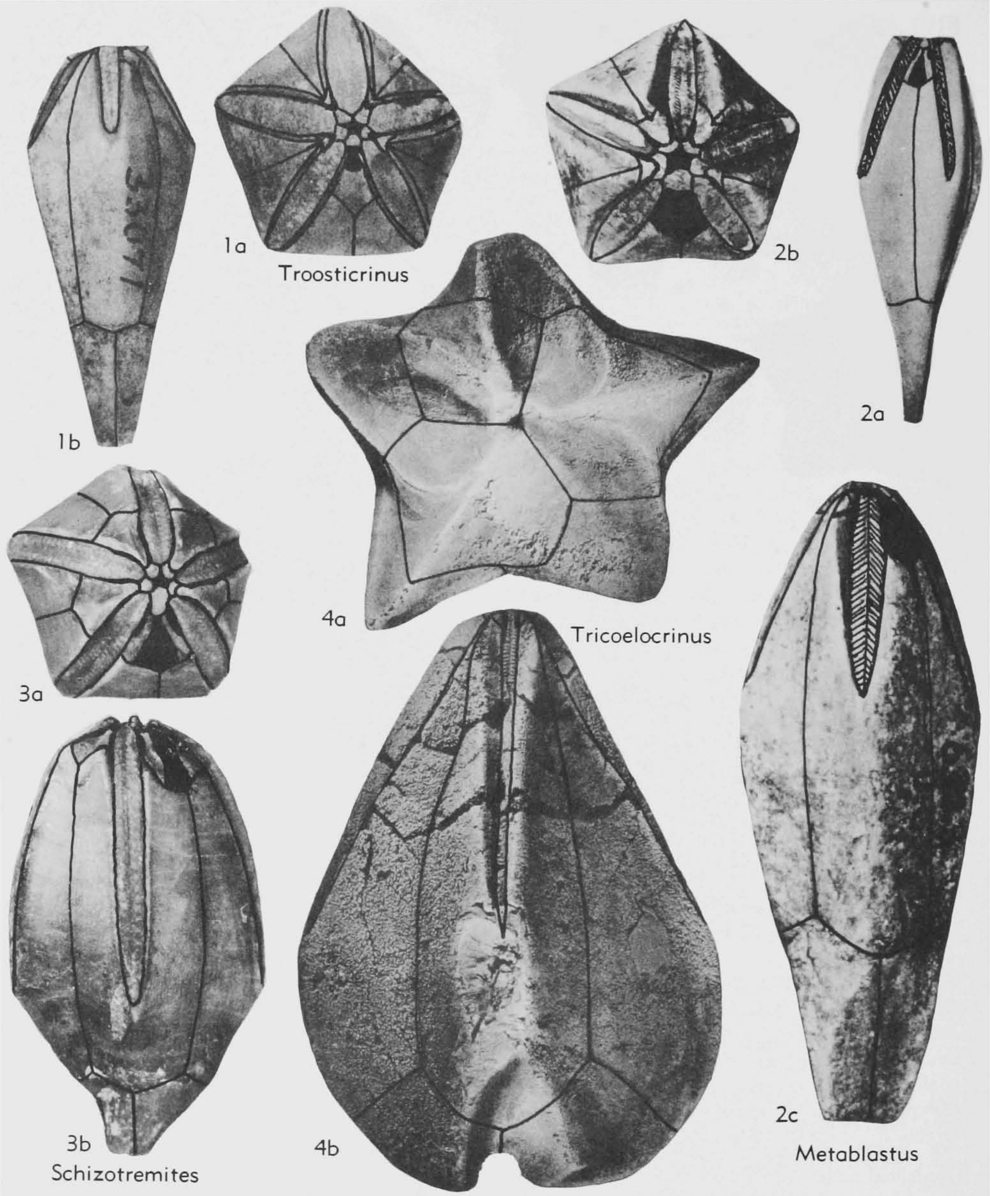

FIG. 258. Troosticrinidae (p. *S*416-*S*419).

BACH, 1903, p. 42 (type, *Pentremites bipyramidalis* HALL, 1858, p. 607)]. Theca subpyramidal, with superdeltoid, 2 cryptodeltoids, and hypodeltoid; lancet covered by side plates; one pore between adjacent side plates along deltoid and radial margins; radials overlapping deltoids; with 3 short hydrospire folds on each side of ambulacrum, extending one-half length of ambulacrum, ending within thick radial plate beneath each ambulacrum; pelvis long, widely inflated outward, subrounded below; deltoids not visible in side view, but large hypodeltoid visible in side view. *Miss.,* N.Am.(Ind.-Tenn.-Ky.-Mo.-Ill.).——FIG. 258,*4*; 260,*1a-e*. **T. woodmani* (MEEK & WORTHEN), M.Miss., Ind.; 258,*4a,b,* aboral, *A*-ray views, ×1.3; 260,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×0.86; 260,*1e,* anal area, diagram. (50, 60, 116).——FIG. 260,*1f. T. obliquatus* (ROEMER), M.Miss., Ind.; cross sec. of ambulacrum, ×4.4 (41).

Family DIPLOBLASTIDAE Fay, 1964

[Diploblastidae FAY, 1964, p. 84]

Theca globular, with five paired spiracles or four paired spiracles and an anispiracle. *Miss.*

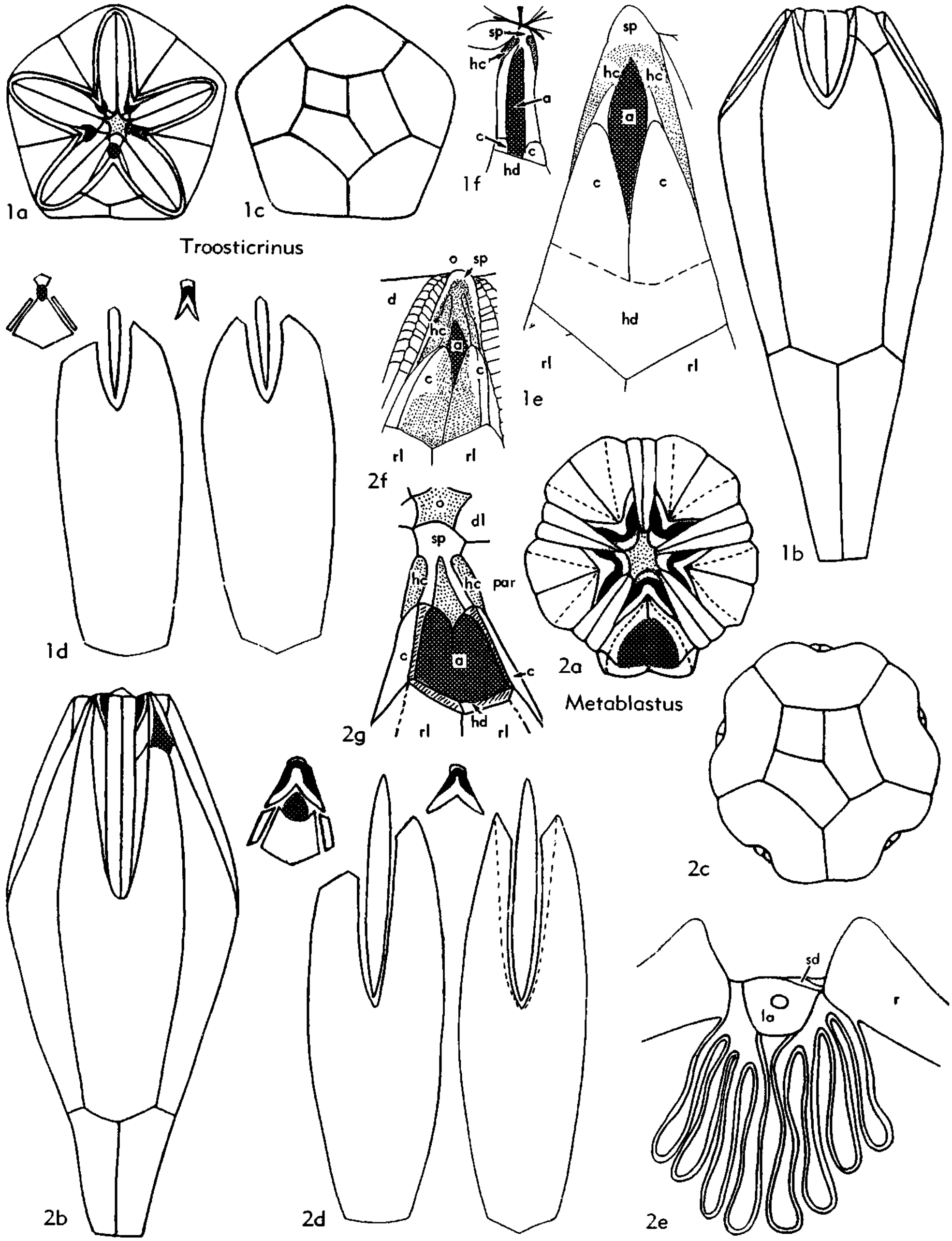

FIG. 259. Troosticrinidae (p. S416). [Explanation: *a,* anal opening; *c,* cryptodeltoid plate; *d,* deltoid plate; *dl,* deltoid lip; *hc,* hydrospire canal; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening; *par,* posterior ambulacrum (right); *r,* radial plate; *rl,* radial limb; *sd,* side plate; *sp,* superdetoid plate.]

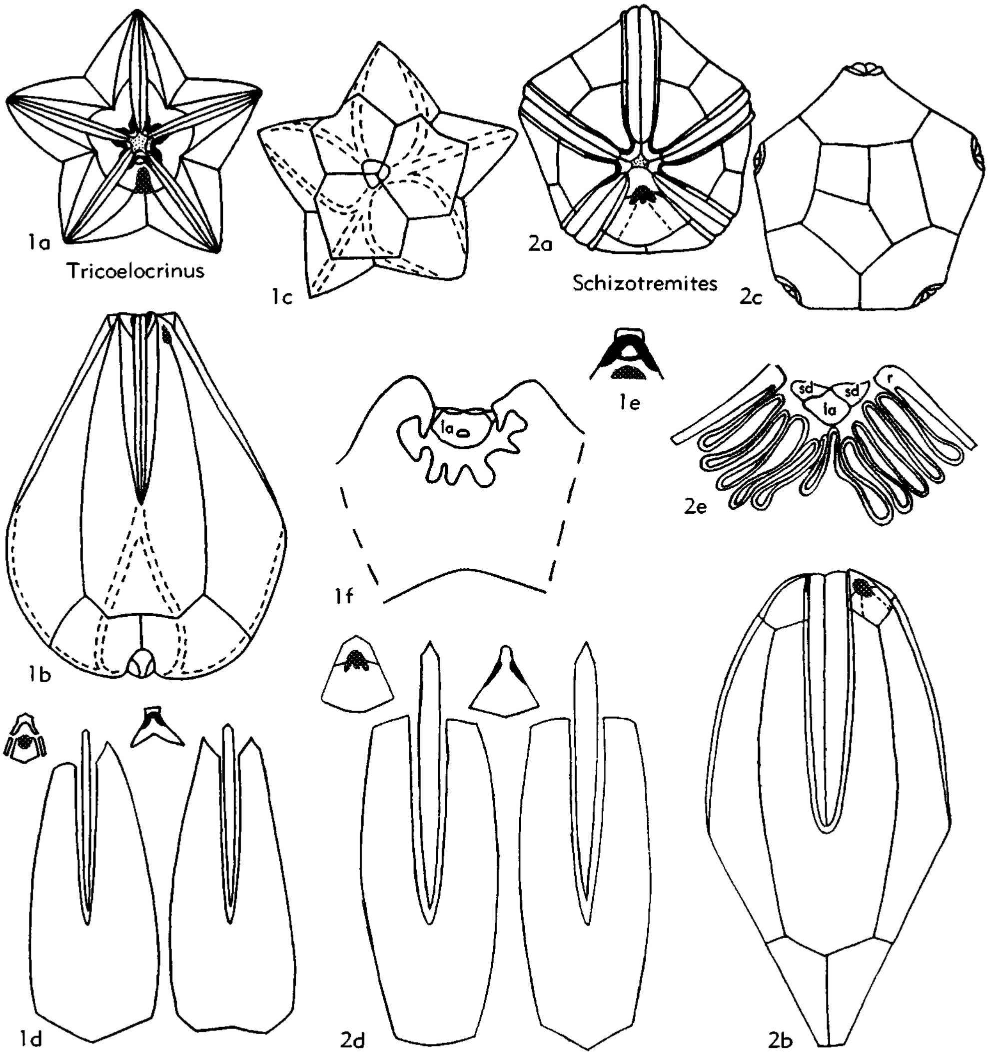

FIG. 260. Troosticrinidae (p. *S*416-*S*419). [Explanation: *la,* lancet plate; *r,* radial plate; *sd,* side plate.]

Diploblastus Fay, 1961 (60), p. 62 [**Granatocrinus glaber* Meek & Worthen, 1869, p. 91; OD]. Theca globular, with superdeltoid, 2 cryptodeltoids, and hypodeltoid; 2 hydrospire folds on each side of an ambulacrum; lancet covered by side plates at aboral end and gradually exposed to 0.3 of its width near adoral end; with one pore between side plates along deltoid and radial margins; radials overlapping deltoids. *Miss.,* N.Am. (Ill.-Mo.-Ky.-Ala.).——Fig. 261,*2*; 262,*1*. **D. glaber* (Meek & Worthen), M.Miss., Ky. (261, *2*), Ill. (262,*1*); 261,*2a,b,* oral, *D*-ray views, ×7.5; 262,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×6.3; 262,*1e,* cross sec. of ambulacrum, ×26.5; 262,*1f,* anal view, ×10 (60).

Nodoblastus Fay, 1963, p. 174 [**Schizoblastus librovitchi* Yakovlev, 1941, p. 71; OD]. Theca bell-shaped to elliptical, with anispiracle located between short epideltoid and long hypodeltoid; deltoids slightly longer than radials which overlap deltoids; one hydrospire fold on each side of an ambulacrum; hydrospire plate present, with about twice as many pores as side plates; basalia small, in slight basal concavity; deltoids nodose, with medium high deltoid crests. *L.Carb.,* Eu. (USSR).——Fig. 261,*1*; 262,*2*. **N. librovitchi* (Yakovlev); 261,*1a,b,* oral, *C*-ray views, ×3.2; 262,*2a-d,* oral, *C*-ray, aboral views, plate diagram, ×3.7; 262,*2e,* transv. sec. of ambulacrum, ×10 (73, 188).

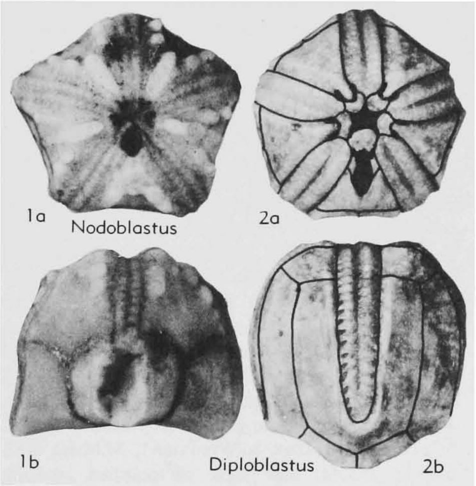

FIG. 261. Diploblastidae (p. S420).

Family GRANATOCRINIDAE Fay, 1961

[Granatocrinidae FAY, 1961 (60), p. 20] [=Granatoblastidae ETHERIDGE & CARPENTER, 1886, p. 237 (invalid, based on nonexistent nominal genus)]

Theca with eight spiracles and anispiracle (or paired anispiracle) around mouth. *Miss.*

Granatocrinus HALL, 1862, p. 146 [**Pentatrematites granulatus* ROEMER, 1851, p. 363; SD SHUMARD, 1866, p. 375] [=*Granatocrinites* TROOST, 1849, p. 420 *(nom. nud.)*; *Cidaroblastus* HAMBACH, 1903, p. 45 (type, *Pentatrematites granulatus* ROEMER)]. Elliptical theca with anispiracle located between epideltoid and hypodeltoid; one hydrospire fold on each side of an ambulacrum; lancet covered by side plates; hydrospire plate present; 2 pores to each side plate along radial and deltoid margins; radials overlapping deltoids; deltoids moderately long. *Miss.*, N.Am.(Ky.-Ind.-Tenn.).——FIG. 263,*1*; 264,*1a-e*. **G. granulatus* (ROEMER), M.Miss., USA(Tenn.); 263,*1a*, oral view,

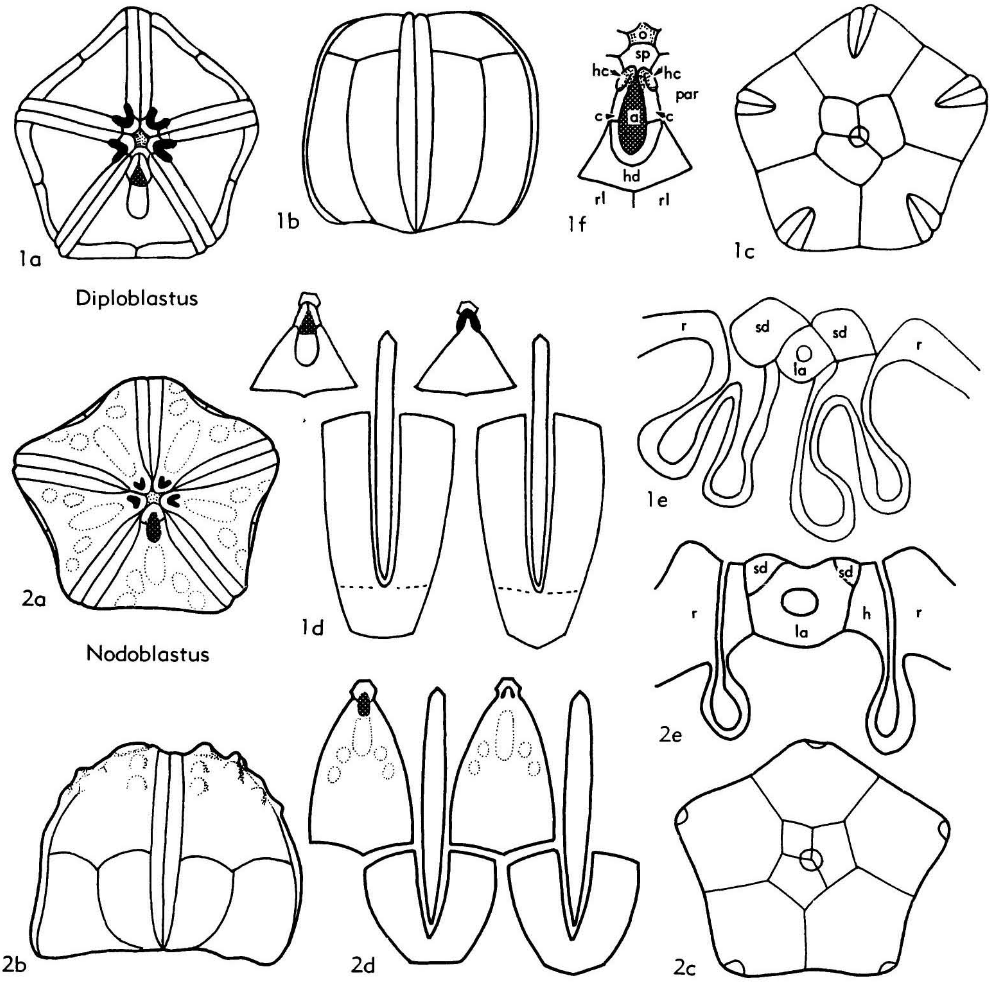

FIG. 262. Diploblastidae (p. S420). [Explanation: *a*, anal opening; *c*, cryptodeltoid plate; *h*, hydrospire plate; *hc*, hydrospire canal; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening; *par*, posterior ambulacrum (right); *r*, radial plate; *rl*, radial limb; *sd*, side plate; *sp*, superdeltoid plate.]

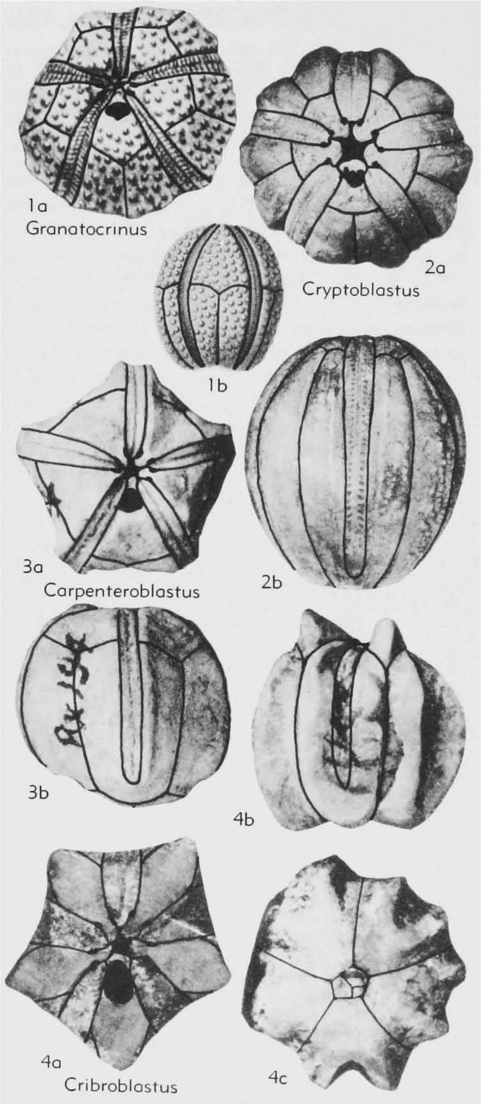

FIG. 263. Granatocrinidae (p. S421-S422).

×1; 263,*1b,* interambulacral view, ×0.5; 264, *1a-d,* oral, *D*-ray, aboral views, plate layout, ×1.3; 264,*1e,* cross sec. of ambulacrum, ×8.7 (60, 86).——FIG. 264,*1f*. *G. kentuckyensis* (CONKIN), M.Miss., Ky.; anal view, ×7.4 (60).

Carpenteroblastus ROWLEY, 1901, p. 347 [**Granatocrinus (Schizoblastus) magnibasis* ROWLEY, 1895, p. 220; OD]. Theca conico-elliptical; anispiracle located between epideltoid and hypodeltoid; lancet exposed along food groove proper; with ?2 hydrospire folds on each side of an ambulacrum; one pore between adjacent side plates along deltoid and radial margins; radials overlapping deltoids; base convex. *Miss.,* N.Am.(Mo.-?Ky.).——FIG. 263,*3*; 264,*2*. **C. magnibasis* (ROWLEY), M.Miss., USA(Mo.); 263,*3a,b,* oral, *D*-ray views, ×2.5; 264,*2a-d,* oral, *D*-ray, aboral views, plate layout, ×3.5; 264,*2e,* cross sec. of ambulacrum, ×35.2; 264,*2f,* anal view, ×10 (60).

Cribroblastus HAMBACH, 1903, p. 39 [**Pentremites cornutus* MEEK & WORTHEN, 1862, p. 141; SD BASSLER, 1938, p. 75]. Ellipsoidal theca; anispiracle located between epideltoid and hypodeltoid; deltoids short, with high coronal processes; radials overlapping deltoids; lancet covered by side plates, with single pore between side plates along radial and deltoid margins; 2 hydrospire folds on each side of an ambulacrum; hydrospire plate present. *Miss.,* N.Am.(Ill.-Mo.).——FIG. 263,*4*; 265,*1*. **C. cornutus* (MEEK & WORTHEN), M.Miss., USA (Mo.); 263,*4a,* oral view of polished summit, ×5; 263,*4b,* side view, ×2.3; 263,*4c,* aboral view, ×3.1; 265,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×3.6; 265,*1e,* cross sec. of ambulacrum, ×17.9; 265,*1f,* anal view, ×3.8 (60).

Cryptoblastus ETHERIDGE & CARPENTER, 1886, p. 229 [**Pentremites melo* OWEN & SHUMARD, 1850, p. 65; OD]. Theca ellipsoidal; anispiracle located between superdeltoid, 2 deep cryptodeltoids, and hypodeltoid; lancet exposed along middle 0.3 of its width except near aboral end; 2 hydrospire folds on each side of an ambulacrum; hydrospire plate present; pores absent along deltoid margins, with about 2 pores per side plate along radial margins; interradial sutures depressed; radials overlapping deltoids except at extreme adoral tip of radial limbs where deltoids project slightly over radials. *Miss.,* N.Am.(Iowa-Mo.).——FIG. 263,*2*; 265,*2*. **C. melo* (OWEN & SHUMARD), M.Miss., USA(Iowa); 263,*2a,b,* oral, *D*-ray views, ×2.6; 265,*2a-d,* oral, *D*-ray, aboral views, plate layout, ×3.6; 265,*2e,* cross sec. of ambulacrum, ×22; 265,*2f,* anal view, ×3.8 (29, 60, 128).

Dentiblastus MACURDA, 1964 (102), p. 370 [**Pentremites sirius* WHITE, 1865, p. 20; OD]. Theca oblate spheroidal; with anispiracle located between epideltoid and hypodeltoid; 2 hydrospire folds on each side of ambulacrum; hydrospire plate present; lancet covered by side plates; single pore between adjacent side plates along radial and deltoid margins; deltoids overlapping radials; radials winglike, with ambulacra extending beyond theca proper. *Miss.,* USA(Iowa-Mo.).——FIG. 266,*1*. **D. sirius* (WHITE), M.Miss., Mo.; *1a-f,* oral, *E*-ray, aboral views, plate layout, oral, *E*-ray views, ×6 (102).

Heteroblastus ETHERIDGE & CARPENTER, 1886, p. 255 [**H. cumberlandi*; OD]. Theca elliptical; anispiracle seemingly located between epideltoid and hypodeltoid; deltoids long, with high coronal processes; lancet covered by side plates; single pore between side plates along radial and deltoid margins; deltoids overlapping radials; probably

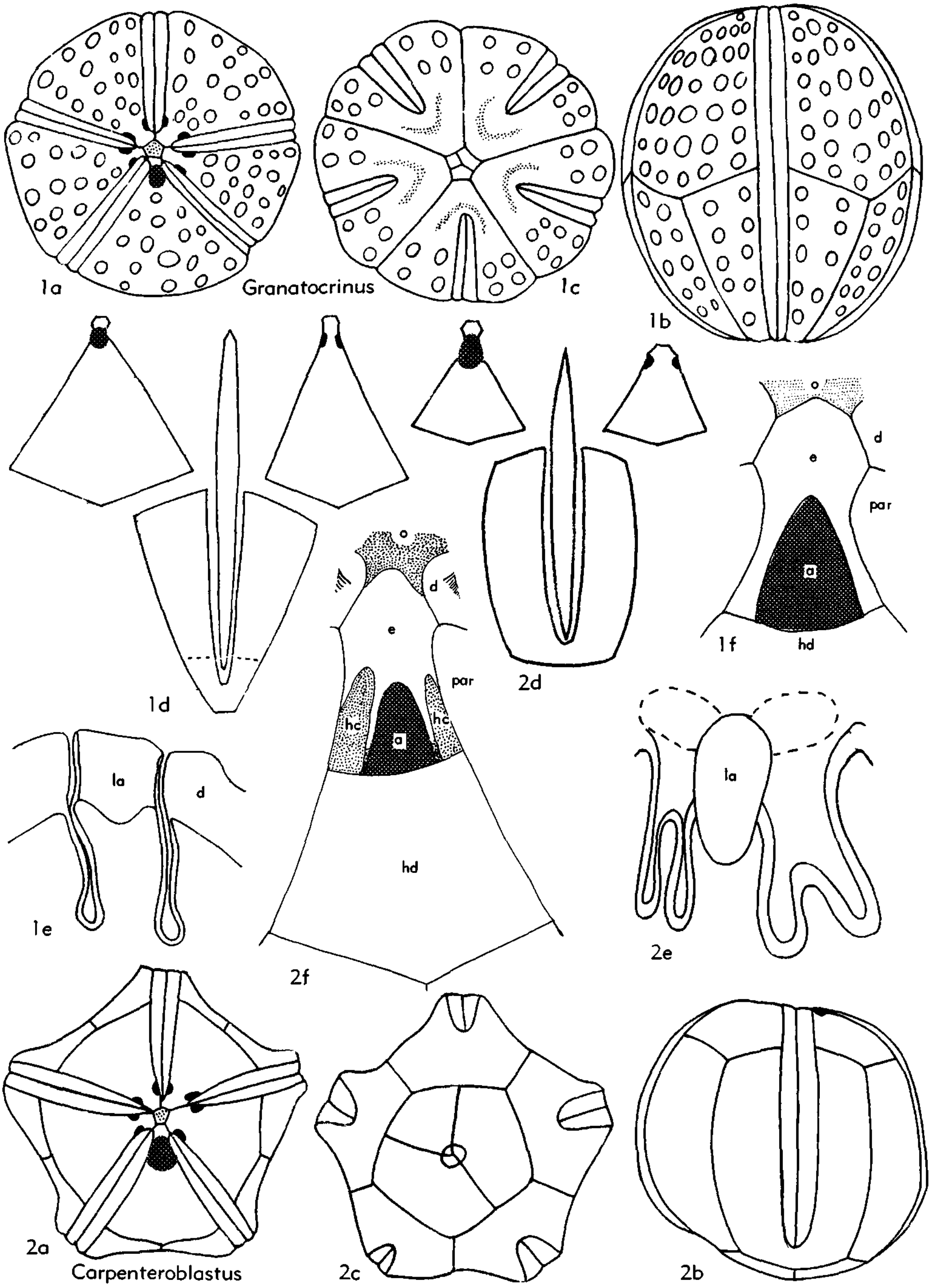

FIG. 264. Granatocrinidae (p. *S*421-*S*423). [Explanation: *a,* anal opening; *d,* deltoid plate; *e,* epideltoid plate; *hc,* hydrospire canal; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening; *par,* posterior ambulacrum (right).]

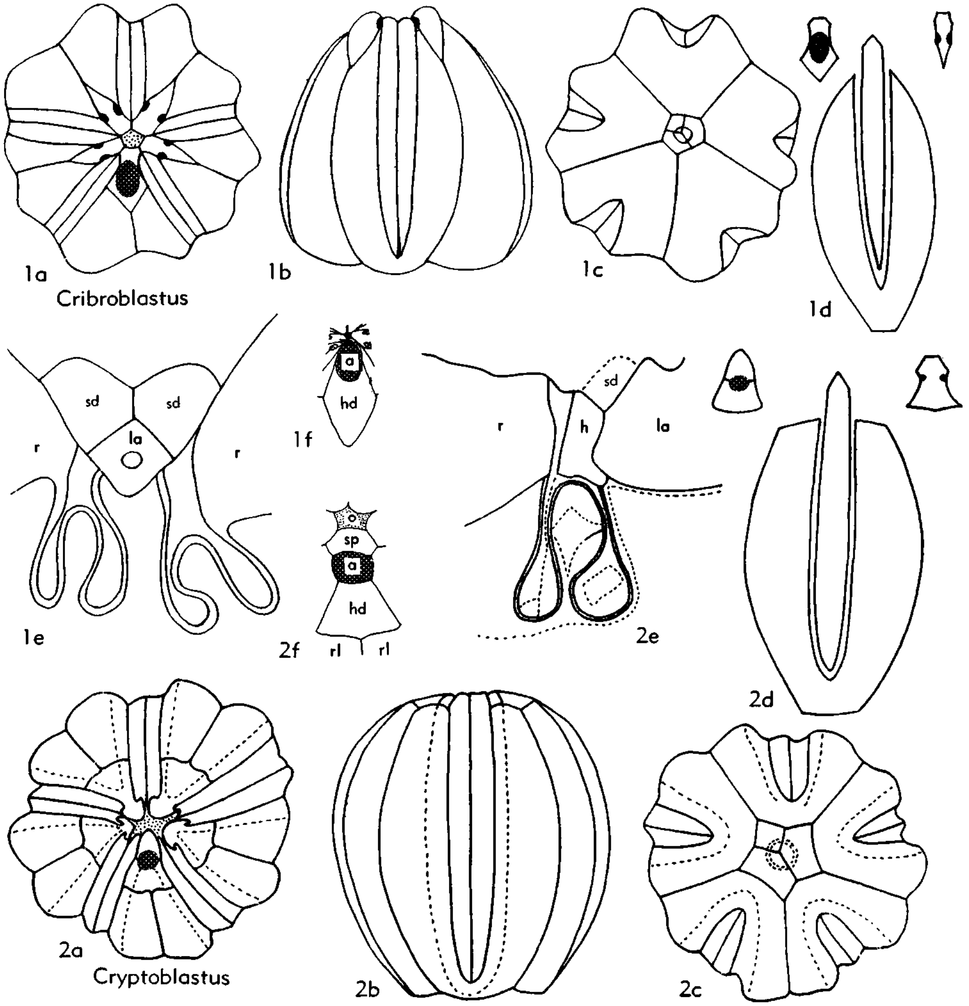

Fig. 265. Granatocrinidae (p. S422). [Explanation: *a,* anal opening; *h,* hydrospire plate; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening; *r,* radial; *rl,* radial limb; *sd,* side plate; *sp,* superdeltoid plate.]

more than one hydrospire fold on each side of an ambulacrum. *L.Carb.,* Eu.(Eng.).——Fig. 267, *1*; 268,*1*. **H. cumberlandi;* 267,*1a,b,* oral, radial views, ×3.8; 268,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×4.4 (41).

Mesoblastus Etheridge & Carpenter, 1886, p. 181 [**Pentatrematites crenulatus* Roemer, 1851, p. 366; OD]. Theca subglobular; superdeltoid, 2 cryptodeltoids, and hypodeltoid; 3 hydrospire folds on each side of ambulacra; thick hydrospire plate, with approximately 5 pores to each side plate infolded into double row; lancet covered by side plates except at adoral end; pores absent along deltoid margins; radials overlapping deltoids. *L. Carb.,* Eu.(Belg.-Eng.-Ger.)-?China.——Fig. 267, *3*; 268,*2a-d, 2f*. **M. crenulatus* (Roemer), Belg.; 267,*3a,b,* oral, *D*-ray views, ×3.2; 268,*2a-d,* oral, *D*-ray, aboral views, plate layout, ×5.8; 268,*2f,* anal view, ×10 (41, 60).——Fig. 268,*2e*. *M. angulatus* (Sowerby), Eng.; cross sec. of ambulacrum, ×11.8 (41).

Monadoblastus Fay, 1961 (60), p. 82 [**M. granulosus*; OD]. Theca elliptical, with anispiracle located between epideltoid and hypodeltoid; hydrospire plate present, and approximately 2 pores to each side plate along radial margins; pores absent along deltoids; one hydrospire fold on each side of ambulacra; lancets covered by side plates except near adoral end; base concave; radials overlapping deltoids. *Miss.,* N.Am.(N.Mex.).——Fig. 267,*2*; 268,*3*. **M. granulosus*; 267,*2a,b,* oral, *D*-ray views, ×6.4; 268,*3a-e,* oral, *D*-ray, aboral views, plate layout, cross sec. of ambulacrum, ×8.8 (60).

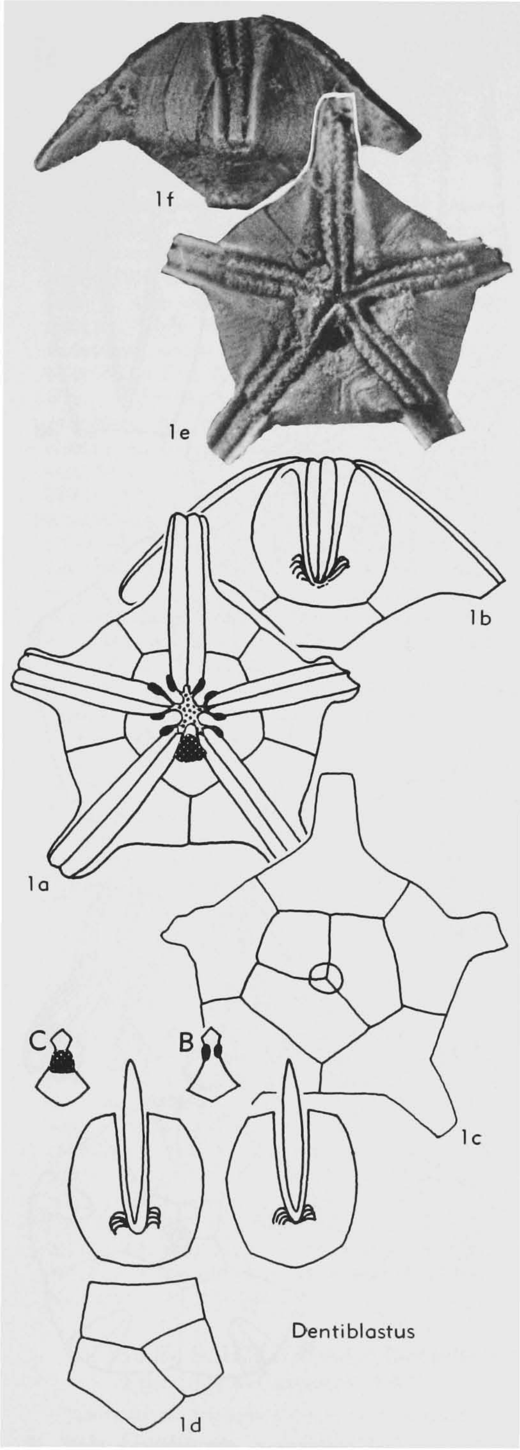

FIG. 266. Granatocrinidae (p. S422).

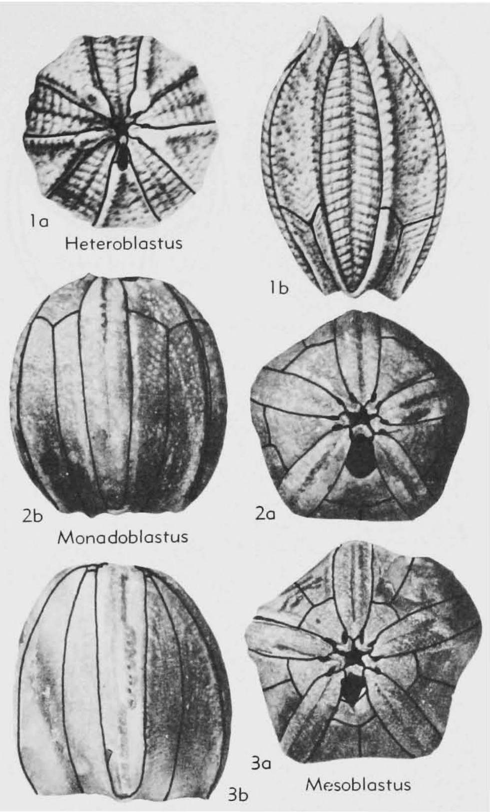

FIG. 267. Granatocrinidae (p. S422, S424).

Monoschizoblastus CLINE, 1936, p. 265 [**Granatocrinus rofei* ETHERIDGE & CARPENTER, 1882, p. 239; OD]. Theca ellipsoidal; anispiracle between small epideltoid and large hypodeltoid; single hydrospire fold on each side of ambulacra; lancet exposed along middle 0.3 of its width; deltoids long, overlapping radials; base concave; with what appears to be single pore between side plates along radial and deltoid margins. *L.Carb.*, Eu.(Eire).——FIG. 269,*1*; 270,*3*. **M. rofei* (ETHERIDGE & CARPENTER); 269,*1a,b*, oral, *A*-ray views, ×4.4; 270,*3a-d*, oral, *D*-ray, aboral views, plate layout, ×7.5; 270,*3e*, cross sec. of ambulacrum, ×13.1 (28, 39, 41, 53).

Poroblastus FAY, 1961 (60), p. 97 [**Pentremites (Granatocrinus) granulosus* MEEK & WORTHEN, 1865, p. 165; OD]. Theca ellipsoidal, with anispiracle between epideltoid and hypodeltoid; radials overlapping deltoids; hydrospire plate present; one pore between side plates along deltoid margins but 2 pores to each side plate along radial margins; single hydrospire fold on each side of ambulacra; lancet covered by side plates at aboral end, gradually exposed to 0.3 of its width

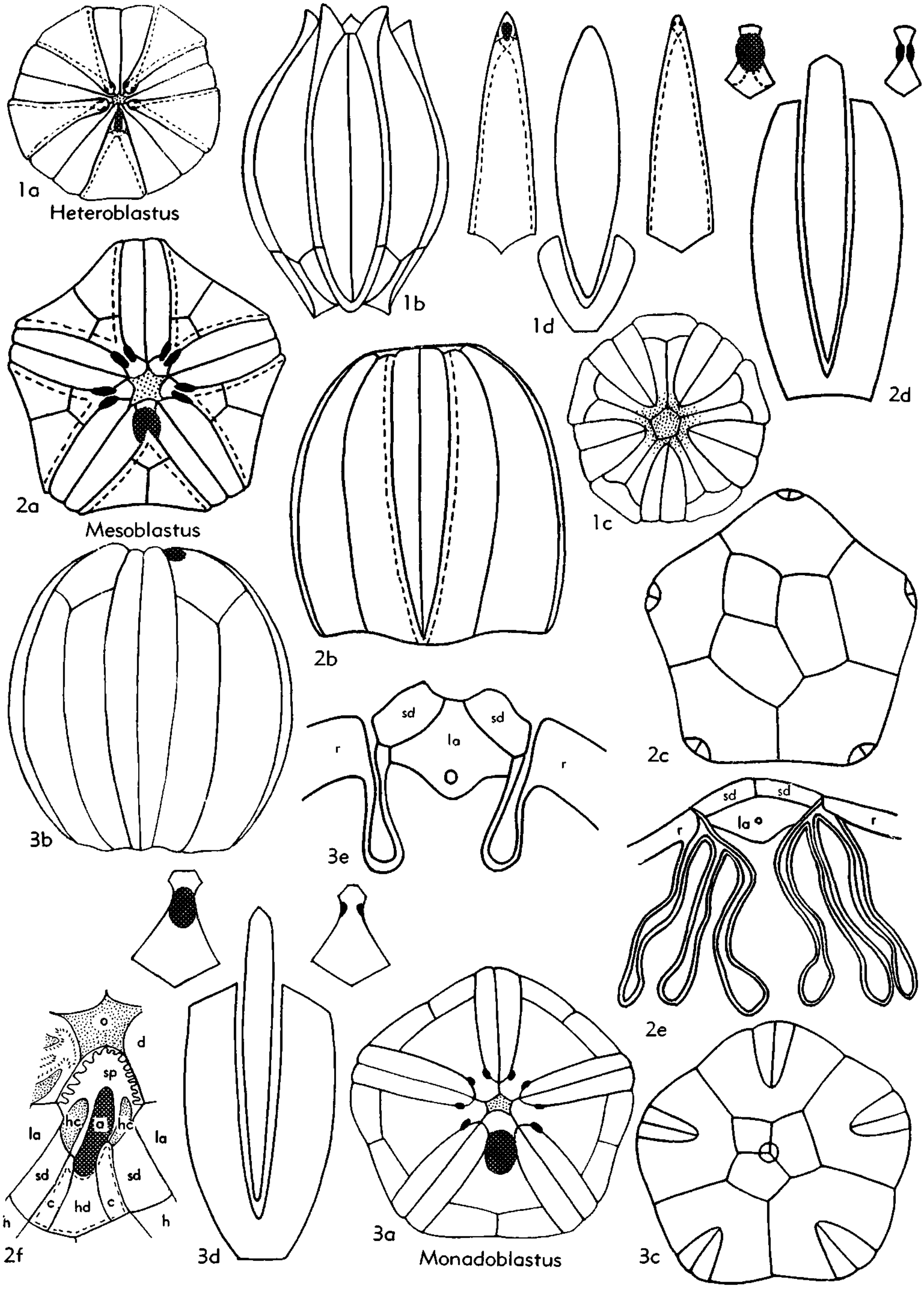

Fig. 268. Granatocrinidae (p. S422, S424). [Explanation: *a,* anal opening; *c,* cryptodeltoid plate; *d,* deltoid plate; *h, h*ydrospire plate; *hc,* hydrospire canal; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening; *r,* radial plate; *sd,* side plate; *sp,* superdeltoid plate.]

near adoral end; base concave. *Miss.*, N.Am.(Ill.-Iowa-Mo.).——FIG. 269,*2*; 270,*2*. **P. granulosus* (MEEK & WORTHEN), M.Miss., USA(Ill.); 269, *2a,b,* oral, *D*-ray views, ×4; 270,*2a-d,* oral, *D*-ray, aboral views, plate layout, ×4.4; 270,*2e,* cross sec. of ambulacrum, ×26.4; 270,*2f,* anal view, ×10 (60).

Ptychoblastus FAY, 1960 (46), p. 1198 [**P. pustulosus*; OD]. Theca ellipsoidal, with anispiracle between epideltoid and hypodeltoid; radials abutting against deltoids; hydrospire plate present; 2 pores to each side plate along deltoid and radial margins; single hydrospire fold on each side of ambulacra; lancets covered at aboral end, gradually exposed to 0.3 of width near adoral end. *Miss.*, N.Am.(Mo.).——FIG. 269,*3*; 270,*1*. **P. pustulosus,* M.Miss.; 269,*3a-c,* oral, *AE* interambulacral, *D*-ray views, ×3.8 (60); 270,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×5.9; 270,*1e,* cross sec. of ambulacrum, ×17.6 (46).

Pyramiblastus MACURDA, 1964 (105), p. 106 [**Orophocrinus fusiformis* WACHSMUTH & SPRINGER, 1888, p. 14; OD]. Theca bipyramidal, with paired anispiracle located between superdeltoid, 2 cryptodeltoids, and hypodeltoid; 6 to 8 hydrospire folds on each side of ambulacrum; lancet exposed along 0.3 of its width; single pore between each side plate along radial and deltoid margins; deltoids overlapping radials; deltoids well exposed in side view. *Miss.*, USA (Iowa).——FIG. 271,*1*. **P. fusiformis* (WACHSMUTH & SPRINGER), L.Miss., Iowa; *1a-f,* oral, *D*-ray, aboral views, plate layout, side view of holotype, *D*-ray view, ×3 (105).

Tanaoblastus FAY, 1961 (60), p. 101 [**Pentremites roemeri* SHUMARD *(partim)*, 1855, p. 186, pl. B, fig. 2a only; OD]. Theca subelliptical, with anispiracle located between superdeltoid and hypodeltoid, with 2 hidden cryptodeltoids; deltoids moderately short; radials overlapping deltoids; pores absent along deltoid margins, but 2 pores to each side plate along radial margins; 2 hydrospire folds on each side of ambulacra; lancet exposed along main food groove; interradial sutures even; base flat to convex. *Miss.*, N.Am.(Mo.-Mont.-?Ariz.-Alta.).——FIG. 272,*1a-h*. **T. roemeri* (SHUMARD), L.Miss., USA(Mo.); *1a,* oral view, ×5.9; *1b,* oral view, ×5.1; *1c, D*-ray view, ×5.9; *1d, D*-ray view, ×5.1; *1e,f,* aboral view, plate layout, ×5.9; *1g,* cross sec. of ambulacrum, ×11.7; *1h,* anal view, ×10 (60).——FIG. 272, *1i*. *T. concinnulus* (ROWLEY & HARE), M.Miss., Mo.; anal view, ×10 (60).

Family SCHIZOBLASTIDAE
Etheridge & Carpenter, 1886

[Schizoblastidae ETHERIDGE & CARPENTER, 1886, p. 220]

Theca with ten spiracles and separate anal opening around mouth; cryptodeltoids (if present) hidden. *Dev.-Perm.*

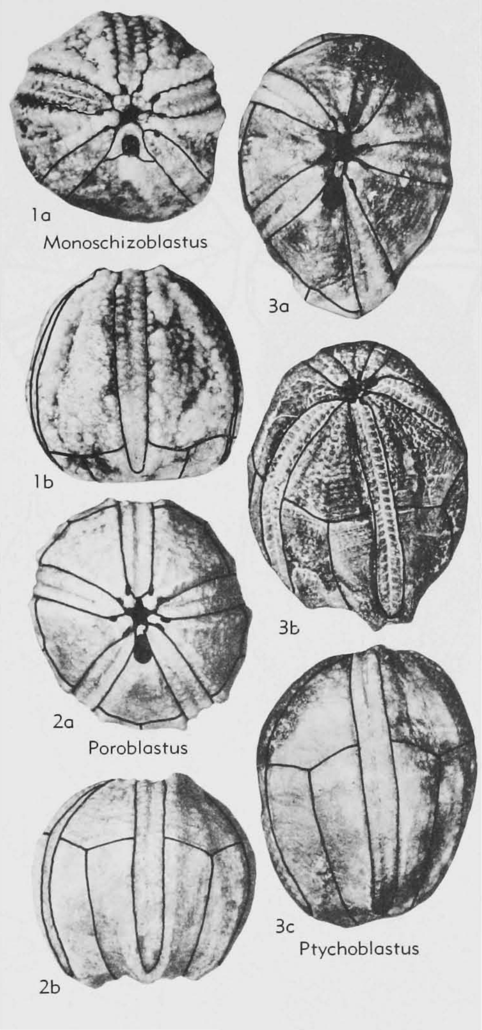

FIG. 269. Granatocrinidae (p. S425, S427).

Schizoblastus ETHERIDGE & CARPENTER, 1882, p. 243 [**Pentremites sayi* SHUMARD, 1855, p. 185; SD ETHERIDGE & CARPENTER, 1886, p. 220]. Theca ellipsoidal; anal opening between epideltoid and hypodeltoid; lancet exposed along main food groove; 1 pore between side plates along deltoid and radial margins; deltoids moderately long, overlapping radials; 2 hydrospire folds on each side of ambulacrum; base slightly concave. *Miss.*, N.Am.(Iowa-Mo.-Ill.).——FIG. 273,*2*; 274,*2*. **S. sayi* (SHUMARD), M.Miss., USA(Mo.); 273,*2a,b,* oral, *A*-ray views, ×2; 274,*2a-d,* oral, D-ray, aboral views, plate layout, ×2.2; 274,*2e,* cross sec. of ambulacrum, ×8.9 (28, 60, 154).

Acentrotremites ETHERIDGE & CARPENTER, 1883, p. 232 [**Mitra elliptica* CUMBERLAND, 1826, p. 33;

OD]. Theca bell-shaped, with spiracles adjacent to radials; anal opening excavated in ?single anal deltoid; hydrospire plate present; pores absent along deltoids; deltoids overlapping radials; 4 or 5 hydrospire folds on each side of an ambulacrum; lancet covered by side plates; basalia seemingly fused to form single plate. *L.Carb.*, Eu. (Eng.).——FIG. 273,*3*; 274,*1*. **A. ellipticus* (CUMBERLAND); 273,*3a,b*, oral, *CD* interambulacral views, ×1.3, ×0.7; 274,*1a-d*, oral, *D*-ray, ab-

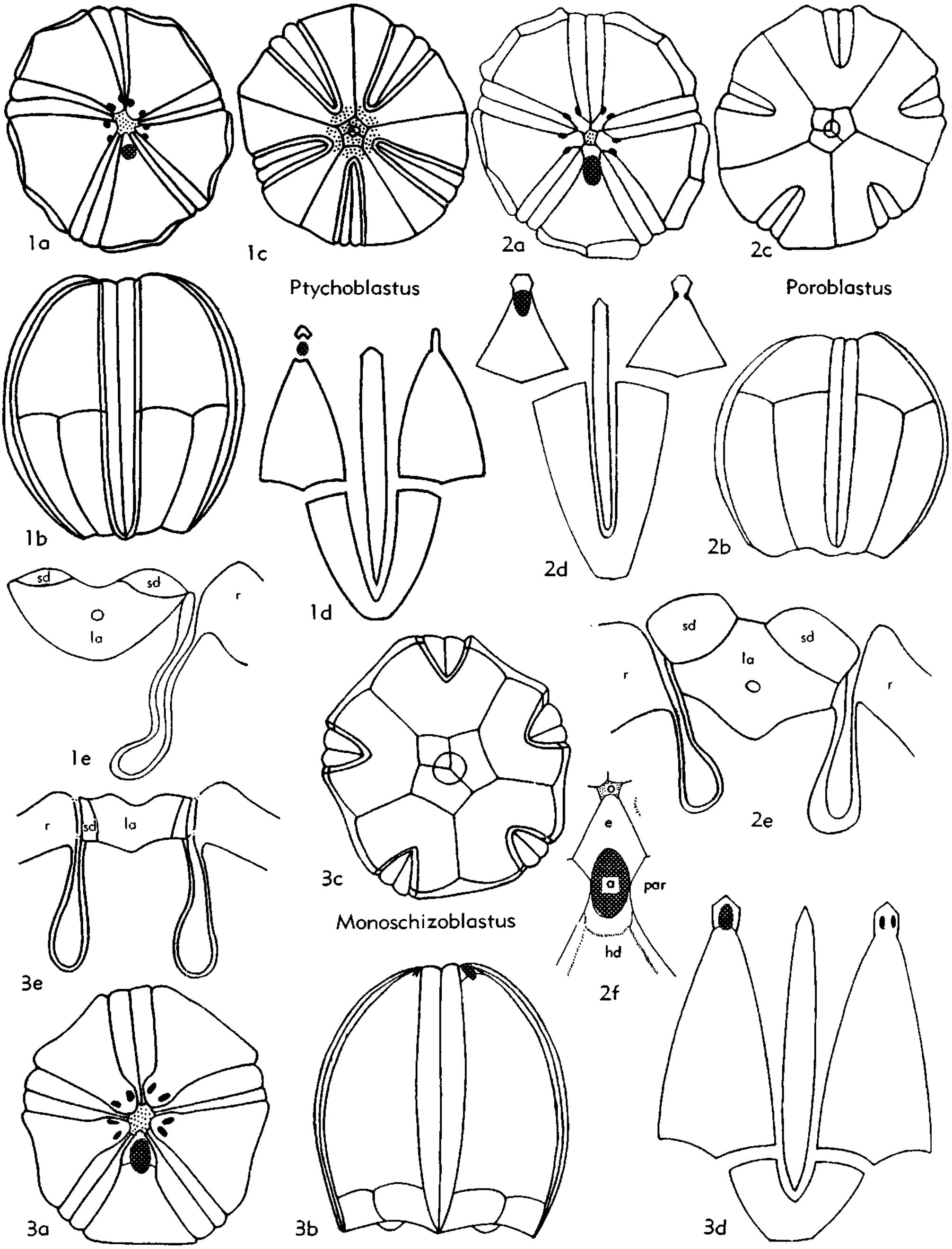

FIG. 270. Granatocrinidae (p. S425, S427). [Explanation*: a,* anal opening; *e,* epideltoid plate; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening; *par,* posterior ambulacrum (right); *r,* radial plate; *sd,* side plate.]

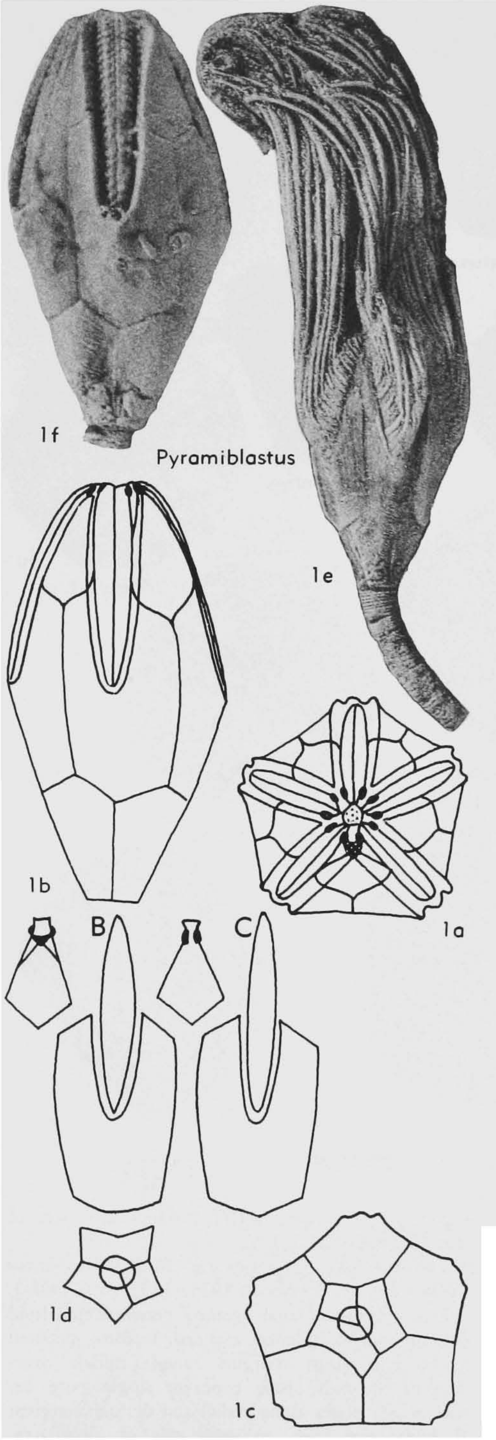

FIG. 271. Granatocrinidae (p. *S*427).

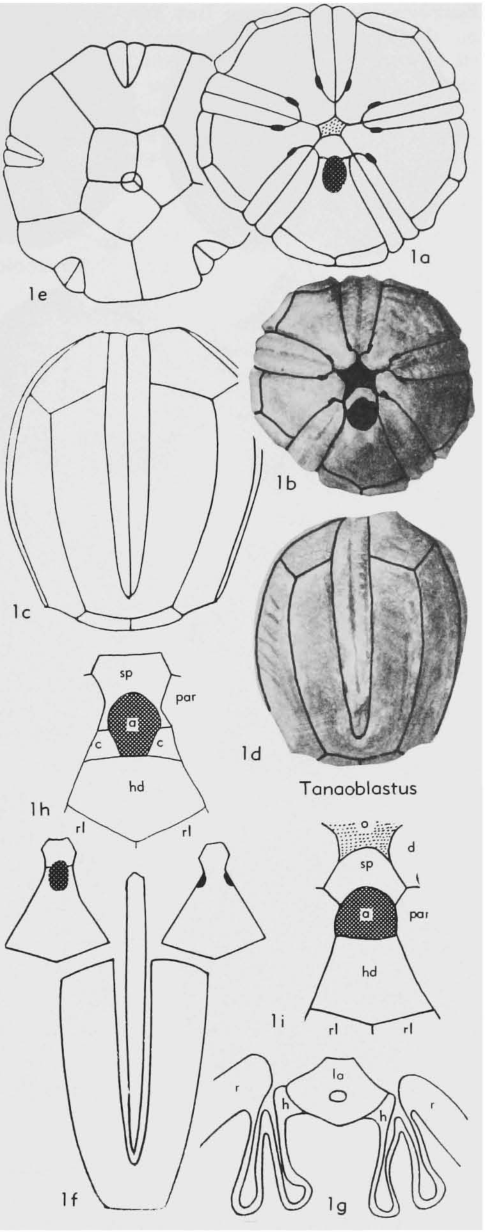

FIG. 272. Granatocrinidae (p. *S*427). [Explanation: *a*, anal opening; *c*, cryptodeltoid plate; *d*, deltoid plate; *h*, hydrospire plate; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening; *par*, posterior ambulacrum (right); *r*, radial plate; *rl*, radial limb; *sp*, superdeltoid plate.]

oral views, plate layout, ×1.3; 274,*1e,f*, cross secs. of ambulacrum, ×3.6 (12, 36, 40, 132).

Auloblastus BEAVER, 1961 (14), p. 1113 [**A. clinei*; OD]. Subspherical form with spiracles near sum-

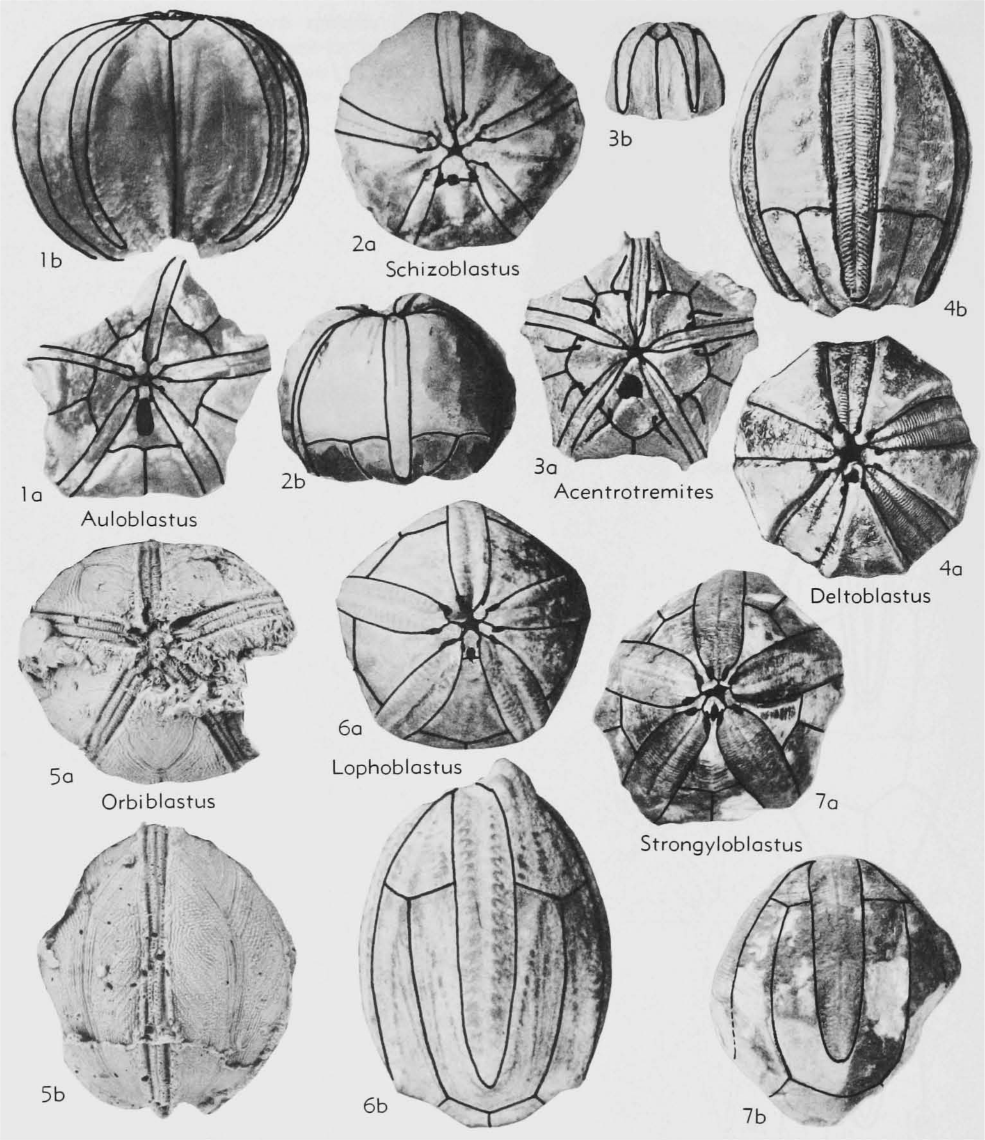

FIG. 273. Schizoblastidae (p. _S_427-_S_432).

mit; anal opening probably separate; basalia small, in concavity; radials long, overlapping deltoids; hydrospire plate absent; single pore between adjacent side plates along ambulacral margins; 4 hydrospire folds on each side of ambulacra; anal opening bordered adorally by superdeltoid, aborally by hypodeltoid, and internally on either side by cryptodeltoids; side plates cover lancets except near adoral tip; lateral canals present. _M.Miss._, N.Am. (Mo.).——FIG. 273,_1_; 274,_3_. *_A. clinei_, USA (Mo.); 273,_1a,b_, oral, interambulacral views, ×1.3; 274,_3a-d_, oral, interambulacral, aboral views, plate layout, ×1.3; 274,_3e_, cross sec. of ambulacrum, ×10 (14).

Deltoblastus FAY, 1961 (49), p. 36 [*_Schizoblastus delta elongatus_ WANNER, 1924 (173), p. 61; OD]. Theca ellipsoidal; anal opening between epideltoid and hypodeltoid; lancet exposed, forming petaloid ambulacra; sinus margins raised; radials overlapping deltoids; base concave; single pore between side plates along radial and deltoid margins; 2 hydrospire folds on each side of ambulacra. _Perm._, E. Indies(Timor)-?Eu.(?Sicily). —— FIG. 275,_1_. _D. permicus_ (WANNER), Timor; 275,_1a-d,_ oral, *D*-ray, aboral views, plate layout, ×3.2; 275, *1e,* cross sec. of ambulacrum, ×7.7 (49).——Fig. 273,*4. D. timorensis* (Bather), Perm., Timor; *4a,b,* oral, *B*-ray views, ×1.3 (11).

Lophoblastus Rowley, 1901, p. 344 [*emend.* Macurda, 1962, p. 1370] [**Codonites inopinatus* Rowley & Hare, 1891, p. 100; OD]. Theca ellipsoidal, with anal opening between epideltoid and hooded hypodeltoid; 3 hydrospire folds on each side of ambulacra; lancet exposed 0.3 of its width; with single pore between adjacent side plates along deltoid and radial margins; deltoids overlapping radials. *Miss.,* N.Am.——Fig. 273,*6;* 276,*3.* **L. inopinatus* (Rowley & Hare), M.Miss.,

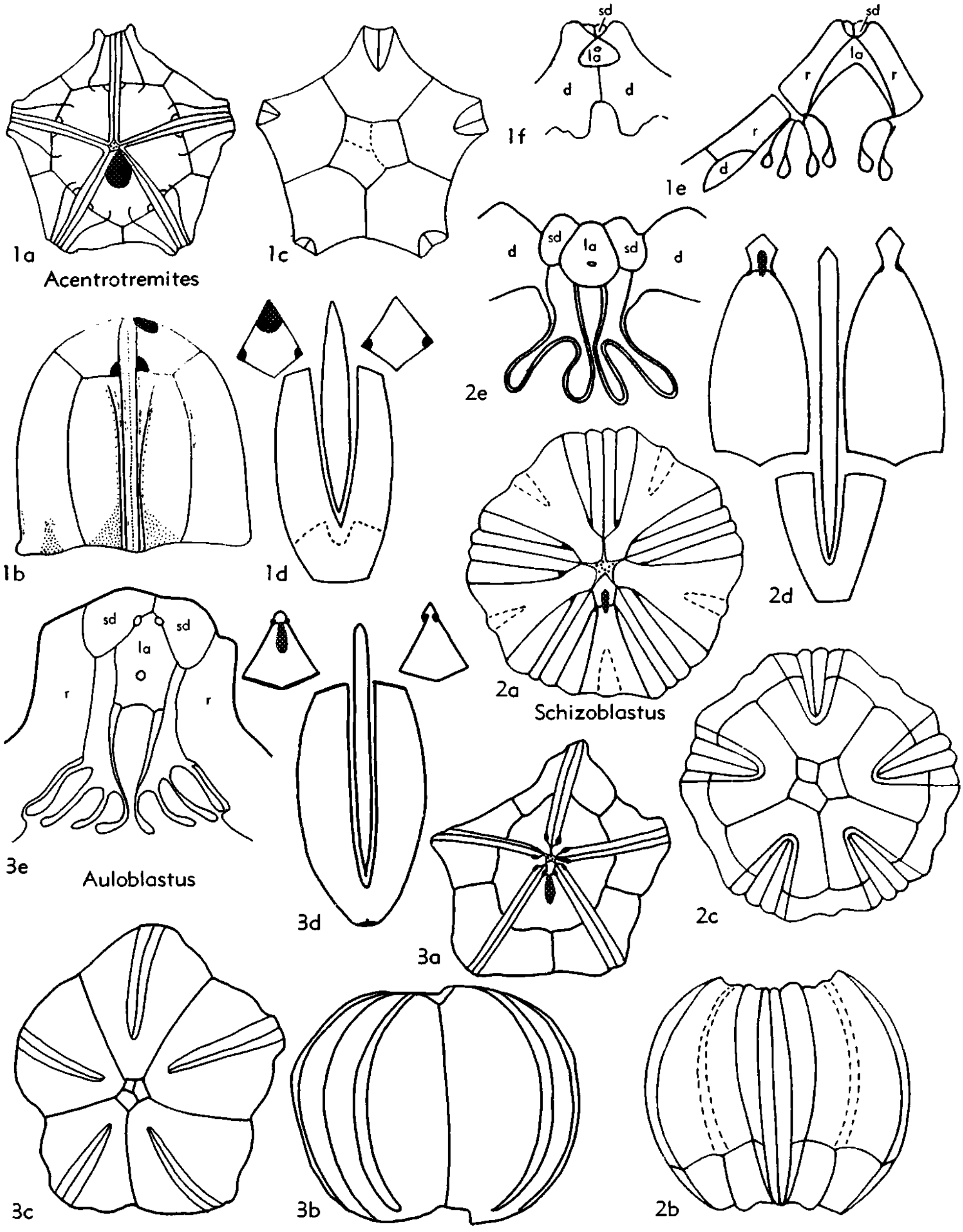

Fig. 274. Schizoblastidae (p. *S*427-*S*430). [Explanation: *d,* deltoid plate; *la,* lancet plate; *r,* radial plate; *sd,* side plate.]

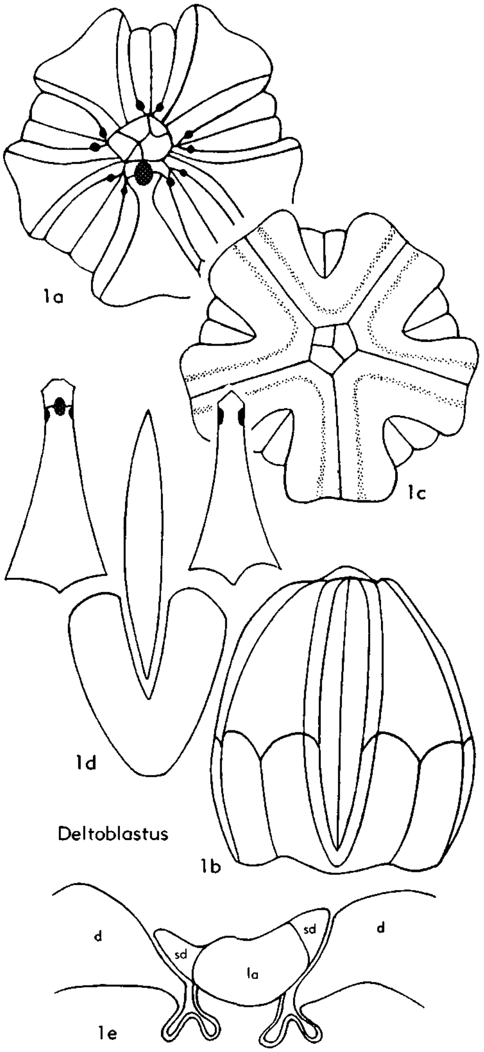

FIG. 275. Schizoblastidae (p. S430). [Explanation: *d*, deltoid plate; *la*, lancet plate; *r*, radial plate; *sd*, side plate.]

USA(Mo.); 273,*6a*, oral view, ×4.2; 273,*6b*, *D*-ray view, ×5.6; 276,*3a-d*, oral, *D*-ray, aboral views, plate layout, ×5.3; 276,*3e*, cross sec. of ambulacrum, ×13.1; 276,*3f*, anal view, ×10 (60).

Orbiblastus MACURDA, 1965 (106), p. 302 [**Orbiblastus hoskynae* MACURDA, 1965 (106), p. 303; OD]. Theca globular, with anal opening between epideltoid and hypodeltoid; 3 hydrospire folds on each side of ambulacra; lancet exposed along main food groove; one pore between each side plate along deltoid and radial margins; radials overlapping deltoids; basalia in basal concavity. *Miss.*, N.Am.(Ark.).——FIG. 273,*5*; 276,*2*. **O. hoskynae*, M.Miss., Ark.; 273,*5a,b*, oral, *D*-ray views, ×1.3; 276,*2a-d*, oral, *D*-ray, aboral views, plate layout, ×1.3 (106).

Strongyloblastus FAY, 1962 (68), p. 132 [**Strongyloblastus petalus* FAY, 1962, p. 132; OD]. Theca suboval, with spiracles near oral opening; anal opening between small epideltoid and moderately long hypodeltoid; deltoids visible in side view, overlapped by radials; lancet widely exposed, with single pore between side plates along radial and deltoid margins; 5 hydrospire folds on each side of ambulacra; ambulacra broadly petaloid and moderately long; periphery at radial lips below mid-height; basalia conical, large; theca subrounded pentagonal in top view. *M.Dev.*, USA (N.Y.).——FIG. 273,*7*; 276,*1*. **S. petalus* FAY; 273,*7a,b*, oral, *E*-ray views, ×1.3; 276,*1a-d*, oral, *E*-ray, aboral views, plate layout, ×1.3; 276,*1e*, cross sec. of *D* ambulacrum, aboral view, ×10 (68).

Family NUCLEOCRINIDAE Bather, 1899

[Nucleocrinidae BATHER, 1899, p. 920] [=Nucleoblastidae ETHERIDGE & CARPENTER, 1886, p. 209 (invalid, based on nonexistent nominal genus); Olivanidae HAMBACH, 1903, p. 48 (invalid, based on nonexistent nominal genus)]

Theca with ten spiracles and anal opening separate around mouth, as in Schizoblastidae, but with two elongate, exposed cryptodeltoids. *Dev.*

Nucleocrinus CONRAD, 1842, p. 280 [**N. elegans*; OD]. Theca ellipsoidal; with 5 large oral plates and 3 exposed anal plates, consisting of 2 cryptodeltoids and hypodeltoid; superdeltoid hidden; anal oral abutting against cryptodeltoids; deltoids long, overlapping radials; 2 hydrospire folds on each side of ambulacra, with short hydrospire canal; lancet covered by side plates, with inner side plate present; one large pore between side plates along deltoid and radial margins. *Dev.*, N.Am.(N.Y.-Iowa-Mich.-Ont.).——FIG. 277,*1a-d*; 278,*1*. **N. elegans*, M.Dev., USA(N.Y.); 277, *1a-d*, oral, *D*-ray, aboral views, plate layout, ×2.6 (34, 60, 83); 278,*1a,b*, oral, *D*-ray views, ×5 (43).——FIG. 277,*1e-h*. *N. meloniformis* (BARRIS), M.Dev., USA(Mich.); *1e*, cross sec. of ambulacrum, ×8.8 (Fay, n); *1f-h*, anal views, ×10 (60).

Elaeacrinus ROEMER, 1851, p. 379 [**E. verneuili*; OD] [=*Olivanites* TROOST, 1849, p. 419 *(nom. nud.)*; *Olivanites* LYON, 1857, p. 487 (type, *Olivanites verneuili* TROOST, 1849); *Eleacrinus* ETHERIDGE & CARPENTER, 1883, p. 228 *(nom. van.)*]. Theca elongate, ellipsoidal; with approximately 18 to 21 oral plates (one of which, however, may be superdeltoid); with 2 prominent, well-exposed cryptodeltoids and hypodeltoid; 1 or 2 anal orals between adoral tips of cryptodeltoids (if 1 it is superdeltoid, and if 2, the aboral one is superdeltoid); deltoids long, overlapping radials; 2 hydrospire folds on each side of ambulacra, with medium-long hydrospire canal; lancet covered by side plates, with inner side plate present; single large pore between side plates along deltoid and radial margins. *Dev.,* N.Am.(Ohio-Ind.-Ky.-Mo.).——Fig. 279,*1a-f*; 280,*1*. **E. verneuili* (Troost), M.Dev., USA(Ind.); 279,*1a-d,* oral,

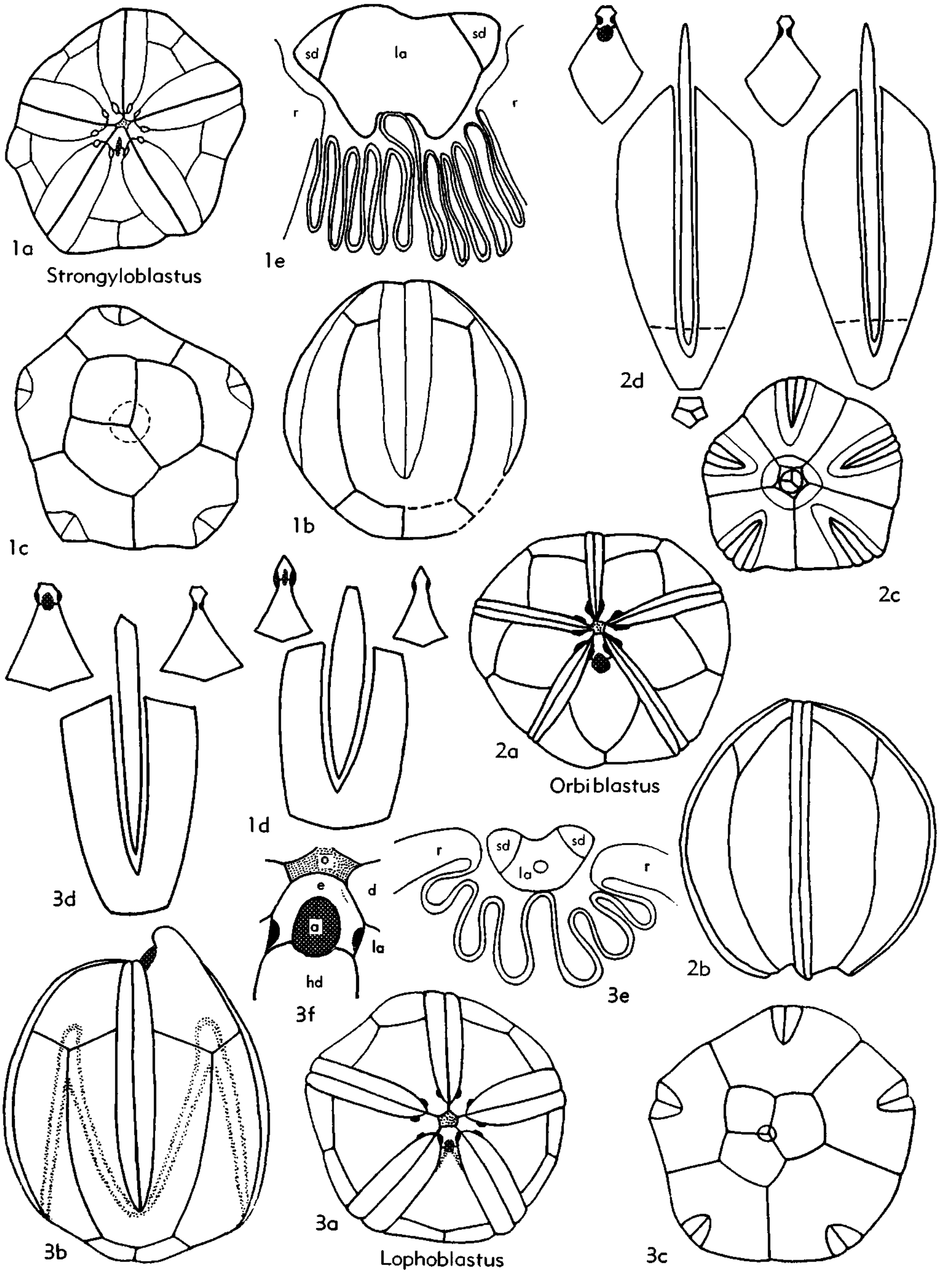

Fig. 276. Schizoblastidae (p. S431-S432). [Explanation: *a,* anal opening; *d,* deltoid plate; *e,* epideltoid plate; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening; *r,* radial plate; *sd,* side plate.]

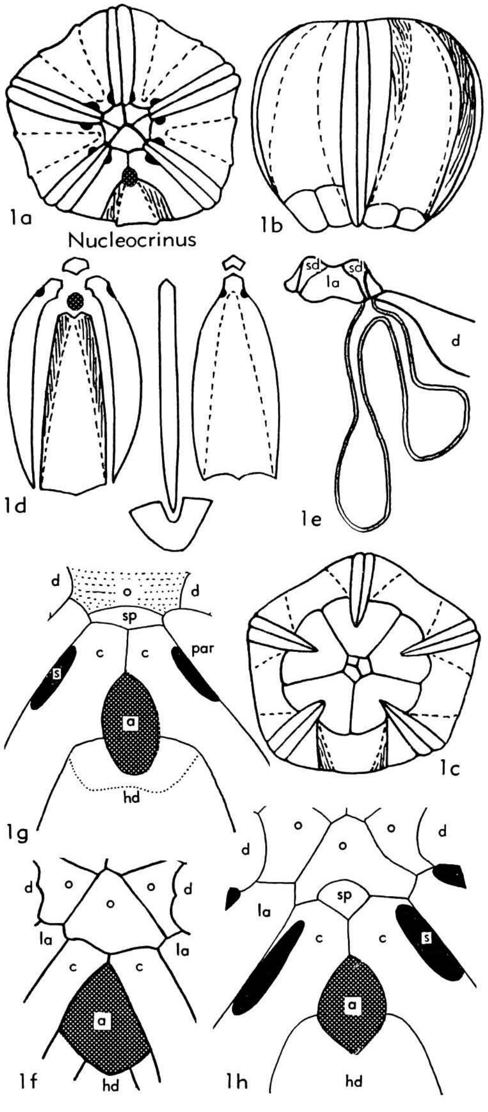

FIG. 277. Nucleocrinidae (p. S432). [Explanation: *a,* anal opening; *c,* cryptodeltoid plate; *d,* deltoid plate; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening or oral plate; *par,* posterior ambulacrum (right); *s,* spiracle; *sd,* side plate; *sp,* superdeltoid plate.]

D-ray, aboral views, plate layout, ×1 (60); 279, *1e,* cross sec. of ambulacrum, ×5 (48); 279,*1f,* anal view, ×4 (60); 280,*1a,b,* oral, *D*-ray views, ×1 (60).——FIG. 279,*1g,h. E. venustus* (MILLER & GURLEY), M.Dev., Ohio; *1g,h,* anal views, ×5.7 (60).

Placoblastus FAY, 1961 (60), p. 92 [**Elaeacrinus obovatus* BARRIS, 1883, p. 358; OD]. Theca elongate ellipsoidal; with prominent, well-exposed cryptodeltoids and hypodeltoid; 6 or 7 large oral plates, one of which is between aboral ends of cryptodeltoids and may be superdeltoid plate; lancet covered by side plates, with inner side plate present; single large pore between side plates along deltoid and radial margins; deltoids long, overlapping radials; 2 hydrospire folds on each side of ambulacra, with long hydrospire canal. *Dev.,* N. Am.(Iowa-Mich.-N. Y.-Ind.-Ohio).——FIG. 280,*2*; 281,*1a-f.* **P. obovatus* (BARRIS), M. Dev., USA(Mich.); 280,*2a,b,* oral, *EA* interambulacral views, ×1.1; 281,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×1.3; 281,*1e,* cross sec. of ambulacrum, ×13.1; 281,*1f,* anal view, ×7.5 (60).——FIG. 281,*1h. P. angularis* (LYON), M. Dev., N.Y.; anal view, ×7.8 (60).——FIG. 281, *1g. P. lucina* (HALL), M.Dev., N.Y.; anal view, ×10 (60).

Family PENTREMITIDAE d'Orbigny, 1851

[*nom. correct.* ETHERIDGE & CARPENTER, 1886, p. 148 (*pro* Pentremitidaea D'ORBIGNY, 1851, p. 139)] [=Eleutherocrinidae BATHER, 1899, p. 920; Eleutheroblastidae, p. 50; Pentremidae, p. 35, HAMBACH, 1903]

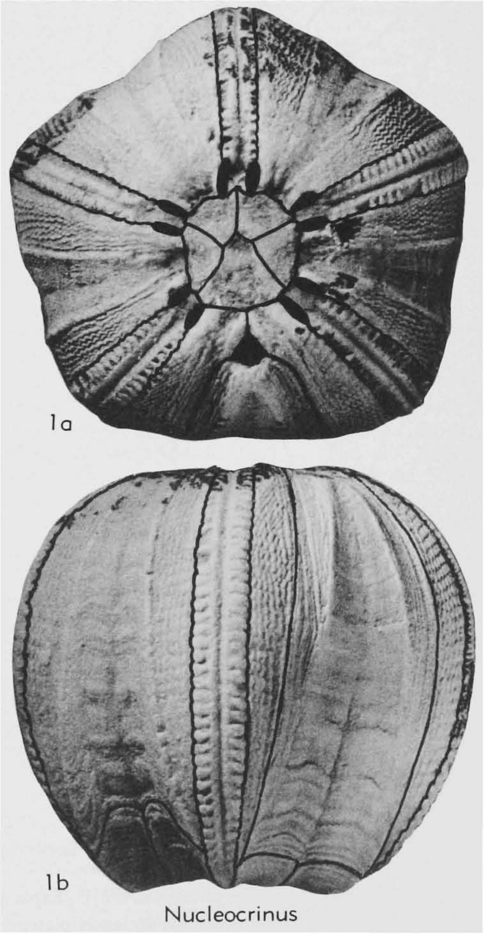

FIG. 278. Nucleocrinidae (p. S432).

Theca subconical or subpyriform with four spiracles and anispiracle around mouth. *Dev.-Perm.*

Pentremites SAY, 1820, p. 36 [**Encrina Godonii* DEFRANCE, 1819, p. 467; SD ETHERIDGE & CARPENTER, 1886, p. 157] [*nom. correct.* SOWERBY, 1825, p. 316 (*pro Pentremite* SAY, 1820)] [=*Asterite, Asterial fossil, Encrina, Encrinites, Pentatrematites, Pentatremites,* AUCTT. *(partim)*]. Theca club-shaped to subpyriform; anispiracle excavated in undivided anal deltoid plate; with 3 to 7 or more hydrospire folds on each side of an ambulacrum; oral and anal areas covered by many imbricate plates; one pore between side plates along radial and deltoid margins; lancet widely exposed, forming petaloid ambulacra; radials overlapping deltoids. *Miss.-Penn.,* N.Am.-S.Am.(Colombia).——FIG. 282,*1*. **P. godoni* (DEFRANCE), U.Miss., USA(Ill.); *1a-d,* oral, *D*-ray, aboral views, plate layout, ×2.6; *1e,* cross sec. of ambulacrum, ×5.3 (Fay, n).——FIG. 283,*3*. *P. sulcatus* (ROEMER), U.Miss., Ill.; *3a,b,* oral, side views, ×1 (78).

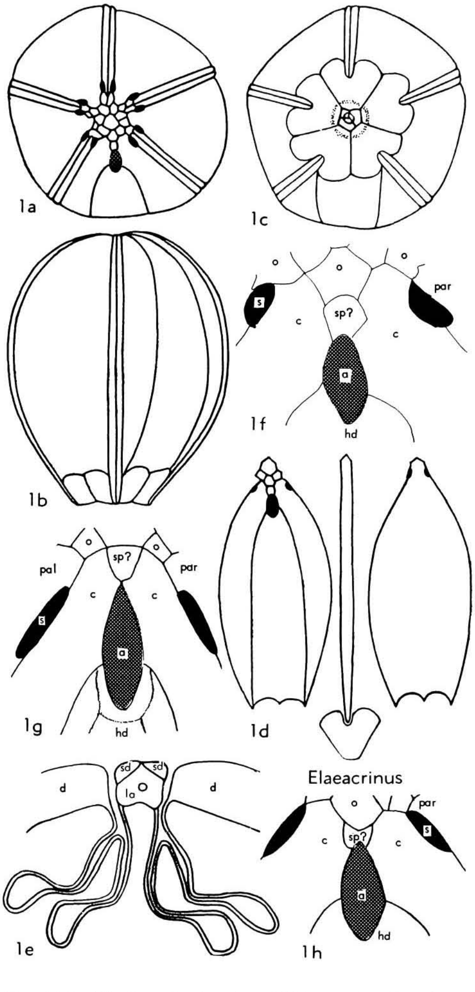

FIG. 279. Nucleocrinidae (p. S432-S434). [Explanation: *a,* anal opening; *c,* cryptodeltoid plate; *d,* deltoid plate; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening or oral plate; *pal,* posterior ambulacrum (left); *par,* posterior ambulacrum (right); *s,* spiracle; *sd,* side plate; *sp,* superdeltoid plate.]

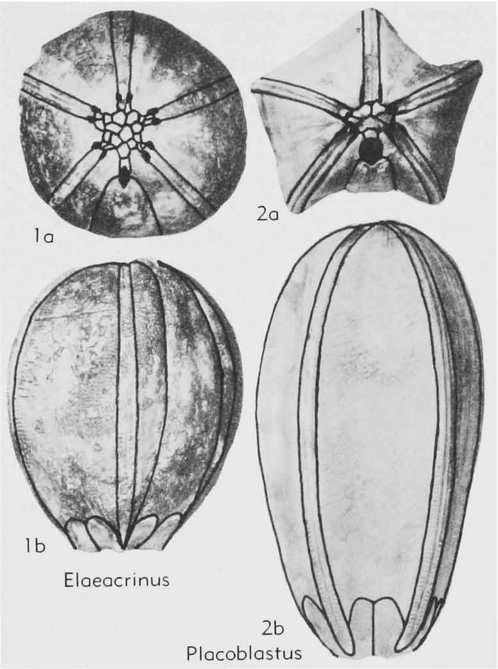

FIG. 280. Nucleocrinidae (p. S432-S434).

Ambolostoma PECK, 1930, p. 104 [**A. baileyi*; OD]. Theca ellipsoidal; anispiracle in undivided anal deltoid plate; 5 large oral plates covering summit; lancet completely exposed; one large pore between adjacent side plates along deltoid and radial margins; 3 hydrospire folds on each side of an ambulacrum. *Miss.,* N.Am.(Utah-Alta.).——FIG. 282,*2*; 284,*6*. **A. baileyi,* USA(Utah); 282,*2a-d,* oral, *D*-ray, aboral views, plate layout, ×0.87; 282,*2e,* cross sec. of ambulacrum, ×17.6; 284,*6a,* oral view, ×1.1; 284,*6b,* interradial view, ×0.8 (130).

Belocrinus MUNIER-CHALMAS, 1881, p. 503 [*emend.* MACURDA, 1966 (110), p. 245] [**Belemnocrinus cottaldi* MUNIER-CHALMAS, 1876, p. 105; OD] [=*Belemnocrinus* MUNIER-CHALMAS, 1876, p. 105 (*non* WHITE, 1862)]. Theca club-shaped, with extremely elongate pelvis; spiracles five, simple, with anispiracle between epideltoid? and hypodeltoid (possibly with two deeply hidden cryptodeltoids); deltoids visible in side view, including hypodeltoid; lancet covered by side plates, with one pore between adjacent side plates along radial and deltoid margins; number of hydrospires unknown but in ten groups or fields. *L.Dev.*, Eu. (NW.Fr.).——Fig. 282,*3*; 283,*4*. **B. cottaldi* (Munier-Chalmas), Eu.(NW.Fr.); 282,*3a-d*, oral, *A*-ray, aboral views, plate layout, ×1.3; 283,*4a,b*, oral, *A*-ray views, ×2 (110).

Calycoblastus Wanner, 1924 (173), p. 35 [*emend.* Breimer & Macurda, 1965, p. 215] [**C. tricavatus*; OD]. Theca subpyramidal, with anispiracle between epideltoid and hypodeltoid; radials overlapping deltoids; 5 hydrospire folds on each

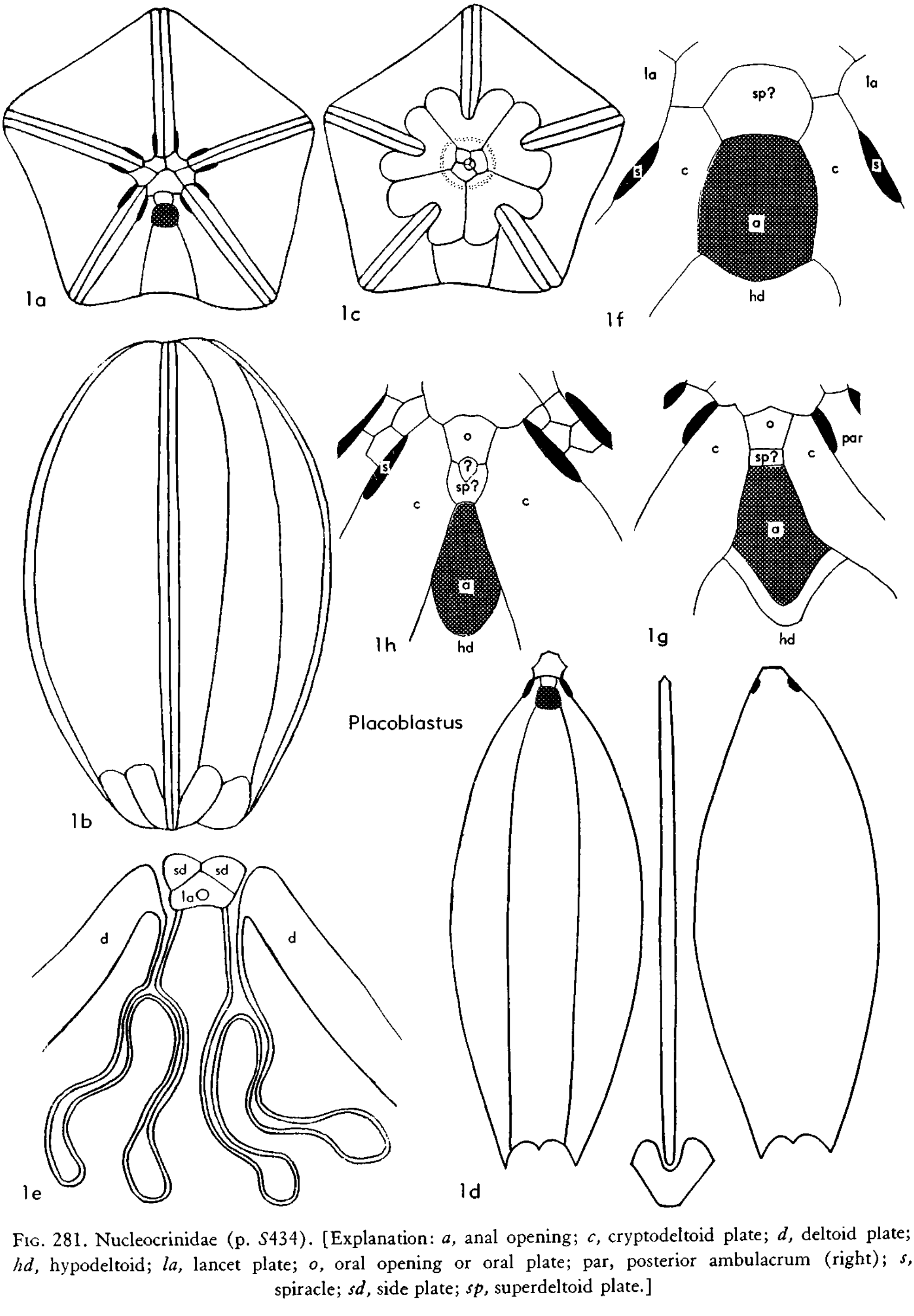

Fig. 281. Nucleocrinidae (p. S434). [Explanation: *a*, anal opening; *c*, cryptodeltoid plate; *d*, deltoid plate; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening or oral plate; par, posterior ambulacrum (right); *s*, spiracle; *sd*, side plate; *sp*, superdeltoid plate.]

side of an ambulacrum; sublancet or fused hydrospire plate present; lancet covered by side plates; deltoids visible in side view. *Perm.*, E.Indies (Timor)-Australia(New S. Wales).——Fig. 283, *1*; 284,*4*; 285,*2*. **C. tricavatus*, Timor, 283,*1*, *A*-ray view, ×1; 284,*4*, oral view, ×1.3; 285, *2a-d*, oral, *D*-ray, aboral views, plate layout, ×1.8; 285,*2e*, cross sec. of ambulacrum, ×3.8 (173).

Cordyloblastus Fay, 1961 (60), p. 52 [**Pentremites*

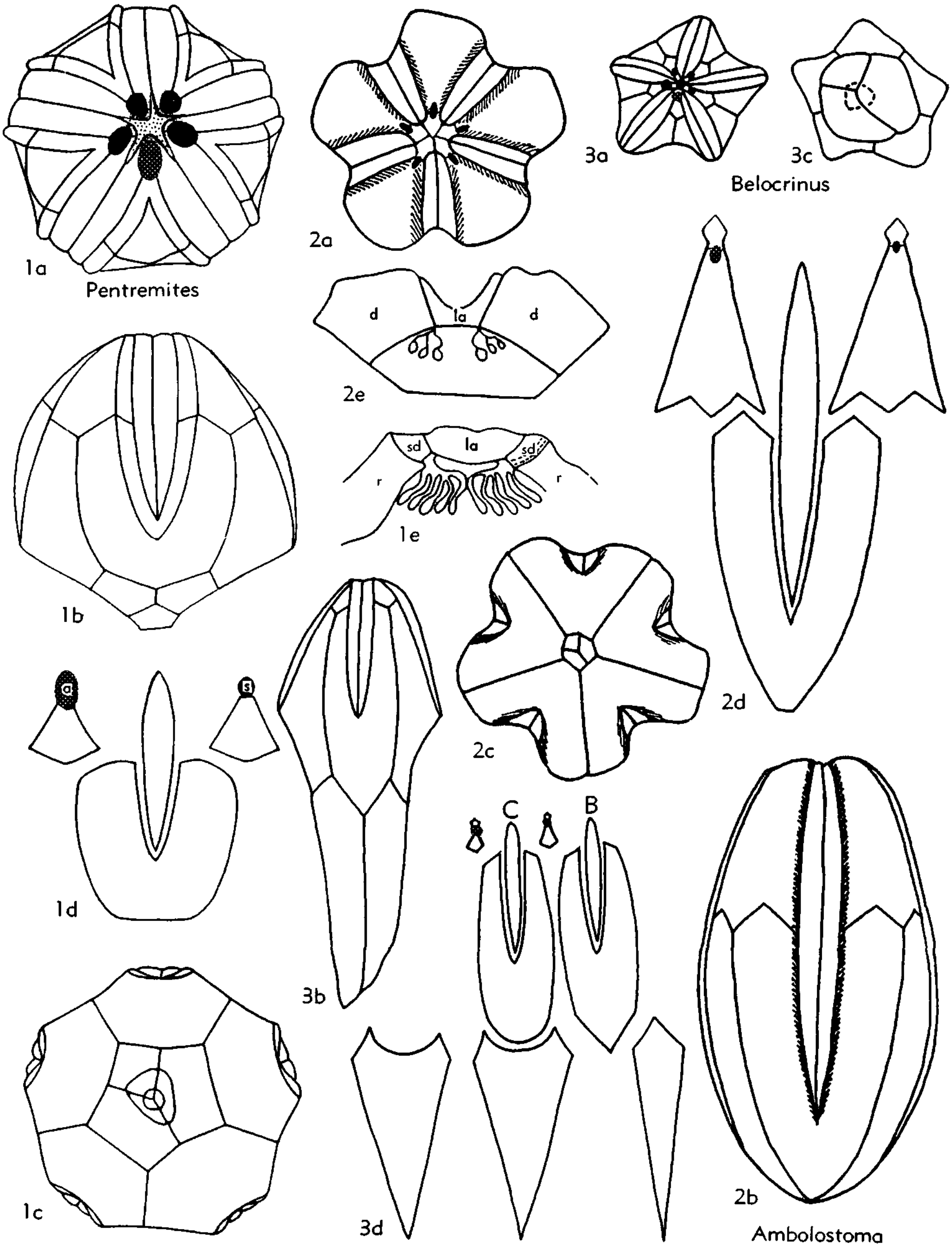

Fig. 282. Pentremitidae (p. S435-S436). [Explanation: *a*, anispiracle; *d*, deltoid plate; *la*, lancet plate; *r*, radial plate; *s*, spiracle; *sd*, side plate.]

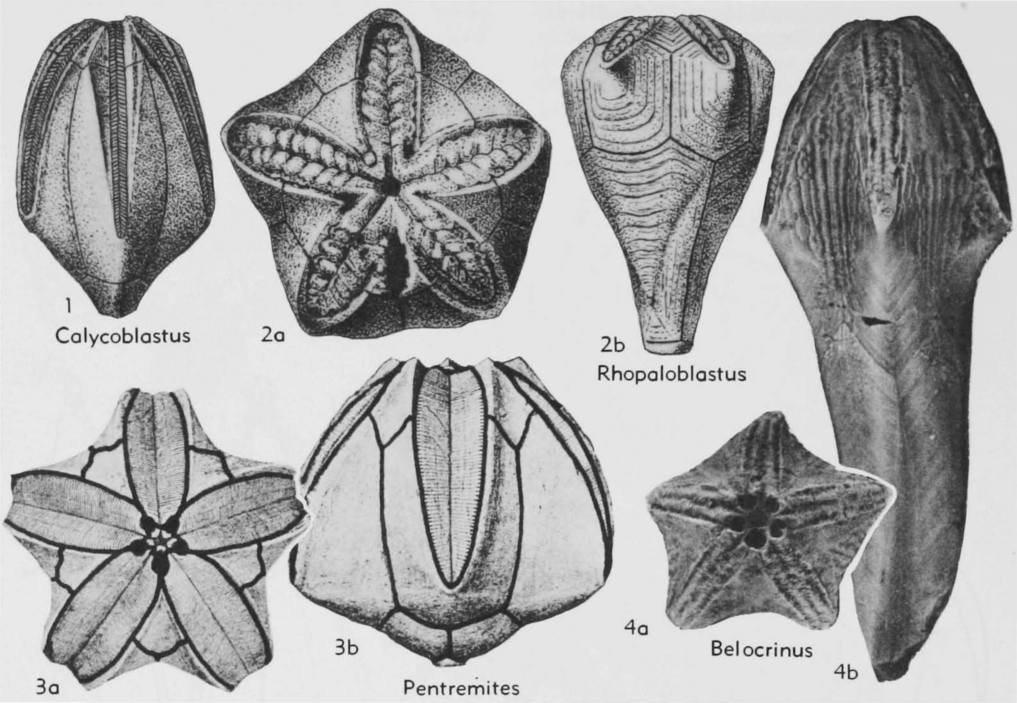

FIG. 283. Pentremitidae (p. *S*435-*S*437, *S*443).

acutangulus SCHULTZE, 1886, p. 225; OD]. Theca club-shaped; with anispiracle between superdeltoid and large hypodeltoid, with 2 internal cryptodeltoids; hypodeltoid seen in side view but not other 4 deltoids; radials overlapping deltoids; lancet covered by side plates; one pore between adjacent side plates along radial margins; with 4 to 9 hydrospire folds on each side of an ambulacrum. *Dev.*, Eu.(Ger.-Spain).——FIG. 284,*3*; 285, *1a-f*. **C. acutangulus* (SCHULTZE), Eifel., Ger.; 284,*3a,b,* oral, *D*-ray views, ×1.7; 285,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×1.8; 285,*1e,* cross sec. of ambulacrum, ×13.1; 285,*1f,* anal view, ×10 (60).——FIG. 285,*1g-i*. *C. eifelensis* (ROEMER), M.Dev., Ger.; *1g,* anal view, ×10; *1h,* anal view, ×30; *1i,* anal view, ×10 (60).

Devonoblastus REIMANN, 1935, p. 30 [**Pentremites leda* HALL, 1862, p. 149; SD REIMANN, 1942, p. 47]. Theca elliptico-conical; anispiracle between superdeltoid and hypodeltoid, with 2 cryptodeltoids beneath hypodeltoid; 5 hydrospire folds on each side of an ambulacrum; lancet covered by side plates except at adoral end; one pore between side plates along radial and deltoid margins; deltoids visible in side view, overlapped by radials. *Dev.*, N. Am.(N.Y.-?Ind.-Ont.)-?Asia(?China).——FIG. 286,*2a-d*. **D. leda* (HALL), M.Dev., USA (N.Y.); *2a-d,* oral, *D*-ray, aboral views, plate layout, ×2.6 (41, 60, 137).——FIG. 284,*5*; 286,*2e-g*. *D. whiteavesi* REIMANN, M.Dev., Ont.; 284,*5a,b,* oral, *D*-ray views, ×2.2; 286,*2e-g,* 3 anal views, ×10 (60).

Eleutherocrinus SHUMARD & YANDELL, 1856, p. 73 [**E. cassedayi*; OD] [=*Eleutheroblastus* HAMBACH, 1903, p. 50 (obj.)]. Theca ellipsoidal, with superdeltoid, 2 cryptodeltoids, and hypodeltoid; short *D* ambulacrum; 6 or 7 hydrospire folds on each side of an ambulacrum; lancet covered by side plates; one pore between adjacent side plates along deltoid and radial margins; radials overlapping deltoids; thecal plates slightly irregular. *Dev.*, N.Am.(Ky.-Ind.-N.Y.-Ont.).——FIG. 284,*1*; 286,*1*. **E. cassedayi,* M.Dev., Can.(Ont.); 284,*1a,* oral view, ×3; 284,*1b, D*-ray view, ×2.8; 284, *1c,* aboral view, ×2.9; 284,*1d, B*-ray view, ×2.9; 284*1e, C*-ray view, ×3.4; 286,*1a-f,* oral, *D*-ray, aboral views, plate layout, cross sec. of middle part of ambulacrum, cross sec. of aboral tip of ambulacrum, ×6.6; 286,*1g,* anal view, ×10 (60, 158).

Pentremoblastus FAY & KOENIG, 1963, p. 267 [**Pentremoblastus conicus*; OD]. Theca conical to obconical, with elongate split-elliptical spiracles; anispiracle between superdeltoid, subdeltoid, and hypodeltoid; elongate radials overlap short deltoids along an inverted V-shaped suture; deltoids barely visible in side view; lancet exposed full width, with one pore between side plates; 2 to 3 hydrospire folds on anal side, but 5 hydrospire folds on each side of other ambulacra; stem round.

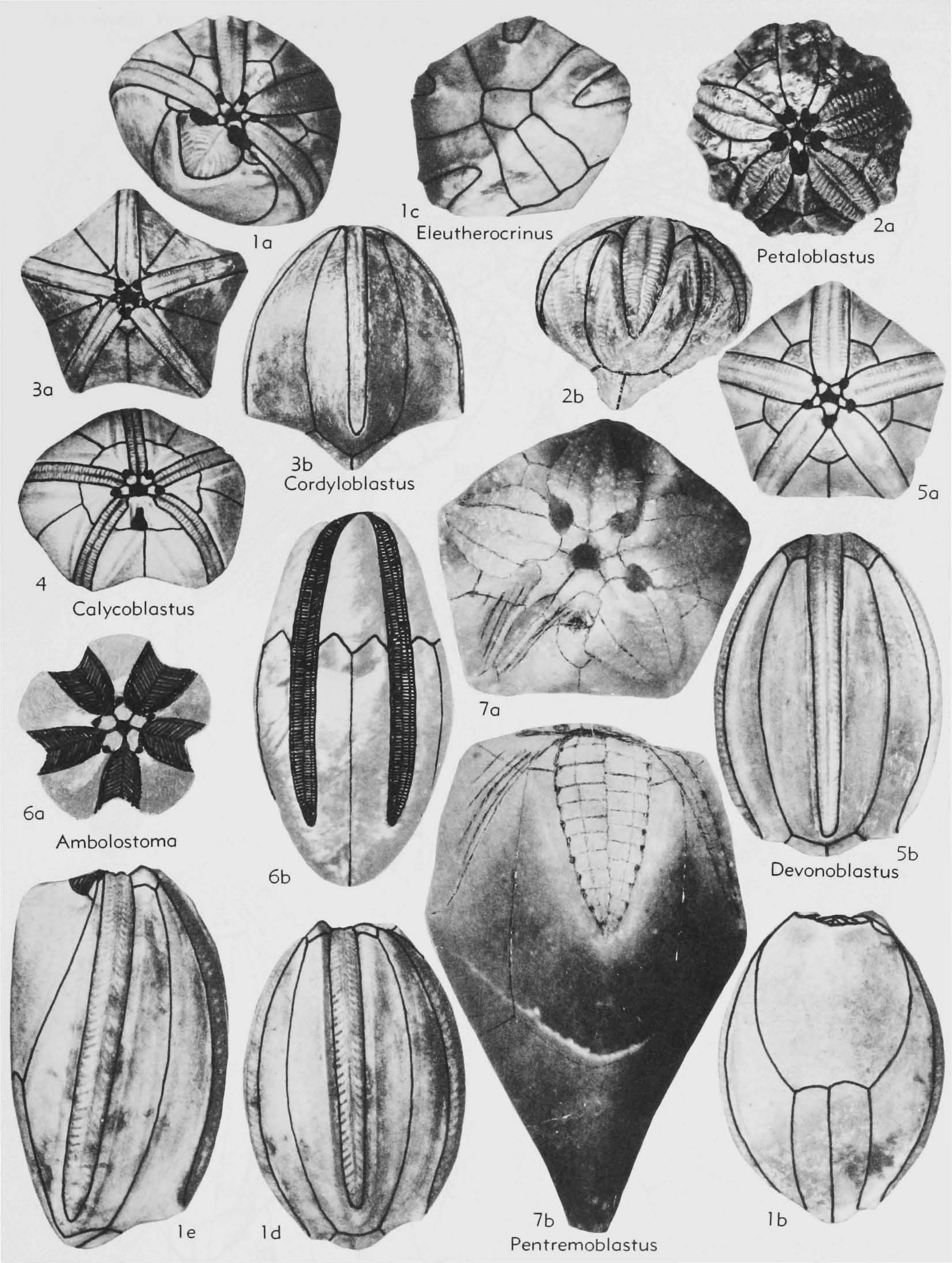

FIG. 284. Pentremitidae (p. S435-S438, S440-S443).

L.Miss., USA(Ill.).——Fig. 284,7; 287,1. **P. conicus*, Kinderhook., Ill.; 284,*7a,b*, oral, *C*-ray views, ×11.4; 287,*1a-d*, oral, *C*-ray, aboral views, plate layout, ×11.4 (75).

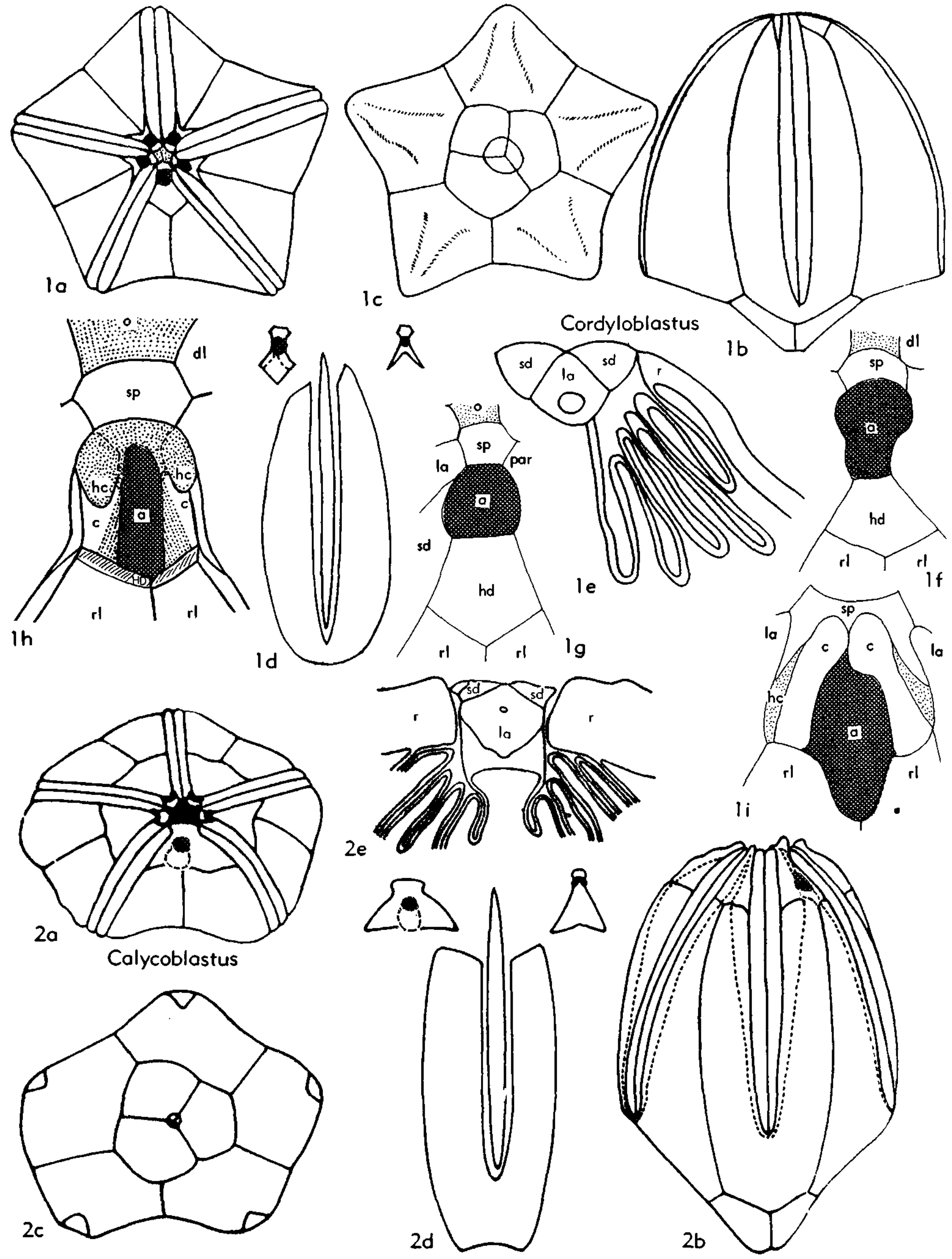

Fig. 285. Pentremitidae (p. *S*436-*S*438). [Explanation: *a*, anal opening; *c*, cryptodeltoid plate; *dl*, deltoid lip; *hc*, hydrospire canal; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening or oral plate; *par*, posterior ambulacrum (right); *r*, radial plate; *rl*, radial limb; *sd*, side plate; *sp*, superdeltoid plate.]

Petaloblastus FAY, 1961 (60), p. 90 [**Pentremites ovalis* GOLDFUSS, 1829, p. 161; OD]. Theca ovoid, with anispiracle located between epideltoid and hypodeltoid; radials overlapping deltoids, but

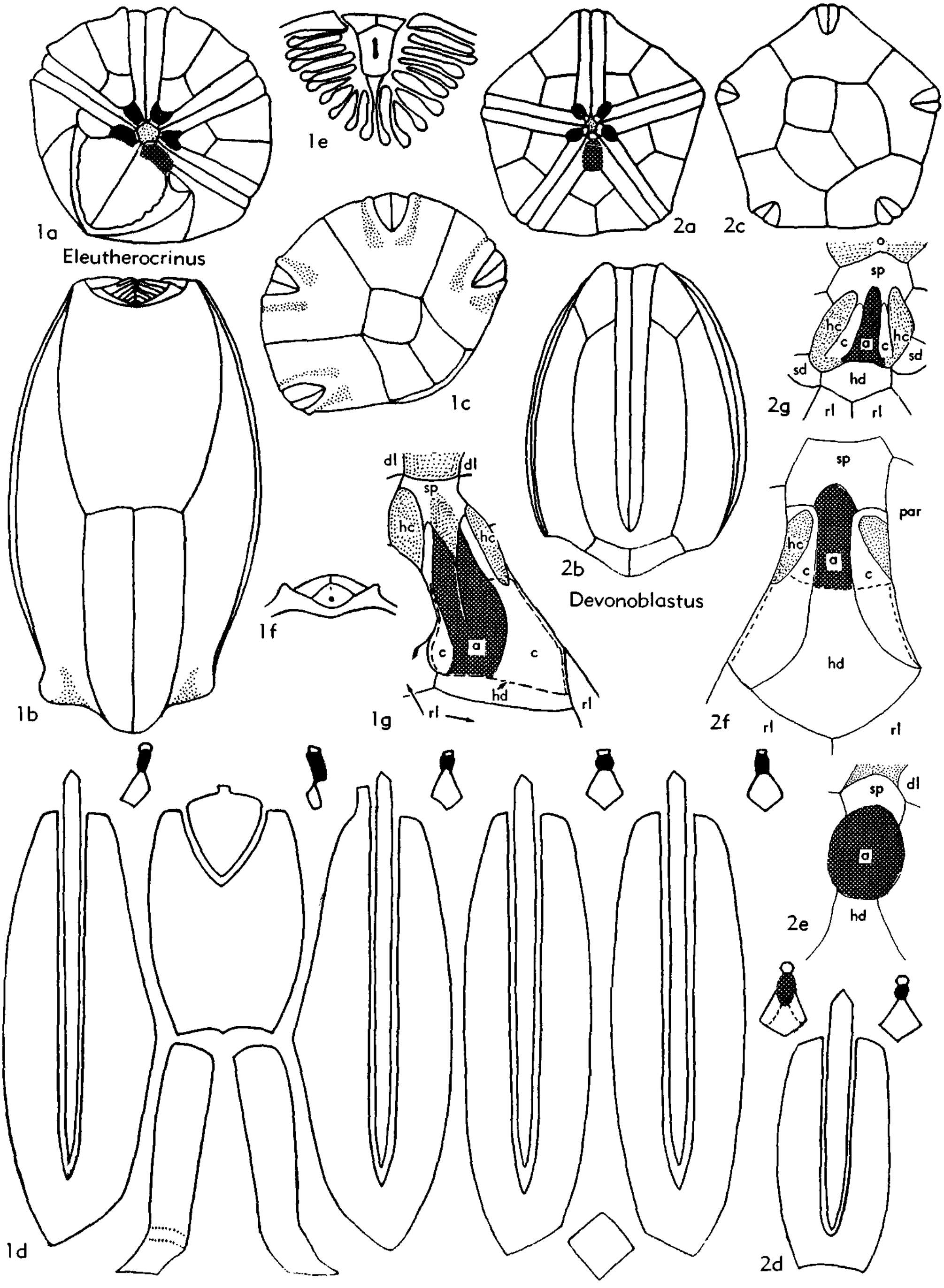

FIG. 286. Pentremitidae (p. S438). [Explanation: *a,* anal opening; *c,* cryptodeltoid plate; *dl,* deltoid lip; *hc,* hydrospire canal; *hd,* hypodeltoid; *o,* oral opening or oral plate; *par,* posterior ambulacrum (right); *rl,* radial lip; *sd,* side plate; *sp,* superdeltoid plate.]

radiodeltoid suture inverted V-shaped (opposite to that seen in *Pentremites*); at least 4 hydrospire folds on each side of an ambulacrum; lancet exposed its full width, forming petaloid ambulacra; one pore between side plates along radial and deltoid margins. *L.Carb.*, Eu.(Ger.).——FIG. 284, 2. *P. boletus* (SCHMIDT), L.Miss., Ger.; *2a,b,* oral, *D*-ray views, ×2.9 (63).——FIG. 287,2. **P. ovalis*

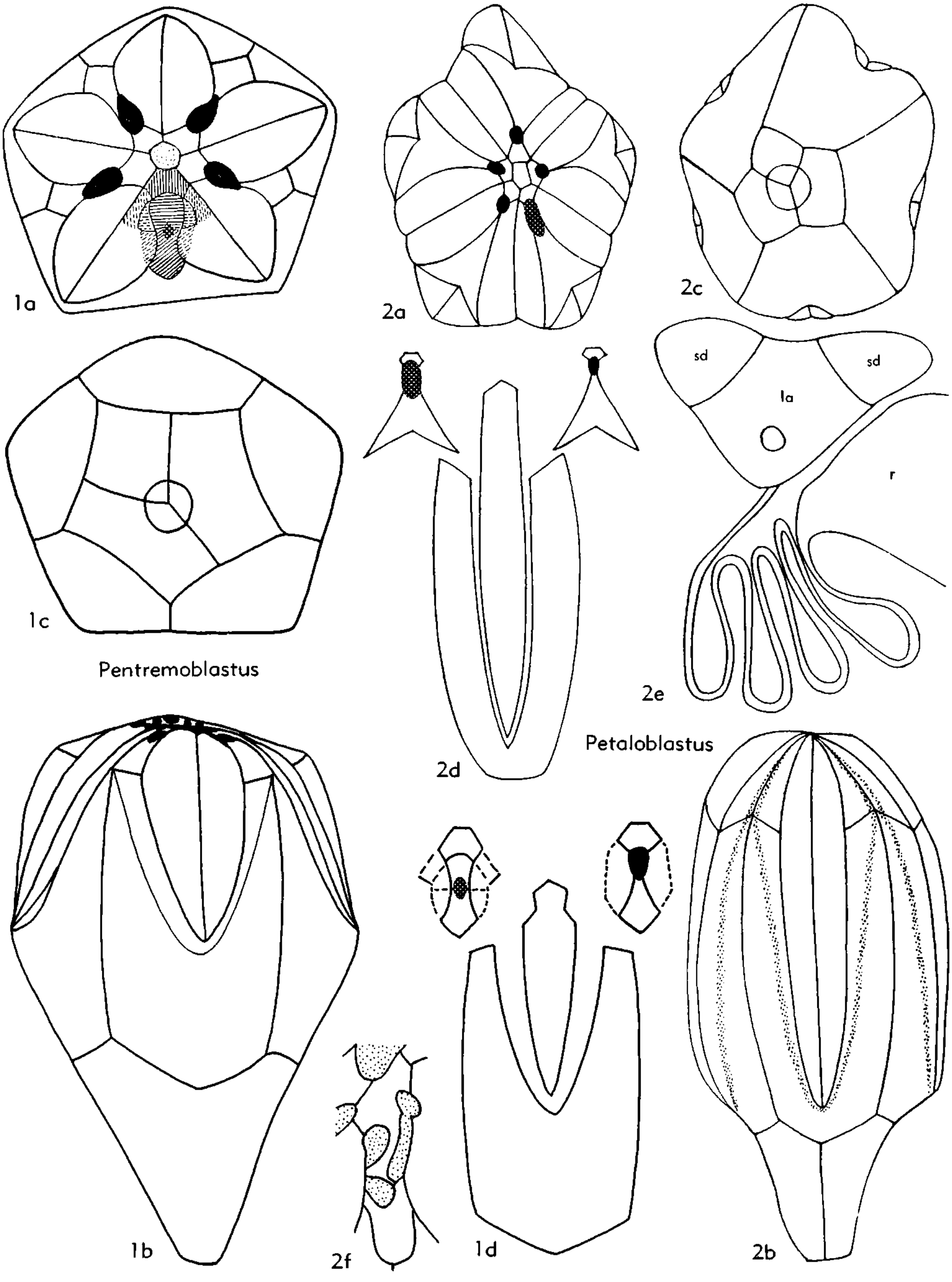

FIG. 287. Pentremitidae (p. S438, S440-S443). [Explanation: *la,* lancet plate; *r,* radial plate; *sd,* side plate.]

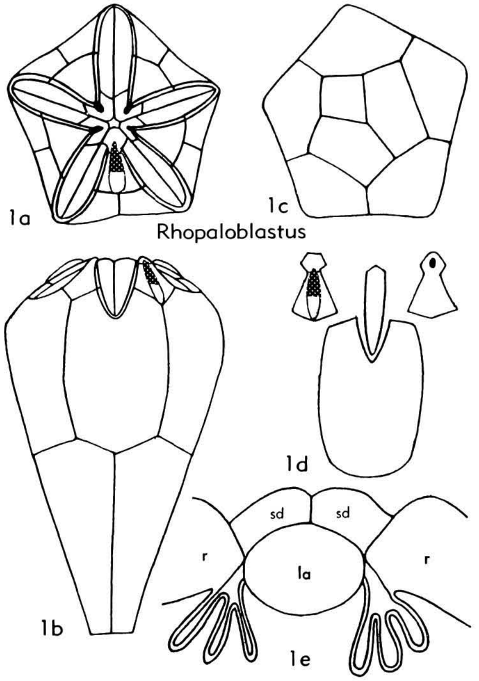

FIG. 288. Pentremitidae (p. S443). [Explanation: *la,* lancet plate; *r,* radial plate; *sd,* side plate.]

(GOLDFUSS), Etroeungt.; *2a-d,* oral, *D*-ray, aboral views, plate layout, ×11.1; *2e,* cross sec. of ambulacrum, ×39.5; *2f,* anal view, ×15 (60).

Rhopaloblastus WANNER, 1924 (174), p. 215 [*emend.* BREIMER & MACURDA, 1965, p. 216] [**R. timoricus*; OD]. Theca obconical, with 4 spiracles plus anispiracle; anispiracle between a superdeltoid, 2 exposed cryptodeltoids, and a hypodeltoid; one pore between side plates along radial and deltoid margins; ambulacra moderately short, almost confined to summit, with lancet stipe away from mouth; lancet covered by side plates; radials short, basals long; 3 hydrospire folds on each side of an ambulacrum. *Perm.,* E.Indies (Timor)-Australia.——FIG. 283,*2*; 288,*1*. **R. timoricus,* Timor; 283,*2a,* oral view, ×4; 283,*2b, BC* inter-ray view, ×2.5; 288,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×2.6; 288,*1e,* cross sec. of ambulacrum, ×13.1 (174, 178).

Family ORBITREMITIDAE Bather, 1899

[Orbitremitidae BATHER, 1899, p. 920]

Theca subglobular with five spiracles (including anispiracle) around mouth. *Miss.*

Orbitremites AUSTIN & AUSTIN, 1842, p. 111 [**Pentremites derbiensis* SOWERBY, 1825, p. 317; SD BATHER, 1899 (9), p. 24] [=*Orbitremites* GRAY, 1840, p. 12 *(nom. nud.)*]. Theca ellipsoidal; with superdeltoid, 2 cryptodeltoids, and hypodeltoid; hydrospire plate present; approximately twice as many pores as side plates along deltoid and radial margins; one hydrospire fold on each side of an ambulacrum; deltoids overlapping radials; lancet exposed along middle one-third of its width. *L.Carb.,* Eu.(Eng.).——FIG. 289,*1*; 290,*1a-g.* **O. derbiensis* (SOWERBY); 289, *1a,b,* oral, *D*-ray views, ×4.2; 290,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×5.9; 290,*1e,* cross sec. of ambulacrum, ×11.7; 290,*1f,g,* 2 anal views, ×10 (3, 41, 60, 161).——FIG. 290,*1h. O. ellipticus* (SOWERBY), L.Carb., Eng.; anal view, ×10 (60).

Doryblastus FAY, 1961 (54), p. 194 [**Mesoblastus melonianus* SCHMIDT, 1930, p. 69; OD]. Theca ellipsoidal, with 4 V-shaped spiracles plus anispiracle; anispiracle located between epideltoid and hypodeltoid, possibly with 2 cryptodeltoids be-

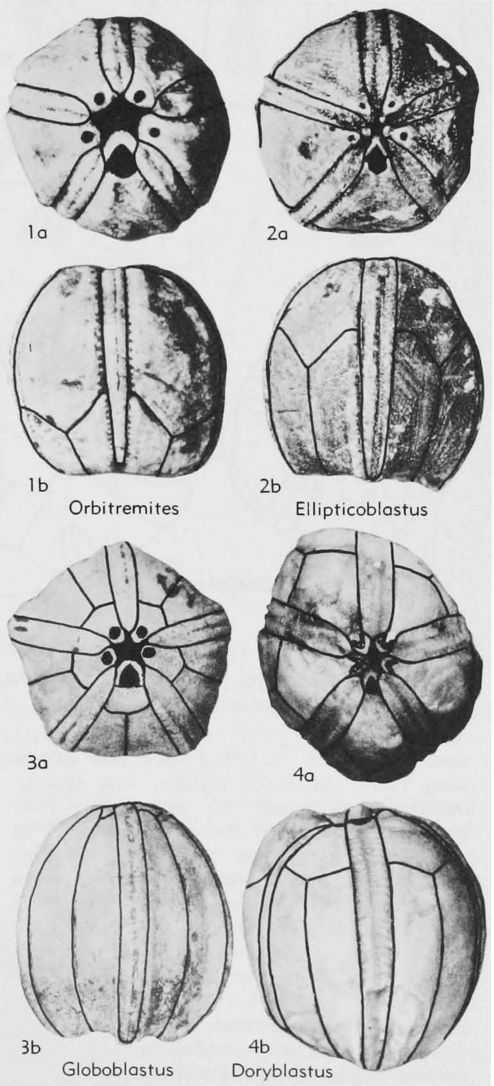

FIG. 289. Orbitremitidae (p. S443-S445).

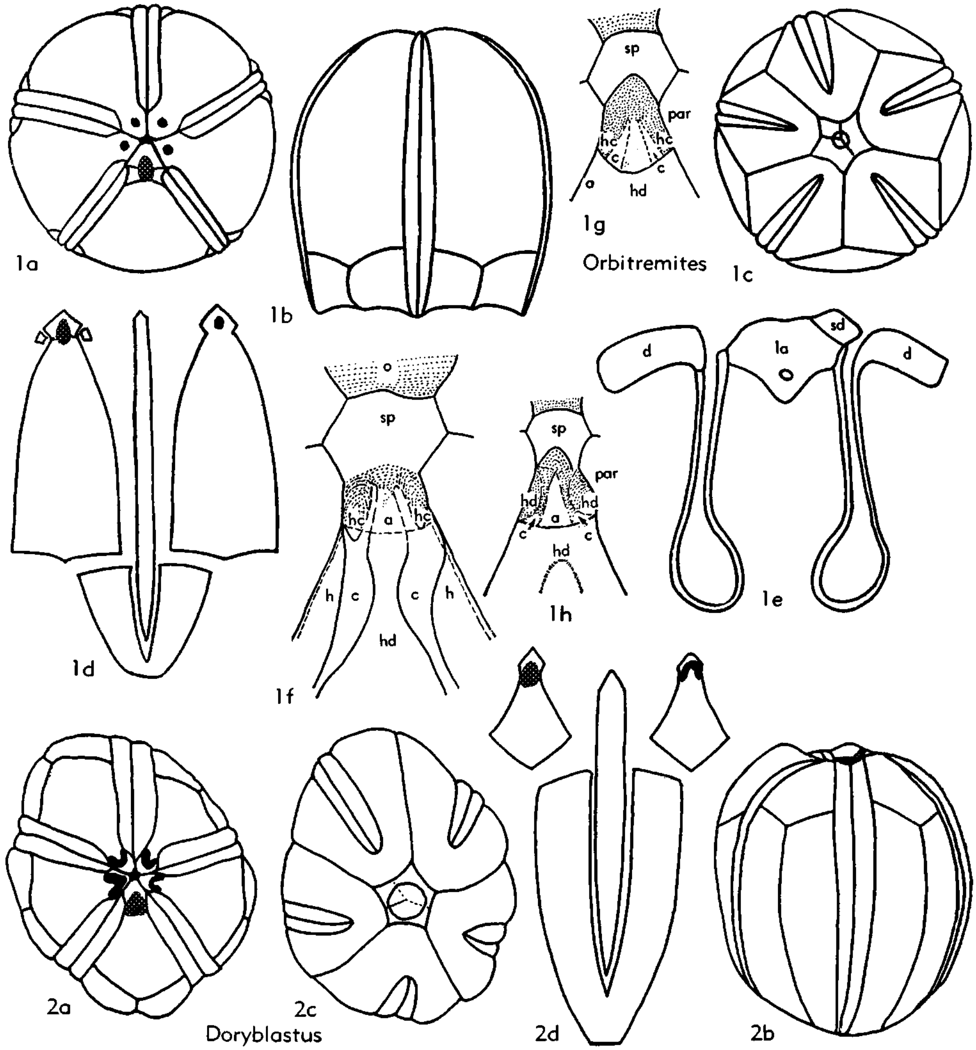

Fig. 290. Orbitremitidae (p. S443-S444). [Explanation: *a,* anispiracle; *c,* cryptodeltoid plate; *d,* deltoid plate; *h,* hydrospire plate; *hc,* hydrospire canal; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening; *par,* posterior ambulacrum (right); *sd,* side plate; *sp,* superdeltoid plate.]

neath hypodeltoid; thick hydrospire plate present along radial and deltoid margins, with approximately 2 pores to each side plate; radials overlapping deltoids; lancet exposed one-third of its width; basalia small, in deep basal concavity; possibly 3 hydrospire folds on each side of an ambulacrum. *M.Miss.,* Ger.——Fig. 289,*4*; 290,*2*. **D. melonianus* (Schmidt), U.Tournais., Ger.; 289,*4a,b,* oral, *D*-ray views, ×4.1; 290,*2a-d,* oral, *D*-ray, aboral views, plate layout, ×4.2 (54).

Ellipticoblastus Fay, 1960 (47), p. 317 [**Pentatrematites orbicularis* Sowerby, 1834, p. 456; OD]. Theca elliptical; with superdeltoid, 2 cryptodeltoids, and hypodeltoid; hydrospire plate present; approximately twice as many pores as side plates along deltoid and radial margins; one long hydrospire fold, curved, on each side of an ambulacrum; radials overlapping deltoids; lancet exposed along middle one-third of its width. *L.Carb.,* Eu. (Eng.).——Fig. 289,*2*; 291,*2*. **E. orbicularis* (Sowerby); 289,*2a,b,* oral, *D*-ray views, ×4.1; 291,*2a-d,* oral, *D*-ray, aboral views, plate layout, ×4.4; 291,*2e,* anal view, ×10 (60); 291,*2f,* cross sec. of ambulacrum, ×6.5 (41).

Globoblastus Hambach, 1903, p. 46 [**Pentremites norwoodi* Owen & Shumard, 1850, p. 64; OD]. Theca subglobular; with superdeltoid, 2 cryptodeltoids, and hypodeltoid; lancet covered by side

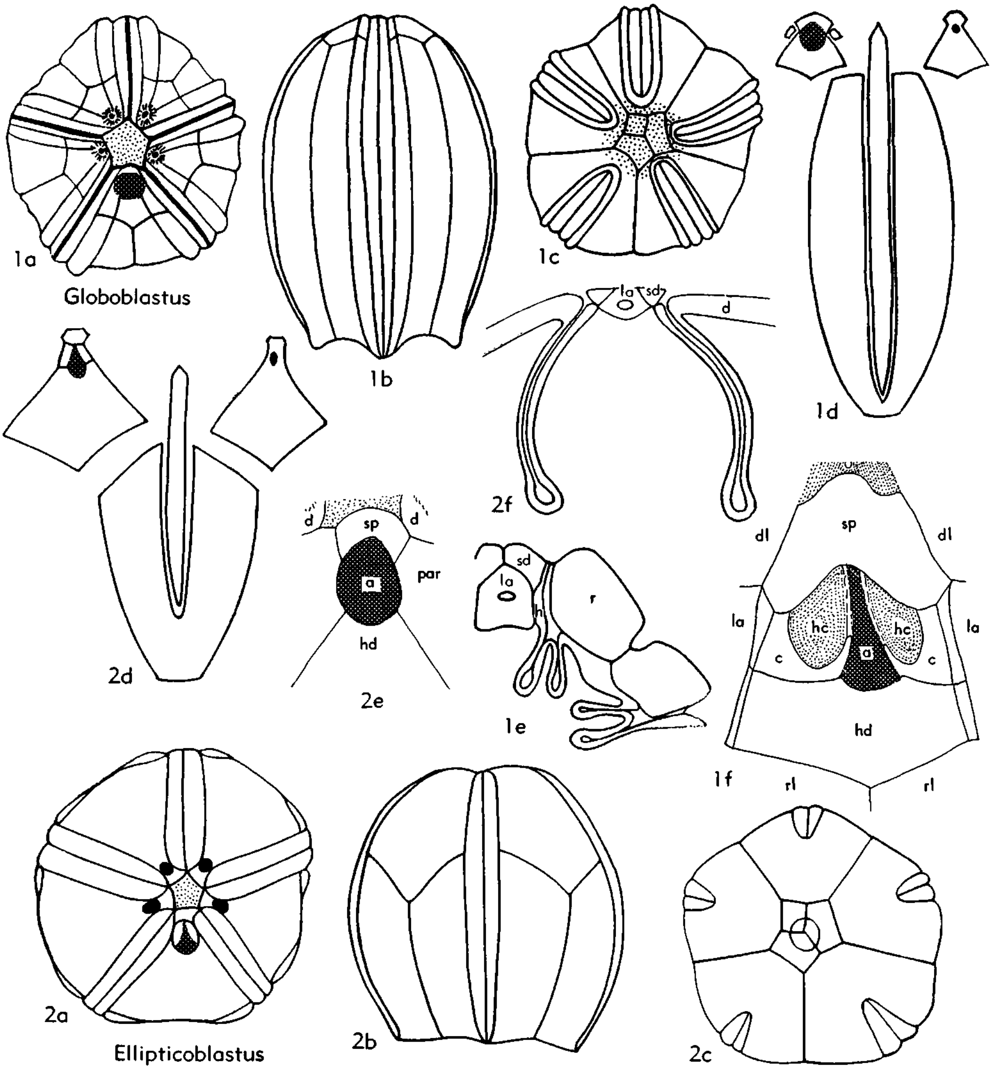

FIG. 291. Orbitremitidae (p. S444-S445). [Explanation: *a*, anispiracle; *c*, cryptodeltoid plate; *d*, deltoid plate; *dl*, deltoid lip; *h*, hydrospire plate; *hc*, hydrospire canal; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening or oral plate; *par*, posterior ambulacrum (right); *r*, radial plate; *rl* radial limb; *sd*, side plate; *sp*, superdeltoid plate.]

plates except near adoral end; radials overlapping short deltoids; hydrospire plate present; 2 hydrospire folds on each side of an ambulacrum; approximately 2 pores to each side plate along radial margins. *Miss.*, N.Am.(Ill.-Iowa-Mo.).——FIG. 289,*3*; 291,*1*. **G. norwoodi* (OWEN & SHUMARD), M.Miss., Iowa; 289,*3a,b*, oral, *D*-ray views, ×2.4; 291,*1a-d*, oral, *D*-ray, aboral views, plate layout, ×3.6; 291,*1e*, cross sec. of ambulacrum, ×8.8; 291,*1f*, anal view, ×11.8 (45, 60, 86, 128).

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(73) 1963, *Nodoblastus, a new Upper Mississippian (Namurian) blastoid from Russia:* Same, v. 23, no. 7, p. 174-180, pl. 1-3.

(74) 1964, *An outline classification of the Blastoidea:* Same, v. 24, no. 4, p. 81-90.

———, & Koenig, J. W.

(75) 1963, *Pentremoblastus, a new Lower Mississippian blastoid from Illinois:* Oklahoma Geol. Survey, Oklahoma Geol. Notes, v. 23, no. 11, p. 267-270, pl. 1.

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(76) 1962, *Some brachiolar and ambulacral structures of blastoids:* Oklahoma Geol. Survey, Oklahoma Geol. Notes, v. 22, no. 2, p. 30-49, text fig. 1-4, pl. 1-4.

(77) 1962, *The paradeltoid plates of Polydeltoideus:* Same, v. 22, no. 2, p. 50-52, pl. 1.

Galloway, J. J., & Kaska, H. V.

(78) 1957, *Genus Pentremites and its species:* Geol. Soc. America, Mem. 69, ix+104 p., 5 text fig., 5 tables, 13 pl.

Goldfuss, August

(79) 1826-1833, *Petrefacta Germaniae:* Theil I, 252 p., 71 pl., Arnz & Co. (Düsseldorf).

Gray, J. E.

(80) 1840, *Synopsis of the contents of the British Museum:* 12 mo., 42nd ed., p. 63 (London).

Gurley, W. F. E. R.

(81) 1884, *New Carboniferous fossils:* Bull. no. 2, 12 p., private publ. (Danville, Ill.).

Hall, James

(82) 1858, *Palaeontology of Iowa:* Iowa Geol. Survey, Rept., v. 1, pt. 2, Palaeontology, p. 473-724, text fig. 53-118, pl. 1-29.

(83) 1862, *Contributions to palaeontology; comprising descriptions of new species of fossils from the Upper Helderberg, Hamilton and Chemung groups; Preliminary notice of some of the species of Crinoidea known in the Upper Helderberg and Hamilton groups of New York:* N.Y. State Cabinet, Ann. Rept. 15, p. 115-153, 2 text fig., 11 pl. (Albany). [Describes *Pentremites calyce, P. leda, P. maia,* (now all *Devonoblastus*), *Pentremites lycorias* (now *Pleuroschisma*), and *Nucleocrinus conradi, N. lucina.*]

(84) 1879, *The fauna of the Niagara group, in central Indiana:* N.Y. State Museum, Ann. Rept. 28, p. 99-203, pl. 3-34 (text printed partly in advance in 1875 or 1876). [Describes *Codaster pentalobus* (now type species of *Decaschisma*).]

Hambach, Gustav

(85) 1884, *Notes about the structure and classification of the Pentremites:* Acad. Sci. St. Louis, Trans., v. 4, no. 3, p. 537-547, text fig. 1-6.

(86) 1903, *Revision of the Blastoidea, with a proposed new classification, and description of new species:* Same, v. 13, no. 1, 67 p., 15 text fig., 6 pl.

Haughton, Samuel

(87) 1859, *On a new Carboniferous echinoderm, from the county of Limerick:* Dublin Geol. Soc., Jour., v. 8, pt. 2, p. 183-184, pl. 12.

Hsu, Chen, et al.

(88) 1957, *Index fossils of China. Invertebrata:* 3 v., illus., in Chinese with English titles; v. 1, p. 1-95, text fig. 1-38, pl. 1-51 (blastoids, p. 87-89, text fig. 23, pl. 51, fig. 10-18), ed. by Paleont. Res. Inst., Academia Sinica, publ. by Geol. Press (Peking). [Lists *Mesoblastus tushanensis* Chi and *Devonoblastus heitaiensis* Mu as only Chinese blastoids described to date. Generic designations may be incorrect.]

Hudson, G. H.

(89) 1907, *On some Pelmatozoa from the Chazy limestone of New York:* N.Y. State Museum, Bull. 107, p. 97-152, pl. 1-10. [Describes *Blastoidocrinus* and introduces new class Parablastoidea.]

Jaekel, Otto

(90) 1918, *Phylogenie und System der Pelmatozoen:* Paläont. Zeitschr., v. 3, no. 1, p. 1-128, text fig. 1-114. [Later publ. in 1921.] [Proposes blastoid orders named Fissiculata, Spiraculata, and Coronata.]

Joysey, K. A.

(91) 1953, *A study of the type-species of the blastoid Codaster McCoy:* Geol. Mag., v. 90, no. 3, p. 208-218, text fig. 1-5, 3 tables.

(92) 1955, *On the geological distribution of Carboniferous blastoids in the Craven area, based on a study of their occurrence in the Yoredale series of Grassington, Yorkshire:* Geol. Soc. London, Quart. Jour., v. 111, p. 209-224, text fig. 1-2, pl. 12.

(93) 1959, *A study of variation and relative growth in the blastoid Orbitremites:* Royal Soc. London, Philos. Trans., ser. B, no. 688, v. 242, p. 99-125, text fig. 1-9, pl. 2.

———, & Breimer, A.

(94) 1963, *The anatomical structure and systematic position of Pentablastus (Blastoidea) from the Carboniferous of Spain:* Palaeontology, v. 6, pt. 3, p. 471-490, text fig. 1-5, pl. 66-69.

Koninck, L. G. de, & LeHon, Henri

(95) 1854, *Recherches sur les crinoïdes du terrain carbonifère de la Belgique:* Acad. Royale Sci. Belgique, Mém., v. 28, 215 p., text fig., 7 pl. [Describes *Pentremites caryophyllatus* (now *Phaenoblastus*), *P. crenulatus* (now *Mesoblastus*), *P. Puzos, P. Orbignyanus,* and *P. Waterhousianus* (now tentatively referred to *Orophocrinus*). Excellent bibliography contains 350 references to publications dated 1558-1853 (18 pre-1700, 110 pre-1800).]

Lehmann, W. M.

(96) 1949, *Pentremitella osoleae n. g. n. sp., ein Blastoid aus dem unterdevonischen Hunsrückschiefer:* Neues Jahrb. Mineralogie, Geologie, Paläontologie, Monatsch., Abt. B, Jahrg. 1949, p. 186-191, text fig. 1-7. [Unrecognizable as to genus but tentatively referred to *Schizotremites.*]

Levin, H. L., & Fay, R. O.

(97) 1964, *The relationship between Diploblastus kirkwoodensis and Platyceras (Platyceras):* Oklahoma Geol. Survey, Oklahoma Geol. Notes, v. 24, no. 2, p. 22-29, text fig. 1, pl. 1-3.

Lucas, M. G.

(98) 1953, *Étude, au microscope polarisant, des hydrospires des blastoides:* in Jean Piveteau, Traité de Paléontologie (v. 3, 1063 p., 17 pl., 1275 fig.), p. 635-637, text fig. 10-12, Masson et Cie (Paris).

Lyon, S. S.

(99) 1857, *Paleontological report. Description of new species of organic remains:* Kentucky Geol. Survey, Rept. 3, p. 465-498, pl. 1-5, maps.

M'Coy, Frederick

(100) 1849, *On some new Palaeozoic Echinodermata:* Ann. & Mag. Nat. History, ser. 2, v. 3, p. 244-254, text fig. 1.

Macurda, D. B., Jr.

(101) 1962, *Observations on the blastoid genera Cryptoblastus, Lophoblastus, and Schizoblastus:* Jour. Paleontology, v. 36, no. 6, p. 1367-1377, text fig. 1-5.

(102) 1964, *Dentiblastus—a new blastoid genus from the Burlington Limestone (Mississippian):* Same, v. 38, no. 2, p. 367-372, text fig. 1, pl. 58.

(103) 1964, *The blastoid Pentremites Say—a trimerous mutant and some new occurrences:* Same, v. 38, no. 4, p. 705-710, text fig. 1-2, pl. 116.

(104) 1964, *The Mississippian blastoid genera Phaenoschisma, Phaenoblastus, and Conoschisma:* Same, v. 38, no. 4, p. 711-724, pl. 117-118.

(105) 1964, *A new spiraculate blastoid, Pyamiblastus, from the Mississippian Hampton Formation of Iowa:* Univ. Michigan, Museum Paleontology, Contrib., v. 19, no. 8, p. 105-114, text fig. 1.

(106) 1965, *Orbiblastus, a new Mississippian blastoid genus from Arkansas:* Michigan Acad. Sci., Arts, & Letters, Papers, v. 50, pt. 1, p. 299-307, text fig. 1, pl. 1-2.

(107) 1965, *The functional morphology and stratigraphic distribution of the Mississippian blastoid genus Orophocrinus:* Jour. Paleontology, v. 39, no. 6, p. 1045-1096, text fig. 1-16, pl. 121-126.

(108) 1965, *The hydrodynamics of the Mississippian blastoid genus Globoblastus:* Same, v. 39, p. 1209-1217, text fig. 1-4.

(109) 1966, *The ontogeny of the Mississippian blastoid Orophocrinus:* Same, v. 40, no. 1, p. 92-124, text fig. 1-10, pl. 11-13.

(110) 1966, *The Devonian blastoid Belocrinus from France:* Palaeontology, v. 9, pt. 2, p. 244-251, text fig. 1, pl. 39.

Matsumoto, Hikoschichirô

(111) 1929, *Outline of a classification of Echinodermata:* Tohoku Imper. Univ., Sci. Rept., ser. 2 (Geology), v. 13, no. 2, p. 27-33.

Meek, F. B., & Worthen, A. H.

(112) 1862, *Descriptions of new Paleozoic fossils from Illinois and Iowa:* Acad. Nat. Sci. Philadelphia, Proc. for 1861, p. 128-148.

(113) 1865, *Descriptions of new Crinoidea, etc., from the Carboniferous rocks of Illinois and some of the adjoining states:* Same, Proc. for 1865, p. 155-166.

(114) 1868, *Remarks on some types of Carboniferous crinoids, with descriptions of new genera and species of the same, and of one echinoid:* Same, Proc. for 1868, p. 335-359. [Describes *Tricoelocrinus woodmani.*]

(115) 1869, *Remarks on the Blastoidea, with descriptions of new species:* Same, Proc. for 1869, p. 83-91. [Describes *Codonites* (now *Orophocrinus*), and *Granatocrinus glaber* (now *Diploblastus*).]

(116) 1873, *Descriptions of invertebrates from Carboniferous system:* Illinois Geol. Survey, v. 5, pt. 2, p. 320-619, 32 pl. [Describes and figures *Tricoelocrinus woodmani.*]

Mitchill, S. L.

(117) 1808, *Uncommon petrifactions, from Georgia and Kentucky:* Medical Repository, v. 11, p. 415-416, fig. A-C (New York). [One of earliest references and figures of a blastoid (now known as *Pentremites godoni*). The specimens were sent to MITCHILL by DR. SAMUEL BROWN, of Lexington, Kentucky, several years prior to 1808.]

Moore, R. C.

(118) 1954, *Status of invertebrate paleontology, 1953, IV. Echinodermata: Pelmatozoa:* Harvard Museum Comp. Zoology, Bull., v. 112, no. 3, p. 125-149, text fig. 1-8.

———, & Strimple, H. L.

(119) 1942, *Blastoids from Middle Pennsylvanian rocks of Oklahoma:* Denison Univ. Jour. Sci. Lab., Bull., v. 37, p. 85-91, text fig. 1. [Describes *Paracodaster dotti* (now classed as *Agmoblastus*).]

Morris, John

(120) 1843, *A catalogue of British fossils comprising all the genera and species hitherto described; with references to their geological distribution and to the localities in which they have been found:* 8 vo., x+222 p., Van Voorst (London). [Introduces *Astrocrinus tetragonus* for *Astracrinites tetragonus* AUSTIN & AUSTIN.]

Mu, A. T.

(121) 1955, *A Devonian blastoid from Kirin:* Acta Palaeont. Sinica, v. 3, no. 2, p. 131-134, 1 pl. [In Chinese, with English summary.] [Describes *Devonoblastus heitaiensis* (Heitai Formation, at Chenchuhoushan near Heitai, Mishan district, Kirin, NE. China). The generic name is misspelled *Devonoboblastus,* and the species may belong to another genus.]

Munier-Chalmas, E. C. P. A.

(122) 1876, *Mollusques nouveaux des terrains paléozoiques des environs de Rennes:* Jour. Conchyliologie, ser. 3, v. 16, whole v. 24, no. 1, p. 102-109. [Describes blastoid from Lower Devonian deposits named *Belemnocrinus* (*non Belemnocrinus* WHITE, 1862, crinoid) later renamed *Belocrinus.* Fossil comprises fragmentary basalia and cannot be assigned to another known genus.]

(123) 1881, *Mollusques nouveaux des terrains paléozoiques des environs de Rennes:* Soc. Géol. France, Bull., ser. 3, v. 9, p. 503.

Nichols, David

(124) 1962, *Echinoderms:* 200 p., 26 text fig., Hutchinson Univ. Library (London).

Nissen, H. U.

(125) 1963, *Röntgegenfügeanalyse am Kalzit von Echinodermenskelleten:* Neues Jahrb. Geologie u. Paläontologie, Abhandl., v. 117, p. 230-234.

Orbigny, A. D. d'

(126) 1850, *Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnées faisant suite au cours élémentaire de paléontologie et de géologie stratigraphiques:* 12 mo. with Atlas 4 to.; v. 1, p. lx+394 p., text fig., Masson (Paris).

(127) 1851, *Cours elèmentaire de paléontologie et géologie stratigraphiques:* 8 vo. with plates 4 to.; v. 2, 841 p., 628 text fig., Masson (Paris). [Erects family Pentremitidaea (*sic*), corrected by Etheridge & Carpenter (1886) to Pentremitidae.]

Owen, D. D., & Shumard, B. F.

(128) 1850, *Descriptions of fifteen new species of Crinoidea from the sub-Carboniferous limestone of Iowa, collected during the U. S. Geological Survey of Wisconsin, Iowa, and Minnesota in the years 1848-1849:* Acad. Nat. Sci. Philadelphia, Jour., new ser., v. 2, pt. 1, p. 57-70, pl. 7. [Describes species now designated as types of *Cryptoblastus, Globoblastus,* and *Orophocrinus.*]

Parkinson, James

(129) 1808, *Organic remains of a former world; The fossil zoophytes:* v. 2, vii+286 p., 19 pl. (London). [Describes and figures what is now *Pentremites godoni,* and is one of the first references to a blastoid.]

Peck, R. E.

(130) 1930, *Blastoids from the Brazer limestones of Utah:* Pan-Am. Geologist, v. 54, no. 2, p. 104-108, pl. 1. [Describes and illustrates *Ambolostoma baileyi.*]

Peetz, H. von

(131) 1907, *Nymphaeoblastus miljukovi, eine neue Gattung und Art der Blastoidea:* Soc. Impér. Nat. St . Pétersbourg, Tiré des Travaux, Geol. et de Min. Sec., v. 35, liv. 5, p. 15-20, 1 pl.

Phillips, Winifred

(132) 1936, *The structure of Acentrotremites:* Swansea Sci. & Field Naturalists' Soc., Proc., v. 1, pt. 10, p. 360-366, text fig. 1-13.

Quenstedt, F. A.

(133) 1874-1876, *Petrefaktenkunde Deutschlands:* Abt. 1, v. 4, no. 7-12, 742 p., pl. 90-114.

Raup, D. M.

(134) 1959, *Crystallography of echinoid calcite:* Jour. Geology, v. 67, p. 661-674, text fig. 1-7, 1 table.

Regnéll, Gerhard

(135) 1945, *Non-crinoid Pelmatozoa from the Paleozoic of Sweden—A taxonomic study:* Lunds Geol.-Mineral. Inst., Medd., no. 108, 255 p., 30 text fig., 15 pl.

(136) 1960, *Données concernant le développement ontogénétique des pelmatozoaires du Paléozoïque (échinodermes):* Soc. Géol. France, Bull., ser. 7, v. 1, no. 7, p. 773-783, text fig. 1-6.

Reimann, I. G.

(137) 1935, *New species and some new occurrences of middle Devonian blastoids:* Buffalo Soc. Nat. Sci., Bull., v. 17, no. 1, p. 23-45, pl. 1-4. [Describes *Brachyschisma* and *Devonoblastus.*]

(138) 1942, *"Tully" blastoids in western New York and genotype of Devonoblastus:* Same, Bull., v. 17, no. 3, p. 46-47, pl. 9.

(139) 1945, *New Devonian blastoids:* Same, Bull., v. 19, no. 2, p. 22-42, pl. 5-9. [Describes *Brachyschisma, Pleuroschisma,* and *Schizotremites.*]

(140) 1948, *New genus of blastoids from the Silurian:* Geol. Soc. America, Bull., v. 59, pt. 2, p. 1346 (abstr.). [Describes but does not name a blastoid *(Polydeltoideus)* from the Henryhouse Shale of Oklahoma.]

(141) 1950, *Possible phylogenetic relationships of some early eublastoids:* Jour. Paleontology, v. 24, no. 4, p. 499-500. [Important contribution to phylogeny because it suggests atrophy of skeletal parts in blastoids as fundamental features in evolutionary trends.]

(142) 1961, *A color-marked Devonian blastoid:* Oklahoma Geol. Survey, Oklahoma Geol. Notes, v. 21, no. 5, p. 153-157, pl. 1-2.

———, & Fay, R. O.

(143) 1961, *Polydeltoideus, a new Silurian blastoid from the Henryhouse formation of Oklahoma:* Same, v. 21, no. 3, p. 86-89, pl. 1.

Roemer, C. F.

(144) 1851, *Monographie der fossilen Crinoidenfamilie der Blastoideen, und der Gattung Pentatrematites in Besondern:* Arch. Naturgesch., Jahrg. 17, v. 1, no. 3, p. 323-397, pl 4-8. [Detailed morphological study in which pores and hydrospires (not then named) were discovered and a classification was presented.]

Rowley, R. R.

(145) 1895, *Description of a new genus and five new species of fossils from the Devonian and sub-Carboniferous rocks of Missouri:* Am. Geologist, v. 16, no. 4, p. 217-223, text fig. 1-20. [Type species of *Carpenteroblastus* described as *Granatocrinus magnibasis.*]

(146) 1900, *New species of crinoids, blastoids, and cystoids from Missouri:* Same, v. 25, no. 2, p. 65-75, pl. 2. [Type species of *Conoschisma* (=*Phaenoschisma*) described as *Codaster laeviusculus.*]

(147) 1901, *Two new genera and some new species of fossils from the upper Paleozoic rocks of northeastern Missouri:* Same, v. 27, no. 6, p. 343-355, pl. 28. [Describes *Carpenteroblastus* and *Lophoblastus.*]

———, & Hare, S. J.

(148) 1891, *Description of some new species of Echinodermata from the sub-Carboniferous rocks of Pike County, Missouri:* Kansas City Scientist, v. 5, no. 7, p. 97-103, pl. 2.

Say, Thomas

(149) 1820, *Observations on some species of zoöphytes and shells principally fossil:* Am. Jour. Sci., v. 2, p. 34-45. [Names *Pentremites,* but spells name as *Pentremite.*]

(150) 1825, *On two genera and several species of Crinoidea:* Acad. Nat. Sci. Philadelphia, Jour., ser. 1, v. 4, pt. 2, p. 289-296. [Proposes name Blastoidea.]

Schmidt, W. E.

(151) 1930, *Die Fauna des deutschen Unterkarbons. 1. Teil, Die Echinodermen:* K. Preuss. Geol. Landesanst., Abhandl., new ser., no. 122, 92 p., 20 text fig., 3 pl., tables. [Describes *Pentremites boletus* and *P. ovalis* (now *Petaloblastus*), and *Mesoblastus melonianus* (now *Doryblastus*).]

Schultze, Ludwig

(152) 1867, *Monographie der Echinodermen des Eifler Kalkes:* K. Akad. Wiss., Math. Naturwiss. Cl., Denkschr., v. 26, Register-Bd., Abt. 2, p. 113-230, pl. 1-13. [Separates dated 1866 in advance.] [Describes *Pentremites acutangulus* and *P. clavatus* (now *Cordyloblastus*).]

Seebach, Karl von

(153) 1864, *Ueber Orophocrinus, ein neues Crinoideen-geschlecht aus der Abtheilung der Blastoideen:* K. Gesell. Wiss. Georg-Augusts-Univ., Nachricht. for 1864, no. 5, p. 110-111.

Shumard, B. F.

(154) 1855, *Description of new species of organic remains:* Missouri Geol. Survey, Ann. Rept. 1-2, p. 185-238, pl. A-C; Dr. Shumard's report, p. 147-184, fig. maps. [Describes

Pentremites sayi (now *Schizoblastus*) and *Pentremites roemeri* (now *Tanaoblastus*).]

(155) 1858, *Descriptions of new species of Blastoidea from the Palaeozoic rocks of the Western States, with some observations on the structure of the summit of the genus Pentremites:* Acad. Sci. St. Louis, Trans., v. 1, p. 238-248, pl. 9.

(156) 1863, *Descriptions of new Palaeozoic fossils:* Same, Trans., v. 2, no. 1, p. 108-113.

(157) 1865-66, *A catalogue of the Palaeozoic fossils of North America. Part 1. Palaeozoic Echinodermata:* Same, Trans., v. 2, no. 2, p. 334-407, publ. in parts at separate times: p. 334-346 (Aug. 24, 1865); p. 347-362 (Sept. 18, 1865); p. 363-378 (Dec. 11, 1865); p. 379-394 (Dec. 5, 1865); p. 395-407 (March 20, 1866). Bound together and published in May, 1866. [Introduces new genus *Troosticrinus* and designates type species of *Granatocrinus*.]

———, & Yandell, L. P.

(158) 1856, *Notice of a new fossil genus belonging to the family Blastoidea, from the Devonian strata near Louisville, Kentucky:* Acad. Nat. Sci. Philadelphia, Proc., v. 8, p. 73-75, pl. 2. [Describes and illustrates *Eleutherocrinus cassedayi*.]

Sieverts-Doreck, Hertha

(159) 1951, *Echinodermen aus dem spanischen Ober-Karbon:* Paläont. Zeitschr., v. 24, pt. 3/4, p. 104-119, text fig. 1-7, pl. 8. [Describes and illustrates *Pentablastus supracarbonicus*.]

Smith, E. A.

(160) 1906, *Development and variation of Pentremites conoideus:* Indiana Dept. Geol. & Nat. Res., Ann. Rept. 30, p. 1219-1242, text fig. 1-3, pl. 43-47.

Sowerby, G. B.

(161) 1825, *Note on the foregoing paper, together with a description of a new species of Pentremites:* Zool. Jour., v. 2, no. 7, p. 316-318, pl. 11. [Describes *Pentremites derbiensis* (now *Orbitremites*) and corrects *Pentremite* to *Pentremites*.]

(162) 1834, *On Pentatrematites orbicularis, acuta, and pentagularis:* Same, v. 5, no. 20, art. 62, p. 456-457, pl. 33, suppl.

Steininger, Johann

(163) 1849, *Die Versteinerungen des Uebergangsgebirges der Eifel:* Jahresb. über den Schul-Corsus. 1848-49 an dem Gymnasium zu Trier, 4 to., 50 p.

Termier, Geneviève, & Termier, Henri

(164) 1950, *Paléontologie Marocaine; II. Invertébrés de l'ère primaire; f. 4, Annélides, arthropodes, échinodermes, conularides et graptolithes:* Service Géol. Maroc, Notes & Mém., v. 79, no. 4, p. 55-105, pl. 207-233. [One of earliest records of blastoids in Africa. Describes and illustrates *Pentremitidea touijinensis* (Strunian) and *Granatocrinus* (Visean) with mention also of *Pentremites* (Visean). These generic assignments may be incorrect.]

Troost, Gerard

(165) 1835, *On the Pentremites reinwardtii, a new fossil; with remarks on the genus Pentremites (Say), and its geognostic position in the state of Tennessee, Alabama and Kentucky:* Pennsylvania Geol. Soc., Trans., v. 1, pt. 2, art. 5, p. 224-231, pl. 10. [Describes and illustrates species now designated as type of *Troosticrinus*.]

Ulrich, E. O.

(166) 1917 (1918), *The formations of the Chester series in western Kentucky and their correlates elsewhere:* in Mississippian formations of western Kentucky, Kentucky Geol. Survey, iv+272 p., 11 pl.

Verneuil, Edouard de

(167) 1844, *Note . . . sur une nouvelle espèce de Pentrémites . . . :* Soc. Géol. France, Bull., ser. 2, v. 1, p. 213-215, pl. 3 [Describes and illustrates *Pentremites pailletti* (now *Pentremitidea*).]

———, & Archiac, E. J. A. d'

(168) 1845, *Note sur les fossiles du terrain Paléozoique des Asturies:* Soc. Géol. France, Bull., ser. 2, v. 2, p. 458-482, pl. 13-15. [Describes and figures *Pentremites Pailletti* and *P. Schultzii* (now *Pentremitidea* and *Cryptoschisma*, respectively).]

Wachsmuth, Charles

(169) 1883, *On a new genus and species of blastoids, with observations upon the structure of the basal plates in Codaster and Pentremites:* Illinois State Geol. Survey, v. 7, p. 346-357, text fig. 1-2.

(170) 1900, *Class 3, Blastoidea:* in Text-book of Palaeontology, by K. A. von Zittel, transl. by Charles R. Eastman: v. 1, p. 188-198, text fig. 312-325, Macmillan & Co. (London). [Classification follows that of Etheridge & Carpenter (1886).]

———, & Springer, Frank

(171) 1879 (1880), *Revision of the Paleocrinoidea:* Acad. Nat. Sci. Philadelphia, Proc., pt. 1, p. 226-378, pl. 15-17.

(172) 1887, *The summit plates in blastoids, crinoids, and cystids, and their morphological relations:* Same, Proc. for 1887, p. 82-114, pl. 4.

Wanner, Johannes

(173) 1924, *Die permischen Echinodermen von Timor, Teil II:* Paläontologie von Timor, Lief. 14, Abhandl. 23, 81 p., pl. 199-206,

31 text fig. [Describes and figures 32 new species and varieties of 7 genera (6 new) from Permian marls and tuffs of Timor Island, collected (1909-11) by Jonker, Molengraff, and Wanner. The types are in Delft, The Netherlands, and Bonn, Germany, but those in Bonn were believed to be destroyed during the war but recent-have been found. The fossils came from 38 different localities. Describes *Calycoblastus, Indoblastus, Neoschisma, Pterotoblastus, Sundablastus, Timoroblastus, and Schizoblastus* (now *Deltoblastus*).]

(174) 1924, *Die permischen Blastoiden von Timor:* Mijnwezen Nederland.-Oost-Indië, Jaarb., Verhandl. I, Jaarg. 51 for 1922, p. 163-233, text fig. 1-11, pl. 1-5. [Describes *Anthoblastus, Nannoblastus, Rhopaloblastus, Sphaeroschisma, Thaumatoblastus.*]

(175) 1931, *Neue Beiträge zur Kenntnis der permischen Echinodermen von Timor. VI. Blastoidea:* Wetensch. Meded. no. 16, Dienst Mijnb. Nederland.-Oost-Indië, p. 38-74, 10 text fig., pl. 1-4. [Describes *Angioblastus* (new), *Nannoblastus, Timoroblastus, Pterotoblastus.*]

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(185) 1937, *Faune des échinodermes du Permo-Carbonifère de l'Oural à Krasnooufimsk, IV:* Vser. Paleont. Obshch., Ezhegod. (Soc. Paléont. Russie, Ann.), v. 11, p. 7-10, pl. 1. [French, with Russian summary.] [Introduces new genus *Sagittoblastus.*]

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EOCRINOIDEA

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CONTENTS

INTRODUCTION

It was OTTO JAEKEL *(23)*[1] who first proposed, in 1899, to remove from the Cystoidea several genera *(Acanthocystites, Ascocystites, Eocystites, Lichenoides, Macrocystella, Mimocystites, Palaeocystites)* which previously had been included in this assemblage, because he judged them to be classifiable as archaic cladocrinoids (=Crinoidea

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[1] Italicized numbers refer to corresponding numbers in the list of references.

Camerata). Later, in 1918 *(25),* he introduced for these and a few other genera a new subclass named Eocrinoidea, which he assigned to the class Crinoidea, despite its inclusion with presumed earliest crinoids forms regarded by him as ancestors of the rhombiferan cystoids and diverse others having aberrant features and ephemeral occurrence. RAYMOND C. MOORE has translated this chapter and for this aid the author expresses sincere thanks.

The echinoderm group known as eocrinoids has been treated quite differently by authors in publications issued subsequent to 1918. Although GEKKER (1938, 1940) and more recently NICHOLS (1962) adopted JAEKEL's placement of these forms as a subclass of Crinoidea, such arrangement was rejected by BASSLER (1938) and BASSLER & MOODEY (1943), who distributed the so-called eocrinoid genera among families of cystoids and did not even cite Eocrinoidea in synonymy. CUÉNOT (1953) accepted the group provisionally as an artificial assemblage, mentioned in a chapter on cystoids in the part devoted to rhombiferans, but omitted recognition of it in classification. ZITTEL (1924) ranked the Eocrinoidea simply as an appendage of the Hydrophoridea (=Cystoidea). Finally, REGNÉLL (1945) distinguished the group as an independent class and in this arrangement has been followed by TERMIER & TERMIER (1948, 1954), BASSLER (1950), HARKER & HUTCHINSON (1951), UBAGHS (1953, 1960, 1963), MOORE (1954), GEKKER (1964), and ROBISON (1965).

The essential basis for REGNÉLL's differentiation of the eocrinoids as an acceptable taxonomic group and his advancement of it in rank was judgment that forms composing the assemblage possess a combination of such cystoid features as the presence of brachioles and typical crinoid characters, such as the absence of thecal pores. As matter of fact, UBAGHS (1953, 1963) and ROBISON (1965) subsequently have demonstrated that some eocrinoids do possess thecal pores, but of a sort unlike those of cystoids.

The Eocrinoidea contain the most ancient known representatives of the Crinozoa and together with the Helicoplacoidea and Edrioasteroidea are the oldest of all known echinoderms, for remains attributable to these groups have been found in the lower half of the Lower Cambrian (DURHAM, *13*). Eocrinoids survived into Silurian time when they vanished without having given rise to known descendants. They are relatively uncommon fossils except in a few favored localities. Many are very inadequately known. Their diversity makes it especially difficult to formulate a satisfactory general definition of them. They comprise a heterogeneous assemblage provisionally treated as a class which better acquaintance perhaps will allow to be subdivided.

MORPHOLOGY

GENERAL FEATURES

The skeleton of complete eocrinoids typically consists of three parts—column or stem, theca, and brachioles (Fig. 292)—but a stem may be lacking.

The **column** is a hollow structure more or less differentiated from the theca and serves for temporary or permanent fixation of the organism to the sea bottom.

The **theca** is composed of plates which enclose the visceral mass and as in cystoids contains only orifices of the peristome and periproct, or additionally in some, one to several pores interpreted as hydropore, gonopore, or hydrogonopore openings. Essentially, the plates are solid skeletal elements composed of crystalline calcite. They are imperforate, although along sutures between the plates in numerous genera are aligned pores which probably served for the protrusion of soft organs functioning for gas exchange between the body interior and surrounding sea water.

In many genera no distinct boundary separates the oral and aboral parts of the theca, and accordingly, unlike crinoids, a tegmen and dorsal cup are not recognizable in eocrinoids. A few forms, however, exhibit a vaulted or plateau-like oral surface well differentiated from the remainder of the theca (e.g., *Akadocrinus, Ascocystites, Mimocystites, Lingulocystis*). These somewhat resemble crinoids, but analysis shows that the similarity is superficial and lacking real significance.

The **brachioles** are simple appendages of the theca which invariably lack branches. They are attached to the extremity of the theca opposite to the stem, and being outside of the theca (exothecal), they have a skeletal structure of their own, adapted for the function of transporting food particles to the mouth. Whereas the thecal cavity may be prolonged into the hollow stem, it does not extend into the brachioles.

Eocrinoids are small to medium in size, with height of the theca unknown to exceed 6 or 7 cm.

ORIENTATION AND SYMMETRY

Eocrinoids are radiate, generally pentaradiate, echinoderms. This symmetry may affect not only the ambulacra and oral surface of the theca (e.g., *Columbocystis*[1]) but extend to the dorsal part as well, although radial symmetry never is complete. Oppositely, radial symmetry may be lacking, as in genera with a compressed theca (e.g., *Batherocystis, Lingulocystis, Rhipidocystis*) in which certain rays have become atrophied or possibly never existed; one cannot choose between these alternatives owing to ignorance of the ancestors of these forms.

In a certain number of genera (e.g., *Columbocystis, Cryptocrinites, Mimocystites*) one of the interrays bears an oral element composed of two closely associated plates with a perforated wartlike swelling located on the suture between them, probably marking the position of the hydropore. Furthermore, in relation to this interray the ambulacra are grouped in a bivium (the two ambulacra bordering the interray) and a trivium (the opposite three ambulacra). This arrangement suffices to define a plane of bilateral symmetry which may be designated as the **madreporite plane.** In genera lacking an observed hydropore (e.g., *Rhopalocystis*), the presence of a double oral or occurrence of a bivium and trivium, or both, allow determination of the same orientation with reasonable confidence. In order to employ the Carpenter system of letter designations for the eocrinoid ambulacra, the ray opposite to the interray containing the hydropore is indicated as *A*, and then, viewing the oral surface of the theca,

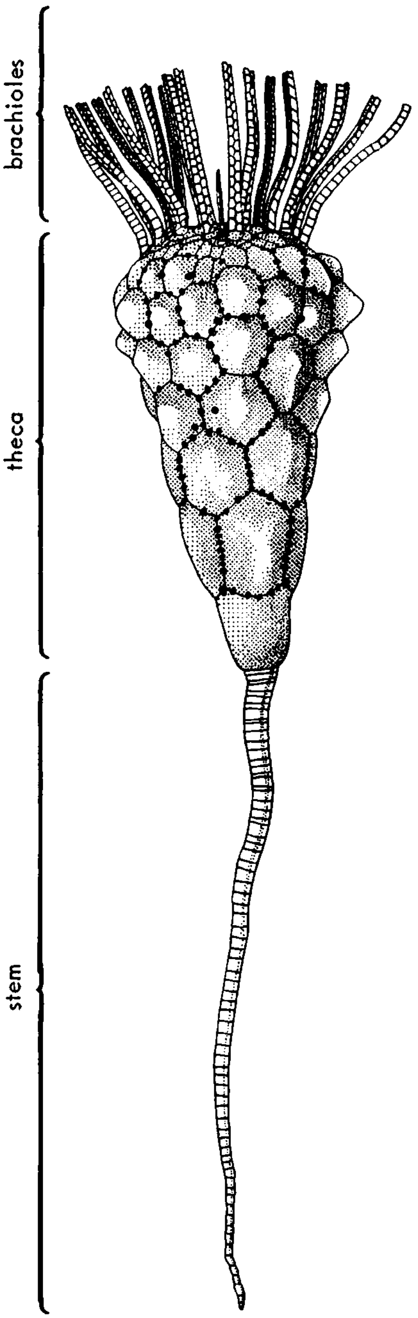

FIG. 292. Entire eocrinoid (reconstr.), showing threefold division of skeleton. *Rhopalocystis destombesi* UBAGHS (Rhopalocystidae), L.Ord., Morocco, ×1 (39).

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[1] Placement of *Columbocystis* in the Eocrinoidea must remain doubtful until the exothecal appendages of this form have been observed.

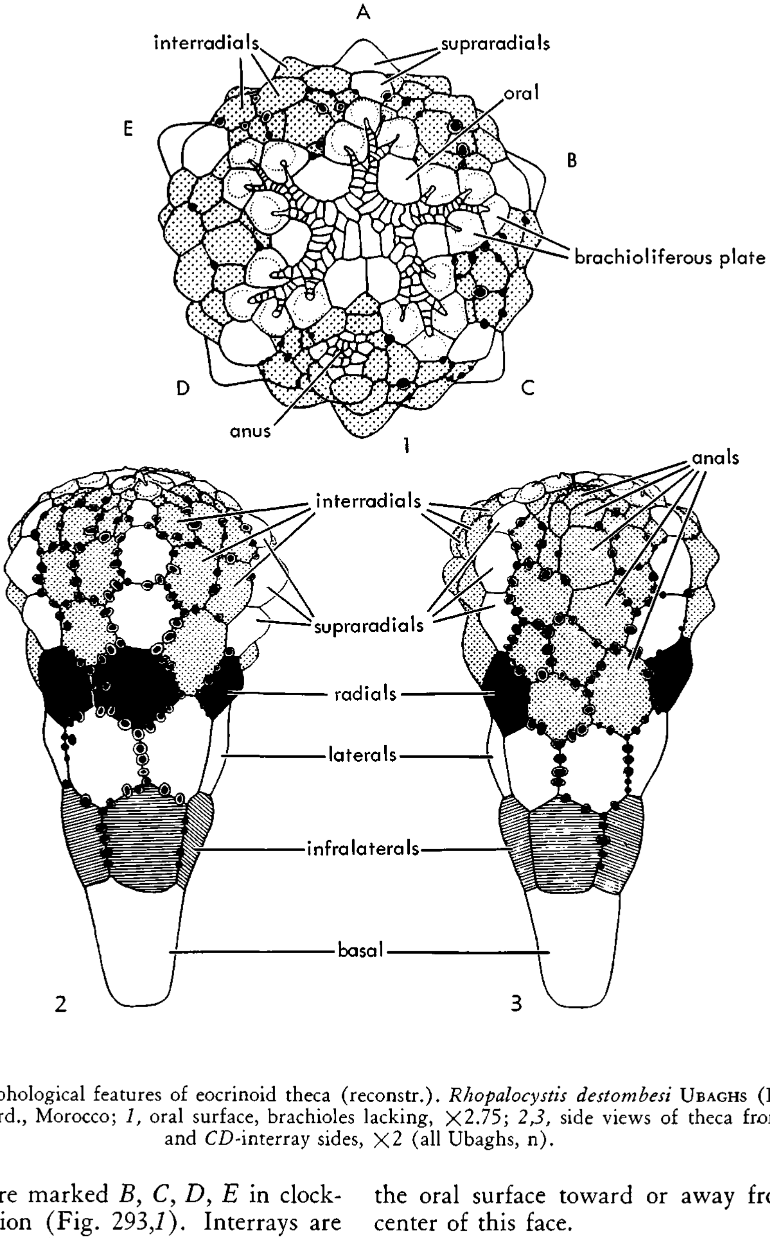

Fig. 293. Morphological features of eocrinoid theca (reconstr.). *Rhopalocystis destombesi* Ubaghs (Rhopalocystidae), L.Ord., Morocco; *1,* oral surface, brachioles lacking, ×2.75; *2,3,* side views of theca from *A*-ray and *CD*-interray sides, ×2 (all Ubaghs, n).

other rays are marked *B, C, D, E* in clockwise succession (Fig. 293,*1*). Interrays are designated by the letters for rays bounding them *(AB, BC, CD, DE, EA)* and thus the hydropore is located in interray *CD.* The anus may occur in interray *CD*, but in several genera it is displaced to a location in *BC*, so that in these forms an anal plane is distinct from the madreporite plane.

The terms **proximal** and **distal** are used as in all Crinozoa, for the skeleton as a whole toward or away from the plane separating theca and stem, and for elements of the oral surface toward or away from the center of this face.

FORM AND COMPOSITION OF THECA

The shape of the theca of eocrinoids may be irregularly spheroidal, ovoid, pyriform, conical, subcylindrical, or combinations of these. Also, it may be laterally compressed so as to offer two flat or weakly convex faces which meet along rounded borders (e.g., *Batherocystis, Cardiocystites, Lingulo-*

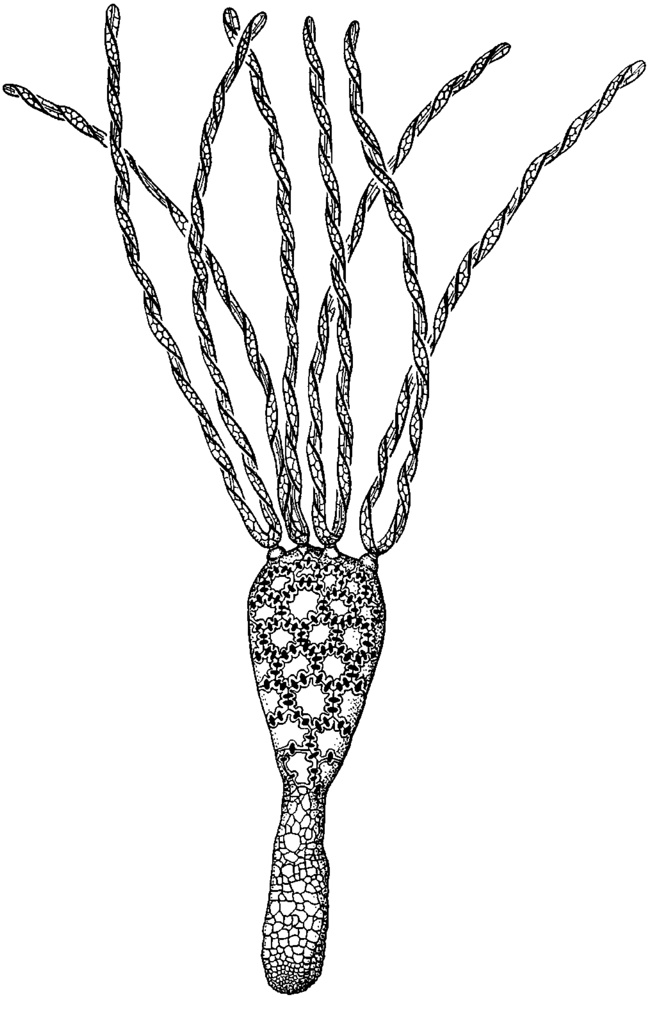

Fig. 294. Entire eocrinoid of rather primitive type (reconstr.), showing dissimilar proximal and distal parts of theca (latter with prominent sutural pores at borders of plates) and helicoidally twisted brachioles, side view. *Gogia spiralis* Robison (Eocrinidae), M.Cam., Can.(B.C.), ×2.3 (31).

cystis, Rhipidocystis). Walls of the theca may be flexible (e.g., *Lingulocystis*) but generally they are rigid. They are composed of polygonal plates which vary in number from relatively few (e.g., approximately 20 in *Cryptocrinites*) to extremely numerous (e.g., several hundred in *Lingulocystis*), and in different genera these numbers may be fixed or very indeterminate (e.g., *Gogia, Bockia*). In arrangement the plates may be precisely regular or extremely irregular. Thus several architectural types may be distinguished, furnishing evidence of quite different modes of growth.

Among oldest known eocrinoid genera, such as *Acanthocystites* and *Gogia* (Fig. 294), both from the Middle Cambrian, the theca is formed of ordinarily numerous polygonal plates arranged irregularly. Their number, which varies according to species and even from one individual to another, may range up to 500 in some species of *Gogia (31)*. The plates are joined by straight sutures with aligned pores, but seemingly these thin skeletal elements, strengthened in some forms by radial folds, are readily dissociated after death of the animal. This type of theca, in which neither the number

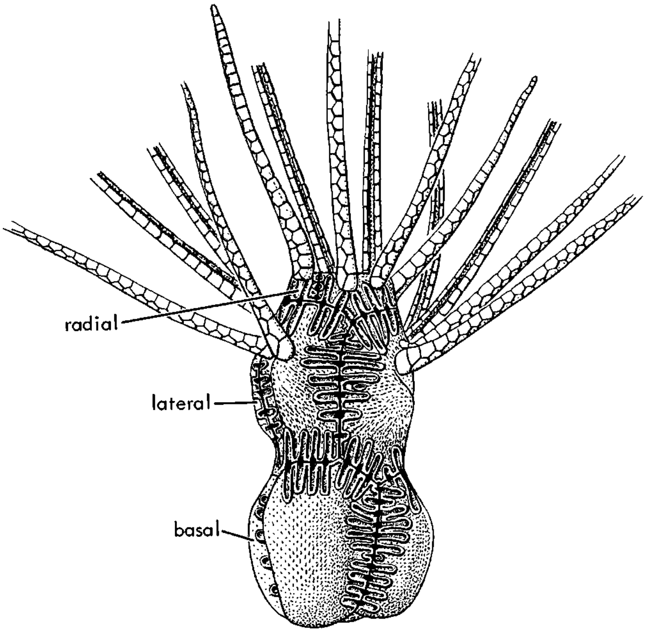

FIG. 295. Entire eocrinoid of type having three circlets of relatively large, regularly arranged thecal plates and well-developed biserial brachioles borne by lateral and radial plates, prominent epispires along sutures between plates (reconstr.). *Lichenoides priscus* BARRANDE (Lichenoididae), M.Cam., Boh., ×3 (Ubaghs, n).

nor disposition of plates is fixed, may represent the most primitive evolutionary stage of the Eocrinoidea.

Another type of thecal structure, which also makes appearance in the Middle Cambrian (e.g., *Lichenoides*), is characterized by arrangement of the plates in successive circlets, as a rule, in alternation. According to their position these plates may be designated by names borrowed from terminology applied to cystoids, that is, from aboral pole to summit 1) a circlet of **basals,** 2) a circlet of **laterals,** and 3) a circlet of **radials** (Fig. 295). In similar manner, a more complex theca may have circlets designated in upward order as 1) basals, 2) **infralaterals,** 3) laterals, 4) radials, and 5) **orals or deltoids** (Fig. 296). Theoretically, each circlet should contain five plates, but there are many exceptions to this rule, because some plates may become divided or new ones come to be inserted, and oppositely because some plates become joined together by fusion or some simply disappear. Examples of these variations can be seen in *Columbocystis, Cryptocrinites, Mimocystites,* and *Rhopalocystis,* in which one of the five oral plates is divided by a suture; in *Mimocystites,* in which the radial circlet contains a supplementary plate; in *Cryptocrinites* and several other genera, in which two of the basals are notably enlarged and modified in shape, seemingly as result of fusion of antecedent pairs of plates; and in *Batherocystis,* in which the two-part base may have originated from elimination of plates. Of course, in none of these examples is the actual mode of plate additions or reductions known.

If the number of plates from circlet to circlet varies somewhat, so that pentameral symmetry of the theca is disturbed, the number of circlets, distribution of plates in different ones, and alternation of plates in contiguous circlets, commonly are far from clearly determinable. As result, a certain amount of transition must be recognized between the thecal organization just described and the preceding one. Moreover, in the course of growth, irregularities commonly tend to be introduced and accentuated. In juvenile individuals of *Bockia,* for instance, plates of the theca comprise a more or less regular pavement, whereas in adults the insertion of new plates between old ones destroys the previous orderly plate

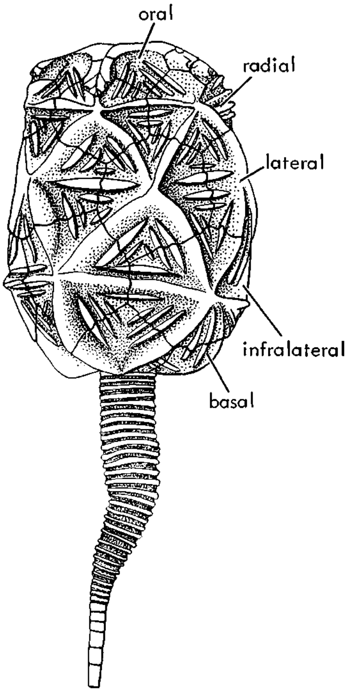

Fig. 296. Side view of theca showing five plate circlets and stem with dissimilar proximal and distal regions, brachioles omitted (reconstr.). *Mimocystites azaisi* Thoral (Macrocystellidae), L.Ord., France, ×2 (Ubaghs, n).

arrangement, making distribution of component thecal elements quite irregular (19).

A third type of thecal construction is encountered in several forms (e.g., *Ascocystites, Palaeocystites, Pareocrinus, Rhopalocystis*) which exhibit disposition of plates throughout a more or less considerable part of the theca no longer in circlets but forming columns or elongate meridional zones. Thus, in *Rhopalocystis* (Fig. 293) the theca is composed of plate circlets from the base to approximately mid-height and then in the upper half exhibits a strongly meridional plate arrangement consisting of five perradial areas (each composed of a **radial** followed by two or three **supraradials**) and five interradial areas (each composed of a much larger number of plates called **interradials,** arranged in four or five successive rows of alternating plates). One of the interradial areas, defined as posterior because of containing the **anus,** is distinguished from others by its greater expanse, by the presence of two plates (instead of one) at its proximal end, and especially by a more or less vertical row of supplementary plates (termed **anals**) distinguished by their large size and conspicuous relief. Such

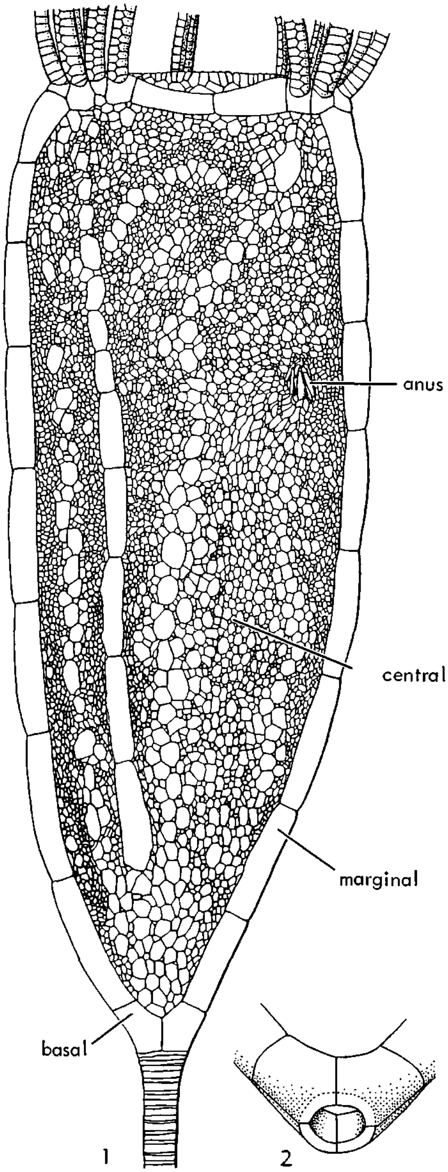

Fig. 297. Eocrinoid with strongly compressed elongate theca rimmed by stout marginal plates and extremely numerous, mostly very minute central plates (reconstr.). *Lingulocystis elongata* Thoral (Lingulocystidae), L.Ord., France; *1,* side view of theca with parts of stem and brachioles, ×4 (38); *2,* oblique view of base, ×6 (38).

organization of the theca in some way resembles that of crinoids, especially that of the Camerata.

Unquestionably, a special place must be reserved for the type of thecal organization seen in compressed forms which rightly or wrongly are included among eocrinoids. A more or less well-differentiated frame accentuates outlines of their theca. It is formed of thick **marginal plates (marginalia).** In *Lingulocystis* (Fig. 297), such plates are elongated, well individualized, and not extended into the pavement of lateral surfaces of the theca. The latter, probably flexible, is composed of innumerable irregular polygonal elements of diminutive size called **centrals (centralia).** In *Rhipidocystis* and *Batherocystis* (see Fig. 318, 319)—perhaps also in *Cardiocystites* (see Fig. 321)—the outer edge of the marginal plates is thickened so as to stand in relief, whereas the remainder of these plates, combined with several central plates, forms a thin but doubtless rigid cover on lateral faces of the theca.

ORAL SURFACE

The region surrounding the peristome in different genera is varyingly distinct from the remainder of the theca. In the Middle Cambrian *Acanthocystites, Gogia,* and especially *Akadocrinus,* it consists of a moderately broad, flat or gently arched area at edges of which the brachioles are attached in bundles, but nothing is known of the structure of this area. In some Ordovician genera (Fig. 298,*1-3*) the peristomial region is formed only by a circlet of **orals,** generally six—each interray having one, except *CD*, which has two, the extra plate considered by YAKOVLEV *(39)* as homologous to the anal plate of crinoids, although this is by no means proved. The brachioles are attached directly to outer edges of the orals (e.g., *Columbocystis,* Fig. 298,*1*) or to pairs of special small plates between the orals which join together beneath them (e.g., *Cryptocrinites,* Fig. 298,*2*).

The oral surface of *Palaeocystites,* from the Middle Ordovician, composed of five orals and five subcircular plates, each serving to support one brachiole, is very little broader than that of the genera previously considered (Fig. 298,*3*). The brachiolar support plates are located along the periphery of the orals and alternate with them. It is unknown whether they rest on other thecal plates or are inserted between them.

In *Rhopalocystis,* from the Lower Ordovician, the oral surface has the form of a slightly raised five-pointed star (Fig. 298,*4*). The interradial areas extend into angles between the perradial branches of the oral surface in such manner that no sharp distinction between oral and aboral parts of the theca exists. Whereas the central disc of the star is composed of six orals grouped around the peristome, each of the branches consists of three to six so-called **brachioliferous plates,** one brachiole being attached to each such plate. The brachioliferous plates are inserted in walls of the theca and take part in forming its inner surface (endothecal condition).

The oral surface attains highest degree of differentiation in *Mimocystites* and *Ascocystites,* both from the Ordovician (Fig. 299,*1,2*). Since the brachioles are attached around its border, a certain analogy with the tegmen of crinoids appears to be offered, but as we shall see later, this resemblance is superficial in nature. The oral surface in these two genera consists of five oral plates *(Ascocystites)* or six *(Mimocystites),* and in addition, a certain number of perradial plates, at outer edges of which the brachioles are attached. The origin of these last plates is unknown. They may be analogous to the brachioliferous plates of *Rhopalocystis.* YAKOVLEV *(43)* called them **adorals.** According to BATHER *(5)*, identical plates in *Cheirocrinus* might arise from proliferation of orals themselves, but this is only an hypothesis. The adoral plates of *Mimocystites* rest partly on the orals and partly on the radials, which form a slotlike support to receive them. They do not take part in making the inner surface of the theca. The perradial plates of *Ascocystites* lie on the upper edge of lateral walls of the theca but larger ones may be endothecal in part.

In *Lingulocystis,* finally, the only eocrinoid with compressed theca in which the oral surface is known, this has an elliptical outline with long axis coinciding with the extension plane of the theca (Fig. 299,*3*). At extremities of this axis are concentrated the plates which bear the brachioles, these plates forming part of the frame of marginals bordering the oral surface; they appear to be modified marginal plates, since sporadically these support isolated brachioles.

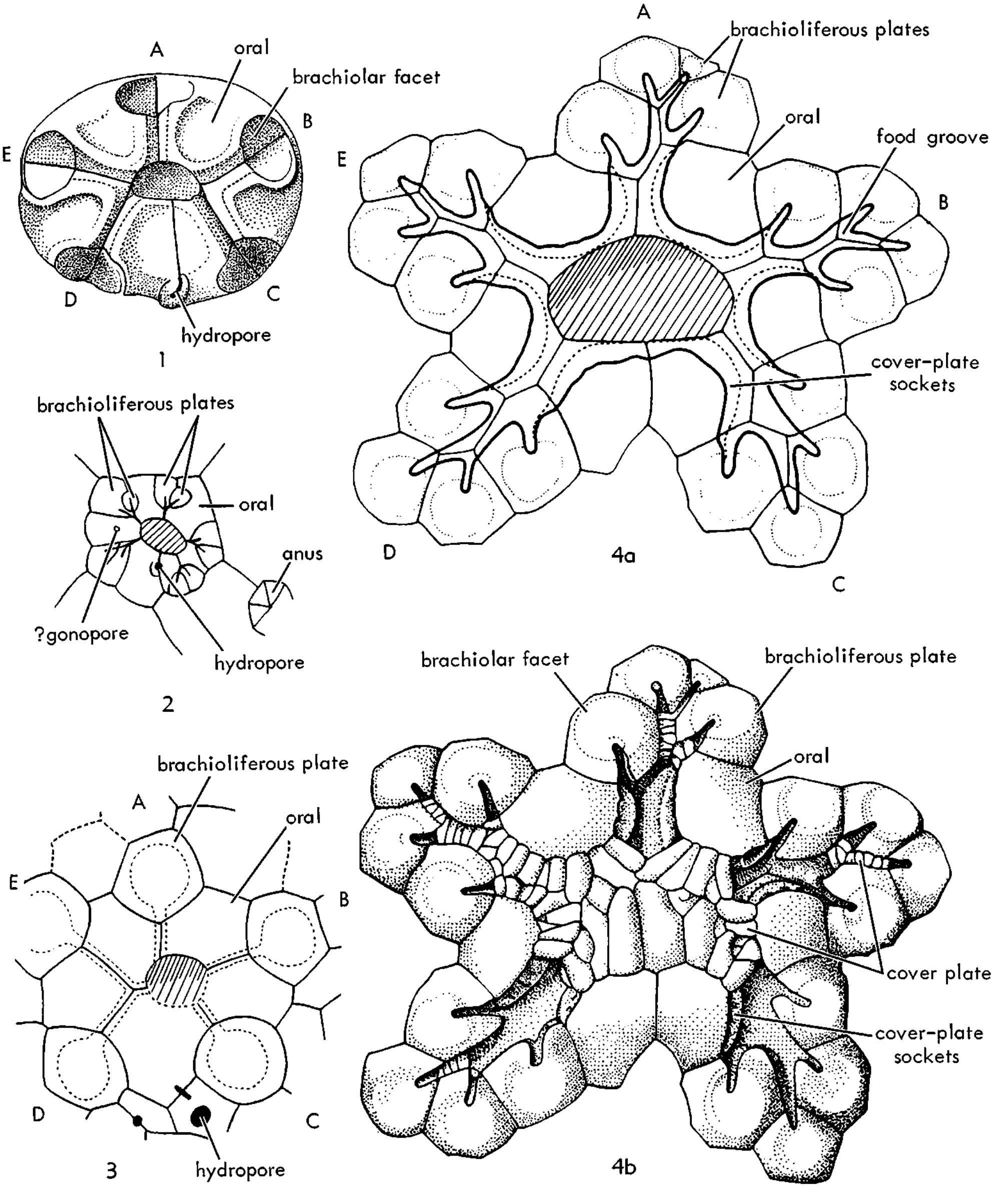

FIG. 298. Morphological features of oral surface of eocrinoid theca.

1. *Columbocystis* BASSLER (?Springerocystidae), M. Ord., N.Am., showing brachiolar facets borne by adjoining pairs of oral plates, ×6 (Ubaghs, n).
2. *Cryptocrinites* VON BUCH (Cryptocrinitidae), M. Ord., E.Baltic, with isotomously branched food grooves leading to pairs of brachioliferous plates, ×4 (Ubaghs, n).
3. *Palaeocystites* BILLINGS (Palaeocystitidae), M. Ord., N.Am., showing short, simple or bifurcating food grooves along interoral sutures, ×7 (22).
4. *Rhopalocystis* UBAGHS (Rhopalocystidae), L.Ord., Morocco, showing heterotomous branching of food grooves leading to clustered brachioliferous plates *(4a)* and cover plates over food grooves *(4b)*, ×10 (39).

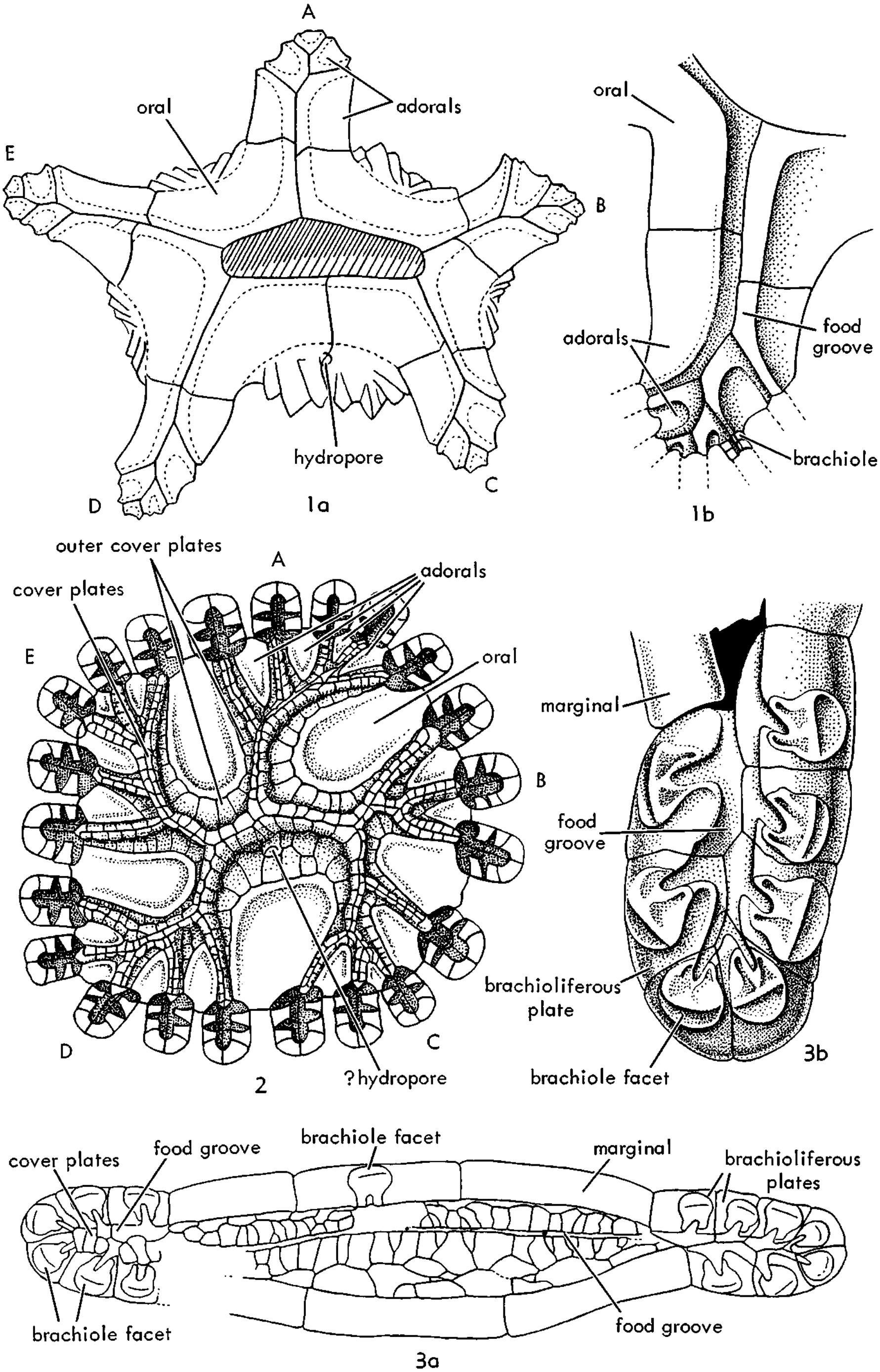

FIG. 299. Morphological features of oral surface of eocrinoid theca.

1. *Mimocystites* BARRANDE (Macrocystellidae), L. Ord.-M.Ord., Eu.-N.Afr., bifurcations of food grooves distally bunched; *1a,* entire oral surface, ×5; *1b,* single ambulacrum, ×7.5 (both Ubaghs, n).

2. *Ascocystites* BARRANDE (Ascocystitidae), M.Ord.,

A pavement of irregular platelets extends between the groups of brachioliferous plates, this pavement being limited on the outer side by the marginal plates. The food grooves and peristome (not observed but probably median) are protected by more or less strongly elevated cover plates.

ORIFICES

In addition to sutural pores, if present, the theca of eocrinoids possesses four orifices at most—mouth, anus, probable hydropore, and small opening of indeterminate function (?gonopore).

The **mouth,** which marks the oral pole, generally is surrounded by a moderately large oval or subpentagonal **peristome,** which tends to be elongated transversely to the madreporite plane. In *Lichenoides* (see Fig. 301,*1c*) its inner margin exhibits a rim formed by the thickened adoral edge of the "radials," which in this genus seems directly to bound the peristome, whereas generally the orals have such position. As sometimes seen in fossils and probably invariably present in living eocrinoids, the peristome is covered by plates **(peristomial cover plates)** of the same sort that protect the food grooves (Fig. 298,*4b*; 299,*2*).

The **anus** may be located on the oral surface not far from the peristome (e.g., *Rhopalocystis,* Fig. 293,*1*) but more commonly it occupies a lateral position. As previously stated, it opens in interray *CD* (e.g., *Rhopalocystis*) or *BC* (e.g., *Columbocystis, Cryptocrinites, Mimocystites, Palaeocystites*) but rarely may be found almost on the meridian of ambulacrum *B* (e.g., *Cryptocrinites*). It is covered by an operculum of small triangular plates **(anal pyramid)** (e.g., *Cryptocrinites, Columbocystis*), in some forms (e.g., *Bockia*) enclosed by very diminutive skeletal elements, or it ends as a small cone formed by elongate plates and probably provided with a terminal sphincter (e.g., *Lingulocystis, Mimocystites, Rhopalocystis*). The anus may be surrounded by a large **periproct,** that of *Mimocystites* being developed mainly on flanks of the theca and covered by an integument reinforced by minute plates; the location and other characters of the periproct are identical with those of the cystoid *Cheirocrinus.*

The orifice considered to be a **hydropore** has been observed in only a few genera. In *Columbocystis* (Fig. 298,*1*), *Cryptocrinites* (Fig. 298,*2*), and *Mimocystites* (Fig. 299, *1a*) it consists of a narrow slit or a perforation opening in a small protuberance set astride of the suture between two plates occupying the place of an oral in interray *CD.* In *Ascocystites* (Fig. 299,*2*) I interpret as hydropore a perforated wart borne by a peristomial cover plate in interray *CD.* A plate adjacent to the *CD* oral and brachioliferous plate *C* in *Palaeocystites* (Fig. 298,*3*) shows a large central pore which may be the hydropore or gonopore *(22)* or these two combined. Calling for notice further is the occurrence in *Cryptocrinites* (Fig. 298,*2*) of a second orifice that pierces oral *DE,* interpreted by BATHER *(5)* as a possible excretory pore and by others *(12, 42)* as a gonopore.

SUTURAL PORES AND EPISPIRES

Many eocrinoids (e.g., *Acanthocystites, Akadocrinus, Cigara, Gogia, Rhopalocystis, Lichenoides,* and others) exhibit the presence of **sutural pores,** generally very numerous, distributed along the sutures between nearly all thecal plates. In simplest and probably most primitive examples (e.g., *Gogia, Akadocrinus*) these pores are small in dimensions (greatest diameter 0.15 to 0.5 mm.) and have the form of ellipses disposed transversely with respect to the sutures along which they open. Externally, they are surrounded by a slightly projecting rim (Fig. 300,*1*).

In *Rhopalocystis,* characterized by relatively thick thecal plates, each pore communicates with the thecal cavity by a generally simple canal excavated in walls of the juxtaposed plates, but such conduits may be double, as in the diplopores of cystoids (Fig. 300,*2a-c*). The inner opening of these

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FIG. 299. [*Explanation continued from facing page.*]

Boh., showing exotomous branching of food grooves with cover plates flanked by outer cover plates, brachioles sectioned slightly above level of their attachment to oral surface, ×5 (Ubaghs, n).

3. Lingulocystis THORAL (Lingulocystidae), L.Ord., France, showing brachioliferous plates chiefly bunched at opposite extremities of the compressed theca; *3a,* entire oral surface, ×10; *3b,* single ambulacrum, ×20 (38).

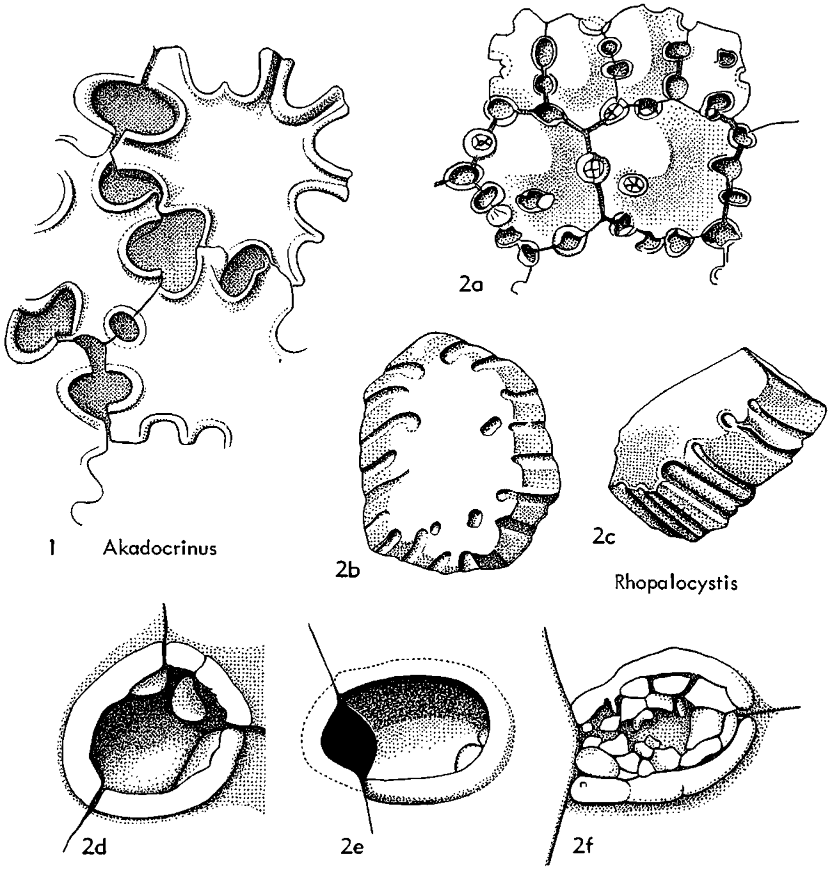

Fig. 300. Morphological features of eocrinoid sutural pores.

1. *Akadocrinus jani* Prokop (Eocrinidae), M.Cam., Boh., showing moderately large sutural pores surrounded by narrow slightly raised rims, ×25 (Ubaghs, n).
2. *Rhopalocystis destombesi* Ubaghs (Rhopalocystidae), L.Ord., Morocco, showing sutural pores bordering several thecal plates; *2a*, exterior of thecal plates with rimmed sutural pores, some penetrating parts of plates at slight distance from sutures and some closed by minute platelets, ×10; *2b*, interior of thecal plate, conduits of pores along sutural faces and inner terminations lacking rims, ×10; *2c*, lateral thecal plate showing sutural pores, ×10; *2d-f*, exterior of sutural pores with more or less numerous cover plates, ×50 (all 39).

canals lacks a rim (Fig. 300,*2b*), whereas the outer opening is located at the bottom of a relatively minute oval basin (maximum diameter 0.25 to 0.35 mm.) which is bounded by a slightly raised edge (Fig. 300, *2e*).

A more complex type of pore apparatus is encountered in *Lichenoides* (Fig. 301, *1a-e*). Here, each sutural pore is prolonged on the outer surface of two juxtaposed thecal plates as an elongated groove bounded by a slightly raised rim, aproximately one-half of the groove being located on one plate and the opposite half in continuation of it on the other plate. Collectively, the grooves tend to produce more or less lozenge-shaped patterns divided by the suture into subequal and symmetrical parts. These occupy nearly the entire surface of the plates, leaving free only median stereomic bosses on the basals and laterals and the brachiolar facets on laterals and radials.

In *Acanthocystites* (Fig. 301,*2a,b*), represented by a single known specimen in which the preservation is much poorer than desirable, the grooves just described appear to have been protected externally by a thin sheet of stereom which covered them com-

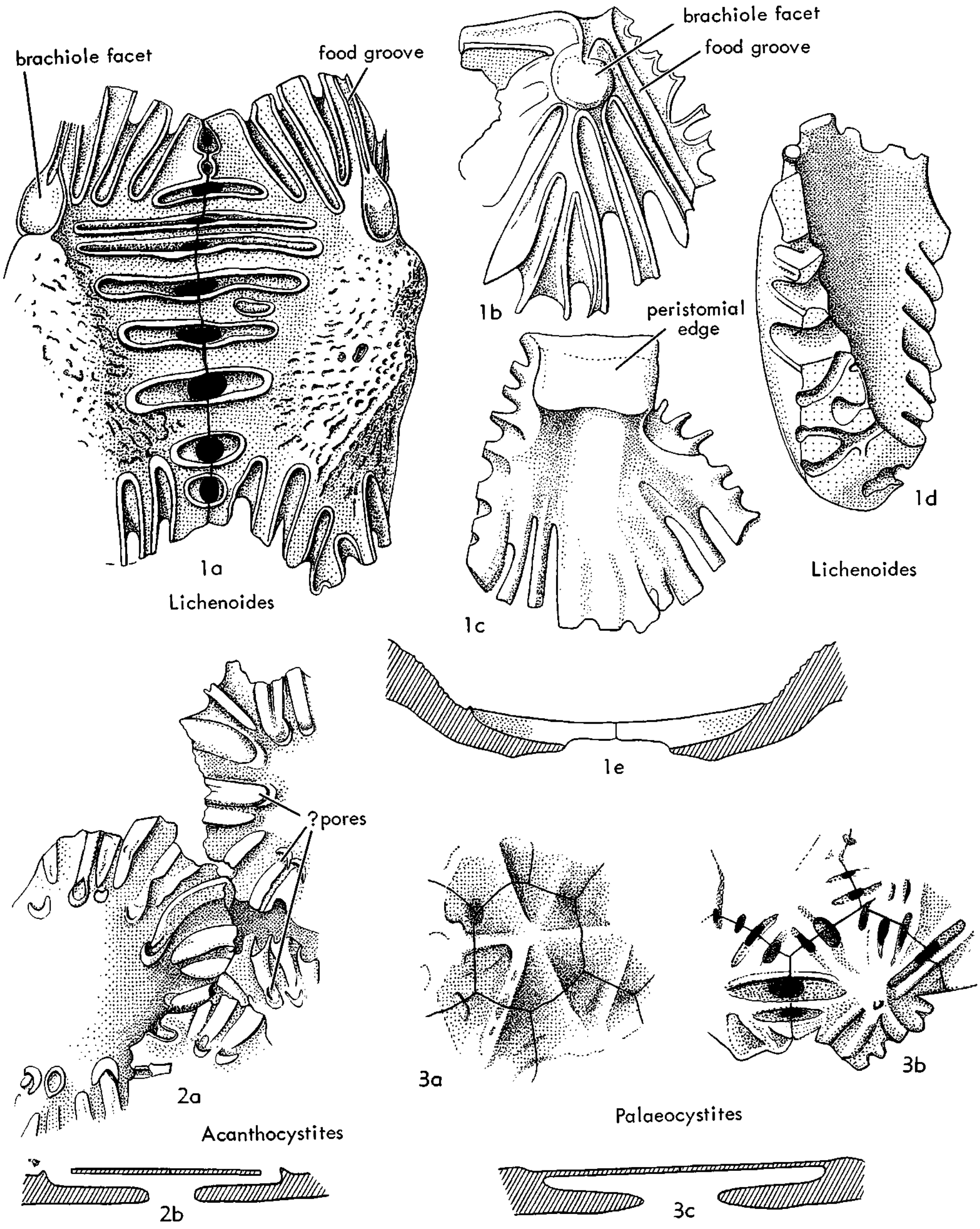

FIG. 301. Morphological features of epispires.

1. *Lichenoides* BARRANDE (Lichenoididae), M.Cam., Boh.; *1a,* two lateral plates with epispires along sutural margins, also showing brachiolar facets and food grooves, ×9; *1b,c,* exterior and interior of radial plate, ×9; *1d,* oblique view of basal plate, ×9; *1e,* section of epispire transverse to suture, enl. *(1a-d,* Ubaghs, n; *1e,* 37).
2. *Acanthocystites* BARRANDE (Eocrinidae), M.Cam., Boh.; *2a,* two thecal plates, exterior side, ×10; *2b,* section of epispire transverse to suture, enl. (both Ubaghs, n).
3. *Palaeocystites dawsoni* BILLINGS (Palaeocystitidae), M.Ord., Canada; *3a,* thecal plates showing radially disposed ridges on exterior, ×5 (22); *3b,* thecal plates with hollow folds opening to exterior, ×5 (22); *3c,* section of epispire transverse to suture, enl. (Ubaghs, n).

pletely except for extremities of each where an opening appears to have been maintained. Accordingly, the grooves are interpreted to have been replaced by hollow wrinkles of the plates, communicating with the thecal cavity by pores along the sutures and with the exterior by pores opening at extremities of the wrinkles.

A comparable arrangement is seen in *Palaeocystites* (Fig. 301,*3a-c*), in which the exterior of the theca bears a complex system of radiating hollow ridges and the interior shows numerous sutural pores. However, external openings of the canals lodged within thickness of the plates have disappeared, so that exchanges between sea water and organic structures within the canals could have been effected only through the thin sheet of stereom which covered them (Fig. 301,*3c*).

Finally, it is proper to ask whether the ridges borne by the thecae of *Ascocystites* and *Mimocystites* may not have the same morphological and functional significance as the lozenge-grouped grooves of *Lichenoides* (Fig. 301,*1a*, 302,*1a,b*) and the canals of *Palaeocystites*. Undoubtedly the ridges constitute stiffening ribs that reinforce solidity of the plates (Fig. 302,*3a*). At the same time, along part of their length—precisely that immediately adjacent to the sutures—they are hollow and thus differ from the structures observed in *Palaeocystites* only in lack of a floor interposed between their cavity and the thecal cavity (Fig. 302,*2,3b*).

Despite their diversity, the structures just described have two common features—all are epithecal and all communicate with the thecal cavity by means of sutural pores, conduits hollowed in sutural faces of thecal plates, or internal grooves cut transversely across the sutures. The structures which opened to the exterior possibly were surmounted by vesicles analogous to the papulae of asteroids. Those which were closed must have contained membranous tubules. The hollow ridges on plates of *Ascocystites* and *Mimocystites* could have contained evaginations of coelom or a stroma permeable to organic fluids. At any rate, these structures must have provided circulation that allowed exchange of gases between parts of the animal enclosed by the theca and sea water. The presumed respiratory function and exterior localization of these organs in relation to the theca make appropriate adoption of the name **epispires** for them, as proposed by Hudson *(22)*.

Reported to occur in *Rhopalocystis* are extremely minute platelets which tend to close off the external orifice of numerous sutural pores (Fig. 300,*2d,f*). These minuscule elements may have formed part of the normal equipment of the pores and they could have served to protect papulae. It is possible also, however, that they were secreted as a seal over pores that for one reason or another had ceased to be functional. As matter of fact, all transitions are observed between largely open pores, partially closed pores, completely blocked pores, and nearly effaced pores *(39)*.

It is not uncommon to find that some pores have lost all contact with the suture along which they originated. They penetrate the stereom of a plate in manner suggesting that in the course of growth they had become completely surrounded (Fig. 300,*2a*). Already stated is observation that in *Rhopalocystis* two sutural canals, instead of one, may open into the bottom of an individual external fossette (Fig. 300,*2c*). Such arrangement is reminiscent of the diplopores of the Diploporita among cystoids and perhaps suggests a certain community of origin, or at least a functional analogy between epispires and diplopores. Likewise, the extremely numerous hollow folds crowded together on the plates of some species of *Mimocystites* suggest the striate rhombs of such cystoids as *Cheirocrinus*. Here again, similarity of structures indicative of comparable functions allows us to entertain the possibility of genetic relationships which only future discoveries can verify.

AMBULACRA

The ambulacra of only a few eocrinoids yet have been observed. They number five wherever known, except that in *Lingulocystis* (and probably *Batherocystis* and *Rhipidocystis*) only two ambulacra occur.

Food grooves either run on the surface of thecal plates (Fig. 301,*1b*) or more commonly follow sutures between these plates, the edges of which then are beveled to form the groove (Fig. 298,*1,4a*, 299, *1a,b*). All of

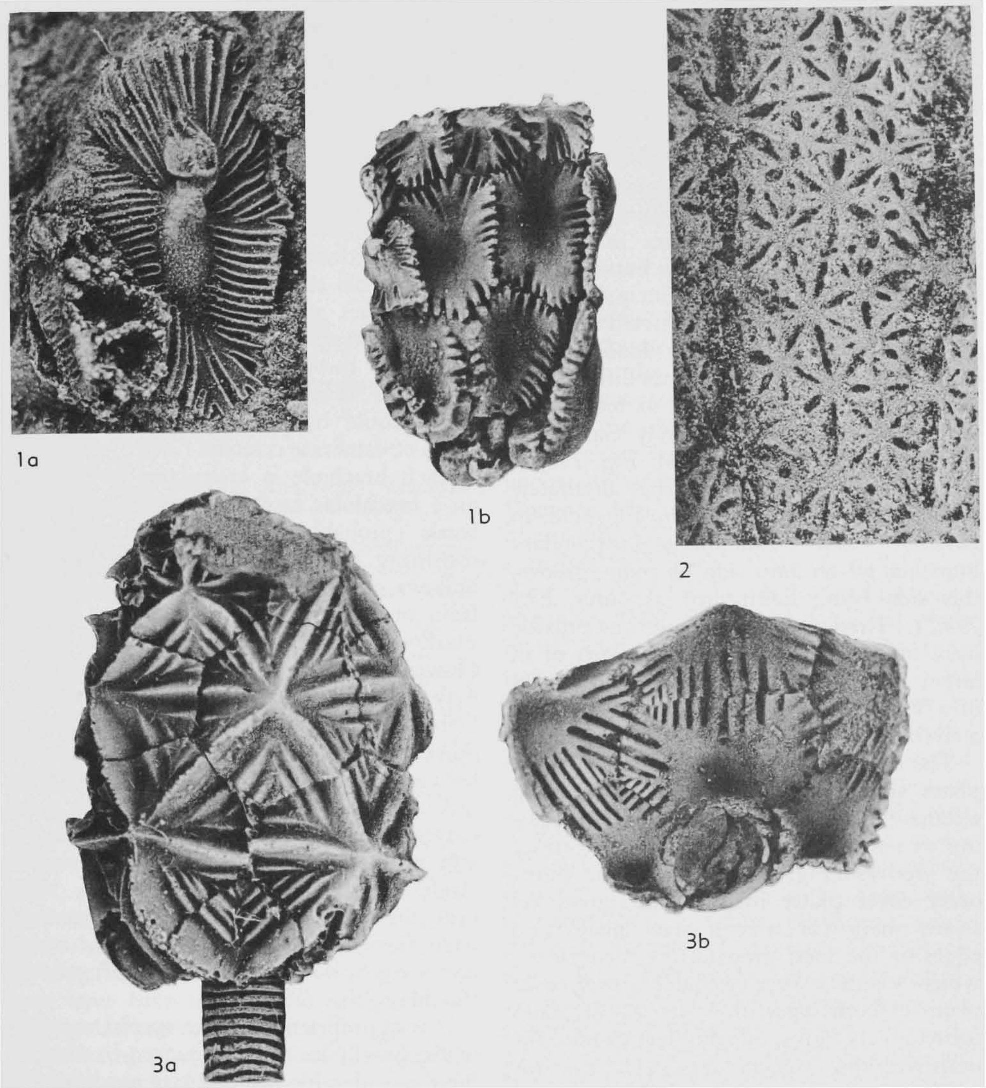

FIG. 302. Morphological features of epispires.

1. *Lichenoides* BARRANDE (Lichenoididae), M.Cam., Boh.; *1a,* external surface of lateral plate showing median boss surrounded by elongate narrow parts of epispires, ×5; *1b,* part of interior of theca showing inner sutural openings, ×3 (both Ubaghs, n).
2. *Ascocystites* BARRANDE (Ascocystitidae), M.Ord., Boh., internal surface of part of thecal wall, ×3 (Ubaghs, n).
3. *Mimocystites azaisi* THORAL (Macrocystellidae), L.Ord., France; *3a,* lateral view of theca and part of attached stem, ×3; *3b,* internal surface of proximal part of theca, ×3 (both Ubaghs, n).

these grooves are short and confined to the oral surface of the theca except in *Lichenoides* where they cross the circlet of radials and descend onto the laterals. They are borne by ordinary thecal plates (orals, radials, laterals, marginals) or by special adoral plates (e.g., *Mimocystites, Ascocystites,* Fig. 299,*1,2*), including the brachioliferous plates of *Rhopalocystis* and *Lingulocystis* (Fig. 298,*4a,b*; 299,*3a,b*).

In general, five food grooves extend directly to edges of the peristome (Fig. 298,*2*) but in some forms two pairs of them next to right and left sides of the madreporite plane came together at a short distance from the peristome border so that only three grooves arrive at this border (Fig. 298,*1,4a*). Exceptionally, four grooves, one of which is bifurcated, reach the peristome (Fig. 298, *3*). The food grooves may be simple unbranched furrows leading directly from a brachiole to the peristome or short secondary furrows may join main ones in treelike manner (Fig. 298,*4a*) or in a bunched pattern at outer extremities of principal grooves (Fig. 299,*1b*). It should be noted that the manner in which secondary food grooves come together or join main ones differs from genus to genus, giving rise to bifurcation patterns which are respectively classifiable as isotomous (branches equal, Fig. 298,*2*), heterotomous (unequal branches alternately meeting from right and left, Fig. 298,*4a*; 299,*3b*), and exotomous (secondary branches all on one side of main groove, this side being interpreted as outer, Fig. 299,*2*). These food-groove patterns provide basis for grouping brachioles in pairs or in larger numbers distributed along branches of a V in each ambulacrum or arranged in a circle around the oral face.

The food grooves were protected by **cover plates** attached on either side generally in alternation, the **cover-plate sockets** appearing as narrow platforms along margins of the grooves (Fig. 298,*4b*). In some forms **outer cover plates** may be interposed between main (or inner) cover plates and edges of the food grooves. In *Ascocystites,* which exhibits very well-developed cover plates of both types, the outer cover plates form a varyingly wide border around the orals with the cover plates raised almost vertically between them (Fig. 299,*2*).

BRACHIOLES

The **brachioles** of eocrinoids are simple exothecal appendages of the theca provided with their own skeleton and excavated on their oral surface are **brachiolar food grooves** which constitute distal extensions of the food grooves on the theca, just discussed. The brachioles are long and narrow—exceptionally slender in some, judging from the size of their facet for attachment. They invariably taper distally and never are branched. They are typically biserial in structure, that is, composed of two rows of alternating diminutive skeletal elements termed **brachiolars,** but a single ossicle may form their proximal extremity and in *Rhipidocystis* the brachioles are uniserial throughout their entire length. *Gogia spiralis* has biserial brachioles twisted on themselves in helicoid spirals (Fig. 294).

The brachiolar food grooves were protected by cover plates, which undoubtedly were capable of being raised. In some the cover plates are so lengthened and so strongly projected above the oral face of the brachioles that they have been misinterpreted as pinnules *(40)* or as structures which could have developed into the pinnules of camerate crinoids *(25)*.

Each brachiole is articulated at its base on a **brachiolar facet** which generally bears weak (probably ligamentary) impressions consisting either of shallow right and left hollows or an aboral depression separated from one or two adoral ones by a faintly marked transverse ridge (Fig. 299,*3b*). However ill-defined the relief of this facet may be, it implies the possibility of at least feeble movements of the brachioles. On the other hand, the great number of sutures between brachiolars must have compensated in some degree the absence of more strongly marked articulations on the facets and it must have rendered the brachioles moderately flexible. On the whole, however, the brachioles of eocrinoids appear to have been rather rigid structures, raised like long spines around the oral pole of the theca (Fig. 295).

It is appropriate to make special mention of the brachioles of *Ascocystites,* in view of their considerable evolutionary modification (Fig. 303). The brachioles of this genus are relatively stout. Each displays a slightly swollen proximal region and a distinctly narrowed distal portion. Their attachments to thecal plates (orals and adorals) are characterized by the presence of deep muscular or ligamentary sockets. Large excavations, especially well developed in the proximal portion of the brachioles, open out between the brachiolars both on aboral and adoral sides. Consequently, each articular face (proximal and distal) of the brachiolars bears two well-marked depressions separated by a transverse fulcral ridge. The depressions evidently served for attachment

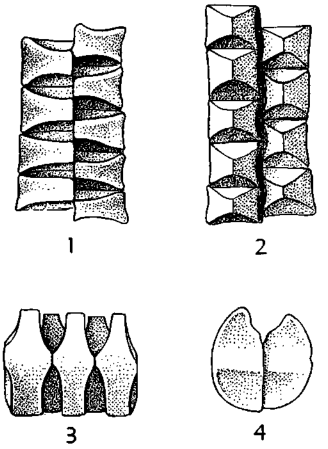

FIG. 303. Brachioles of *Ascocystites* BARRANDE (Ascocystitidae), M.Ord., Boh. (all Ubaghs, n).

1. Dorsal (outer) side of part of brachiole clearly showing biserial arrangement of brachiolars and large excavations between those of each series, ×10.
2. Oral (inner) side of specimen shown in *1,* showing excavations between brachiolars of series on opposite sides of median food groove, ×10.
3. Lateral view of part of brachioles, oral side up, dorsal side down, showing interbrachiolar excavations on each, ×10.
4. Sutural surfaces of pair of brachiolars, oral side up, ×10.

of powerful bundles of contractile or elastic fibers, antagonistic action of which would have produced extension and flexion of the brachioles. Distributed around the circumference of the oral surface of the theca, they must have been able to spread apart and pull toward one another (Fig. 299,*2*).

The number of brachioles varies in different genera and probably also in individuals of different age, as well as in different rays of the same individual. Five brachioles are observed in *Columbocystis,* ten in *Cryptocrinites,* about 15 in *Lingulocystis,* 15 to 30 in *Rhopalocystis,* approximately 23 in *Ascocystites,* and 8 to 22 (or even 44) in *Gogia.*

The brachioles of eocrinoids are attached to the theca in various ways; 1) attachment of each to an individual plate, which may be an ordinary one (radial, lateral, marginal) (Fig. 299,*3a*) or special (adoral, brachioliferous plate) (Fig. 298,*2,3*; 299, *1b,3b*); 2) attachment of two or even three brachioles to a single plate (e.g., laterals of *Lichenoides* with one to three brachioles) (Fig. 295); 3) attachment of each brachiole to a pair of adjoining plates (e.g., two orals, two adorals, an oral and adoral) (Fig. 298, *1*; 299,*1b,2*). To be noted in the third type is the fact that the brachioles are attached to the outer lateral edge of thecal plates and not to their adoral part.

COLUMN

All known eocrinoids possess a column, with exception of *Lichenoides,* which lacks one. Also, the more or less atrophied stem of *Rhipidocystis* and *Batherocystis* appears to be on the way to disappearance.

The most archaic sort of eocrinoid stem appears to be that seen in *Gogia* (Fig. 294), from the Middle Cambrian, in which it is a more or less elongated hollow organ consisting actually of an aboral evagination of the theca. The walls are formed by many irregularly arranged small polygonal plates joined rather loosely together. The most proximal ones may be transitional with plates of the theca, or oppositely, may be very dissimilar in size. The distal extremity of the column may be a narrowly rounded point composed of minuscule platelets or it may become enlarged into a flattened sole.

The structure of the column of *Gogia* possibly explains the origin of the varyingly numerous small plates at the aboral pole of *Lichenoides,* for these correspond rather closely to the skeletal elements of the *Gogia* stem. Indeed, if this indicates their morphological significance, the proximally located small plates of *Lichenoides* may represent a rudimentary stem which never developed. Other hypotheses have postulated that these plates are remnants of an atrophied circlet of thecal plates *(44)* or secondary skeletal elements produced for closure of the axial canal when a supposed peduncle was lost in the course of ontogenetic development *(37).*

The column of *Akadocrinus* (Fig. 304), another Middle Cambrian genus, exhibits structure unlike that of the stem of *Gogia.* Its length is five or six times the height of the theca. Equal to the theca in diameter at its proximal extremity, it progressively diminishes distally to a termination in a probably hollow holdfast disc with upper surface paved by irregular small polygonal

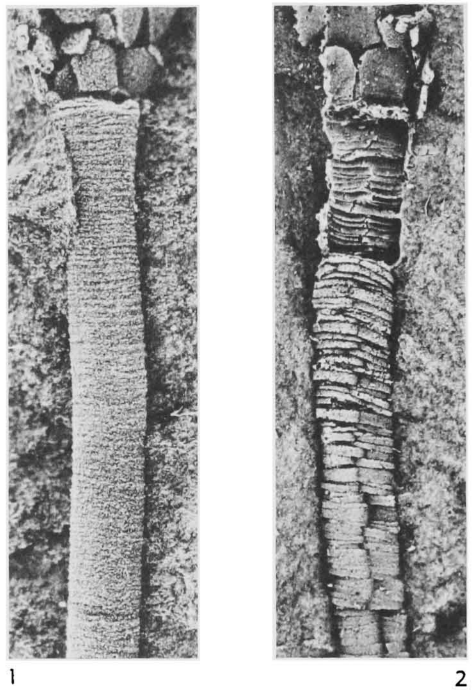

FIG. 304. Morphologic features of eocrinoid stem illustrated by *Akadocrinus nuntius* PROKOP (Eocrinidae), M.Cam., Boh. (Ubaghs, n).——*1.* Proximal part of theca and attached stem composed of wide, very short circular columnals, ×5.——*2.* Similar view of specimen showing large hollow interior of stem continuous with thecal cavity, ×5.

plates (Fig. 305) and lower surface unknown. The thin walls of the column are formed by short ossicles unevenly joined together. They enclose a large space which without restriction is continuous with the thecal cavity (Fig. 304,*2*). This broad communication between the stem and thecal cavities is doubtless a primitive characteristic, for it is found also in other eocrinoids, as well as cystoids and archaic crinoids.

Where eocrinoid columns are known in genera not already discussed, they are found to be composed of cylindrical columnals diverse in height (length) and pierced by an axial canal of large diameter, especially in the proximal region. Whether short or moderately long, the stem generally diminishes in diameter distally, terminating or apparently terminating in a point (Fig. 292). Its proximal extremity, attached to the aboral pole of the theca, is well separated from it both by smaller diameter of the column and by nature of the columnals. Commonly, near the theca very short columnals alternate with longer ones but progressively toward the free end of the stem the columnals become elongated and they tend to resemble one another closely. Their articulations, in so far as observed, are indicated by little or no differentiated features of the columnal facets and sutures between columnals are not crenulate.

Longitudinal differentiation of the column in genera of the Macrocystellidae allows distinction of two quite dissimilar regions, joined by a short transitional zone (Fig. 296; see also Fig. 313). The expanded proximal region is characterized by a relatively very large axial cavity which opens broadly into the thecal cavity. It is composed of regularly alternating annular columnals of two different types, one having a strongly salient peripheral flange accompanied internally by a narrow depressed zone which becomes enlarged at two diametrically opposite points where a small protuberance appears (see Fig. 313,*3*), and the other fitting exactly into the depressed zones of the just-described columnals and bearing also a pointed enlargement with small depression corresponding to the small protuberance on the inner side of the first-type columnals *(32)*. The distal part of the column, greatly reduced in diameter, is uniformly built of cylindrical columnals which increase in length while decreasing in width

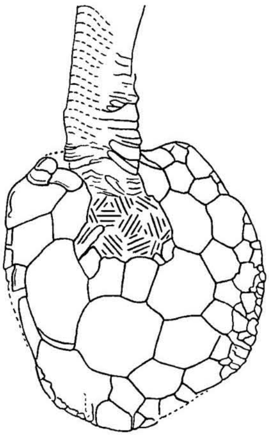

FIG. 305. Holdfast disc at distal extremity of stem of *Akadocrinus nuntius* PROKOP, M.Cam., Boh., ×9 (Ubaghs, n).

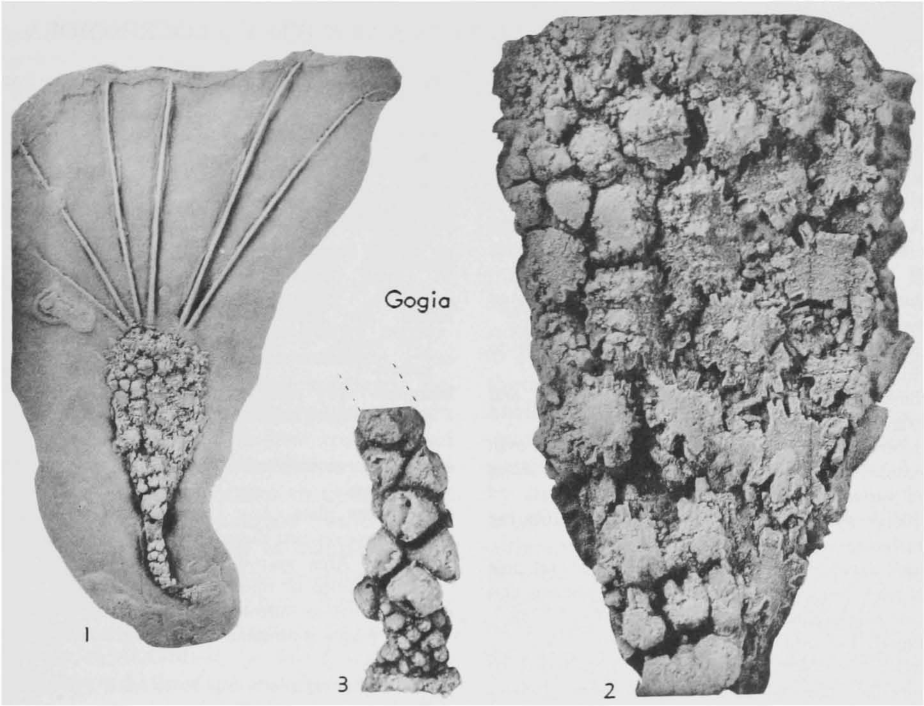

FIG. 306. Eocrinidae (p. S478).

in direction away from the theca (see Fig. 313,*1*).

In the Rhipidocystidae the column appears to be tending toward reduction. That of *Batherocystis* is composed of a few abnormally developed columnals having ovoid or somewhat irregular shape and transversely elliptical section (see Fig. 319,*3*). Perhaps these eocrinoids lived in prone position on the sea floor, like most "carpoids" *(18)*, although similarity of the two opposite flattened faces of the theca does not favor this hypothesis.

In no eocrinoid, other than *Akadocrinus*, has the presence of differentiated anchorage structures been ascertained. Without doubt, the column, implanted in mud or attached to some foreign body by its attenuated and recurved extremity, served to moor the animal at least temporarily. The relatively large hollow stem of *Gogia* may have functioned as ballast to orient the organism in a vertical position; in some individuals the stem is enlarged distally and terminates in a plane surface that may have aided fixation (Fig. 306,*3*). The manner of preservation of several specimens of *Lichenoides* suggests that this stemless form lived in sea-bottom mud implanted by its aboral extremity; also, this extremity, made heavier by its very thick walls, perhaps was utilized as ballast. We may recall that JAEKEL *(23)* considered *Cigara dusli, Lapillocystis fragilis,* and *Pilocystites primitivus* as bulbous radicular fragments belonging to eocrinoids (possibly *Acanthocystites*) and interpreted as a hollow root *(Hohlwurzel)* a curious structure found in Middle Ordovician beds containing *Ascocystites (25)*. In fact, *Cigara* comprises the remains of a ?theca prolonged toward the base by a hollow extension (?stem); *Lapillocystis* is an enigmatic, poorly preserved fossil; *Pilocystites* seemingly is not an echinoderm; the presumed *Hohlwurzel* of *Ascocystites* is an object (*?Conularia* shell) to which conical shells (probably brachiopods, perhaps Craniacea) are attached; consequently, the postulate advanced by JAEKEL and supported by EHRENBERG that the *Hohlwurzel* represents the most primitive type of echinoderm attachment root seems to lack any basis.

GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO EOCRINOIDEA

adoral. Any plate associated with orals, supporting food grooves on their beveled common edges and carrying brachioles on their outer margin.

ambulacrum. All food grooves, including brachiolar food grooves, of any single ray.

anal. Supplementary plate in *CD* interray.

anal pyramid. Valvular structure of triangular plates serving to close anus.

basal. Any plate of proximal circlet.

brachiolar. Any ossicle of brachiole (exclusive of cover plates).

brachiolar facet. Scarlike area on thecal plate to which brachiole was attached.

brachiolar food groove. Furrow running along oral surface of brachiolar ossicles.

brachiole. Exothecal structure supported by its own endoskeleton and bearing food groove along oral surface.

brachioliferous plate. Special thecal plate bearing brachiole.

column. Stalklike structure attached to aboral pole of theca and presumably used for supporting and anchoring organism.

columnal. Individual ossicle of column.

central. Any plate located in area surrounded by marginal framework on flattened faces of theca in compressed genera.

cover plate. Small plate covering part of food groove.

cover plate socket. Any place of attachment for cover plates.

deltoid. See oral.

epispire. Epithecal structure, open or covered, associated with sutural pore or slit, and presumably serving for respiration.

food groove. Furrow running along adoral surface of brachioles (brachiolar food groove) and on surface of theca to mouth; used for conveying food.

gonopore. Presumed outlet of genital products.

hydropore. Presumed orifice of water-vascular system.

infralateral. Any plate of circlet between basals and laterals.

interradial. Any interray plate above laterals (exclusive of orals).

lateral. Any plate of circlet between infralaterals (or basals, if infralaterals are lacking) and radials.

marginal. Any plate forming framework in compressed genera such as *Lingulocystis* and *Rhipidocystis.*

oral. Any of interradially disposed plates around peristome.

outer cover plate. Any small plate present along food grooves just outside of cover plates.

periproct. Area surrounding anus, covered with anal pyramid or finely plated integument.

peristome. Area surrounding mouth, protected by cover plates continuous with those covering food grooves.

peristomial cover plate. Any small plate participating to covering of peristome.

radial. Any plate of circlet next distal to laterals.

stem. See column.

supraradial. Any plate of meridionally disposed column resting on radial, exclusive of brachioliferous plate.

sutural pore. Any diminutive opening in theca, generally very numerous, distributed along sutures in many eocrinoids.

theca. Plated investment of visceral mass; body exclusive of column and brachiole.

TAXONOMIC POSITION

The problem of the taxonomic position of the Eocrinoidea is made difficult by their diversity, probable heterogeneity of their relationships, and insufficience of knowledge concerning the organization of numerous genera. In order to discuss genetic connections with other echinoderms it is desirable to confine initial consideration to forms in which structural features are reasonably well known and among these chiefly ones judged most suitable to serve as morphological types, later grouping others around them.

The first point that seems to be well established is appurtenance of the Eocrinoidea to the Crinozoa, all diagnostic characters of which are found in eocrinoids—visceral mass enclosed by a calcified theca formed of plates, oral surface typically directed upward, aboral surface resting on the substrate or attached to it permanently or temporarily generally by means of a stem, presence of exothecal processes along which ambulacral grooves designed for collection and transport of food particles to the mouth are developed, and anus located on the adoral half of the theca.

Among crinozoans, the eocrinoids appear to be related most closely to the cystoids. This is true not only of such forms as *Mimocystites* but it applies to the whole eocrinoid assemblage, in which essential features of organization clearly are cystoid-like. Such characters include 1) theca in form of a completely enclosed capsule except for a few openings, 2) absence generally of a true tegmen comparable to that of crinoids, 3) construction of theca similar or identical to that of cystoids, 4) organization of ambulacra as in cystoid ambulacra, 5) presence of true brachioles instead of arms. Only the absence of thecal pores or distinction between the sutural pores of eocrinoids and the diplopores or pore rhombs of typical cystoids allows separation of these echinoderm assemblages, even though morphological intermediates between sutural pores and diplopores are seen *(39)* and though the hollow trans-sutural folds of such eocrinoids as *Mimocystites* undeniably show resemblance to cystoid pore rhombs. Indeed, maximum similarity of the two classes is found in comparing the genus just mentioned with the rhombiferan cystoid *Cheirocrinus.* These forms differ essentially neither in structure of the stem nor in construction of the theca, which has the same number of plates arranged in the same manner, nor in organization of the ambulacra nor in nature and position of the thecal orifices, especially the anus, in both forms located in a wide elliptical finely plated area. Except for the complete lack of thecal pores in one and the presence of pore rhombs in the other, the two genera could easily be confused. Such great similarity in so many characters hardly can be fortuitous. It denotes close relationship in parentage between at least certain eocrinoids, (e.g., Macrocystellidae), and certain cystoids (e.g., Cheirocrinidae), as JAEKEL *(23)* recognized long ago when he interpreted *Mimocystites* (probable synonym of *Macrocystella*) as the immediate ancestor of *Cheirocrinus.* When the general organization of the compared forms is thus nearly identical, one may well ask if the diagnostic importance of the presence or absence of a certain type of thecal pores has not been exaggerated.

Another form particularly cited in considering the relationships of eocrinoids and cystoids is *Cryptocrinites.* As represented by this genus, they are ambiguous, however. If the nature of its ambulacral grooves, the presence of brachioles, the ventrolateral location of the anus, and the discovery by YAKOVLEV *(42)* in a normal specimen of supernumerary plates including one with traces of pore rhombs provide support for arguments favoring genetic relationship with rhombiferan cystoids—indeed, derivation of *Cryptocrinites* from them *(5, 42)*—other characters, such as the tricyclic construction of the theca, the lack of thecal pores, and the morphologic significance attributed by YAKOVLEV *(42)* to plates immediately surrounding the peristome, have suggested to some authors a possible connection with crinoids.

The hypothesis of crinoid affinities, though dependent on very superficial analogies, accords with often expressed opinion that the eocrinoids contain the source of crinoids. JAEKEL *(25)* tested this by study of Middle Cambrian forms such as *Acanthocystites,* in which the still-undifferentiated theca is composed of numerous irregularly arranged plates, with "arms" grouped in five bundles, as if at their level a tendency toward pentamerous division of the body already is manifest. These five arm groups, according to JAEKEL, by influence exerted on the theca, would have led to its progressive differentiation and especially the formation of median columns of thick plates as a kind of vertical ribs suited for support of the arm groups as well as the anal region. A stage illustrated by *Ascocystites* would have preceded appearance of true crinoids, including especially the Camerata. MOORE *(26)* contributed to the problem in undertaking to demonstrate by diagrams that "the respective dorsal-cup patterns of all types of camerate crinoids are directly derivable from eocrinoids, or conceivably from regular rhombiferan cystoids of sorts that belong either to the Cheirocrinidae or Caryocrinitidae; this calls merely for longitudinal shifting of thecal plates in a manner clearly shown within the cystoid assemblage."

It is appropriate to inquire whether these theoretical considerations are confirmed by any facts. Assuredly, many analogies, some of which are very striking, associate the theca of certain eocrinoids, such as *Ascocystites, Palaeocystites, Rhopalocystis,* and *Lichenoides* (termed a "cystocrinoid" by BERNARD, 1895), with that of crinoids. These analogies, never all manifested in a single genus, include 1) division of the theca into a dorsal cup and "tegmen," 2) tricyclic arrangement of dorsal-cup plates in several genera and division of the plates into alternating perradial and interradial meridional zones, 3) presence of supplemental plates interpreted as anals in the posterior interray, 4) more or less pronounced pentameral symmetry, 5) massive and imperforate nature of the plates, and 6) presence of sutural pores and epispires recalling comparable structures in some archaic crinoids.

Analysis indicates that a majority of these resemblances of eocrinoids and crinoids are essentially superficial. Thus, among eocrinoids one cannot find a true tegmen in the crinoid sense of the term, for in crinoids the tegmen is circumscribed by a circle passing through bases of the arms which are supported by plates of the dorsal cup. The brachioles of eocrinoids, which perform the function of the arms of crinoids, are attached to plates that comprise an integral part of the "tegmen" (except in *Lichenoides*) and even in *Ascocystites,* with brachioles distributed in a circle around the "tegmen," these depend entirely on plates (orals, adorals) belonging to it and none on plates belonging to the aboral part of the theca. Accordingly, the "tegmen" of eocrinoids is indicated by its organization, nature of its constituent elements, and relationship with the brachioles to be much more cystoid-like than crinoid-like.

The tricyclic arrangement of thecal plates in a few eocrinoid genera proves nothing as to genetic affinities with crinoids, for such grouping of plates around the visceral mass recurs frequently in the evolutionary history of echinoderms. For the same reason, partition of the theca into alternating perradial and interradial meridional zones lacks significance. Furthermore, the perradial plate columns of eocrinoids are not homologous with those formed by radials and fixed brachials in crinoids, because true arms are nonexistent in eocrinoids. Also, quite unproved is the assumption that supplemental plates of the *CD* interray observed in some eocrinoid genera correspond to anal plates of crinoids. As previously observed, neither in organization of the theca nor in the nature of its component elements is any sure indication found of relationship between eocrinoids and crinoids, and still less of descent of the latter from the former. Finally, the best suggestion of a possible genetic link between the two classes perhaps lies in the absence of thecal pores or the presence of sutural pores and epispires similar to those of archaic crinoids *(37),* although this is far from decisive.

In my view, a main objection to the hypothesis of descent of crinoids from eocrinoids or forms similar to them is the fundamentally different nature of crinoid arms and eocrinoid brachioles. The latter are distinguished from the former 1) in being exothecal appendages, that is, occurring outside of the thecal wall instead of comprising evaginations of it, 2) in lacking any continuity of their skeletal support with plates of the aboral part of the theca, 3) in not being attached to plates homologous with crinoid radials but generally instead to plates of the oral region of the theca, 4) in providing for intercommunication which their soft parts could have with organs and cavities enclosed by the theca by way of the peristome and the epithecal part of the food grooves instead of through an orifice at the base of each brachiole, and 5) in having biserial structure in contrast to the probable initial uniserial nature of crinoid arms. These many profound differences deter guesswork in the present state of knowledge concerning the manner in which one type of appendage could have given rise to the other.

When account is taken of the fact that the eocrinoids most similar to crinoids are contemporaneous with genera of the latter which already exhibit all attributes of this class, it is necessary to admit that the observed resemblances can only signify convergence or evolutionary parallelism, according to judgment that the forms considered are descendants of different or common ancestors. No presently available paleontological evidence allows choice between these alternatives. On the other hand, nothing firmly opposes phyletic relationship between certain cystoids and certain eocrinoids, even though the nature of these relationships cannot yet be specified.

Finally, we may note that some authors (e.g., Fell, *14*; Jaekel, *25*; Nichols, *27*) have assigned to eocrinoids the role of common source of all echinoderms. This entirely speculative concept is denied by the fact that in lowest Cambrian strata such complex forms as *Helicoplacus* and *Stromatocystites* are associated with plates probably attributable to eocrinoids. Also, it is self-evident that no known eocrinoid can represent the ancestral type of *all* echinoderms *(13)*. In addition, how could an echinoderm that had attained the stage of radial symmetry give rise to such forms as the "carpoids," which in all likelihood belong to a preradial-symmetry stage of the phylum? How also could the eocrinoids, already well advanced along the path of the Crinozoa, possibly be ancestors of the Echinozoa? The simple asking of these questions suffices to show the inanity of such suppositions.

CLASSIFICATION

A majority of the genera brought together in the class Eocrinoidea previously have been considered to belong to the Cystoidea *(sensu lato)* and generally classed partly in the Amphoridea and partly in the Aporita. Jaekel *(23)* was first to withdraw this assemblage from the cystoids, later *(25)* grouping them as a subclass of the Crinoidea. Still later, Regnéll *(29)* elevated the subclass to the rank of class.

Again it is Jaekel *(25)* who must be credited for the only published classification of the group, a classification which recognizes four orders, seven families, and 15 genera, with *Amygdalocystites* and *Comarocystites* (now assigned to the Paracrinoidea) provisionally included as an appendix.

Jaekel's first order, named Atava, contained the two families Eocrinidae and Ascocystidae (*recte* Ascocystitidae), intended for inclusion of such forms as *Acanthocystites* and *Ascocystites,* characterized by a theca containing very numerous plates not arranged in circlets and having a flattened upper surface with five attached groups of brachioles. The genus *Eocrinus,* which is a junior subjective synonym of *Gogia (31),* contained in the order, is the type not only of the family Eocrinidae but of the class Eocrinoidea.

The second order, named Reducta by Jaekel, was composed of the families Lichenoidae (*recte* Lichenoididae), Cryptocrinidae (*recte* Cryptocrinitidae), and with reservation, Paractocrinidae. Representatives of the first two families are characterized by a theca composed of only a few circlets, generally with five plates in each, without sharp separation of oral and aboral parts, and with a variable number of brachioles unevenly distributed around the summit. The Paractocrinidae was proposed for three new, rather poorly known genera from Ordovician rocks of the Leningrad region. Since they seem to show greater affinities with crinoids than eocrinoids *(2),* they are omitted from consideration here.

The third order, called Plicata, was erected for the single family Macrocystellidae, in which the theca contains more numerous plate circlets than in the preceding order and five groups of brachioles are supported by plates designated as radials. As indicated by the name of the order, thecal plates are ornamented by a number of folds. The Macrocystellidae were considered as intermediate forms leading directly to the regular cystoids, especially *Cheirocrinus,* which differs from the macrocystellids only in the possession of pore rhombs.

The fourth order, Deviata, was grouped in the Eocrinoidea doubtfully, and Jaekel placed in it the Malocystidae (*recte* Malocystitidae), containing the single genus *Malocystites*. This form now is classed in the Paracrinoidea.

Subsequently to the time of Jaekel's work, several families and numerous genera have been assigned to the Eocrinoidea (*3, 16-18, 28, 38, 39, 46*). Some of these genera (e.g., *Lingulocystis, Rhipidocystis*) originally were thought to be "carpoids" *(17, 18)*, but they differ essentially from these echinoderms in having typical brachioles and a stem that is markedly different from the stele of the Homostelea and Homoiostelea. Ubaghs *(38)* recognized that both should be transferred to the Eocrinoidea. *Lepidocystis,* on the other hand, provisionally classified as an eocrinoid by Foerste *(16)*, has an organization radically unlike that of this class; since it cannot be attributed to some other known class, perhaps it merits a class of its own. Some genera (e.g., *Columbocystis, Foerstecystis, Springerocystis*), in which the nature of exothecal appendages is unknown, may ultimately prove to belong outside of the Eocrinoidea, though they are included here in the class provisionally.

As delimited in the *Treatise,* the Eocrinoidea contain approximately a score of genera, to which are added a few forms too poorly known for definite classification. In comparing these genera with one another, it is possible to set forth characters found to be present in common and on this basis to recognize families. It is difficult to determine the relative importance of these characters, because their phylogenetic significance is unknown. At any rate, the principal features used in classification of the eocrinoids are 1) number and mode of arrangement of thecal plates, 2) presence or absence of sutural pores (or structures associated with them), 3) symmetry of the theca, and 4) disposition of the brachioles. To be noticed is the relatively large number of monotypic families, though this should not be surprising in view of the probable numerous genera and lineages which are unrepresented in the small fraction of once-living forms now available in fossil collections.

The difficulty in constructing a hierarchy of familial morphological characters indicates that the establishment of systematic categories of superfamilial rank would be highly precarious. They could not be based on criteria other than those having fairly well-established phylogenetic signification. One might, indeed, undertake to distinguish two main groups of eocrinoids defined by possession or lack of possession of sutural pores. Since nothing would prove common origin of families that come to be placed on this basis in either group, it is better not to arrange families in this way. Accordingly, they are here presented in a sequence that takes maximum account of degree of similarities.

SYSTEMATIC DESCRIPTIONS

Class EOCRINOIDEA Jaekel, 1918

[*nom. transl.* Regnéll, 1945 (*ex* subclass Eocrinoidea Jaekel, 1918)] [The term Eocrinites, created but not defined by Jaekel in 1899 (23, p. 174), has no taxonomic status; it served apparently to designate collectively such genera as *Acanthocystites, Eocystites* or *Lichenoides,* which were regarded by him as primitive Cladocrinoidea (=Crinoidea Camerata)]

Extinct, stalked or rarely stemless Crinozoa, with theca closed up to peristome, and with or without tegminal region differentiated from aboral part. Radial (generally pentamerous) symmetry affecting food grooves and (in several families) thecal plates, which are solid, without pores (except tiny pores of stereom meshwork). Sutural pores present in many genera, opening directly to exterior or accompanied by epithecal grooves or covered passageways (i.e., epispires) at right angles to sutures of thecal plates. No true arms, but food grooves extended on exothecal skeletal, unbranched, typically biserial, processes (brachioles), which are inserted either on ordinary thecal plates or on special brachioliferous plates lying outside or between thecal plates. *L. Cam.-Sil.*

Family EOCRINIDAE Jaekel, 1918

[=subfamily Acanthocystida Haeckel, 1896 (invalid family-group name)]

Thecal plates numerous, polygonal, indefinite in number, without any regular arrangement or in many alternating transverse rows, but never in well-defined circlets. Brachioles long, slender, biserial, originating in probably five clusters located at periphery of oral face. Stem enclosing wide central cavity. *M.Cam.*

Gogia Walcott, 1917 [**G. prolifica*; OD] [=*Eocrinus* Jaekel, 1918, type, *Eocystites?? longidactylus* Walcott, 1886]. Theca conical, subspherical or subcylindrical. Plates numerous, polygonal, without any definite arrangement, smooth or ornamented with granules or radiating ridges. Sutural pores rimmed by slightly raised ridges. Brachioles 8 to about 22 and probably as many as 44, twisted in *G. spiralis,* originating in clusters. Stem covered by numerous small irregularly arranged polygonal plates that may be gradational with those of theca or of distinctly different size; distal end of stem characterized by cluster of relatively small plates, which may or may not form an expanded flat-based process. *M.Cam.,* N.Am.——Fig. 306,*1-3*. **G. prolifica,* Can.(B.C.); *1,* lectotype, ×1; *2,* theca of same, ×4; *3,* distal end of stem with expanded, flat-based process, ×6 *(31)*. [See also Fig. 294.]

Acanthocystites Barrande, 1887 [**A. briareus*; OD] [=*Acanthocystis* Bather, 1889 *(nom. van.)*]. Theca elongate, apparently conical. Thecal

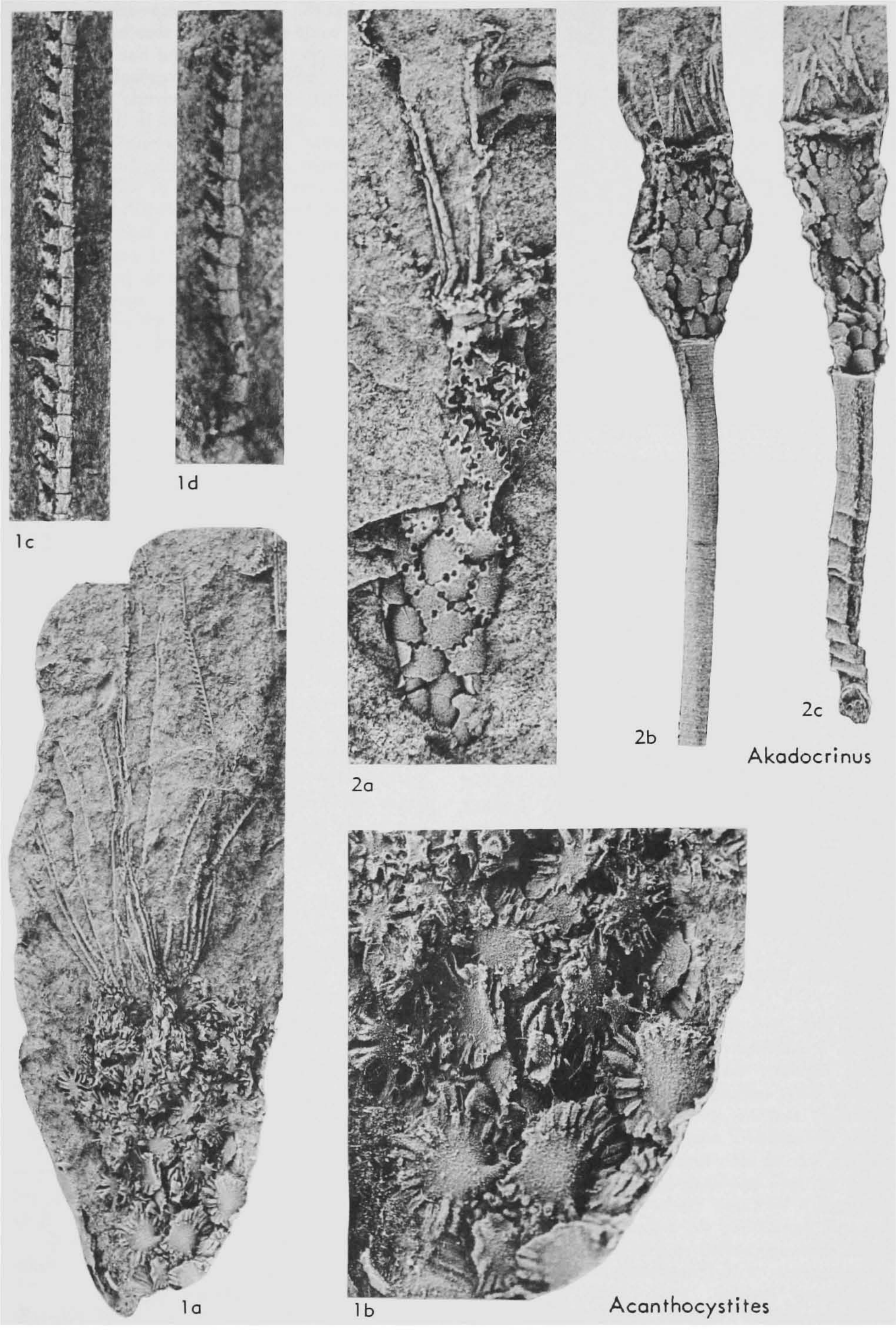

FIG. 307. Eocrinidae (p. *S*478, *S*480).

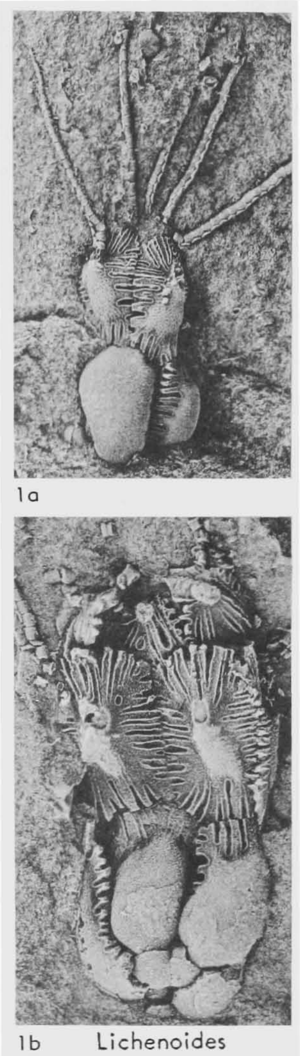

FIG. 308. Lichenoididae (p. S481).

plates thin, irregularly arranged, flat or slightly tumid, ornamented with minute granules; size of plates regularly diminishing in distal direction. Sutural pores leading into covered epispires with seemingly exterior openings at both ends. Cover plates of brachioles relatively large, obliquely protruding, one to each brachiolar ossicle. [Proximal regon of theca and stem lacking in single known specimen.] *M.Cam.*, Boh.——FIG. 307,*1*. **A. briareus,* Jince beds; *1a*, holotype, ×2; *1b*, thecal plates showing covered epispires, ×5; *1c,d*, brachioles, lat. view, ×10 (Ubaghs, n).

Akadocrinus PROKOP, 1962 [**A. jani*; OD] [=*Compsocrinus*[1] ŽELÍZKO, 1911 *(nom. nud.)* (*non* MILLER, 1883)]. Theca relatively small, elongate, bottle-shaped. Oral area between brachiole insertions rather large and flat. Thecal plates irregularly pentagonal or hexagonal, arranged in more or less alternating transverse rows, becoming smaller and more irregular in distal direction. Sutural pores fairly large, rimmed by slightly raised, narrow ridges. Brachioles numerous. Stem long, with proximal diameter as wide as proximal diameter of theca, tapering distally, composed of very low columnals which may meet along irregular zigzag sutures in proximal region. *M.Cam.*, Boh.——FIG. 307,*2a*. **A. jani,* Jince beds; incomplete theca, ×5 (Ubaghs, n).——FIG. 307, *2b,c*. *A. nuntius* PROKOP, Jince beds; *2b,* holotype; *2c,* another specimen, both ×2 (Ubaghs, n).

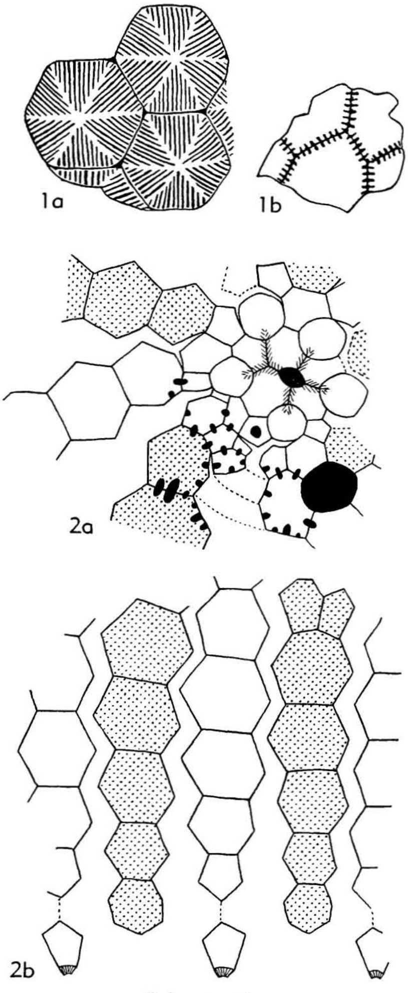

FIG. 309. Palaeocystitidae (p. S481-S482).

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[1] Name introduced by PERNER in typescript, seemingly first published by ŽELÍZKO in 1911 as *nomen nudum*.

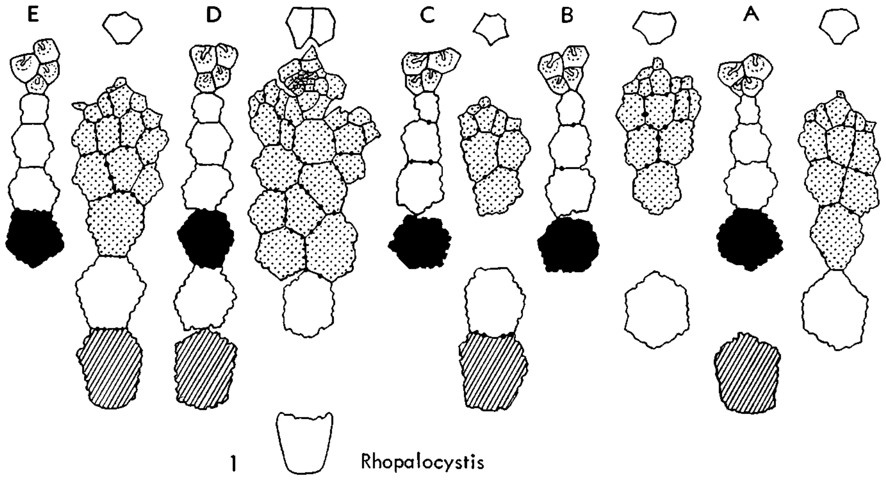

FIG. 310. Rhopalocystidae (p. S481-S482).

Family LICHENOIDIDAE Jaekel, 1918

[*nom. correct.* UBAGHS, herein (*pro* Lichenoidae JAEKEL, 1918)]

Theca composed of three alternating circlets of typically five plates each, plus variable number of small ossicles at aboral pole. Sutural pores numerous, each one passing into an open, well-developed epispire. No "tegmen," but peristome directly surrounded by third circlet of plates (radials). Food grooves epithecal, simple or branching. Brachioles long, biserial, apparently rigid, inserted on second (lateral) and third (radial) circlet of thecal plates. No stem. *M.Cam.*

Lichenoides BARRANDE, 1846 [*L. priscus*; OD] [=*Lichenocystis* HAECKEL, 1896 *(nom. van.)*]. Theca ovoid. Base forming thick-walled cup of large unequal basal plates with their aboral ends partially separated by variable number of small thick ossicles. Middle circlet comprising subpentagonal or subhexagonal lateral plates, largest elements of theca. Upper circlet composed of subpentagonal, rather small radial plates, with thickened inner adoral margin. Epispires rimmed by slightly raised narrow ridges and covering whole surface of plates except brachiole insertions and median stereomic protuberances on basal and lateral plates. Brachioles single or in clusters of 2 or 3 on lateral and radial plates. *M.Cam.*, Boh.——FIG. 308,*1*. **L. priscus*, Jince beds; two specimens; *1a*, ×2; *1b*, ×3 (1). [See also Fig. 295.]

Family RHOPALOCYSTIDAE Ubaghs, new family

Theca divided into 1) proximal part made of single basal ossicle and two alternating circlets of infralateral and lateral plates, 2) middle part composed of five meridional perradial series of plates separated from each other by five interradial plated areas, and 3) oral part comprising circlet of six oral plates and five endothecal ambulacra. Sutural pores numerous, each one opening exteriorly into small depression that is rimmed by narrow ridge. Anus located at adoral end of *CD* interray. Brachioles attached to special plates inserted between other thecal plates. Stem round, progressively tapering distally, composed of low cylindrical columnals. *L.Ord.*

Rhopalocystis UBAGHS, 1963 [**R. destombesi*; OD]. Theca club-shaped, thick-walled. Basal ossicle very thick, cup-shaped; infralaterals 4, pentagonal or hexagonal, largest plates of theca; laterals 6, hexagonal or heptagonal; perradial series of 4 or 5 plates each (one radial and 2 or generally 3 supraradials); interradial areas typically resting on laterals, composed of 4 or 5 rows of interradials; *CD* interray larger than others, asymmetrically divided by a column of extra plates (anals). Peristome central, subpentagonal. Periproct with small anal pyramid. Ambulacra occupying a small stellate area around oral pole, each one composed of 3 to 6 brachioliferous endothecal plates. Brachioles 20 to 30. *L.Ord.*, Morocco.——FIG. 310,*1*. **R. destombesi*, U.Tremadoc, S.Morocco; diagram of theca *(39)*. [See also Fig. 293.]

Family PALAEOCYSTITIDAE Ubaghs, new name (1896)

[=family Palaeocystida HAECKEL, 1896 (invalid family-group name)]

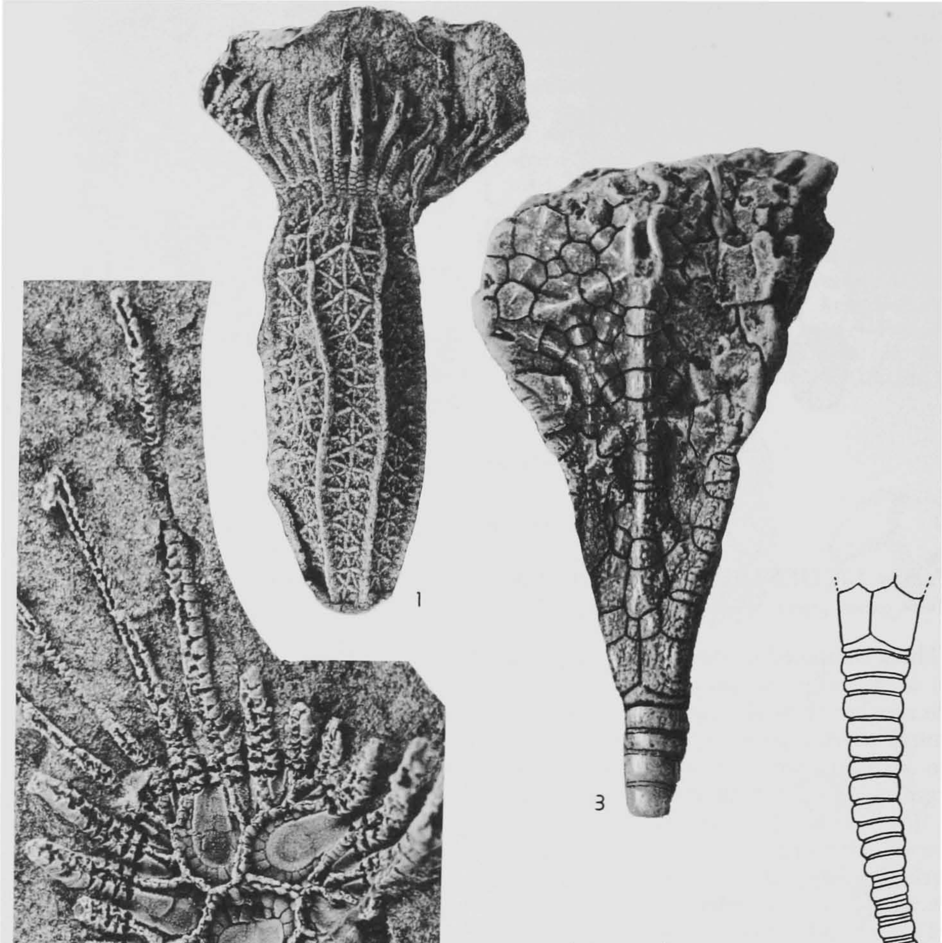

FIG. 311. Ascocystitidae (p. *S*483).

Theca comprising 1) proximal part of two alternating circlets of five plates each, 2) middle lateral part of ten meridional series of plates, 3) small oral area made of doubled circlet of five orals and five brachioliferous plates, surrounded by more or less complete belt of small irregular plates. Sutural pores opening into covered epispires which externally form elaborate system of strongly raised, radiating ridges. Anus between oral and middle lateral part of theca, in *BC* interray. Pore (?hydropore) in small plate close to oral circlet. Brachioles and stem unknown. *M.Ord.,* N.Am.

Palaeocystites BILLINGS, 1858 [**Actinocrinus tenuiradiatus* HALL, 1847; SD S. A. MILLER, 1889] [=*Palaeocystis* HAECKEL, 1896 *(nom. van.)*]. Theca elongate, somewhat cylindrical in upper half, conical and proximally tapering in lower half, with hemispherical oral face. Peristome central, rather small. Food grooves along interoral sutures, short, simple or bifurcating into 2 short branches. *M.Ord.,* N.Am.——FIG. 309,*1*. **P. tenuiradiatus* (HALL), Chazyan, USA(N.Y.); *1a,b*, outer and inner sides of thecal plates, enl. *(47)*.——FIG. 309,*2*. *P. dawsoni* BILLINGS, Chazyan, Can.; *2a,* oral area, ×3; *2b,* part of proximal and middle lateral walls of theca, diagram., ×3 *(22)*.

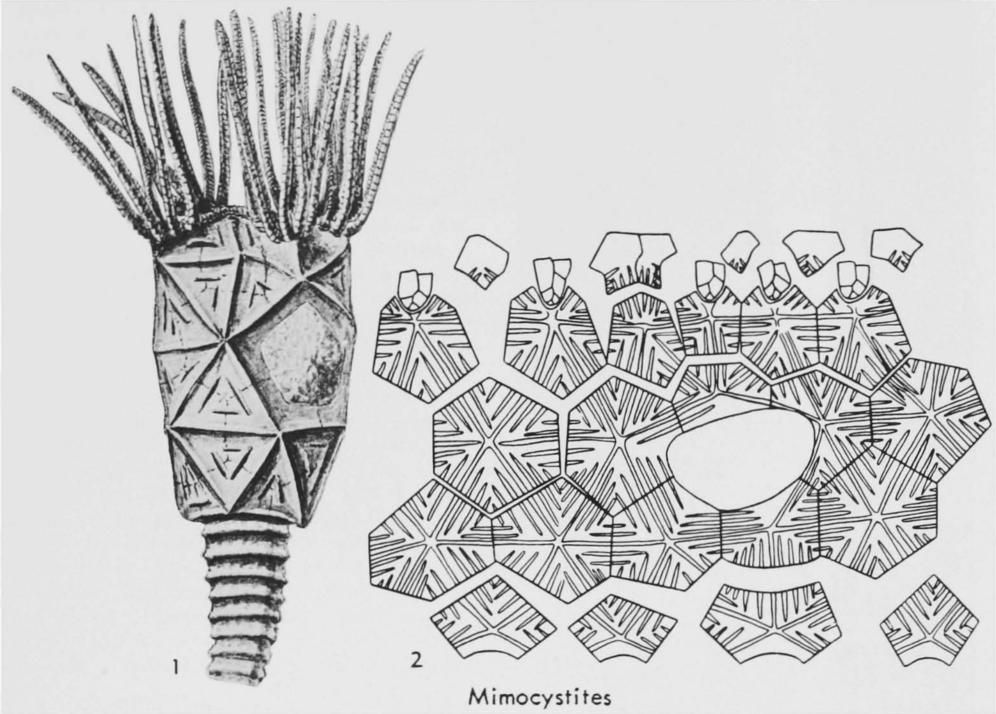

FIG. 312. Macrocystellidae (p. S484-S486).

Family ASCOCYSTITIDAE Ubaghs, new name (1896)

[=family Ascocystida HAECKEL, 1896 (invalid family-group name); Ascocystidae JAEKEL, 1918 (invalid family-group name)]

Theca divided into flat tegmen and elongate aboral part, hexagonal in cross section; aboral part comprising very numerous polygonal plates with subquadrate platelets between them, distributed in six vertical columns and six intermediate fields. No sutural pores, but partially hollow radiating ridges cross sutures. Tegmen composed of five large orals and variable number of adorals. Food grooves exotomously branching. Peristome and food grooves protected by cover plates and outer cover plates. Hydropore? in outer cover plate of *CD* interray. Brachioles 20 to 30, biserial, with deep ventral and dorsal muscle or ligamentary insertions between successive ossicles, forming circle around tegmen; each brachiole inserted on outer edge of an oral and adoral or of two adorals. Anus unknown. Stem round, tapering distally, composed of alternating very thin and thicker columnals. *M.Ord.*

Ascocystites BARRANDE, 1887 [**A. drabowensis*; OD] [=*Ascocrinus* BARRANDE, 1887 (*non* TROMELIN & LEBESCONTE, 1876) *(nom. nud.)*; *Ascocystis* BATHER, 1889 *(nom. van.)*]. Thecal plates united by elaborate system of radiating ridges perpendicular to plate sutures and by 6 powerful vertical ridges, running along vertical columns of plates from proximal end to distal margin. *M.Ord.*, Boh.——FIG. 311,*1-4*. **A. drabowensis*; *1*, theca, ×1; *2*, tegmen, ×3; *3*, proximal portion of theca, ×5; *4*, stem, ×5. [The structure figured by JAEKEL [*25*, fig. 9D-F, p. 17] as a hollow root of *Ascocystites* is a foreign body (shell of *?Conularia*) covered by epizoans (probably brachiopods)] (Ubaghs, n).

Family MACROCYSTELLIDAE Bather, 1899

Theca divided into elongate aboral cup and tegminal portion, and composed of strongly radiately ridged or folded plates, displaying more or less regular pentamerism. Brachioles in five groups. No sutural pores, but radiating hollow ridges cross sutures of thecal plates. Stem round, comprising rapidly tapering proximal region composed of low columnals with wide flange, and gradually tapering distal region composed of long narrow columnals with narrower lumen. *L.Ord.-M.Ord.*

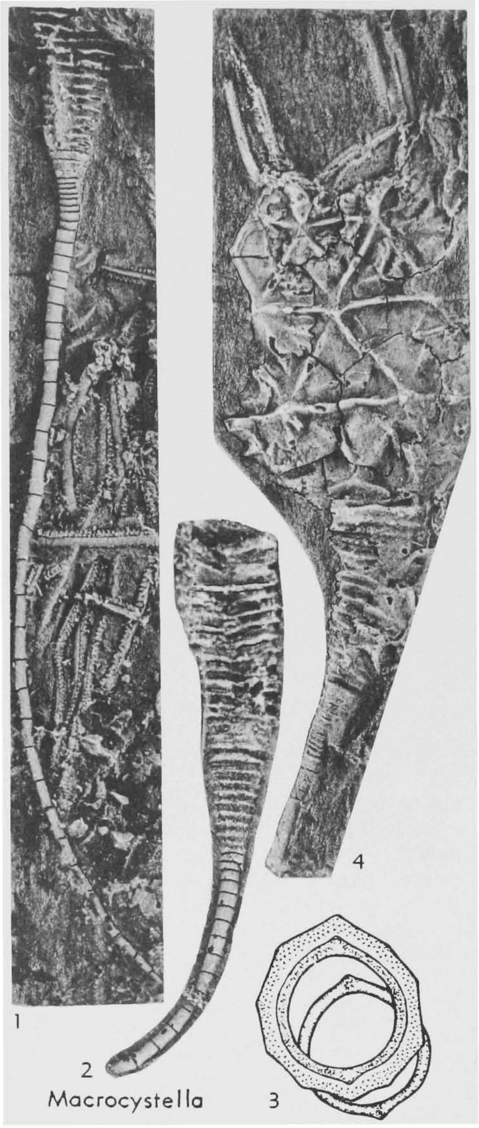

FIG. 313. Macrocystellidae (p. S484).

Macrocystella CALLAWAY, 1877 [*M. *mariae*; OD]. Aboral cup showing 4 circlets of plates; those of aboral circlet low, those of 2nd and 3rd circlets relatively large, and of 4th circlet about half size of those in 3rd circlet. Brachioles long, slender, biserial and unbranched, probably inserted on small tegminal elements borne by plates of 4th circlet; cover plates distinct. Aboral thecal plates strongly marked by radiating ridges, which divide surface into triangles, inside of which are smaller folds. [This genus, based on crushed material, is inadequately known; neither the tegmen nor anal side of theca has been observed. The statement by BATHER (5) that each plate of the 4th circlet bears a brachiole, which almost immediately bifurcates, is probably erroneous. So far as determinable from available data, *Macrocystella* does not differ from *Mimocystites,* which is kept apart only provisionally.] *L. Ord.,* Eng.-Ger. (Bavaria)-? Fr.-?Greenl.——FIG. 313,*1-4*. **M. mariae,* Tremadoc, Shineton Shales, Eng.; *1,* almost complete stem, ×3; *2,* proximal and median stem region, ×3; *3,* proximal columns, ×1; *4,* theca, ×3 *(1,2,4,* Ubaghs, n; *3, 32).*

Mimocystites BARRANDE, 1887 [**M. bohemicus*; OD] [=*Mimocystis* CARPENTER, 1891 *(nom. van.)*]. Theca irregularly ovoid, divided into elongate aboral cup and slightly convex oral face, theca composed of 5 circlets of generally alternating plates. Basal circlet of 3 relatively small pentagonal plates and 4th one probably formed by fusion of 2 somewhat larger hexagonal plates. Each of next 2 circlets composed of 5 plates, which are large, theoretically hexagonal or pentagonal, but some variously modified in shape for accommodation of anal area. Plates of 4th circlet relatively small, generally hexagonal, somewhat unequal in size, and distally notched (except one in *CD* interray) for reception of ambulacra. Fifth circlet of 6 orals (2 in *CD* interray), relatively

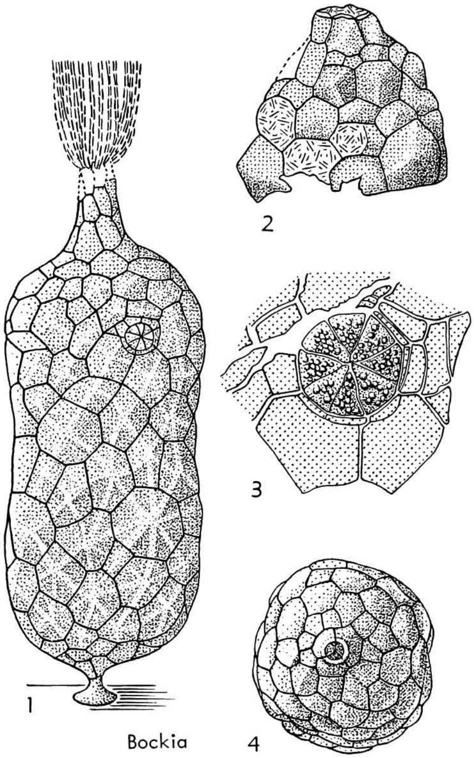

FIG. 314. Springerocystidae (p. S486-S487).

small, lozenge-shaped or subpentagonal in outline, bordering peristome; ambulacra V-shaped, composed of small adorals, bearing brachioles on their outer edge (each brachiole inserted on 2 contiguous adorals). Peristome and food grooves protected by alternating cover plates. Hydropore on suture between orals of *CD* interray. Periproctal area large, oval, lateral, between 2nd and 3rd circlets, filled with small plates and comprising small anal pyramid in *BC* interray. Thecal surface divided into triangles by strongly marked radiating ridges, between which are smaller folds.

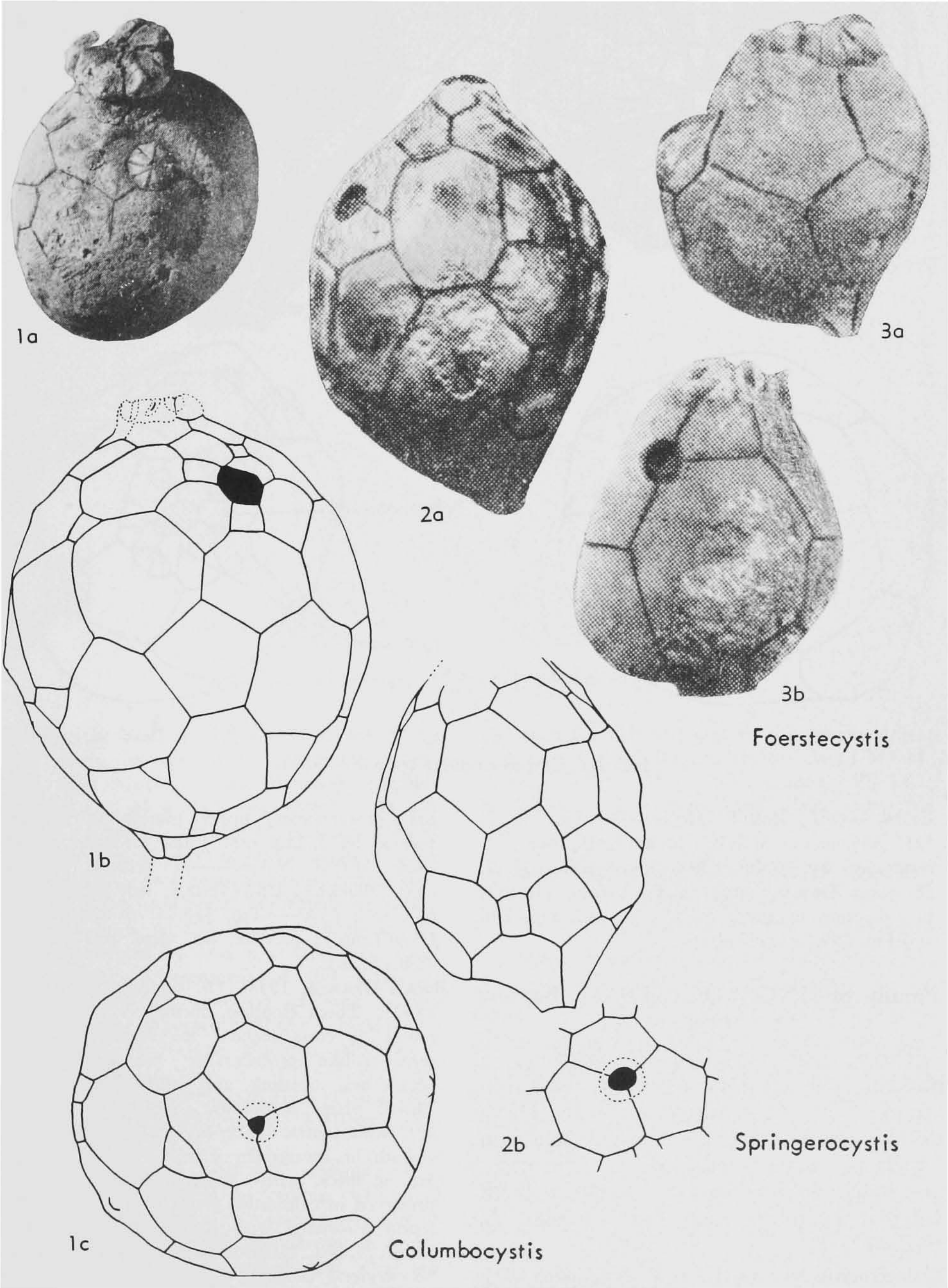

Fig. 315. Springerocystidae (p. *S*486-*S*487).

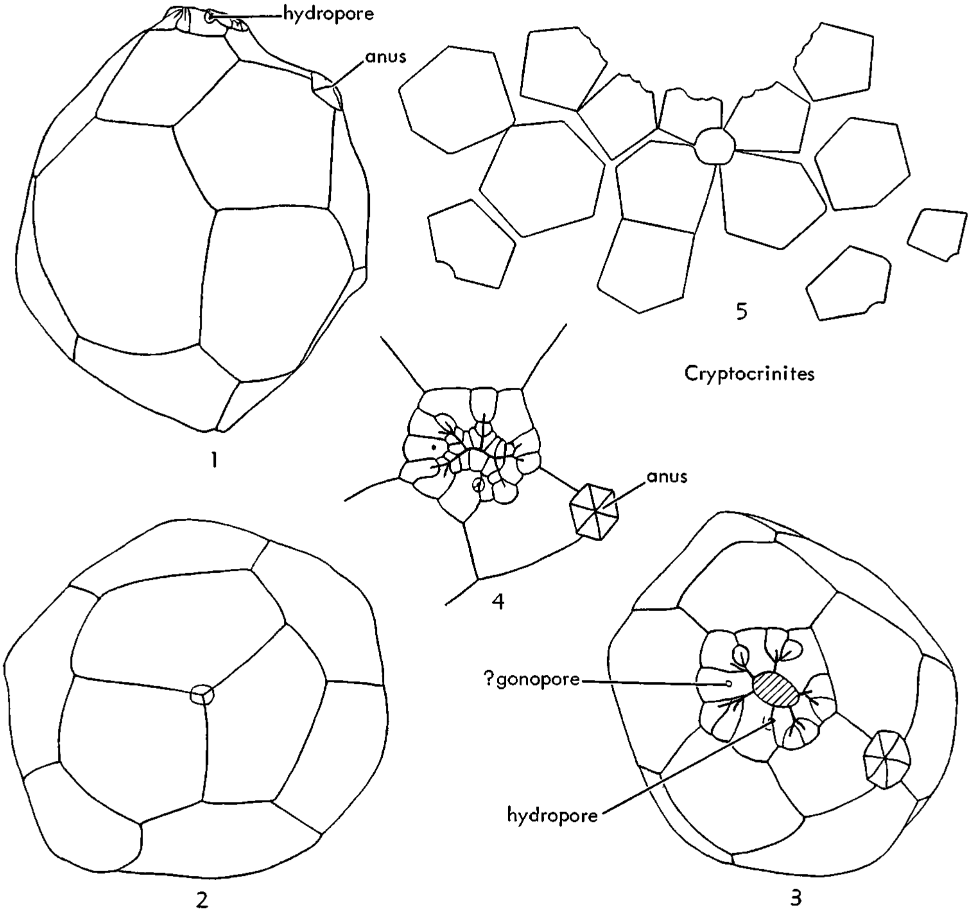

Fig. 316. Cryptocrinitidae (p. *S*487-*S*488).

L.Ord.-M.Ord., Boh.-Fr.-Morocco.——Fig. 312,*1*. **M. bohemicus*, M.Ord., Letná beds, Boh.; *1*, restoration by Jaekel *(23)*, ×4.——Fig. 312,*2*. *M. azaisi* Thoral, L.Ord.(U.Tremadoc), Hérault, Fr.; diagram of theca *(36)*. [See also Fig. 296 and Fig. 299,*1* (oral face).]

Family SPRINGEROCYSTIDAE Bassler, 1950

Thecal plates polygonal, indefinite in number and irregular in shape, size, and arrangement. Basals three, unequal. Theca distally elevated into short protuberance on which are located peristome, food grooves, and brachiole insertions. Anus lateral, with valvular pyramid. Stem facet circular. *L. Ord.-M.Ord.*

Springerocystis Bassler, 1950 [**S. longicollis*; OD]. Theca ovoid or pyriform, proximally produced into short point, distally elevated into tubelike, oral protuberance, upper margin of which is formed by 5 thin oral plates arranged in small circlet. *M.Ord.*, N.Am.——Fig. 315,*2a*. **S. longicollis*, Blackriv., USA(Tenn.); side view of holotype, ×2 *(3)*.——Fig. 315,*2b*. *S.* sp., Blackriv., USA(Tenn.); part of lat. view and base, ×3 (Ubaghs, n).

Bockia Gekker, 1938 [**B. neglecta*; SD Gekker, 1940]. Theca elongate, cucumber- or sac-shaped, round in cross section, terminating distally in proboscis-like protuberance, which must have borne oral opening and ambulacral structures. Thecal plates numerous, generally slightly convex, with central umbo and radiating flat ridges, smooth or covered by granules. Anus on upper 3rd of theca, with valvular pyramid. Stem not preserved in connection with theca; discoidal roots found associated with genus may belong to it. *L.Ord.-M.Ord.*, USSR-?Sweden.——Fig. 314,*1-4*. **B. neglecta*, M.Ord., E. Baltic region; *1*, reconstruction, ×1; *2*, distal part of theca, ×1.5; *3*, periproctal area, ×3; *4*, aboral face, ×1.5 *(18)*.

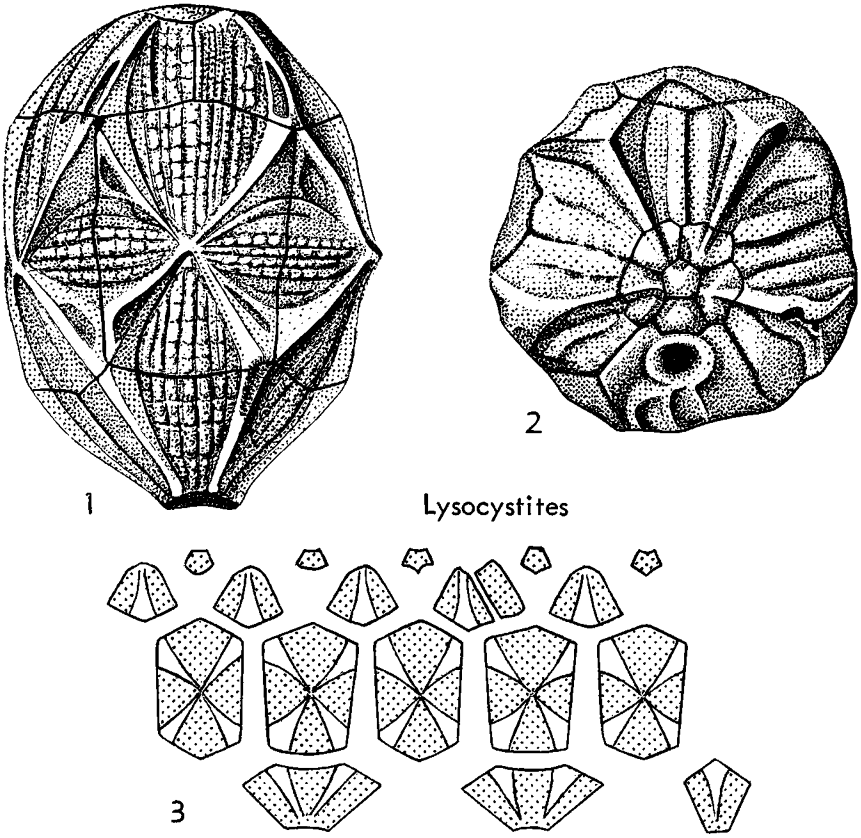

FIG. 317. Cryptocrinitidae (p. S488-S489).

?**Columbocystis** BASSLER, 1950 [**C. typica*; OD]. Theca ovoid or subglobose, somewhat asymmetric, with conspicuous oral flattened protuberance composed of 6 thick oral plates (2 in *CD* interray) centering about small peristome. Food grooves on apposed edges of orals. Brachiole facets very large, on outer edge of protuberance, each carried by 2 adjoined orals. Hydropore on suture between 2 orals of *CD* interray. Anus in *BC* interray, protected by anal pyramid. Stem facet small, circular. [Assignment of this genus to Eocrinoidea will be uncertain as long as the "arms" remain unknown.] *M.Ord.*, N.Am.——FIG. 315,*1a*. **C. typica,* Blackriv., USA(Va.); slightly oblique lat. view, ×2 *(3)*.——FIG. 315, *1b,c*. *C. sp.,* Blackriv., USA(Tenn.); side view (*CD* interray) and aboral face, ×2 (Ubaghs, n). [See also Fig. 298,*1*.]

?**Foerstecystis** BASSLER, 1950 [**F. obliqua*; OD]. Theca irregularly rotund in outline, with anal side very gibbous, especially toward lower end of theca, where it is angularly protuberant in nearly horizontal direction. Thecal plates few. Oral end supporting 5 relatively broad "arms" recumbent on top of theca. [This poorly known genus (no specimen available for study by the present writer) may turn out to belong to another class.] *M.Ord.*, N.Am.——FIG. 315,*3*. **F. obliqua,* Blackriv., USA(Tenn.); *3a,b,* abanal and adanal sides, ×4 *(3)*.

Family CRYPTOCRINITIDAE Bassler, 1938 (1895)

[=Cryptocrinidae ZITTEL, 1895 (invalid family-group name)]

Theca regularly composed of four circlets of plates and more or less completely affected by pentamerous symmetry. Thecal plates in definite number, shape, size, and arrangement; three in basal circlet, unequal, probably produced from five by fusion; five in second circlet; five or six (according to genus) in third circlet; five or six (according to genus) in fourth circlet, which occupies very restricted area around oral pole. No sutural pores. Peristome small. Anus lateral. Brachiole insertions tiny. Stem facet circular. *M.Ord.-Sil.*

Cryptocrinites VON BUCH, 1840 [**C. regularis*

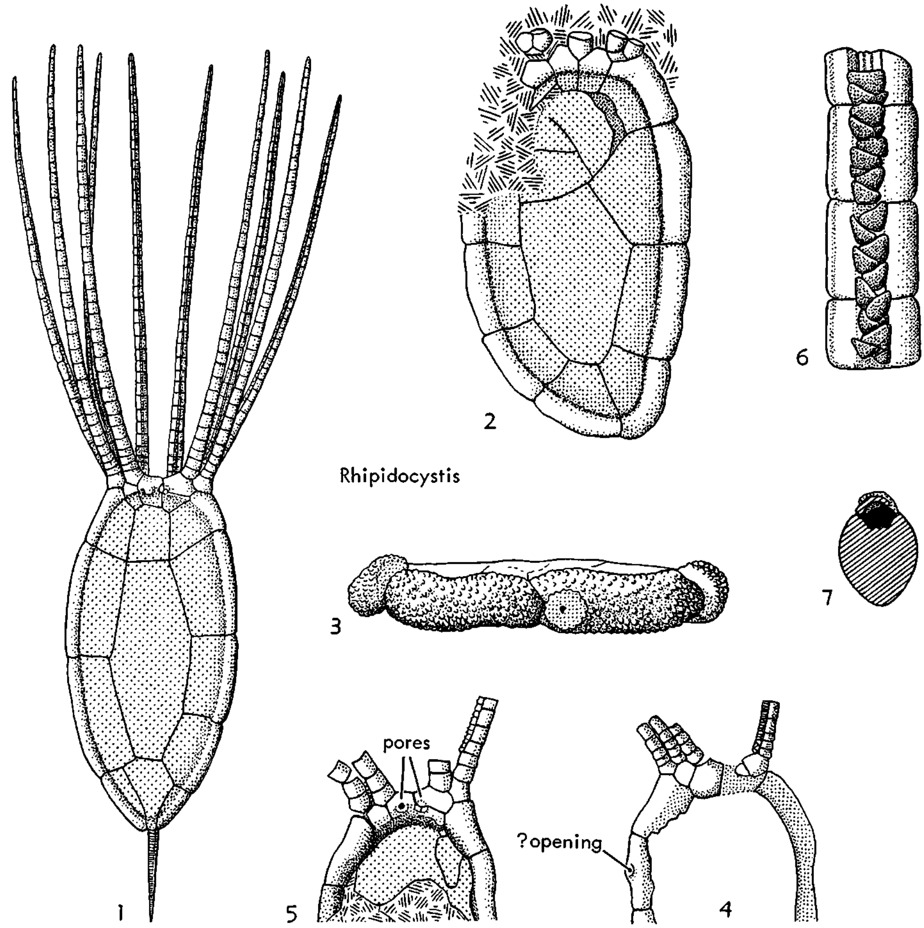

FIG. 318. Rhipidocystidae (p. S489).

(=*Echinosphaerites laevis Pander, 1830); SD von Buch, 1841] [=Cryptocrinus Geinitz, 1846 *(nom. van.)*]. Theca small, irregularly spheroidal. Plates of 2nd circlet large, unequal in size and shape; plates of 3rd circlet 5, smaller, subpentagonal, most of them alternating with plates of preceding circlet; large supplementary plate between 2nd and 3rd circlet; contiguous to periproct; 4th circlet irregularly pentagonal, composed of 6 small oral plates (2 in *CD* interray) surrounding peristome. Food grooves 5, epithecal, very short, on sutures between orals, bifurcating and leading to 10 minute paired brachiole-bearing platelets, which rest on apposed edges of orals. Peristome pentagonal, protected by double series of cover plates (rarely preserved). Periproct hexagonal, with valvular pyramid of 6 plates, located in *BC* interray between 2nd and 3rd circlets of plates. Hydropore on suture between paired orals in *CD* interray; another pore (gonopore?) piercing oral of DE interray. *M.Ord.*, USSR-Sweden.——FIG. 316,*1-5*. **C. laevis* (Pander), E.Baltic region; *1-3*, lat., aboral, and oral faces, ×4 (Ubaghs, n); *4*, peristome area, cover plates preserved, enl. *(42)*; *5*, diagram of theca, orals excluded (Ubaghs, n).

Lysocystites S. A. Miller, 1889 [*nom. subst. pro Echinocystites* Hall, 1864 (*non* Wyville Thomson, 1861)] [**Echinocystites nodosus* Hall, 1864; OD] [=*Aethocystites* S. A. Miller, 1892; *Echinocystis* Haeckel, 1896 *(nom. van.)*; *Lysocystis* Bather, 1897 *(nom. van.)*; *Scolocystis* Gregory, 1897 (*nom. subst. pro Echinocystites* Hall, 1864); *Aethocystis* Bather, 1900 *(nom. van.)*]. Theca subspheroidal or ovoid. Plates of 2nd circlet very large, elongate, hexagonal; plates of 3rd circlet 6, smaller, pentagonal or quadrate, converging adorally; 4th circlet of 5 very small subtriangular elements enclosing small central peristome, from which shallow and short food grooves extend outward. Anus located near apex of plates of 3rd circlet. Ornamentation consisting of tubular thin-

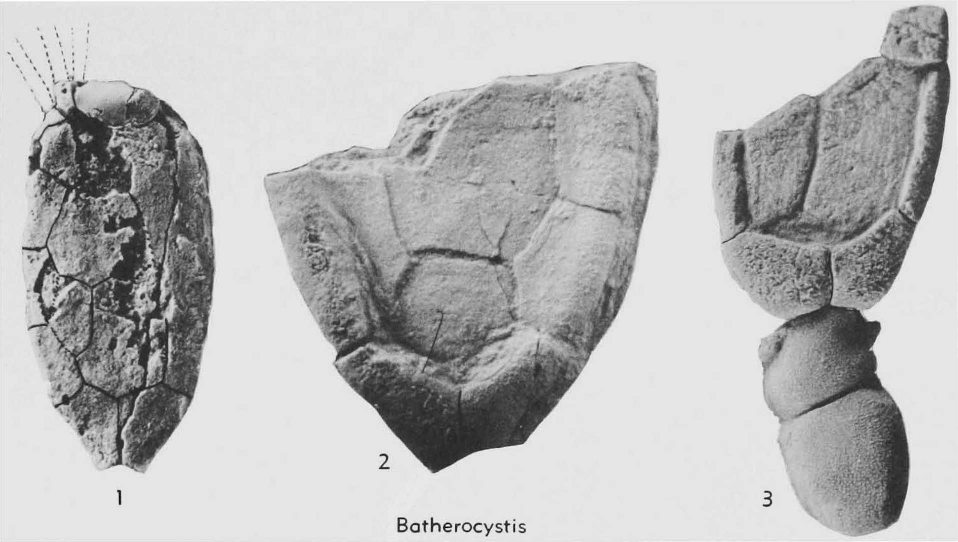

Fig. 319. Rhipidocystidae (p. S489-S490).

walled folds surrounding diamond-shaped striated areas. *Sil.*, N.Am.——Fig. 317,*1-3*. *L. sculptus* (S. A. Miller), Sil.(Niagaran), USA(Ind.); *1*, lat. face showing striation and tubular folds, latter broken in several places, ×1.7 *(33)*; *2*, oral face, ×2.25 *(33)*; *3*, diagram of theca *(15)*.

Family RHIPIDOCYSTIDAE Jaekel, 1901

[=Batherocystidae Bassler, 1950]

Theca elongate, strongly depressed, presenting two flat faces framed by limited number of marginals surrounding relatively large polygonal central plates. Marginals with thickened outer margins and participating more or less in pavement of flat faces. Brachioles on oral margin of both faces. Stem more or less reduced. *L.Ord.-M.Ord.*

Rhipidocystis Jaekel, 1900, p. 672 [**R. gigas*; SD Bather, 1913, p. 369]. Theca subelliptical in outline, with blunt oral and tapering aboral ends. Outer edge of marginals massive and raised, forming framework usually quite distinct from flat and relatively thin pavement of 2 main faces. Basal marginals 3, with proximal ends thickened. Central plates large and few. One or 2 tiny apertures (hydropore?) on adoral marginals and single supplementary one or pit in some on one of lateral marginals. Brachioles long, uniserial, unbranched, inserted in 2 series between or upon adoral marginals. Brachiole ossicles long and massive, with alternating cover plates. Stem facet small, circular, borne by generally single and rarely 2 basal marginals. Stem apparently reduced. Axial canal round and narrow. [*Rhipidocystis*, as originally conceived by Jaekel *(24)*, comprised remains of four genera, belonging to three different classes. It was demonstrated by Gekker *(17, 18)* that the "cup-plates" of this "genus" partially belong to the ophiocistioid *Volchovia* and partially to the eocrinoid *Bockia*; the "stem-plates" belong to *Dendrocystites kuckersiana* (now *Heckericystis kuckersiana*), of the Homoiostelea; the flat "appendages of the stem" refer to the genus for which Gekker retained the name *Rhipidocystis*; the "saclike roots" are the thecae of the eocrinoid *Bockia*. *Rhipidocystis* as emended by Gekker was regarded by him as a "carpoid," for which he proposed the new order Digitata. Later, Ubaghs *(38)* placed it among the eocrinoids.] *L.Ord.-M.Ord.*, USSR.——Fig. 318,*1-3*. *R. baltica* Jaekel, L.Ord., Leningrad area; *1*, "upper" face (reconstr.), ×0.7; *2*, theca, "lower" face, ×2; *3*, proximal end of theca and stem facet, ×5 *(24)*.——Fig. 318,*4*. *R. öpiki* Gekker, M.Ord., Estonia; distal part of theca, "lower" face, with (?) opening in one marginal *(17)*.——Fig. 318,*5-7*, *R. sp.* Gekker, M.Ord., Estonia; *5*, distal part of theca, "upper" face, with pores on adoral margin, ×2; *6, 7*, oral face of a few brachiolars and cross section, ×10 *(18)*.

Batherocystis Bassler, 1950 [**B. appressa*; OD]. Theca oblong. Basal marginals 2, with common sutures along middle of flat faces. Central plates more numerous than in *Rhipidocystis*, but probably no more than 7 to 10. Anal? opening relatively large, located slightly below distal end of lateral margins, and surrounded by 3 marginals. Prominent pit on one plate of adoral margin. Brachioles unknown, probably inserted on or between adoral marginals. Stem facet elliptical, relatively large, borne by both basal marginals; columnals apparently very few, inflated, ovoid or somewhat irregularly shaped, elliptical in cross section, abnormally large and massive. [I am greatly indebted to R. L. PARSLEY for information concerning this genus.] *M.Ord.*, N.Am.——FIG. 319,*1*. **B. appressa*, Chazyan, USA(Tenn.); holotype ×2 (Parsley, n).——FIG. 319,*2*. *B. sp.*, USA (Ky.); proximal portion of theca, *ca.* ×3 (Ubaghs, n).——FIG. 319,*3*. *B. sp.*, Blackriv., USA (Va.); proximal portion of theca and 2 columnals, ×4 (Parsley, n).

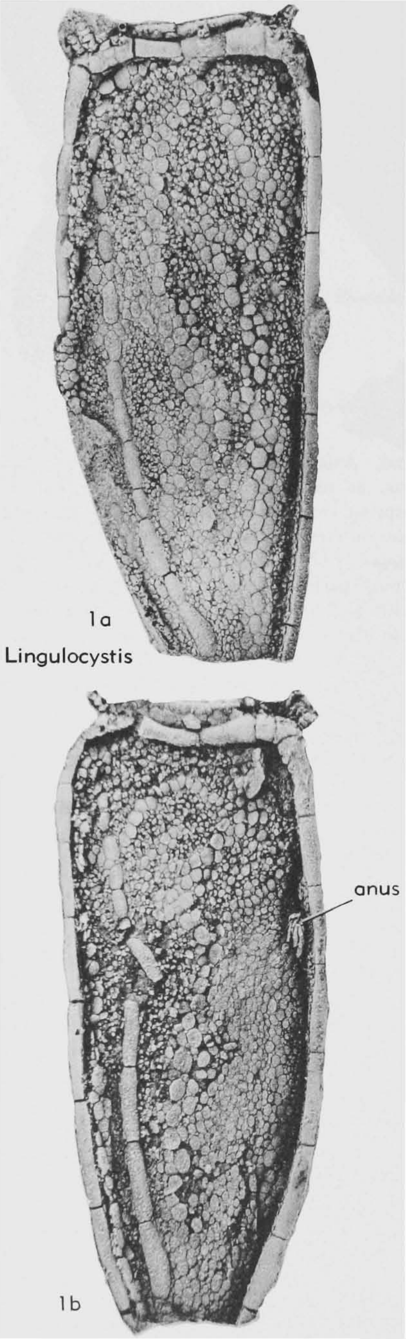

FIG. 320. Lingulocystidae (p. S490-S491).

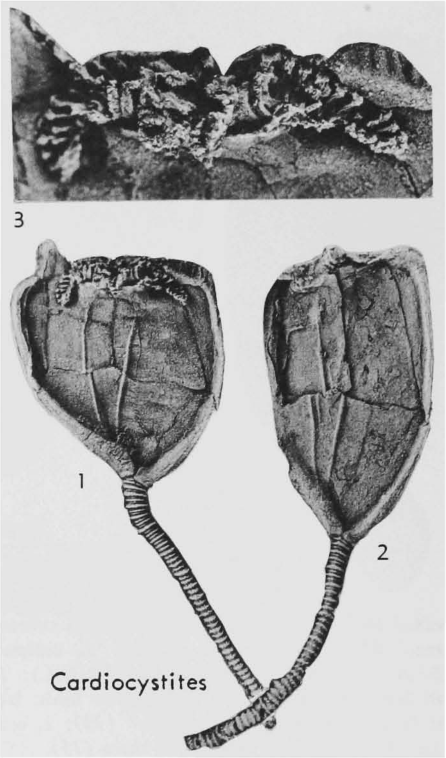

FIG. 321. Unclassified genera (*Cardiocystites*) (p. S491-S492).

Family LINGULOCYSTIDAE Ubaghs, 1960

Theca elongate, depressed, clearly divided into elongate aboral part and low convex oral surface. Marginals numerous, not participating in pavement of flattened faces, which are covered by finely plated integuments. Basals four, equal. Anus lateral. Brachioles carried on special plates inserted in marginal framework at both ends of oral face and in some specimens on ordinary oral marginals. Stem long, round, distally tapering. *L.Ord.*

Lingulocystis THORAL, 1935 [**L. elongata*; OD]. Theca paddle-shaped, probably elliptical in cross section during life. Marginals numerous, elongate, thick and narrow, surrounding both aboral part

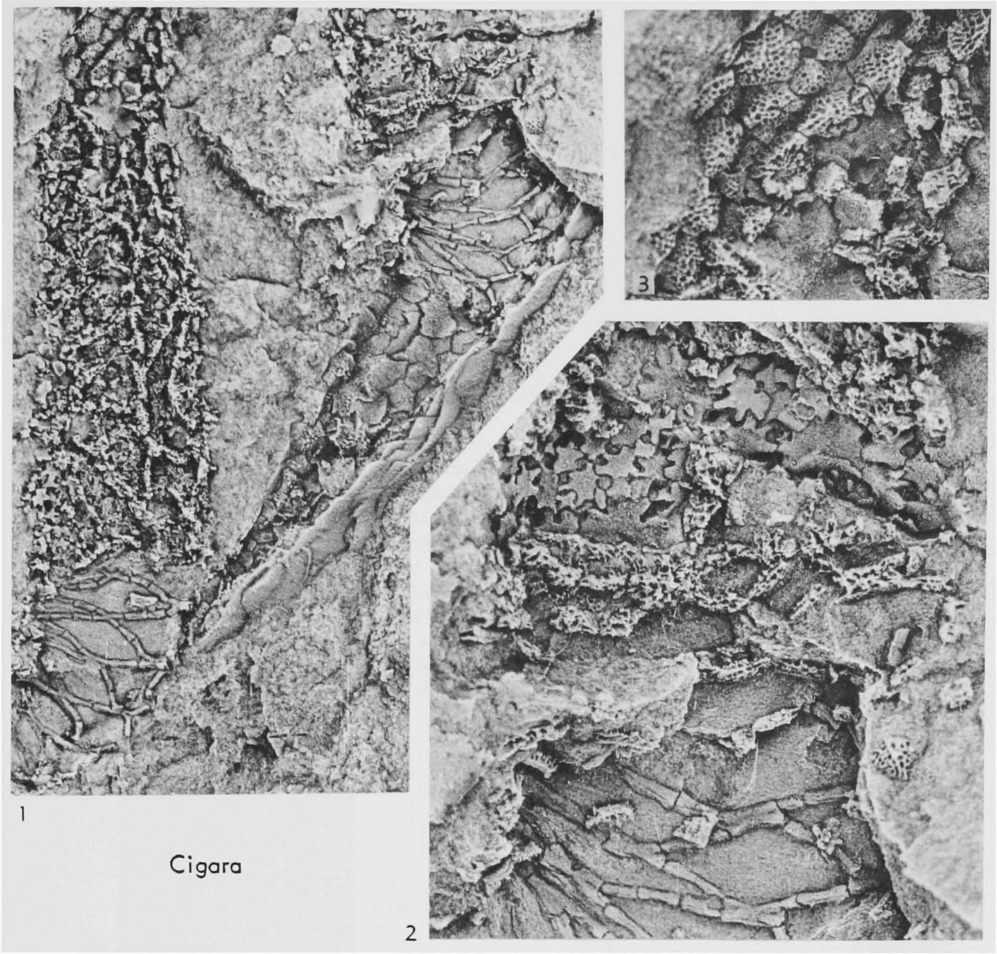

FIG. 322. Unclassified genera *(Cigara)* (p. *S*492-*S*493).

and oral surface. Flattened faces apparently pliant, each unequally divided by longitudinal series of relatively large, elongate, slightly convex plates. Anus protected by pyramid of numerous needlelike platelets, located at distal 3rd of theca, near margin. Oral face covered by small plates, with probably subcentral peristome and 2 food grooves leading to clusters of brachioles located at both ends; peristome and food grooves concealed under raised cover plates. *L.Ord.,* France.——FIG. 320, *1.* **L. elongata,* U.Tremadoc-M.Arenig., Hérault; *1a,b,* lectotype, ×3 *(37).* [See also FIG. 297; 299,*3*.]

UNCLASSIFIED GENERA

?**Archaeocystites** BARRANDE, 1887 [=*Archaeocystis* HAECKEL, 1896 *(nom. van.)*].

Cardiocystites BARRANDE, 1887 [**C. bohemicus;* OD] [=*Cardiocystis* BATHER, 1900 *(nom. van.)*]. Theca depressed, moderately elongate, with tapering proximal end and convex lateral margins; distal margin abruptly narrowing and provided on one side with distinct rounded protuberance. Margins strongly thickened and bearing longitudinal groove on large portion of their external face. Theca (only one side known) composed apparently of 2 transverse rows of plates, proximal row of 2 basal marginals and distal row of 2 marginals and probably 2 centrals; admedian parts of marginals and centrals thin. Starting from near proximal end of one of thickened margin, 2 narrow diverging ridges forming V-shaped figure open in distal direction. "Arms" at least 3, apparently short and possibly recumbent, biserial, with sutural faces of successive brachials deeply excavated. Stem long, cylindrical, tapering distally; proximal columnals of unequal height, arranged in more or less regular alternation, each provided with distinct flange; distal columnals higher, all of nearly same size, barrel-shaped and spinose. *M.Ord.,*

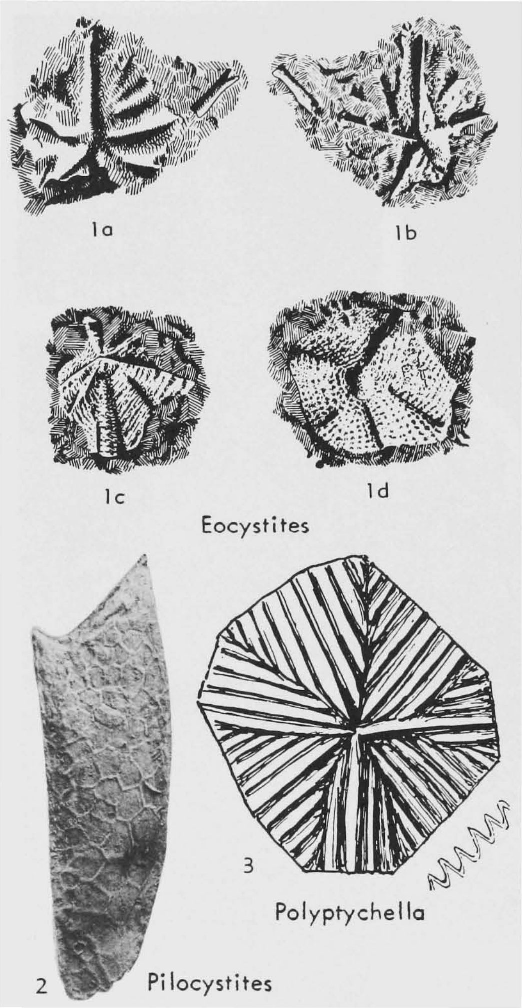

Fig. 323. Unclassified genera *(Eocystites, Pilocystites, Polyptychella)* (p. S492-S493).

Boh.——Fig. 321,_1-3. *C. bohemicus; 1,2,_ specimens figured by Barrande, 1887 (pl. 31, fig. 10-12), ×2; *3,* "arms" of specimen *1,* ×3 (Ubaghs, n).

Cigara Barrande, 1887 [_*C. dusli_; OD]. Body elongate, composed of 3 regions; 1st or proximal region conical, strongly tapering, covered by thin, polygonal, irregular, and apparently imbricating plates, with delicate radiate ornamentation; middle region characterized by lattice-work of rodlike and X-shaped, exteriorly coarsely ornamented ossicles that enclose diamond shaped, apparently uncalcified or poorly calcified areas; 3rd or distal region slightly tapering distally, composed of numerous, small, stellate plates joining by their ray ends; some plates of distal region distinguished from others by their strongly convex and coarsely pitted outer surface, linked together in such manner as to form irregular, more or less continuous meshwork of ridges, which probably prolong lattice-work of middle region; numerous sutural pores present between all plates of distal region, except most distal ones, which are larger, more convex, and more closely set than others and disposed in oblique, perhaps helicoidal, series. [This enigmatic fossil is represented only by two incomplete specimens on a small slab of shale. Bather *(5)* thought that it resembles the stem of *Dendrocystites,* in which genus it was placed by Bassler

Fig. 324. Unclassified genera *(Pareocrinus)* (p. S493).

(2) and by BASSLER & MOODEY *(4)* as a synonym. JAEKEL *(23, 25)* interpreted the proximal region as a stem passing into a saclike hollow root (distal region) and possibly belonging to *Acanthocystites*. These interpretations are unacceptable. The main region (as indicated by the nature of its plates) probably represents a theca prolonged downward by a many-plated extension; such a theca is structurally distinct from that of *Acanthocystites*. No connection with this genus or Homoiostelea are suggested.] *M.Cam.*, Boh.——FIG. 322,*1-3*. **C. dusli,* Jince beds; *1,* specimens figured by BARRANDE (1887, pl. 2. fig. 34), ×2; 2, middle region and proximal part of distal region, showing lattice-work and platelets in outer and inner aspects, ×5; *3,* distal part of distal region, ×5 (Ubaghs, n).

Eocystites BILLINGS, 1868 [**E. primaevus*; OD] [=*Eocystis* BATHER, 1900 *(nom. van.)*]. Genus founded on isolated stellate, probably thecal, plates, having central umbo and variable number of folds which radiate like wheel spokes, most prominent folds reaching umbo and directed toward plate angles. [Discovery of similar plates has been reported from the Middle Cambrian of France, Spain, Morocco, and elsewhere but their assignment to *Eocystites* is uncertain.] *M.Cam.*, N.Am. ——FIG. 323,*1*. **E. primaevus*; *1a,c,* internal, and *1b,d,* external imprints of plates, ×4 *(6)*.

Lapillocystites BARRANDE, 1887 [**L. fragilis;* OD] [=*Lapillocystis* BATHER, 1889 *(nom. van.)*]. Body ovoid in outline, composed of many small, irregular, polygonal plates; inadequately known. [According to JAEKEL (23), this fossil comprises the hollow root of an eocrinoid, possibly *Acanthocystites*.] *M.Cam.*, Boh.

Pareocrinus YAKOVLEV, 1956 [**P. ljubzovi*; OD]. Theca small, proximally conical, medially cylindrical, distally truncated by flat oral surface. Cylindrical part composed of 5 or 6 vertical alternating columns of very thin plates, each centrally elevated into conical protuberance. Small circular opening (anus?, hydropore?) at top of one vertical column. Brachioles about 10, slightly longer than theca, attached to elevated processes on margin of oral face. Stem cylindrical, narrow, distally tapering. *M.Cam.* or *U.Cam.*, USSR(Sib.).——FIG. 324,*1*. **P. ljubzovi,* up. M. Cam. or low. U. Cam., E.Sib.; holotype, ×3 *(46)*.

Pilocystites BARRANDE, 1887 [**P. primitivus*; OD]. Body elongate, rounded at one end, obliquely truncated at other, divided into polygonal areas by slightly raised limits. [This genus, generally assigned to cystoids, was regarded by JAEKEL *(23)* as a doubtful root fragment of a cladocrinoid but probably it is not even an echinoderm.] *M.Cam.*, Boh.——FIG. 323,*2*. **P. primitivus*; holotype, ×1 (Ubaghs, n).

Polyptychella JAEKEL, 1918 [**P. esthona*; OD]. Genus based on isolated polygonal plates characterized by many radial folds set at right angles to plate sutures. [Placed by JAEKEL *(25)* among Macrocystellidae.] *M.Ord.*, Est.——FIG. 323,*3*. **P. esthona,* Brandschiefer; holotype, enlarged *(25)*.

?**Protocystites** HICKS, 1872 [*non* SALTER, 1865 *(nom. nud.)*; =*Protocystis* BATHER, 1900 *(nom. van.)*, *non* WALLICH, 1862].

?**Trachelocrinus** ULRICH, 1929.

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HOMALOZOANS

By Georges Ubaghs and K. E. Caster

Included in this assemblage are the "carpoid" classes Stylophora, Homostelea, and Homoiostelea, all of which are represented in Cambrian strata but none in post-Devonian deposits.

STYLOPHORA

By Georges Ubaghs

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CONTENTS

INTRODUCTION

The class Stylophora corresponds to the superorder Stylophora (class Carpoidea) proposed by GILL & CASTER (1960, *43*) and embraces the orders Mitrata and Cornuta of JAEKEL (1918,*55*). Forms belonging to these two orders possess the same basic organization, which differs profoundly from that of both Homostelea and Homoiostelea.

Like other "carpoid" echinoderms, stylophorans are asymmetrical flattened organisms which lack any trace of radial symmetry. Their body is composed of a **theca** made of plates, attached to which is a highly characteristic jointed appendage known as the **aulacophore,** here interpreted as a brachial process. Until recently, it was considered erroneously to be homologous to the stele (peduncle) of other "carpoids" *(88).* The mouth, probably intrathecal, was located at the base of the aulacophore and the anus at or near the opposite extremity of the theca. The placement of these orifices at opposite poles of the theca, combined with presence of an aulacophore, absence of a stele or other sort of peduncular process, and lack of marginal external grooves clearly distinguish the Stylophora from the Homostelea. Stylophorans differ from the Homoiostelea in lacking a stele and in having a brachial process (aulacophore) differentiated into three distinct regions, instead of an arm with the same composition throughout.

In contrast to other "carpoids" so far known, the Stylophora comprise a great diversity of forms. These range from the very peculiar, quite asymmetrical *Cothurnocystis* to genera like *Placocystites* with nearly developed bilateral symmetry. In the Old World stylophorans are known from Middle Cambrian to Middle Devonian, and in the New World from Upper Cambrian to Lower Devonian.

MORPHOLOGY AND FUNCTION

GENERAL CHARACTERS

The skeleton of Stylophora is composed of two parts—a theca that incloses the body, and a unique brachial process termed the aulacophore (Fig. 325). No stele or peduncle is observed. As in other "carpoids," organization of the theca is fundamentally asymmetrical, but several groups, especially within the Mitrata, exhibit a tendency to acquire bilateral symmetry. This is never perfect, however, and must be considered as secondary, since it appears late in the history of the groups.

A stylophoran theca lying flat on a horizontal surface invariably slants downward away from the aulacophore. In the Mitrata

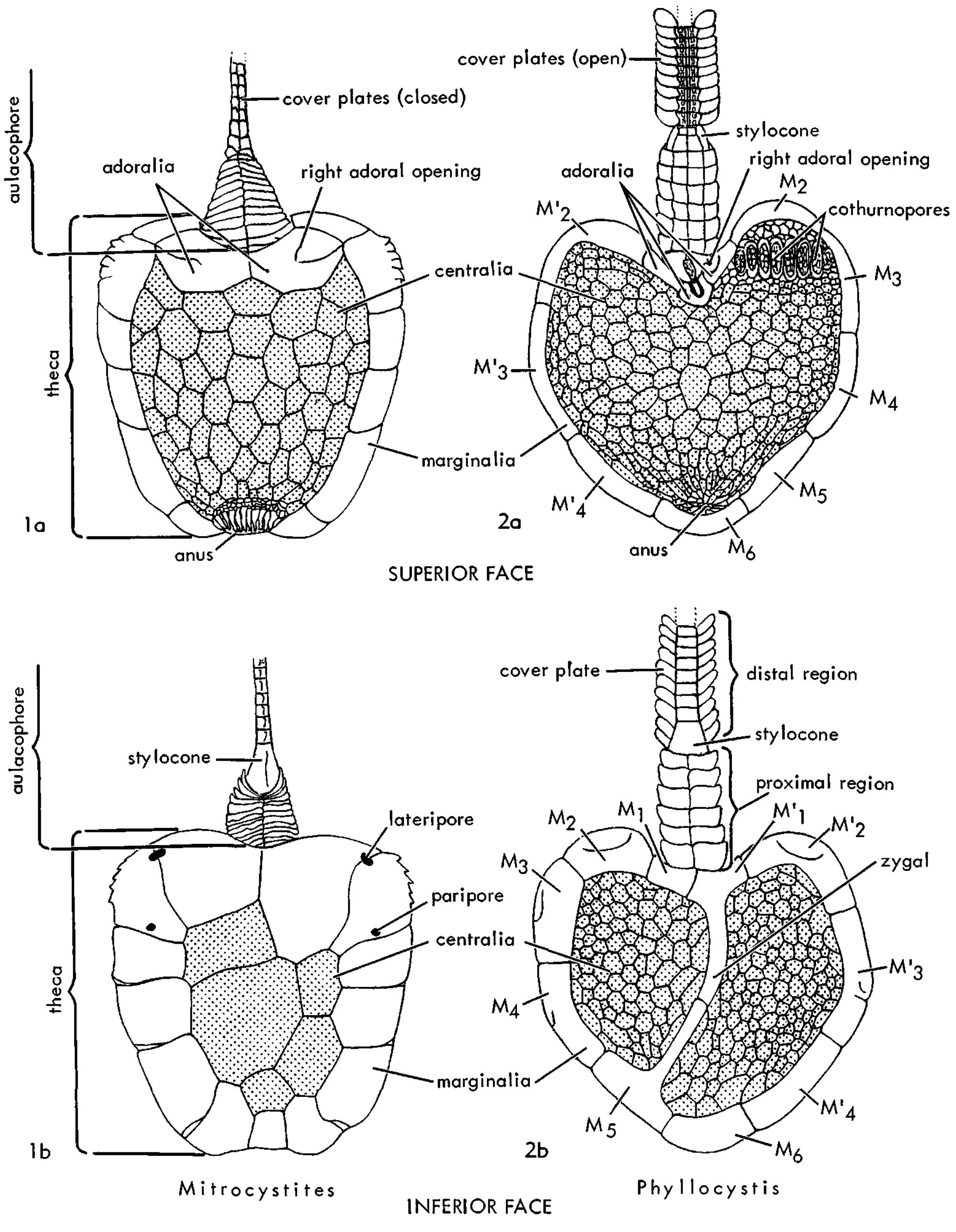

FIG. 325. General features of Stylophora.——*1. Mitrocystites mitra* BARRANDE, M.Ord., Boh; *1a,b,* superior and inferior faces, ×2.2 (Ubaghs, n).——*2. Phyllocystis blayaci* THORAL, L.Ord., Fr.; *2a,b,* superior and inferior faces, ×1.5 (Ubaghs, n) (M_1-M_6, right marginalia; M'_1-M'_4, left marginalia; centralia stippled).

the theca generally is oval or subrectangular in outline (Fig. 325,*1*); it is somewhat elongate and more or less symmetrical. As a rule, at least one of the faces is covered by large plates. In the Cornuta the theca ordinarily is much more asymmetrical and less regular in shape (Fig. 325,*2*), for instance, with outline resembling that of a pointed boot (e.g., *Cothurnocystis*) or a playing-card heart (e.g., *Phyllocystis*). It may be

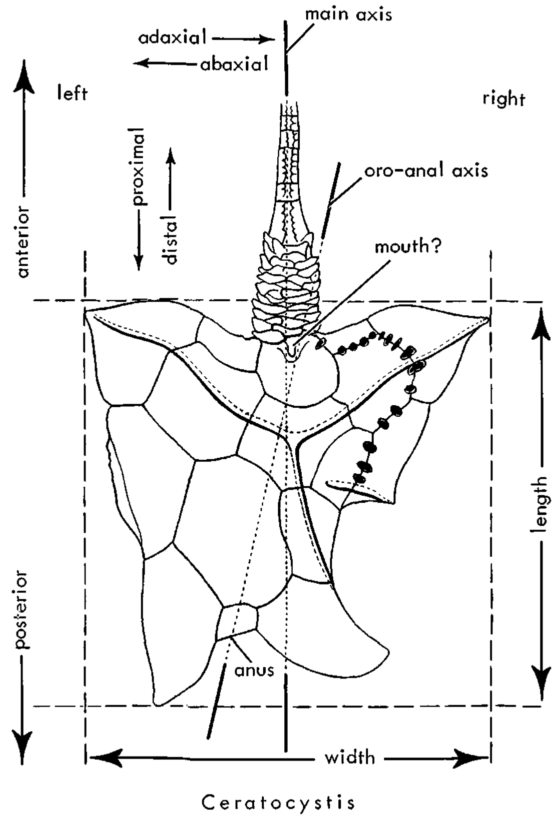

FIG. 326. Orientation of Stylophora. *Ceratocystis perneri* JAEKEL, M.Cam., Boh.; superior face, ×1.8 (Ubaghs, n).

entirely composed of large plates, but more commonly a framework of marginal pieces is sharply set off from sheets of pavement platelets which occupy the two faces. In both groups articulated or fixed appendages may extend outward from the framework, adding to the strange appearance of these creatures.

The two faces of the depressed theca differ in form and composition. The lower one **(inferior face)**, upon which the animal presumably reposed in life, is flat or concave, and the upper one **(superior face)** is convex. The border of the theca consists of a framework of marginal pieces **(marginalia)** which surround a variably large number of plates or platelets **(centralia)** on faces of the theca, those of the lower face being called **infracentrals (infracentralia)** and those of the upper face **supracentrals (supracentralia)**[1] (Fig. 325).

The insertion of the aulacophore is surrounded typically by four or five plates—two marginal plates below and two or three adorals **(adoralia)** above (Fig. 325,*1a,2a*). Some authors have designated these plates erroneously as basals. The adorals form part of the border framework of the theca in Cornuta and generally do not participate appreciably in the covering pavement of the upper face. In the Mitrata, on the other hand, the adorals always occupy part of the upper face and in a few genera (e.g., *Balanocystites*) all of it. According to my interpretation, the two main apertures (mouth, anus) of the body were situated respectively at or near the base of the aulacophore and at the opposite extremity of the theca or in its immediate vicinity. The mouth cannot be observed, however; it is

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[1] JAEKEL (55) termed these plates hypocentrals and epicentrals, which are hybrid Greek-Latin designations; here all-Latin names are substituted.

judged to have been intrathecal, as in the Homoiostelea.

An orifice called the **right adoral opening,** presumed to be a hydropore (possibly combined with gonopore), is seen in some genera, notching or piercing one of the adoralia (Fig. 325,*1a,2a*). The role of other orifices (e.g., lateripores, paripores, cothurnopores, Fig. 325,*1b,2a*) remains conjectural.

The aulacophore of stylophorans invariably is divisible into three distinct parts (Fig. 325,*2b*). Next to the theca is an inflated hollow **proximal region,** the cavity of which communicates with that of the theca. An intermediate solid piece is termed the **stylocone.** A **distal region** consists of a single series of ossicles placed end to end. The upper face of the stylocone and distal ossicles bears a groove which is interpreted here as an **ambulacral furrow.** It is protected by a double series of **cover plates** which may open and close (Fig. 325,*1a,2a*).

ORIENTATION AND TERMINOLOGY

The major plane of the depressed stylophoran theca has been called the **extension plane** by Bather (1913,*13*) and the **extensiplane** by Gill & Caster (1960,*43*). The two faces of the theca, as previously noted, are the upper or superior (=obverse of Bather, 1913,*13*) and lower or inferior (=reverse of Bather, 1913,*13*); this terminology is based on the inferred natural position of the living animals. In the Mitrata Caster (1925,*25*) has employed carapace for the upper surface of the theca and plastron for the lower one, terms which are very descriptive for this group but ill-suited for application to the Cornuta. Designations such as ventral, dorsal, oral, and aboral have been employed diversely by authors in referring to the two faces of the depressed theca, but use of them is inadvisable because of uncertainty of the implied morphological interpretation. The upper and lower sides of the aulacophore, however, could be differentiated appropriately in this way.

The aulacophore, with the mouth probably located near its base, marks the **anterior extremity** of the body, and opposite to it the margin of the theca adjacent to the anus marks the **posterior extremity** (Fig. 326). By placing the skeleton on its inferior face with the aulacophore directed away from an observer (upward on figures), one can make the conventional distinction between right and left sides.

The aulacophore is bilaterally symmetrical, and the intersection of its plane of symmetry with the extension plane of the theca defines the **main axis** of the body (Fig. 326). The plane through this axis perpendicular to the extension plane is here called the **median plane,** instead of symmetry plane (Bather, 1913,*13*), inasmuch as the never perfectly symmetrical theca is generally very asymmetrical with reference to this plane. The straight line from the aulacophore insertion center, marking the presumed location of the mouth, to the anus defines the **oro-anal axis.** In the mitrates this line approximates or may coincide with the main axis, whereas in the cornutes the two axes generally are quite distinct (Fig. 326). The terms proximal and distal are not useful in describing parts of the theca but may be employed for parts of appendages, then respectively denoting directions toward and away from the insertion. Directions toward and away from the main axis are termed **adaxial** and **abaxial** (Fig. 326).

Length of the aulacophore is measured along the main axis and width perpendicular to this axis in the extension plane; height (or thickness) is determined by measurements perpendicular to the other two lines. Length of the theca is defined as the distance between two lines normal to the median plane and respectively tangent to the most anterior and posterior points (Fig. 326). Width of the theca is the distance between two lines parallel to the median axis and respectively tangent to the right and left sides. Height (or thickness) of the theca is the distance between two planes parallel to the extension plane and respectively tangent to the lower and upper faces.

Individual plates of the marginal framework are distinguished by a conventional system of symbols (Fig. 325,*2a,b*). Marginals on the right side of the oro-anal axis, viewing the superior face of the theca, are indicated from front to back by the symbols M_1, M_2, M_3, etc., and those on the left side similarly by M'_1, M'_2, M'_3, etc. The

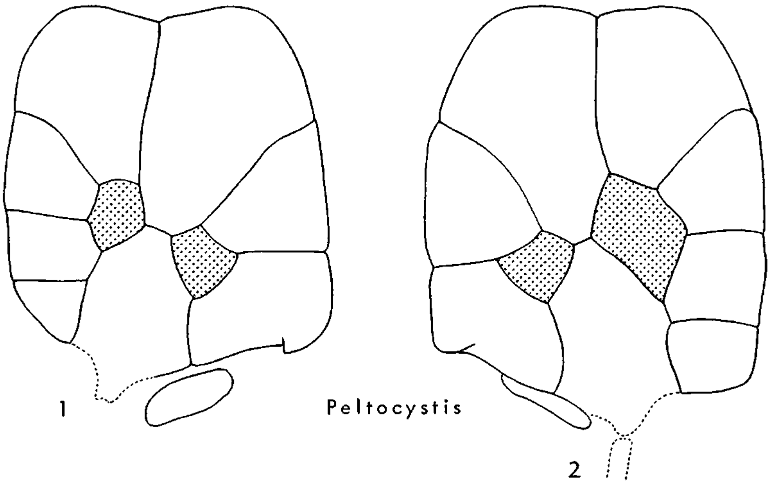

FIG. 327. Reversed asymmetry. *Peltocystis cornuta* THORAL, L.Ord., Fr.; *1,2,* inferior face, of normal and abnormal specimens, ×4.1 (Ubaghs, n).

posterior marginal traversed by the oro-anal axis is arbitrarily attributed to the right-hand series. This method of notation was introduced by JAEKEL (1918,*55*) but here is modified by accepting as anterior what that author considered to be posterior and vice versa.

A few other symbols have been found useful, especially for designations of plates shown in figures. Thus, among centralia, *A* identifies the "anomalocystid plate" and *P* the "placocystid plate; the right, median, and left adoralia are respectively marked by *r.ad., m.ad.,* and *l.ad.* Infracentrals (=hypocentrals of JAEKEL) of the Mitrata are individually designated by H_1, H_2, H_3, etc., according to a plan introduced by CHAUVEL (1941,*30*). These notations are preferred rather than more elaborate systems such as have been proposed for the Mitrocystitida by GISLÉN (1930,*45*) and for the Anomalocystitida by CASTER (1952,*25*).

ASYMMETRY

All stylophorans are asymmetrical, though varying in degree. Their asymmetry, more evident in the Cornuta than in the Mitrata, is manifested by (1) outlines of the theca, except in some Anomalocystitida, (2) distribution, form, and dimensions of thecal plates, especially those of the inferior face, (3) almost invariable divergence of the oro-anal axis from the main axis, even though this may be slight, and (4) the presence and location of numerous structures such as the zygal and accessory orifices of the Cornuta, the septum of the Mitrata, and the infundibulum and right adoral orifice of both Cornuta and Mitrata, all of which are placed laterally from the median plane without symmetrical counterparts on the other side of this plane.

The prevalence and diversity of these characteristics indicate that asymmetry is a fundamental attribute of the Stylophora. It is true that the asymmetry often has been considered to be secondary and derived from a perfect bilateral symmetry that is most completely expressed by the aulacophore, erroneously regarded as a stem. The validity of this interpretation is denied by factual observations and especially by the chronologic succession of genera and families. Not only has no fossil trace of a stage with perfect bilateral symmetry been discovered, but the oldest known representatives of the group (e.g., *Ceratocystis, Nevadaecystis, Chinianocarpos, Peltocystis*) are some of the most asymmetrical. Further, genera in which the theca is most nearly symmetrical (e.g., *Australocystis, Basslerocystis, Placocystites, Rhenocystis*) are confined to relatively high stratigraphic levels. They seem to be very specialized forms in which bilateral symmetry, though imperfect, almost surely is a secondary adaptation to some particular mode of life. The bilateral symmetry of the aulacophore probably has no more morphologic and phylogenetic significance than a single crinoid arm or starfish ray.

Finally, the occurrence of **inverted asymmetry** should be mentioned, although examples of it are rare (Fig. 327). Some abnormal individuals show all characters

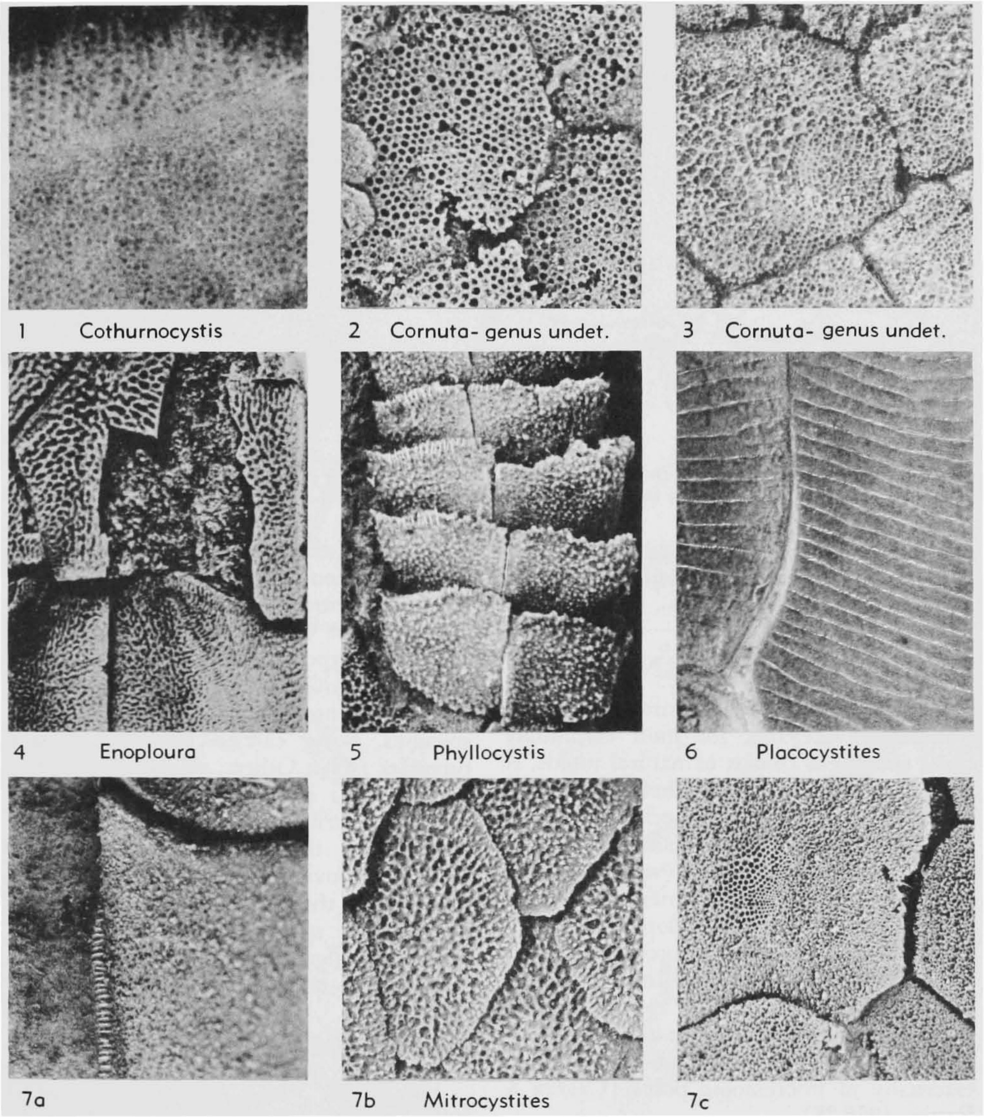

FIG. 328. Stereom and ornament among Stylophora.——*1. Cothurnocystis elizae* BATHER, U.Ord., Scot.; longitudinal section through a marginal, ×35 (Ubaghs, n).——*2.* Cornuta, genus and species indet., M.Ord., Boh.; external surface of supracentralia, ×15 (Ubaghs, n).——*3.* Cornuta, genus and species indet., L.Ord., Fr., ornamentation of supracentralia, ×15 (Ubaghs, n).——*4. Enoploura popei* CASTER, U.Ord., Ohio; ornamentation of part of lower face, ×8.3 (25).——*5. Phyllocystis* sp., L.Ord., Fr.; proximal region of aulacophore, inferior face, ×15 (Ubaghs, n).——*6. Placocystites forbesianus* DE KONINCK, Sil., Eng.; ornamentation of part of superior face, ×8 (Ubaghs, n).——*7. Mitrocystites mitra* BARRANDE, M.Ord., Boh.; *7a,* striated edge of a marginal, inferior face, ×14; *7b,* ornamentation of supracentralia, ×15 (Ubaghs, n); *7c,* special reticulated subcentral area on infracentral (holotype of *M. latus* JAEKEL, considered as syn. of *M. mitra*), ×12 (Ubaghs, n).

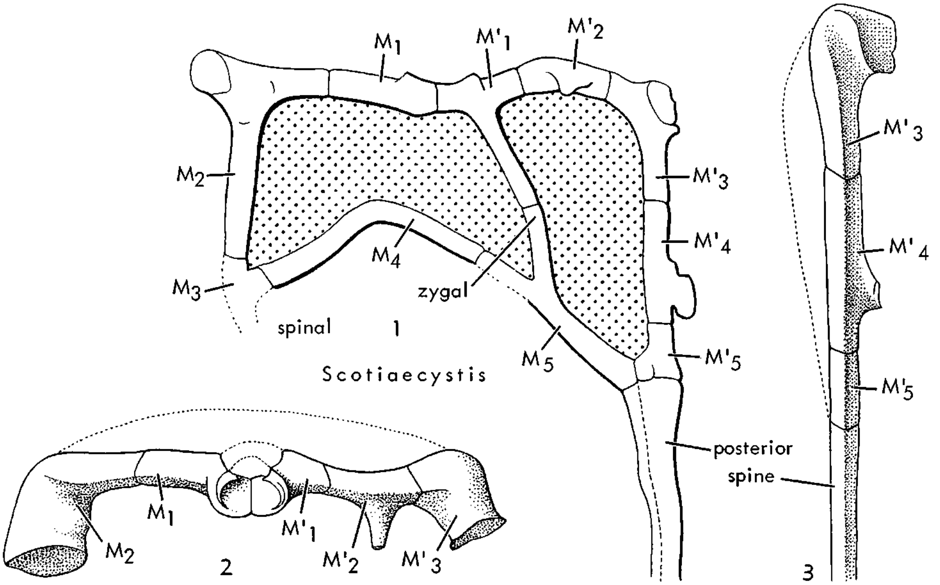

Fig. 329. Marginal frame of a cornute Stylophora.——*1-3, Scotiaecystis curvata* (Bather), U.Ord., Scot.; inferior, anterior, and right lateral faces, ×3 (*M_1-M_5*, right marginalia; *M'_1-M'_5*, left marginalia) (Ubaghs, n).

transposed to the opposite side of the median plane, as compared with normal individuals.

STEREOM AND ORNAMENT

Little is known as to histology of the stylophoran skeleton, for most commonly fossil specimens consist of natural molds. It is certain, however, that their hard parts were composed, as in other echinoderms, of calcareous stereom with included organic stroma. The characteristic reticulation of echinodermal skeletal elements often is clearly recognizable in stylophoran fossils (Fig. 328,*1,2*). The stroma occupied meshes of the calcareous network. In some specimens (e.g., *Paranacystis*) it appears to have filled a labyrinth of minute canals extending from one plate to another and opening externally in microscopic pores (Caster & Eaton, 1956,*28*).

Ornament of the stylophoran skeleton is varied (Fig. 328). A particularly characteristic pattern on the surface of thecal plates consists of equidistant fine wrinkles, sinuous and parallel, disposed transversely or obliquely to plate margins (Fig. 328,*6*). This type of ornament strikingly resembles the terrace lines of trilobites or markings on machaeridian plates (e.g., *Turrilepas*). It is commonly seen in genera of the Anomalocystitida, rarely in other Mitrata, and never in Cornuta.

Various types of spines have been observed in Stylophora, articulated with marginals or central plates. Some are inconspicuous, being carried probably by tiny tubercles (*89*). Others, of hairlike appearance, form a sort of brush along margins of an undescribed Lower Ordovician representative of the Scotiaecystidae. In new Lower Ordovician Cornuta, club-shaped spines cover the entire upper surface of the theca in one species and flattened elongate spines are aligned on the marginal framework of two others.

MARGINALIA

The plates which form the marginal framework of the theca are termed marginals (or **marginalia**) (Fig. 325). In all representatives of the Cornuta, save *Ceratocystis,* they are clearly distinct from plates of the pavements which cover the two thecal faces and they barely participate as skeletal elements of these faces (Fig. 325, *2a,b*). They are elongate, relatively narrow and thick pieces which typically are constant in number and position within a given species but may vary somewhat within a genus. Generally they are U-shaped in cross section and have a rounded lower external edge. Some genera (e.g., *Ceratocystis, Phyllocystis, Scotiaecystis, Bohemiaecystis*) have ten marginals; in *Cothurnocystis* their number is ten or 11 (exceptionally 12).

Certain marginals of the cornute Stylo-

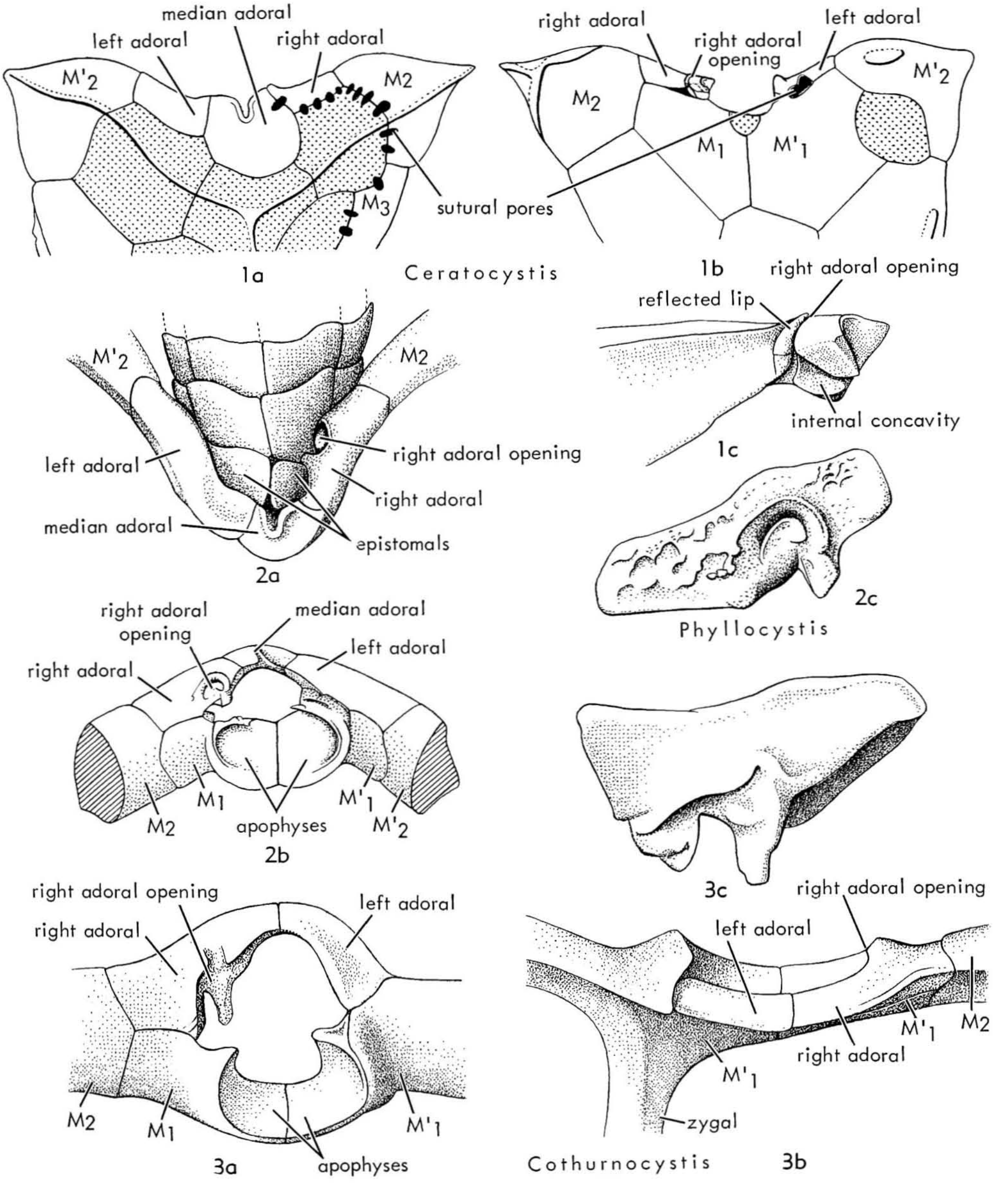

FIG. 330. Adoralia among cornute Stylophora.——*1. Ceratocystis perneri* JAEKEL, M.Cam., Boh.; *1a,b,* superior and inferior faces, ×2.2; *1c,* adaxial part of right adoral, inferior face, ×8.3 (Ubaghs, n).——*2. Phyllocystis crassimarginata* THORAL, L.Ord., Fr.; *2a,b,* superior and anterior faces, ×5; *2c,* right adoral, anterior face, ×12 (Ubaghs, n).——*3. Cothurnocystis elizae* BATHER, U.Ord., Scot.; *3a,b,* anterior and superior faces, ×5; *3c,* right adoral, anterior face, ×10 (Ubaghs, n). (M_1, M_2, . . . , right marginalia; M'_1, M'_2. . . , left marginalia).

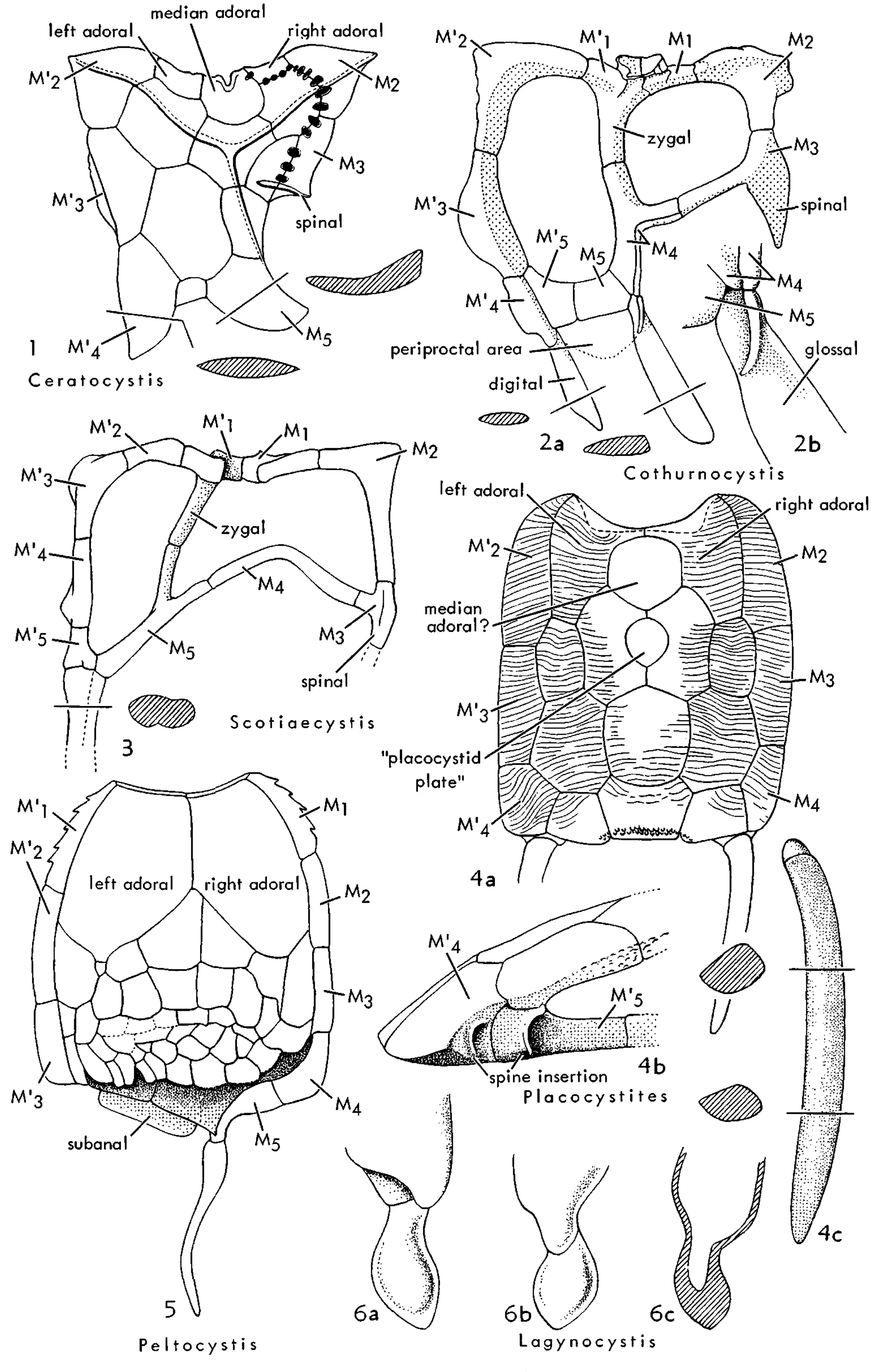

FIG. 331. [*Explanation on facing page.*]

phora generally bear protuberances on their lower side (Fig. 329). These project more or less obliquely or at right angle to the extension plane. Some are simple or denticulated knobs. Others consist of rather long spines which are pointed, truncated, or spatulate in form, depending on the species, nature of the immediate environment, or location on the frame. Typically, the protuberances occur at main angles of the frame on the anterior half of the theca, probably serving for its support and maintenance of balance of the whole body. Also they doubtless prevented displacement of the theca by currents and by movements of the aulacophore. In species provided with flexible integuments, they raised the theca above the sea floor enough to allow the inferior face to take advantage of its flexibility *(13, 14)*.

The two median anterior marginals of the Cornuta (M_1, M'_1) call for special notice in that (1) they form part of the thecal frame only on the inferior face (Fig. 325,*2b*), being covered by adorals on the superior face (Fig. 325,*2a*); (2) the inner side of each bears a powerful apophysis on which proximal muscles of the aulacophore were inserted (Fig. 330,*2b,3a*); and (3) the left marginal (M'_1) sends off a backwardly directed long process which is fused to a similar process generally borne by a marginal on the opposite side of the oro-anal axis.[1] This last-mentioned structure, termed the **zygal** by UBAGHS (1963,*89*) (=strut, BATHER, *13*), is restricted to the inferior face of the theca and divides it into two unequal fields (Fig. 325,*2b*; 329,*1*). It is observed in all cornute stylophorans except *Ceratocystis* and apparently *Nevadaecystis.* Probably the zygal served to brace the theca, impeding distention or rupture of the inferior face integument resulting from pressures exerted by thecal contents and providing a place for attachment of internal organs *(13, 14)*. In several Lower Ordovician species of *Cothurnocystis* the marginal that furnished the posterior branch of the zygal is formed by two superposed pieces which join along a horizontal suture, suggesting a possible double origin for the marginal. The zygal process originates entirely from the lower piece (Fig. 331,*2a*).

The marginals form a less obvious frame in the Mitrata than in the Cornuta. On the upper side of the mitrate theca they typically form only a narrow border which is interrupted for insertion of the aulacophore and generally also for the area around the anus (Fig. 325,*1a*). In *Chinianocarpos,* however, the two most posterior marginals are extended on the upper face enough to cover the entire posterior area. On the lower side of the theca the marginals generally cover a relatively large part of the surface (Fig. 332) and in some genera (e.g., *Lagynocystis*) almost the whole area (Fig. 332,*10*). The plates are generally V- or J-shaped in cross section and in some genera are more or less thickened along their lower external edge, which may be either sharp or blunt. As in the Cornuta, the two median anterior marginals carry a powerful apophysis on their inner side for attachment of the proximal muscles of the aulacophore; manifestly the mitrate M_1 and M'_1 are homologous to similarly designated marginals of the Cornuta. *Mitrocystites* and *Mitrocystella* (Fig. 332,*2,3*) have 12 or 13 marginals, most Anomalocystitida (Fig. 332,*4-7*) 11, *Australocystis* (Fig. 332,*8*) ten, *Chinianocarpos* (Fig. 332,*1*) nine, *Peltocystis* (Fig. 332,9) eight, *Lagynocystis* (Fig. 332,*10*) seven, and *Balanocystites* and *Anatiferocystis* (Fig. 332,*11, 12*) only two. If only

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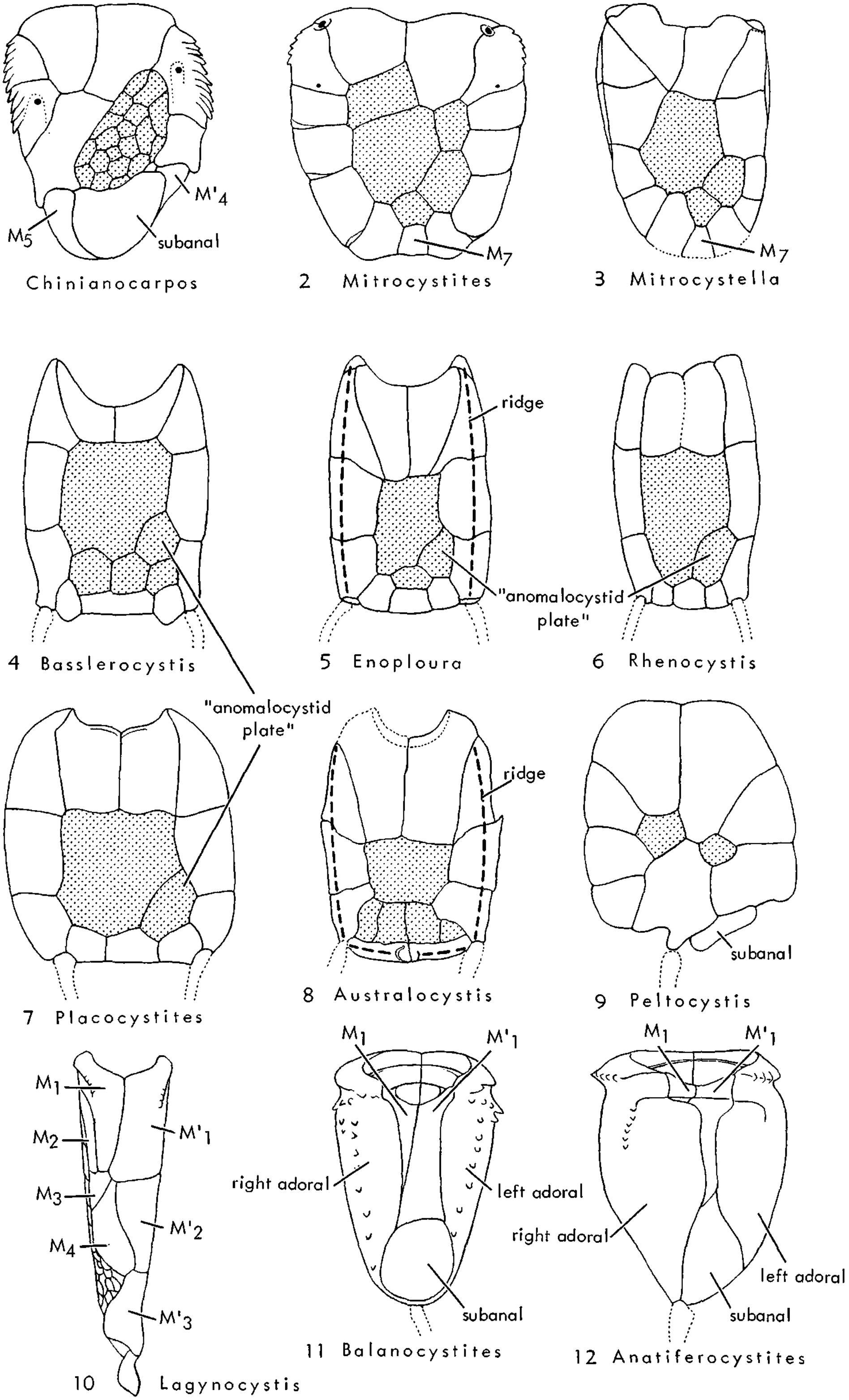
[1] In a new undescribed genus from the Lower Ordovician of France, the posterior part of the zygal is not a process borne by a marginal but an independent ossicle united to the marginal framework by a distinct suture.

FIG. 331. Marginal appendages among Stylophora.——*1. Ceratocystis perneri* JAEKEL, M.Cam., Boh.; superior face, ×1.6 (Ubaghs, n).——*2. Cothurnocystis primaeva* THORAL, L.Ord., Fr.; *2a,* superior face of whole frame, ×3.4; *2b,* proximal part of glossal, superior face, enl. (Ubaghs, n).——*3. Scotiaecystis curvata* (BATHER), U.Ord., Scot.; superior face, ×2.5 (Ubaghs, n).——*4. Placocystites forbesianus* DE KONINCK, Sil., Eng.; *4a,* superior face of theca, ×2; *4b,* left half of posterior face of theca, ×4; *4c,* posterior spine, superior face, ×4 (Ubaghs, n).——*5. Peltocystis cornuta* THORAL, L.Ord., Fr.; superior face, ×3.8 (Ubaghs, n).——*6. Lagynocystis pyramidalis* (BARRANDE), M.Ord., Boh; posterior appendage, *6a,b,* lower and upper side; *6c,* longitudinal section, ×5.4 (Ubaghs, n) (M_1, M_2 . . . right marginalia; M'_1, M'_2 . . . left marginalia).



1 Chinianocarpos
2 Mitrocystites
3 Mitrocystella
4 Basslerocystis
5 Enoploura
6 Rhenocystis
7 Placocystites
8 Australocystis
9 Peltocystis
10 Lagynocystis
11 Balanocystites
12 Anatiferocystites

FIG. 332. [*Explanation on facing page.*]

two marginals are present, these are M_1 and M'_1, identified by their location and role for insertion of the aulacophore.

Marginals of the Mitrata never develop protuberances analogous to those of the Cornuta, although their lateral inferior borders may be produced downward as prominent rounded edges which support the theca on flat surfaces (e.g., *Enoploura, Basslerocystis*). A similar ridge occurs along the posterior margin of *Australocystis.* The theca of *Lagynocystis* and *Placocystites* was partially raised above the bottom by a median longitudinal keel extending rearward from the front margin. The marginals of some Mitrata (e.g., *Chinianocarpos, Mitrocystites*) may have a lower denticulated external edge (Fig. 325,*1a,b*) or a narrow striated border (Fig. 328,*7a*) or a flat thin flange stretched out in the extension plane, serving apparently to prevent sinking of the theca into a particularly soft bottom (Chauvel, *30*).

MARGINAL APPENDAGES

Stylophoran marginalia commonly bear fixed or articulated appendages. As previously noted, the marginals of many Cornuta carry knoblike or spinose processes on their lower side. The exaggerated growth of such a protuberance on the "toe" of the boot-shaped theca of *Cothurnocystis* and *Scotiaecystis* produces the long point or blade termed **spinal** (Jaekel, *55*) (=toe spine, Bather, *13*) (Fig. 329,*1*; 331,*2a,3*). The spinal of *Ceratocystis* is a triangular projection extending from the middle of the right lateral margin and from its summit a short transverse ridge runs onto the upper surface (Fig. 331,*1*). The two posterolateral marginals (M_5, M'_4) in this genus have the form of horns, which are fixed and partly hollow. In *Cothurnocystis* corresponding horns are massive spines of unequal size and dissimilar form, designated by Jaekel *(55)* respectively as **digital** (=tag, Bather, *13*) and **glossal** (=tongue, Bather, *13*) (Fig. 331,*2a*). The glossal is joined to the marginals by two sutures, one at a distinct angle to the other, indicating that the spine possibly could be lifted or lowered but not displaced laterally. The digital seems to have been more freely articulated on the framework of the marginals and probably movable in almost any direction. Instead of these two appendages, *Scotiaecystis* has a single long process joined by sutures to the posterior left truncated corner of the theca (Fig. 329; 331,*3*). The presence of longitudinal grooves on its upper and lower sides suggests that the process was formed by union of two pieces.

Among the Mitrata, a single posterior appendage characterizes the Lagynocystida. It is short, somewhat inflated, and partially hollow in *Lagynocystis,* with cavity apparently communicating with the interior of the theca (Fig. 331,*6a-c*). In *Peltocystis* it is long, narrow, seemingly massive, and probably articulated on a posterior thecal prominence (Fig. 331,*5*). The process was rather long and variously shaped in *Balanocystites* and *Anatiferocystis,* articulating with the lower side of the posterior corner of the theca. All Anomalocystitida possess two movable spines (variously called arms, brachial arms, buccal arms, brachioles, tentacles, etc.), symmetrically placed at the two ends of the posterior margin, with attachment by highly differentiated articulations (Fig. 331,*4a-c*). Bases of the spines are constricted and proximally rounded; in *Placocystites* their evenly convex lower face and asymmetrically angulated upper face

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Fig. 332. Marginalia, infracentralia and subanal among mitrate Stylophora. [All figures show inferior faces.]——*1. Chinianocarpos thorali* Ubaghs, L.Ord., Fr.; ×3.5 (Ubaghs, n).——*2. Mitrocystites mitra* Barrande, M.Ord., Boh.; ×1.6 (Ubaghs, n).——*3. Mitrocystella barrandei* Jaekel, M.Ord., Boh.; ×1.5 (Ubaghs, n).——*4. Basslerocystis disparilis* (Hall), L.Dev., N.Y.; ×2.3 *(25)*.——*5. Enoploura popei* Caster, U.Ord., Ohio; ×1.4 *(25)*.——*6. Rhenocystis latipedunculata* Dehm, L.Dev., Ger.; ×1.4 *(25)*.——*7. Placocystites forbesianus* de Koninck, Sil., Eng.; ×1.6 (Ubaghs, n).——8. *Australocystis langei* Caster, L.Dev., Brazil; ×2.6 *(27)*.——*9. Peltocystis cornuta* Thoral, L.Ord., Fr.; ×2.6 (Ubaghs, n).——*10. Lagyno*pyramidalis (Barrande), M.Ord., Boh.; ×1.8 (Ubaghs, n).——*11. Balanocystites lagenula* Barrande, M.Ord., Boh.; ×2.5 (Ubaghs, n).——*12. Anatiferocystis barrandei* Chauvel, M.Ord., Boh.; ×2.4 (Ubaghs, n) (M_1, M_2 . . . right marginalia; M'_1, M'_2 . . left marginalia).

meet in a rather sharp edge (Fig. 331,*4c*, cross sections). They have no communication with the thecal cavity and musculature controlling their movements was external.

Spines of this sort in *Enoploura* were supposed by Pope *(70)* to be enveloped by "cover plates" identical to the scales of the machaeridian *Lepidocoleus*, but this has not been confirmed by examination of other anomalocystids. In *Paranacystis* and the Mitrocystitidae no exothecal process of any sort is seen, but the posterior thecal plates of *Paranacystis* form a subtriangular projection interpreted as an ostial cover by Caster *(26)*.

All stylophoran thecal appendages are directly related to the marginals, or even considered to be modified marginal plates themselves (Kirk, *56*). Certainly, this applies to the two posterior "horns" of *Ceratocystis*. Probably the processes evolved independently in different lineages and, in view of the diversity of their shapes, it is very likely that they served diverse functions. All of them probably contributed to anchoring the animal and their localization at the posterior extremity of the body suggests that they were a counterweight to the aulacophore.

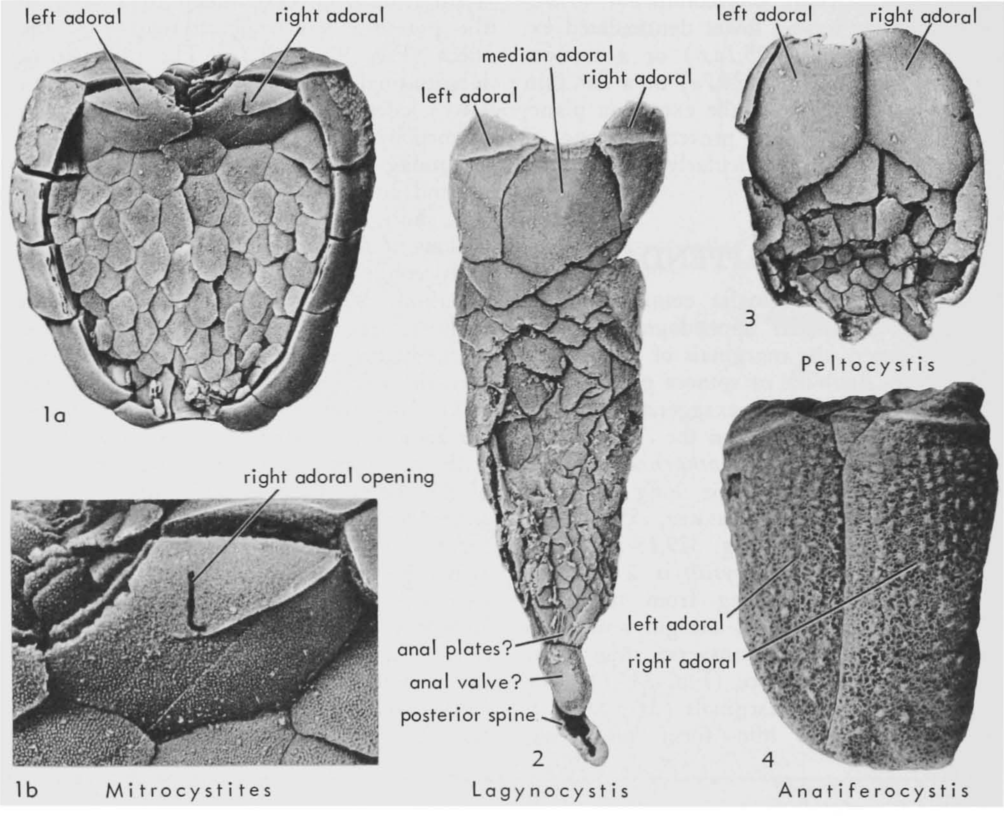

Fig. 333. Adoralia among mitrate Stylophora.——*1. Mitrocystites mitra* Barrande, M.Ord., Boh.; *1a,* superior face of theca, ×2.2; *1b,* right adoral, ×6 (Ubaghs, n).——*2. Lagynocystis pyramidalis* (Barrande), M.Ord., Boh.; superior face of theca, ×3 (Ubaghs, n).——*3. Peltocystis cornuta* Thoral, L.Ord., Fr., superior face of theca, ×4.1 (Ubaghs, n).——*4. Anatiferocystis punctata* (Bassler), M.Ord., Tenn.; superior face of theca, ×7 (Ubaghs, n).

ADORALIA

Plates here designated as adorals are those which in combination with the median anterior marginals *(M_1, M'_1)* frame the insertion of the aulacophore.[1] They correspond to the *épibasales* of Chauvel *(30)* and adcolumnals of Caster *(25)*. In *Ceratocystis* (Fig. 330,*1a,b*) they are represented by three plates, those at right and left contributing to formation of the anterior thecal border on upper and lower faces equally and the middle one pertaining only to the upper face. The lower surface of the right adoral bears a narrow slit which is a distinct aperture (*see* right adoral orifice, p. S515). The median plate, which is relatively large, has a V-shaped re-entrant bordered by an elevated lip on its anterior margin. The adorals of all other Cornuta, where known, form part of the frame and are restricted to the superior face of the theca (Fig. 330,*2,3*). Whether two or three in number, they form a broad arc with ends resting on the two median anterior marginals *(M_1,M'_1)*. The lower edge of the right adoral is notched by an orifice (Fig. 330,*2b,c, 3a,c*). The middle plate seems to be regressive, being present (though small) in Lower Ordovician forms but unknown in the Upper Ordovician. In *Phyllocystis* (Fig. 330,*2a*) this plate shows a median depression provided with a slightly projecting rim, probably homologous with the notch that is seen in the median adoral of *Ceratocystis*.

At first glance, adorals of the Mitrata seem quite unlike the similarly designated plates in the Cornuta (Fig. 333). Invariably they are much more developed and either partly or completely cover the superior face. Even so, they are held to be homologous to the adorals of Cornuta, since they have the same relationship to the M_1 and M'_1 plates and the aulacophore and since the right adoral (e.g., in *Mitrocystites*) may be pierced by an unpaired orifice, as in the Cornuta (Fig. 333,*1a,b*). They are two or three in number (Fig. 333,*1,2*). The median plate does not attain the anterior upper margin in some genera (e.g., *Placocystites,* Fig. 331,*4a*), and in others it creases to be distinct from adjacent supracentrals (Fig. 333,*3*) or disappears altogether. The adorals may be small (e.g., *Mitrocystites,* Fig. 333,*1*), intermediate in size (e.g., *Placocystites*), or very large (e.g., *Peltocystis,* Fig. 333,*3*). They completely cover the superior face of *Balanocystites* and *Anatiferocystis* (Fig. 333,*4*) and folding over the lateral borders, they occupy most of the inferior face as well (Fig. 332,*11,12*).

EPISTOMALIA

In *Phyllocystis* the triangular space between the adorals and the first skeletal ring segment of the aulacophore is occupied by two small plates which (as they are interpreted as protecting the mouth) are here called **epistomalia (epistomals)** (Fig. 330, *2a*). They are apparently attached to the left and right adorals by their abaxial edges and sutured (or at least contiguous) to the median adoral by their posterior edge, with other margins free. Rarely they join one another along the median plane but more commonly are separated, their adaxial edges prolonging the U-shaped ridge that surrounds the axial depression of the median adoral, this depression thus seeming to be confluent with an empty space between the epistomals. The origin of these plates is obscure, since no equivalents of them have been observed with certainty in other genera. In broad aspect they closely resemble plates which protect the upper face of the proximal region of the aulacophore, but these are parts of skeletal rings, whereas the epistomals are not. Seemingly they could open at least slightly, unlike proximal upper plates of the aulacophore, which always are closed.

CENTRALIA

The variably large number of plates or platelets on the superior and inferior faces

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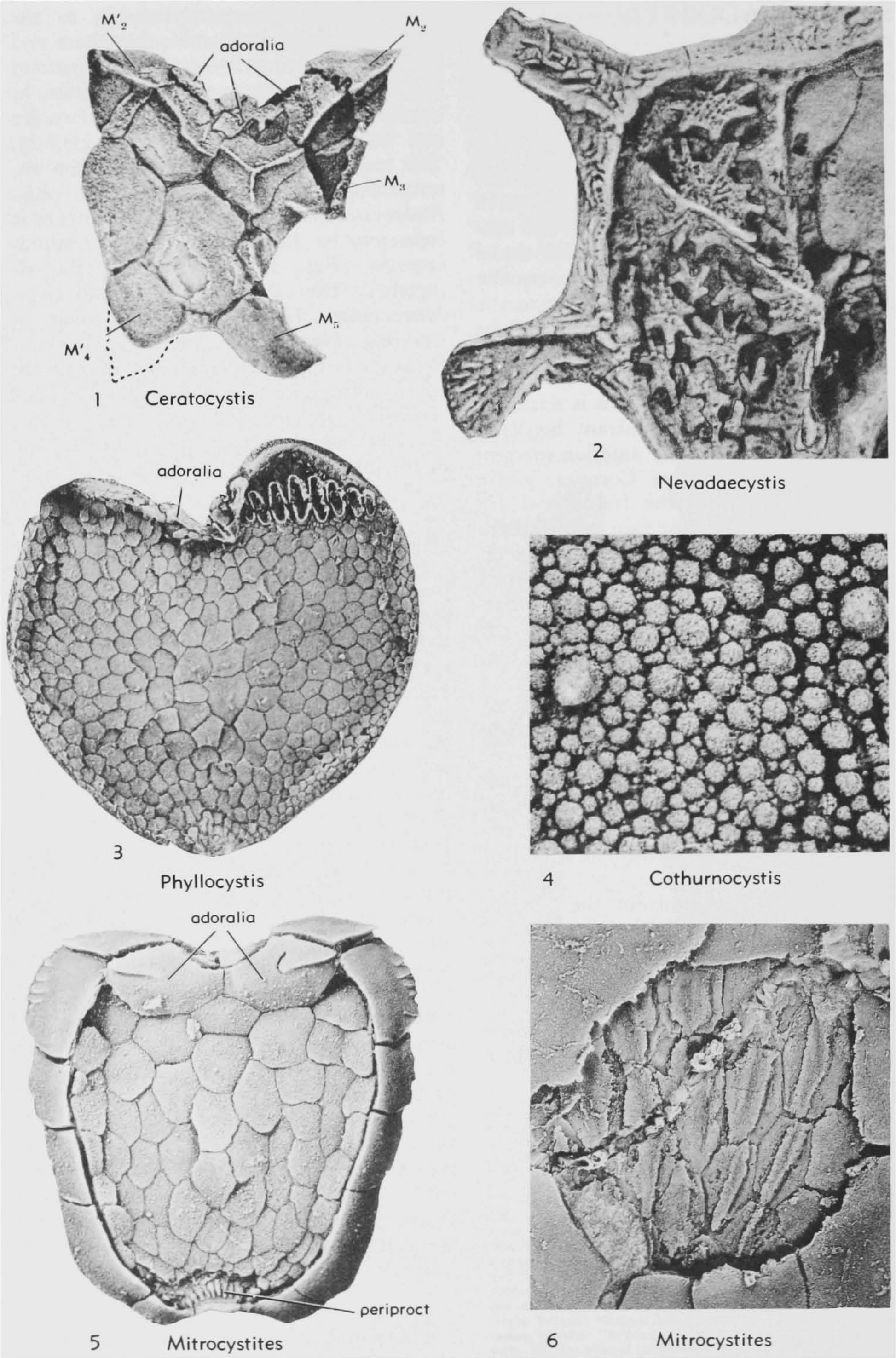
[1] The aulacophore insertion typically is surrounded by four or five plates—*M_1* and *M'_1* below and two or three adorals above. In *Rhenocystis* and possibly some specimens of *Placocystites* additional marginals (*M_9, M'_9*) may form part of this anterior ring, bringing to six the number of plates around the base of the aulacophore. Also, the presence of two deltoid "interbasal" plates between the marginals and adorals has been recorded in *Mitrocystella* by Chauvel (30) and in *Enoploura* by Caster (25). Carefully made latex casts of *Mitrocystella*, however, demonstrate that the presumed extra plates are merely reflected downward margins of adorals separated from other adorals by a ridge (see Fig. 340,*3*). The so-called interbasals of *Enoploura,* which admittedly are very small, may be sutural wrinkles. In any case, the "hexabasal" pattern of the anterior ring of plates is no more significant than the "tetrabasal" scheme postulated by Jaekel (55) as a diagnostic feature of his class Carpoidea.



1 Ceratocystis

2 Nevadaecystis

3 Phyllocystis

4 Cothurnocystis

5 Mitrocystites

6 Mitrocystites

FIG. 334. [*Explanation on facing page.*]

of the theca, inclosed by the marginal frame, composes the **centrals (centralia).** In *Ceratocystis,* which is the most ancient known representative (Middle Cambrian) of the Stylophora, centrals are separable from marginals with difficulty, for all are large plates which contribute subequally to formation of the rigid box that surrounded soft parts of the animal (Fig. 334,*1*). On the inferior face are five **infracentrals (infracentralia)** and on the superior face are eight **supracentrals (supracentralia)** (see Fig. 345,*1*,*2*). The upper face of the theca is crossed by a tripartite crest, with branches that meet near the middle.

Morphologically intermediate in some respects between *Ceratocystis* and *Cothurnocystis* is *Nevadaecystis* (Upper Cambrian), which still has large plates on the lower face but numerous stelliform supracentrals on the upper face, joined to one another only at points of their rays so as to leave large oval orifices which doubtless represent uncalcified areas of the integument that served for gaseous exchange between fluids inside and outside of the theca. As in *Ceratocystis,* an apparently triradiate crest (one branch lacking in the only known specimen) may be seen on the upper thecal surface.

The two thecal faces of all other known representatives of the Cornuta are protected by a finely plated, probably flexible integument attached to inner borders of the marginals. Generally the plates are tessellated but in some forms (e.g., *Scotiaecystis*) they appear to be imbricate in many places, possibly owing to defective preservation.

Supracentrals of Cornuta invariably differ from infracentrals in size and commonly also in ornament. The supracentrals may be slightly the larger (e.g., *Phyllocystis*) but in most genera they are ordinarily the smaller. Also, the plating is not the same all over. As a rule, the size of plates decreases toward the periphery and around openings in the integument (Fig. 334,*3*), thus providing greater flexibility of the theca in these regions. The infracentrals next to the zygal in *Bohemiaecystis* and *Phyllocystis* are elongated in a direction parallel to this piece. On the upper face of several species of *Cothurnocystis* (e.g., *C. elizae* in particular), the plating consists of relatively large rounded and swollen plates which in full-grown specimens are surrounded by smaller ones (Fig. 334,*4*). Plates of the left posterior region are more closely set than in other parts of the same side and in some individuals an arcuate row of spines or conical protuberances may be observed at some distance from the upper anterior margin. The supracentrals of *Scotiaecystis* are polygonal plates, each bearing a low, convex-topped spine (see Fig. 348,*2*), and where the spines are contiguous they may form a sort of false test beneath which empty spaces possibly were maintained.

The infracentralia of most Mitrata[1] are large to small plates which are essentially constant in number according to genera and species—four to six in *Mitrocystites* (Fig. 332,*2*), three in *Mitrocystella* (Fig. 332,*3*), two in *Peltocystis* (Fig. 332,*9*), and one to five in Anomalocystitida (Fig. 332,*4-8*). They are entirely lacking in *Lagynocystis, Balanocystites,* and *Anatiferocystis* (Fig. 332,*10-12*) but in *Chinianocarpos* (Fig. 332,*1*) replaced by some 20 platelets in a subcentral elliptical area. Their distribution is almost symmetrical in *Allanicytidium* and *Australocystis* (Fig. 332,*8*) but is very asymmetrical in all other genera. Generally, the center of the inferior face is occupied by a single large plate (two in *Mitrocystites*) in contact with M_1 and M'_1 (in *Mitrocystella* rarely with M'_1 alone). The large infracentral ordinarily is accompanied by smaller plates, one of which designated

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[1] Gislén (1930, 28) designated these according to their position as hypocentral (large middle plate), dextrolaterals (plates on right side) and sinistrolaterals (plates on left side), but orientation used by him is the reverse of that adopted here.

Fig. 334. Supracentralia among Stylophora.——*1. Ceratocystis perneri* Jaekel, M.Cam., Boh., ×1.5 (Ubaghs, n).——*2. Nevadaecystis americana* (Ubaghs), U.Cam., Nev.; stelliform supracentralia, ×6 (Ubaghs, 1963).——*3. Phyllocystis blayaci* Thoral, L.Ord., Fr.; ×3 (Ubaghs, n).——*4. Cothurnocystis elizae* Bather, U.Ord., Scot.; ×10 (Ubaghs, n).——*5. Mitrocystites mitra* Barrande, M.Ord., Boh.; ×3 (Ubaghs, n).——*6. Mitrocystites mitra hanusi* Chauvel, M.Ord., Boh.; internal aspect of supracentralia (center) showing median elevation, ×3 (Ubaghs, n) (M_2, M_3, M_5, right marginalia, 2, 3, and 5; M'_2, M'_4, right marginalia, 2, 4).

as the "anomalocystid plate" by Caster *(25)* truncates the left posterior corner of the large plate and seems to characterize many Anomalocystitida (Fig. 332,*4-7*). An anomalocystitid plate is lacking in *Australocystis* (Fig. 332,*8*).

Supracentrals of the Mitrata, complemented by adorals, cover the upper thecal surface except for the generally narrow border formed by the marginals. In the Mitrocystida (Fig. 331,*1*; 334,*5*) and some Lagynocystida (Fig. 333,*2,3*) they are rather small, numerous, irregular in outline and arrangement, imbricated or tessellated, and diminishing in size in a backward direction. They are more or less sharply differentiated from the adorals. The integument which they reinforced seems to have been somewhat flexible, rather than rigid. Inner sides of the plates bear median elevations which probably served for attachment of muscle or ligament strands used to control movement of the integument (Fig. 334,*6*). The supracentrals of anomalocystid genera are much larger, fewer, never imbricated, and constant in very symmetrically arranged positions (Fig. 331,*4a*). Together with the adorals, from which they are little distinguished, the supracentrals contributed to a rigid thecal covering for which the term **carapace** (Caster, *25*) is well suited. A supracentral called the "placocystid plate" by Caster *(25)*, observed in *Placocystites* (Fig. 331,*4a*) and probably present also in *Rhenocystis*, is remarkable on account of its circular to elliptical outline and smooth (unstriated) outer surface. Earlier (de Koninck, *58*; Woodward, *95*) this plate was thought to be an anal structure. Supracentrals are entirely lacking in *Balanocystites* and *Anatiferocystis* (Fig. 333,*4*), in which two large adorals completely protect the upper face.

SUBANALIA

The lower face of the theca in some stylophoran genera (e.g., *Chinianocarpos, Balanocystites, Anatiferocystis*) (Fig. 332, *1,11,12*) bears a large subcircular terminal plate, the morphologic and functional meaning of which is obscure. Possibly it is a modified marginal, homologous with the median posterior marginal *(M_7)* that forms the floor of the anal area in *Mitrocystites* and *Mitrocystella* (Fig. 332,*2,3*).

A somewhat different element occurs in *Peltocystis* (Fig. 332,*9*). This is a rectangular plate located beyond the two posterior marginals and thus outside the normal limits of the theca, yet seemingly placed below the anal structures as in the two last-mentioned genera. For all of these similarly located posterior plates of uncertain origin, some perhaps different from others, the designation **subanals (subanalia)** here is adopted.

THECAL ORIFICES

The theca of Stylophora may possess openings of various sorts. For example, four types are observed in *Mitrocystites.* The function of some of these orifices is reasonably certain, whereas the physiological significance of others is entirely conjectural. Names without functional implication should be used for the latter.

MOUTH AND ANUS

The inlet and outlet of the digestive tube in stylophorans are treated together because they are interrelated and because separate consideration of them would be measurably artificial.

Opinions concerning locations of the mouth and anus in the strange echinoderms here discussed are extraordinarily divergent. For the sake of simplicity and avoidance of ambiguity, all references to them are converted to the orientation of Stylophora adopted in the *Treatise,* which requires that the usage of most authors for directional terms (anterior, posterior, right, left) except upper (or superior) and lower (or inferior) must be transposed. Given in these terms, different judgments can be recorded as follows.

(1) Mouth and anus both placed at posterior extremity of the body—Bather *(11)*, Jaekel *(54)*, Kirk *(56)*, Caster *(25)* in *Enoploura*, Cuénot *(32)* in all Mitrata, Gill & Caster *(43)* in *Victoriacystis,* Nichols *(68)*.

(2) Single orifice serving as mouth-anus placed at posterior extremity of the body—Jaekel *(55)*, Gislén *(45)*, Spencer *(80)*. The first two authors postulated that the morphological anus by reason of a com-

plete reversal of food currents in the digestive tube functions also as the physiological mouth. Spencer thought that the posterior opening of *Cothurnocystis* was the aperture of a vestibule which held both mouth and anus.

(3) Mouth located in anterior position adjacent to the aulacophoral insertion and anus at opposite (posterior) extremity of the body—Bather *(21)* in *Placocystites,* Chauvel *(30)* in Mitrata, Termier & Termier *(82)* in Mitrata.

(4) Mouth located at or near posterior pole and anus placed variously—Haeckel *(49),* anus on upper face near right anterior corner of theca in *Mitrocystites* and on mid-line of lower face at base of the aulacophore in Anomalocystitidae; Jaekel *(54),* anus on right lateral margin of theca in *Ceratocystis*; Caster *(27)*, anus close to the aulacophore insertion in *Paranacystis.*

(5) Anus located on mid-line of superior face, position of mouth indeterminate—de Koninck *(58)* in *Placocystites,* Schuchert *(78)* in *Anomalocystites* and *Basslerocystis.*

(6) Anus placed at or near posterior extremity of body and inlets to digestive tube consisting of elliptical organs or sutural pores along the upper right anterior margin of the theca in many Cornuta—Bather *(13, 14)*, Chauvel *(30)*, Delpey *(35)*, Termier & Termier *(82)*, Cuénot *(32)*. Also Bather *(14)* considered that pores on the lower face of *Mitrocystites* served as food intakes.

The extreme diversity of these opinions stems mainly from the absence of any thecal opening in the Stylophora that can be identified with certainty as the mouth. This suggests that the mouth did not open on the outer surface of the theca but probably, as in Homoiostelea, was located inside the theca. Its approximate position may be inferred from the fact that the aulacophore carries a median groove and lateral depressions which are protected by mobile cover plates. Such features in echinoderms are characteristic of ambulacral tracts, and in all Recent and fossil echinoderms these tracts lead to the mouth. Accordingly, if the aulacophoral groove is ambulacral, the mouth of Stylophora must have been placed at or near its proximal end. Several features are possibly related to the presence of this orifice: 1) the presence in *Phyllocystis* of epistomalia which apparently form a protective roof over an aperture (Fig. 330,*2a*), 2) the occurrence in *Phyllocystis* and *Ceratocystis* of a small notch-and-groove on the anterior edge of the median adoral plate seemingly related to an opening just beneath (Fig. 330,*1a,2a*), and 3) the presence of an almost complete separation between the proximal aulacophoral cavity and the thecal cavity in *Lagynocystis,* impeding the passage of a digestive tube (see Fig. 341, *2,3*), and 4) the occurrence of comblike organs on the most anterior part of the theca in this genus, which must have been just in front of the mouth if they functioned as a filter (see Fig. 341,*3,4*).

The anus is placed on the superior face of the theca at or near its posterior extremity in all stylophorans where it has been observed. A radiating arrangement of small plates in this position in *Cothurnocystis* (see Fig. 346,*1*), *Phyllocystis* (Fig. 335,*2a,b*) and *Scotiaecystis* (see Fig. 348,*4*) suggests the presence of an anal pyramid during life. The surrounding thecal integument **(periproctal area)** is judged to have been very flexible and extensible, suggesting that the anal orifice could have been protruded and retracted. The most posterior marginals of *Cothurnocystis* (see Fig. 346,*1*) form a transverse or oblique bar on the lower thecal side only and the periproctal area placed partly on their flattened upper (internal) surface probably extended beyond them into a conical projection. The extension was framed on the left by the proximal part of the digital and on the right by the concave crest of the prolonged upper edge of the adjacent right marginal on the glossal. Retractor and protractor muscles of the anal pyramid could have been attached to all of these skeletal structures (Fig. 331,*2a*).

The upper edge of the posterior marginal of *Phyllocystis* slopes more or less distinctly downward to the level of the periproctal area (Fig. 335,*2a,b*) and the upper (internal) surface of this marginal in some specimens carries two symmetrically placed small knobs which probably provided for insertion of the rectal retractor muscles. In *Scotiaecystis* the anal pyramid was not placed at the apex of the angle formed by marginals M_5 and M'_5 but was shifted toward M'_4 (see Fig. 338,*1a*; 348,*1a*).

The periproctal area surrounding the

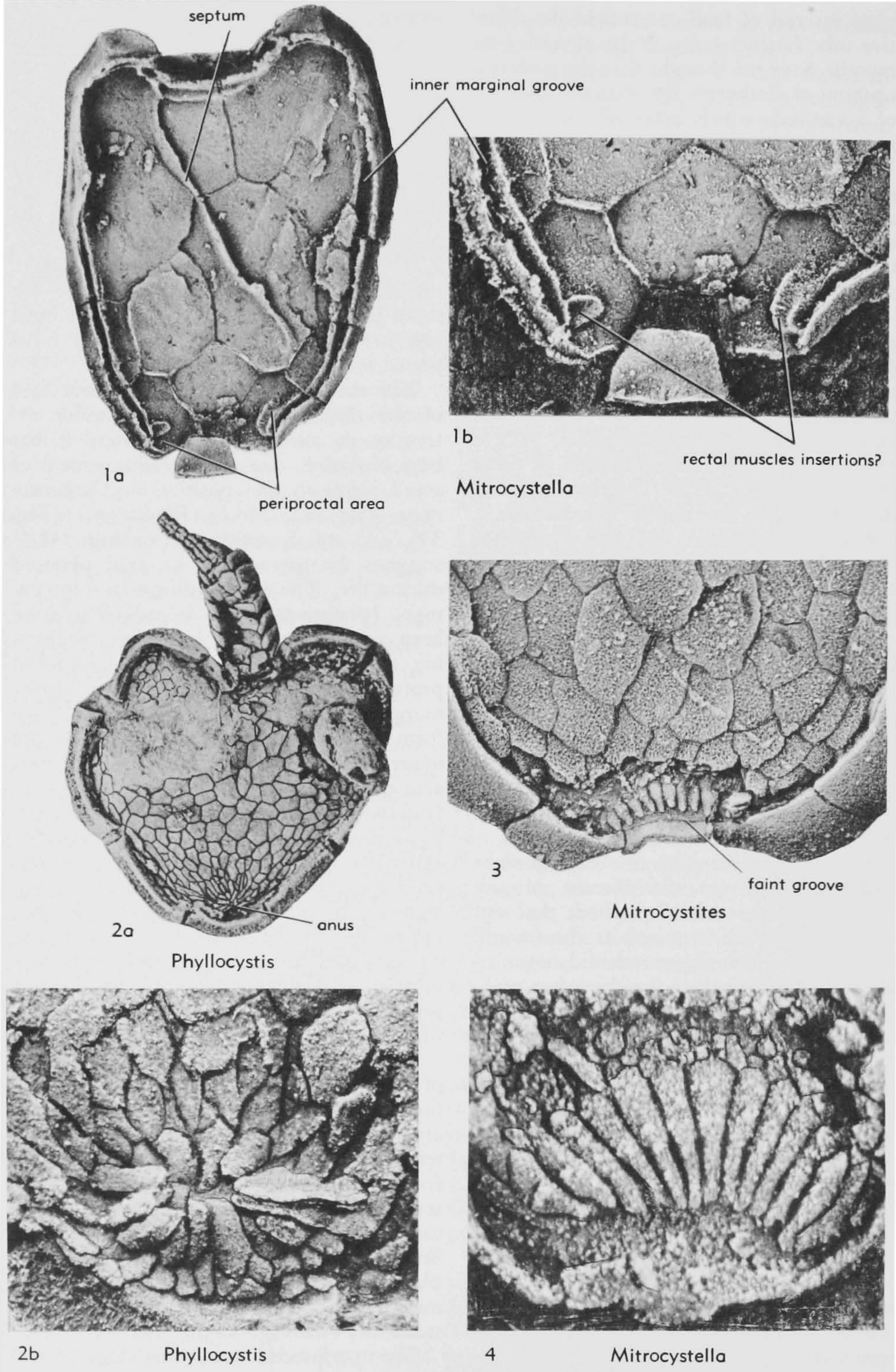

FIG. 335. [*Explanation on facing page.*]

anus in *Mitrocystites* and *Mitrocystella* is limited by a semicircular row of small supracentrals, and the upper edge of the marginal frame slopes downward at its level in manner that interrupts the frame and allows the rectal region to be pushed out and drawn back (Fig. 335,*3,4*). The periproctal area is finely plated and the anus bordered by an arcuate row of toothlike platelets which diminish in size toward both extremities. Each platelet of the row has a somewhat spatulate proximal part in close contact with adjacent ones and a narrower distal part separate from its neighbors by distinct empty spaces (Fig. 335,*4*). The faintly convex proximal regions, made of finely reticulate stereom, probably were embedded in the integument, whereas the more convex distal regions, marked by tiny superficial wrinkles, doubtless protruded at least partly from it. Presumably, the platelets were bound together by transverse fibers, short and elastic between proximal portions, longer and contractile between distal portions. The anal orifice could be opened or closed very readily by opposite action of these fibers. The floor of the periproctal area in these genera, formed by the three most posterior marginals, also deserves attention. In some specimens of *Mitrocystites* the median one carries a faint transverse groove disposed parallel to the posterior margin attachment of the plate, probably marking the attachment of the contractile tissues of the lower lip of the anus (Fig. 335,*3*). Both in *Mitrocystites* and *Mitrocystella,* some portions of the internal surface of the two lateral posterior marginals may be raised into small shelves which apparently served for attachment of muscles or ligaments operating the rectal part of the digestive tube (Fig. 335,*1a,b*).

The anus of *Lagynocystis* is unknown, but a transverse row of very narrow ?anal plates at the posterior end of the supracentral covering abuts against a conical hollow ossicle that may represent a kind of anal valve (Fig. 333,*2*).

The subanals of *Chinianocarpos, Balanocystites,* and *Anatiferocystis* may have served as a floor of the periproctal areas (Fig. 332, *1,11,12*).A small gap at the posterior edge of the subanal should have been sufficient for ejection of excreta. No other indication of an anus is found in these genera.

In at least some Anomalocystitida *(Basslerocystis, Placocystites)* a large transversely elongate opening is observable on the posterior face of the theca (Fig. 331,*4b*). According to SCHUCHERT *(78)* and KIRK *(56),* a sort of trapdoor flap hanging from the upper margin of the aperture apparently served to close the terminal orifice of *Basslerocystis.* In *Placocystites* the orifice is surrounded by a smooth narrow band (bordered on the upper side by a row of small denticles); this band probably marks the attachment of a periproctal membrane. *Victoriacystis* exhibits small plates (termed tegminals by GILL & CASTER, *43*) in series with the supracentrals, geniculated to form a presumed cover surface probably over the anus. CASTER (in *43*) has reported the occurrence of similar platelets in *Enoploura.*

RIGHT ADORAL ORIFICE

A single thecal opening present in *Ceratocystis, Phyllocystis, Cothurnocystis,* and *Mitrocystites* is termed the **right adoral orifice** because invariably it is related to the right adoral plate. It leads more or less directly into a funnel-shaped depression known as the **infundibulum,** which is hollowed out on the internal face of marginal M_1. In *Ceratocystis* this orifice, found on the lower side of the theca, consists of a narrow slit with reflected right margin, followed inside by a concavity which forms a ceiling for the infundibulum (Fig. 330, *1b,c*). The right adoral orifice of *Phyllocystis* and *Cothurnocystis* is located on the anterior thecal margin above the aulacophoral insertion and slightly to the right of it, making a rather deep notch in the lower edge of the right adoral plate (Fig. 330, *2a-c,3a-c*). A somewhat ear-shaped project-

FIG. 335. Anal area among Stylophora.——*1. Mitrocystella incipiens miloni* CHAUVEL, M.Ord., Fr.; *1a,* internal side of inferior thecal face, ×3 (Ubaghs, n); *1b,* posterior part of same, details of floor of anal area, ×6 (Ubaghs, n).——*2. Phyllocystis crassimarginata* THORAL, L.Ord., Fr.; *2a,* superior face of theca, ×3 (Ubaghs, n); *2b,* anal pyramid, ×15 (Ubaghs, n).——*3. Mitrocystites mitra* BARRANDE, M.Ord., Boh.; post. part of superior thecal face, ×6 (Ubaghs, n).——*4. Mitrocystella barrandei* JAEKEL, M.Ord., Boh.; periproctal area, details, ×15 (Ubaghs, n).

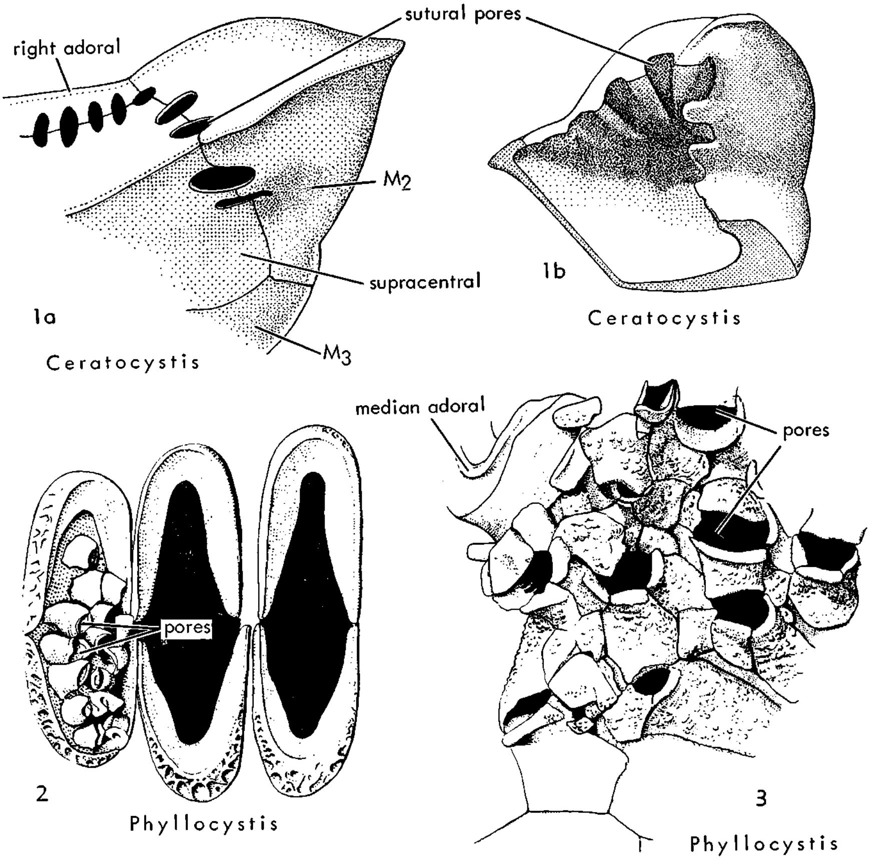

FIG. 336. Sutural pores and cothurnopores among cornute Stylophora.——*1. Ceratocystis perneri* JAEKEL, M.Cam., Boh.; *1a,* right anterior corner of theca, details, ×5 (Ubaghs, n); *1b,* right anterior marginal, oblique view showing internal grooves leading to sutural pores, ×5 (Ubaghs, n).——*2. Phyllocystis blayaci* THORAL, L.Ord., Fr.; cothurnopores, the left one with platelets preserved, ×15 (Ubaghs, n).——*3. Phyllocystis crassimarginata* THORAL, L.Ord., Fr.; sutural pores; ×15 (Ubaghs, n) (M_2, M_3, right marginalia).

ing rim borders it above and laterally in *Phyllocystis* but soft tissues must have adjoined it on the lower side. In *Mitrocystites* the upper surface of both adorals shows a fold running transversely from their outer anterior corners to their centers. A narrow slit in the right adoral near the inner (adaxial) end of this fold extends toward the anterior edge of the plate without reaching it (Fig. 333,*1a,b*). As in other genera mentioned, the orifice lies above the infundibulum but seems not to open directly into it, since exfoliated stereomic projections that conceal its inner edge come between it and the depression (see Fig. 340, *2c*). A similar orifice has not been discovered in *Mitrocystella,* although an infundibulum exists, suggesting that the opening was located close to the right adoral plate rather than in it, probably in soft tissues.

The constant relationships of the right adoral orifice to the right adoral plate and infundibulum in all genera where the open-

FIG. 337. Sutural pores and cothurnopores in Cothurnocystidae.——*1. Phyllocystis crassimarginata* THORAL, L.Ord., Fr.; *1a,* theca, superior face; *1b,* upper right anterior area, details, ×10 (Ubaghs, n); *1c,* sutural pores, internal aspect, ×10 (Ubaghs, n).——*2. Phyllocystis blayaci* THORAL, L.Ord., Fr.; *2a,* theca, superior face, ×2 (Ubaghs, n); *2b,* cothurnopores, details, ×15 (Ubaghs, n); *2c,* a few cothurnopores, internal aspect, ×7.5 (Ubaghs, n).

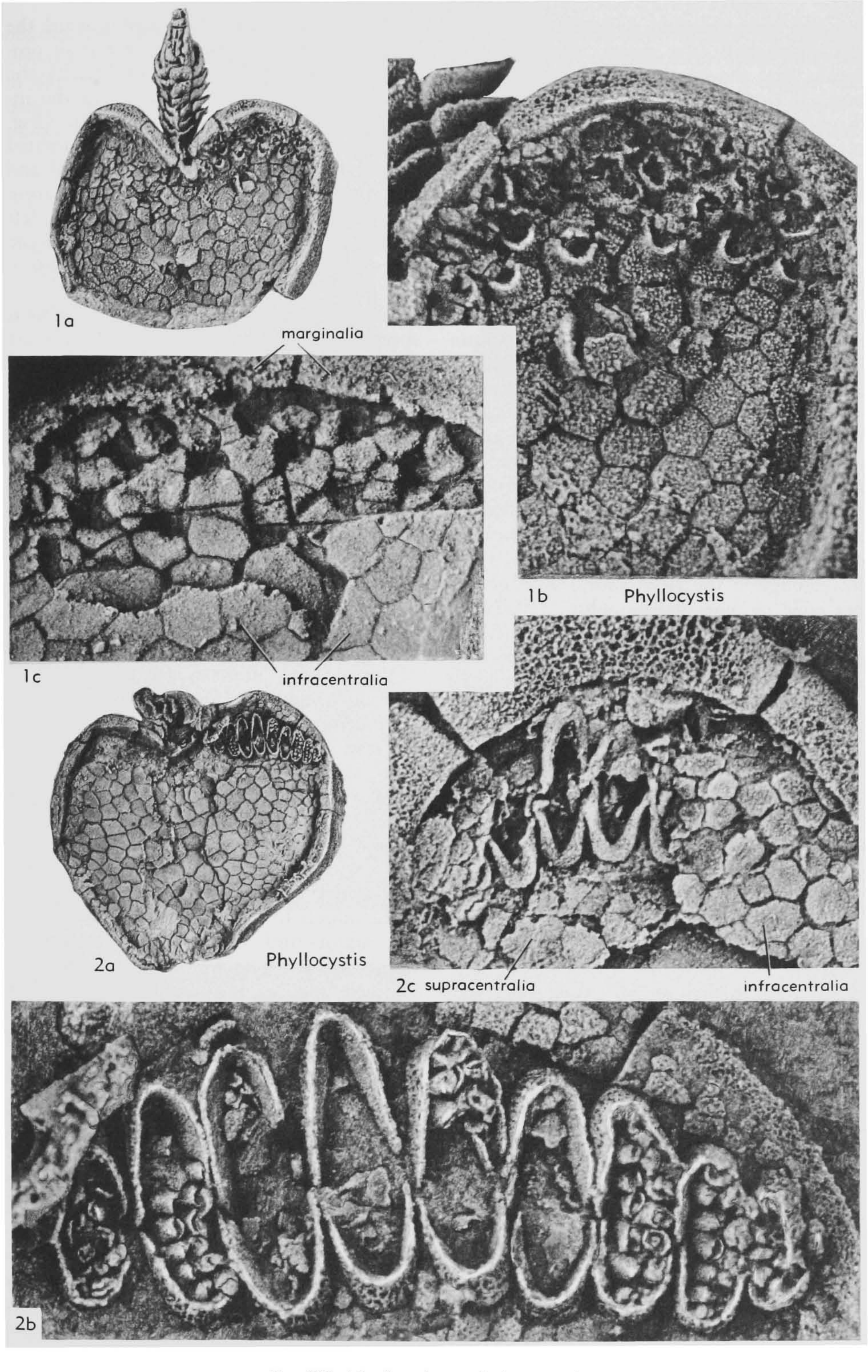

FIG. 337. [*Explanation on facing page.*]

ing has been observed indicates its homology throughout the group. Probably this means that the aperture migrated from an original location on the inferior face of the theca (e.g., *Ceratocystis*) to an ultimate placement on the superior face (e.g., *Mitrocystites*). A similar displacement from one face of the body to the other is seen in the postmetamorphic development of the hydropore in ophiuroids, which migrates from a dorsomarginal to adoral position. Of course, this may be pure analogy, yet it gives hint that the right adoral orifice in stylophorans might represent the hydropore, which is an interpretation supported by its singleness and asymmetrical location in *Ceratocystis* and *Mitrocystites,* as well as its narrowness. In particular, its appearance in *Mitrocystites* (Fig. 333,*1a,b*) is very similar to that of the hydropore groove of some echinoids (e.g., *Cubanaster torrei*). In *Phyllocystis* and *Cothurnocystis* soft tissues must have occupied the triangular space between the lower edge of the right adoral and the upper edge of marginal M_1 (Fig. 330,*2b,3a*), and since the hydropore was located in these soft tissues, we do not know its size and shape. Another possibility is that the hydropore was combined with the outlet for genital products. Close association of hydropore and gonopore in such primitive echinoderms would not be surprising, since the primordium of the gonad in developing individuals of the phylum arises from the wall of one of the coelomic pouches in contact with the complex of organs invariably located in the madreporitic interray.

SUTURAL PORES

All cornute Stylophora, except some undescribed forms, possess orifices in the right anterior part of the superior face of the theca which probably performed similar functions despite their large variety of morphological aspects. One type of these openings consists of rather simple sutural pores, first observed in *Ceratocystis* and called to attention by Bather *(13)*. In this genus they comprise a series of more or less even-spaced apertures located along sutures that join the median and right adorals and that occur between contiguous supracentrals and the latter, along with marginals M_2 and M_3 (Fig. 330,*1a,b*). The pores vary in size, have rounded edges bent toward the thecal cavity, and lack an external projecting rim (Fig. 336,*1a*). Ordinarily the pores are prolonged by grooves on the inner surface of plates next to them (Fig. 336,*1b*). A single similar orifice is located on the suture between the left adoral and marginal M'_2 at the left anterior margin of the theca and another between the left adoral and M'_1 on the inferior face of the theca (Fig. 330,*1b*). The maximum diameter of the pores is less than 2 mm.

Sutural pores of another sort, in different specimens ranging from a few to more than 50, are seen in *Phyllocystis crassimarginata* Thoral (Fig. 336,*3*; 337,*1a-c*). They open between small supracentrals which have convex corrugated surfaces. Each pore is surrounded by the upturned edges of two or three, or as many as five of these plates. Their maximum diameter is 0.3 to 0.6 mm. As viewed from inside the theca, they appear as subquadrate openings 0.7 in greatest diameter (Fig. 337,*1c*).

COTHURNOPORES

Very curious elliptical structures observed first by Bather *(13)* on the theca of *Cothurnocystis elizae* and found later by Thoral *(85)* in *Phyllocystis blayaci* are here named **cothurnopores,** as suggested by Caster (personal communication) (Fig. 336,*2*; 337,*2a-c*). They are present also in several undescribed species of *Cothurnocystis* and in *Nevadaecystis (89),* occupying a tract that extends from the vicinity of the right adoral to the right lateral margin of the frame and projecting slightly above adjacent thecal plates smaller than ordinary supracentrals. The latter suggest a particularly flexible thecal wall. The cothurnopores lie contiguous to one another or nearly so and with diminishing size of individuals toward ends of their tract form a very elongate rhombic figure. They vary in number according to species and size (?reflecting age or growth stage)—eight in *Nevadaecystis,* eight or nine in *Phyllocystis,* and 18 or more in *Cothurnocystis elizae.*

The long axis of each cothurnopore lies approximately at right angle to the adjacent portion of the frame (Fig. 337,*2a*). The elliptical structures are surrounded by a raised rim formed by two unequal U-shaped ossicles, an inner short one and outer long one that meet at their free ends. According to BATHER *(13, 14)*, the short U, which borders a semicircular orifice without cover plates, could be bent over on its hinge so as to protect the opening like the hood of a carriage or perambulator. The long U, with sides sloping down to a V-shaped slit, is protected by a double row of alternating cover plates which are similar in appear-

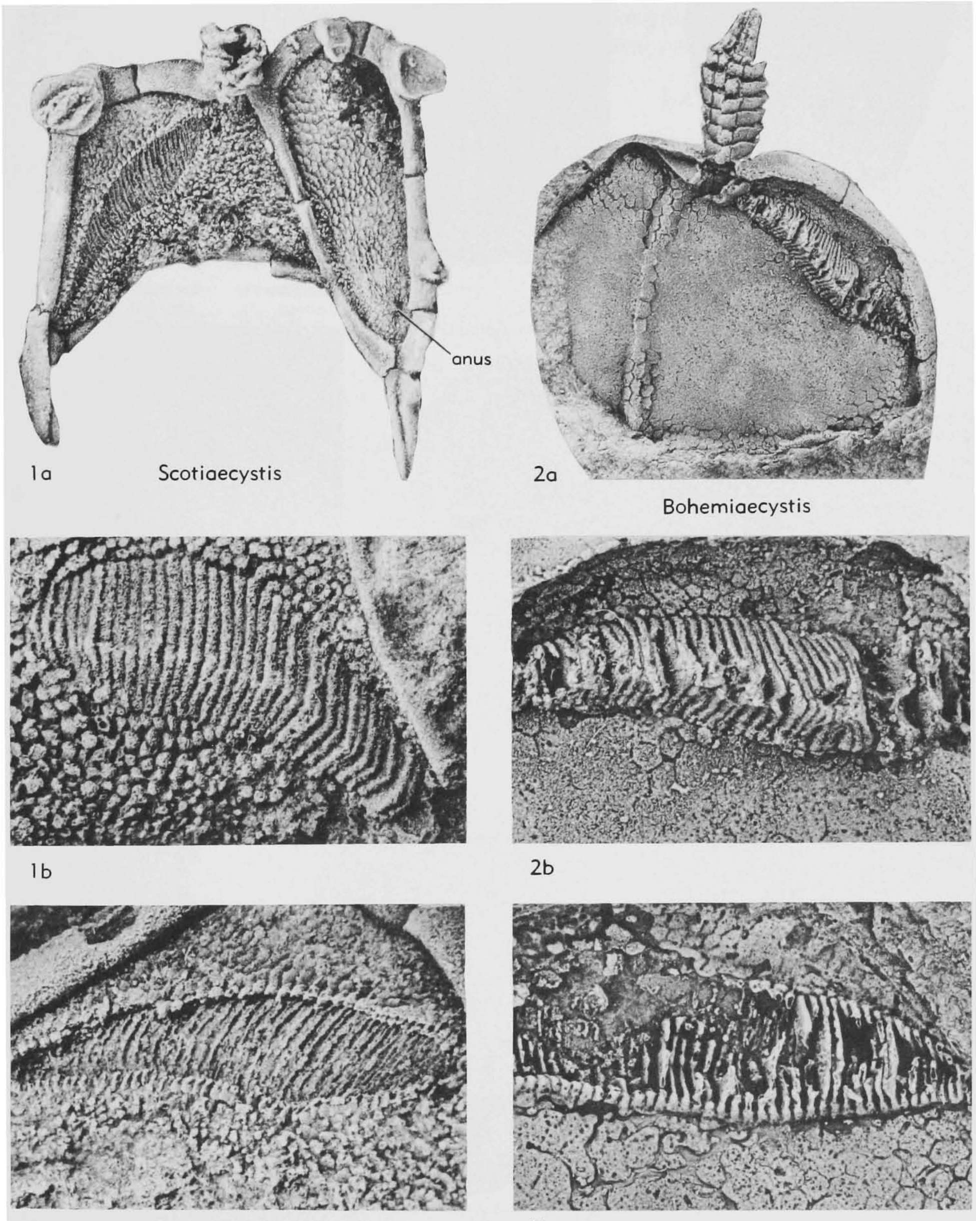

FIG. 338. Lamellipores in Scotiaecystidae.——*1. Scotiaecystis curvata* (BATHER), U.Ord., Scot.; *1a,* theca, superior face, ×2.5 (Ubaghs, n); *1b,c,* lamellate organ, external and internal aspects, ×5 (Ubaghs, n).——*2. Bohemiaecystis bouceki* CASTER, n. genus, n. species, M.Ord., Boh.; *2a,* theca, superior face, ×2 (Ubaghs, n); *2b,c,* lamellate organ, external and internal aspects, ×5 (Ubaghs, n).

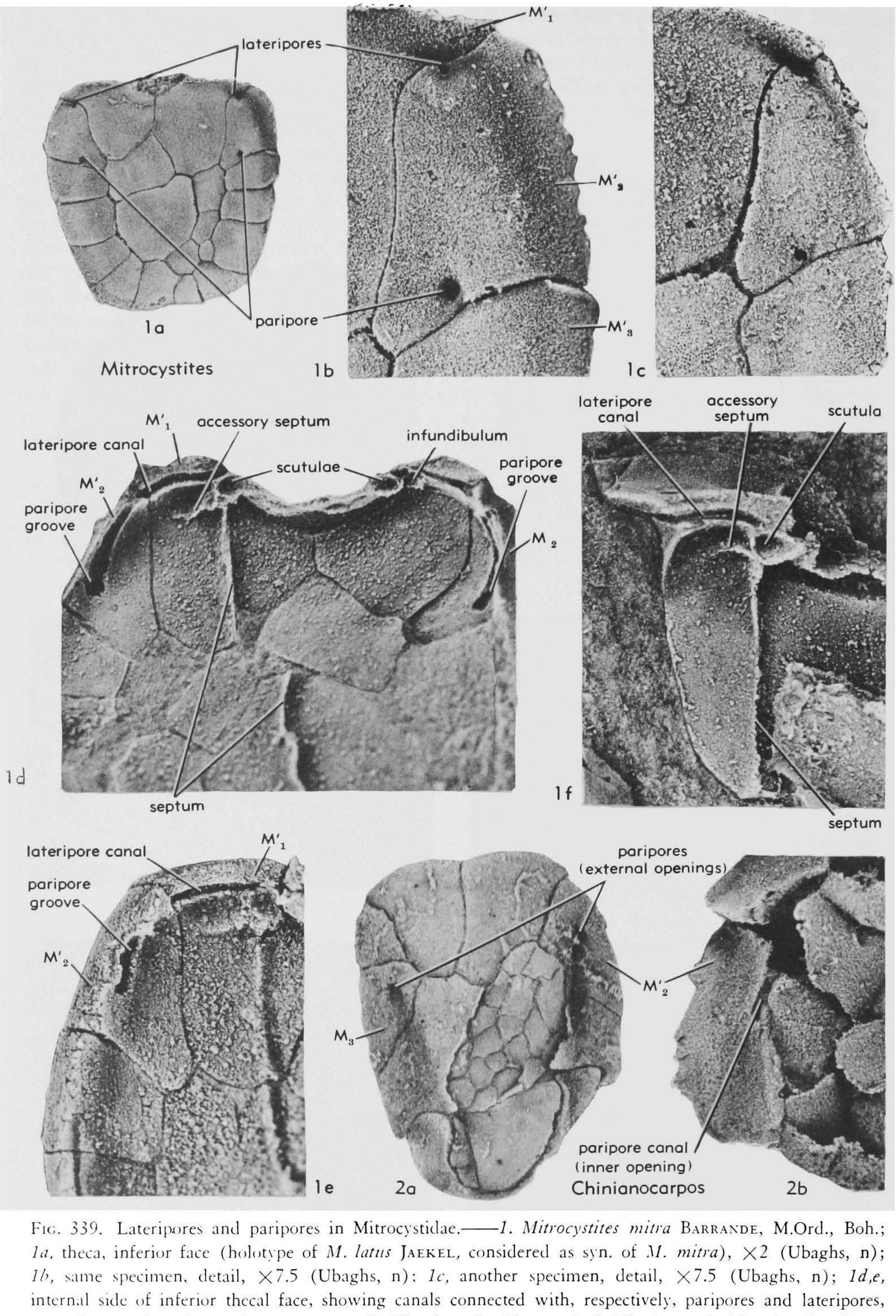

FIG. 339. Lateripores and paripores in Mitrocystidae.——*1. Mitrocystites mitra* BARRANDE, M.Ord., Boh.; *1a*, theca, inferior face (holotype of *M. latus* JAEKEL, considered as syn. of *M. mitra*), ×2 (Ubaghs, n); *1b*, same specimen, detail, ×7.5 (Ubaghs, n); *1c*, another specimen, detail, ×7.5 (Ubaghs, n); *1d,e*, internal side of inferior thecal face, showing canals connected with, respectively, paripores and lateripores, as well as various internal structures, ×5 (Ubaghs, n); *1f*, marginal *M'1*, internal side, showing inner

ance and probable function to those of ordinary crinozoan food grooves.

Study of specimens of *Phyllocystis blayaci* preserved in matrix finer-grained than that associated with *Cothurnocystis elizae,* supplemented by examination of latex casts, indicates that the true structure of the cothurnopores—at least in *P. blayaci*—differs from the interpretation given by Bather. Neither orifice nor cover plates exist. Instead, the entire space enclosed by the cothurnopore rim is occupied by tiny platelets which are paired to form minute cones, each with a minute apical pore (Fig. 336,*2*; 337,*2b*). Therefore cothurnopores seem to be a very complex type of porous organs having no structural relationship with the subvective system of pelmatozoan echinoderms.

LAMELLIPORES

An additional type of openings occurs on the upper thecal face of *Scotiaecystis* and *Bohemiaecystis* (Fig. 338). It consists of narrow slits between vertical calcareous lamellae, very numerous, closely set, and grouped to form elongate rhombic structures similar to the conjunct pore rhombs of some cystoids. The individual slits here are named **lamellipores** and their combined structure a **lamellate organ.** The outer surface of the organ is slightly ridged, whereas its inner surface is apparently concave in *Scotiaecystis* and strongly convex in *Bohemiaecystis* (Fig. 338,*1b,c, 2b,c*). The internal face of each lamella is prolonged into the thecal cavity *(Bohemiaecystis)* or marked by a median very shallow groove that possibly served for attachment of soft partitions on both lateral edges *(Scotiaecystis).* The entire margin of the lamellate organ of *Scotiaecystis* on its internal side bears curious imbricate platelets, not matched by similar ones in *Bohemiaecystis* (Fig. 337,*1c,2c*). Bather *(13,14)* thought that minute irregular plates covered the slits of *Scotiaecystis,* but study of latex casts indicates that this is a misinterpretation probably based on the coarse appearance of external edges of the lamellae. In neither genus have cover plates actually been detected. In an undescribed species from the Lower Ordovician of France, some lamellae appear to be divided into two subequal parts by a very faint suture; this may suggest that originally at least the lamellipores were sutural pores of some sort.

LATERIPORES

Among accessory orifices in the theca of mitrate Stylophora are two types that first were observed by Jaekel *(55)* on the inferior face of *Mitrocystites* (Fig. 339,*1a*). He termed them *Seitenporen* and *paarige Gruben,* names which here are replaced by lateripores and paripores, respectively.

Lateripores comprise two symmetrically placed openings near the anterolateral angles of the lower thecal face, one striding the suture between marginals M_1 and M_2 and the other that of the suture between M'_1 and M'_2. Each opens on the floor of depressions which vary in depth and span in different specimens (Fig. 339,*1b,c*). The depressions commonly are extended parallel to borders of the theca by shallow furrows, one directed obliquely forward toward the main axis of the body and the other backward. The first of these quickly vanishes, but the second may reach as far as M_3 and M'_3, length varying among individuals, and they may even be absent. The pores themselves indent the edges of the marginals next to them more or less deeply. Each is the external orifice of a vertical canal excavated in the upturned sutural surfaces of the marginals (Fig. 339,*1d-f*; 340,*2b*). At the level of the upper edge of these plates each canal is extended horizontally and adaxially by a furrow on the surface of M_1 or M'_1, that is to say along the border of these marginals which supports corresponding adorals. The canals terminate close to special structures (scutulae, infundibulum, described subsequently) without opening into them.

The occurrence of lateripores in *Mitrocystella* is uncertain. Jaekel *(55)* figured

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Fig. 339. [*Explanation continued from facing page.*]

canal from left lateripore, ×5 (Ubaghs, n).——*2. Chinianocarpos thorali* Ubaghs, L.Ord., Fr.; *2a,* theca, inferior face, ×5 (Ubaghs, n); *2b,* inner opening and inner groove of paripore canal on superior edge of marginal M'_2, ×7.5 (Ubaghs, n) (M_2, M_3, right marginals 2 and 3; M'_1, M'_2, left marginals 1 and 2).

them in *M. barrandei,* and CHAUVEL *(30)* thought that probably they were present in *M. incipiens miloni*; but all specimens studied by me show only doubtful indications of them or none at all. On the upper edge of marginal M_1 in two individuals, however, I have observed a furrow comparable to that found in the same posi-

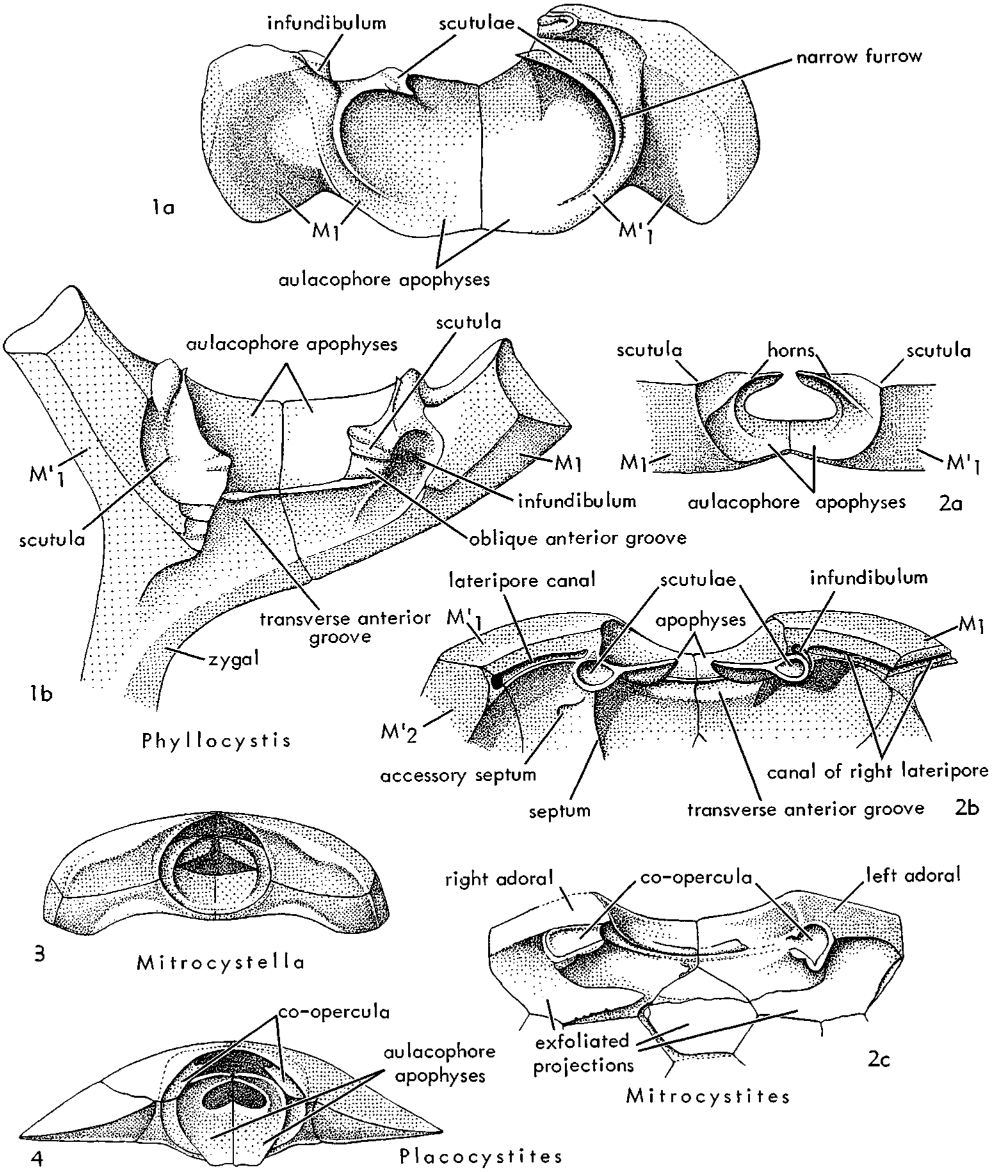

FIG. 340. Internal thecal structures among Stylophora.——*1. Phyllocystis blayaci* THORAL, L.Ord., Fr.; *1a,b,* aulacophore insertion and adjacent structures, in anterior and superior aspects, ×16 (Ubaghs, n).——*2. Mitrocystites mitra* BARRANDE, M.Ord., Boh.; *2a,b,* aulacophore insertion and adjacent structures, in anterior and superior aspects, ×4.4 (Ubaghs, n); *2c,* adoralia, internal side, ×4.4 (Ubaghs, n).——*3. Mitrocystella barrandei* JAEKEL, M.Ord., Boh.; anterior face of theca, ×2.5 (Ubaghs, n).——*4. Placocystites forbesianus* DE KONINCK, Sil. (Wenlock Ser.), Eng.; anterior face of theca, ×1.6 (Ubaghs, n) (M_1, M'_1, median anterior marginals).

tion in *Mitrocystites* communicating with the right lateripore. Perhaps the lateripores of *Mitrocystella,* if they existed, did not open on the inferior face of the theca but instead opened laterally between the marginals and adorals.

The marginals M_1 and M'_1 of *Lagynocystis* are extended well upward and forward by an incurved hornlike portion which laterally encloses the insertion of the aulacophore (see Fig. 341,*1*). The inner side of this horn is hollowed as a trough and probably this trough opened to the exterior by means of a sutural pore located at the front of the theca (see Fig. 342,*2*), possibly equivalent to a lateripore of *Mitrocystites.*

PARIPORES

Symmetrically placed on opposite sides of the main body axis of *Mitrocystites* and commonly somewhat closer to this axis than the lateripores are two small thecal openings named **paripores.** They are not simple excavations on plates of the inferior face, as JAEKEL's term *Gruben* suggests, but true orifices which pierce marginals M_2 and M'_2 near the posterior sutures of these plates (Fig. 339,*1a-c,2a*). Their nature as pores is demonstrated by their connection with a deeply impressed groove on the inner surface of each marginal (Fig. 339,*1d,e*). The grooves extend from the paripores obliquely forward and upward and terminate on the upper edge of these marginals not far from the sutures between them and M_1 and M'_1. The internal grooves vary in length in different specimens, and in at least a part of their course they seem to be separated from the thecal cavity by a thin wall.

The inferior face of the theca of *Chinianocarpos* shows two pores approximately at the centers of marginals M_3 and M'_2 (Fig. 339,*2a*). They are more or less symmetrical with respect to the axial plane and seem undoubtedly to correspond to the paripores of *Mitrocystites,* even though the inner side of the theca shows neither openings nor grooves associated with these pores. Consequently, the conduits that end in the pores must have been included entirely within the thickness of the thecal wall, a conclusion that seems to be confirmed by the presence of two other pores on the upper edges of M_3 and M'_2, each accompanied by a short forward-trending furrow (Fig. 339,*2b*). The latter pores are presumed to represent internal (intrathecal) orifices of conduits leading to the external orifices identified as paripores.

FUNCTION OF ACCESSORY ORIFICES IN STYLOPHORA

Interpretations of the possible function of the several sorts of accessory orifices seen in the Stylophora differ from one another approximately as much as cothurnopores differ from sutural pores, or lamellipores from lateripores and paripores. Such apertures in the Cornuta were considered by BATHER *(13, 14)* to be inhalant orifices for entrance of food particles which were carried by ciliary currents to an internal mouth and his opinion was accepted by CHAUVEL *(30)*, DELPEY *(35)*, TERMIER & TERMIER *(82)*, and CUÉNOT *(32)*. They were judged by JAEKEL *(55)* to represent genital apertures and by GISLÉN *(45)* to be branchial slits formed by intestinal diverticula which coalesced with the surface of the body and opened upon it, the slits serving to strain off water and allow food particles to remain in the digestive tube. Cothurnopores were thought by SPENCER *(80)* to be respiratory pouches which probably lacked any communication with the alimentary canal and were imagined by NICHOLS *(68)* to house respiratory organs which could be retracted and covered by plates when the animal was disturbed.

The first of these interpretations is the most improbable, if one admits that the food-catching organ of stylophorans is the aulacophore, as all evidence indicates. Then, cothurnopores and analogous orifices were not needed for collecting nutrient particles.

JAEKEL *(55)* suggested that cothurnopores were multiple gonopores but furnished no supporting reasons for such an assumption. BATHER *(14)* rejected this interpretation because their structure, in his view, suggested food-intake organs. GISLÉN *(45)* likewise denied the possibility that cothurnopores could be a series of gonopores, for this would demand a corresponding number of gonads within the theca and call for an extremely improbable segmented body. NICHOLS *(68)* pointed out that gonopores

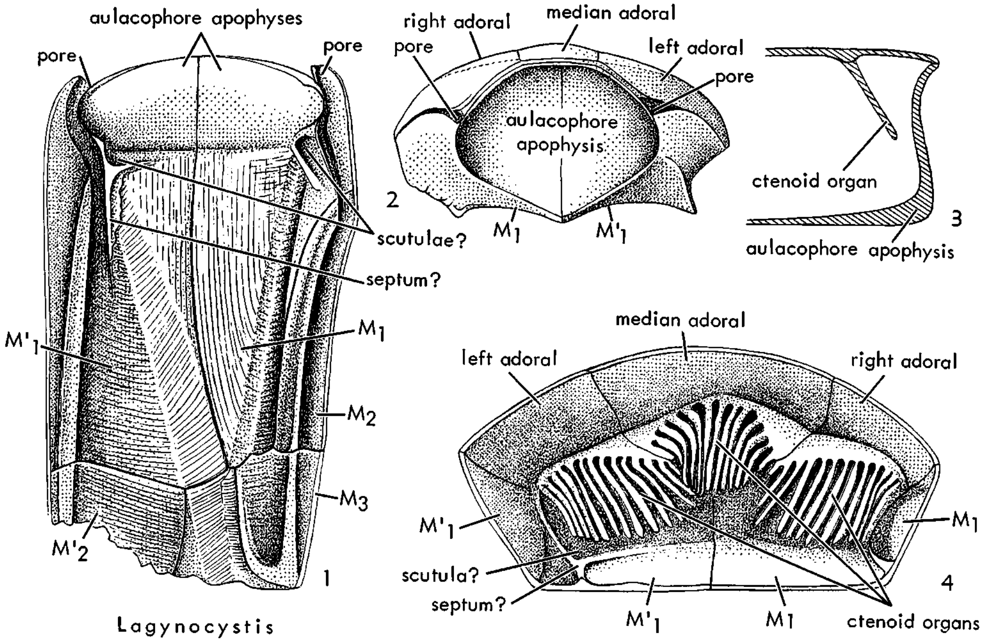

FIG. 341. Morphology of *Lagynocystis pyramidalis* (BARRANDE), M.Ord., Boh.——*1*. Internal anterior thecal structures of inferior face, ×5 (Ubaghs, n).——*2*. Anterior face of theca, ×5.3 (Ubaghs, n).——*3*. Schematic longitudinal median section through anterior part of theca, ×5.3 (Ubaghs, n).——*4*. Ctenoid organs, posterior face, ×8 (Ubaghs, n) (M_1, M_2, M_3, right marginalia 1, 2, 3; M'_1, M'_2, left marginalia 1, 2).

would not require the complex plate structure of cothurnopores and that multiple gonopores surely would not be needed by Stylophora. Arguments like these do not lead to a definitive judgment, especially since secondary metamerism of gonads is a possibility in archaic echinoderms. It is known in rather primitive Deuterostomia (e.g., Enteropneusta).

The possibility that the stylophoran accessory orifices and structures associated with them served a respiratory function is suggested by their analogy with the hydrospires, pore rhombs, and sutural pores of other primitive echinoderms. It seems hardly conceivable however that in *Nevadaecystis* they were used as simple respiratory pores, for respiratory exchange must have been readily accomplished through the many uncalcified areas between the supracentrals. Furthermore their complex morphology and their narrow location in a definite part of the body suggest that they housed specialized structures or were connected with internal organs such as the alimentary canal. This leads to consideration of the possibility that they were branchial openings related to the pharyngeal part of the digestive tract (and not to the intestinal part, as supposed by GISLÉN), since they are close to what seems to have been the mouth region. Other deuterostomian invertebrates (e.g., Stomochorda) have developed pharyngotremy. Such a feature might have arisen as means of securing an outlet for the water that entered the pharynx with the food, but it must also have helped to provide respiratory exchange. The accessory pores of Stylophora, however, could not have been gill slits opening directly to the exterior, for the cothurnopores in many specimens of *Cothurnocystis elizae* penetrate so deeply into the posterolateral (spinal) corner of the theca that the digestive tube would have been bent at an acute angle at the end of the branchial region, which is unlikely. Therefore, if they were connected with the alimentary canal, they could only have been external openings of branchial sacs or diverticles. But in such case why did they require the complex plated structure of cothurnopores, why are they so different from one genus to another and even from one species to another species of the same genus, and how it is possible that they are entirely lacking in some species?

Such questions, which remain without satisfactory answers, show that the evidence at hand does not permit elucidation of the real nature of stylophoran accessory orifices. Among various interpretations that have been proposed none seem conclusive and none (except perhaps BATHER's opinion that the cothurnopores were part of a subvective system) can be definitively rejected.

The significance of accessory thecal orifices in the mitrate Stylophora is as difficult to determine as in genera of the Cornuta. For example, both BATHER *(14,19,20)* and GISLÉN *(45)* judged that the morphological attributes and functions of lateripores and paripores in the Mitrata corresponded to cothurnopores and other accessory orifices in the Cornuta. BATHER, however, viewed the pores as entries leading to the digestive tube, passageways to the mouth being invaginated and transformed into a tunnel. GISLÉN interpreted them as branchial orifices produced by coalescence of the body wall with intestinal respiratory diverticula. CHAUVEL *(30)* and CASTER *(26)* have concluded that the small thecal openings in Mitrata cannot be homologized with the complex pore apparatuses of the Cothurnocystidae. Noting that lateripores and paripores are confined to a small number of mitrate forms, CHAUVEL has supposed that they represent organs for optional communication with the exterior or that they could emit their products in diverse ways without need for specialized openings. On the basis of this he developed his hypothesis that lateripores are gonopores and paripores are hydropores, an opinion shared by CASTER *(26)*.

The observed placements of accessory thecal orifices in *Lagynocystis* possibly throws light on the morphologic and functional significance of these pores in the Mitrata generally. On the ceiling of the anterior part of the thecal cavity in this genus are comblike structures (ctenoid organs) so arranged that they could have served to filter water entering the digestive tube (Fig. 341,*3,4*). A sort of entry appears to have been located just in front of the thecal cavity, water entering it by way of the aulacophore and probably escaping from it by sutural pores located at the base of this organ on both sides of its insertion (Fig. 341,*1,2*). Although ctenoid organs have not been found in other genera, it may be assumed that their general organization differed in no essential way from that of *Lagynocystis*. In genera having a single pair of pores, these may be exhalant orifices, as in *Lagynocystis*. Where two pairs of pores are present, an exhalant function is assignable to one of them and a different (?inhalant, ?genital) function to the other pair. We must recognize, however, that this sort of reasoning rests on structural analogies and that the true significance of pores in Mitrata, like those of Cornuta, remains entirely conjectural.

INTERNAL CHARACTERS OF THECA

INSERTION OF AULACOPHORE

The aulacophore is attached to the middle of the anterior face of the theca. Among cornute genera other than *Ceratocystis* its proximal lower edge overlaps against the forward-projecting parts of marginals M_1 and M'_1 (e.g., *Phyllocystis blayaci*) or abuts against it (e.g., *Cothurnocystis elizae*). In *Ceratocystis* and all Mitrata its base penetrates a cavity provided at the front of the theca. Except for this difference, the mode of insertion of the aulacophore is practically the same in the two groups.

On the inner faces of M_1 and M'_1 are two elevations **(aulacophore apophyses)** which plainly serve for attachment of proximal muscles of the aulacophore (Fig. 330,*2b,3a*; 340,*1a,2a,3,4*). These apophyses are somewhat reduced and separated in *Ceratocystis* but strongly developed and closely adjoined in all other genera where they have been observed. Thick at the base, they become slender upward and on internal molds their former presence is shown by a deep incision which CHAUVEL *(30)* named *sillon pédonculaire*. Symmetrical and similar to one another, the apophyses together form a small cup that is directed forward and somewhat upward.

The just-described cup commonly is divided into four unequal concave fields—

two adaxial large ones and two abaxial small ones—separated by a pair of ridges which are raised from the floor of the cup and ascend in a curve parallel to its lateral borders. The upper extremities of the ridges protrude only a little in the Cornuta but are prolonged in the Mitrata into incurved horns with points convergent on one another and by twisting of their axes the horns overhang the cup (Fig. 340, *1a,2a,b,3,4*). The upper surfaces of the horns, which are relatively flat and expanded slightly, furnish attachment and support for the first plate ring of the aulacophore. In the Mitrata the horns divide the passageway between cavities of the aulacophore and theca into lower and upper orifices which are more or less completely separated from each other (Fig. 340, *3,4*). On the other hand, the passage is not divided in the Cornuta and is large, for the adorals above it generally form an elevated arch (Fig. 340,*2b,3a*).

The nature of these features is somewhat different in *Lagynocystis* (Fig. 341,*1-3*). The apophyses of M_1 and M'_1 in this genus have neither ridges nor horns, and they are produced upward to form a wall or diaphragm that separates the aulacophoral and thecal cavities almost completely. The diaphragm is very peculiarly shaped, since its lower half has a median convex portion between two moderately deep concave lateral portions and its upper half is concave, curving forward and down. Communication between the aulacophoral and thecal cavities could have been effected only over the upper edge of the diphragm. Indeed, the internal (posterior) surface of this partition bears an oblique channel descending toward right from the top, possibly representing the path along which water and food particles entered the thecal cavity. The existence of a similar channel descending leftward has not been determined but seems probable.

SCUTULAE

Near the two abaxial extremities of the upper edges of apophyses belonging to M_1 and M'_1 and symmetrically placed with respect to the main body axis is a pair of concave platforms here named **scutulae** (sing., **scutula**), from the Latin for plate or saucer. Among cornute stylophorans they are quite unequal, that on the right side barely developed. The left scutula comprises the floor of a rather large cavity supported by the upper overhanging edge of M'_1 and the adoral above this marginal. Each scutula is prolonged forward (i.e., toward the aulacophore) by a very narrow furrow which descends along one of the two ridges borne by the concave anterior face of the aulacophore apophyses and becomes lost on the floor of these (Fig. 340,*1a*).

The scutulae of mitrate genera are subequal and well developed (Fig. 340,*2b*). Their outline is subtrigonal and their floor rises from a strongly depressed abaxial corner toward the main body axis, merging insensibly with the upper surface of the apophysis horns. It may be noted in passing that on internal molds each scutular depression is marked by a nipple-like protuberance, which CHAUVEL *(30)*, who was first to observe it, called "mamelon" and interpreted as an unpaired feature on the left side of the theca (*Treatise* orientation). In fact, two mamelons are present, one on either side. Scutulae seem to be lacking in *Ceratocystis,* at least in the form which has been described. In *Lagynocystis* a more or less well-marked depression can be seen at left near the base of the diaphragm between the aulacophoral and thecal cavities (Fig. 341,*1*). This depression, matched on the other side by a much more vague concavity, may be the equivalent of a scutula.

CO-OPERCULA

In at least some Mitrata, structures similar to contour to scutulae, with concave surface bounded by a projecting rim, occur in the inner surface of adoral plates and are inferred to correspond to the scutulae. They are here designated as **co-opercula** (sing., **co-operculum**), from the Latin for lid or cap. Undoubtedly, these structures lie above the scutulae and with them contribute to isolating small parts of the thecal cavity more or less completely (Fig. 340,*2c*). Their described placement and nature have been observed in *Mitrocystites* and they probably occur also in *Placocystites* (Fig. 340,*4*). In *Mitrocystella incipiens miloni* one may see identically placed slight prominences from each of which five wrinkles radiate in as many directions *(30)*, and a similar feature occurs in *Paranacystis (26)*. Comparable structures are lacking in *Lagynocystis, Balanocystites,* and *Anatiferocystis.* Their existence in other genera is unknown, but only in rarest circumstances can the inner side of adoral plates be examined.

The role of co-opercula and scutulae is uncertain. CHAUVEL *(30)* postulated that they marked the placement of ganglionic masses from which nerves extended in thickened thecal elements, such as the wrinkles mentioned in *Microcystella incipiens miloni* and *Paranacystis.* The presence of nerve concentrations in this region of the theca seems reasonable in view of the large development and apparently considerable importance of the proximal musculature of the aulacophore. Thus, one is tempted to consider scutulae as possible sites of nerve centers.

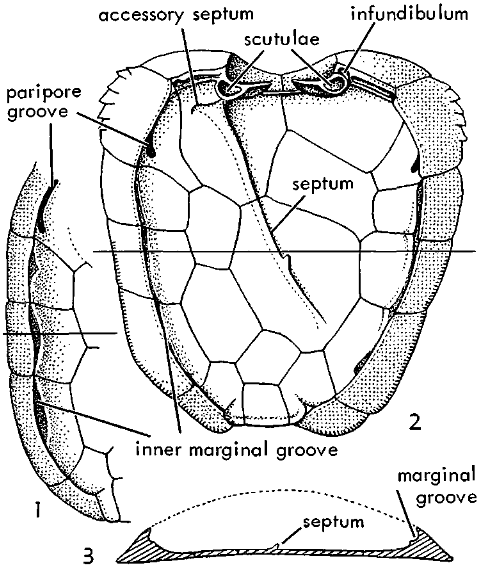

FIG. 342. Internal thecal structures of *Mitrocystites mitra* BARRANDE, M.Ord., Boh.——*1.* Left lateral side of inferior face of theca, slightly oblique view to show inner marginal groove, ×2.2 (Ubaghs, n).——*2.* Inner side of same, ×2.2 (Ubaghs, n).——*3.* Cross section of theca, ×2.2 (Ubaghs, n).

INFUNDIBULUM

A depression excavated between the right scutula and upper edge of the inner side of marginal M_1 is here termed the **infundibulum** (Latin, funnel). Its topographic relationships to the right adoral orifice have been noted previously. In *Ceratocystis* the infundibulum is shallow and rounded, but in other Cornuta (e.g., *Cothurnocystis, Phyllocystis*) and the Mitrata (e.g., *Mitrocystites, Mitrocystella*) wherever observable it is deeply impressed in the substance of the plate (Fig. 340,*1b,2b*). A generally well-marked furrow **(transverse anterior groove)** hollowed on inner surfaces of M_1 and M'_1 runs from its base along the posterior face of the aulacophore apophyses, passes beneath the scutulae, and becomes lost either on the inner surface of the zygal (in Cornuta) or at the origin of the septum (in Mitrata), described subsequently. Another furrow **(oblique anterior groove),** which is much narrower and weaker than the transverse groove, may be seen in some specimens of *Cothurnocystis* and *Phyllocystis.* This leaves the bottom of the infundibulum, rises obliquely, and ends at the summit of the adjacent apophysis just beneath the adaxial angle of the right scutula (Fig. 340, *1b*). Seemingly, it connects the infundibulum with the aulacophore. Finally, in *Ceratocystis* and some specimens of *Phyllocystis* and *Mitrocystella,* a third groove, which generally is very weak, runs from the infundibulum toward the right and disappears on the inner face of the anterior marginals on this side of the theca. Thus it appears that the infundibulum is a sort of center toward which a group of structures converge, and this supports the inference that it exercised a complex role.

If, as previously supposed, the orifice by which the infundibulum communicated with the exterior (right adoral orifice) represents a hydropore, possibly combined with a gonopore, the infundibulum should be the seat of a part of what presently constitutes the axial complex of echinoderms. At any rate, it must have inclosed the hydroporic canal, perhaps accompanied by the small ampulla (remnant of the left axocoel) which in modern echinoderms is placed at its junction with the stone canal.

The anterior oblique groove of stylophorans probably inclosed the hydrocoel branch which penetrated into the aulacophore, and the anterior transverse groove may have contained another hydrocoel diverticle passing beneath the esophagus and possibly corresponding to the stone canal and the periesophageal ring of radially symmetrical echinoderms. The transverse groove may also have contained part of the axial sinus. The faint groove on the inner surface of the right anterior marginals perhaps marks the course of the genital rhachis.

SEPTUM

A low wall or ridge observed on the floor of the thecal cavity of most Mitrata is termed the **septum** (Fig. 335,*1a*; 342,*2,3*). It originates on the M'_1 marginal slightly below the level of the left scutula and runs obliquely toward the right posterior corner of the theca without reaching it. The course of the septum is slightly irregular and its height is steadily reduced toward the rear. It leans toward the left in its anterior part so as to have an asymmetrical transverse section but straightens up in the posterior part, providing a more symmetrical section. Presence of the septum is marked on internal molds by a very characteristic strong incision, which was clearly illustrated by BARRANDE *(2)* and was called *sillon transversal* by CHAUVEL *(30)*, who was the first to draw attention to its existence.

A small **accessory septum** diverges in a general leftward direction near the anterior extremity of the septum (Fig. 340,*2b*; 342, *2*). Also, a diminutive spur is seen on the right side of the septum in the posterior third of its length in some specimens (Fig. 335,*1a*; 342,*2*).

ZYGAL

Among the Cornuta a septum is lacking, but this structure appears to be replaced by a skeletal bar extending from M_1 to the right posterior margin of the lower thecal face. This bar, named the **zygal** *(89)*, is probably equivalent in function to the septum and perhaps also in morphology. The two structures are closely similar in position and connection with other parts of the theca—for example, with the marginal M_1, the anterior transverse groove, and the left scutula—and they show a like oblique placement with respect to the main axis of the body. A median crest runs on the inner surface of the zygal, serving possibly for attachment of organs or mesenteries, as likewise in the case of the septum. The marginal M'_1 of the mitrate *Anatiferocystis*, which is almost identical in form with that of the equivalent marginal of *Cothurnocystis*, is a thin narrow plate that forms a ridge on the floor of the thecal cavity. This is curiously similar to the zygal of the Cornuta.

Ceratocystis and *Nevadaecystis* seem to have neither a zygal nor a septum. *Lagynocystis* also lacks a septum but has a much shorter ridge parallel to the left border of the theca, and possibly this is homologous to the septum seen in other Mitrata (Fig. 341,*1*). According to CASTER *(26)*, the superior face of the theca of *Paranacystis* has an internal groove that externally is marked by a rounded ridge, and this structure may correspond to the normally developed septum.

FUNCTIONS OF SEPTUM AND ZYGAL

CHAUVEL *(30)* viewed the septum of Mitrata as the place of attachment for a mesenteric membrane that supported one of the loops of the digestive tube. He thought to have discovered traces of two other mesenteries, at right and left, running along the marginals, and assigned to them a comparable role in fixation of the digestive canal. Thus he judged that he could determine the approximate course of this organ, concluding that it turned around like that of crinoids and holothuroids. This interpretation lacks the anatomical foundation inferred by CHAUVEL, for what he

FIG. 343. Morphology of aulacophore in cornute Stylophora.——*1-5. Phyllocystis crassimarginata* THORAL, L.Ord., Fr.; *1*, proximal region, stylocone, and proximal part of distal region, aboral face *(1a)*, oral face *(1b)*, ×7 (Ubaghs, n); *2*, stylocone, oral face *(2a)*, left lateral face *(2b)*, longitudinal median section *(2c)*, ×30 (Ubaghs, n); *3*, ossicles of distal region, oral face *(3a)*, left lateral face *(3b)*, proximal face *(3c)*, distal face *(3d)*, ×30 (Ubaghs, n); *4*, two cover plates, inner or oral face, ×30 (Ubaghs, n); *5*, diagrammatic reconstruction of a portion of distal region, with cover plates widely open and water-vascular organs (in black) (M_1, M_2, right marginalia 1, 2; M'_1, M'_2, left marginalia 1, 2).

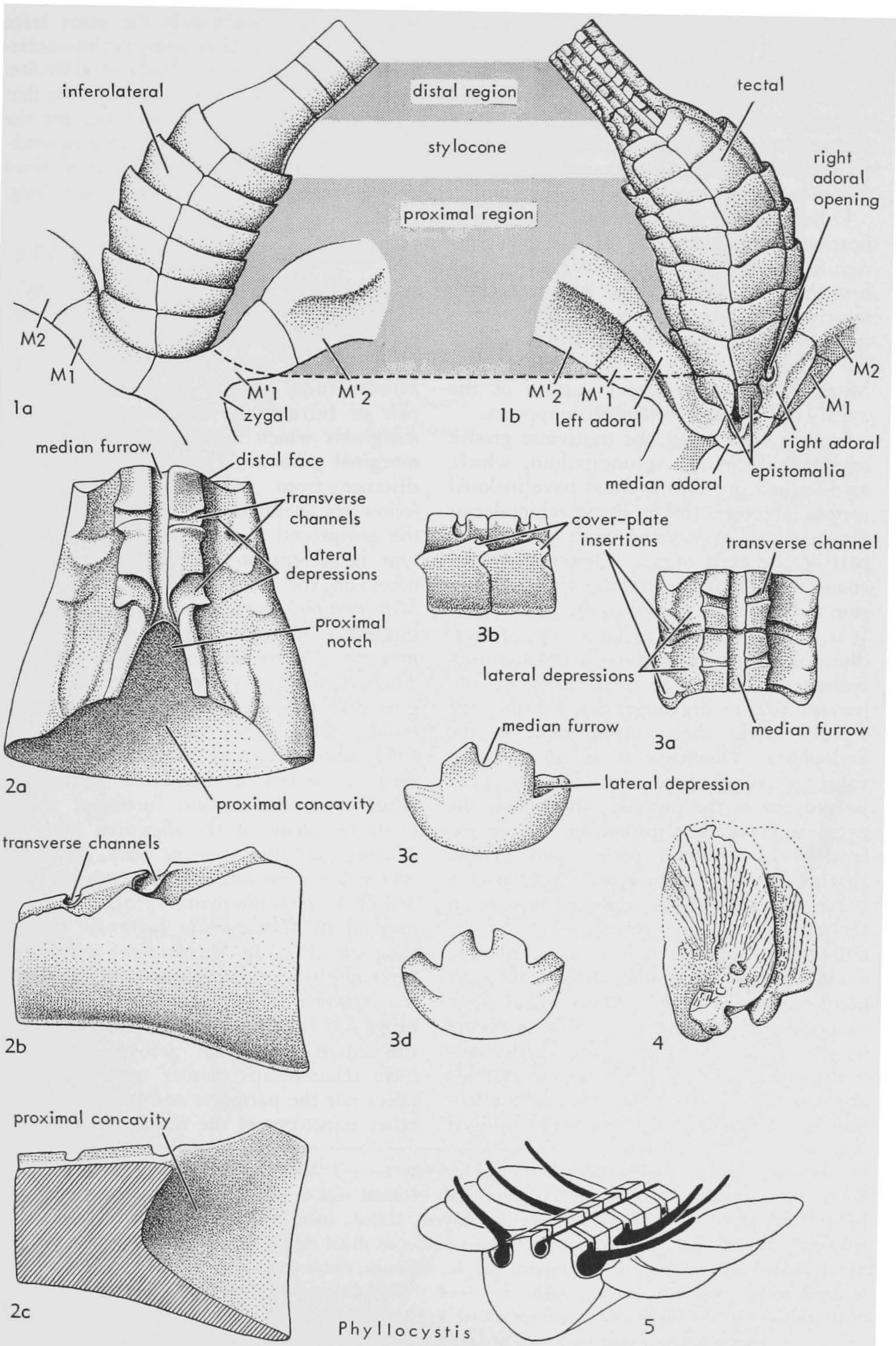

FIG. 343. [*Explanation on facing page.*]

considered to be emplacements of lateral mesenteries in reality represents the projecting adaxial borders of grooves excavated on the inner surface of the lateral marginals (Fig. 335,*1a*). CASTER *(26)*, who inferred a similar function of the septum, arrived at a much simpler course for the digestive tube, almost in a straight line.

Other considerations perhaps allow clarification in some degree of the morphological significance of the septum. We may recall first the close relationships which seem to associate this structure with the anterior transverse groove. This groove leads to the point of origin of the septum (in Mitrata) or to the upper surface of the zygal (in Cornuta), where it disappears.

On the other hand, the transverse groove originates from the infundibulum, which, as discussed previously, could have inclosed certain structures that in living echinoderms are narrowly associated with the aboral part of the axial organ. These anatomical connections seem to indicate that the septum also could be related to the axial organ. It is well known that in larvae the primordium of this organ appears in the accessory mesenteries and that these play an important role in organogenesis. Possibly the septum marks their emplacement in the Stylophora. Doubtless it is not without value to recall here that BATHER *(13)* judged one of the possible functions of the zygal to have been protection of the extensions of a blood plexus and genital rhachis, in addition to a prolongation of a nerve center which he supposed to exist in the opening of the proximal region of the aulacophore—that is to say in summation, a kind of axial complex. Finally, we may point out that a more or less vertical ridge suggestive of the septum in Mitrata occurs on the inner side of the theca in the posterior interray of certain Paleozoic cystoids and crinoids. JAEKEL *(55)*, who drew attention to the presence of this ridge, judged that it had approximately the same trace as that of the vertical mesenteries—accessory mesenteries—in the larva of *Antedon*. For all these reasons we may postulate that the septum of stylophorans served for the attachment of mesenteric membranes, within the thickness of which the axial sinus and axial organ possibly could find lodgment.

INTERNAL MARGINAL GROOVES

In addition to already described stylophoran grooves or canals, such as the paripore grooves, lateripore canals, and transverse anterior groove, some genera of the Mitrata (and possibly Cornuta) possess a pair of furrows on the inner side of the marginals which here are named **internal marginal grooves.** They begin at variable distance from the front of the theca, follow its lateral borders, and disappear in the periproctal region (Fig. 335,*1a*; 342). One is present on the right side and the other on the left. They are constant in *Mitrocystites,* sporadic in *Mitrocystella,* and unknown in other mitrates. [They appear to exist also in an undescribed cornute.] Their somewhat projecting adaxial margins may produce narrow slits on internal molds, called *sillons latéraux* by CHAUVEL *(30)*, who discovered them and interpreted them as traces of mesenteric membranes which with the septum furnished attachment for loops of the digestive tube. In *Mitrocystites* the grooves tend to vanish where they cross intermarginal sutures (Fig. 342,*1*). In opposite manner, they are clearly marked in *Mitrocystella barrandei* only at these crossings. In *M. incipiens miloni* features of the grooves are unmodified where they traverse sutures between the marginals (Fig. 335,*1a*). At their anterior extremity the internal marginal grooves appear to have relationships neither with the lateripores nor the paripores and indeed with no other structures of the theca. They cannot

FIG. 344. Morphology of aulacophore in mitrate Stylophora.——*1. Mitrocystella barrandei* JAEKEL, M.Ord., Boh.; proximal region, stylocone and proximal part of distal region; *1a,* oral face; *1b,* left lateral face, ×7.5 (Ubaghs, n).——*2. Enoploura wetherbyi* CASTER, U.Ord., Ind.; ×1 (90).——*3. Mitrocystites mitra* BARRANDE, M.Ord., Boh.; *3a,* stylocone and three ossicles of distal region, left lateral face, ×15 (Ubaghs, n); *3b,* stylocone, oral face, ×10 (Ubaghs, n); *3c,* stylocone, distal face, ×15 (Ubaghs, n); *3d,* ossicles of distal region, oral face, ×15 (Ubaghs, n).——*4. Peltocystis cornuta* THORAL, L.Ord., Fr.; ossicle of distal region in laterodistal *(4a)*, lateroproximal *(4b)*, and oral *(4c)* views, ×30 (Ubaghs, n); *4d,* diagrammatic reconstruction of two articulated ossicles to show how they can move.

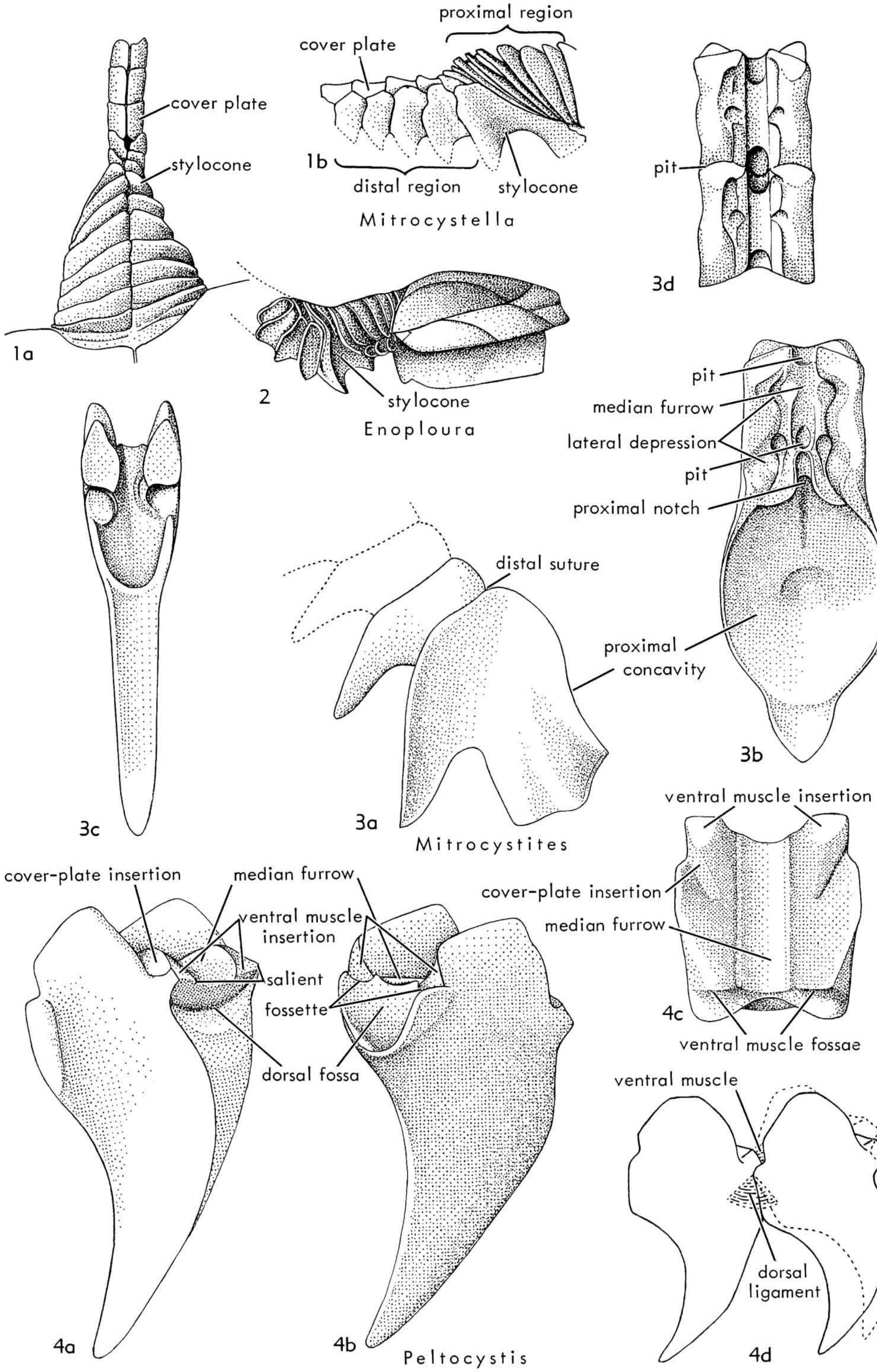

FIG. 344. [*Explanation on facing page.*]

be interpreted reasonably as these invaginated subvective grooves which Bather *(14)* supposed to exist in *Mitrocystites*. Perhaps they are the passageways of nerves leading to the rectum or some other posterior organ. Their actual function is unknown.

CTENOID ORGANS

Structures composed of lamellae in arrangements that resemble the teeth of a comb are here named **ctenoid organs.** They were discovered by Chauvel *(30)* in *Lagynocystis pyramidalis* and as yet are unknown in other stylophoran genera. They occur in three groups, one median and the other two placed laterally (Fig. 341,*4*). Each ctenoid organ is supported by a ridge on the inner surface of an adoral and end to end the three ridges together form an arc which is thin at its center and extremities but thickened at crossings of sutures between the adorals. The lamellae of the organs converge at the same time in three directions—downward, forward, and toward the median axis of the body. Thus they form a sort of grill or filter in the anterior part of the theca. Previously evoked is the possible existence of an atrium in front of the thecal cavity in which a water current charged with food particles must have been induced by the aulacophore, perhaps emerging through exhalant orifices at right and left. The function of the ctenoid organs then would have been to catch food particles suspended in the water, agglutinate them with mucus, and conduct them toward the mouth. The possibility that the organs exercised a respiratory function also is not to be excluded, for they may have served as support for gill structures.

AULACOPHORE

The name **aulacophore** has been introduced by Ubaghs *(88)* for the appendage of Stylophora that formerly was thought to be the same as the stele in Homostelea and Homoiostelea. The designation is morphologically descriptive in indicating that the appendage bears a groove (Greek, *aulacos,* furrow or groove, +*phoros,* bearer). It is in no sense a peduncular process or stem, but is here interpreted as a brachial appendage provided with an ambulacrum. Its unique nature warrants the adoption of a special morphological term.

The aulacophore comprises three parts—(1) a proximal hollow region which is inflated, relatively large, and protected by imbricated plates or by quadripartite rings generally one inserted within another, (2) a massive intermediate piece named the **stylocone,** and (3) a distal region composed of a single series of massive ossicles placed end to end and each provided with a pair of cover plates (Fig. 325; 343,*1a,b*; 344, *1a,b*).

PROXIMAL REGION

Next to the theca is part of the aulacophore defined as the **proximal region.** It encloses a wide hollow space which communicates with the thecal cavity. A covering composed of numerous imbricated scale-like plates is seen in *Ceratocystis* and *Lagynocystis* (see Fig. 345, 354), but in other genera, where known, of a fixed number of four-piece rings which generally are telescoped together, but not invariably so. The ring elements are subequal in the Mitrata, with sutures between them located in mid-superior, mid-inferior, and two mid-lateral positions. The pieces are unequal in size in the Cornuta but symmetrically disposed with respect to the aulacophore plane of symmetry, which coincides with the sutures between plates on the upper and lower sides. Each lateral half ring contains a small plate, above, here called **tectal,** and a large one, below, here termed **inferolateral,** the tectal covering less than half of the mid-part of the upper surface, whereas the inferolateral not only covers an entire half of the lower surface but much of a side as well (Fig. 343,*1a,b*). Each ring was joined to its contiguous neighbor or neighbors by muscles and probably also by ligaments. In addition, powerful muscles attached them in a proximal direction to the inner apophyses of marginals M_1 and M'_1 and in a distal direction to the stylocone. Without doubt, the proximal region of the aulacophore enjoyed great freedom of movement both vertically and laterally and probably it controlled general movements of the whole appendage.

STYLOCONE

The intermediate part of the aulacophore, interposed between its proximal and distal regions, is the unique ossicle named *stylocone*[1] (*Styloconus* or *Styloid* of JAEKEL, *55*). Lengthwise, it is a minor portion of the appendage, though important in reducing within a very short distance the broad width of the proximal region to the narrow diameter of the distal region. Its constant presence and complex nature prove that it must have had considerable functional significance. Its structure is essentially the same in cornute and mitrate Stylophora, thus denying a morphological basis for JAEKEL's *(55)* usage of stylocone for Cornuta and styloid for Mitrata. Nevertheless, the stylocones of the two groups are readily distinguished by external characters, whether viewed from the inferior face or in profile. It appears smooth and regularly rounded in the Cornuta (Fig. 343,*1a,b, 2a-c*), whereas in the Mitrata it bears diverse excrescences—1) a narrow crest in the plane of symmetry, 2) a single long spine incurved toward the theca (e.g., *Mitrocystites, Chinianocarpos*), 3) a series of points (e.g., to six in *Lagynocystis*), or 4) transverse blades resembling plowshares (e.g., *Enoploura*) (Fig. 344,*1-3*). The excrescences just mentioned doubtless served as fulcra for lifting the distal region, which normally was raised at an angle (Fig. 344,*2,3a*). According to CASTER *(43)*, the stylocone blades of *Enoploura* contain coarse radial canals of unknown function and morphological significance.

The stylocone has the general form of a funnel with excavated relatively wide proximal part and narrower semicylindrical distal part. The obliquely chiseled proximal face (more so in Mitrata than Cornuta) is occupied entirely by a deep concavity directed upward and toward the theca (Fig. 343, *2a,c*; 344,*3b*). It served for insertion of the distal extremities of muscles occupying a part of the cavity of aulacophoral proximal region. The distal face of the stylocone in Cornuta is perpendicular to the longitudinal axis of the ossicle, serving for a little or not at all differentiated sort of ligamentary articulation with the proximal plate of the distal region (Fig. 343,*2b*). In the Mitrata this distal stylocone face is oblique and directed upward (Fig. 343,*3a*) and is joined to the first ossicle of the distal region by a very highly differentiated articulation, like those uniting the distal ossicles with one another (Fig. 344,*3c*).

In Mitrata the rather short upper face of the stylocone is framed by steep elevated walls which give it the appearance of a rather narrow throat (Fig. 344,*3b*). The walls are much lower in the Cornuta, being less elevated even than the axial structures which they border on each side (Fig. 343, *2a*). In both Cornuta and Mitrata a deep notch, bordered by raised lips, occurs on the proximal border of the upper face at its middle. This notch leads to a groove **(median furrow)** which extends to the distal extremity of the stylocone, passing there onto ossicles of the distal region. The groove is somewhat raised in the Cornuta and limited by relatively wide rims (Fig. 343,*2a*). It is flanked from place to place by **lateral depressions** and at two points both margins of the groove are generally interrupted by a short **transverse channel** leading to lateral depressions on either side. In Mitrata the median furrow lies in the middle of the throat, which occupies the entire width of the upper face (Fig. 344,*3b*). It is not elevated noticeably and is bordered on each side by a very narrow ridge. The ridges are continuous in some genera (e.g., *Peltocystis*) but interrupted at two points on each side in others (e.g., *Mitrocystites*). Where interrupted, the furrow communicates with small lateral depressions, two on each side, which lie slightly lower than the furrow, but they are not observed in *Peltocystis*. It may be noted also that in some Mitrata (e.g., *Mitrocystites, Mitrocystella*) a small pit or fossa occurs in the floor of the groove at each end, the distal one being divided by the suture between stylocone and first ossicle of the distal region (Fig. 344,*3b*).

The upper face of the stylocone was protected by plates, four pairs of them having been counted in Cornuta. The two proximal pairs closely resemble the median upper plates in rings of the adjacent aula-

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[1] GILL & CASTER (43) report that the stylocone of *Victoriacystis* has multiple segments. Probably only the most proximal of these represents the real stylocone, others belonging to the distal region. Also, CASTER (43) has described the stylocone of *Enoploura* as composed of several ossicles which become dissociated upon weathering. If correct, this suggests that the stylocone originally was a composite structure resulting from differentiation and fusing of the most proximal ossicles of the distal region.

cophoral proximal region, and they form the ceiling, probably fixed, of the excavated proximal part of the stylocone (Fig. 343, *1b*). The two distal pairs, which overlie the groove and accompanying structures, are mobile plates identical to the cover plates of the aulacophoral distal region (Fig. 343, *4*). A large part of the upper face of the stylocone in Mitrata is covered by rings or half rings of the adjacent aulacophoral proximal region, the remainder being protected by a pair of cover plates (Fig. 344, *1b,2*). This explains why JAEKEL *(55)* thought that the stylocone in the Mitrata was only a half cylinder inserted in the lower face of the organ, and not a solid piece that just as in the Cornuta joins the proximal and distal regions of the aulacophore.

DISTAL REGION

Invariably, the longest and narrowest part of the aulacophore is found in the **distal region.** Its diameter at the extremity nearest to the theca equals that of the distal end of the stylocone. Away from this point it tapers more or less rapidly to its free end. It is entirely composed of semicylindrical, bilaterally symmetrical, very short ossicles which abut end to end and are protected by a pair of cover plates. The ossicles of this region in the Cornuta have rounded inferior and lateral faces (Fig. 343, *3a-d*), whereas their upper face carries an elevated median grove or furrow which generally connects by a short transverse canal with a lateral depression on each side. The median groove is an extension of the similar furrow on the stylocone. The cover plates were movable and each articulated with a salient on the outer margin of the ossicle beneath it. These plates resemble scales strongly imbricated in the distal direction (Fig. 343,*4*).

Ossicles of the aulacophoral distal region of the Cornuta were closely joined by synostosis or by barely differentiated articulations (Fig. 343,*3c,d*). The distal face of each bears two lateral salients which fit into hollowed fossettes on the proximal face of its next-placed neighbor. Slight movement in a vertical plane was permitted by this rudimentary sort of hingement. The distal region must have been relatively rigid and certainly incapable of enrolling on itself.

Construction of the distal-region ossicles is essentially the same in all stylophorans, but in the Mitrata some distinctive traits are seen (Fig. 344,*3d, 4a,b*). Firstly, the lower side of each ossicle bears a spine, point, or blade in the plane of symmetry, ordinarily incurved toward the theca; the projections are most prominent on proximal segments, diminishing and disappearing distally.

Secondly, the upper face of the ossicles, like the upper face of the stylocone, shows 1) a median furrow sunk between high lateral walls and bordered by fine ridges, 2) a shallow short depression on each side of the groove (though seemingly not in all forms), and 3) presence of a fossa or pit in the floor of the groove at the level of each suture, at least in some genera (Fig. 344,*3d*). Thirdly, the cover plates attached at outer borders of the ossicles alternate somewhat with these plates and are not imbricated when the arm was extended (Fig. 344,*1b*). Finally, the ossicles are joined to one another by very well-developed articulations, having on distal faces a pair of salients slightly below the median furrow and on proximal faces corresponding fossettes to receive these projections (Fig. 344,*4a,b*). The salients determine an articulatory axis around which the ossicle could pivot (Fig. 344,*4d*) and above each salient and fossette is a small triangular area which marks the insertion of a flexing **ventral muscle.** A large unpaired concavity **(dorsal fossa)** is seen on both the distal and proximal articular faces of the ossicles below the articulation axis. These concavities doubtless served to accommodate an elastic **dorsal ligament** which operated in opposition to the flexing muscles. The articulations afforded arm movements in a vertical plane. The aulacophore of Mitrata frequently is seen to be recurved toward the superior face of the theca and it may even be enrolled in a spiral, with spines of its inferior face turned outward as though in an attitude of defense.

FUNCTIONS OF AULACOPHORE

How may structures of the aulacophore just described be interpreted? The median furrow, short transverse channels, lateral depressions, and movable cover plates of its upper surface comprise an ensemble nowhere found among echinoderms except in their ambulacra. In living stylophorans, the median furrow must have housed an axial ambulacral canal, and in addition, it probably carried nerve, blood, and coelomic structures such as accompany the canal in living echinoderms. The lateral depressions are presumed to have received tentacles connected to the axial canal by short branches placed in the transverse channels (Fig. 343,*5*). In at least some genera, a distinct widening of the transverse channels at their abaxial extremity (Fig. 343, *2a,3a*) suggests the possible existence of ampulla-like expansions at the base of tentacles such as those present in the podia of some Recent ophiuroids. The sutural pits on the floor of the median groove of some Mitrata could have accommodated saclike expansions of the axial canal, serving as reservoirs lodged in similar hollow cavities of the vertebrae in some living ophiuroids.

The descriptions and discussion which have been given support the following important conclusions. 1) The aulacophore of Stylophora is not a tail, column, or peduncle, for its organization lacks the structures and indicated functions belonging to these morphological features—in particular having nothing in common with the stele of the Homostelea and Homoiostelea. 2) The aulacophore is a mobile brachial process which bears an ambulacrum, and the main function of this ambulacrum can hardly have been other than collection of food particles and transport of them to the mouth. 3) The peculiar structure of the aulacophore and lack of its association with similar appendages borne by any one stylophoran cannot be homologized with the multiple radial brachial processes of other echinoderms. 4) The aulacophore differs structurally from the single arm of the Homoiostelea. 5) The aulacophores of Cornuta and Mitrata are very similar and entirely homologous to one another.

GENERAL ORGANIZATION OF BODY

Information concerning the anatomy of stylophorans derived from study of their skeletal remains evidently is insufficient for reconstruction in detail of the soft parts of these animals. Even so, it may not be too ambitious an undertaking to seek determination of the main divisions of the body and recognition of their morphological significance.

In order to attain these goals, it would be fruitless to depend heavily on comparisons with living adult echinoderms, which by acquisition of radial symmetry have been transformed profoundly and seem to be utterly different. It is permissible, however, to refer to the ontogenetic stages which precede the appearance of this symmetry among them and which, as apparently in the Stylophora, are characterized by pronounced asymmetry in development of their structures.

The skeleton of stylophorans encloses two clearly distinct cavities—that of the theca and that of the proximal region of the aulacophore. It is probable that the first comprised the general body cavity produced by the somatocoels and the second perhaps corresponded to the axocoels and hydrocoel, which in echinoderms always are closely associated. Data supporting this hypothesis are presented in the following paragraphs.

The structure of the aulacophore indicates that this organ served to support a tentacle-bearing diverticle such as only the hydrocoel produces in echinoderms. If this interpretation is correct, the aulacophore diverticle could only depend from the left hydrocoel, for the right one never plays any role in the organogenesis of echinoderms. The aulacophore is fixed to the middle of the front border of the theca, however, and not to its left half. This requires us to suppose that it has migrated, along with the hydrocoel diverticle enclosed by it, so as to become placed in the main axis of the body. Such a movement doubtless represents a phenomenon of secondary symmetrization, comparable to that shown by larvae of modern echinoderms, which, following a stage of asymmetry, tend to develop bilateral symmetry (*sekundär symmetrische Stufe* of HEIDER). It is noteworthy that this tendency toward acquisition of bilateral symmetry with respect to the principal body axis, invariably discernible in the Stylophora, may be very conspicuous (e.g., Anomalocystitida).

Furthermore, the inferred stylophoran hydrocoel appears to have opened outward through an orifice in the right adoral plate. This coelomic compartment, from which the aulacophoral diverticle extended, must have been localized, then, in the immediate vicinity of the attachment of the aulacophore to the theca. In larvae, the hydrocoel lies behind the axocoel and is more or less distinct from it. In adults, the axocoel produces structures (e.g., ampulla at junction of stone canal and hydropore canal, madreporic vesicle, axial sinus) that remain closely associated with unpaired organs (e.g., madreporite, stone canal) of the hydrocoel apparatus. Thus is developed a complex of organs that originates in the anterior and median coelomic compartments of the larva. Perhaps, then, it is not a pure coincidence that the part of the body of stylophorans located in the immediate proximity of the aulacophore attachment is also characterized by a large complex of internal skeletal structures (e.g., infundibulum, anterior transverse groove, origin of septum, scutulae, co-opercula, diverse canals and grooves leading to external orifices or toward posterior regions of the body). This complex, suggestive of that found in the mesosomal region of enteropneusts and pterobranchs, may include (for reasons given in previous chapters) a diversity of organs derived from the two axocoels and left hydrocoel, as well as ganglionic masses needed in particular for control of the aulacophore muscles.

The remaining part of the thecal interior undoubtedly was occupied by the digestive tube, which can be localized with some degree of certainty by the principal thecal orifices, by the gonads, and by the general cavity derived from the larval somatocoels. This cavity must have been divided asymmetrically in diagonal manner, as shown by the course of the septum or zygal, which doubtless furnished attachment for mesenteric membranes and which may have marked, as suggested previously, the position of some elongate unpaired structure such as the axial sinus and axial organ.

We may see, then, that several diverse lines of evidence seem to support the hypothesis initially offered in this discussion. Thus, the two main parts of the body in Stylophora would be axohydrocoelian (in front) and somatocoelian (behind). The first would include the proximal region of the aulacophore and part of the thecal cavity closely adjacent to the aulacophoral attachment, and the second would include the large remaining part of the thecal cavity.

This interpretation allows the fundamental organization of Stylophora to be correlated easily with that of the presumed ancestral echinoderm suggested by embryology. Derived from this ancestor (a least distorted picture of which possibly is offered by the pterobranch *Cephalodiscus*) would be the unattached stylophoran mode of life, the division of the body into two or three successive coelomic regions—separation of the axocoel and hydrocoel is far from well defined in all echinoderms—and the presence of one of an antecedent pair of lophophorian arms, an arm (represented by the aulacophore) which from the outset must have assured nutrition and respiration for the animal. The main transformations marking the passage from this hypothetical ancestor to the Stylophora would be connected with the appearance and accentuation of an asymmetry which would be the same as that demonstrated in the ontogeny of living echinoderms from the beginning of larval development or even from the egg.

Finally, what was the morphological orientation of the body of Stylophora? If attention is directed to the natural position of these organisms during life, distinctions can be made between a superior and inferior face, between an anterior extremity marked by the mouth and a posterior extremity marked by the anus, and between a right side and a left side. These terms evidently have only topographic significance. Orientation in terms of morphology may be very different. If the principal orifices of the theca are adopted for reference, the location of the anus may be considered as posterior, that of the mouth (directed forward and upward) as both anterior and ventral, and that of the hydropore—its most primitive position seemingly observed in *Ceratocystis*—as indicating the dorsal face and left side. From this viewpoint, the conclusion may be reached that the Stylophora reposed on their morphologically dorsal face and that their morphologically ventral surface was directed upward. This conclusion would be permissible if these organisms had maintained the orientation of the bilaterally symmetrical form supposed to exist in echinoderms at their beginning. In fact, the stylophorans are asymmetrical, which proves that their ancestors, like those of other echinoderms, had undergone transformations that could have been accompanied by more or less considerable displacements of the orifices toward faces of the body originally defined as lateral. It follows that their median plane may very well have been newly acquired, not coincident with the ancestral median plane but cutting across it at an indeterminable angle. Likewise, the upper face of stylophorans does not coincide necessarily with the ventral surface of the antecedent primitive form, or the lower face with its dorsal surface. In sum, the problems of morphological orientation of the Stylophora are the same as for other echinoderms and it would be vain to seek in their complex and transformed organization axes of symmetry belonging to the source of the phylum.

GLOSSARY OF MORPHOLOGICAL TERMS USED FOR STYLOPHORA

[Terms considered as synonyms or terms of lesser importance are printed in italics]

abaxial. Directed away from main axis.

aboral. Applied to surface (or structure) of aulacophore situated on face opposite that bearing median groove (*syn.* dorsal, lower, or inferior face of aulacophore).

accessory septum. Small left branch of septum near its anterior extremity.

adaxial. Directed toward main axis.

adcolumnal. See adoral.

adoral (pl., **adorals, adoralia**). One of two or three upper thecal plates which frame aulacophore insertion.

anomalocystid plate. Special infracentral plate truncating left posterior corner of largest infracentral, distinguished by its rather great constancy among Mitrata.

anterior. Applied to part of theca (or thecal structure) located at or adjacent to aulacophore insertion; front of theca; directed toward anterior margin; opposite to posterior.

anterior margin. Part of margin in middle of which aulacophore is inserted.

anus. Vent of alimentary canal.

apophysis (**apophyses**). *See* aulacophore apophysis (apophyses).

aulacophore. Single jointed exothecal appendage, here interpreted as brachial process carrying ambulacrum.

aulacophore apophysis. Inner projection for attachment of aulacophore proximal muscles, carried by each of two median anterior marginals.

carapace. Upper face of theca in Mitrata.

central (centralia). Plate(s) located inside marginal framework either on lower or upper face of theca (*see* supracentral and infracentral).

co-operculum (pl., **co-opercula**). Endoskeletal structure on internal face of adoral plate, serving as partial lid to corresponding scutula; observed in a few mitrates.

cothurnopore. Specialized porous organ in right anterior upper thecal area of *Cothurnocystis* and other Cornuta.

cover plate. One of many small plates which protect oral face of stylocone and ossicles of distal region in aulacophore.

ctenoid organ. Comblike calcareous structure attached to inner side of adorals and protruding into thecal cavity in *Lagynocystis.*

dextrolateral. Infracentral located on right side.

digital. Spine attached to marginal framework directly on left of anal opening of *Cothurnocystis.*

distal. Direction away from insertion in aulacophore or any appendage; opposite of proximal.

dorsal. See aboral.

épibasale. See adoral.

epicentral (epicentralia). See supracentral (supracentralia).

epistomal (epistomalia). Seemingly movable plate(s) in small triangular space between adorals and proximal ring segment of aulacophore.

extension plane. Plane in which theca is depressed (*syn.,* extensiplane).

extensiplane. See extension plane.

frame (framework). Series of plates which constitute margin of theca, i.e., marginals and (in Cornuta) adorals.

glossal. Spine attached to marginal frame directly on right of anal opening in *Cothurnocystis.*

hypocentral (hypocentralia). See infracentral (infracentralia).

inferior. Directed toward inferior face of theca.

inferior face. Flat or concave side of theca, presumably toward sea bottom in life position (*syn.,* lower, reverse).

inferolateral. Lower plate of half ring in proximal region of aulacophore.

infracentral (infracentralia). Plate(s) located inside marginal framework on lower face of theca.

infundibulum. Distinct depression between right scutula and inner upper edge of marginal M_1, located just below and probably related to right adoral opening.

internal marginal groove. Furrow on inner side of lateral marginals in some Mitrata.

lamellate organ. All lamellipores taken together.

lamellipore. Elongated very narrow slit in right anterior upper thecal area in Scotiaecystidae.

lateral depression. Elongate depression on oral face of stylocone and ossicles of distal region of aulacophore in which ambulacral tentacle is presumed to have been located.

lateripore. One of two openings in *Mitrocystites,* symmetrically located on lower thecal face near anterolateral corners, on sutures uniting two first right or left marginals (*syn., Seitenpore*).

left. Referring to side corresponding with left of observer, when theca is placed on its lower face, with aulacophore away; opposite of right.

lower face. *See* inferior face.

main axis. Straight line which corresponds to intersection of extension plane with plane of bilateral symmetry of aulacophore and which is prolonged across theca.

marginal (marginalia). Ossicle(s) of a series framing theca (except adoral).

median groove. Axial furrow along oral surface of stylocone and ossicles of distal region of aulacophore, presumably housing axial ambulacral structures.

median plane. Plane passing through main axis and perpendicular to extension plane (*syn.,* symmetry plane).

mouth. Entrance to alimentary canal, presumably located at or near proximal end of aulacophore inside theca.

oblique anterior groove. Faint groove uniting infundibulum to aulacophore insertion.

obverse. See superior.

oral. Applied to face of aulacophore which carries median groove (*syn.,* ventral, upper or superior face of aulacophore).

oro-anal axis. Straight line from anus to center of aulacophore insertion (presumed mouth position).

paarige Gruben. See paripore.

paripore. One of two openings through marginals M_2 and M'_2 in *Mitrocystites* or marginals M_3 and M'_2 in *Chinianocarpos* symmetrically placed on lower face of theca (*syn., paarige Gruben*).

periproct (periproctal area). Presumed flexible and extensible thecal integument surrounding anus.

placocystid plate. Special supracentral located on mid-line of theca and generally surrounded by its two neighbors, distinguished by its smooth surface and its rounded (rather than polygonal) outline; present in a few Anomalocystitidae (*Placocystites, Rhenocystis*).

plastron. Lower face of theca in Mitrata.

posterior. Applied to part (or structures) of theca located at or adjacent to anal area; direction opposite to anterior; backward.

posterior margin. Opposite to anterior margin.

proximal. Referring to direction toward insertion in aulacophore or any appendage; opposite of distal.

reverse. See inferior.

right. Side of theca corresponding with right of observer when it is placed on its lower face with aulacophore away; opposite of left.

right adoral orifice. Thecal opening which notches or pierces right adoral plate.

scutula (pl., **scutulae**). One of two concave calcareous platforms on internal face of marginals M_1 and M'_1, near abaxial ends of aulacophore apophysis.

Seitenpore. See lateripore.

septum. Calcareous wall on floor of thecal cavity running obliquely from abaxial end of left aulacophore apophysis toward right posterior thecal margin in most Mitrata.

sinistrolateral. Infracentral located on left side.

spinal. Point or fixed spine prolonging right posterior corner of theca in some Cornuta.

strut. See zygal.

stylocone. Cone-shaped ossicle forming middle region of aulacophore (*syn.,* styloid).

styloid. See stylocone.

subanal (subanalia). Special thecal plate(s) in some mitrates located below anal structures.

superior face. Convex side of theca presumably directed upward in life position; opposite of inferior face (*syn.,* upper face, obverse face).

supracentral (supracentralia). Plate(s) located inside marginal framework on superior face of theca.

sutural pore. Pore located on suture between two or several thecal plates.

symmetry plane. See median plane.

tectal. Upper small plate in lateral half ring of proximal part of aulacophore.

tegminal. Supracentral close to posterior margin, possibly serving as cover to posterior opening in some genera.

theca. Body skeleton exclusive of aulacophore.

toe spine. See spinal.

transverse anterior groove. Shallow transverse furrow on internal face of marginals M_1 and M'_1, running from infundibulum to zygal (Cornuta) or septum (Mitrata).

transverse channel. Short groove connecting median furrow with lateral depression on aulacophore.

upper face. *See* superior face.

ventral. See oral.

zygal. Skeletal bar uniting marginal M'_1 with right posterior margin on lower face of most Cornuta.

ONTOGENY

Knowledge of the ontogenetic development of the Stylophora, decidedly meager at best, rests on three sorts of evidence—1) observation of young individuals, 2) study of growth series, and 3) examination of growth lines. All relate to fairly advanced stages, which invariably are subsequent to the metamorphosis.

CHAUVEL *(30)* has shown that in many species of Mitrocystitidae young individuals differ little from adults, at least in organization of their inferior face, nothing exactly being known about development of the superior face. Growth of the theca is effected not by introduction of new plates but simply by enlargement of existing plates which are constant in number and placement from early youth. Only the proportions and outlines of the theca may be modified.

The number of plates in the frame of the theca in Cornuta likewise seems to have been established at an early growth stage, but the shape and proportions of these plates tend to be altered in the course of development. In a general way, among diminutive individuals the frame seems to be relatively larger than in adults. It seems also that the size of the centralia rather than their number increase with age; if new elements were introduced during growth, it must have been at the periphery where very small plates are generally crowded. The number of cothurnopores or comparable orifices varies among individuals, possibly being greater with age, and their decreasing size toward the two extremities of each series suggests that new pores were introduced in these terminal regions.

Occasionally, striae parallel to edges of plates can be observed on the inner surface of the stylophoran theca. This is especially true of *Lagynocystis* and genera of the Kirkocystidae, in which the inner side of the marginals or adorals bear numerous striae that may be considered as growth lines (Fig. 341,*1*). They show that these plates have undergone changes in proportion in the course of their development.

The mode of growth of the aulacophore is not known. Probably the number and arrangement of plate rings in the proximal region were fixed at a very early age in individuals, but it is very likely that new ossicles were added to the distal extremity of the appendage throughout growth, as in the arms of crinoids.

MODE OF LIFE

LIVING POSITION

Stylophorans lived resting on the sea bottom, as proved by 1) absence of a stem, 2) flattened form of the theca and its lateral extension, 3) marked dissimilarity of the two faces of the theca inferred to be upper and lower, and 4) the presence of one of the thecal faces (lower) in many species of spines or longitudinal ridges which doubtless served to elevate the body and assure equilibrium, as well as eventually for anchoring it.

With respect to the face just referred to, the organism can be oriented unequivocally, for the face that in life was directed upward and accordingly designated as the superior face is evidently the one toward which the ambulacral furrow opened. It is also the more convex face and that which generally bears the mouth and anus. It never shows the presence of protuberances and other excrescences of the sort just mentioned as characteristic of the other face.

LOCOMOTION

The absence of a stem and organs comparable to a root indicates that the Stylophora were not sessile animals but rested free on the sea floor or other support. The aulacophore, considered as stem, peduncle, or tail, often has been supposed to be a means of anchorage, operating like the cirrus of a crinoid *(25)*, sinking into clefts or between roots on the substrata *(14)*, or standing vertically on its tapered extremity with the theca extended horizontally in the water *(82)*. The stylocone, especially in the Mitrata, has commonly been considered to be a device for clinging, and BATHER *(17)* judged it to be "a support on which the internal muscles could raise the theca as on an elbow, or swivel it round to meet the food-currents." Among other functions which have been assigned to the aulacophore is that of a rudder *(13,25)* and that of a propeller *(49)*. Referring to mitrocystids, GISLÉN *(45)* thought "that the animal moved itself forward [backward in terms of *Treatise*-adopted orientation] with jerks to the right and left of the strongly muscular proximal part of the stem." Thus the so-called stem would become "a swim tail" *(46)*. Even *Cothurnocystis*—despite its extreme asymmetry, its protuberances, and its long marginal processes—was judged capable of swimming by pirouetting about on itself *(45)*.

Other authors have imagined that stylophorans crawled, using the aulacophore to push themselves backward or pull them forward. KIRK *(56)* described in some detail how the mitrate *Bassleroeystis* glided over the sea floor by movement of its aulacophore with the aid of its two posterior spines and CASTER *(25)* explained how *Enoploura* traveled on the sea bottom by "upflexings" of the body at junction of the aulacophore with the theca, in manner recalling the mode of progression of measuring worms.

If, as here interpreted, the aulacophore is not a stem or peduncle but rather a brachial process serving to carry the single ambulacrum of the stylophoran and therefore functioning essentially for capture of food, most of the hypotheses which have been outlined evidently lose all significance. It remains conceivable, however, that the aulacophore, in addition to its function as an organ for obtaining nourishment, could have acted to keep the animal favorably oriented in water currents or to shift them somewhat in case of need. Just as the arms of comatulids enable them to swim or crawl on the sea bottom, the aulacophore of stylophorans, with its powerful proximal musculature, might conceivably have been capable of performing similarly.

Opposed to unqualified adoption of the hypothesis just stated are several anatomical considerations which apply to the Stylophora. 1) The high degree of asymmetry seen in the theca of most Cornuta, and the not uncommon considerable development of their protuberances, spines, and marginal processes make a judgment that these "carpoids" crawled or swam improbable. 2) The rearward thinning down of the theca which is observed in all Stylophora provides a hydrodynamic condition unfavorable for displacement of the body in a backward direction, for very generally aquatic animals move with their big end forward. 3) Similarly the rearward imbrication of the supracentrals of some genera *(Mitrocystella, Lagynocystis)* or of the scalelike covering of the lower face of *Allanicytidium* makes unlikely a backward progression of the organisms. 4) In *Mitrocystites* and *Chinianocarpos* the spines borne by the lateral anterior marginals point obliquely backward and downward in such a way as to impede sliding of the theca sideward and toward the rear. Projections on the lower surface of the stylocone and distal ossicles of the aulacophore in Mitrata have their points generally directed toward the theca—an arrangement that would hinder any propulsive force that movements of this organ could have generated in a posterior direction. Such considerations suggest that the Stylophora either led an essentially static existence, reposing in the same place as long as conditions were favorable, or, if they moved, progressed forward. For moving, they could use their aulacophore to pull them in a manner described by CASTER *(14)* or expel water from the anus, making a jet which served to propel the animal forward. One may here call attention on the occurrence of projections apparently serving for attachment of muscles or ligaments on the inner side of the supracentrals of some Mitrata, suggesting that rhythmical contraction and expansion could have resulted in a bellows-like action of the body wall. In very asymmetrical forms (e.g., *Cothurnocystis*) a forcible expulsion of water from the anus should have induced gyration of the theca, which was probably checked by the protuberances on the lower side of marginals, the spinal and the aulacophore *(13)*. In more symmetrical forms, however, an effective leap forward could probably have been realized in this way. On the other hand, this does not mean that the Stylophora were active swimmers. It seems more likely that they used such possibility occasionally, when, for instance, it was necessary to shift their position. Doubtless JAEKEL *(55)* was right in comparing their behavior to that of holothuroids. One may well imagine that stylophorans lived most of the time in the manner of certain psolid dendrochirotes, which have depressed bodies and cling to the substrate by their flattened ventral sides.

NUTRITION

Interpretation of the aulacophore which has been given indicates that this organ served principally for the collection of nourishment. The nature of the articulations between distal segments of the aulacophore in Mitrata shows that this region was held in a position directed more or less upward. It was inflected or formed an elbow at the level of the stylocone, which served it for support and as a sort of hinge. Many fossils (e.g., *Lagynocystis, Enoploura, Rhenocystis*) show the aulacophore preserved in this bent position. It is not to be doubted that in at least some circumstances this appendage could partially enroll on itself so as to protect soft structures lodged in the furrow of its oral face.

Capability of enrollment assuredly was lacking in the aulacophore of the Cornuta, which was much more rigid, with principal movements, if not only ones, controlled by the proximal region. Even so, it is probable that the aulacophore of these stylophorans did not lie flat on the sea floor, since its aboral surface never is depressed. With little doubt it moved in the water with equilibrium of the body maintained by disposition of the protuberances that served for support of the theca and by the presence of appendages (glossal, digital) or posterior marginal expansions designed to provide a counterweight.

The nature of the median groove and other structures which characterize the oral surface of the stylophoran aulacophore suggest, by analogy with the endoskeletal ambulacral structures of living echinoderms, that these animals were microphagous, capturing minute particles suspended in the sea water or catching tiny prey by play of their tentacles and mucociliary mechanisms. In summation, the nature of the aulacophore furnishes no confirmation at all of hypotheses postulating that these "carpoids" were 1) scavengers *(26)*, 2) sea-bottom mud-swallowers *(56)*, 3) nourished by pumping water inward through the anus *(34,45,46,55)*, and 4) fed through inhalant pores such as cothurnopores, sutural pores of *Ceratocystis*, and lamellipores *(13, 14,32)*.

Among other morphological features that may have been concerned with nutrition are the ctenoid organs of *Lagynocystis*. Seemingly located at the back of an entrance-way atrium, they appear to be adapted for straining out food particles suspended in water currents, embedding them in mucus, and conducting them to the mouth.

RESPIRATION

Respiration of the Stylophora may have been accomplished in various ways—1) directly through the thecal integument when covered by a thin pavement or provided with uncalcified spaces (e.g., *Nevadaecystis*; and according to CASTER *(26)*, very abundant stroma in the plates of *Paranacystis* must have allowed gas exchanges within the skeleton); 2) by extensions of the hydrocoelian apparatus (e.g., tentacles of the aulacophore); 3) through walls of the digestive tube; 4) by introduction and expulsion of water through the anus as in living crinoids and holothuroids *(45,55)*, possibly controlled by pulsations of the upper thecal face when, as seems to have been common in many, it had sufficient flexibility; 5) perhaps by means of specialized organs such as the cothurnopores and lamellipores, if these organs, which in some stylophorans are closely analogous to hydrospires and pore rhombs, actually had a respiratory function; and 6) possibly also through the agency of ctenoid organs (e.g., *Lagynocystis*), which in addition to filtering water from the atrial chamber could have aided aeration of fluids filling the gills that perhaps they supported. It is probable then that, as in other echinoderms, respiration was effected by various means.

ECOLOGY

Little precise information is available as to the environment of living Stylophora. A majority of them appear to have existed in the places where their fossil remains are found, or very close to these places. In view of their relatively large size and delicacy of their complex organization, they could hardly have been transported very far from sites occupied in life to places of burial.

Remains of these animals are found most

commonly in clayey sediments, either on bedding planes of shale or enclosed by siliceous or sand-carbonate concretions occurring in essentially pelitic deposits. Only rarely have they been collected from strongly arenaceous or calcareous formations. This common association of the fossils with argillaceous sediments indicates that most known stylophorans lived in marine environments sufficiently calm to have allowed predominant deposition of clay particles and mica flakes. Although generally true, the stated rule is not universal—for example, dissociated plates of *Enoploura* are found in large numbers in coquinites and calcarenites of the Cincinnati-arch region in Ohio and Indiana, indicating that this mitrate preferred a habitat in which the water was so agitated by waves and currents that clay-size particles could not be deposited but were swept away *(25)*. The diversity in morphology of stylophoran genera and species suggests a corresponding diversity of ecologic niches adapted to each.

Stylophora are rare as fossils. Their rarity may reflect modest size of populations, possibly associated with special ecologic exigencies, but it may mean that they have been neglected by collectors or that conditions of fossilization render finding of them exceptional. Thus, in the Lower Ordovician of southern France (Hérault) in strata which have furnished the most diversified assemblage of stylophorans yet known, only specimens contained in small quartzitic concretions distributed through the shaly mass have a chance of being collected; others which might be found in the shale are entirely irretrievable owing to fracture of the rock into tiny pieces. This may explain why a majority of the species recorded from this region—approximately a dozen—are represented by a single specimen or a small number at most. On the other hand, deposits elsewhere which seem to indicate conditions of fossilization closely similar to those just noted have furnished very numerous stylophoran fossils. Thus, the Šárka Shale, in the Middle Ordovician of Bohemia, has yielded several hundred specimens of *Lagynocystis pyramidalis,* all preserved in siliceous concretions. That this species was especially abundant can hardly be doubted. Another example from the same region is seen in the *Ceratocystis perneri* Zone of the Skryje Shale, Middle Cambrian, which contains heaps of specimens piled together pell-mell. Like many other echinoderms, some stylophoran species must have led a gregarious existence.

It is difficult to determine in what type of sea and under what special conditions a majority of stylophoran species lived, for critical paleoecologic investigations have not been made of any of the deposits that contain these fossils. The few published discussions on this subject relate only to *Cothurnocystis elizae (13), Paranacystis petrii (26), Victoriacystis wilkinsi (43), Dalejocystis casteri (71),* and the genus *Enoploura (25).* No worthwhile synthesis can be offered.

PHYLOGENY

ORIGIN AND RELATIONSHIP OF STYLOPHORA

From the outset of their appearance in Middle Cambrian time the Stylophora display all attributes of their class. Consequently, their source is unknown.

Like other "carpoids," they have long been interpreted and by many still are considered to be modified Pelmatozoa (Crinozoa) which abandoned a fixed mode of life and erect position to assume a partially eleutherozoic habit and a horizontally reclining attitude. No evidence supports this hypothesis, however. On the contrary, the Stylophora display an ensemble of features that oppose them to pelmatozoans. These are: 1) the fundamental asymmetry of their organization and entire absence of radial symmetry; 2) the lack of a peduncle or homologous organ or any means of fixation at all; 3) the presence of a single ambulacrum and hence the probable absence of a hydrocoelian ring and the five primary tentacles which form origins of the rays in other echinoderms; 4) the structure of their aulacophore, which resembles neither a crinoid arm nor a cystoid brachiole; 5) localization of the mouth at the front of the body and the anus at the rear.

All these characters contribute to definition of an organization peculiar to itself, suggesting an independent origin and evolutionary trends unlike those seen in crinoids, cystoids, and sessile echinoderms generally. Moreover, the Crinozoa and pelmatozoic Echinozoa already were represented when the Stylophora first appeared in the Middle Cambrian and no convergence toward a common source is definable among these archaic forms.

Likewise, the stylophorans cannot be placed close to radiate free echinoderms, despite the seeming fact that they never were attached, at least as adults. Indeed, their asymmetrical construction and lack of any mark of radial symmetry, accompanied by their single ambulacrum and morphologic peculiarities of their aulacophore, definitely remove them from echinoderm types such as the Asterozoa and Echinozoa.

What origin is suitable for assignment to this group? In various discussions Bather *(14, 15, 20, 21)* has outlined an hypothesis according to which the Stylophora could have been derived from a dipleurula attached by its ventral surface rather than by the preoral lobe, in this way acquiring the shape of a Y with the lower part of the letter represented by a stem and the upper part by the body with its mouth at the extremity of one branch of the Y and its anus at the extremity of the other branch. The different types of "carpoids" would have been produced from the Y-shaped form by divergent evolution. Chauvel *(30)* accepted the Y plan as fundamental but instead of deriving it from the primitive dipleurula, postulated that it came from a modified one which already had arrived at the generalized sort of pelmatozoic stage approximately represented by the cystoid *Aristocystites*. His concept has a twofold advantage over Bather's hypothesis in connecting the Stylophora with an ancestor that would be common to all echinoderms and in explaining the asymmetry of stylophorans. It is mistaken, however, in accepting the aulacophore as a stem, which otherwise is unknown in these organisms, and in deriving the Stylophora from an ancestor that already is too far advanced on the path leading to the Crinozoa.

Is it advisable, consequently, to choose Bather's *(21)* opposed view in affirming that the Stylophora, like other "carpoids," "have never traversed the evolutionary roads followed by the other classes and [that they] do not possess the most familiar characters of the Phylum"? In my opinion, this would be going too far. We have seen that the general organization of stylophorans can be explained in some measure by comparison with the ontogenetic stages which precede the appearance of radial symmetry. Phylogenetically, this indicates that the group must have separated from the remainder of the phylum before radial symmetry was acquired but after asymmetry had become a main echinodermal characteristic. In other words, if they cannot be connected directly with some ancestral dipleurula—any more than can the radial classes—nothing prevents considering them, along with the Homostelea and Homoiostelea, as records of preradial divergences of the echinoderm stock the origin of which doubtless occurred long before the dawn of Cambrian time. In this perspective, the Stylophora and other "carpoids" merit recognition with the Helicoplacoidea as the most primitive echinoderms.

Despite their fundamental archaic nature, the Stylophora exhibit such morphologic and functional specializations that they cannot be considered as possible ancestors of other echinoderms. They became extinct without leaving known descendants.

The hypothesis sometimes has been advanced that the chordates might have been derived from echinoderms similar to the Stylophora. According to Gislén *(45)*, the asymmetry of the theca of *Cothurnocystis* and its unique row of cothurnopores may recall a development stage of *Amphioxus*, and the mitrocystids in some respects may resemble the tunicate appendicularians. Gregory *(48)* has called attention to the astonishing, though possibly superficial, similarity of the theca of *Mitrocystella* or that of *Placocystites* to the cephalothorax of the cyclostome fish *Drepanaspis*. Caster *(25)* and Caster & Eaton *(28)* have emphasized the analogy which in their eyes exists between the ornament and microstructure of certain stylophoran plates and plates in the exoskeleton of ostracoderms. Such resemblances, however, may be purely accidental and surely do not prove that the

Stylophora had an organization close to that of ancestors of the chordates. At any rate, we know that during the time of their existence vertebrates of already highly organized type lived. If echinoderms are related to chordates, the connection between them must date back so remotely that the fossil record can hardly preserve a trace of it.

In common with the other "carpoids," stylophorans display a depressed body form, presence of a single ambulacrum (bifurcated in the Homostelea), and asymmetry without trace of radial symmetry. As previously suggested, all may belong to an extremely ancient preradial echinoderm radiation, and if this is true, the Stylophora represent an independent branch without known relations to other branches of the radiation. Supposition that *Microcystites* was derived from a form not distant from *Trochocystites (13, 20)* or that the Mitrata and Cincta constitute a morphological series characterized by reduction of ambulacral grooves *(45, 55)* is without foundation. Every comparison between the Stylophora and Homostelea (Cincta) brings essential differences to light. The former are distinguished from the latter by: 1) absence of a stele and in general any peduncular prolongation of the body; 2) presence of the highly organized brachial process termed aulacophore; 3) position of the mouth and anus at opposite poles of the theca; and 4) presence of accessory orifices and such internal structures as the septum, infundibulum, scutulae, and marginal grooves, without known equivalent in *Trochocystites* and its allies.

In equal degree the Stylophora differ from the Homoiostelea, and to some extent in the same ways as from the Homostelea, as shown by: 1) absence of a stele; 2) specialized structure of their aulacophore; 3) constant presence of a framework of marginal plates around the theca; 4) much more pronounced differentiation of the two thecal faces; and 5) presence of internal structures and accessory orifices peculiar to themselves.

These are profound differences and suggest dissimilar general organization. For a given feature, homology cannot be demonstrated. No proof can be found, for example, that the marginal plates of the Stylophora are homologous with those of the Homostelea, since they may have been acquired independently, and likewise the marginals observed in some representatives of other echinoderm classes. In any event they do not correspond exactly either in number, or position, or in relation to the orifices or to other parts of the theca. Further, no form having characters morphologically intermediate between Stylophora, on one hand, and Homostelea and Homoiostelea, on the other is known. For these reasons I concur with Cuénot *(32)*, Gekker *(41)*, and others in judgment that the "carpoids" comprise a heterogeneous assemblage which needs to be separated into three distinct classes.

EVOLUTION WITHIN STYLOPHORA

The Stylophora include two orders, which are named Cornuta and Mitrata. If these orders at first glance seem to be very different, actually they exhibit many strong resemblances, quite in contrast to that shown by comparison of the stylophorans with other "carpoids." Obviously, their fundamental organization is the same, since their body comprises the same parts, disposed in the same way and it has such similarity of plan or identity of connections that homologies cannot be doubted. Particular attention may be directed to the following points: 1) the body is composed in one as in the other of a theca and an aulacophore; 2) it bears no stem or peduncular prolongation; 3) the principal orifices have the same emplacement; 4) the theca and aulacophore possess the same structural elements; 5) attachment of the aulacophore to the theca is effected in the same way; and 6) many internal structures (e.g., muscular apophyses, scutulae, infundibulum) are seen in representatives of both orders. This structural unity seems incontestable and supports the conclusion that the Cornuta and Mitrata are orders derived from a common source.

When they first appear in the stratigraphic records, however, both the Cornuta and Mitrata are seen to be already highly specialized. Their oldest known representatives—*Ceratocystis*, from the Middle Cambrian of Bohemia, of the Cornuta, and

Chinianocarpos and *Peltocystis,* from the Lower Ordovician of Hérault, France, of the Mitrata—are so greatly advanced along lines peculiar to each that it is impossible to ascertain any interrelationships or to determine which of the two groups is the more primitive. Possibly the weak differentiation of the marginals from central plates in *Ceratocystis,* in combination with some other characters, may be identified as archaic traits, but this genus is established as an authentic cornute by the form and composition of its theca, the nature of its orifices, and the structure of its aulacophore. *Ceratocystis* cannot possibly be an ancestor of the Mitrata. On the basis of well-established observations, the Cornuta and Mitrata are recognized as groups having equal phylogenetic values, closely related to one another without doubt but with unknown interrelationships. Their common source must antedate considerably the time represented by the oldest fossils.

The fossil record is much too incomplete to allow steps in the evolution of either order to be followed, though some general trends are discernible by examining the stratigraphic succession of genera. The evolution indicated is difficult to prove, since neither genera nor species are connected by trustworthy lines of descent. However, comparison of *Ceratocystis* with *Nevadaecystis* and other cornute genera suggests that the following changes occurred during history of the group: 1) differentiation of marginal plates in relation to the centrals; 2) appearance of a zygal as reinforcement of the thecal frame and development of various appendages (spinal, glossal, digital) joined to it; 3) fragmentation of the thecal faces into a multitude of platelets, thus providing suppleness to the originally rigid pavements; 4) restriction of the adoral plates to the upper thecal face and gradual integration of them into the marginal framework; 5) regression of the median adoral to its ultimate disappearance; 6) migration of the right adoral orifice from a location on the inferior face to the right anterior edge of the theca; 7) substitution of sutural pores by generally more complex types of openings which retain narrowly localized placement in the upper right anterior area; 8) strengthening of internal structures of the theca, especially the aulacophore apophyses; 9) replacement of imbricated scales, which in *Ceratocystis* enclose the cavity of the aulacophoral proximal region, by a number of quadripartite rings articulating on one another; and 10) enlargement and thickening of the ridges along borders of the median groove of the aulacophore, with associated differentiation of transverse channels and lateral depressions. These alterations, already in progress at the end of Cambrian time (e.g., *Nevadaecystis*), were mostly completed in the Early Ordovician. During this epoch two assemblages became clearly differentiated—the Cothurnocystidae, characterized by the presence of cothurnopores or simple sutural pores, and the Scotiaecystidae, distinguished by the occurrence of lamellipores. They followed parallel lines of evolution until their apparent extinction in the Late Ordovician, for no post-Ordovician cornutes are known.

The Mitrata are represented in the Lower Ordovician by the suborders Mitrocystitida and Lagynocystida. In addition to these, the Middle Ordovician contains representatives of the Anomalocystitida. The Mitrocystitida appear to be the least specialized of the three groups, for they display characters (e.g., arrangement of infracentrals) found to be more or less modified in the other suborders. This does not prove that mitrocystids are the source of other mitrates classed as lagynocystids or anomalocystids or both of them, for all three groups could have been derived from a common trunk or separately descended from different ancestors. Questions of their origin are answerable neither by chronologic nor comparative morphologic evidence.

The Mitrocystitida and Anomalocystitida appear to be homogeneous assemblages, for their most typical representatives, at least, differ from one another respectively only in unimportant ways. The anomalocystids differ from the mitrocystids in having a pair of posterior movable spines and in being much more symmetrically organized with respect to the main axis of the body. As previously emphasized, this bilateral symmetry is superposed on a fundamental asymmetry. It is incomplete and probably denotes a secondary adaptation.

The Lagynocystida, by way of contrast, appear to be more diversified, with constituents modified by several different evolutionary trends. Among these are: 1) appearance of a unique calcareous process at the posterior extremity of the body; 2) retention of thecal asymmetry, or rather an increase of it; 3) reduction in the number of thecal plates; and 4) increase of the adoral plates to the point of hypertrophy. The first three of the cited trends affect all known genera, but in varying degree, and thus indicate the homogeneity of the suborder. The fourth trend is seen only in *Anatiferocystis* and *Balanocystites,* showing that the assemblage as a whole contains some diversification. On this basis two lineages which make appearance in the Middle Ordovician can be distinguished—the Lagynocystidae, containing *Lagynocystis* as its single genus, and the Kirkocystidae, containing *Anatiferocystis* and *Balanocystites* (=*Kirkocystis*). These two families are possibly related to the Peltocystidae, which are less specialized and are already present in the Lower Ordovician.

Finally, a resemblance that seems to relate *Paranacystis* to the Lagynocystida may be noted, though it may be the product of convergent evolution. According to CASTER *(26), Paranacystis,* as well as the Lagynocystida, would have been derived independently from Cambrian or Ordovician Mitrocystitida, considered to be the principal source of the Mitrata. This is agreed to at least provisionally by assigning this genus to the Mitrocystitida because, like representatives of this suborder and unlike the Lagynocystida, *Paranacystis* lacks a posterior exothecal process.

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION

The oldest known stylophoran is the cornute *Ceratocystis perneri* JAEKEL *(54)* from the Skryje Shale, Middle Cambrian, of Bohemia (BATHER, 1913). To find the next representatives of the Cornuta one must go to the uppermost Cambrian of the New World, for Trempealeauan rocks of Nevada contain *Cothurnocystis americana* UBAGHS (=*Nevadaecystis*) and *Phyllocystis* sp. *(89).*

The Lower Ordovician (upper Tremadoc and lower Arenig) of southern France (Hérault) has yielded a highly varied stylophoran fauna *(85)* characterized by: 1) great development of Cothurnocystidae, possibly representing the peak of this family, containing numerous species of *Cothurnocystis*—mostly undescribed—and *Phyllocystis*; 2) first appearance of the Scotiaecystidae, represented by an undescribed species; and 3) first appearance of the Mitrata, represented by two of its three suborders—the Mitrocystitida, with *Chinianocarpos,* and the Lagynocystida, with *Peltocystis.* Fossils identical or closely related to constituents of this fauna have been discovered in the Lower Ordovician of Morocco *(42)* (CHAUVEL, personal communication).

In the Middle Ordovician the Cornuta appear to become more rare, whereas the Mitrata are multiplied in number. The Šárka Shale (Llanvirnian) of Bohemia has yielded many species of *Mitrocystites,* two species of *Mitrocystella,* and one each of *Anatiferocystis, Balanocystites, Lagynocystis,* and *Spermacystis* (new name for *Anomocystis* JAEKEL, 1918, *non* HAECKEL, 1896) *(2,30,54,55).* Llandeilian strata of Brittany, in France, contain a comparable fauna but less rich *(30).* From the Middle Ordovician of the United States, *Anatiferocystis papillata* BASSLER has been recorded in Oklahoma and *Enoploura punctata* BASSLER in Tennessee. In Canada *Ateleocystites huxleyi* BILLINGS is the oldest known representative of the Anomalocystitidae. As for the Cornuta, only *Bohemiaecystis,* of the Scotiaecystidae and two undescribed genera are found in the Šárka Shale and Sv. Dobrotivá Shale of Bohemia.

Only a small number of Stylophora are known from the Upper Ordovician. From Bohemia, BARRANDE *(2)* has described an anomalocystid of uncertain generic affinities, named by him *Anomalocystites bohemicus (25,30).* In Brittany *Mitrocystites riadanensis* CHAUVEL *(30)* has been recorded. The celebrated Starfish Bed (Ashgillian) of Lady Burn, in the Girvan region of Scotland, is the source of two species described by BATHER *(13),* named by him *Cothurnocystis elizae* and *C. curvata,* the latter now designated as the type species of *Scotiaecystis.* These are the last known representatives of the Cornuta. From Ashgillian beds in Yorkshire, England, MARR (1913) has called attention to the occurrence of an undescribed mitrate by him attributed to *Ateleocystites.* Finally, Cincinnatian strata in Ohio and Indiana have yielded five species of *Enoploura (25).*

From the Silurian onward, only genera of the Anomalocystitidae, Allanicytidiidae, and Paranacystidae are found, with the possible exception of a doubtful form referred to the Mitrocystitidae. From Australia, in beds identified as Lower Silurian, GILL & CASTER *(43)* have reported *Victoriacystis* sp. aff. *V. wilkinsi* and from Upper Silurian rocks of the same region they have described *V. wilkinsi.* The Upper Silurian (Wenlock) of England has furnished *Placocystites forbesianus* DE KONINCK (1869) *(95).* These species belong to the Anomalocystitidae.

In the Lower Devonian, the Anomalocystitidae are represented by: 1) *Rhenocystis latipedunculata* DEHM *(33, 34)* in Germany; 2) *Anomalocystites disparilis* HALL (1859) *(25, 56, 78)* in Maryland (=*Basslerocystis*); 3) *Anomalocystites cornutus* HALL (1859) *(25, 78)* in New York; 4) *"Placocystites" africanus* REED *(72)* in South Africa; and 5) *Victoriacystis* sp. aff. *V. wilkinsi* GILL & CASTER *(43)* in Victoria, Australia. The Australocystidae contain *Australocystis langei* CASTER *(27)* from Paraná, Brazil, and *Placocystella capensis* RENNIE (1936, *77*) from South Africa, both from the Lower Devonian. Allanicytidiidae are represented by one genus *Allanicytidium* (herein described) from the Lower Devonian of New Zealand. The Paranacystidae contain the single form named *Paranacystis petrii* CASTER *(26)* from the Lower Devonian of Parana, in Brazil. The stylophoran species doubtfully assigned to the Mitrocystitidae is *Mitrocystites? styloideus* DEHM *(34)* from the Bundenbach Shale (Hunsrückian) in Germany.

The geologically latest known member of the Stylophora is the Middle Devonian *Dalejocystis casteri* PROKOP *(71)* from Bohemia. Possibly it belongs to the Lagynocystida but here is classified as suborder and family uncertain.

Although the taxonomic diversity of the stylophorans seems to be modest, their geographic range is surprisingly extensive.

SYSTEMATIC DESCRIPTIONS

Class STYLOPHORA Gill & Caster, 1960

[*nom. transl.* CASTER & UBAGHS, herein, *ex* superorder Stylophora GILL & CASTER, 1960]

Homalozoa in which the body comprises theca and brachial appendage (aulacophore) but no stele, stem, or peduncle; theca depressed, thickening forward, with very distinct upper and lower faces framed by marginals; mouth intrathecal, at or near proximal end of aulacophore; anus at opposite thecal extremity; aulacophore comprising three parts—a wide hollow proximal region, covered by imbricating scalelike platelets or more generally by tetramerous rings, a median region consisting of a conical reducing piece (stylocone), and a distal region composed of a single series of ossicles; stylocone and ossicles of the distal region carrying a median groove, typically flanked by lateral depressions, groove and depressions being both protected by movable cover plates. *M. Cam.-M.Dev.*

Order CORNUTA Jaekel, 1901

[*nom. transl.* JAEKEL, 1918 (*ex* suborder Cornuta JAEKEL, 1901)]

Stylophora with asymmetrical outlines; oro-anal axis ordinarily making quite distinct angle with main axis; exothecal processes or some protruding marginals generally present; marginals typically thick and narrow, ordinarily well differentiated from centrals, some of them commonly carrying knobs or spines on lower side; adoralia generally forming part of frame and not markedly participating to covering of both faces; right adoral notched by opening situated on lower face or more typically on anterior margin of theca; pores of various types ordinarily present in upper right anterior area; stylocone with rounded aboral face, without any knob or spine; median furrow of aulacophore raised on median ridge that is flanked by lateral depressions; transverse channels generally connecting median furrow with lateral depressions; cover plates imbricate. *M.Cam.-U.Ord.*

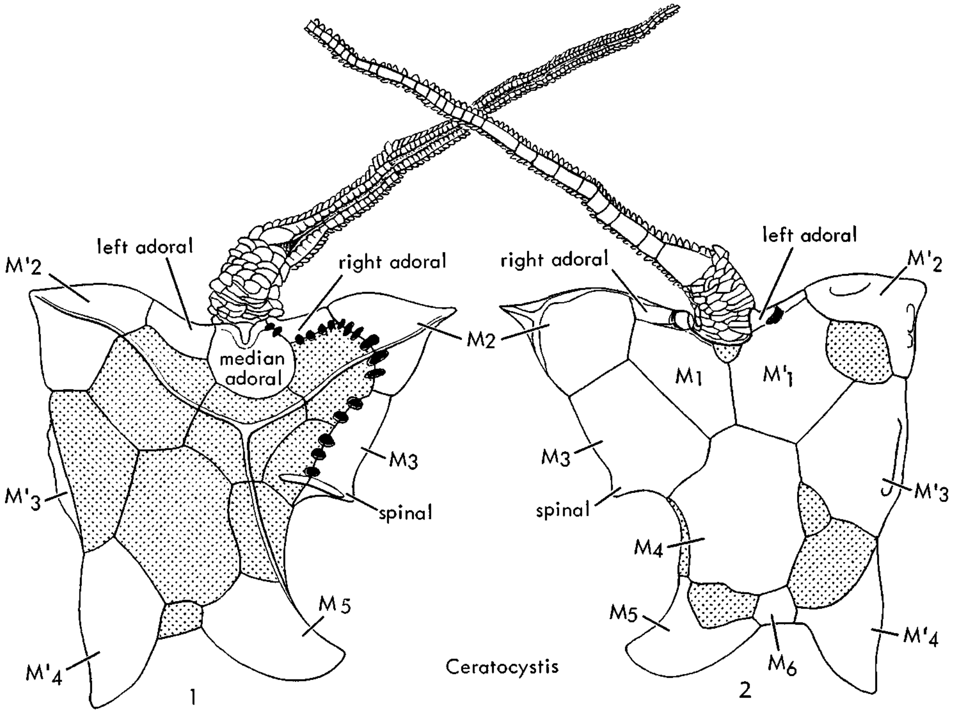


FIG. 345. Ceratocystidae (p. S548).

Family CERATOCYSTIDAE Jaekel, 1901

Theca with outlines not unlike those of pointed shoe; anterolateral corners protruding and thickened; right lateral margin divided by median triangular spinal projection; posterolateral marginals horn-shaped; frame slightly differentiated from central covering; knobs on lower face of M_2, M'_2 and M'_3, M_3 with downward-produced external edge; centrals few and not markedly smaller than marginals; upper thecal face characterized by triradiate ridge and short transverse ridge connected with spinal projection; adoralia 3, left and right, forming anterior thecal margin on both sides of aulacophore insertion and extending on both lower and upper thecal faces into narrow rim; median adoral located on upper thecal face only, its anterior edge with triangular median notch; slitlike opening emarginating lower margin of right adoral; anus unknown, probably located between two posterior horns; pores along sutures joining median adoral with right adoral, and right adoral and marginals M_2 and M_3 with contiguous supracentrals; single similar pore on anterior left thecal margin between M'_2 and left adoral, and on lower face between left adoral and M'_1; proximal region of aulacophore covered by imbricating scalelike platelets; median aulacophore furrow limited by narrow ridge; transverse channels indistinct and lateral depressions slightly marked. *M.Cam.*

Ceratocystis JAEKEL, 1901 [**C. perneri*; OD]. Characters of family. *M.Cam.*, Boh.——FIG. 345, *1,2*. **C. perneri*, Skryje Sh.; *1*, upper face, ×1.8; *2*, lower face, ×1.8 (Ubaghs, n).

Family COTHURNOCYSTIDAE Bather, 1913

Theca very depressed, boot-shaped or heart-shaped in outline, framed by narrow elongate marginals between which stretch either a pavement of large plates or, more generally, finely plated integuments; lower face typically divided into two unequal parts by a zygal; adorals 2 or 3, resting on M_1 and M'_1, confined to upper thecal side; lower anterior edge of right adoral notched

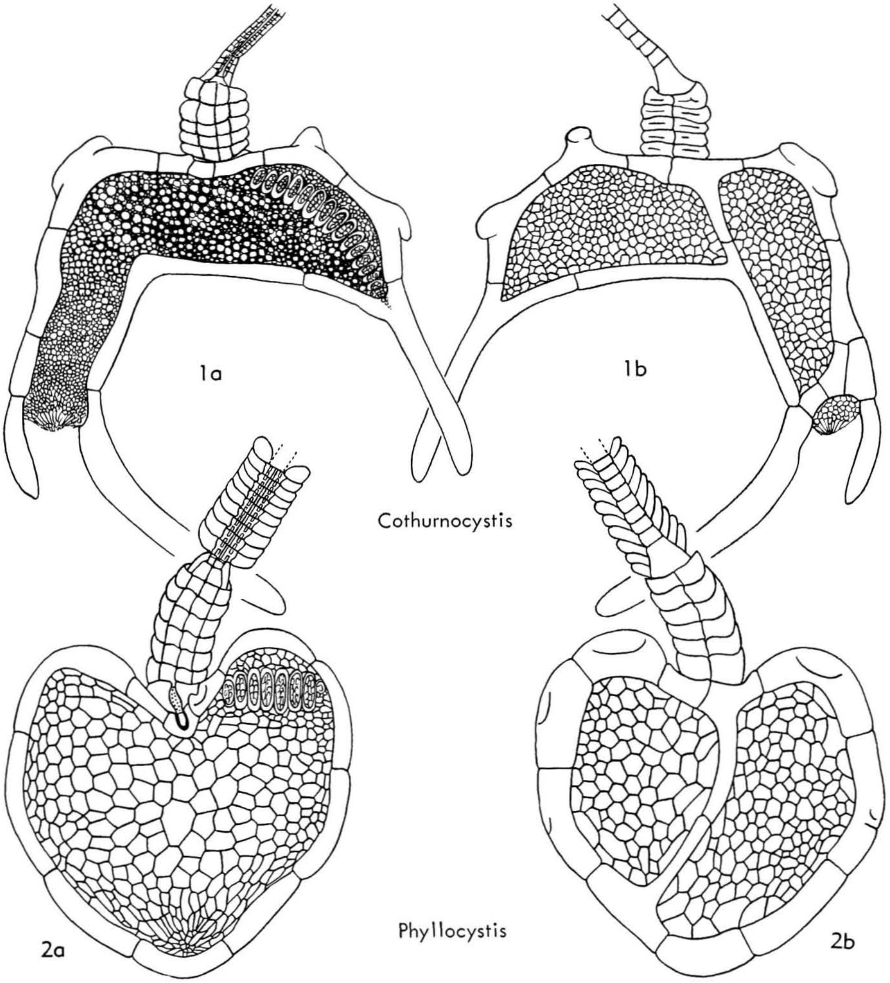


FIG. 346. Cothurnocystidae (p. S549-S550).

by distinct opening; anus terminal at posterior upper end of theca; cothurnopores arranged in row or simple pores scattered between supracentrals in upper right anterior area; proximal region of aulacophore protected by rings, each composed of four unequal plates, two smallest covering mid-part of superior face; median furrow limited by relatively wide rims; transverse channels and lateral depressions well marked. *U. Cam.-U.Ord.*

Cothurnocystis BATHER, 1913 [**C. elizae*; OD]. Theca very asymmetrical, transversely elongate, having boot-shaped outlines; left posterior area forming long narrow protrusion; spinal, glossal, digital, and generally marginal knobs or spines well developed; infracentralia flattened and tessellate; supracentralia generally rounded and slightly swollen; upper integument stretching over 2 most posterior marginals which close frame on its lower side only; cothurnopores arranged in row running from left adoral to spinal corner. *L.Ord.-U.Ord.*, Scot., Fr.——FIG. 346,*1*. **C. elizae*, U. Ord., Ashgill Ser., Girvan, Scot.; *1a*, upper face, ×1.2; *1b*, lower face, ×1.2 (Ubaghs, n).

Nevadaecystis UBAGHS, **new genus** herein [**Cothurnocystis americana* UBAGHS, 1963]. Similar to *Cothurnocystis* but having lower face covered by few large plates and upper face by numerous stellate ossicles with uncalcified areas between their joining rays; no zygal; marginal spine prominent; ridge, probably triradiate, on upper side as in *Ceratocystis*. *U.Cam.*, USA(Nev.).——FIG. 347, *1*. **N. americana* (UBAGHS), Trempealeau; upper face, ×3 (89).

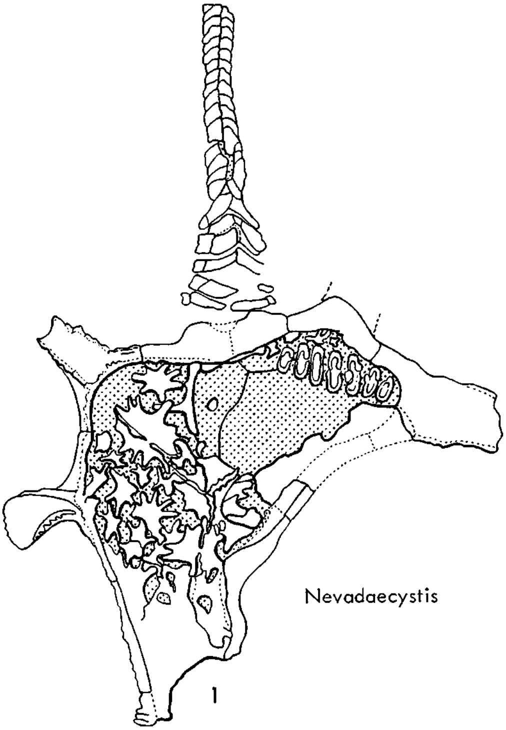


FIG. 347. Cothurnocystidae (p. S549).

Phyllocystis THORAL, 1935 [*P. blayaci; OD]. Differs from *Cothurnocystis* in having heart-shaped outlines, marginals completely framing theca on both faces, supracentrals as well as infracentrals tessellate, and no exothecal process; simple or denticulate knobs but no spines on lower side of marginals; adorals 3, median one with anterior median notch (as in *Ceratocystis*); row of cothurnopores or numerous scattered openings in upper right anterior area according to species. *U. Cam.-L. Ord.,* USA (Nev.)-Eu.(France)-N. Afr. (Morocco).——FIG. 346,*2*. **P. blayaci*, L.Ord., France; *2a*, upper face, ×3; *2b*, lower face, ×3 (Ubaghs, n).

Family SCOTIAECYSTIDAE
Caster & Ubaghs, new family

Theca very depressed and asymmetrical, with complicated outlines; frame well distinct from central covering, completely surrounding theca on both sides; marginals narrow and elongate; lower and upper integument finely plated; lamellipores numerous, occupying curved tract between right adoral to near right posterior corner; aulacophore similar to that in Cothurnocystidae. [An undescribed species is known from the Lower Ordovician of France.] *L.Ord.-U.Ord.*

Scotiaecystis CASTER & UBAGHS, **new genus,** herein [**Cothurnocystis curvata* BATHER, 1913; OD]. Theca junk-shaped, transversely elongate; left posterior area not markedly protruding and ending in truncated angle that carries single long posterior spine; spinal short and thick; prominent knobs on lower side of some anterior and lateral marginals; zygal sloping in direction of left posterior corner; infracentrals flattened and tessellate; supracentrals with low convex-topped spines; anus not terminal, but near left posterior margin; lamellae between lamellipores not prolonged into thecal cavity; lower face of ossicles of distal aulacophore region angulate. *U.Ord.,* Scot.——FIG. 348,*1-4*. **S. curvata* (BATHER), Ashgill Ser., Girvan; *1a,b,* upper and lower faces, ×3.3; *2,* supracentrals, ×9; *3,* infracentrals, ×9; *4,* anal area, ×10 (all Ubaghs, n).

Bohemiaecystis CASTER, **new genus,** herein [**B. bouceki* CASTER, **new species,** herein; OD]. Theca sabot-shaped, moderately wide; left posterior end rounded, ?without posterior spine; ?no spinal; simple low knobs on some anterior and lateral marginals; zygal slightly oblique to main axis; supracentrals as well as infracentrals flattened and tessellate; lamellae between lamellipores protruding into thecal cavity. *M.Ord.,* Boh.——FIG. 349, *1,2*. **B. bouceki*, M.Ord., Sv. Dobrotivá and Šárka Shales, Boh.; *1,2,* upper and lower faces, ×1.5 (Caster, n).

Order MITRATA Jaekel, 1918

Stylophora with asymmetrical to bilaterally symmetrical outlines; oro-anal axis approximating or coinciding with main axis; lower thecal face plane or slightly concave; upper thecal face invariably convex; both thecal faces covered by relatively large plates; marginals generally not very distinct from centrals, never carrying knobs or protuberances on their lower side; no zygal, but generally an intrathecal septum in corresponding position on floor of thecal cavity; adorals covering more or less large area on upper surface; right adoral pierced (in *Mitrocystites* only) by slitlike opening; one or two pairs of pores present in some genera on lower or anterior thecal face; stylocone with aboral knob or spine; median furrow in deep groove, with lateral depressions slightly marked, if at all; cover plates not imbricating in extended position of aulacophore. *L.Ord.-M.Dev.*

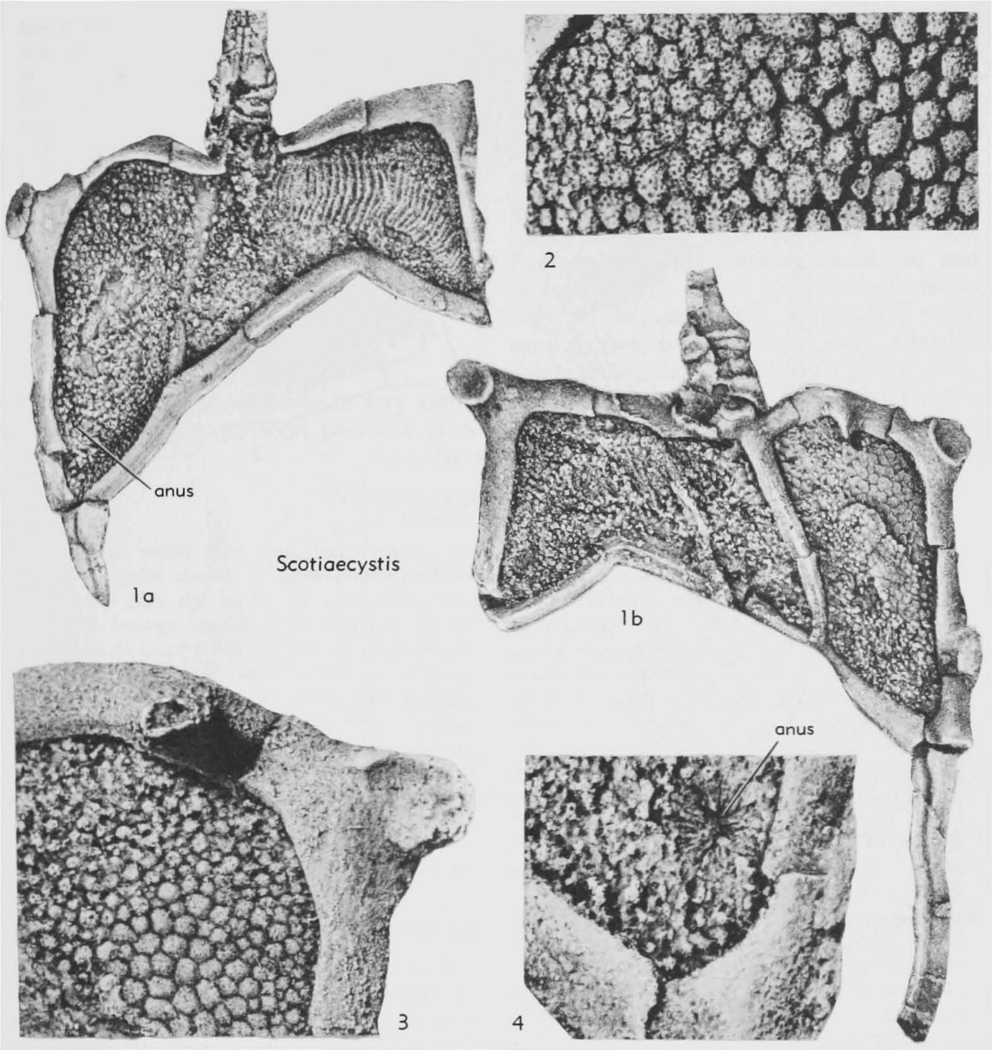


FIG. 348. Scotiaecystidae (p. S550).

Suborder MITROCYSTITIDA Caster, 1952

[*nom. correct.* UBAGHS, herein (*pro* Mitrocystida CASTER, 1952)]

Thecal outlines slightly to moderately asymmetrical; no exothecal posterior process; adorals two. *L.Ord.-L.Dev.*

Family MITROCYSTITIDAE Ubaghs, new family

[=Mitrocystidae JAEKEL, 1901 (invalid family-group name based on *nom. van.*, Code, Art. 11,e)]

Posterior margin evenly arcuate or slightly notched; infracentrals numerous, either small and nearly equal in size, or few and very unequal; adorals moderately developed; supracentrals rather small and more or less numerous; proximal region of aulacophore covered by imbricating quadripartite rings; aboral face of stylocone and following distal ossicles each with strong median curved spine. *L.Ord.-U.Ord.*

Mitrocystites BARRANDE, 1887 [**M. mitra*; OD] [=*Mitrocystis* BATHER, 1889]. Thecal outlines subtrapezoidal or subrectangular, somewhat asymmetrical, slightly notched at both ends; marginals 12 or more, generally 13 (5 or 6 on left side, 7 on right side), relatively thick and folded upward at an acute angle; M'_1 distinctly larger than M_1; lower outer edge of M_2 and M'_2 denticulate;

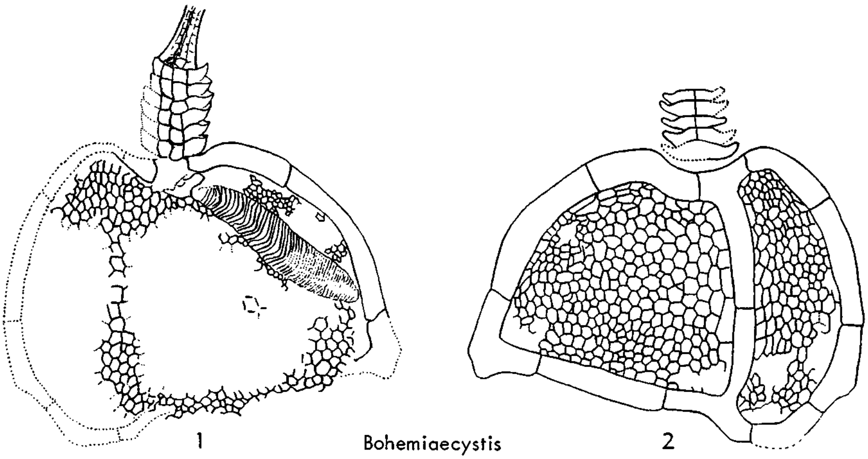


FIG. 349. Scotiaecystidae (p. S550).

infracentrals 4 to 6, largest one subcentral and separated from M_1 by median-sized plate; adorals bearing transverse fold, right one pierced by slitlike opening; supracentrals not imbricate or only slightly so, if at all; periproct semicircular, on upper side, covered by granular integument surrounding perianal row of elongate toothlike platelets; paripores on M_2 and M'_2; lateripores near outer extremity of sutures M_1, M_2 and M'_1, M'_2. *M.Ord.-U.Ord.*, Boh.-Fr. [A very doubtful species has been recorded by DEHM (1934) in the Lower Devonian (Hunsrück Sh.) of Germany].——FIG. 350,*1*. **M. mitra* M.Ord. (Šárka Shale), Boh.; *1a-c,* lower, upper, lat. faces; *1d,* cross section of theca, ×2 (Ubaghs, n).

Chinianocarpos UBAGHS, 1961 [**C. thorali; OD*]. Thecal outlines asymmetrical; posterior margin evenly arcuate, anterior margin hardly notched on lower side, moderately so on upper side; no anterolateral lobes; marginals 9 (4 on left side, 5 on right side), relatively thick, folded upward at acute angle, all of them more extended on lower than on upper side, except M'_4 and M_5 which cover whole upper posterior area; lower external border of M_2, M_3 and M'_2 denticulate; M'_1 larger than M_1; M_4 separating M_1, M_2, and M_3 from infracentrals, which are numerous, small, polygonal, subequal, and tessellate, occupying median elliptical area; one large subanal between infracentral area and marginals M_4, M_5, and M'_4; adorals without transverse fold and opening; supracentrals moderately numerous, tessellate; paripores on M_3 and M'_2; periproct unknown. *L.Ord.*, Fr.——FIG. 351,*1-4*. **C. thorali; 1,2,4,* upper, lower, and lat. faces; *3,* cross section of theca, ×4 (Ubaghs, n).

Mitrocystella JAEKEL, 1901 [**Anomalocystites incipiens* BARRANDE, 1887; OD]. Similar to *Mitrocystites,* but theca relatively more elongate and more asymmetrical, rounded or barely notched at posterior end, and with rather deep median embayment between 2 distinct lobes at anterior end; marginals 13 (6 on left side, 7 on right side), relatively thin, folded upward almost at right angle; M_1 and M'_1 about equal in size; infracentrals 2, one of them very large, always in contact with M'_1, and generally also with M_1; adorals without transverse fold and opening, transversely striated in some species; supracentrals apparently imbricate; paripores and lateripores unknown. *M.Ord.*, Boh.-Fr.——FIG. 350,*2*. *M. barrandei* JAEKEL, 1901, Šárka Sh., Boh.; *2a-c,* lower, upper and lat. faces; *2d,* cross section of theca, ×2 (Ubaghs, n).

Family PARANACYSTIDAE Caster, 1954

Posterior margin acute and prominent; infracentrals few, about equal in size, elongate and roughly hexagonal; adorals very large, covering half or more of upper surface; infracentrals few and rather large. *L.Dev.*

For this monotypic family alone, CASTER (1954) proposed the new suborder Paranacystida. It does not seem that our present knowledge is sufficient to justify recognition of a higher category than family for this rather admittedly aberrant assemblage of Mitrata.

Paranacystis CASTER, 1954 [**P. petrii;* OD]. Theca lancet-shaped to ovate, with nearly vertical lateral surfaces; anterior corners of upper side moderately inflated, produced subangularly; anterior margin more excavated for aulacophore insertion on lower than on upper face; posterior thecal plates seemingly imbricated and prolonged into beak-shaped structure; 2 (possibly 3) marginals on each lateral surface, taking no part in covering of upper side; infracentrals 2 (possibly 3); supracentrals 3 or 4, rather large; anteromedian supracentral quadrangular; aulacophore considerably longer than theca; stylocone 2-bladed, ossicles of aulacophoral distal region with strong median aboral spines. *L.Dev.*, S.Am.(Paraná, Brazil).——FIG. 352,*1-3*. **P. petrii*; *1,* paratype, external mold, upper side, ×10; *2a,b,* holotype, external molds, upper and lower faces, ×5.3; *3,* paratype, external mold, lower face, ×5 *(26)*.

Suborder LAGYNOCYSTIDA Caster, 1952

Thecal outlines moderately to very asymmetrical; a single exothecal posterior process. *M.Ord.*

Family PELTOCYSTIDAE Ubaghs, new family

Thecal outlines moderately asymmetrical, irregularly pentagonal, slightly excavated for aulacophore insertion on both sides; posterior margin unequally divided by marginal protuberance bearing elongate sigmoid spine; marginals eight (three on left side, five on right side), taking almost no part in covering of upper face; lower external edge of M_1 and M'_1 denticulate; infracentrals two, small, not in contact; subanal subquadrangular, outside marginal frame; adorals two, large, extending to mid-length of theca; supracentrals numerous and small, seemingly tessellate; proximal region of

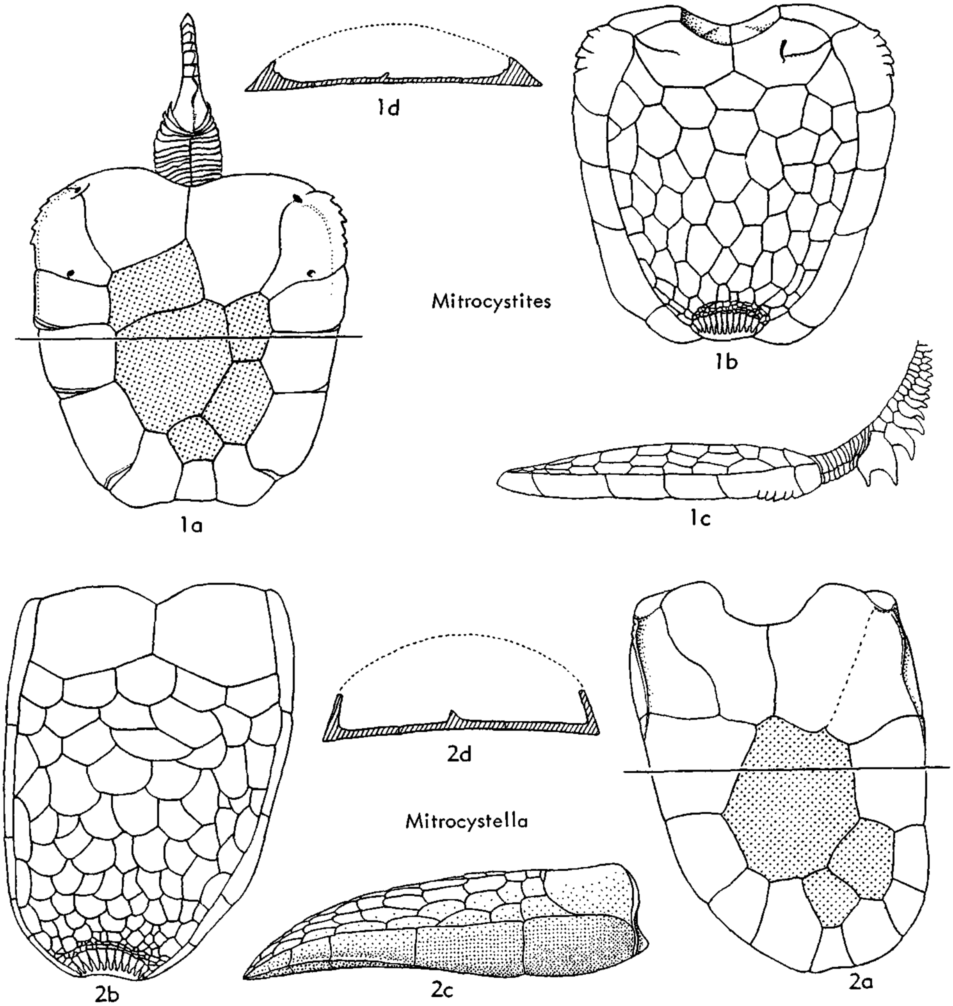


FIG. 350. Mitrocystitidae (p. S551-S552).

aulacophore covered by imbricating tetramerous ring; stylocone and following distal ossicles with strong curved aboral spines. *L.Ord.*

Peltocystis Thoral, 1935 [**P. cornuta*; OD]. Characters of family. *L.Ord.*, Fr.——Fig. 353,*1-4*. **P. cornuta*; *1,3,* interior and exterior of lower face; *2,* upper face; *4,* anterior face; ×3 (Ubaghs, n).

Family LAGYNOCYSTIDAE Jaekel, 1918

Theca elongate, pyramidal, subquadrate in cross section, very asymmetrical; posterior end obliquely truncated, with short hollow calcareous process attached to left posterior corner; left lateral surface higher than right one; lower left lateral edge sharper than right one; no infracentrals, whole inferior face being covered by seven marginals (three on left side, four on right side) and few scalelike platelets in lateral connection with supracentrals; adorals three, moderately large; supracentrals numerous, imbricating; posterior hollow conical piece (?anal valve) terminating upper face; sutural pore on each side of aulacophore insertion; proximal part of aulacophore protected by spinous scalelike imbricated platelets; stylocone elongate, very shallow, with median aboral row of four or five spines; distal region of aulacophore composed of elongate ossicles, each with short distal triangular aboral projection. *M.Ord.*

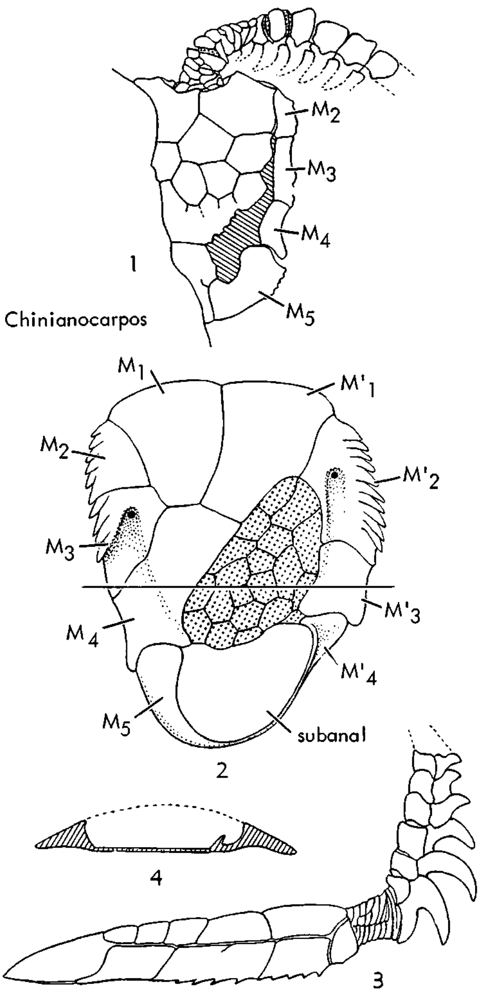


Fig. 351. Mitrocystitidae (p. S552).

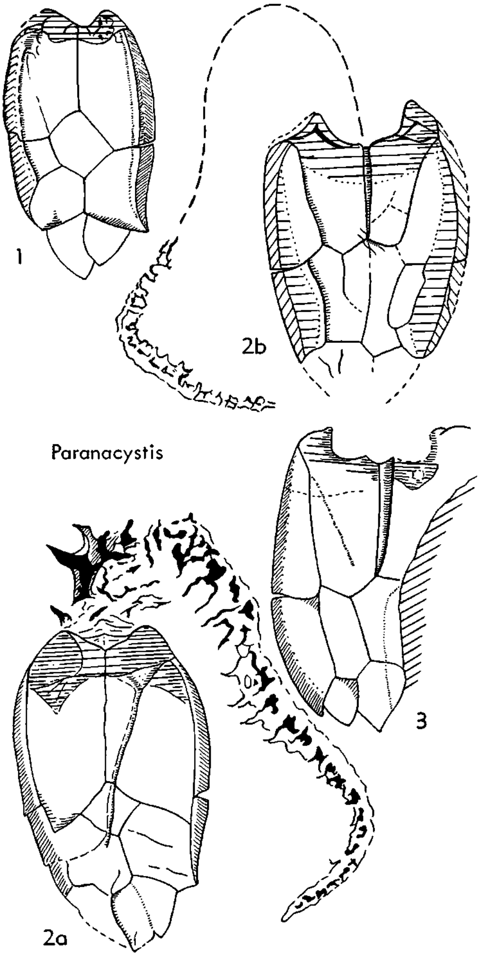


Fig. 352. Paranacystidae (p. S552-S553).

Lagynocystis JAEKEL, 1918 [**Anomalocystites pyramidalis* BARRANDE, 1887; OD]. Characters of family. *M.Ord.*, Boh.——354,*1-5*. **L. pyramidalis* (BARRANDE), Šárka Sh.; *1-4*, lower, upper, right lateral and ant. faces; *5*, cross section of theca, ×3 (Ubaghs, n).

Family KIRKOCYSTIDAE Caster, 1952

[*nom. transl.* UBAGHS, herein (*ex* Kirkocystinae CASTER, 1952)]

Theca plano-convex, asymmetrical, composed of only two adorals, two marginals (M_1, M'_1) and one subanal, and with calcareous posterior process; adorals convex, elongate, subequal, very large, covering entire upper face and large part of lower face as well; M_1 and M'_1 more or less reduced, M_1 smaller than M'_1, which touches large subanal inserted between posterior and adaxial lower margins of adorals; proximal region of aulacophore protected by quadripartite rings; stylocone and following distal ossicles each with aboral spine. *M.Ord.*

Balanocystites BARRANDE, 1887 [**B. lagenula;* OD]. M'_1 relatively large, widening in posterior direction and broadly in contact with subanal; M_1 triangular, extending for some distance along side of M'_1; subanal suparallel to extension plane. *M.Ord.*, Boh.-?Fr.——FIG. 355,*1*. **B. lagenula,* Šárka Sh.; *1a-c,* lower, anterior, upper faces of theca, ×3 (Ubaghs, n).

Anatiferocystis CHAUVEL, 1941 [**A. barrandei*; OD] [=*Kirkocystis* BASSLER, 1950 (type, *Enoploura? papillata* BASSLER, 1943)]. M'_1 narrow, in contact with subanal by short suture; M_1 subquadrate, not extending along side of M'_1; subanal oblique to extension plane. *M.Ord.*, Boh.-Fr.-USA (Okla.).——FIG. 355,*2*. **A. barrandei,* Šárka Sh., Boh.; *2a,b,* lower, upper faces, ×3 (Ubaghs, n).——FIG. 355,*3*. *A. papillata* (BASSLER), Blackriv., USA(Okla.); *3a-e,* lower, posterior, upper, right and left lateral faces of theca, ×6 (Ubaghs, n).

Suborder ANOMALOCYSTITIDA Caster, 1952

[*nom. correct.* UBAGHS, herein (*pro* Anomalocystida CASTER, 1952)] [=suborder Placocystida CASTER, 1952]

Thecal outlines nearly bilaterally symmetrical, with two exothecal posterior spinous processes articulated at base. *M. Ord.-L.Dev.*

The genera classified herein under this suborder were placed by CASTER (1952) under two new monotypic suborders—Anomalocystida and Placocystida—under the erroneous assumption that the Anomalocystitida are provided with segmented brachia and the Placocystida with unsegmented rodlike processes. In fact, as demonstrated by Caster (see under *Anomalocystites*), the Anomalocystitida have no jointed brachia at the posterior end of the body. Therefore they do not differ in any essential way from the placocystid genera.

Family ANOMALOCYSTITIDAE Bassler, 1938

[=Anomalocystidae MEEK, 1872 (invalid family-group name based on *nom. van.*, Code, Art. 11,e); fam. Anomocystida HAECKEL, 1896 (invalid) (*partim*); subfam. Placocystida HAECKEL, 1896 (invalid) (*partim*); fam. Atelocystida HAECKEL, 1896 (invalid) (*partim*); Placocystidae CASTER, 1952 (invalid); Placocystinae CASTER, 1952 (invalid); Enoplourinae CASTER, 1952; Basslerocystinae CASTER, 1952; Placocystitidae GILL & CASTER, 1960]

Theca achieving high degree of bilateral symmetry in general outlines, as well as in

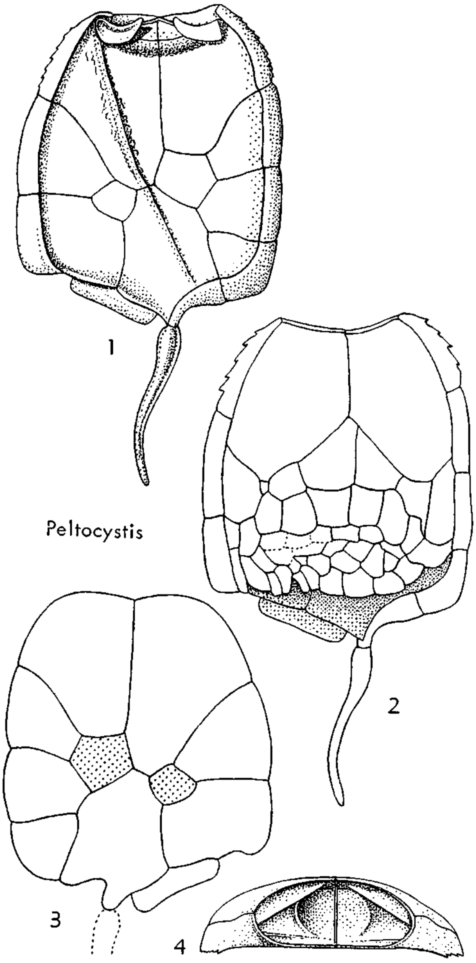


FIG. 353. Peltocystidae (p. S554).

shape and arrangement of plates, particularly on upper face; marginals 11 (two on anterior face, three on each lateral face, and three on posterior face; infracentrals few, including one large plate usually in median position accompanied by small "anomalocystid" plate at its left posterior corner and possibly by one to four additional posteriorly placed small plates; supracentrals tessellate, forming apparently solid pavement; thecal ornament typically consisting of transverse wavy lines. *M.Ord.-L.Dev.*

Partition of the anomalocystitid genera into subfamilies, seems inadvisable to me, at least until better understanding of phyletic relationships has been obtained.

Anomalocystites Hall, 1859 [**A. cornutus*; SD S. A. Miller, 1889] [=*Anomalocystis* Bather, 1889 *(nom. van.)*; *Anomocystis* Haeckel, 1896 *(nom. van.)*] [Diagnosis furnished by K. E. Caster after study by him of Hall's types.]. Theca subovoid in outline, upper face convex and lower one concave, with lateral rim; lateral faces longitudinally arcuate, posterior and anterior upper margins transversely arcuate, inferior face deeply arcuate for reception of aulacophore. Upper thecal surface composed of 12 laterals, 3 large adorals (median one touching margin), 3 large adprocteals, and 14 supracentrals arranged in 4 transverse rows (3 in proximal row, 5 in 2nd, 4 in 3rd, 2 in 4th). Lower thecal face composed of 6 marginals, 2 large adaulacophorals deeply excavated proximally, 3 adprocteals, and 2 infracentrals. Theca partially ornamented by transverse wavy lines, at distal lateral extremities bearing 2 articulated spines. Aulacophore broad proximally, formed of 8 or 9 telescoping rings which imbricate axially on lower side; styloid with 3 axial elements, short blades; distal part of aulacophore long and narrow, apparently biserial. [According to Schuchert (1904), 2 segmented brachia bearing exothecal ambulacra were inserted on the posterior thecal margin. This conclusion is er-

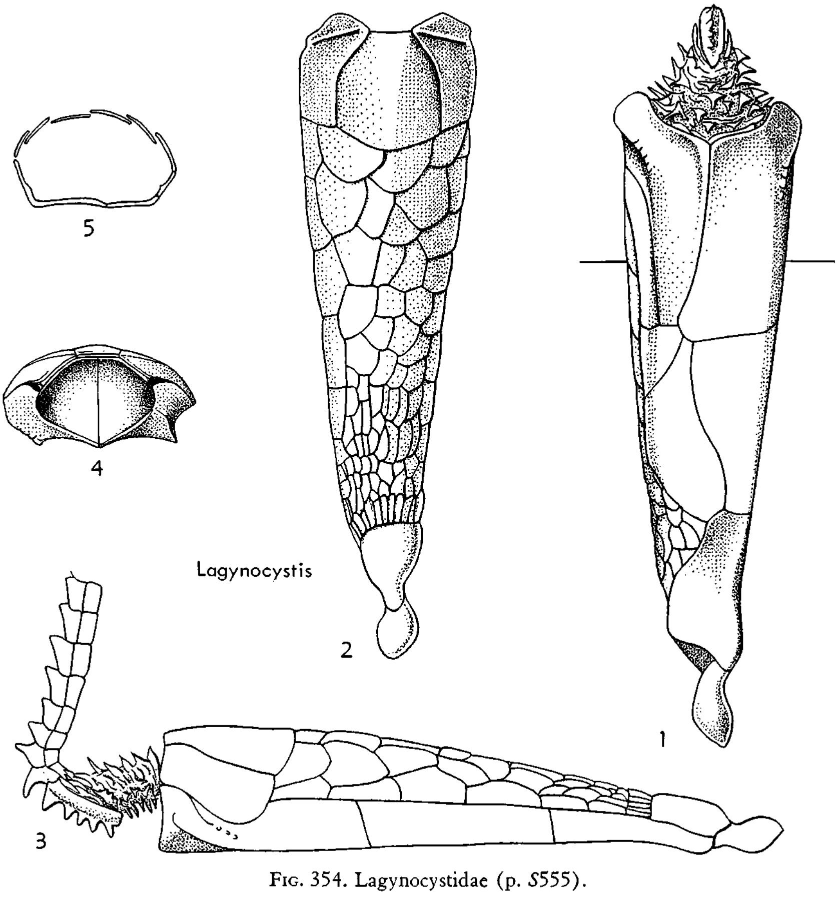


Fig. 354. Lagynocystidae (p. S555).

roneous, for it was based on the distal stele of an adjacent specimen on the same slab (USNM no. 35078). Hall's types preserve the bases of articulated spines in the position of Schuchert's inferred ambulacra.] *L.Dev.*, USA(N.Y.).——Fig. 356,*1*; 357,*1*. **A. cornutus*; 356,*1a-d*, four of Hall's type specimens (AMNH no. 2288); 356, *1a* (holotype), *1b* (previously unfigured paratype), showing superior face; 356,*1c,d*, paratypes showing inferior face (356,*1c*, figured by Hall, 356,*1d*, previously unfigured); all ×3 (Caster, n); 357,*1a,b*, plate arrangements of superior face (holotype) and inferior face (paratype, ×4.5 (Caster, n).

Ateleocystites Billings, 1838 [**A. huxleyi*; OD] [=*Ateleocystis* Lindström, 1888 *(nom. van.)*; *Atelecystis* Bather, 1889 *(nom. van.)*; *Atelocystis* Haeckel, 1896 *(nom. van.)*] [Diagnosis furnished by K. E. Caster after study by him of Billings' types]. Small anomalocystitid mitrates

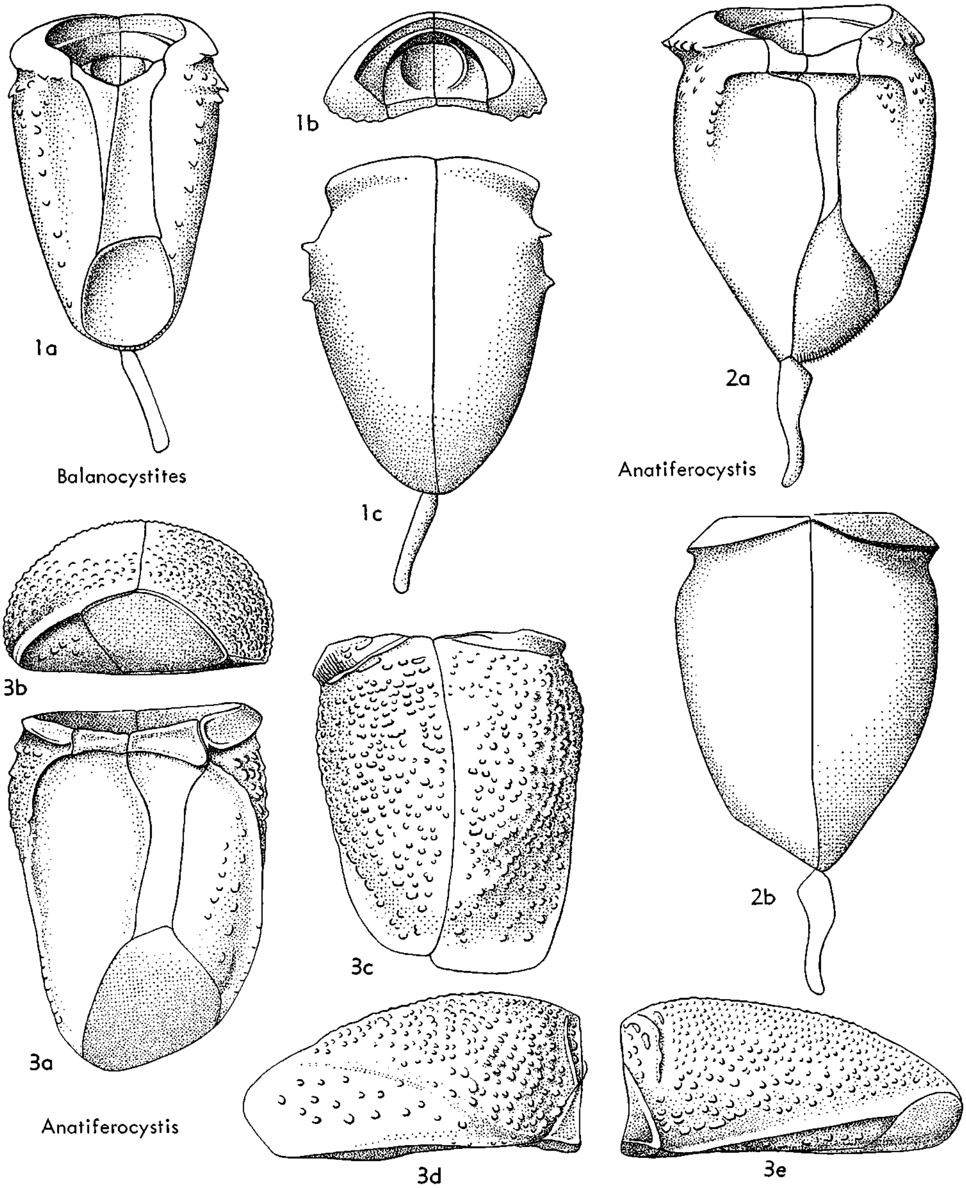
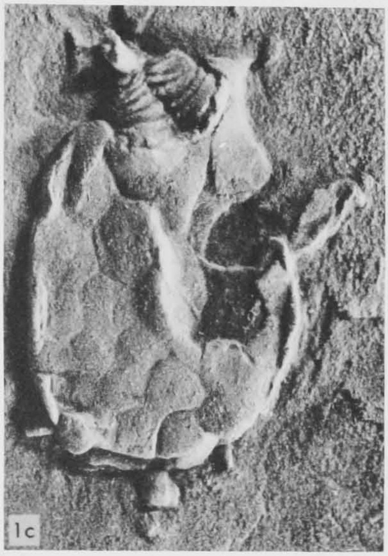
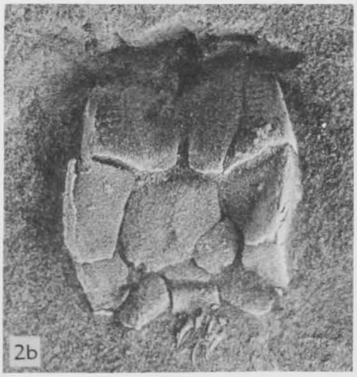


Fig. 355. Kirkocystidae (p. *S*555).



Anomalocystites



Ateleocystites

with inferior (plastron) surface composed of 14 plates, of which 3 are somatic and others marginal, as in *Enoploura*; superior (carapace) surface poorly known, but with more numerous somatic plates and considerably narrower adaulacophore axial plate than in *Enoploura,* superior

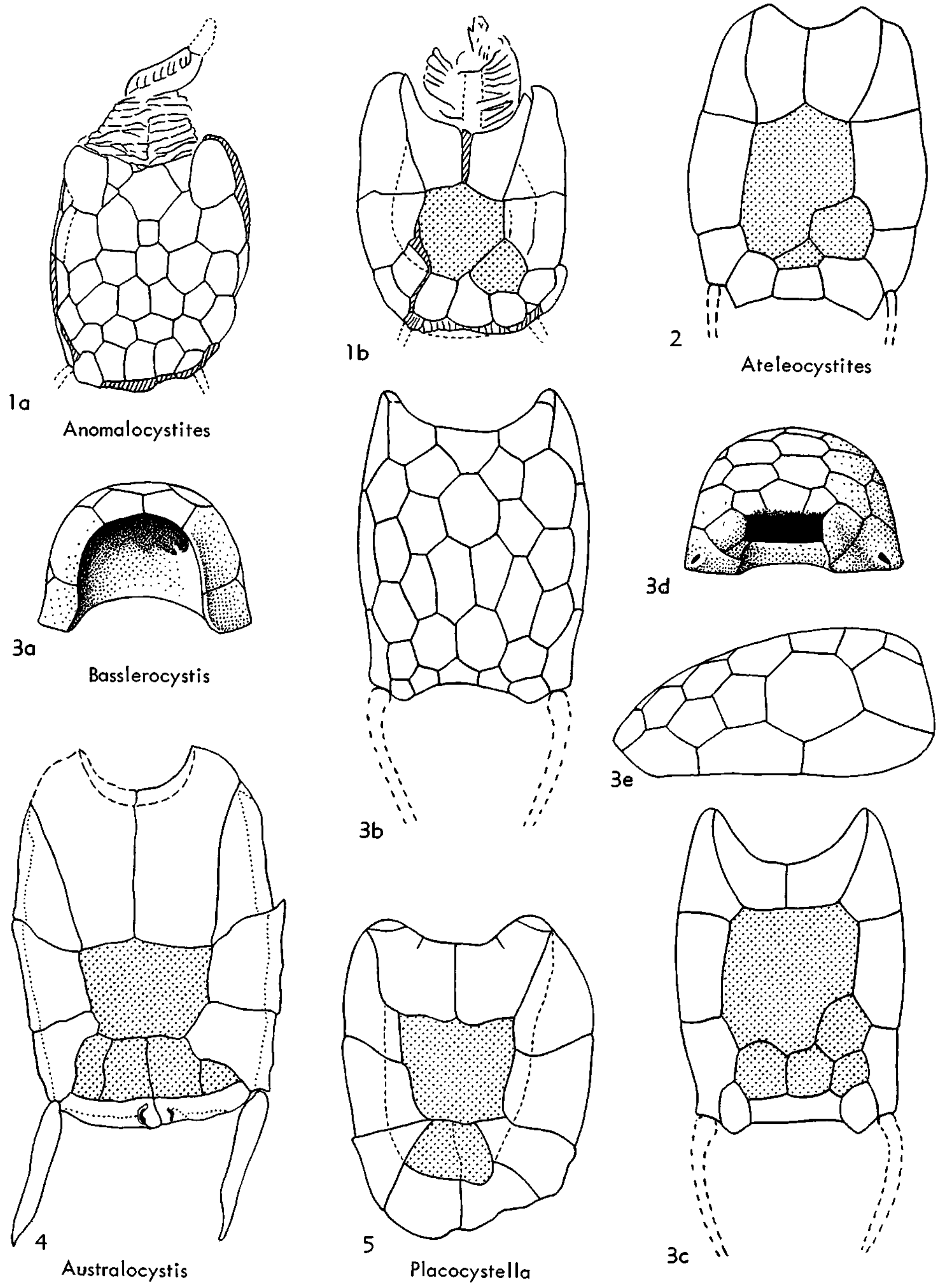
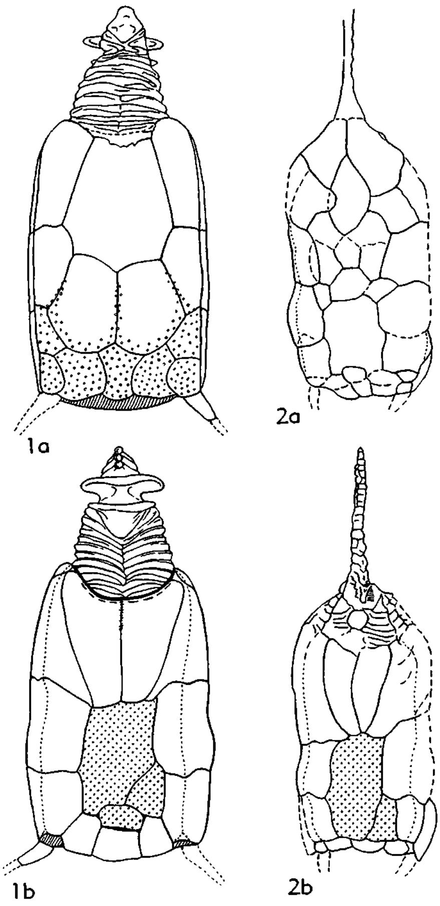


FIG. 357. Anomalocystitidae *(1-3)*; Australocystidae *(4-5)* (p. S556-S557, S559-S560).

FIG. 356. Anomalocystitidae (p. S556-S557, S559-S560) [*On facing page*].



Enoploura Victoriacystis

FIG. 358. Anomalocystitidae (p. S560-S561).

face extending posteriorly well beyond inferior margin, this part apparently formed by single thick posterior marginal plate that served as hood over large posterior orifice (?anus), interior surface of this hood bearing prominent rounded longitudinal carinae nodosely expanded distally. Two distal-lateral articulated "arm" spines known mainly from thecal articulatory surface. Aulacophore 3-zoned, proximal region composed of thin-walled smooth tetrameres which imbricate deeply, styloid part massive and bearing 2 short stout blades, distal region apparently dimerous, inferiorly carinate, and probably long and narrow; surface of inferior adaulacophore plates with prominent pseudoimbricating transverse ridges which grade into seemingly imbricated squamae adaxially; ornament apparently overlapping away from aulacophore. *M.Ord.(Trenton.),* Canada (Ottawa Valley).——FIG. 356,*2*; 357,*2*. **A. huxleyi*; 356,*2a,b,* inferior face of two syntypes (Geol. Survey Canada, nos. 1392A,H) showing longitudinal ridges on posterior, interior of superior (carapace) cover, ×4 (Caster, n); 357,*2,* lower face, ×3.8 (25, mod.).

Basslerocystis CASTER, 1952 [**Anomalocystites disparilis* HALL, 1859; OD]. Theca egg-shaped; lateral faces longitudinally arcuate, more or less steep; lower face concave, with downward produced lateral margins; upper face rather strongly convex; posterior face invaginated for length of quadrate, transverse opening, which apparently could be closed by single, hinged, ?opercular plate; anterior side rather deeply emarginated for aulacophore insertion; infracentrals 5, comprising large central plate and 4 small ones in left posterior and posterior positions; adorals 3; supracentrals numerous. *L.Dev.,* USA(Md.).——FIG. 357,*3*. **B. disparilis* (HALL), Oriskany; *3a-e,* ant., upper, lower, post., and right lat. faces, ×1.4 (*3a,d,e,* Kirk, 1911; *3b,c,* Caster, 1952).

Enoploura WETHERBY, 1879 [**Anomalocystites (Ateleocystites?) balanoides* MEEK, 1872; OD]. Theca subrectangular, larger than wide; lateral faces axially arcuate and nearly vertical, making almost right angle with upper side; anterior margin deeply emarginated for aulacophore insertion, posterior margin slightly arcuate; lower face concave; theca resting on downward-produced edges of lateral marginals; infracentrals 3, one large central plate and two small ones in left posterior and submedian posterior positions; adorals 3, one large median reaching about mid-length of theca and two smaller lateral ones; supracentrals 11; thecal ornament finely granular, coarsely pitted, labyrinthine, or transversely striated. *U.Ord.,* USA(Ohio-Ind.).——FIG. 358,*1*. *E. popei* CASTER, Ohio; *1a,b,* upper and lower faces, ×1.4 (Caster, 1952).

Placocystites DE KONINCK, 1869 [**P. forbesianus*; OD] [=*Placocystis* HAECKEL, 1896 *(nom. van.)*]. Theca flattened subquadrate, somewhat longer than wide; lateral margins slightly arcuate longitudinally; anterior margin deeply emarginated by aulacophore insertion; posterior margin almost straight; lower face slightly concave, upper face moderately convex, both faces joined at acute angle; infracentrals 2, one large central plate and one small one at left posterior corner; adorals 2, moderately developed, almost completely separated by subpentagonal median plate (?third adoral) which does not reach anterior margin; supracentrals 11, in 3 transverse rows, those belonging to most anterior row including median rounded plate ("placocystid plate") generally quite surrounded by its two neighbors; large posterior opening; most thecal plates ornamented with transverse wavy lines on both faces. *U.Sil.,* Eng.-?Gotl.——FIG. 359,*2*. **P. forbesianus,* Wenlock; *2a,b,* upper and lower faces, ×1.5 (Ubaghs, n).

Rhenocystis DEHM, 1932 [**R. latipedunculata*; OD]. Theca subrectangular, elongate, plano- and more probably concavo-convex; lateral margins slightly arcuate longitudinally; posterior margin straight, anterior margin apparently almost entirely occupied by aulacophore insertion; infracentrals 2, large central plate and small one at its left posterior corner; adorals 2, almost completely separated by narrow median plate (?third adoral) which typically does not reach anterior margin; supracentrals 15, in 4 transverse rows; "placocystid plate" narrow, longitudinally elongate; aulacophore very long, ossicles of distal region with long aboral spines. *L.Dev.*, Ger.——Fig. 359,*1*. **R. latipedunculata*, Hunsrück Sh.; *1a,b*, upper and lower faces, ×1.5 (Ubaghs, n).

Victoriacystis Gill & Caster, 1960 [**V. wilkinsi*; OD]. Theca elongate, with subpentagonal outline; lower face flat or slightly concave; upper face strongly convex; lateral margins nearly vertical; upper anterior border overarching proximal region of aulacophore, lower anterior margin arcuately excavated by wide aulacophore insertion; four most anterior marginals occupying nearly half of lower thecal face; infracentrals 2, moderately large median plate and small one at its left posterior corner ("anomalocystid plate"); adorals 2, small, posteriorly separated by lozenge-shaped plate (?third adoral); supracentrals numerous and rather small, except relatively large one in median posterior position; anterior upper plates ornamented with transverse wavy lines. *U.Sil.*, Australia.——Fig. 358,*2*. **V. wilkinsi*, Victoria; *2a,b*, upper and lower faces, ×1.5 *(43)*.

Family AUSTRALOCYSTIDAE Caster, 1954 [1956]

[*nom. transl.* Ubaghs, herein (*ex* Australocystinae Caster, 1954 [1956])]

Theca achieving high degree of bilateral symmetry in general outlines, as well as in shape and arrangement of plates on both thecal faces; marginals 10, two on anterior face, three on each lateral face, and two on posterior face; infracentrals few, comprising one large subcentral plate and generally some additional smaller ones. *L.Dev.*

Australocystis Caster, 1954 [1956] [**A. langei*; OD]. Theca subrectangular in outline arcuately excavated for reception of aulacophore on lower face (only one known); lateral and posterior inferior margins raised in prominent rounded flanges; marginals 10 (12 according to Caster) and infracentrals 5 (3 according to Caster) almost symmetrically arranged; no "anomalocystid plate"; transverse row of 4 small infracentrals immediately behind large central plate; posterior margin entirely occupied by only 2 massive transversely elongate marginals. *L.Dev.*, S.Am.(Paraná, Brazil).——Fig. 357,*4*. **A. langei*; lower face, ×3.6 (27).

Placocystella Rennie, 1936 [**P. capensis*; OD]. Theca apparently cordiform in outline; lower face made of ?12 plates (10 marginals, 2 infracentrals), more or less symmetrically arranged. *L.Dev.*, S.Afr.——Fig. 357,*5*. **P. capensis*, Bokkeveld Ser.; lower face, ×2.5 (27, modified).

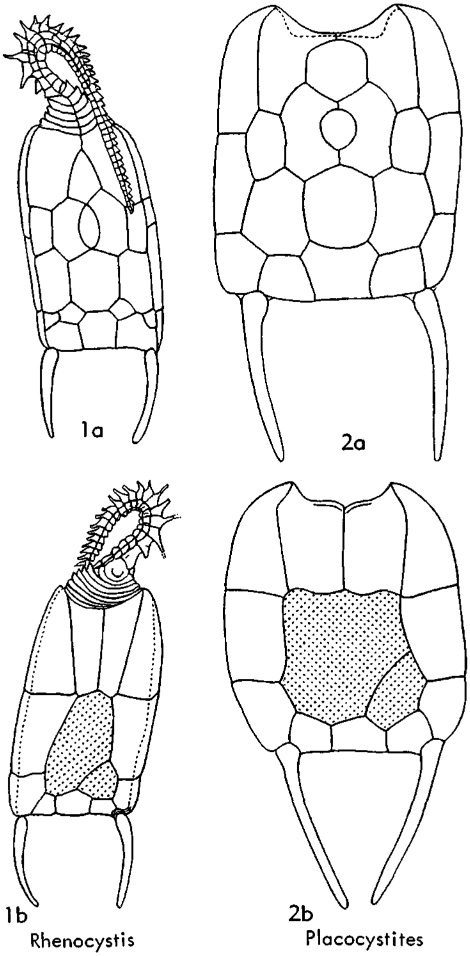


Fig. 359. Anomalocystitidae (p. *S*560-*S*561).

Family ALLANICYTIDIIDAE
Caster & Gill, new family

Mitrate, anomalocystid Stylophora of nearly perfect bilateral symmetry both in outline and thecal plate arrangement; with pair of articulated distal lateral spines, articulatory bases for which are seen on thecal corners; one large somatic plate in superior (carapace) face, and two subequal, paired somatics in inferior (plastron) face; aulacophore large, three-zoned, one styloid blade of quite exceptional width. *L.Dev.*

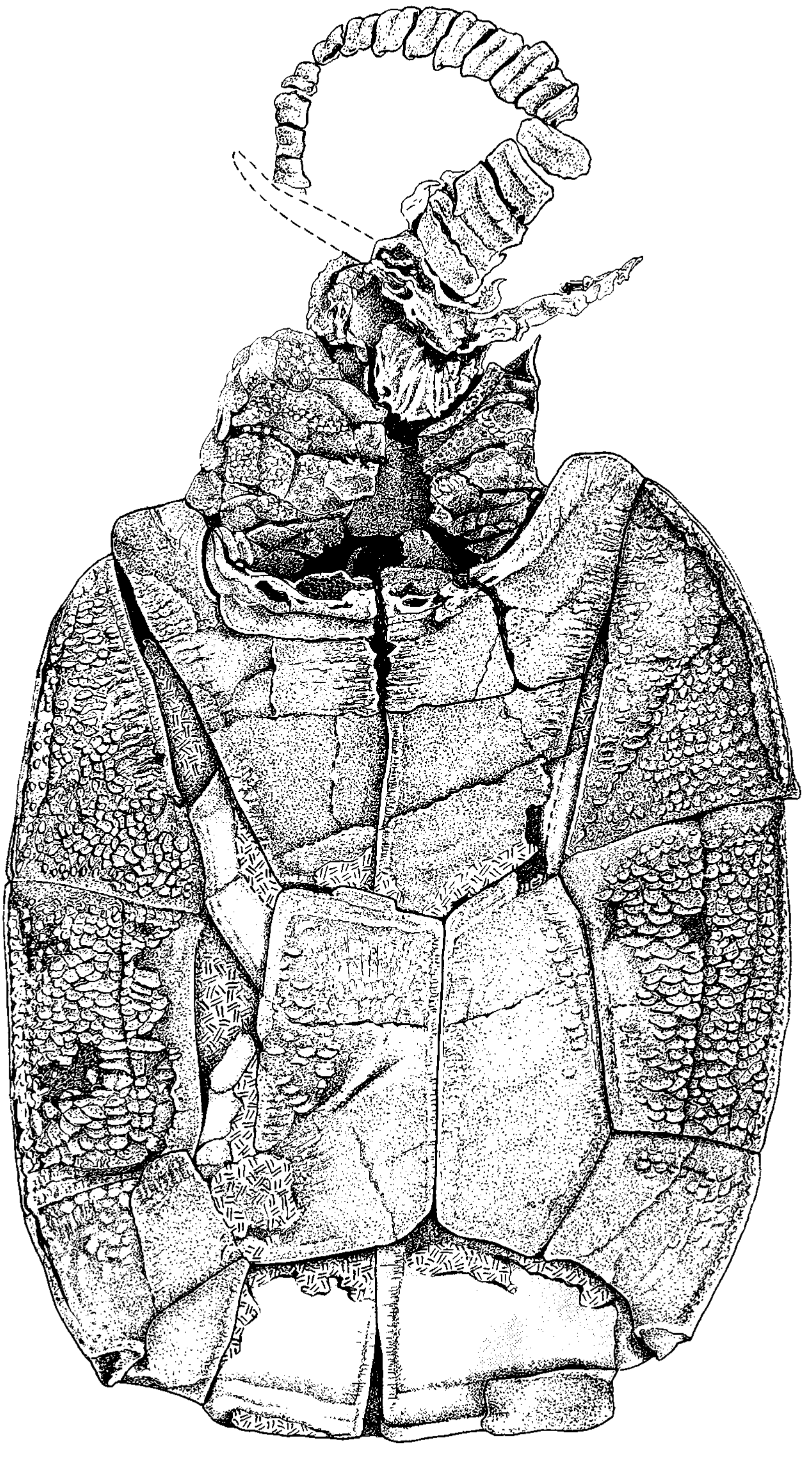


FIG. 360. *Allanicytidium flemingi* CASTER & GILL (Allanicytidiidae) (p. S564).

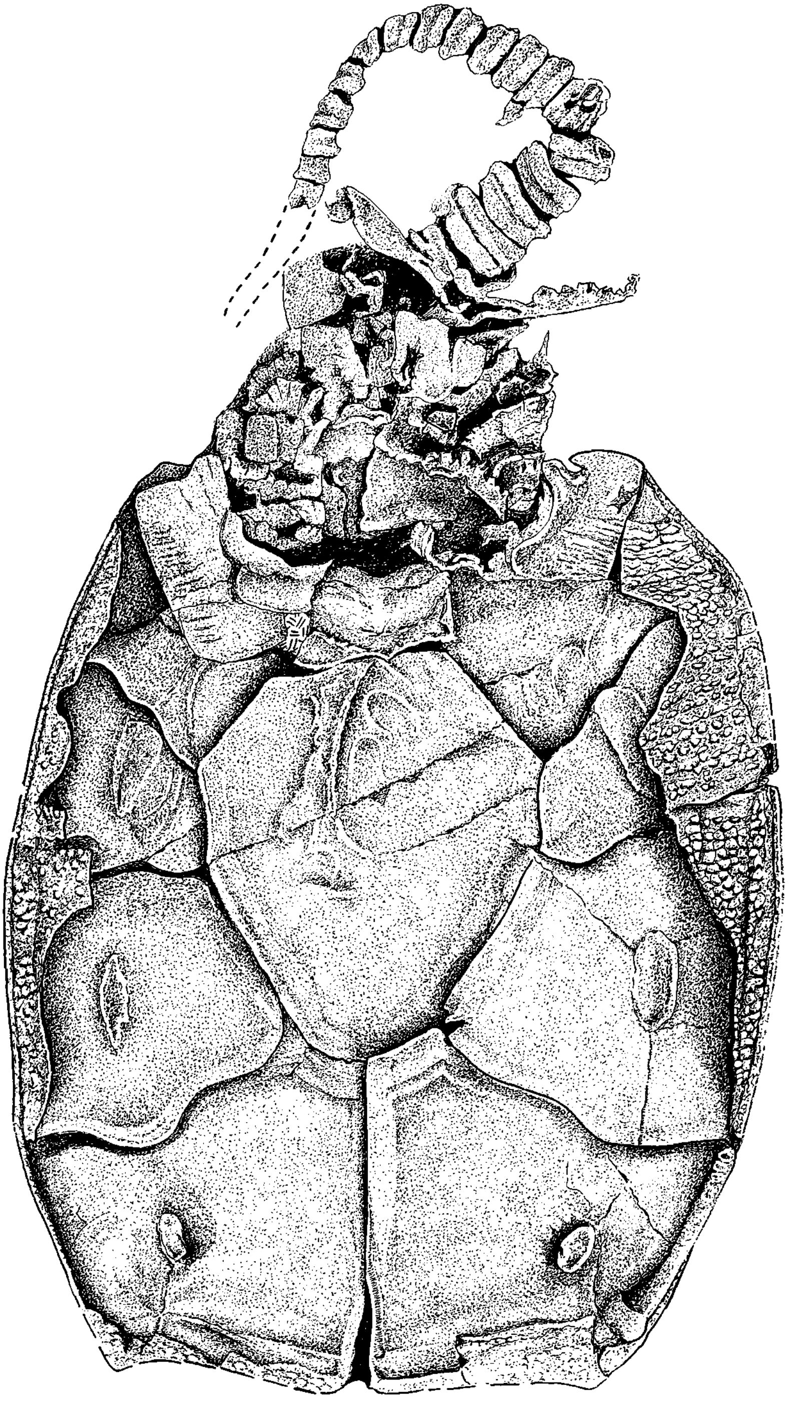


FIG. 361. *Allanicytidium flemingi* CASTER & GILL (Allanicytidiidae) (p. S564).

Allanicytidium Caster & Gill, **new genus,** herein (named for Robin S. Allan; *cytidium,* little box) [**A. flemingi* Caster & Gill, n.sp.; OD]. Large placocystoid, with boxlike theca, tripartite aulacophore and paired, basally articulating distal-lateral spines. Theca quadrately ovoid in plan; broadly convexi-concave in cross section; length to width as 13:11; broad-margined re-entrant of both thecal faces for aulacophore insertion. Surface of thecal plates prominently scaly in appearance, with pseudo-overlap away from aulacophore; imbrice scale aspect merging into typically mitrate transverse ridging on the adaulacophore plates (surface ornament seen so far only on inferior thecal face). Coarse granular ornament on proximal aulacophore tetrameres. Inferior (concave, plastron) thecal surface covered by probably 13 large nonimbricating plates, only 2 of which are somatic. Plates seemingly flexibly united in life (holoperipheral growth lines prominent on interior of plates), except possibly at margins of theca, where either there was fusion of plates of both thecal surfaces, or more likely marginal plates bend laterally so as to form lateral surface and extend onto both thecal surfaces. [For purposes of description here, the marginal plates seen on each surface are treated as though separate plates.] Lateral thecal margin bears narrow, downwardly directed keel; remainder of inferior surface forming broad vault. Holotype has 9 marginal plates but 2 more are reasonably inferred at distal margin; somatic pair are elongate, subequal in size and shape, meeting on axial plane. Right somatic (as seen with theca inverted and aulacophore directed away from viewer) is slightly smaller in area and pentagonal, rather than quadrate. Superior (convex, carapace) thecal surface covered by 9 large plates, only one of which has appearance of being somatic, but in reality is large adaulacophore basal axial plate. (Only the interior surface on the carapace plates is known.) The disposition of the plates and the circumperipheral lines of growth indicate that the plate sutures were flexible and integumentary. Most of the superior plates bear prominent, cuplike calcareous myophores. *L.Dev.,* N.Z.——Fig. 360, 361. **A. flemingi*; Reefton Beds, South Island, N.Z. (Rain Creek, Waitahn); views of holotype (N.Z. Geol. Survey no. 38/370203), 360, 361, inferior (plastron) and superior (carapace) surfaces, ×8 (Gill & Caster, n).

[These new taxa differ markedly from any other Stylophora in nature of the plate arrangement; they are mainly covered by the homologues of marginal plates in other forms; the somatic elements are as a correlate much reduced in number and highly modified. The right somatic of the plastron appears to be the homologue of the small asymmetric "anomalocystid" plate in other mitrates (e.g., *Placocystites, Enoploura*). The central "somatic" of the carapace is a distally migrated and enlarged central basal plate of other forms; in this genus it no longer makes contact with the aulacophore. Only the Australocystidae (*Australocystis,* L.Dev., Brazil; *Placocystella,* L.Dev., S. Afr.) approach the Allanicytidiidae in bilaterality; however, the plate arrangements of the two families are quite different. The new genus, being monotypic, is characterized by large size, pseudosquamose ornament, and extraordinary large styloid blade.]

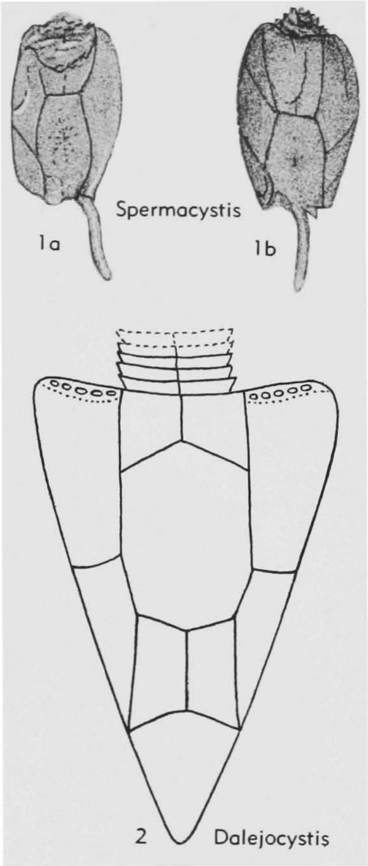


Fig. 362. Stylophora, Suborder and Family uncertain (p. S564-S565).

Suborder and Family UNCERTAIN

Dalejocystis Prokop, 1963 [**D. casteri*; OD]. Theca symmetrical, showing form of rounded isosceles triangle; upper face composed of fairly large symmetrically arranged plates and ending in rounded massive triangular plate; anterior margin bearing row of conical tubercles on both sides of aulacophore insertion; lower face unknown. *M.Dev.,* Boh.——Fig. 362,2. **D. casteri,* Daleje Sh. (Couvinian); upper face, schematic reconstruction, ×6 (71).

Spermacystis Ubaghs, herein [*nom. subst. pro Anomocystis* Jaekel, 1918, p. 122 (*non* Haeckel, 1896)] [**Anomalocystites ensifer* Barrande, 1887; OD]. Thecal outline nearly symmetrical; anterior border emarginated for aulacophore insertion, lateral margins longitudinally arcuate, posterior margin straight; one (possibly 2 according to Barrande) posterior exothecal rodlike process;

number and arrangement of plates, as well as aulacophore, unknown. [This nominal genus, based on scanty and poorly preserved material, was placed among Anomalocystidae by JAEKEL (1918) and CHAUVEL (1941). Possibly it belongs in the Lagynocystida.] *M.Ord.*, Boh.——FIG. 362, *1*. **S. ensifer* (BARRANDE); *1a,b*, different specimens, orientation unknown, ×1.5 (2).

[References for the chapter on Stylophora are included with those for Homostelea and Homoiostelea (*see* p. *S*624).]

HOMOSTELEA

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[Université de Liège, Belgium]

CONTENTS

INTRODUCTION

The subclass Homostelea, here elevated to class rank, was proposed by GILL & CASTER (1960,*43*) to embrace the two orders Cincta JAEKEL *(55)*[2] and Digitata GEKKER (1938,*39*), which GILL & CASTER included in the class Carpoidea JAEKEL *(54)*. Subsequently, the Digitata were assigned to the class Eocrinoidea by UBAGHS (1950,*86*). Therefore, as here understood, the Homostelea contain only the single order Cincta.

Within the Cincta are placed *Trochocystites* BARRANDE (1887) and a few related genera, all of which belong to the Middle Cambrian of the Old World. That it is appropriate to classify *Trochocystites* in a family group of its own was first recognized by JAEKEL when he defined the Trochocystitidae. At the same time he united this assemblage with the Mitrocystidae *(54)* in a suborder named Marginata of the order Heterostelea (class Carpoidea). The Mitrocystitidae now are recognized as a family of the order Mitrata in the class Stylophora. BATHER *(13)* maintained the Trochocystitidae—incorrectly spelled Trochocystidae, as given by him (BATHER, 1902, in Zoological Record) earlier and generally

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[1] I am much indebted to KENNETH E. CASTER and RAYMOND C. MOORE for translating my manuscript, and to the following persons for loan of specimens or permission to study collections: Prof. JACQUES AVIAS, Université de Montpellier, France; Dr. ALBERT BREIMER, Vrije Universteit, Amsterdam, Netherlands; Abbé ROBERT COURTESSOLE et M. GÉRARD GRIFFE, Carcassonne, France; Dr. HERMANN JAEGER, Humboldt-Universität, Berlin, Germany; Dr. R. P. S. JEFFERIES, British Museum (Natural History), London, Great Britain; Dr. FERDINAND PRANTL, Národní Museum, Prague, Czechoslovakia; Dr. GERTA WEHRLI-OLBERTZ, Ernst-Moritz-Arndt-Universität, Greifswald, Germany. Photographs, drawings and assemblage of figures have been prepared by Mrs. MARIE MASSON. To all these people I express deep thanks.

[2] Numbers enclosed by parentheses, other than years, indicate serially numbered publications in the list of references at end of this chapter.

accepted by other authors—but rejected the Marginata, assigning the family instead to the suborder Heterostelea of the order Amphoridea (class Cystoidea).

In 1918 Jaekel *(55)* described two new genera of echinoderms more or less similar to *Trochocystites* and grouped all of them together in a new order named Cincta. The genus designated as *Trochocystoides* was placed in the Trochocystitidae and one named *Gyrocystis* in the new family Gyrocystidae.

Other authors generally have treated the genera mentioned as members of a single family of the class Carpoidea *(32,41)* or grouped them with most other "carpoids" as mere so-called cystoids referred to the family Anomalocystidae of Meek (1872) (Zittel, 1895, 1910, 1913; Bather, 1900; Delage & Hérouard, 1903) or its equivalent, correctly designated, Anomalocystitidae Bassler (1938) (Bassler & Moodey, 1943). The Anomalocystitidae now are classified as a family of the Mitrata in the class Stylophora.

The Homostelea have nothing in common with other "carpoids" except the depressed form of their asymmetrical body girdled by a marginal framework and their complete lack of radial symmetry. They differ from all of them in the localization of their two main thecal orifices near one pole of the body and in having one or two epithecal grooves on the marginal frame leading to one of the orifices. In addition, they differ from the Stylophora in possessing a pedunculate appendage or stele and in lacking a brachial appendage comparable to the stylophoran aulacophore. They are separated from the Homoiostelea by the nature of the stele, primarily composed throughout its length of a double series of similar plates, and likewise by the absence of an arm.

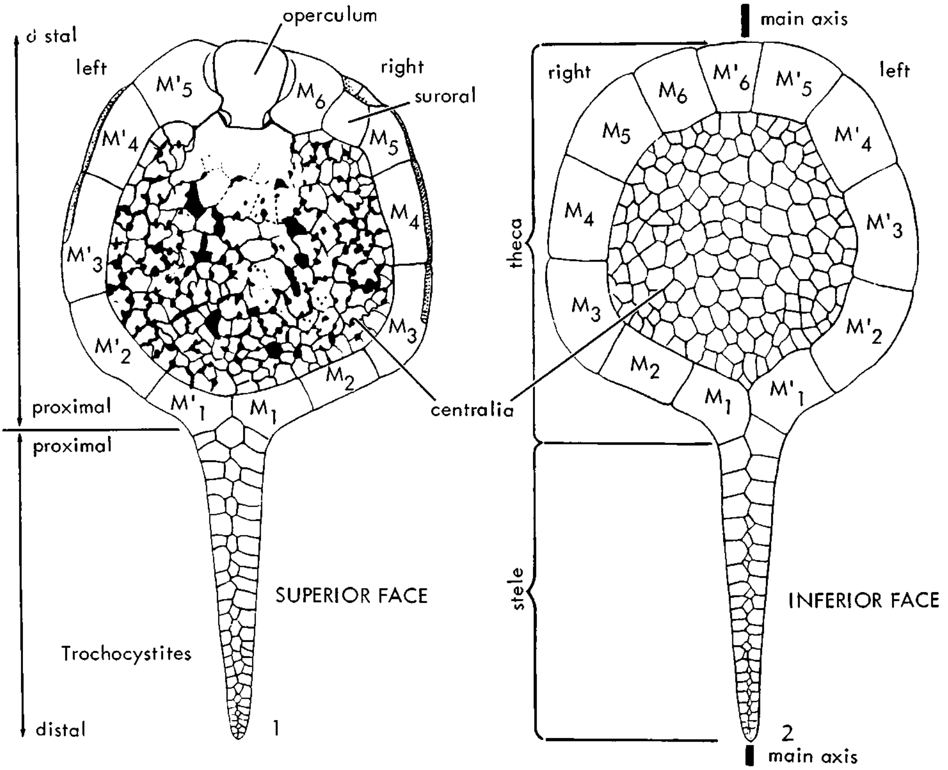

Fig. 363. Morphological features of Homostelea, based on **Trochocystites bohemicus* Barrande, M.Cam., Boh.; *1,2,* upper and lower faces, ×3 (Ubaghs, n).

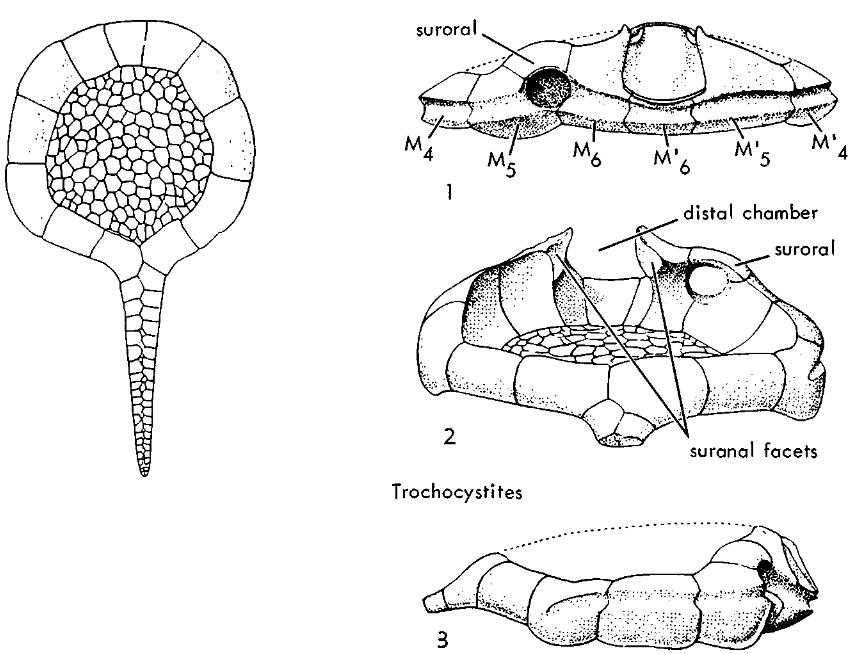

FIG. 364. Morphological features of Homostelea, based on **Trochocystites bohemicus* BARRANDE, M.Cam., Boh.; *1-3,* distal, proximal, and right lat. views, ×3 (Ubaghs, n).

MORPHOLOGY

GENERAL FEATURES

The skeletal parts of the Homostelea consist of a **theca** and a **stele,** the latter being essentially only a much-narrowed and tapering extension of the former. The theca is asymmetrical, although it may display some tendency toward bilateral symmetry (Fig. 363).

In outline the theca may be almost circular, oval, pyriform, or subtriangular. When pyriform, the stele emerges from the constricted part of the theca, and when subtriangular, from the apex of the triangle. Invariably, the theca grows thinner toward the stele.

The theca is flattened and shows two very dissimilar faces—a flat or concave one, on which the living animal presumably reposed, and an opposite convex one. The integuments covering a large median part of the two faces contain many small plates named **centralia** or **centrals.** Peripherally these meet the inner edges of thick plates that form the stout marginal framework of the theca and accordingly are named **marginalia** or **marginals.** On the convex upper face of the theca the marginal frame is pierced by two orifices which are located near to one another at the extremity opposite to the stele (Fig. 364,*1,2*). The smaller of the orifices is bounded laterally by a pair of marginals and above by a supplementary fixed plate named **suroral** (=eporal, JAEKEL, 1918[1]) resting on edges of the marginals (Fig. 364,*1,2*; 365,*3,4*). One or two epithecal grooves hollowed into the outer face of some of the marginals lead to this orifice. The neighboring relatively large orifice is bounded by three marginals, two laterally and one below, and is protected above by an apparently movable plate designated as **operculum** (Fig. 363,*1*; 364,*1*; 365,*3*).

The stele is flattened like the theca. It tapers distally away from the theca and shows the same organization throughout its length. It is composed of two series of opposed or alternating plates which meet along the mid-line of each face except

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[1] Such terms as eporal, epanal, epicentral, and hypocentral, of combined Greek-Latin origin, here are replaced by terms with components derived from a single one of these languages.

where a varying number of tiny ossicles is intercalated between them. A narrow axial canal enclosed by the stele opens between two of the marginals into the thecal cavity.

ORIENTATION AND NOMENCLATURE

The plane in which the theca is flattened is termed the **extension plane** (Bather, 1913) or extensiplane (Gill & Caster, 1960). The two faces of the theca are differentiated with respect to this plane and the probable attitude of the living animal as **superior or upper face** (=obverse face, Bather, 1913) and **inferior or lower face** (=reverse face, Bather, 1913). The **main axis** of the theca and stele runs longitudinally midway between their lateral margins and marks the position of the **symmetry plane** (Bather, 1913) oriented at right angles to the extension plane. The body tends toward bilateral symmetry as defined by this plane.

Length is measured along the main axis and **width** normal to this axis in the extension plane. **Height or thickness** is defined as the distance between the two thecal faces normal to the extension plane.

For purposes of description, the junction of theca and stele is defined as marking the most **proximal or adsteleal** pole of the theca and the opposite extremity along the main axis of the **distal or absteleal** pole of the theca (Fig. 363). Similarly, the proximal part of the stele lies closest to the theca and the distal part nearest to its tip.

Right side and **left side** are purely conventional designations of halves of the

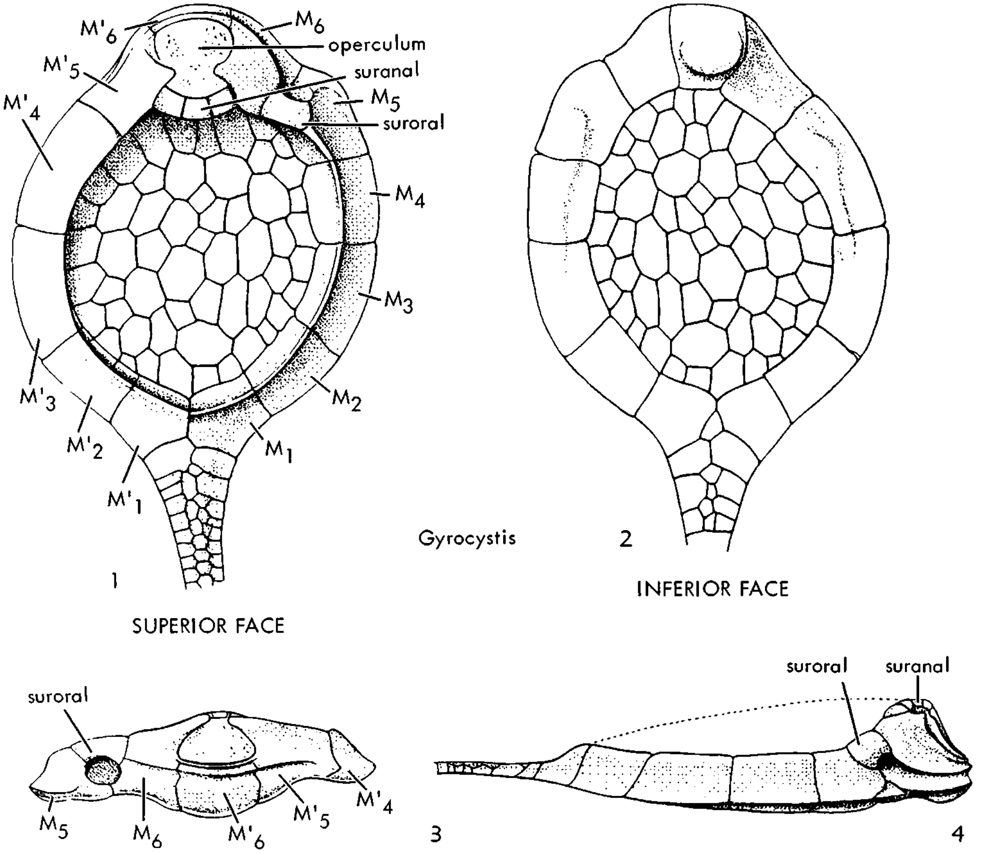

Fig. 365. Morphological features of Homostelea, based on _*Gyrocystis barrandei_ (Munier-Chalmas & Bergeron), M.Cam., Fr.; *1,* upper face, supracentrals lacking, ×3; *2-4,* lower, distal, and right lat. views, ×3 (Ubaghs, n).

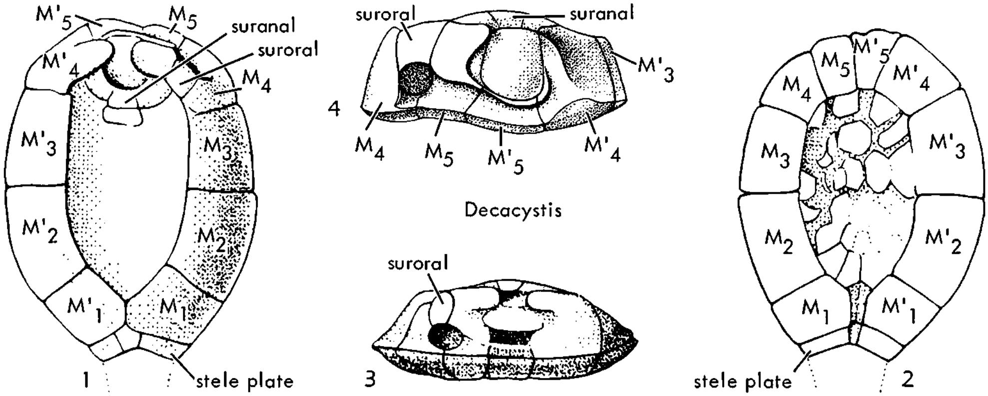

FIG. 366. Morphological features of Homostelea, based on *Decacystis*.——*1-3*. **D. hispanica* GISLÉN, M. Cam., Spain; upper, lower, and distal views, ×3 (10).——*4*. *D.* sp. cf. **D. hispanica* GISLÉN, M.Cam., Spain; distal view, ×5 (Ubaghs, n).

theca and stele on opposite sides of the symmetry plane when the fossil is oriented with the inferior thecal face directed downward and the stele toward the observer (downward in figures). According to convention, the marginal plates are designated by the symbols M_1, M_2, M_3 . . . on the right side of the theca beginning at the stele and by the symbols M'_1, M'_2, M'_3 . . . on the left side similarly (Fig. 363). It should be observed that identity in form of these symbols does not indicate homologies of the marginals in Homostelea and Stylophora.

MARGINALIA

The framework formed by the marginal plates comprises the strong peripheral part of the theca. The mode of designating individual marginal plates has just been explained. All are thick and they are joined firmly to one another. Both their positions and numbers (10 to 12 in different genera) are constant. The upper face of each plate may be distinctly convex (e.g., *Trochocystites*, Fig. 364,*2,3*), slightly convex to slightly concave (e.g., *Trochocystoides*), flat (e.g., *Decacystis*, Fig. 366,*3,4*), or almost flat to strongly concave (e.g., *Gyrocystis*, Fig. 365,*1*), whereas the lower face of each plate invariably is flat or convex and the inner (interior) face concave (Fig. 364,*2*). The external intersection of the upper and lower faces may be sharp-angled or regularly rounded and consequently its cross section varies from triangular (e.g., *Decacystis, Gyrocystis*) or inverted T-shaped (e.g., *Gyrocystis*) to more or less U-shaped (e.g., *Trochocystites*).

Prominent localized swellings or tumescences generally characterize the lower face of the marginals, but never in the proximal part of the theca. The swellings have lateral positions in *Trochocystites* and extend over several plates on both sides (Fig. 364,*2,3*). Opposite to the stele in *Gyrocystis* a large boss is seen beneath the main thecal orifice, generally flanked on both sides by less prominent elongate swellings (Fig. 365,*2*). The variations in shape and size of the prominences may reflect the microenvironments of individuals, though the precise nature of their function is unknown. Probably they helped to anchor the animals.

CENTRALIA

The superior and inferior plated integuments of the median part of the theca are affixed to the upper and lower inner edges of the marginal framework. Along the lines of attachment many small depressions observed in some specimens probably mark the sites of supple ligamentary bundles (see Fig. 370,*3*). Collectively, the plates of the central regions of the theca are designated as **centralia or centrals.**

The centrals of the superior thecal face are distinguished as **supracentralia or supracentrals** [=epicentralia, JAEKEL, 1918]. For the most part these small plates are discrete and in the living animal were probably united flexibly, thus accounting for their rare preservation. They are almost unknown in *Gyrocystis* and *Decacystis* except for isolated platelets, but in *Trochocystites bohemicus* they consist of small irregular and maladjusted ossicles with uneven integumentary spaces between them (Fig. 367,*1*). The spaces may have the aspect of generally distributed sutural pores with elliptical outlines. In places they are bordered internally by calcareous crests, and collectively they may form a transverse crescent (Fig. 367,*2-4*). As in eocrinoids and some other primitive echinoderms, these sutural

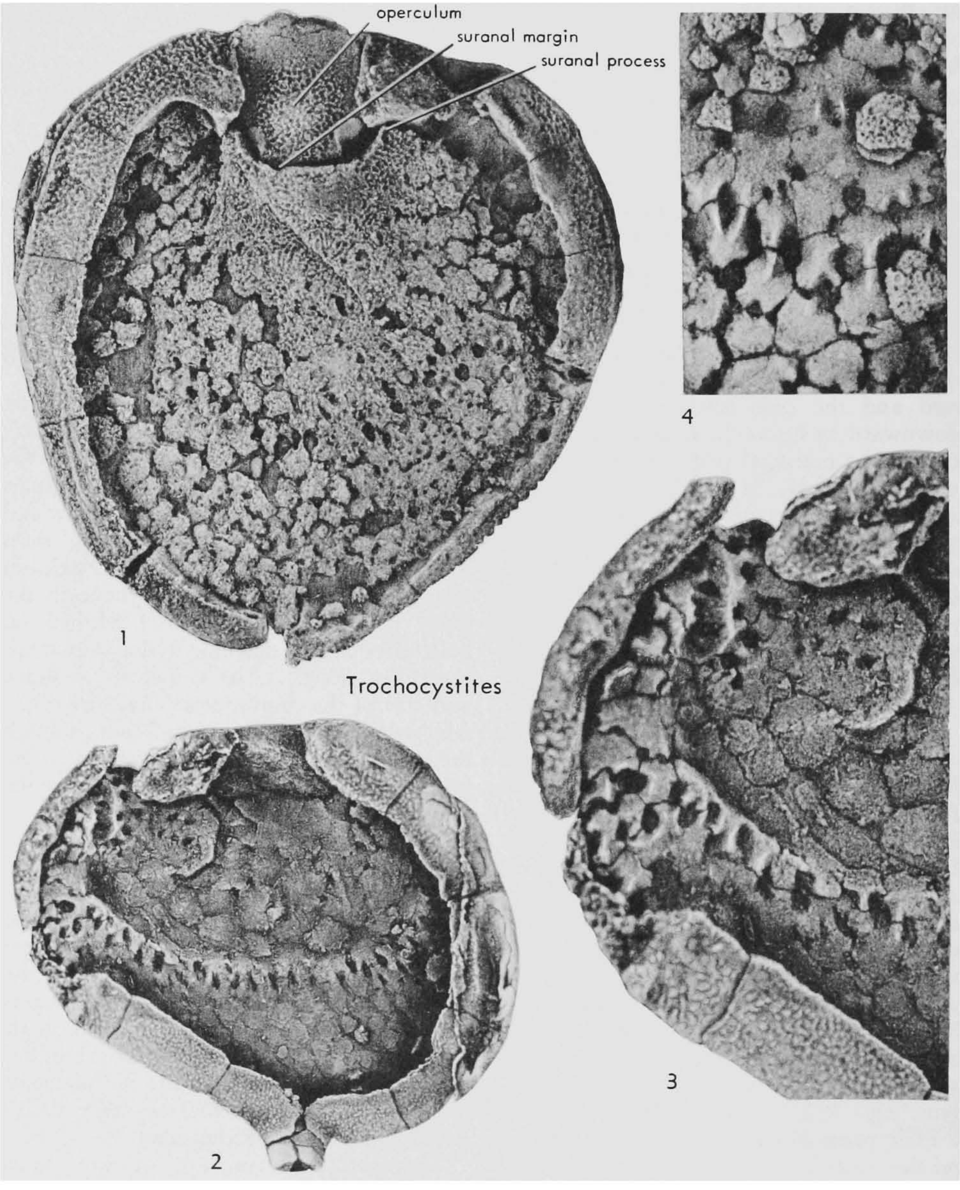

FIG. 367. Centrals of superior thecal face in **Trochocystites bohemicus* BARRANDE, M.Cam., Boh.; *1,* upper face, external side, ×4; *2,3,* internal side of supracentral pavement, ×4; *4,* internal side of some supracentrals showing sutural pores, ×7.5 (Ubaghs, n).

"pores" probably were not actual openings in the theca but merely small uncalcified parts of the integument or spaces occupied by papulae-like organs that served for gaseous exchange between coelomic fluids and sea water.

The integument of the lower thecal surface inside of the marginal frame was occupied completely by more or less numerous polygonal plates which formed a tessellated pavement (Fig. 363,*2*; 365,*2*). These plates are called **infracentralia or infracentrals** [=hypocentralia, Jaekel, 1918].

A few special features of the superior face of the theca call for notice. In *Trochocystites* from near the middle, plates of the centralia become more tightly united in a distal direction toward the large thecal orifice so as to form a thick firm border around it, which is distinguished as the **suranal margin** (Fig. 367,*1*). Laterally and distally this margin is produced into two **suranal processes,** each of which rests against the **suranal facet** of a large apophysis borne by one of the pair of marginals that frame the orifice laterally (Fig. 364,*2*; 367,*1*). No

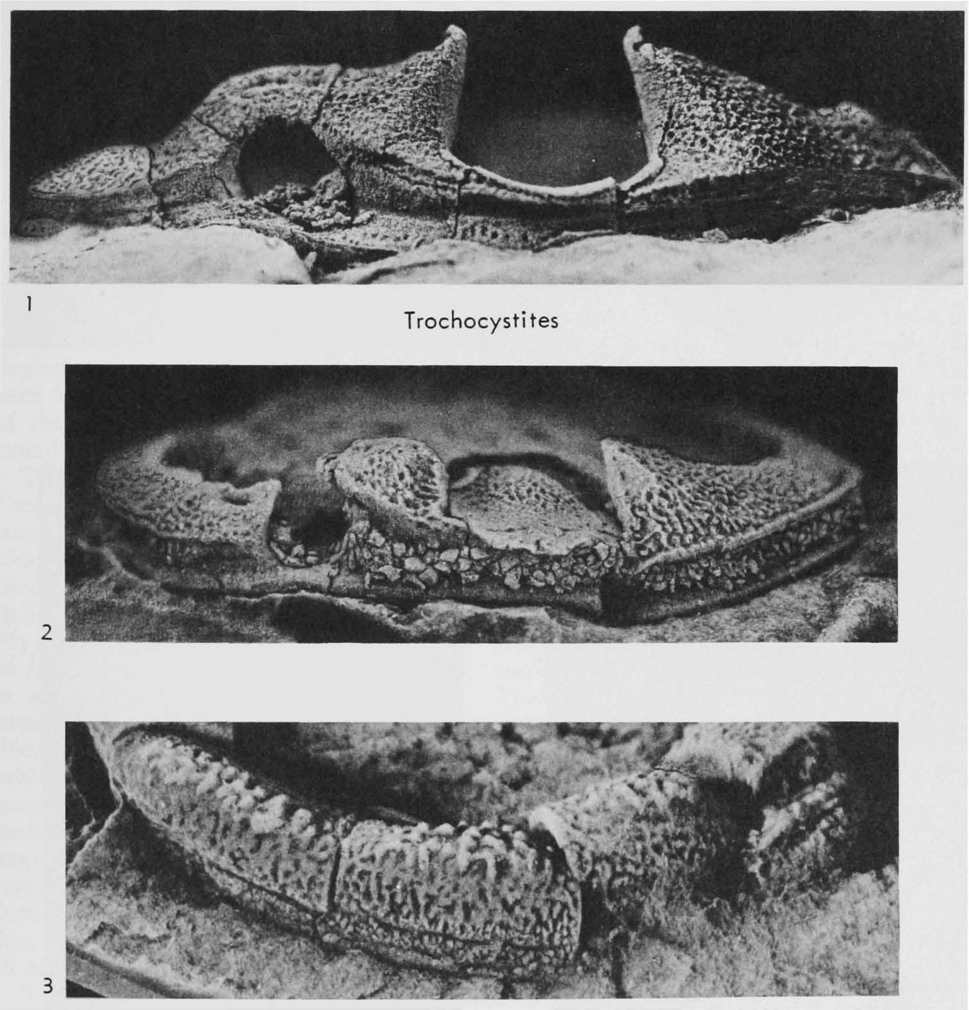

Fig. 368. Marginal grooves of **Trochocystites bohemicus* Barrande, M.Cam., Boh.; *1,* distal view showing empty grooves with tiny serial depressions which presumably served for attachment of cover plates along their margins, ×7.5; *2,* distal view of specimen showing grooves partially filled with cover plates, ×7.5; *3,* right lat. view showing grooves protected by cover plates, ×7.5 (Ubaghs, n).

continuous suranal margin is seen in *Decacystis* and *Gyrocystis,* but instead the larger orifice is bordered proximally by three or four thick **suranal plates** (=epanals, Jaekel, 1918) (Fig. 365,*1*; 366,*1*).

ORIFICES AND MARGINAL GROOVES

The marginal framework on the upper face of the theca is pierced by two openings—not three, as reported erroneously by Barrande (1887), Haeckel (1897), and Bather (1900). The orifices are unequal in size and shape and they differ constantly in location. The larger one is found near the absteleal pole of the theca and the smaller at a short distance from it to the right.

The small orifice is located between two marginal plates and is circular. Above it is an arched plate known as the **suroral** which laterally rests on edges of the marginals (Fig. 364,*1*; 365,*4*; 366,*3,4*). A groove leading to right from the orifice and another

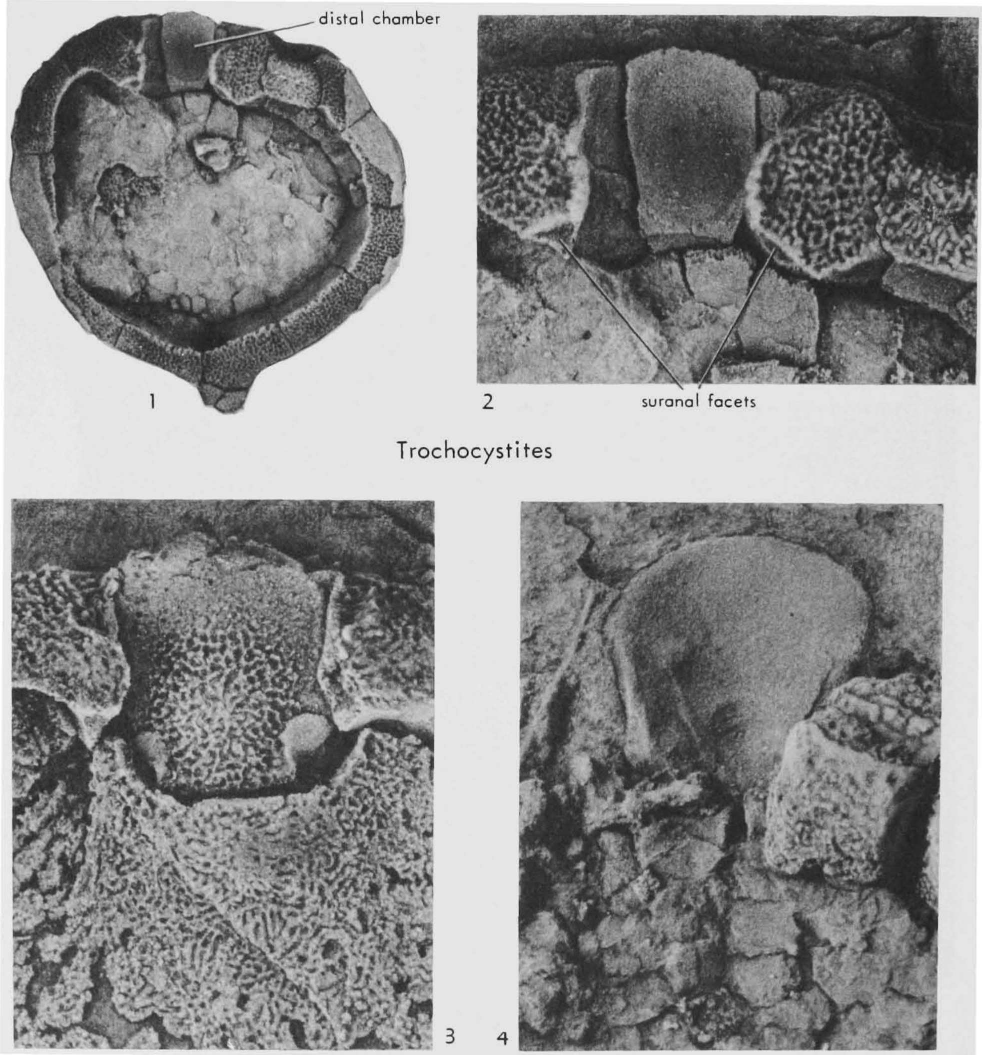

Fig. 369. Distal chamber and operculum of **Trochocystites bohemicus* Barrande, M.Cam., Boh.; *1,* upper face of theca with centrals not preserved, distal chamber open (without operculum), ×3; *2,* distal chamber, ×7.5; *3,4,* external and internal sides of operculum, ×7.5 (Ubaghs, n).

to the left are excavated in the outer face of adjacent marginals along the periphery of the theca just above the boundary between its superior and inferior faces. The grooves are long in *Trochocystites* and *Trochocystoides*, shorter in *Gyrocystis*, and still shorter in *Decacystis*. The right groove traverses marginals M_5 and M_4 in *Trochocystites* to a termination on M_3 (Fig. 363,*1*; 364,*1-3*), whereas in *Trochocystoides* it is confined to M_4 and M_3. The right-hand groove remains undeveloped in *Decacystis* or can barely be detected in a few specimens (Fig. 366,*4*). The left groove passes under the salient lower lip of the large orifice and is terminated on M'_3 in *Trochocystites* (Fig. 363,*1*; 364,*1*), and *Trochocystoides*. In *Gyrocystis* the left groove ends on M'_5 (Fig. 365,*1,3*) and in *Decacystis* on M'_4 (Fig. 366,*4*).

The marginal grooves of Homostelea range from shallow to deep. Those of *Trochocystites* and *Trochocystoides* are deep and in some specimens of the former marked by distinct borders (Fig. 368,*2*). The floor of the grooves is angular and smooth but each side bears a series of tiny depressions which seem to be attachment seats for cover plates (Fig. 368,*1*). The ends of the grooves away from the orifice are rounded and generally quite distinct.

The floor of the grooves in *Gyrocystis* rises rather abruptly near their distal extremity and their termination is not always clear. The right groove, in particular, leaves hardly any trace—at best only a very faint indication on the superior faces of M_5 and M_4 (Fig. 365,*1*). The corresponding groove of *Decacystis* is generally not differentiated at all, whereas the left one, deeply impressed proximally, vanishes on M_4 (Fig. 366,*4*). The grooves and the opening to which they lead are observed in many specimens to be filled with very tiny irregular ossicles, which may be so associated as to suggest that they are remnants of a pavement (Fig. 368,*2,3*). Morphologically and functionally the ossicles seem to be equivalent to the cover plates of the food grooves of many pelmatozoans.

The relatively large orifice of the theca opens into a sort of chamber—here called **distal chamber**—which is hollowed entirely into the thick framework of marginals at the absteleal pole of the theca. The chamber is truncate cone-shaped, expanding toward the interior of the theca, with which it is confluent (Fig. 364,*2*; 369,*1,2*). Its lower distal margin extends laterally outward as a lip which projects over the left marginal groove (Fig. 368,*1*). The walls of the chamber are smooth. Its concave floor, sloping toward the thecal interior, is formed by the upper surface of M'_6 in *Trochocystites* and *Gyrocystis* or of M'_5 in *Decacystis*. The side walls are cut into the two adjacent marginals and its ceiling is formed by a special plate termed the **operculum** (=*Analklappe*, JAEKEL, 1918; anal valve, GISLÉN, 1927; *clapet buccal*, CUÉNOT, 1953). The marginals which flank the orifice and partially overhang the operculum bear strong apophyses which extend more or less convergently inward and upward at the sides of the orifice (Fig. 364,*2*;368,*1*). A little below the summit of each apophysis is an articulatory fossette named the **suranal facet,** which receives a suranal process (e.g., *Trochocystites,* Fig. 364,*2*) or plate (e.g., *Decacystis, Gyrocystis,* Fig. 365,*1*; 366,*1*).

The operculum is a convex oval plate, wrinkled externally and smoothly concave internally (Fig. 369,*3,4*). It expands slightly in a distal direction with its lateral and distal edges adjusted to the walls of the chamber covered by it, but neither fused to these walls nor articulated with them. The proximal edge of the operculum is joined to the suranals (e.g., *Gyrocystis, Decacystis*) or suranal margin (e.g., *Trochocystites*) probably by a loose suture or ligamentary articulation and both extremities of this edge are more or less deeply notched. The notches are bordered in some specimens of *Trochocystites* by a smooth upbent lip which probably provided the attachment for muscles that served to open the operculum (Fig. 369,*3*). In closed position, the operculum sloped steeply downward distally, and when opened, probably an elliptical orifice was left between it and the lower margin of the distal chamber.

The structures just described have been subjects of diverse and often conflicting interpretations.

In view of SPENCER *(80)*, CUÉNOT *(32)*, NICHOLS *(68)*, and GEKKER *(41)*, the chamber of the large orifice (distal chamber) represents a stomodeal pouch or vestibule that was protected by the operculum and provided with protrusible tentacles for the capture of nutrients. It functioned then as a mouth and the small orifice was inferred to be the anus. CUÉNOT and GEKKER supposed that the marginal grooves on either side of the "anus" served for transport of excreta away from the oral field, whereas SPENCER and NICHOLS offered no guess concerning their function. If the grooves really carried excreta, in the case of *Decacystis* they would bring this waste into contact with the mouth.

JAEKEL *(54, 55)*, BATHER *(13)*, and GISLÉN *(45)* adopted an opposite interpretation, concluding that the large orifice corresponds morphologically to the anus and the small one to the mouth. These suppositions are based mainly on the presence of the marginal grooves connected to the small orifice and the resemblance of these grooves to the food grooves of pelmatozoans—certainly a fact. Since the grooves are much shorter in *Gyrocystis* and especially *Decacystis* than in *Trochocystites*, JAEKEL (1918) and GISLÉN (1930, 1934) judged that by evolution they tended to disappear, their reduction being correlated with change from buccal to anal feeding. They imagined that anal respiration analogous to that in crinoids and holothuroids existed in the Homostelea. If so, introduction of water into the digestive tube through the anus would have brought in small food particles and would have led eventually to reversal of the alimentary current, rendering the presence of nutritive grooves superfluous.

The interpretation just stated is opposed by the following observations: 1) though anal respiration does occur in crinoids and holothuroids, anal nutrition is entirely unknown in any echinoderm; 2) it is by no means established that the approximately contemporaneous genera *Trochocystites, Gyrocystis,* and *Decacystis* are progressive stages of a single lineage and consequently an inferred trend toward disappearance of their marginal prooves is quite unproved, for the contrary is possible or the three genera may belong to different lineages; 3) the alleged reduction of the grooves affects neither the dimensions of the small orifice nor the width of the left groove near it, and even in *Decacystis* the well-developed nature of the orifice and associated groove indicates that they must have been functional.

Differences between characters of the grooves in various genera and even in individuals belonging to the same genus (mainly *Gyrocystis* and *Decacystis*) suggest another explanation. In *Trochocystites,* which has long, deep, sharply terminated grooves, the food-capturing organs housed by them must have been totally affixed to the theca (epithecal) or nearly so. In *Gyrocystis* and above all in *Decacystis,* which have shorter and shallower grooves, difficult to perceive in some individuals and generally without clear terminations, the food-gathering organs must have projected more or less freely into the water (exothecal) away from their proximal attachments. This does not signify that the Homostelea possessed a pair of brachioles inserted on either side of the oral aperture, as imagined by HAECKEL *(49)* and MELÉNDEZ *(62)*. Instead, the organization suggests the presence of a sort of two-branched lophophore which was epithecal in some genera and partly exothecal in others.

What then are the morphological implications of the large orifice, distal chamber, and operculum, and how did they probably function? The infundibular shape of the distal chamber and its protruding lower lip suggest the existence of a protrusive organ, which perhaps was a kind of tube designed for jet expulsion of excreta, or possibly a cloaca *(45)* into which not only the digestive tube but organs such as gonads could have emptied. The operculum doubtless would have protected these organs. BATHER (1925) considered this cover to be "a movable shield to guide the excreta [away] from the inflowing food-stream." Certainly, the fact that the operculum is attached by its proximal border, with apophyses of the adjacent marginals overhanging it, proves that this plate could not turn its distal edge so as to extend in front of the theca to support food-catching organs of some sort, as supposed by JAEKEL *(55)*, CUÉNOT *(32)*, NICHOLS *(68)*, and MÜLLER (1963).

STELE

The stele tapers throughout its length and shows the same organization from one end to the other (Fig. 363, 370). Consequently, it is impossible to differentiate dissimilar parts, as in the Homoiostelea. The stele is depressed and like the theca shows a flattened inferior surface, which is slightly and regularly rounded, and a gabled superior surface with a median ridge above planate or slightly concave flanks. The two surfaces meet laterally in keels (Fig. 370,*1,2*).

Passage from the stele to the marginal framework of the theca is entirely gradational, for outlines of the stele comprise prolongation of the thecal contours. Also, the upper surface of the stele rises evenly to the superior face of the proximal marginals M_1 and M'_1 meeting it confluently. Its lower surface is at the level of the inferior face of these marginals and continuous with it. Above all, the form, size, and ornament of the first stele ossicles (most proximal ones) are transitional to plates of the thecal frame (Fig. 370,*1,2*). The passage is so gradual in *Decacystis* that GISLÉN *(44)* classed as marginals two plates that by analogy with other genera belong to the stele (Fig. 366,*1,2*).

The stele is composed basically of two series of opposed or alternating ossicles (called sphenoids by JAEKEL, 1918), with both conditions commonly present in the same stele. Along the mid-line of both faces a variable number of small supplementary plates (called intersphenoids by JAEKEL, 1918) generally are intercalated. They are polygonal or lozenge-shaped platelets inserted like wedges between the main plates and those on opposite surfaces of the stele do not correspond to each other.

An axial canal of very small diameter extends throughout the stele but becomes enlarged toward its proximal end where it opens into the thecal cavity through a short

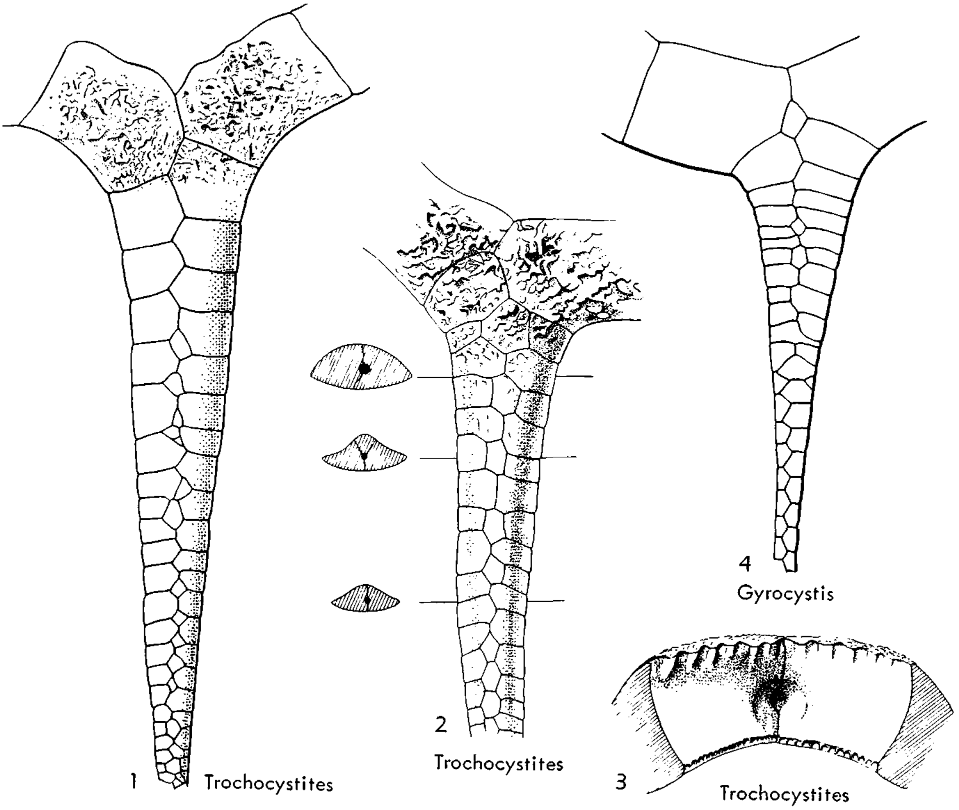

FIG. 370. Stele of Homostelea.——*1-3.* **Trochocystites bohemicus* BARRANDE, M.Cam., Boh.; *1,* lower face; *2,* upper face and transverse sections; *3,* thecal opening of axial canal of stele, all ×3.75 (Ubaghs, n).——*4.* **Gyrocystis barrandei* (MUNIER-CHALMAS & BERGERON), M.Cam., Fr.; lower face, × 3.75 (Ubaghs, n).

funnel excavated in the junction faces of marginals M_1 and M'_1. The floor of the funnel is at the level of the internal faces of the infracentrals, but its ceiling is well below the internal faces of the supracentrals (Fig. 370,*3*).

The stele of the Homostelea thus can be considered as a tubular extension of the theca having the morphologic nature of a peduncle. Nothing indicates that it is homologous to the stem of a Crinozoa, however, and in fact it may have been developed from quite a different body region. Further, nothing indicates that the stele served the same function as the crinozoan stem. Its depressed form, lack of flexible union with the theca, as well as union of its component ossicles, its rigid aspect, the lack of evidence that it served as means of fixation, seems to indicate that the stele never fulfilled the role of support, although it may have helped to stabilize the animal. Many fossils show the stele pointed obliquely downward from the plane of the lower thecal surface, suggesting that it was thrust into sea-bottom sediment during life.

THEORETICAL CONSIDERATIONS

According to Walther (1886) and Haeckel (1896), the symmetry plane of the Homostelea should correspond to the plane of bilateral symmetry of the dipleurula and the theca interpreted as depressed dorsoventrally. This homology was challenged by Neumayr (1889) and rejected by Bather *(11, 13, 21)*, of whom the latter judged that the extension plane of the homostelean theca should be considered as equivalent to the sagittal plane of the dipleurula, and its two surfaces then would be right and left. It may be noted that in 1900 Bather identified the concave (inferior) thecal face as right and the opposite convex (superior) face as left, but in 1913 transposed these identifications. Subsequently (Bather, *20, 21*) became convinced that the "carpoids" comprise a group of their own, distinct from all other echinoderms, and postulated that they were derived from a dipleurula fixed by its ventral surface and not by its preoral lobe. Thus attached, the ancestral organism would have reversed positions of its head and tail, acquiring a Y-shaped form with the tail pointed downward and the body upward with mouth and anus located at extremities of the divergent upper branches of the Y. No torsion of internal organs is postulated by this hypothesis. The Homostelea would have been derived from this archetype by shortening of the stem and branches and close approach of the two apertures to one another.

Chauvel *(30)* adopted another initial premise and consequences deduced from it, namely, a dipleurula attached by its preoral lobe rather than its ventral surface, thus having at the outset the imagined ancestral pelmatozoan condition with mouth at the body pole opposite to its point of fixation, with anus in lateral position, and with internal organs, particularly the digestive tube, subjected to a characteristic torsion. Then appearance of the two lobes bearing the mouth and anus would have led, as in the preceding hypothesis, to a Y-shaped ancestor which by convergence of the two apertures and development of ambulacral grooves could have yielded *Trochocystites* and genera allied to it. In sum, the Homostelea and other "carpoids" would have the same origin as the pelmatozoan echinoderms but because of their very early separation from the primitive stock would retain in common with others only the stem (stele), constructed on a very special plan, however.

Based on the postulate that the digestive tube of most primitive echinoderms had an arcuate shape with concavity on the ventral side, Gislén *(45)* concluded that the space between the mouth and anus represents an extremely shortened ventral surface. The approach of mouth and anus toward one another and their displacement to the superior face of the theca must constitute secondary phenomena, however, corresponding to the stage of asymmetry distinguished by Heider (1912) in the ontogenetic development of echinoderms generally. If the Homostelea belong to an equivalent phylogenetic stage, their left somatocoel should be found beneath the superior thecal face and the right one next to the inferior face. Also, the right axocoel should have been already much reduced and the left one well developed, located possibly beneath the anal operculum. The left hydrocoel should have extended beneath the ambulacral groove, thus being confined to the right anterior border of the body, whereas the right hydrocoel probably was much reduced.

Even if the concept of Gislén seems to accord with indications drawn from the study of early ontogenetic stages of living echinoderms, like other hypotheses it remains purely speculative. The interior of the homostelean theca has preserved such little trace of the organs and cavities enclosed by it that effort to reconstruct their true organization seems futile. No basis allows assertion that their stele is homologous to the pelmatozoan stem or that their digestive tube displayed the helicoidal torsion characteristically present in crinoids.

GLOSSARY OF MORPHOLOGICAL TERMS USED FOR HOMOSTELEA

[Terms considered as synonyms or terms of lesser importance are printed in italics].

absteleal. Directed away from stele.

adsteleal. Directed toward stele.

Analklappe. See operculum.

anal valve. See operculum.

axial canal. Longitudinal passageway through stele.

central(s) (pl., **centralia**). Plate(s) located inside marginal framework either on lower or upper face of theca *(see* infracentral and supracentral). theca *(see* infracentral and supracentral).

clapet buccal. See operculum.

dimere. Any ossicle of two main series which compose stele.

distal. Referring to direction away from junction of theca and stele.

distal chamber. Enclosed space hollowed into marginal framework between large orifice and thecal cavity.

epanal. See suranal plate.

epicentral(s) (epicentralia). See supracentral(s) (pl., supracentralia).

eporal. See suroral.

extension plane. Plane in which theca is depressed (syn., extensiplane).

extensiplane. See extension plane.

frame (framework). Series of plates which constitute margin of theca, i.e., marginals and suroral.

hypocentral(s) (hypocentralia). See infracentral(s) (pl., infracentralia).

inferior. Directed toward inferior face.

inferior face. Flattened or concave side of theca or stele, presumably toward sea bottom in life position *(syn.,* lower face, reverse face).

infracentral(s) (pl., **infracentralia**). Plate(s) located inside framework on inferior face of theca.

intersphenoid. Any supplementary small plate along mid-line of stele.

left side. Referring to side corresponding with left of observer, when theca is placed on its inferior face with aulacophore toward observer; opposite of right side.

lower. See inferior.

main axis. Imaginary longitudinal straight line through stele and prolonged across theca.

marginal(s) (pl., **marginalia**). Ossicle(s) of series framing theca.

marginal groove. Furrow running on outer side of marginals and leading to small orifice (mouth) (considered as ambulacral furrow).

obverse. See superior.

operculum. Seemingly movable plate covering distal chamber.

proximal. Referring to direction toward junction of theca and stele.

reverse. See inferior.

right side. Referring to side corresponding with right of observer, when theca is placed on its inferior face with aulacophore toward observer; opposite of left side.

sphenoid. See dimere.

stele. Relatively slender and tapering peduncular prolongation of body.

superior. Directed toward superior face.

superior face. Convex side of theca or stele presumably directed upward in life position; opposite of inferior face *(syn.,* upper face, obverse face).

supracentral(s) (pl., **supracentralia**). Plate(s) located inside marginal framework on superior face of theca.

suranal facet. Small slightly concave surface on framework serving for articulation of suranal process or suranal plate.

suranal margin. Thick firm proximal upper border of distal chamber; apparently composed of fused supracentrals.

suranal plate. Ossicle of series forming proximal upper margin of distal chamber.

suranal process. Lateral outgrowth uniting suranal margin with marginal framework.

suroral. Fixed thecal place above small orifice (mouth); included in marginal framework.

symmetry plane. Plane passing through main axis and perpendicular to extension plane.

theca. Body skeleton exclusive of stele.

upper. See superior.

MODE OF LIFE

That the Homostelea reposed on one of their thecal faces is proved beyond doubt by the depressed form of their body, by differentiation of the two surfaces of their theca and stele, and by the distal termination of the stele in a point, indicating that it was manifestly incapable of serving for vertical support. The surface of the theca that rested on the substrate can only be the one designated as inferior, as denoted by its flat or concave form, conformation of the marginal frame, and absence on this side of the body of orifices and associated structures having presumed respiratory function, which are concentrated on the opposite face.

Nonetheless, Bather *(13)* considered it difficult to imagine such organisms as resting directly on a sea bottom occupied by the kind of sediments—muddy sands or marly limes—which is represented by the rocks commonly associated with the remains of these "carpoids," for in his view the sand grains and clay particles would have fouled the food grooves and filled the mouth much too easily. Accordingly, he supposed that the animals attached themselves like a cupping glass to the thallus of algae, no traces of which are preserved, of course. The protuberances and other inequalities of the underside of the marginal frame make a sucking action of the inferior thecal face quite impossible, however. It appears, then, that the Homostelea could not have lived in the manner imagined by Bather.

We may recall that the nutritive grooves of the homostelean theca are protected by a cover of platelets. Possibly, as suggested by Nichols *(68)*, these animals led a semisessile existence on the sea bottom, exploring with their tentacles the area around them while fixed at a given place by their stele dug into the sediment—indicated, as previously mentioned, by the oblique downward attitude of the stele in many fossils. Perhaps they lived in still more fixed location, for the stele appears to have had almost no capacity for movement—indeed, they may have led a partial burrowing existence, limited to gathering food particles suspended in the sea water by their tentacular or mucociliary action and to producing vibratile respiratory currents on the surface of their body. Previously stated are reasons for support of the hypothesis that a sort of lophophore functioned in relation to the marginal grooves.

PHYLOGENY

The origin of the Homostelea and their descent—if such there may be—are equally mysterious. Confined within limits of the Middle Cambrian, these "carpoids" are tied to other echinoderms by no known intermediate links. They have long been regarded, it is true, as Pelmatozoa (Crinozoa), the modified ancestral characters of which must have been produced correlatively with acquisition of a recumbent and partially free mode of life. In support of this interpretation their possession of epithecal furrows analogous to the food grooves of pelmatozoans and close association of their mouth and anus near the thecal pole opposite to the stem have been cited. Accordingly, *Trochocystites* was said to be derived from a form resembling *Aristocystites* by lateral compression of the body *(11)*, or from a vermiform eocrinoid similar to *Cigara (55)*, or from a form *(Eikocystis)* supposedly related to *Stromatocystites (24)*.

These are only conjectures, at best. Detailed comparisons reveal no real resemblance of Homostelea to the pelmatozoan echinoderms and bring to light no certain homology with them. Quite unlike these echinoderms which display a fundamental radial symmetry from the moment of their appearance, the Homostelea exhibit not a trace of such symmetry. Their stele has a twofold structure that is unmatched by the stem of crinozoans. Their principal orifices of the theca possess entirely individual traits, and if the depressed form of their body, girdled by a massive frame, is not an exclusive attribute, at least these are constant characters which canont be explained—by lateral compression or play of secondary transformations—as derivatives of diagnostic pelmatozoan features.

When compared with other "carpoids," some of the Cornuta are not to be overlooked, for their theca, like that of the Homostelea, is framed by thick marginal plates and the integument of their superior and inferior faces is reinforced by small plates. Kirk *(56)* saw in *Trochocystites* the possible source of other "carpoids," Bather *(20)* viewed *Mitrocystites* and its allies as derivatives of a form close to *Trochocystites,* and Gislén *(45)* in agreement with Jaekel *(55)* delineated a morphological series beginning with *Trochocystites* and ending in the Mitrata which was thought to illustrate the progressive reduction and ultimate disappearance of ambulacral grooves in the course of evolution.

Nothing is less certain, however, than descent of the Mitrata from the Homostelea, or more broadly, any kinship whatever between the Homostelea and Stylophora. The former are distinguished from the latter by: 1) the presence of a stele, comprising a peduncular prolongation of the theca; 2) the absence of a brachial process possibly correlatable with the stylophoran aulacophore; 3) adjacent location of the two main thecal orifices near one pole of the body in contrast to their positions at opposite extremities of the theca in the Stylophora; 4) the peculiar nature of the homostelean orifices and their close association with the marginal frame; 5) the presence of one or two epithecal grooves excavated in the marginals and connected to one of the orifices; 6) the existence of a special plate termed operculum protecting the large orifice, quite without equivalent in the Stylophora; and 7) entire absence of such structures as the infundibulum, scutulae, septum, and internal marginal grooves which are found inside the theca of stylophorans.

Among the Homostelea and Stylophora, then, not a single morphological character can be considered to be homologous. The presence of a marginal framework in each group is not a significant phylogenetic link, since the same structure is seen in other classes (e.g., Eocrinoidea, Edrioasteroidea) with a high degree of resemblance.

A comparison of homosteleans with the Homoiostelea yields no more certain indication of affinities. To be sure, a peduncular prolongation of the theca is found in both groups, but in the Homostelea this displays the same organization throughout its length, whereas in the Homoiostelea it is clearly divided in characteristic manner into two quite distinct regions. Moreover, the relations of stele to theca and of the axial cavity of the stele, narrow in the one group and wide in the other, to the cavity of the theca show no similitude. Other features show still greater differences. For example, the Homostelea lack a brachial process such as occurs in the Homoiostelea. The mouth and anus lie close together in the former group but far apart in the latter. The two thecal faces generally are much less differentiated in the Homostelea than in the Homoiostelea, and the marginal frame, which is a constant attribute of the first, ordinarily is lacking in the second. Therefore, no justification seems to exist for placing the two groups in the same class, as hitherto done.

Concerning interrelationships of *Trochocystites, Gyrocystis,* and *Decacystis,* no significant facts allow elucidation. These genera are contemporaneous, or nearly so. Intermediate forms are lacking and the trends of their evolution are unknown.

SYSTEMATIC DESCRIPTIONS

Class HOMOSTELEA
Gill & Caster, 1960

[*nom. transl.* Ubaghs, herein *(ex* subclass Homostelea Gill & Caster, 1950)]

Homalozoa with skeleton composed of theca and stele; theca depressed in plane (extension plane) passing through main orifices and stele attachment, with convex surface (superior face) and opposite flat or slightly concave surface (inferior face) united in girdling frame of thick marginal plates; superior face formed within marginals by numerous loosely joined plates termed supracentrals except near pole opposed to stele where they fuse or are replaced by row of stout suranal plates; at absteleal pole and excavated in marginal frame is large thecal orifice inferred to mark location of anus; it is protected by apparently movable plate designated as operculum; adjacent is smaller circular orifice that probably represents mouth; periphery of theca adjacent to presumed mouth bearing one or generally two epithecal grooves hollowed in outer face of marginals, grooves connected to mouth and protected by multitude of minute cover plates; inferior thecal face formed within marginals of close-fitting polygonal infracentrals, without orifices. Stele tapered, depressed in same plane as theca, with convex superior

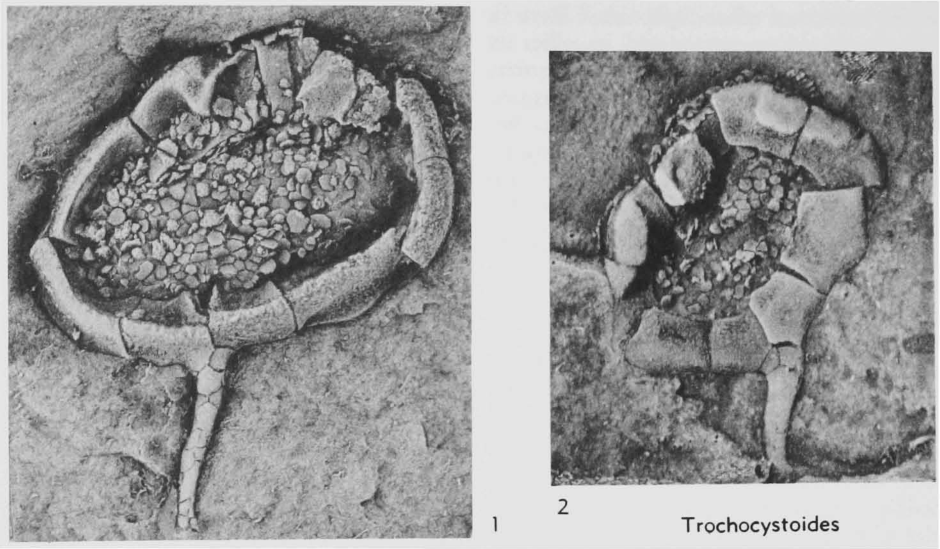

FIG. 371. *Trochocystitidae.*——*1. Trochocystoides* sp. cf. **T. parvus* JAEKEL, M.Cam., Boh.; upper face, ×5 (Ubaghs, n).——*2.* **T. parvus* JAEKEL, M.Cam., Boh.; lower face (?holotype), ×5 (Ubaghs, n).

face in form of ridge and flat or slightly convex inferior face which meet laterally as angled keels, constructed of two rows of opposed or alternating ossicles (dimeres) between which variable number of small irregular platelets commonly are intercalated on superior and inferior faces; narrow axial cavity of stele confluent with thecal cavity. *M.Cam.*

Order CINCTA Jaekel, 1918

[=suborder Marginata JAEKEL, 1901 *(partim)*]

Characters of class. *M.Cam.*

Family TROCHOCYSTITIDAE Jaekel, 1901

[=Trochocystidae BATHER, 1902 *(nom. van.)*]

Well-developed marginal groove on each side of small circular orifice (mouth), both of them long and deep; centrals of inferior thecal face small and numerous. *M.Cam.*

Trochocystites BARRANDE, 1887 [**T. bohemicus*; M] [=*Trochocystites* BARRANDE, 1859 *(nom. nud.)*; *Trochocystis* HAECKEL, 1896 *(nom. van.)* (obj.); *Trigonocystis* HAECKEL, 1896 (type, *T. trigona*)]. Marginals typically 12, with rounded upper external slope, knobs on lower face of M_2, M_3, M_4 and M'_2, M'_3, M'_4; marginal grooves generally ending on M_3 and M'_3; suranals indistinctly separable from adjoining centrals. *M.Cam.*, Boh.-?Ger.(Bavaria)-?Fr.——FIG. 364,*1-3*. **T. bohemicus*, Boh.; *1-3*, distal, proximal, lat. views of theca, ×3 (Ubaghs, n). [See also Fig. 363, 367-370.]

Trochocystoides JAEKEL, 1918 [**T. parvus;* M]. Marginals typically 10, with slightly convex to concave upper external slope, knobs on lower face of M_3, M_4 and M'_3, M'_4; marginal grooves ending on M_3 and M'_3; stele relatively narrow, distinctly convex on upper face, slightly so on lower face. [A single specimen identified by JAEKEL as **T. parvus* which I have been able to study shows only the lower side (Fig. 371,*2*). It seems to belong to the same species as a small form that was confounded by BARRANDE with **Trochocystites bohemicus*. None of the specimens examined by me, however, exactly show features reported by JAEKEL to be diagnostic of this genus.] *M.Cam.*, Boh.——FIG. 371,*1,2*. **T. parvus*; *1*, upper side of specimen (cf. **T. parvus*) figured by BARRANDE (1887, pl. 3, fig. 6, 7), ×5 (Ubaghs, n); *2*, lower side of another specimen (?holotype), ×5 (Ubaghs, n).

Family GYROCYSTIDAE Jaekel, 1918

Marginal grooves relatively short, right one very much reduced or even wanting; centrals of inferior thecal face comparatively larger and fewer than in Trochocystitidae; suranals distinct, three or four. *M.Cam.*

Gyrocystis JAEKEL, 1918 [**G. platessa*; M (=**Trochocystites barrandei* MUNIER-CHALMAS & BERGERON, 1889; ?*T. occidentalis* JAEKEL, 1901)] [=*Sucocystis* TERMIER & TERMIER, 1958 (type, *S. theronensis*)]. Marginals typically 12, with flat or concave upper external face, generally with prominent knob on marginal beneath large thecal orifice and less prominent swellings on either side; marginal grooves ending on M_5 and M'_5. *M.Cam.*, Fr.-Morocco.——FIG. 365,*1-4*. **G. barrandei* (MUNIER-CHALMAS & BERGERON), Fr.; *1-4,* upper, lower, distal, and right lat. views of theca, ×3 (Ubaghs, n).

Decacystis GISLÉN, 1927 [**D. hispanica*; M]. Marginals 10, with flat upper external face; right marginal groove wanting, left one ending on M'_4. *M.Cam.*, Spain-France.——FIG. 366,*1-3*. **D. hispanica,* Spain; *1-3,* upper, lower, and distal views of theca, ×3 (10).——FIG. 366,*4*. *D.* sp. cf. **D. hispanica,* Spain; distal view of theca, ×5 (Ubaghs, n).

[References for the chapter on Homostelea are included with those for Stylophora and Homoiostelea (*see* p. *S*624).]

HOMOIOSTELEA

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[In the preparation of this section it has been necessary to re-examine much original type materials of BARRANDE, BATHER, JAEKEL, THORAL, and UBAGHS, and to study extensive supplementary material. To the officers and staff of the Narodni Museum, Prague; British Museum (Natural History), London; Museum of Humboldt University, East Berlin; Department of Geology, University of Lyon; Montpellier University, Lyon; University of Greifswald; Hunter Museum, Glasgow; United States National Museum, Washington; Geological Survey of Canada; Victoria National Museum, Melbourne; and to private collectors, R. COURTESSOLE and G. and G. GRIFFE, Carcassonne, FR. KRANTZ, Bonn, and many others, deepest thanks. Very special thanks go to GEORGES UBAGHS, RONALD PARSLEY, and EDMUND D. GILL.]

CONTENTS

INTRODUCTION

The Homoiostelea (U.Cam.-L.Dev.) form a part of the former class Carpoidea JAEKEL (1902) and are coextensive taxonomically, as herein revised, with JAEKEL's order Soluta. They share with other "carpoids" the possession of fundamental asymmetry of skeletal organization and show varying degrees of superimposed bilateralization; moreover, a tendency toward flatness (depression) is common to all. They possess an exothecal arm, plated theca and tail-like stele (heterostele).

THECAL APPENDAGES

The name Homoiostelea (similar stele) comes from GILL & CASTER (1960), who attempted to point up axial differentiation of the "tails" in the Soluta, and also in the Cornuta and Mitrata (Stylophora), into three zones, as against the condition in the Homostelea (=JAEKEL's Cincta) where zonation does not exist. It was the assumption of previous authors that all carpoid steles are homologous, both in origin and function. It now appears, as a result of work by UBAGHS (1961) on Cornuta and (elsewhere in this volume) on Mitrata (these two orders of JAEKEL comprising the new class Stylophora), that the functions of the solutan "tail" and arm were both performed by the single serial appendage of stylophorans, the aulacophore. Herein lies the basis for a difference of opinion as to the homologies and orientation of the whole organism as between the Soluta and Cincta on one hand and the Stylophora on the other.

UBAGHS (*Treatise,* p. S496) correlates the stylophoran aulacophore with the solutan arm because of their common subvective function. Consequently, he prefers to designate the base of the aulacophore, like the base of the arm, as anterior (see Fig. 325-326, 343-350, this volume), since both presumably lead to the mouth of the organisms. But, whereas mouths are always anterior in position in primordial bilaterians, "carpoids" appear to have undergone two stages of metamorphism beyond that condition: some degree of radial superimposition, perhaps associated with fixation; and secondary freedom and very advanced secondary superimposition of bilateralization, which is never complete. In most eleutherozoic echinoderms "anterior" is conventionally the direction of forward movement, and this seldom coincides with the position of the oral-anal axis or mouth.

It is my opinion that in this complex of convergently adapted eleutherozoans, which might be termed the "cladus Carpoidea," all exothecal tetramerous organs are modified biserial arms, and hence are all radial homologues. According to this view, all "carpoid" heterosteles are radially homologous. The stylophoran aulacophore has primitively retained the radiate subvective function, the while also serving the free-moving "tail" function of the heterostele in other "carpoid" classes. All seem best designated as heterosteles in accord with JAEKEL's original proposal (1901). The aulacophore is, then, a special kind of heterostele.

The convergent form of "carpoids" seems to have been selectively determined in accord with hydrodynamic principles and correlated with bottom-moving in a flatfish-like manner. A swollen anterior body (theca), usually rounded anteriorly, and depressed, more or less parallel-sided, and bearing a posterior caudal appendage (heterostele) for steering and locomotion, is the recurrent plan. The recurrent analogy of the heterostele to a fish tail in all three classes of "carpoids" seems to have orientational validity.

The steles ("tails") of Homostelea and Homoiostelea are apparently completely homologous both in origin (probably from a biserial arm) and in caudal, wholly locomotor, function. In the former, however, the mosaic plating and lack of axial zonation of the component meres bespeak much less motility of the stele than in the homoiosteles, where zonation and either marked imbrication or flexible integumentary suturing of the proximal stele meres is usual. In both classes the proximal steles (proxisteles) are tetramerous and the distal steles (dististeles) dimerous; this is achieved in both instances by the distal diminution of alternate series of tetrameres (see Fig. 378). In the Stylophora, the dististele (distal aulacophore) appears to be uniserial. In the homosteles the close proximity of mouth and anus on the anterior thecal margin localizes the oral-anal axis to a short line on the distal margin, whereas in the homoiosteles the axis is lateral (never in the axial plane) or diagonal, due to the wide separation of the two apertures. If mouth and anus determine anterior and posterior orientation of the organisms, in neither case is the caudal stele posterior. In no instance has the solutan mouth been observed to fall on the morphologic axial plane of the organism. In some stylophorans, where derived bilateral symmetry is most advanced among "carpoids," the oral-anal axis and axial or bisymmetry-plane do seem to coincide. However, in this last class, the anus lies on the leading, distal (anterior) margin of the theca and the mouth at the base of the aulacophore (subvective tail).

SYMMETRY AND ORIENTATION

Inasmuch as the homoiosteles are depressed (that is, flattened[1]) asymmetric

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[1] Like all echinoderms, the homoiosteles were presumably bilaterians showing a fundamental asymmetry in their embryological development. However, the identification of their original bilaterian coordinates is highly speculative, as is also the degree to which their observed skeletal asymmetry correlates, if in any wise, with that of the dipleurulan

creatures which exhibit bilateral tendencies, they pose special problems in geometric nomenclature. It is quite impossible to employ the terms dorsum (dorsal), venter (ventral), and right and left sides in their true bilaterian morphologic sense. However, it now develops that the last two can be used pretty consistently in the Soluta in a purely descriptive conventional sense, thus rendering unnecessary the substitute and less clear terms which BATHER (1913) proposed. Synonymous names for morphology and symmetry components are indicated (Fig. 372).

Two planes of reference can be distinguished in the Homoiostelea: 1) the plane of flattening, which BATHER (1913) called the **extension plane,** and GILL & CASTER (1960) the **extensiplane;** and 2) the plane normal to this and passing through the axis, which BATHER termed the **symmetry plane,** with respect to which all forms show some degree of bilateralism, hence sometimes called the "bilateral plane" or bisymmetry plane. The main course of the organic axis is judged from the symmetry plane of the stele, which is then projected through the theca. Shortening normal to the extensiplane is **depression** (flattening), and in the extensiplane, normal to the symmetry plane, **compression** (shortening of the width).

Whereas in unmodified bilaterians the **oral-anal axis** coincides with the axial and bisymmetry planes, and hence determines the historic anterior and posterior orientation, in homoiosteles, like most other "carpoids," there is no such coincidence. In fact, the two axes usually meet at a high angle, or, exceptionally, cross one another. Hence the "anterior" and "posterior" labels on solutans are conventional and ecologic rather than historical and physiologic. Being, like all "carpoids," vagile benthos, the solutans (=homoiosteles) possessed a caudal organ that served a propulsive or steering function, or both. This organ was the tail, *"tige,"* or stele (heterostele), or, in the Stylophora, the aulacophore, a subvective stele. The caudal appendage was **functionally posterior.** Neither the position of the mouth or anus nor the trend of the oral-anal axis serves among homoiosteles (or in other "carpoids") to establish conventional, functional anterior and posterior.

The depression of the theca usually results in the existence of two thecal surfaces or **faces.** In the past, these, where recognized, have been variously denominated with respect to the correlation with arm-mouth or anus. Thus BATHER (1913) distinguished the "adbrachial" (="brachial" of authors) and "antibrachial," or "anal," and "antanal" faces. (In "carpoid" descriptions **ant-, anti-, counter** and **opposite** have been used synonymously.) BATHER (1913) also employed **obverse** and **reverse** for the thecal faces which he judged to have been respectively upper and lower in life. However, he was unable consistently to employ these terms, and did not attempt to use them in describing homoiosteles. With exception of the seemingly almost fusiform (data for this conclusion doubtful) *Heckericystis,* the seemingly truly globular *Dehmicystis,* and the nummuloid *Rutroclypeus,* the two faces can be identified consistently and homologized. Therefore, the denominations obverse (upper, carapace) and reverse (lower, plastron) are quite acceptable. Since the position of the anus is highly variable, both as to the side and face on which it occurs—and to some degree the same is true of the solutan arm—face denominations with respect to these organs are misleading. BATHER (1913) also identified the **sides** (flanks) in terms of the anus and arm position. Since top and bottom faces are now pretty generally recognizable in homoiosteles, there seems to be no good reason for not using the simple terms right and left for the sides.

The distance between the two faces of the theca is the **height** or **thickness;** it is usually measured in the symmetry plane. The distance between the sides is **width; length** is an axial dimension. The plane of contact of the stele and theca is conventionally known as the **proximal plane.** However, it is notable that this is apparently not the same plane of reference commonly employed among Crinozoa. Directions toward the proximal plane are **proximal** and away from it **distal.**

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larva. It now seems quite probable that more than one mode of flattening of the bilaterian body has occurred among "carpoids" and that to characterize them all as pleuronect creatures (lying on one side, like flounders) is too comprehensive a generalization, and possibly quite a wrong one. This is a certainty: every "carpoid" is a multiple palimpsest of superimposed symmetries.

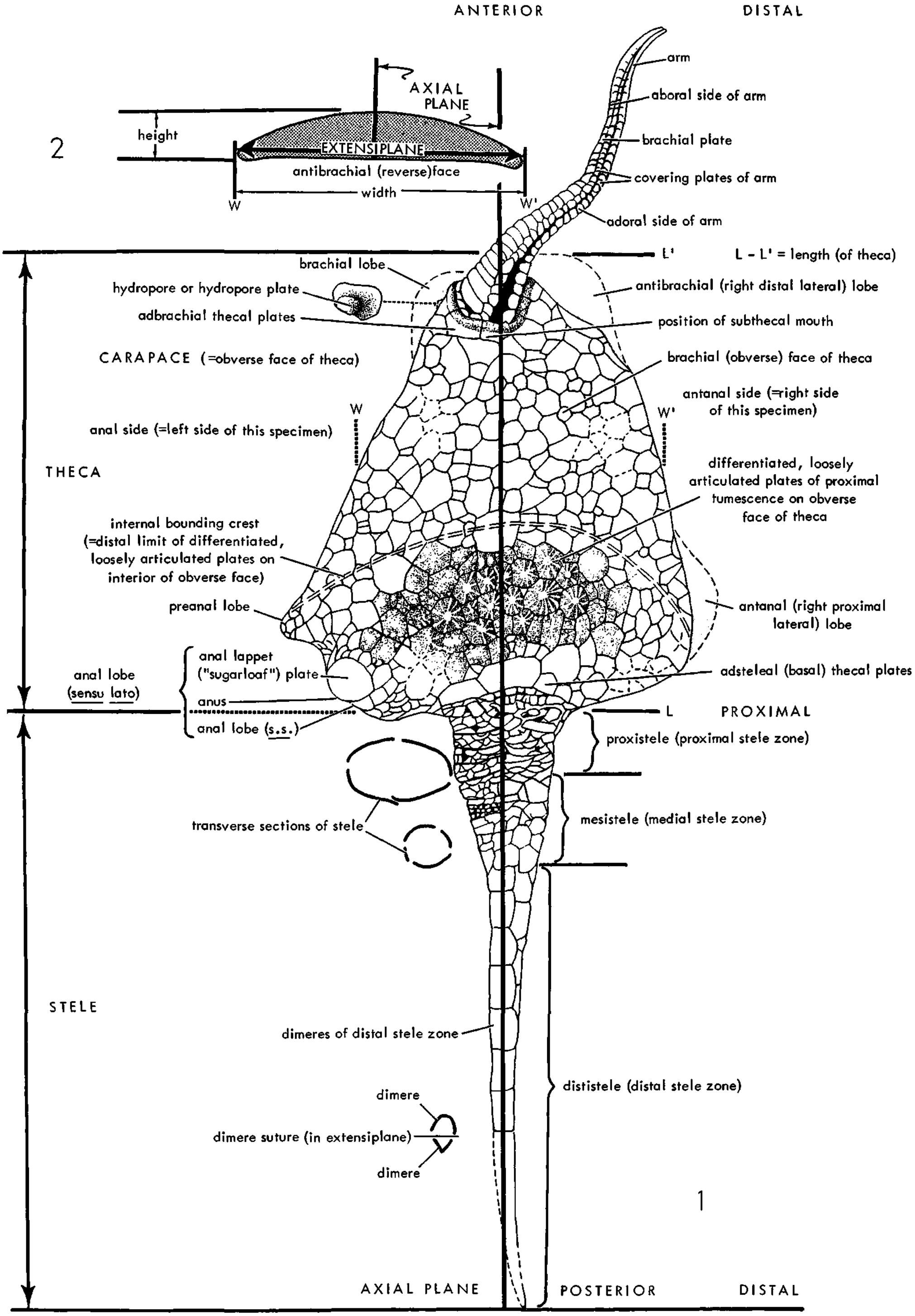

FIG. 372. Homoiostele morphology and orientation (based on **Dendrocystites sedgwicki* (BARRANDE), a generalized solutan "carpoid"). *1*, extensiplane view obverse side, ×1.7; *2*, generalized cross section of theca, ×1.7 (Caster, n; drawn by Elizabeth A. Dalvé from photos and sketches of Barrande specimens from Praha).

MORPHOLOGY

GENERALITIES

The morphologic nomenclature of the Homoiostelea is given in Figure 372. However, this figure hardly conveys the aspect of more advanced members of the class which are commonly strongly homeomorphic with the stylophorans. The body is composed of three regions: 1) the anterior (really anterolateral) biserial **arm,** which commonly has been called a "brachiole" *(13, 43)*; 2) the main body, which was invested with a **theca** of calcareous plates; and 3) the **stele** or **heterostele,** as JAEKEL *(54)* preferred in order to counter the common mistake of referring to the posterior appendage as a "column" or "stem" under the misapprehension that it is homologous with the pelmatozoan column. It is also commonly called a tail or *"tige,"* which best describes its apparent function in life. Undoubtedly, there was in life the usual echinodermal mesodermal fleshy investiture of all calcareous parts. The labyrinthine canals in the skeleton (stereom), occupied in life by fleshy strands (stroma), are commonly preserved (e.g., CASTER & EATON, 1956, described similar histology in Mitrata). Most of the fleshy anatomy of the organism was housed in the theca, but significant extensions undoubtedly reached into the large lumens of the arm and proxistele. The plates of both arm and stele are **bilaterally** arranged; those of the theca quite imperfectly so (*Syringocrinus,* see Fig. 393; *Iowacystis,* see Fig. 394) or not at all (*Dendrocystites,* Fig. 372; *Dehmicystis,* see Fig. 388; *Rutroclypeus,* see Fig. 391, 392; *Girvanicystis,* Fig. 373, 374, see Fig. 389, 390). Plates adjacent to arm, anus, and stele are to some degree regularized, and consistently identifiable in certain genera and to some degree homologous. In some forms, the plate size, number, arrangement, and ornament differ on the two faces, sometimes markedly so; this is termed **facial differentiation.** There may also be **regional differentiation** of plates within a face or organ.

ARM AND RELATED STRUCTURES

Although the exothecal subvective organ

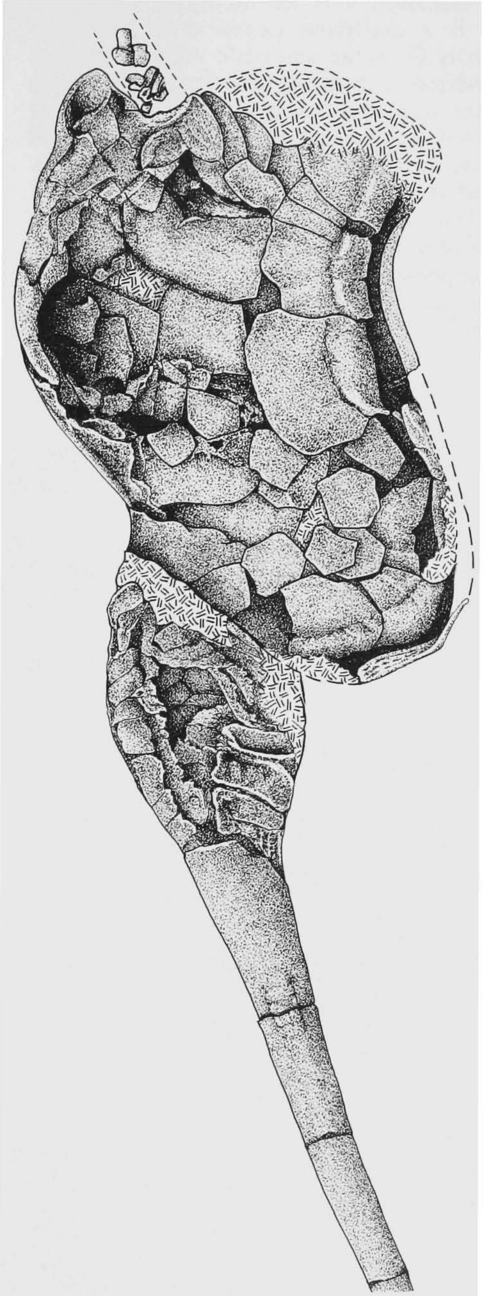

FIG. 373. Morphological features of **Girvanicystis batheri* CASTER, n. gen., n. sp., U.Ord., Scot. (Girvan), showing obverse face of somewhat deformed paratype having well-defined marginal groove for reception of thickened margin of reverse face, ×2.4 (Caster, n; drawn by E. A. Dalvé from photo of BMNH, Begg Coll. no. E5830).

in homoiosteles has been commonly called a brachiole, it is technically an **arm** since it is a skeletized extension of the body cavity (as is the stele) and not a solid serial skeleton such as are true brachioles. It has been termed a "proboscis," under the mistaken impression that it bore a terminal mouth; it also has been erroneously identified as an anal structure. The arm is usually a long, tapering, broadly based organ (e.g., *Dendrocystites*), subterete or somewhat compressed, and covered by two matching but unequal biseries of plates (i.e., it is essentially tetramerously invested) arranged bilaterally. The larger biseries, termed **brachial plates,** usually cover about two-thirds of the arm flanks and meet tightly or flexibly on the **aboral** side; the aboral suture is usually zigzag, reflecting the alternation of the brachial biseries; no aboral suture has been found in *Minervaecystis* (See Fig. 381). There may be slight distal imbrication of the brachial plates. Each plate is about twice as wide as long, and bowed. The adoral gape between the bowed brachials is covered by the matching lesser biseries of plates, the **cover plates,** which articulated with the brachials and met ad-

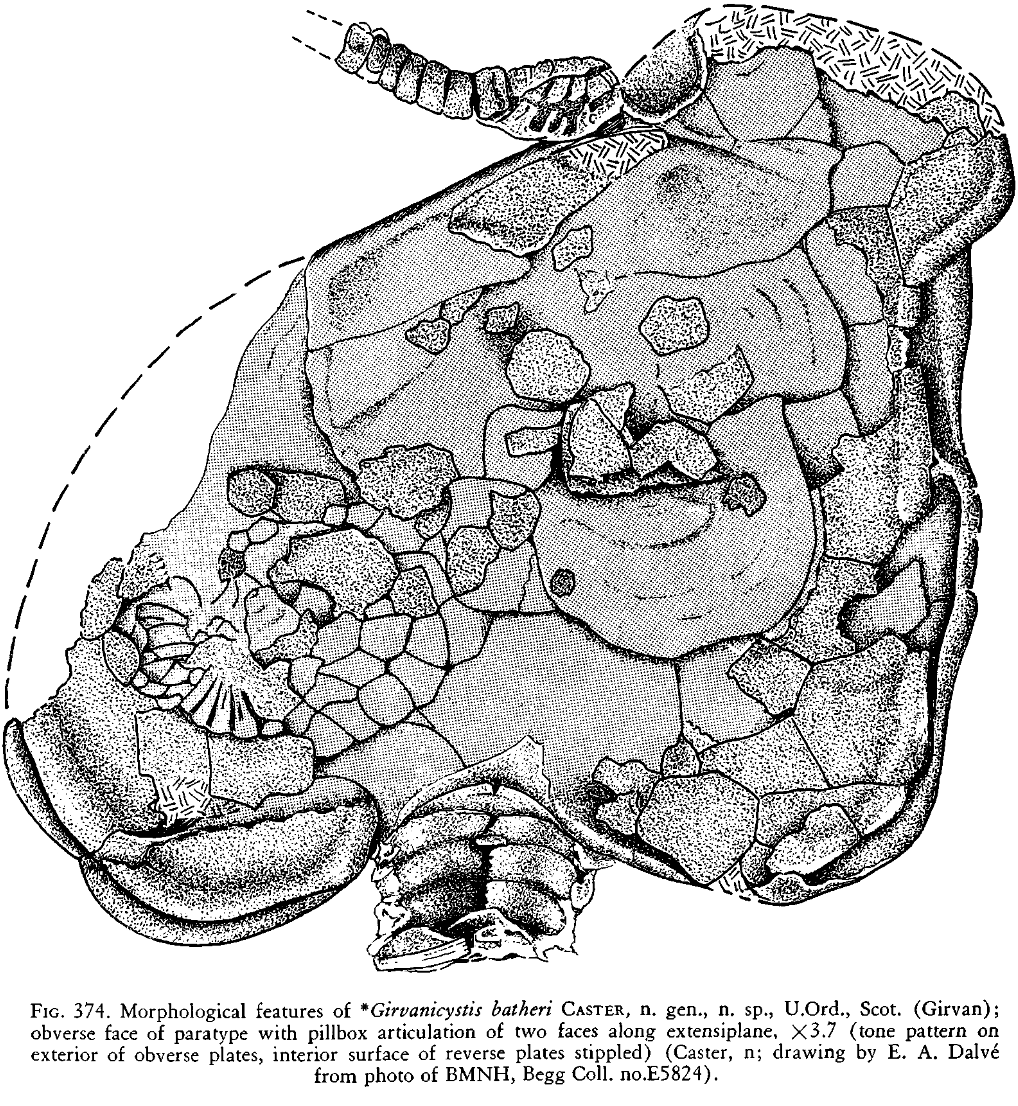

Fig. 374. Morphological features of **Girvanicystis batheri* Caster, n. gen., n. sp., U.Ord., Scot. (Girvan); obverse face of paratype with pillbox articulation of two faces along extensiplane, ×3.7 (tone pattern on exterior of obverse plates, interior surface of reverse plates stippled) (Caster, n; drawing by E. A. Dalvé from photo of BMNH, Begg Coll. no.E5824).

orally along a zigzag line. The relative width of brachials and cover plates is variable within taxa; they may form a confluent arm surface, or the cover plates may rise in a gable on the adoral side and their articulation with the brachials be a depressed line. Internally both brachials and cover plates bear articulatory muscle scars. The adoral gape of the brachial plates presumably defines the ciliated food groove (ambulacrum) of the living animal. This leads to the concealed mouth, which presumably was situated near the end of the groove, within the theca. As in all other echinoderms, the normal feeding position of the arm was undoubtedly with the adoral side of the arm and the associated ambulacral groove upwardly exposed when the cover plates were open. Thus, the life position of the arm determines the orientation of the whole organism. This is the ultimate recourse in the sometimes perplexing problem of thecal orientation and face determination of the fossil. The adoral features of the arm correspond in position to the obverse side of the theca.

The mouth and gut being unknown, the intestinal course is speculative between the base of the arm and the anus. Of a certainty, it does not follow the oral-anal axis, and the asymmetrical form of the homoiostele theca suggests that it has an arcuate, or perhaps even looped course, and that it probably does not lie wholly in the extensiplane.

The transition from arm to theca is abrupt; nothing has been observed which would support Bather's (1913) contention that the solutan arm skeleton passes gradationally into thecal skeleton (Fig. 375). The arms, so far as known, are consistently tetrameral (except possibly in *Minervaecystis*, see Fig. 381, where quite probably the lack of an aboral suture reflects ankylosis of a biseries). Adbrachial thecal plating is rarely four-part, and the junction between the theca and arm is consistently integumentary, in keeping with the manifest motility of the arm as a whole. In *Dendrocystites sedgwicki* (Fig. 372, see Fig. 383) adults many small polygonal plates occupy the contact zone. These may be sclerites of the integument, or more likely represent the breakup of larger adbrachial plates in the same man-

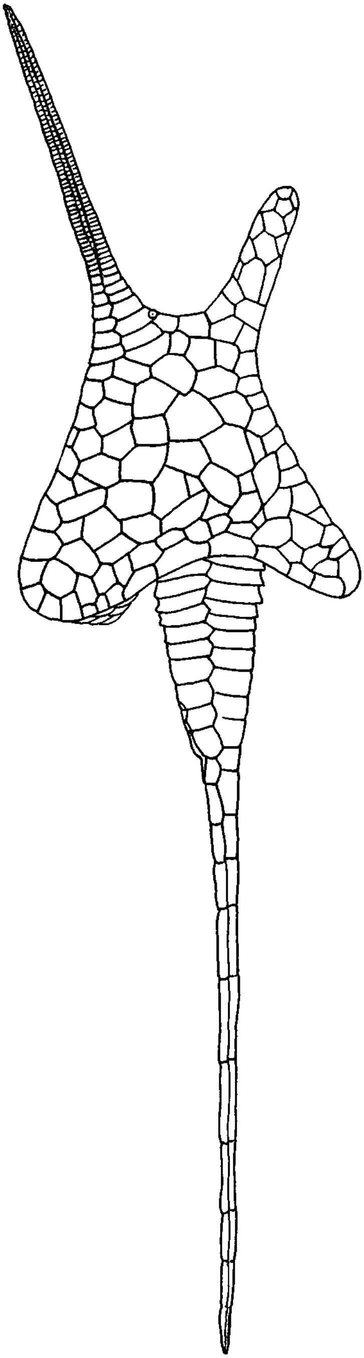

Fig. 375. Complete skeleton of **Dendrocystoides scoticus* (Bather) viewed from obverse side (reconstr.), U.Ord., Scot. (Girvan), ×1.3 (Bather, 1913).

ner as observed in the proxistele of this species. These small plates may have been the basis for much of BATHER's speculation about the relation of arm plating to thecal.

The large adbrachial plates of the theca are always distinctive. They are generically consistent in number and form. They may be a more or less rigid circlet of strongly fused plates, as in *D. sedgwicki* adults; a thickened rim may be developed on them around the arm orifice, as in *Girvanicystis;* this becomes a prominent bordering flange in *Iowacystis* (see Fig. 394). In *D. barrandei* (see Fig. 384, 385), and the Scottish *Dendrocystoides* (Fig. 375, 387), and the French *Minervaecystis* (see Fig. 381), adbrachials strongly geniculate to encircle the arm base and laterally imbricate to form a scalelike sheath. The number of adbrachials in the circlet varies from perhaps six in *Dendrocystites* to four (or fewer) in *Iowacystis.* In In *Girvanicystis* (see Fig. 389, 390) there are apparently four adbrachials, two obverse and two reverse, which are deeply excavated to form the brachial foramen. The size and shape of this foramen depends on the configuration of the proximal arm. Certainly within genera, and possibly more widely, the various adbrachial plates can be homologized.

One adbrachial, lying on the left side of the arm base and usually extending well onto the adoral surface, consistently bears an organ which probably represents a hydropore. In *Dendrocystites* and *Dendrocystoides* this takes the form of a single (see Fig. 386) or multiple (Fig. 376) warty tumescence on the plate. In *Minervaecystis* (see Fig. 381) two distinct prominences, one of which may be gonadal, appear on this plate. In *Girvanicystis* (see Fig. 390) a rimmed pore is developed in the same position, and two produced phialine pores in *Iowacystis* (see Fig. 394); here again, the lesser pore tube may be gonadal. Some of the illustrations of *Rutroclypeus* (see Fig. 391, 392) suggest the presence of a similarly located warty prominence, although it was not originally observed. Since the hydropore structures in most solutans are usually in a slightly inferior position on the adoral side of the arm aperture, they are best seen on specimens revealing the reverse face of the theca.

The arm generally emerges from the left distal area of the theca and from the marginal zone of the obverse face. In *Girvanicystis* (Fig. 373, 374) the arm position is normal, but the foramen is excavated on the peculiar bounding suture between the two faces; also, more of its excavation lies in the two reverse adbrachials than in the obverse ones. Correlating with a recurrent tendency among homoiosteles for the distal theca to become narrow, the arm becomes nearly axial in position (e.g., *Heckericystis,* see Fig. 384,*1*; *Dendrocystites barrandei,* see Fig. 384,*2*; *Dendrocystoides*), or crosses the axis to lie consistently on the right distal side of the theca, as in the deltoidal *Iowacystis* (see Fig. 394). Probably the arm commonly lies in the plane of balance of these usually highly irregular organisms; this seems very much the case in the anomalous girvanicystids.

In *Dendrocystites* and *Dendrocystoides* (and no doubt elsewhere) occur what might be termed mirror anomalies in the position of the arm. Thus, right-armed individuals may occur in a dominantly left-armed assemblage. Only the locus of the arm shifts, however, without any reversal of orientation of correlated structures (i.e., in right-armed forms, the adbrachial hydropore plate is still consistently on the left side of the brachial foramen).

The arm and anus commonly occur on the left side of the theca, as seen in *Dendrocystites, Dendrocystoides,* and *Girvanicystis.* When the arm shifts to an axial or near-axial position this may be hard to prove, and in *Iowacystis* (see Fig. 394) the oral-anal axis crosses the symmetry plane. In forms exhibiting the mirror anomaly, the arm and anus are on opposite sides. But in quite another category is *Minervaecystis* (see Fig. 381), the oldest well-documented homoiostele, where the anus lies on the left proximal lobe and the arm in the exceptional right distal position. This is the best example of the "opposite" condition of mouth and anus. In this inadequately known genus we may be observing a mirror anomaly with respect to the anus. No transitional stages in either the brachial "mirrors" or in attaining the reversed anal position are known.

THECA

The homoiostele theca is depressed, asymmetrical, and multiplated, and recurrently it exhibits a tendency toward bilateralism. The differential flattening in the extensiplane results in a wide variety of depressed thecae. The degree of flattening has usually been exaggerated during fossilization and thecal topography commonly is masked thereby. Moreover, what were tight sutures between thecal plates have been opened in the process and an illusion of thecal flexibility created, whereas in life the form was fixed and relatively rigid. However, since the inferior thecal face, usually the reverse face (*Girvanicystis* is resupinated in this respect), is commonly planate or nearly so, it is less deformed and usually gives a fair clue to the living thecal outline.

But since all homoiosteles are essentially asymmetrical, the form of the thecal perimeter in the extensiplane is difficult to describe. *Dendrocystites* is subcordiform; *D. barrandei* and *Heckericystis* subvasiform?; *Dendrocystoides* irregularly shrubby or tunicate; *Girvanicystis* obliquely subcordiform; *Minervaecystis* and *Syringocrinus* ovoid; *Iowacystis* triangular; *Rutroclypeus* circular; *Dehmicystis* probably globular. In addition, hourglass-shaped, subquadrate, and subtrapezoidal forms are known.

Lateral lobation is especially characteristic of the dendrocystitid solutans, but is seldom seen elsewhere in the class. There are two broad unequal **proximal lobes,** the left being usually the larger. In most specimens the left lobe would correlate with BATHER's (1913) "anal" lobe and the right with his "antanal" lobe. In *Minervaecystis* the larger proximal lobe and "anal" lobe is on the right. Both lobes are usually broadly, but asymmetrically, curved and the left one especially may have considerable posterior development *(Dendrocystites)*. In some *Dendrocystoides* either proximal lobe may be produced posterolaterally as an attenuate process. In *Dendrocystoides,* and in *Girvanicystis* especially, a broad, rounded, right **distal lateral lobe** (BATHER's "antibrachial" lobe) is developed. In right-armed variants a corresponding lobation may occur on the left side, but never to the same degree as on the right. The distal lateral lobe may grade into or be distinct from a **distal lobe,** which is rarely developed on the thecal asymmetry axis; the distal lobe, when developed, extends forward from the base of the arm. In *Dendrocystites sedgwicki* the distal lobe is commonly well developed, but distal lateral lobation is inconspicuous. Both a distal and a distal lateral lobe occur in *Girvanicystis* (see Fig. 390) and are broadly confluent. In addition to these broad and usually depressed extensions of the thecal faces, long, hollow, hornlike plated processes occur in *Dendrocystoides* (Fig. 376, see 386, 387). The most frequently encountered of these lies in an "antibrachial" position, usually right distolateral. However, these processes can develop almost anywhere on the theca, reverse or obverse face. The "antibrachial" horn may arise from either face, or on the flank, or may arise in common with the arm from a distal thecal tumescence. Several such horns have been observed on a single specimen. In a few specimens what appears to be a terminal perforation of a horn has been seen.

The left proximal lobe (usually the "anal" lobe) shows secondary lobation in several genera, especially where the anus is marginal or nearly so. The anus itself is in these specimens associated with the larger, rounded, posterior lobe, the true anal lobe, usually bearing BATHER's "sugarloaf" plate, the anal plate, or anal lappet; this is the **anal lobe,** *s.s. (Dendrocystites, Dendrocystoides)* (see discussion of anus, below). Distally from the true anal lobe and usually marking the widest part of the theca, is a subangular **preanal lobe,** best seen in the above two genera. In *Dendrocystites* this lobe is swollen and possibly bears a marginal aperture. Internally the inside surface of the obverse thecal plates bears an undulatory imprint of a soft-part structure which leads to the apex of this lobe; this may be an organ or conduit.

Heckericystis, as restored by GEKKER [HECKER] (1940), was inflated and not facially differentiated; however, it does show a proximal lateral bulge on the anal side. At the present time it is impossible to assess the accuracy of the restoration of this form.

Although the thecal plates of homoiosteles are commonly imbricated when encountered, this seems to be due to deformation. The plating appears to have been mosaic, with either firm sutures or integumentary junctures. Even among the supposedly wholly flexible dendrocystitids, there is good evidence that the thecal configuration was quite constant in life and that many of the plates were firmly joined (e.g., Fig. 382,*1*).

Restudy of the types of the Bohemian *Dendrocystites sedgwicki* and of considerable new material indicates that young specimens bore fewer and relatively larger

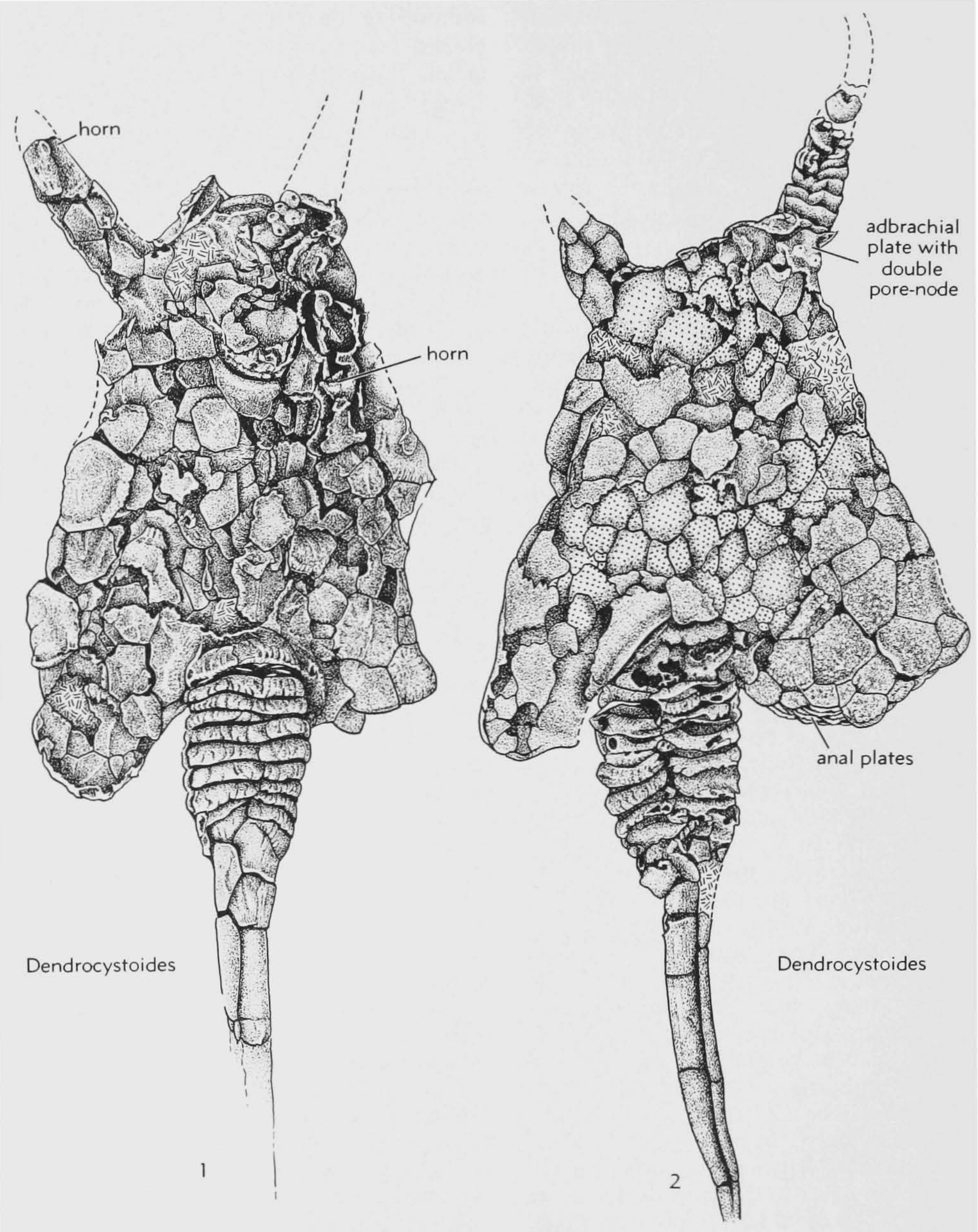

FIG. 376. Morphological features of **Dendrocystoides scoticus* (BATHER), U.Ord., Scot. (Girvan); *1,* reverse face of theca with thecal spine arising from deep in face, stele well preserved, ×2.3; *2,* reverse face of another specimen with double pore node on adbrachial plate, coarse dot pattern indicating interior of obverse plates, ×2.2 (Caster, n; drawings by E. A. Dalvé from photos from BMNH specimens H5A and H103A).

plates than adults (see Fig. 383). New plates seem to have been added in rosettes around previously introduced plates. A very similar mode of plate increment was noted by GILL & CASTER (1961) in the Australian rutroclypeids.

Around the arm, anus, and stele foramina considerable regularization of plate number and form is seen; there is also considerable plate differentiation on the two faces of convexi-planate forms, such as *Dendrocystites, Dendrocystoides, Iowacystis, Syringocrinus,* and *Girvanicystis.* The only known exceptions to the rule of facial differentiation among homoiosteles are the apparently vasiform *Heckericystis,* globular *Dehmicystis,* and biplanate, nummuloidal *Rutroclypeus* (see Fig. 391, 392). The planate face bears fewer and larger plates than the convex one, as a rule, although the reverse is true in *Minervaecystis* and *Iowacystis.* Moreover, the plates of the planate face (usually the reverse) commonly are tightly sutured, whereas those of the convex face (usually obverse) are generally wholly or in part joined integumentally. In *Girvanicystis* (Fig. 373, 374) the convexities are reversed, and both faces are covered by tightly joined plates.

In the dendrocystitids the obverse topography is complex. Both a proximal and a distal plated swelling is present. A **distal tumescence** lies just proximal to the arm insertion and most probably correlates with the forward part of the gut. This prominence was firmly plated. *Dendrocystites barrandei* shows a localized distention adjacent to the arm; this, when flattened in preservation, is probably what BATHER had before him when he described an "antibrachial hump." This may correlate with the common antibrachial process or horn in *Dendrocystoides,* although other plated protuberances, horns, spines, etc., occur on other regions of the theca in this genus.

The **proximal tumescence** (Fig. 372) is a far larger and presumably more important elevation of the theca. This is a transversely oval zone, occupying the widest part of the obverse theca. The plates covering this area have usually collapsed and become imbricated during fossilization, reflecting their integumentary union in life. The proximal border of the zone is the firmly sutured adsteleal circlet of plates; the distal border is a bounding arc of thecal plates, firmly sutured and usually medially upbent proximally, to which the plates of the tumescence were flexibly united. Internally, along the transplate line of geniculation of the bounding arc, there is a sulcar ridge. This extends from the apex of the "antanal" right proximal lobe to the apex of the preanal lobe of the left proximal lobe. Both the bending of the plates of the bounding arc and the internal sulcus serve as indices of the obverse face of the theca, a matter that is often not easy to determine in fragmental material. In *Dendrocystites sedgwicki* the loosely joined plates of the proximal tumescence are somewhat larger than those over the rest of the theca, also thicker and umbonate, with marginal bosses at the plate angles (and in some specimens between them) or with prominent radial ridges (not plicae as usually described), which are not visible on the interior surface. In *D. barrandei* the plates of this tumescence are unornamented. In *Syringocrinus* (see Fig. 393) and *Iowacystis* (see Fig. 394) much of the obverse face seems to be occupied by the homologue of this tumescence, likewise covered by flexibly united plates. In some specimens of *D. sedgwicki* there is a secondary out-pouching of the theca on the adanal side of the proximal tumescence, which may have accommodated a large cloaca, perhaps bearing respiratory trees.

In the convexi-planate forms, where, to employ turtle nomenclature, the obverse face was carapace-like and the reverse, plastron-like, the latter was possibly flexibly conformable to the substrate surface, although seemingly generally more or less rigid and somewhat concave. In the resupinate *Girvanicystis* (Fig. 373, 374) the reverse face is very convex, and bears striking prominences which involve the flexuring of plates; the obverse face was apparently concave and essentially "opercular" in relation to the reverse. The juncture of the two faces, except possibly at the distal margin, was like that of a pillbox (Fig. 374) and conspicuously integumental on the extensiplane; both faces seem to have been composed of rigidly united plates.

Clearly in most, if not all homoiosteles, there is provision in the thecal organization for expansion and contraction of the soft anatomy, or pumping action of the cloaca.

This seems clearly to be the meaning of the proximal tumescence in dendrocystitids, of the many and loosely united plates of the obverse faces in *Iowacystis* and *Syringocrinus,* and of the extensiplane peripheral suture in *Girvanicystis.*

In *Syringocrinus* and *Iowacystis,* and to some degree in *Minervaecystis,* the thecae are homeomorphic with the Stylophora. This entails the development of a turtle-like (testudinate) investiture wherein the obverse face is very like a carapace and the reverse like a plastron. Some thecal plates become definitely lateral in position. In *Minervaecystis* and *Syringocrinus* a loaf-like thecal form is invested with thin plates which form a curved mosaic on the flanks. In *Iowacystis* the lateral plates are constant in number and position, very thick, and geniculate onto both faces to form a **marginal frame** within which are the **somatic plates;** obverse somatics are **supracentrals;** reverse, **infracentrals.** *Rutroclypeus* has the aspect of having been pressed in a die, the polyplating being but little, if to any degree, correlated with the nummuloidal thecal form that results.

The thecal plates adjacent to orifices have been to some extent regularized so that some of them can be consistently identified and homologized. This is especially true of adbrachials and adsteleals, but less so of adanals. Adsteleal plates are commonly larger, thicker, and more firmly united than most thecal plates; thus they form an **adsteleal girdle** about the steleal foramen. In *Dendrocystites* the girdle is well developed, but the number of plates in it is variable. However, a single axial one on the obverse and two adaxial ones on the reverse face are constant. *Girvanicystis* and *Iowacystis* have single axial adsteleal plates on each face. Four symmetrically disposed adsteleals encircle the steleal aperture in *Syringocrinus.* In *Girvanicystis* the extensiplane peripheral suture passes through both the arm and stele apertures. In *Dendrocystites sedgwicki,* and probably elsewhere, the median adsteleal plates bear internal, elevated muscle ridges or platforms, some with apophyses, for attachment of the strong proxistele muscles. Around the inner margin of the adsteleal girdle there is commonly a shallow, narrow groove, presumably for the attachment of integument.

ORNAMENT

The thecal plates are commonly granular *(Dendrocystites, Girvanicystis),* but *Minervaecystis* seems to be smooth. *Iowacystis* is extremely granular and papillose with a prominent labyrinthine ornament on the marginal plates. Central plate bosses *(Heckericystis),* umbones *(D. sedgwicki),* and long spines *(Rutroclypeus),* marginal bosses and radial ribs are external ornament. In *Girvanicystis* certain thecal plates are warped into spines and comblike excrescences which affect the entire plate, as do radial plicae of certain large plates in this genus. The supracentrals of *Iowacystis* are radially plicated. The plated spines and excrescences of *Dendrocystoides* are unique.

ANUS

The homoiostele anus is usually very large, although it has not been discovered in *Rutroclypeus* despite an abundance of fossil materials. It commonly lies in the left proximal lobe; however, in *Minervaecystis* it is right proximal. The aperture is usually near or at the thecal margin, but may invade either the obverse or reverse face. *Girvanicystis* is unusual in that it deeply invades the reverse face of the left proximal lobe. When the anus is at or near the margin its presence is usually indicated by the development of the anal lobe *(s.s.)* on the proximal lobe.

Usually special anal plates effect the anal closure; **adanal plates** surround the anal orifice; between them there may be many flexibly united platelets constituting a periproctal zone. In *Minervaecystis* the anus is closed by a low pyramid of long trigonal plates which radially imbricate over the aperture. In *Dendrocystoides* many small platelets are puckered around the anus, and the closure seems to have been sphincteral, as BATHER (1913) supposed. Here the anus is in a posterior inframarginal position. The adanal plates of the obverse face form a trigonal lappet over the anal area and extend posteriorly to form a projecting anal lobe. The lappet plates are coarsely grained and ridged externally. In *Dendrocystites sedgwicki* the anal lappet bears a swollen median plate of subtrigonal outline. This is BATHER's "sugarloaf" or epianal **(suranal)**

plate. Laterally and subjacent to the lappet there were on either side of the anus itself groups of long platelets which may represent relics of an anal pyramid or specialized periproct.

In *Dendrocystites barrandei* (see Fig. 384,*2*) the anal orifice lies on the posterior left flank or slightly on the reverse face of the rounded flank. Although an ovate anal lobe exists on the flattened specimens, indicating an anal bulge of the theca, no lappet has been observed, despite BATHER's (1913) drawing of both lappet and "epianal" plate. A large, truncated oval adanal plate is present and usually stands at a high angle in the fossils. This may be the antecedent homologue of the suranal in *D. sedgwicki*. But in *D. barrandei,* the older species, its position is *beneath* the anus (subanal), rather than above it (suranal). The broad base of this plate seems to bear articulatory apophyses and is notched as though a sutural pore of some kind were present.

Iowacystis bears the most specialized of homoiostele anal apparatuses. The marginal anus, located at the left posterior angle of the triangular theca, is closed by a pair of calcareous quarter-spheres which serve as opposable valves, opening on the extensiplane and making, when closed, a large hemispherical boss. The valves are probably modified subanal and suranal plates. Surrounding the anal boss is a rosette of quadrangular adanal plates.

The anuses of *Minervaecystis* and *Girvanicystis* (see Fig. 389) lie well within the proximal lateral thecal face. It is left and obverse in the former, and left, reverse in the latter. In *Girvanicystis* the suranal plate is seen to be large and near the center of a large proctal area which is otherwise occupied by tessellated, or perhaps slightly imbricating, periproct plates. Although previous studies of the Rhenish Devonian solute *Dehmicystis globulus* (DEHM) had not revealed the anal apparatus, it is now quite clear (see Fig. 388,*2*). The theca is here reevaluated as having been essentially globular in life, rather than flattened in the rutroclypeid manner, as GILL & CASTER (1960) supposed. The anal zone is large and circular and, although postlateral and marginal on the flattened specimen, does not appear to be associated with thecal lobation. Narrow trigonal plates form a low pyramid over the anal aperture; additional periproctal or adanal plates surround the pyramid, and a large suranal plate seems to be poorly preserved. The anus of *Syringocrinus* remains problematic despite rather full knowledge of the thecal anatomy (PARSLEY & CASTER, 1965). The many small, flexibly united, supracentral plates are probably the homologue of the proximal tumescence of *Dendrocystites,* developed as the pumping apparatus; still the appearance is very much like a periproct zone in other echinoderms. However, there is no aperture within this supracentral area.

STELE

The very name of the class signifies that the stele is a primary taxobasis thereof. It is also an organ of fundamental import in the economy of homoiosteles. Like the arm, the demarcation between stele and theca is sharp, rather than gradational; the juncture is always muscular and integumental, the skeletal plating on the two sides of this juncture, of distinct organization (Fig. 377, 378). Like the arm, the stele (heterostele) or tail is bilaterally tetramerous, i.e., is composed of four series of plates, and possesses, at least proximally, a large central lumen. Among homoiosteles, in contrast to the Stylophora, where the stele (aulacophore) is quite similar in plane and caudal function, the homoiostele organ had no subvective function, although it may well have evolved from an arm.

Three axial zones of the heterostele are differentiable: the proximal zone or **proxistele,** mesial or **mesistele,** and distal or **dististele** (Fig. 372, 375; see Fig. 381, 384). The proxistele is fundamentally tetraserial, i.e., tetramerous, four plates completing a circle; and the dististele biserial, i.e., dimerous. The transition from four-part to two-part symmetry occurs in the mesistele (see Fig. 384). This is achieved through distal suppression of alternate series of tetrameres and concomitant rotation of the resulting biseries, so that the dimere suture lies for most of its length in the projected extensiplane of the theca, and the dimeres thus take on a corresponding obverse and reverse orientation.

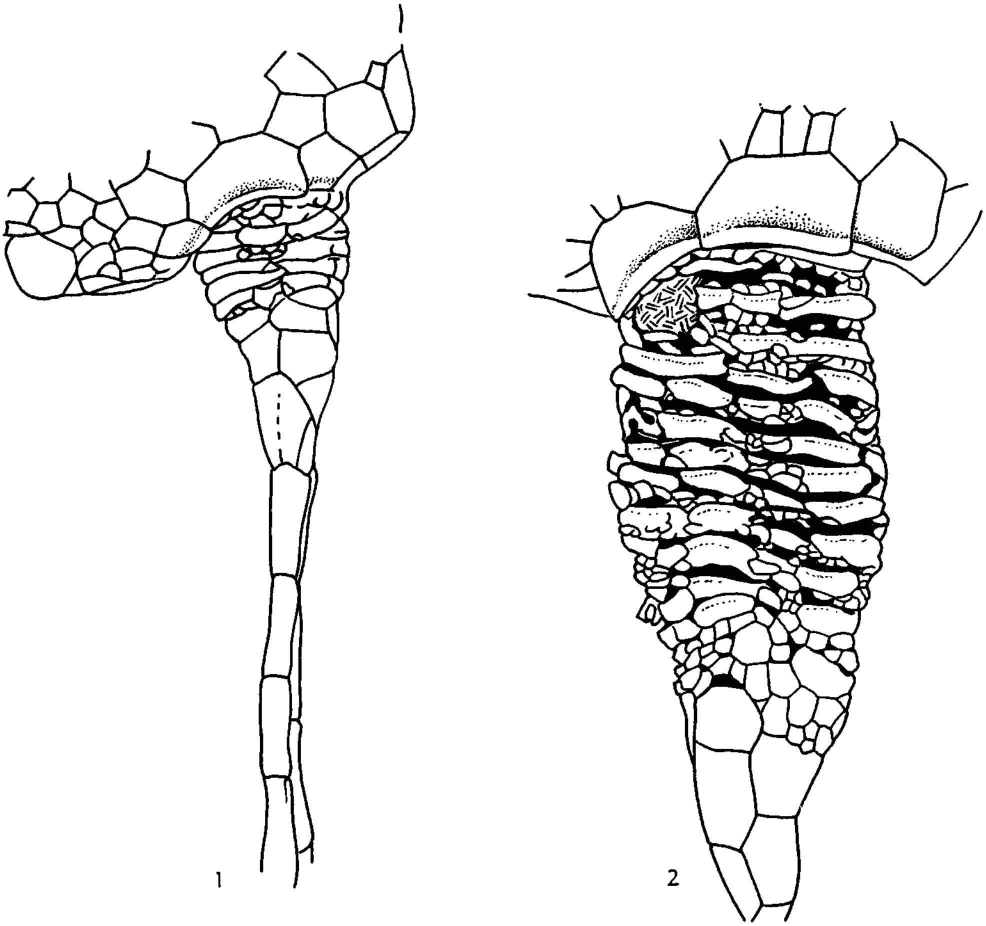

FIG. 377. Morphological features of homoiostelean steles illustrated by obverse views of immature specimens showing two stages in stele development, both identified as **Dendrocystites sedgwicki* (BARRANDE), M.Ord., Eu.(Boh.); *1,* tetramerous proxistele with few platelets both between annuli and between tetrameres of same ring but distal transition from proxistele to mesistele unobscured by platelets, ×3.8; *2,* specimen showing later stage of stele ontogeny in which each annulus is composed of at least 8 meres with many platelets between them in ring, as well as between adjacent rings, transition from proxistele to mesistele obscured by rosetting around major plates, ×3.3 (Caster, n; drawings by E. A. Dalvé based on specimens from Narodni Museum, Praha, Frič and Barrande Colls.).

PROXISTELE

The proximal stele, or proxistele, was the main zone of mobility in the homoiostele. It is strongly plated, usually in the form of telescopically imbricating tetramere rings. Internally the large lumen presumably contained a complex of muscle fibers which served as attachment of the heterostele to the theca and performed as the main locomotor organ of the creature. Movements of extension and contraction of the ring-covered area, right and left, up and down and, by differential contraction of the muscles, somewhat rotatory, are implied. Prominent ridges or platforms inside the stele aperture of the theca were the concentrated zone of proximal muscle fixation; the inside surface of the bourrelets of the rings were distal fixation sites; the conical lumen of the mesistele probably served as the main seat of distal attachment of lengthening and shortening muscles. Probably the main locomotor function of the dististele was controlled in the proxistele.

The archetypical proxistele plan would seem to be that of the single unnamed Upper Cambrian homoiostele described (1963) by UBAGHS from Nevada, and the Lower Ordovician *Minervaecystis* from France. In both, well-developed, axially imbricating, tetramere rings are present. This organization, which is the dominant one in the Homoiostelea, is shared with the mitrate Stylophora (anomalocystitids), where the aulacophore shows an identical organization, which is here assumed to be homologous. This proxistele condition is termed **anomalocystitoid** (Fig. 379, see Fig. 381,*6*). The archetypic proxistele was essentially terete (possibly slightly compressed), the tetrameres of each ring flexibly meeting end-to-end on the obverse symmetry-plane, on the extensiplane laterally, and slightly imbricating on the reverse symmetry plane. The combined telescoping of rings and sagittal imbrication of the tetrameres on the reverse face creates a characteristic zigzag shingling on the reverse mid-line; all of which is "anomalocystitoid," although in most homoiosteles and Stylophora the proxistele (proximal aulacophore) tends to be somewhat depressed.

In *Minervaecystis* (see Fig. 381) the proxistele is exceptionally long, distally tapering, and comprising some 25 to 30 long, thin, imbricating rings. Since both in this genus and in the Nevada form the proxisteles are preserved in an inflated condition, it seems that the constituent tetrameres of the telescoping rings were relatively firmly joined obversely and laterally; reversely they show a slight zigzag imbrication.

Each tetramere is thickened proximally into a **bourrelet** which curves outward as a thickened rim; distally the rings thin to a feather edge. Because of axial imbrication, the bourrelet is normally deeply concealed beneath the thin margin of the proximally adjacent ring.

Several solutans show a marked tendency for the distal stele to twist to the right, thus bringing what are proximally and serially (and probably historically) obverse skeletal elements to a lateral position, and concomitantly lateral ones to the reverse position (see Fig. 384). Correlated with this torsion, the tetramerous condition of the proxistele passes within the mesistele zone into the dimerous condition of the dististele. In this process the distal dimere suture, which is continuous with the sagittal sutures of the proxistele, comes to lie in the extensiplane. In *Minervaecystis* this dextral torsion (Fig. 378,*2d*) of the mid-stele zone is uniquely recorded by a crest which passes across the mesistele diagonally onto the distal proxistele plates: the left reverse tetrameres (to the right of the observer when the reverse surface is viewed) each bear subangular longitudinal median folds which continue as a low keel onto the mesistele where the fold axis crosses the symmetry plane. It appears that in life the organism lay with the left half proxistele distally twisted toward the right, so that the keel came to lie in a position normal to the sea floor. It was functionally a proximal continuation of the pectinate keel or rudder on the proximal reverse dimeres.

In *Syringocrinus* (see Fig. 393) of the Middle Ordovician of Canada the slightly compressed proxistele comprises 11 or 12 smooth, imbricating rings, of which the tetrameres imbricate both obversely and reversely on the symmetry plane. In *Iowacystis*, of the Upper Ordovician, the proxistele is very short, comprising 5 or 6 rings, each of which bears an encircling railroad rail-like flange at its mid-length. The ring margins are smooth and apparently without a bourrelet; they imbricate telescopically. The lateral tetramere sutures are tight, but those on the symmetry plane imbricate slightly on both faces. The whole proxistele is slightly depressed. *Rutroclypeus* of the Australian Lower Devonian has a remarkably depressed theca and a correspondingly much-depressed proxistele of unusual trigonal outline, which first led to its identification as the buckler of a xiphosuran. All of the tetrameres were loosely joined and the two faces in close proximity. The tetrameres strongly imbricate on the symmetry plane of both faces. In keeping with the spinose theca, most specimens show a prominent spine on each tetramere. This is perhaps the most anomalocystitoid of solutan proxisteles.

Heckericystis, of the Baltic Middle Ordovician, is shown by GEKKER [HECKER] as possessing a terete proxistele, recalling the swollen proximal columnals of the cystoid *Pleurocystites,* of 12 or 13 narrow rings. Although it is supposed that the rings are tetramerous, no sutures have been reported. Both GEKKER (1940) and GILL & CASTER (1961) assumed that the rings were non-imbricating and united by integument only. This may be a misconception.

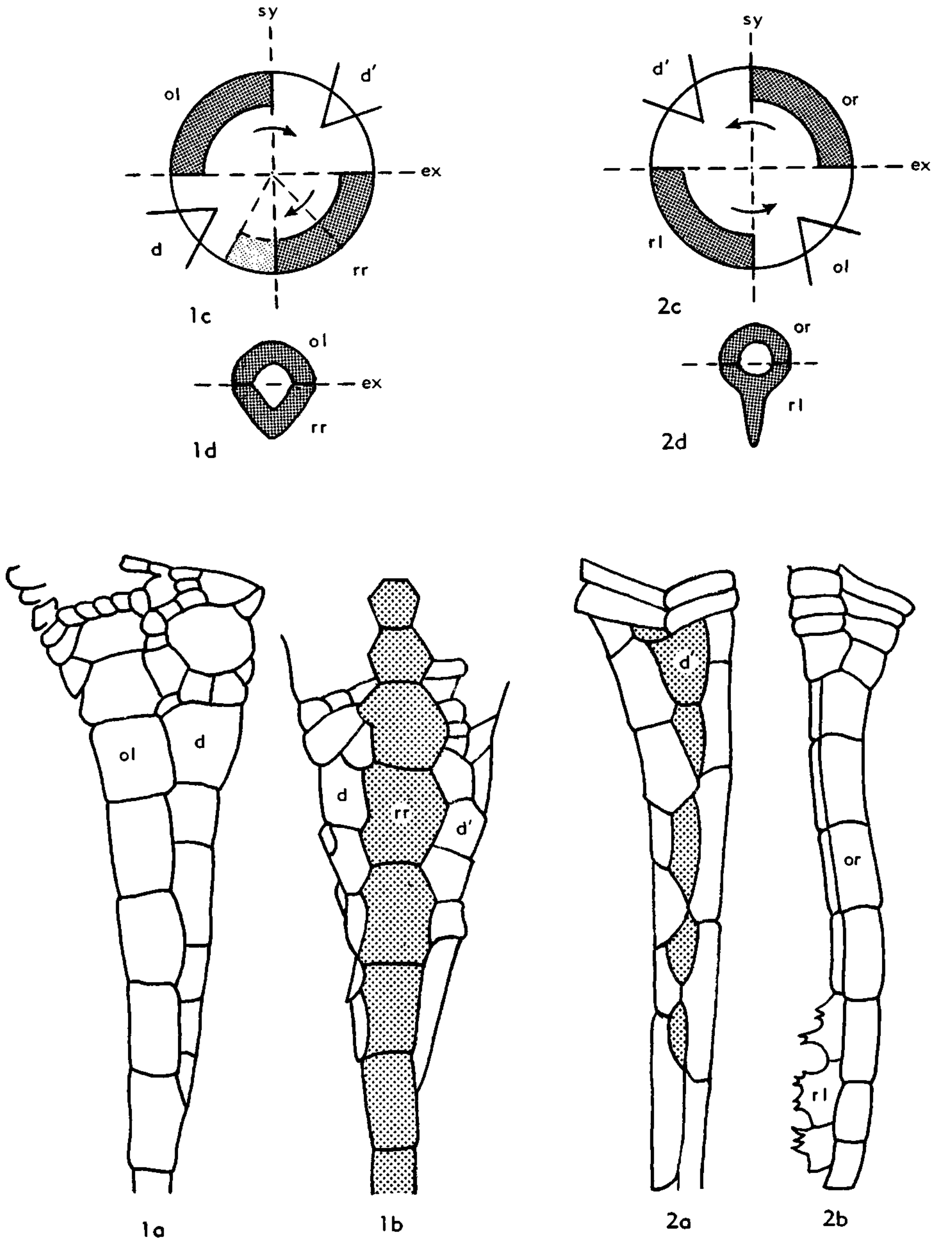

FIG 378. Mesistele transition from tetrameral condition of proxistele to dimeral condition of dististele in Homoiostelea.

1. **Dendrocystites sedgwicki* (Barrande), M.Ord., *1a,b,* obverse and reverse faces of stele (reverse tetramere series stippled); *1c,* schematic cross section of proxistele in which those tetramere series which persist through mesistele and into dististele are stippled, and those which become evanescent in this passage are indicated by chevrons; *1d,* dimere disposition in dististele (Caster, n; based on materials in Narodni Museum, Praha).

2. *Minervaecystis* Ubaghs & Caster, n. gen., L.Ord.; *2a,* left view of mesistele (left obverse tetramere series dotted; *2b,* obverse face of same stele (keeled reverse dimeres turned sideward during fossilization); *2c,d,* same analysis of this genus as shown in *1c,d* (Caster, n; based on holotype of **M. vidali,* courtesy G. Ubaghs).

[Explanation: Arrows indicate direction of rotation of persisting tetramere series when traced through

The Bohemian Middle Ordovician *Dendrocystites sedgwicki* and the Scottish Upper Ordovician *Dendrocystoides* and *Girvanicystis* show many small platelets in association with the proxistele tetrameres, or, in the first instance, seemingly in lieu of them (Fig. 372, see Fig. 382). Every stage from complete tetrameres to rudimentary remnants submerged in a melange of platelets can be seen. *Dendrocystites barrandei* (BATHER), of the Lower Middle Ordovician of Bohemia, and related undescribed forms, commonly preserve distinct tetrameres, or identifiable remnants thereof, the while adding platelets in the annulus series with them so as to create penta-, hexa- or polymere annuli. Between the flanged rings of the tetramere plates many very small platelets occupy the zone of integumentary junction. In what appear to be young individuals of *D. sedgwicki*, the *D. barrandei* plan is closely approximated and the tetramere elements readily identified. In adult and typical *D. sedgwicki* most evidence of the tetramerous proxistele is eradicated by the multiplicity of platelet development and the reduction in size of the tetramere elements. This proliferation occurs both within the annuli and between them, all sclerites being flexibly joined. This is the most inflated of homoiostele proxisteles and certainly the most flexible one. However, close scrutiny does reveal among the platelets a few which exhibit the characteristic flange and bourrelet of the tetrameres. These are found in the circles of larger platelets. The wider zones of small plates seem to have been folded into rugae between the more prominent rings. The whole proxistele lumen of the fossils is commonly choked with discrete platelets.

In some specimens of *Dendrocystites sedgwicki* the disposition of the platelets in the prominent rings suggests that they may derive from the splitting of tetrameres. It is also clear that in *Dendrocystites* the process of rosetting, by which small plates develop in the sutures around large plates, operates both in the theca and the proxistele-mesistele.

Dendrocystoides (Fig. 376; see Fig. 386) of the Upper Ordovician consistently shows many small polygonal plates in the proxistele lumen, but little or no evidence of them externally; they probably were embedded in the integument which connected the telescoping rings. Here, too, there is a remarkable range in surface nature of the tetrameres, and apparently all at the same growth stages of the type species. Thin, smooth, squamose tetrameres are found along with thick, rugose, pitted or radiately ribbed ones, with frayed or spinose distal margins (Fig. 379). *Girvanicystis,* from the same beds, has a depressed anomalocystitoid proxistele with rugosely flanged and carinate tetrameres (Fig. 374, see Fig. 390). Adjacent to the flange both distally and proximally there are many external adherent subpolygonal platelets which seem to pertain to tissues originally covering the stele. Here no platelets have been observed inside the lumen.

BATHER (1913 and elsewhere) apparently largely employed the proxistele morphology of *Dendrocystites sedgwicki* in formulating his idea that the solutan stele derived from thecal plates by regularization. He imagined the regularized stele to grade into the essentially chaotic theca. In the process, perhaps by fusion of platelets or by differential growth and reduction, tetrameres would emerge. However, in this species no gradation from stele to theca occurs, and instead of being a primitive solutan, it now appears to be one of the most advanced, at any rate in stele development. The multiplating is derived from the anomalocystitoid condition, from tetrameres (plus supplements), rather than being antecedent to them. What are judged to be young forms of the species, in association with adults, show tetrameres along with a few platelets. The antecedent *D. barrandei* BATHER of Bohemia, which was still recognizably anomalocystitoid in adulthood, closely parallels the young forms

[*Continued from facing page*]

mesistele; plate sutures or margins which were on symmetry-plane in proxistele come to lie on extensiplane of dististele; *d,d'*, tetrameres of series which distally disappear; *d*, reverse; *d'*, obverse; *ex*, extensiplane of theca projected through stele; *ol*, obverse left tetramere; *or*, obverse right tetramere; *rl*, reverse left tetramere; *rr*, reverse right tetramere; *sy*, bisymmetry-plane.]

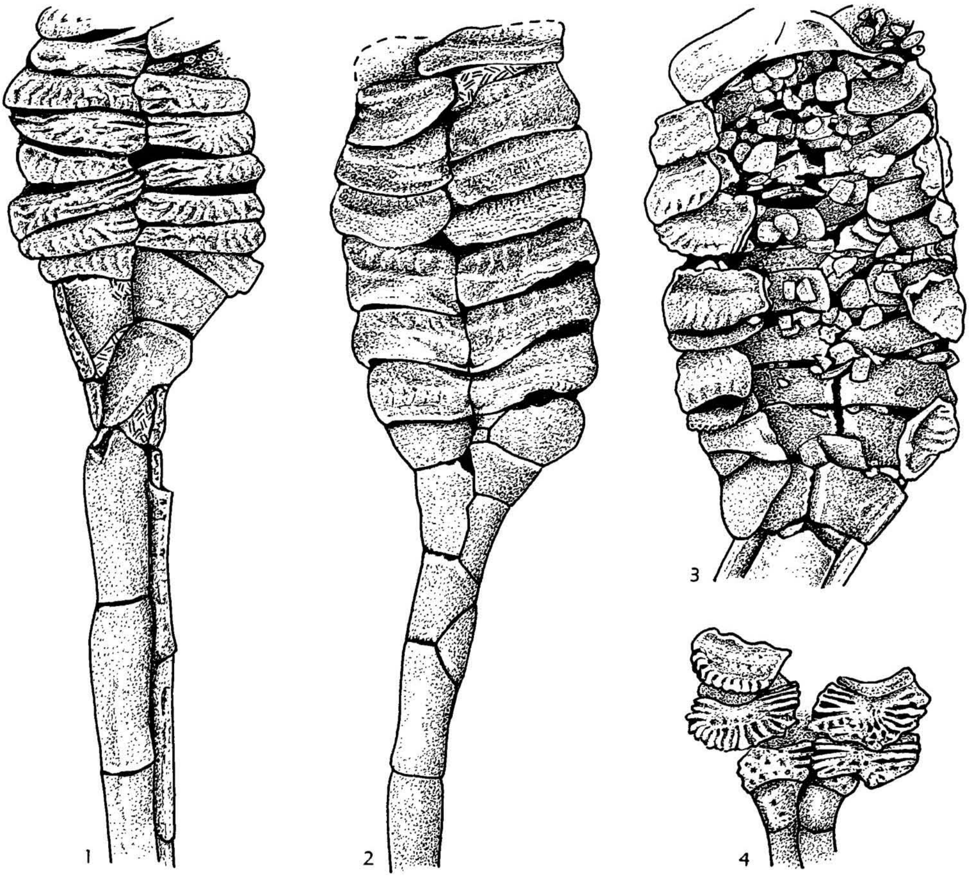

FIG. 379. Reverse views of four anomalocystitoid steles of **Dendrocystoides scoticus* (BATHER), U.Ord., Scot. (Girvan), showing variations within the species, in specimens of essentially same stage of growth, in nature of ornament and presence of internal integumental platelets. *1,2,4,* exterior reverse faces, torsion of mesistele well shown in *1* and aspects of radial ribbing in *2,4*; *3,* internal view of obverse face showing many small platelets concentrated mainly in integumental zone between annuli. (Caster, n; drawings by E. A. Dalvé based on specimens in Hunterian Museum, University of Glasgow: *1,* no. E5803, ×4; *2,* no. E5718, ×3.5; *3,* no. E5827, ×3.8; *4,* no. E5719, ×4.3).

of *D. sedgwicki,* and was at about the same stage of platelet development as the Scottish *Dendrocystoides* and *Girvanicystis.*

PROXISTELE INSERTION

The proxistele is inserted well within the stele foramen, which is usually recessed into the proximal thecal margin. The aperture conforms in shape to the proxistele, from circular to very depressedly ovate. The adsteleal plates of both thecal faces are to some degree regularized and can be homologized within limits. They were commonly rigidly fused to form an adsteleal girdle, a marginal flange of which extended over the proximal proxistele. Just inside the flange there is usually a shallow groove, probably for integument attachment; deeper within the aperture, and mainly developed on or adjacent to the symmetry plane, each genus shows characteristic scars, calluses, or paired apophyses which were places of attachment of the powerful proxistele muscles. In *Dendrocystites sedgwicki* strong bilateral apophyses are present both reversely and obversely, so tilted as to suggest that obverse tetrameres were connected by muscles to the reverse apophyses, and reverse to the obverse.

MESISTELE

The mesistele is a relatively rigidly plated conical coupling between the proxistele and the dististele. It served mainly as the distal termination of proximal muscle strands responsible for the main movements of the dististele "tail." Within the mesistele the transition from the proximal tetramerous condition to distal dimerous was made. It is usually possible, especially in anomalocystitoid forms, to trace across the mesistele (Fig. 378) the serial homologies between tetrameres and dimeres, or biseries. (Biseries, biserial, is employed for **alternate** positioning of plates, with a resultant zigzag suture; dimeres, dimerous, for **opposite,** semicylindrical plates having a rectilinear suture.) In these the distal tracing of tetramere series reveals that alternate ones persist and diminish in the passage of the mesistele zone. Alternate series commonly become evanescent in the distal mesistele. However, in *Iowacystis* (see Fig. 394) and *Syringocrinus* remnants of the diminishing series persist as discontinuous intercalates on the zigzag sutures of the distal biseries. The correlation between tetramere quadrants and dimeres or biseries have taxonomic import (Fig. 376).

In *Minervaecystis* (Fig. 378), the oldest well-known solutan, the mesistele is relatively simple. The obverse right series of tetrameres passes directly into the tightly sutured right series of the mesistele, which in turn is serially continuous with the right dimere series of the proximal dististele; the left obverse tetrameres align with two or three plates which appear as intercalates on the mesistele equivalent of the proximally zigzag and distally dimerous suture of the dististele. Tracing the left obverse tetramere series distally, it is seen to diminish serially in size and finally to disappear in transit of the mesistele. On the reverse face the left tetramere series continues the length of the mesistele and aligns with the left series of the proximal dististele; the right reverse tetramere series, similarly traced, peters out in two or three distally diminishing plates.

This general plan, alternate tetrameres aligned serially with dimeres and their alternates disappearing distally within the mesistele, seems usual among homoiosteles. In *Dendrocystites* (Fig. 378,*1*) wherein the general structural scheme is common to all other anomalocystitoid solutes, quadrants antipodal to those in *Minervaecystis* persist and diminish distally; however, the basic relationships are the same, and the dimere series is thus to be identified and serially homologized with proxistele tetrameres.

In *Dendrocystites sedgwicki* (Fig. 372, 377), where auxiliary platelets and rosetting obscure serial relationships, the juveniles suggest that the prevailing homologies pertain.

Throughout the class the same modifications of the meres take place in the transition from a tetraseries to a biseries. Those tetramere quadrants which are serially vacated by the distally diminishing alternate series are serially invaded by the persisting series as their configuration changes from quarter circles to semicircles. On both faces the proportional serial enlargement is across the symmetry plane; the original extensiplane (lateral) sutures remain constant in position. The effect of this opposing proportional enlargement of the serially persisting plates is that of distal rotation of the stele. When the dimere condition is fully attained, the two half cylinders meet on the extensiplane and in obverse and reverse position, each astride the symmetry plane, rather than being half-right and half-left, as in the proxistele. Customary representations of the dimeres meeting on the symmetry plane seem to be in all cases 90 degrees out of life orientation. The diagonal carina of the reverse face of the *Minervaecystis* proximal stele, mentioned above, which crosses the symmetry plane, conforms to this principle of distal stele rotation. Apparently the rotation is one of the oldest of homoiostele traits, and seems to correlate with the development of an obverse keel or "caudal" fin in free-moving animals. In *Iowacystis,* where no such modification is known, the rotation seems to be suppressed, and for that matter, mesistele plate organization persists through much, if not all, of the distal stele.

The nature of serial transitions of *Minervaecystis* suggests that historically the whole stele was covered by a tetraseries of alternating plates. In this respect *Iowacystis* is the most generalized solute yet encountered; however, the rest of the highly specialized anatomy of this genus suggests that this is a derived simplicity. Unfortunately, there are as yet no ontogenetic data available on stele development, and neither the mode of, nor focus of, stele plate origination is known.

The mesistele of *Syringocrinus,* M.Ord., Canada, is both anomalous and instructive. It has been called a dendrostyloid by PARSLEY & CASTER (1965) because of its homeomorphic resemblance to the styloid of the Stylophora. It is unusually long, petiolate, and covered by rigidly sutured asymmetrical plates (see Fig. 393). It is lachrymal in cross section, i.e., rounded on the obverse face (in life) and keeled on the reverse (see Fig. 393,*1a*). Prominent nodes occur on the left side of the keel; none on the right. The plating is triserial, the right side being invested by a biseries, while the left has a continuous axial row of long plates separating the plates of the biseries. These axials are serial homologies of discontinuous left intercalates which extend through most of the dististele. In the mesistele the axial plates cover most of the rounded surface. The suture between the biseries on the right side of the mesistele is rectilinear and continues as a straight suture to the end of the dististele.

The main mesistele plating in this genus is a disparate biseries, three long plates on the obverse face occupying exactly the same distance as five nodose ones on the keel side. The five plates bear the nodes or bosses at mid-length and marginally on the left side of the keel; these continue onto the first two dististele keeled plates. The distal keel margins are subspinously produced as imbricating caps which give the keel a characteristic serrate appearance; this continues essentially for the length of the tail. These serrations and nodes on the rigid mesistele are the basis for comparing this organ with the mitrate stylocone.

The presence of a narrow, apparently unsutured, annulus between the proxistele and mesistele makes direct correlation between the serial plating of the two zones difficult. The annulus may bespeak unusual rotational activity in this zone in the living organism. It is also no doubt correlated with the usual sinistral rotation of plate series in the mesistele. It is assumed that the keeled edge of the distal mesistele and dististele was, in the main, downwardly directed in life, and that the lanceolate expansion of the dististele served mainly as a laterally moving caudal fin. However, the nodes on the left side of the keel-forming plates of the middle stele zone, and the markedly different plating on the two sides of the post-proxistele tail, pose problems of symmetry, balance, and serial homology. It is no doubt significant that the asymmetrical ornament and the direction of the distal serial rotation are both sinistral. The nodes may have served as a counterbalance to inherent muscular forces tending to return the tail to a primordial orientation, such that the dimere suture would lie in the sagittal plane. The extra plating on the left side of the tail may have a similar correlation. As for the serial homologies between the proxistele and the rest of the tail, this is most speculative. Probably, as in other sinistrally rotating homoiosteles, the axial plates of the mesistele, and their discontinuous correlates along the zigzag suture of the left dististele, are serial homologues of the right obverse quadrants of the proxistele. If this is so, then what is the meaning of a single small plate (see Fig. 393,*1a*) on the suture between the first axial and an adjacent nodose plate? It may be adventitious; in other solutes one would tend to correlate it with a tetramere series, it being the only tetramerous element in the mesistele. If this is elected, then *Syringocrinus* is unique in having distally diminished both obverse tetramere series, and in having the resultant biseries wholly of reverse derivation. On the other hand, the compelling evidence of sinistral rotation argues for disregarding this platelet, and correlating the nodose keel plates of the biseries as left obverse in origin, as in *Dendrocystites.* In this genus the left reverse tetrameres diminish distally in the mesistele, but in *Syringocrinus,* if the right plates of the biseries are to be correlated, as is conventional, with the right reverse series, they do not appear in the mesistele. The left reverse series would seem to have no postannulus correlates. This reasoning is supported by the rectilinear suture on the right side of the tail. Intercalated plates, representing a distally diminishing tetramere series, are generally associated with the biserial zigzag relationship of plates; straight sutures derive from zigzag, just as opposite plates derive from alternate. In these terms the right side of the *Syringocrinus* tail is considerably more specialized than the left. The annulus of this genus might be likened to a temporal hiatus, in the crossing of which much that transpired has been eliminated from the record.

In *Dendrocystites sedgwicki* (Fig. 372, 377) the mesistele is a tessellated, multiplated, conical connection between the very flexible and profusely plated proxistele and the dimerous dististele. The adult mesisteles usually show an advanced condition of rosetting by which earlier-formed plates become isolated among many platelets which form in circles around them. However, on both larger steles and especially so on immature ones, it is possible to trace through five or six large plates the continuous serial course of dimeres into the tetramere series (Fig. 377). On the obverse mesistele the left half of the face is occupied by a continuation of the distal dimere series; the right side, by a distally diminishing series of six or seven plates which alternate with the left series. Laterally and at the junction with the dimere series, small plates may be intercalated; proximally the initial large plate of the diminishing series is commonly rosetted. This series disappears at a shoulder on the first obverse dimere. On the reverse face of the mesistele the inferiorly oriented dististele dimeres pass without interruption through a series of six or seven median plates. This median series of mesistele plates seems to correspond to a right proxistele series. A low axial keel is present on these median plates, and continues onto the corresponding dististele plates. On the right side of the median series the distally diminishing series of the obverse face covers about one-third of the reverse face; on the left there is another distally diminishing series of plates bounding the reverse medians; this series disappears on a left shoulder of the first dististele dimere on this side. Obviously, the mesistele bears tetramerous elements, just as in the much older *Minervaecystis,* but with this basic difference: the apparent rotation in the mesistele zone is in an opposite direction in the two genera (Fig. 378,*1c,2c*), and antipodal quadrants distally continue and diminish.

Dendrocystoides show the basic mesistele gradation from four-part to two-part symmetry, accompanied by lateral rotation of keeled dimeres to a reverse position, the dististele being largely biserial. In *Iowacystis* the mesistele is undifferentiated from the dististele. In the mesistele zone there are no axial intercalates on the obverse face; on the reverse, one series of axial inserts is preserved. Both mesistele and dististele are somewhat depressed, and no rotation is in evidence.

DISTISTELE

Ordinarily the dististele is a long, rather firmly plated "tail," subequal in length to the remainder of the stele and in some specimens as long as the rest of the organism (some specimens of *Dendrocystoides*). Its plating is dominantly biserial or dimerous, usually passing from the first condition to the second distally. The basic orientation of the biseries, as described in morphology of the mesistele, is bilateral, one element deriving from the right or left obverse face, and the other from the left or right reverse, and consistently in a antipodal manner. Distal rotation either to right or left usually brings the biseries-dimeres to a fully obverse-reverse orientation with the sutures between the semicylinders lying in the projection of the thecal extensiplane. In *Dendrocystites sedgwicki* the dististele is attenuated and nearly terete, only a low keel occurring on the reverse dimere. In *Dendrocystites* and *Rutroclypeus* some specimens suggest a slight degree of prehensileness in the distal "tail." In *Heckericystis* a terete and highly attenuate dististele has been illustrated by GEKKER [HECKER] (1940). Usually the dististele is markedly flattened, and commonly asymmetrically. Whereas this flattening is always morphologic *depression,* the accompanying distal rotation creates the appearance of compression. The obverse members of the biseries are usually somewhat horseshoe-shaped in section; the reverse ones angular or keeled, some extending downward in a blade or comb. This asymmetry creates a caudal fin. This is lanceolate in profile in *Syringocrinus,* with serrations along the reverse edge created by distal imbrications of reverse dimeres; in *Minervaecystis* the pectinate comb of the keel might be likened to a "heterocercal" fish tail. In *Iowacystis* the biserial elements are essentially symmetrical and bilaterally disposed. They are depressed, being somewhat flattened in the extensiplane. Either no rotation occurs here, or in terms of the conditions illustrated in Figure 378 the two distally persisting homologues of the proxistele tetrameres rotate in opposite directions to occupy the vacated quadrants.

Because of the asymmetry and flattening of the dististele in most homoiosteles, the organ is usually preserved with the plane of depression parallel to the bedding; hence the usual restorations show the zigzag or rectilinear suture in the sagittal plane rather than the extensiplane. *Iowacystis* is the only form known so far in which the fossil dististele is actually preserved wholly in life position, and in this unique genus the suture was sagittal. *Girvanicystis* (Fig. 373) appears to have a very long dististele, composed of unequal but very long dimeres, but the suture lies in the extensiplane.

OCCURRENCE

DISTRIBUTION

Homoiostelea range in time from the Cambrian of Nevada and Upper Tremadocian (Lower Ordovician) of France well into the Lower Devonian of Victoria, Australia, and Germany. The maximum expansion came in the Middle and Upper Ordovician of Europe and North America. No Silurian representatives are yet known, and none from Asia, Africa, South America, or Antarctica.

PRESERVATION

Although homoiosteles, like other "carpoids," are among the rarest fossils, under exceptional circumstances they are abundant (see Fig. 385). In the Girvan Upper Ordovician of Scotland, the Middle Ordovician of Drabov and Zahorǎny, Bohemia, and the Kingland district of Victoria, Australia, extraordinary concentrations have been encountered. Such deposits are clastic polymict sediments, and the fossil concentrations are commonly on single bedding planes. This probably represents the death setting under conditions of roily flow. The carcasses seem to be hydrodynamically oriented (see Fig. 385). Presumably roiliness was especially injurious to microphages such as these. The occurrences usually preserve the fossils as collapsed thecae, quite probably attesting to their rapid burial. Moreover, they are now encountered as ochre-stained molds comprising the residue from solution of the stereom lime and reduction of a pyrite filling of the stroma canals of the skeleton. Rapid burial of the living animal would probably create a reducing environment inside the labyrinth of canals of the skeleton; this setting is commonly one propitious for pyrite deposition. The resultant sediment, being relatively porous, permits ready circulation of water during weathering, and resultant solution of lime and oxidation of the pyrite. The sulphuric acid released in the transition from pyrite to limonite abetted solution of the calcium carbonate. In less porous clastics, like the fine-grained micaceous shales such as cover some specimens (see Fig. 383), the stereom is still intact. Lime ooze was especially fine for the preservation of dead skeletal parts in essentially living articulation. No concentrations of remains have yet been found in such deposits. Probably homoiosteles, like other "carpoids," were far more abundant in Paleozoic seas than fossils indicate; their delicate and commonly inflated thecae, whether tightly or loosely plated, were prone to destruction. Dissociated plates have never been reported. However, this is more artifactual than real. Commonly, beds which contain homoiosteles also contain many other echinoderms, starfishes, other "carpoids," cystoids, machaerids, and eocrinoids. Other organisms are usually rare in this echinoderm facies.

PHYLOGENY AND EVOLUTION

"Carpoids" as a whole have proved enigmatic as to broader phylogenetic relationship.

Homoiostelea share with other "carpoids" indubitable echinoderm relationships. They appear, however, to lie completely outside

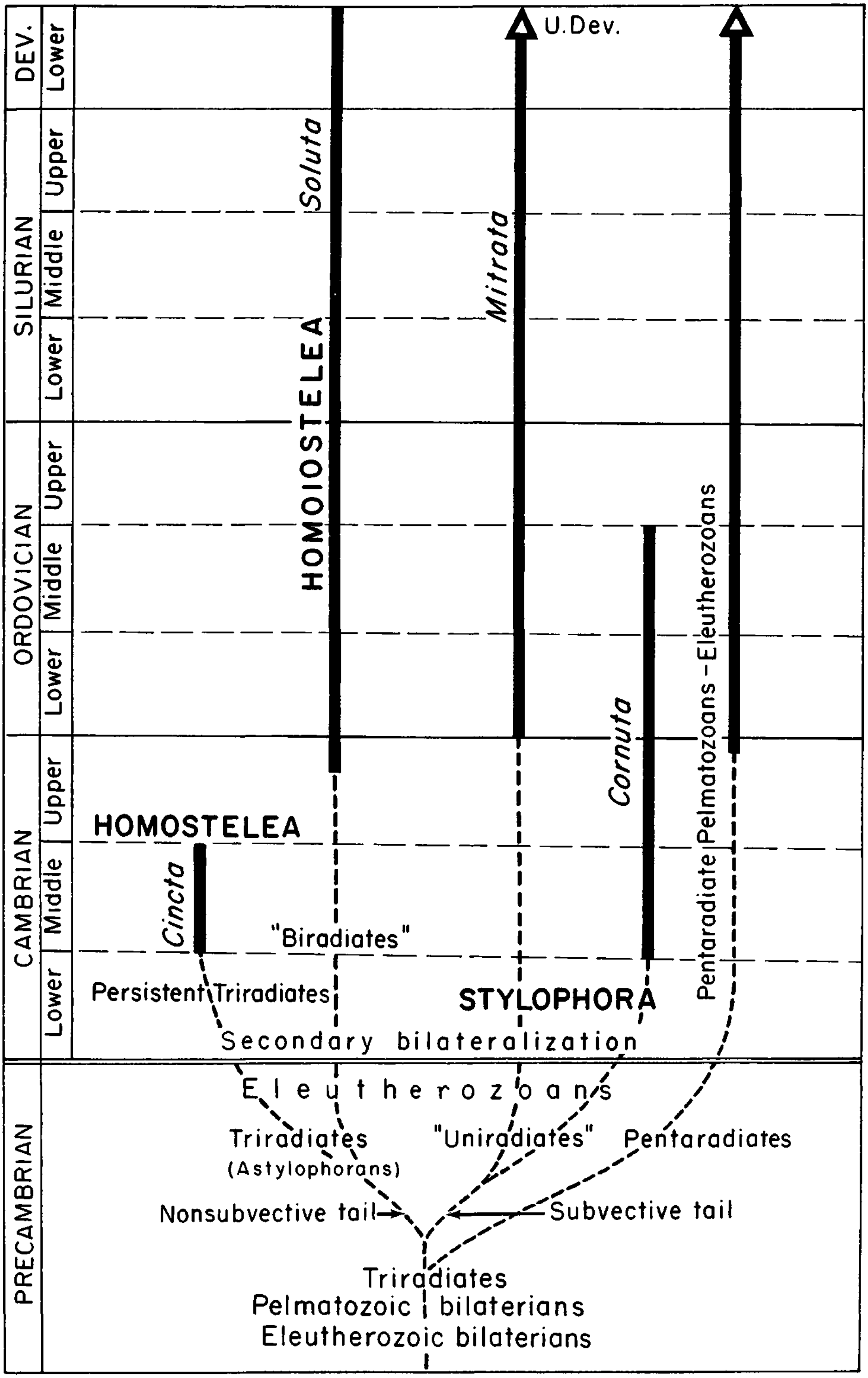

Fig. 380. Speculative phylogeny of "carpoid" classes (Caster, n).

any other echinoderm evolution. This is so fundamental that it presumably denotes a separate course, or courses, since pre-Phanerozoic times. It is my opinion that comparative "carpoid" morphology bespeaks a common ancestry of the three classes (Fig. 380). The still quite unknown triradial archetype would lie not only in the "carpoid" ancestry, but presumably also in that of all pentaradial pelmatozoans or pelmatozoan-derived classes.

This hypothesis entails the radial homologizing of arm and stele in the homoiosteles; according to this theory both were originally biserial subvective organs. Hence, the homoiosteles are termed "biradiates" (Fig. 380), the third radius having been suppressed prior to our encounter with the class. The aulacophore "tail-arm" of the Stylophora was the sole radial survivor there, and this group is labeled "uniradiates."

Within the class Homoiostelea there are too many hiatuses in the record and too much morphologic differentiation between the forms so far encountered to make phylogenetic speculation very meaningful. However, a few generalities are in order. Much has been discovered since the speculations of Bather (1900, 1913, 1930) and Jaekel (1899, 1901, 1921), which have largely colored all subsequent thinking about "carpoid" relations. In that phase of echinodermology the "Amphoridea" concept played a prominent role; since the "carpoids" were thought of as Pelmatozoa, and all fixed forms were supposed to derive from a loosely plated saclike form fixed at one extremity, regularization of plates was postulated as focusing on the point of fixation and at the arm base; both arms and peduncle were thought of as regularized extensions of the theca. Thus, when Barrande's *Dendrocystites sedgwicki* of the Bohemian Middle Ordovician was supposed to be one of the oldest "carpoids" (although the Cincta: Homostelea were then and still are oldest of all), its theca composed of many, apparently loosely articulated and little-if-at-all-regularized plates, its polyplated proxistele, and many small plates in the zone between first plates of the arm biseries and large thecal plates, all seemed —especially to Bather—to support the "Amphoridea" hypothesis. Now, with better knowledge of the organization of Bather's *D. barrandei,* from somewhat lower in the Bohemian Ordovician, of the juvenile stages of *D. sedgwicki* itself, and especially with the discovery of the Tremadocian *Minervaecystis* and a comparable stele from the Nevada Cambrian, the *Dendrocystites* support of the "Amphoridea" hypothesis fails. Instead of polyplating of the stele and gradational plating from theca to arm being archetypical, both are now seen to be specializations. In both the oldest forms and in juveniles of the specialized ones, tetramerous proxisteles and adbrachial regularized plates are the rule. *D. sedgwicki,* in the new light, is a highly specialized form, in which interstitial platelets and fractionation of antecedent large plates both occur.

Minervaecystis is far from a primitive homoiostele, and in many respects (e.g., its pectinate dististele keel) is very specialized. In its stele anatomy, however, it probably is the most primitive form yet known. Thus, far, no data are available which might indicate what organization of the proxistele may have antedated the tetramerous one. If the appendage is a modified arm, as here urged, its biserial nature and cover-plate series may be very ancient indeed (e.g., eocrinoids). Certainly this genus possesses the largest number of tetramere annuli known. Even so, its mesistele and dististele represent advanced locomotor specialization.

Until it is known how stele plates proliferated, any biogenetic interpretation of the axial differentiation of the stele is risky. When the stele was thought of as "another kind of stele," (i.e., column, hence "heterostele"), small attention was paid it. Its growth would be presumed to be mainly by intercalation of new skeletal elements at the proximal plane as in "other Pelmatozoa." Thus, if any biogenetic significance were to be attached to axial differentiation, the more distal elements would reflect an older phylogenetic state. If, on the other hand, the stele is a modified arm, it presumably grew like arms, with distal increments of parts. Thus it might be, and here is urged, that the distal succession from tetrameres to biseries to dimeres is quite possibly palingenetic[1] and Jacksonian,[2] hence of considerable phylogenetic importance. The very long series of tetrameres in *Minervaecystis* would seem to support this concept; likewise the well-documented transition from four-part to two-part symmetry of the oldest mesisteles, and distal transition from biseries to dimeres in many dististeles. (However, in *Minervaecystis* and *Dendrocysittes sedgwicki* the distal sequence is from dimeres to biseries. Thus the latter may well correlate with the prehensile flexibility of the tip of the tail.) In general, the older solutes have more armlike steles, solutan arms being basically tetramerous.

Within the Homoiostelea too many geologic and morphologic gaps separate the known genera to make lineage speculation worthwhile. Except at the species level, relationships are obscure. Although Gill & Caster (1960) indulged in a bit of speculation in this field, further information does not especially enhance their surmises. As the classification brings out, the generic differentia are, for the most part, comparable to family taxobases used elsewhere in the phylum.

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[1] Palingenesis, a succession of ontogenetic events which appear in the same order as the phylogenetic events which they supposedly recapitulate; this would be documentation of biogenesis.

[2] Robert Tracy Jackson attempted to apply the "biogenetic law" (biogenesis) to serially developing organs such as an ambulacral series of plates. It was his contention that the ontogeny of such a series tends to rehearse the evolutionary history of the organ.

SYSTEMATIC DESCRIPTIONS

Class HOMOIOSTELEA
Gill & Caster, 1960

[*nom. transl.* Caster, herein (*ex* subclass Homoiostelea Gill & Caster, 1960) (of the class Carpoidea Jaekel)] [=order Amphoridea Haeckel, 1896 (of class Cystidea) *(partim)*; Dendrocystidae Bather, 1899 (of order Amphoridea); order Soluta Jaekel, 1901 (of class Carpoidea, subclass Heterostelea); suborder Heterostelea Bather, 1913 (of order Amphoridea); class Carpoidea Bather, 1929 *(partim)*; superorder Astylophora Gill & Caster, 1960 (of subclass Homoiostelea)]

Ancient, eleutherozoic, asymmetrical echinoderms without obvious radial symmetry elements; usually depressed, and tending toward bisymmetry; theca of fixed form, multiplated; plates usually both facially and regionally differentiated (adsteleal, abbrachial, adanal); some regional provision for visceral expansion and contraction usual in thecal plating; single biserial, usually distal-lateral, arm bearing biserial cover plates; mouth subthecal; anus posterolateral in most forms; heterostele ("tail") posterior, long and composed of axially differentiated plates: proxistele flexible and fundamentally tetramerous; mesistele transitional from four-part to two-part plate symmetry: dististele usually biserial proximally and dimerous distally; adbrachial plate bearing hydropore and gonopore, where known. *U.Cam.-L.Dev.*

Order SOLUTA Jaekel, 1901

[=suborder Soluta Jaekel, 1901 (of class Carpoidea, order Heterostelea, *partim*); suborder Soluta Jaekel, 1918; order Soluta, Gill & Caster, 1960]

Characters of class. *U.Cam.-L.Dev.*

Seven families and ten genera of Soluta are recognized as follows:

1) Minervaecystidae Ubaghs & Caster, n.fam., *?U. Cam.,L.Ord.,* Eu.(France)-N.Am.(USA).
    Minervaecystis Ubaghs & Caster, n.gen., *U. Cam.,* N.Am.(Nev.) ("unnamed solutan," Ubaghs, 1963); *L.Ord.,* Eu.(France). (**Dendrocystis vidali* Thoral).
2) Dendrocystitidae Bassler, *M.Ord.-L.Dev.,* Eu.-N.Am.
    Dendrocystites Barrande, *M.Ord.,* Eu.(Boh.). (**Cystidea sedgwicki* Barrande); *D. barrandei* Bather.
    Dendrocystoides Jaekel, *U.Ord.,* Eu.(Scot.). (**Dendrocystis scotica* Bather).
    Heckericystis Gill & Caster, *M.Ord.,* Eu. (Est.). (**Dendrocystites kuckersianus* Hecker).
    Dehmicystis Caster, n.gen., *L.Dev.,* Eu.(Ger.). (**Dendrocystites (Dendrocystoides?) globulus* Dehm).
3) Girvanicystidae Caster, n.fam., *U.Ord.,* Eu. (Scot.).
    Girvanicystis Caster, n.gen., *U.Ord.,* Eu. (Scot.). (**G. batheri* Caster, n.sp.).
4) Rutroclypeidae Gill & Caster, *L.Dev.,* Australia.
    Rutroclypeus Withers, *L.Dev.,* Australia (Victoria). (**R. junori* Withers); *R. withersi* Gill & Caster.
5) Syringocrinidae Parsley & Caster, *M.Ord.,* N. Am.(Can.).
    Syringocrinus Billings, *M.Ord.,* Can.(Ont.). (**S. paradoxicus* Billings); *S. sinclairi* Parsley & Caster.
6) Iowacystidae Gill & Caster, *U.Ord.,* N.Am. (USA).

Iowacystis Thomas & Ladd, *U.Ord.*, USA (Iowa). (**I. sagittaria* Thomas & Ladd).

7) Belemnocystitidae Parsley, n.fam.[1] *M.Ord.*, USA.

Belemnocystites Miller & Gurley, *M.Ord.*, USA(Ky.). (**B. wetherbyi* Miller & Gurley).

Family MINERVAECYSTIDAE
Ubaghs and Caster, new family

Characters of *Minervaecystis*. *?U.Cam.*, *L. Ord.*

Minervaecystis Ubaghs & Caster, **new genus** [**Dendrocystites vidali* Thoral, 1935; M] [=*Dendrocystis* sp., Bather, 1913]. Large solutans with inflated, somewhat depressed theca, unequally biconvex, or possibly convexisubplanate; ovoid in profile, without lobation; thecal plates large, thin, nonimbricate, unornamented except near anus where they are granular; obverse plates somewhat smaller than reverse ones; flanks covered by regularly curving tessellation; facial differentiation gradual over the flanks. Arm and anus opposite; arm emerging abruptly, without plate gradation, from distal right margin of obverse face or slightly on flank; anus on proximal left in obverse face near posterior margin; arm long, narrow and very flexible in life, compressed, slightly angular aborally, presumably biserial and composed of opposite brachial plates, however, no aboral suture in evidence; confluent brachiole pairs imbricate distally; cover plates large, subequal in width to brachial flank, meeting in low arch over ambulacral groove, apparently not quite in series with brachials. Adbrachial circlet of plates forms imbricating collar or sheath about arm base; left, obverse, lateral sheath plate bearing 2 hemispherical prominences which presumably represent hydropore and gonopore. Anus covered by low circular "pyramid" of elongate subtrigonal plates. Stele very long and complexly zoned; proxistele inflated, slightly compressed, nearly terete, tetramerous and anomalocystitoid, comprising some 25 to 30 annular, telescopically imbricating rings, last 6 or 7 progressively diminishing in diameter toward mesistele and last tetrameres about twice as long as others, each tetramere bearing proximal external bourrelet or thickened lip which deeply imbricates beneath proximal adjacent tetramere, distal margins of tetrameres scalelike and feather-edged, also with low angular fold crossing each left reverse tetramere at mid-width in alignment with carina which diagonally crosses mesistele and becomes prominent keel on proximal dististele; mesistele short, mainly covered by 2 series of plates, one of which aligns with right obverse tetrameres and other, with left reverse, distally continuing as dististele dimeres-biseries (Fig. 378); alternate tetrameres aligned with 2 series of 2 or 3 distally diminishing plates which lie between dominant series of mesistele; mesistele zone short, and making distal transition from 4-part to 2-part symmetry; almost no mesistele in some specimens; dististele very long, narrow tail showing compression of double series of plates, and rotation (Fig. 378); proximal dististele composed of 2 or 3 long dimeres, suturing on extensiplane, reverse dimeres being carinate; mesial zone of long plates which show distal transition from dimerous to biserial, each of 3 proximal plates in this zone reversely bearing very high, comblike blade at about mid-length of postproxistele tail; distal dististele forms narrowly lanceolate, caudal fin composed of biserial plates, flattened in extensiplane (plane of zigzag suture); obverse fin plates asymmetrically rounded, reverse ones angular; stele elements all flexibly joined *?U.Cam.*, N.Am.(Nev.); *L.Ord.(Tremadoc.)*, Eu.(France).——Fig. 381. **M. vidali* (Thoral), Tremadoc., France; *1*, reverse face of holotype, ×2; *2*, oral detail of holotype arm and adbrachial pore plate, ×6; *3*, aboral view of holotype arm (note lack of aboral suture), ×6; *4*, anal pyramid of holotype, ×6; *5*, lateral view of mesistele and proximal dististele, ×4; *6*, obverse aspect of complete stele with cross sections at indicated places, ×3.5; *7*, detail of distal 2 pectinate dimeres of dististele, ×12 (Ubaghs, n). [See Fig. 378,*2*.]

Family DENDROCYSTITIDAE
Bassler, 1938

[=Dendrocystidae Bather, 1899]

Theca widely variable, but always asymmetrical; usually depressedly inflated; faces poorly or well differentiated; most plates tessellated and firmly joined; always some provision for expansion and contraction of viscera by flexible union of some thecal plates; arm and anus commonly on left side, but variable in position; proxistele fundamentally tetramerous and anomalocystitoid, but commonly modified by the addition of secondary platelets and possibly modified by tetramere fusing into narrow annuli; mesistele showing distal transition from four-part to two-part symmetry of plate series; obverse left and reverse right tetramere series distally continuous with biseries-dimeres of dististele. *M.Ord.-L.Dev.*

Dendrocystites Barrande, 1887, p. 142[2] [**Cystidea*

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[1] While this section of the *Treatise* was in preparation, *Belemnocystites* was discovered by Ronald L. Parsley of the University of Cincinnati to be a solutan and in Parsley's opinion a new family is essential for its inclusion. His more detailed analysis will appear elsewhere.

[2] Several authors have attributed new taxa published in *Système Silurien . . . de la Bohême: Classe de Echinodermes, Ordre des Cystidées* (v. 7, pt. 1) to Waagen, who served as Barrande's posthumous editor. In the introduction to the volume, Waagen took pains to deny any share in authorship; thus the new taxa presented therein belong to Barrande.

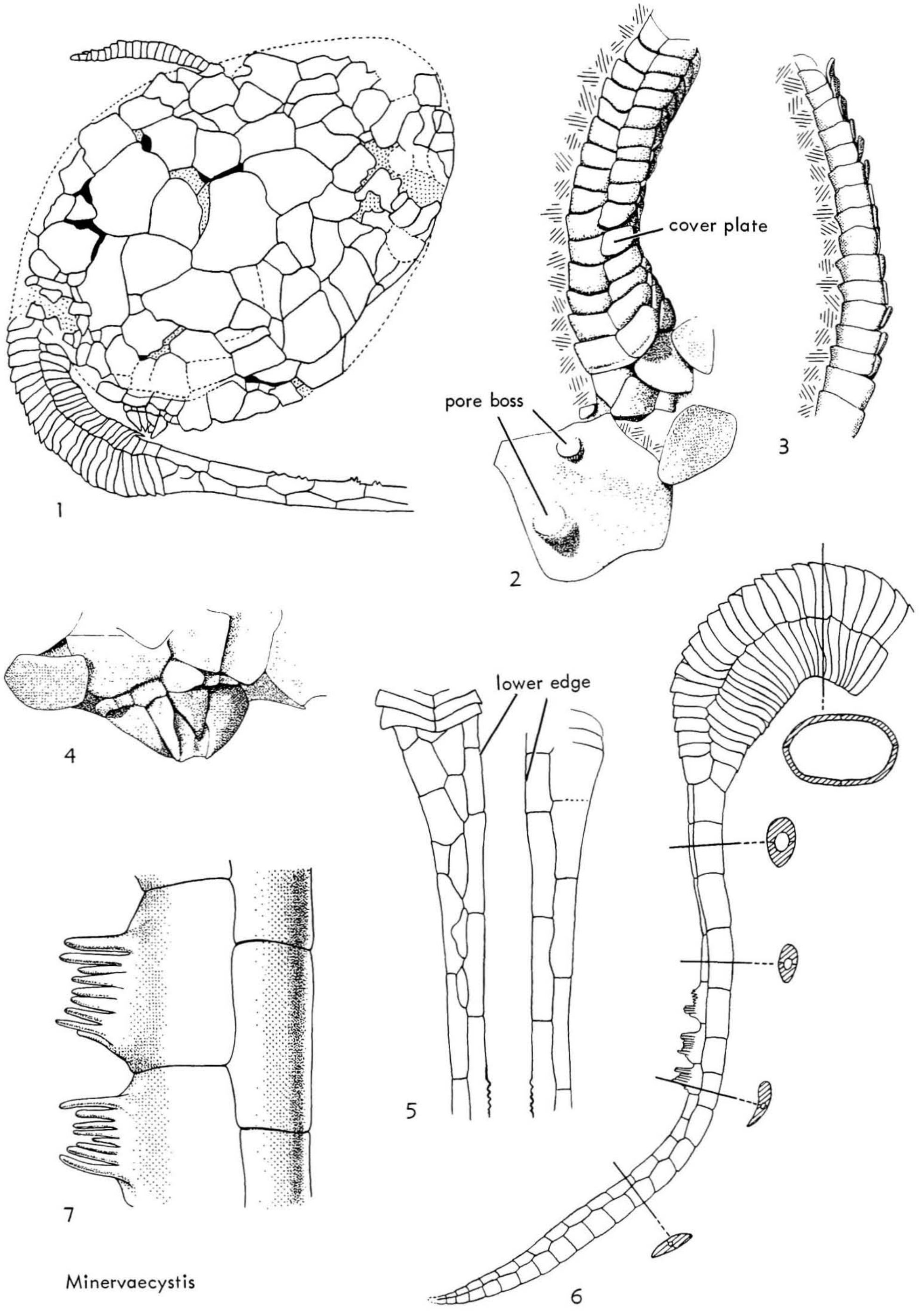

Fig. 381. Minervaecystidae (p. S606).

Sedgwicki BARRANDE, 1867, p. 179; OD] [=*Dendrocystis* BATHER, 1889, p. 268 (obj.) *(nom. van.)*]. (Diagnosis based on type species.) Large dendrocystitids with lobately triangular thecal outline, especially in usual flattened state; theca depressedly inflated, obverse and reverse faces differentiated both in configuration and in plate details, obverse face usually convex and topographically complex, reverse flat to concave and simple; thecal margins usually rounded, may be subangular or sutural; position of arm, anus and thecal lobation asymmetrical; prominent, angular left proximal lobe, but only very faint lobate rounding on right side; left lobe composite, with large angular preanal lobe and rounded anal lobe *(s.s.)*; distal margin moderately lobate. Arm commonly distal and sinistral, emerging from obverse thecal face; may be nearly axial and in some individuals dextral. Anus marginal and usually on posterior lateral face of left proximal lobe, rarely on right side, when large proximal lobe is also dextral. Thecal plates many, tessellated, firmly united in life (not imbricated as in usual crushed specimen), except for localized flexible junction, these plates about equal in size and number on both faces, relatively large and few in juveniles but abundant and smaller in adults; plate increment mainly by sutural intercalates (rosetting). Obverse face somewhat swollen in distal third, with broad oval tumescence of flexibly joined, large, ornamented, polygonal plates in widest proximal part of theca (apparently to accommodate expansion and contraction of viscera); larger movable plates bearing central boss and radiating costae; ribs increase in width and elevation toward plate margins, smaller (younger) plates bearing low central umbo and peripheral nodes, latter increasing in prominence and extending toward center of plate with increase in plate size. Mobile tumescence proximally bordered by tightly fused girdle of adsteleal plates and distally by bounding arc of unornamented, firmly united thecal plates, each of which upwardly geniculates at low angle toward tumescent area, and on inner surface bears low bounding ridge on line of geniculation. This ridge can be traced across plates of internal obverse face from preanal lobe to widest part of right proximal lobation. [The bounding ridge and geniculated plates serve in complexly preserved and incomplete specimens as an excellent key to the obverse face.] Brachial orifice nearly circular and surrounded by constant number of adbrachial plates, one on left side bearing wartlike node which is apparently madrepore-hydropore. Adbrachials, like entire distal thecal plates, firmly joined in life, with low flange developed adjacent to orifice; between adbrachials and tetramerous arm, several circlets of small platelets intervene in largest specimens and are inconspicuous in juveniles. Marginal anus covered above by rounded lappet which makes outline of anal lobe *(s.s.)*; center of lappet occupied by ovate-subtrigonal, convex suranal plate (BATHER's "sugarloaf plate"); this is distally margined by arc of small, polygonal plates, and laterally-reversely by radiating narrow plates (probably periproctal); preanal lobe very prominent and angular. Arm slightly compressed and longer than theca; aboral suture between brachial biseries apparently open; brachials about twice as wide as cover plates, with which they are essentially in annular series; cover plates meeting in zigzag adorally. Stele long and axially differentiated into 3 zones: proxistele basically anomalocystitoid, but in adulthood many small platelets are developed so as to conceal juvenile 4-part symmetry. [This is especially true of *Dendrocystites* where young forms show tetrameres (or octameres) between which platelets form on all sides.] The ephebic proxistele is an alternating series of 6 to 8 larger and smaller rings of platelets, the first being composed of larger firmly united elements, and the second of many plates loosely joined. Despite rosetting, the mesistele bears evidence of tetramere series, 2 of which persist distally into the dimerous series; 2 alternates diminish in size and disappear in length of the mesistele. Here, as in *Minervaecystis,* the dististele is proximally dimerous and distally biserial; plates of distal extremity loosely joined, and faceted so as to permit some prehension; dististele may be somewhat compressed, and reversely keeled. *M.Ord.,* En.(Boh.), questionable elsewhere.——FIG. 382, 383. **D. sedgwicki* (BARRANDE), M.Ord., Boh.; 382, rubber molds of type and topotype specimens in National Museum, Praha (all photos Caster, n); 382,*1,* oblique view into undeformed proximal interior of obverse thecal face (proxistele insertion as in life, anal lappet at right) showing tessellation of plates and rigidity of test (BARRANDE type), ×2; 382,*2,* obverse view of immature form in which proxistele tetrameres are in process of fractionation (note rosetting of proximal mesistele), ×2; 382, *3,* reverse view of interior surface of obverse plates showing usual imbrication of plates due to compression during fossilization (note hydropore pustule on adbrachial plate, multiple platelets of proxistele, and carination of axial series of mesistele) (BARRANDE type), ×1.5; 382,*4,* obverse view of topotype with complete stele which lacks evident keeling and shows distal dimere sutures beveled as for some degree of prehension (Barrandium, Praha), ×1; 382,*5,* obverse view of young individual with short tetramerous proxistele and tessellated thecal plates which are relatively few and very large (topotype, Barrandium, Praha), ×2; 383,*1-3,* obverse views of new material (Narodni Museum, Praha) showing calcareous plates intact, ×1 (Caster, n.).——FIG. 384,*2;* 385. *D. barrandei* BATHER, Low.M.Ord., Boh.; 384,*2,* specimen figured by BATHER (1913), ×1.7; 385, rubber mold of part of slab covered by oriented specimens in usual state of preservation of homoio-

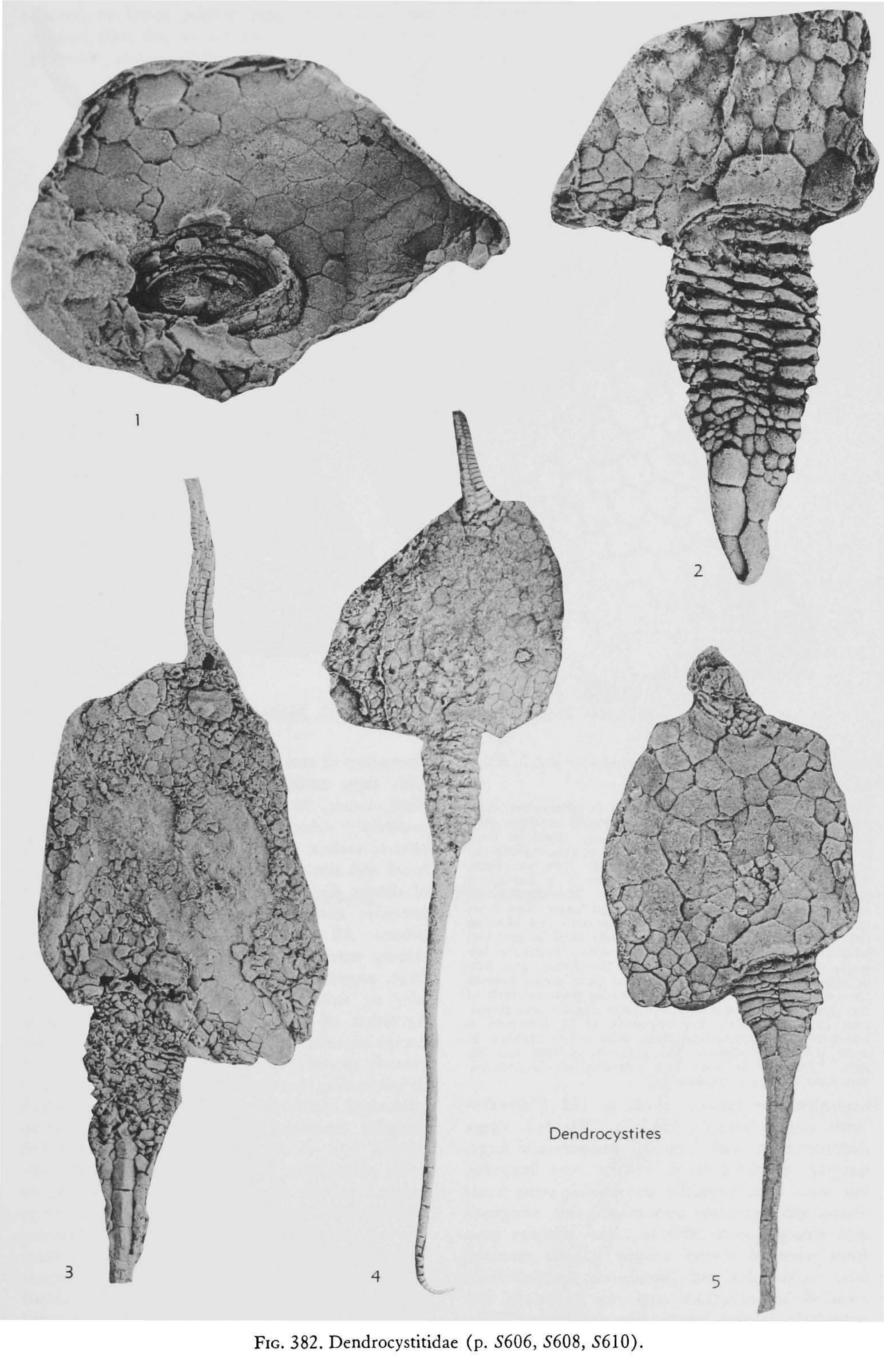

FIG. 382. Dendrocystitidae (p. *S*606, *S*608, *S*610).

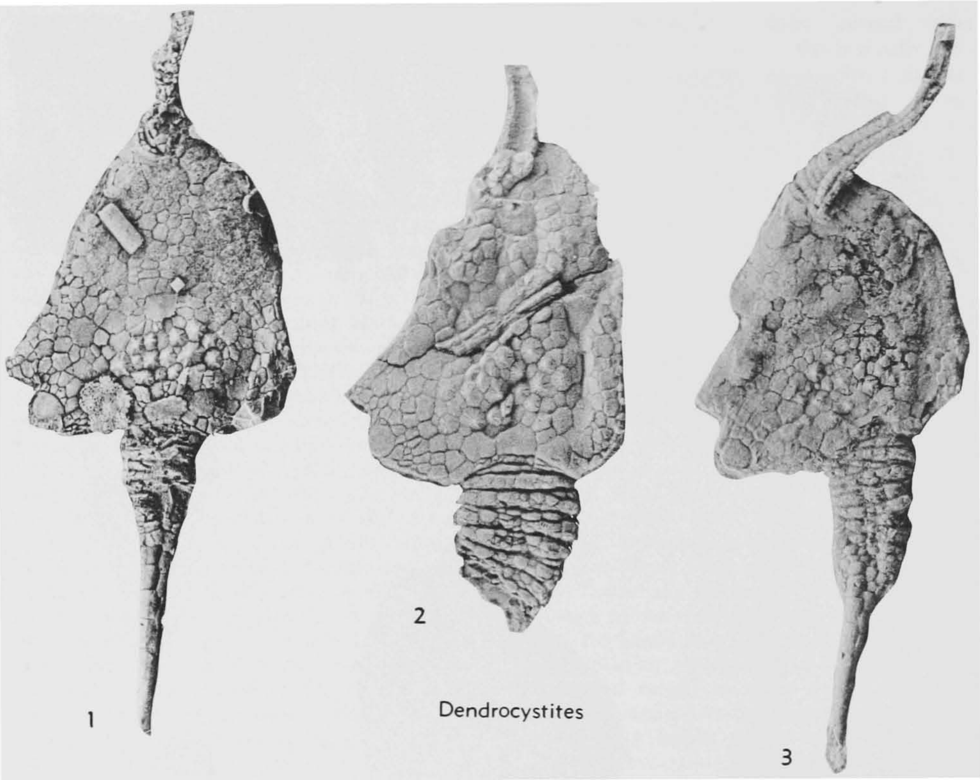

FIG. 383. Dendrocystitidae (p. S606, S608, S610).

steles (note tetramerous proxisteles), ×2.7 (Caster, n). [See Fig. 387.]

[Although it shares several traits with *Dendrocystites sedgwicki,* the form designated as *D. barrandei* is more pyriform, less lobate, and more symmetrical. Also, its faces are less well differentiated and more of its thecal plates are loosely articulated, a maximal tumescent zone not being distinguished. Probably the species named by BATHER is generically distinct from *Dendrocystites.* The thecal plates of *D. barrandei* are relatively fewer and larger than those of *D. sedgwicki,* with rosetting unimportant and platelets few. The arm of *D. barrandei* is nearly axial in position, with large geniculating adbrachials which imbricate laterally to form an adbrachial sheath. No obvious anal lobe or lappet is seen and a single subanal plate occurs beneath the anus on the reverse side or rounded posterior wall of the theca. The preanal lobe is equally angular and prominent in both species. The proxistele of *D. barrandei* is tetramerous and anomalocystitoid, with a few platelets in some individuals between the tetramere sutures and annuli. The mesistele bears clear indication of distal transition from tetrameres to dimeres.]

Dendrocystoides JAEKEL, 1918, p. 123 [**Dendrocystis scotica* BATHER, 1913, p. 391; M]. Large dendrocystitids with hornlike processes and large, unequal, proximal lobes. Outline very irregular, but main theca generally trapezoidal; some hourglass-shaped; arm and anus on left side, marginal; arm emerges from obverse distal margin; anus from posterior reverse margin of left proximal lobe; subangular and protuberant preanal lobe; rounded inconspicuous anal one. Obverse face irregularly convex; reverse face nearly flat. Theca commonly much constricted just proximal of emergence of arm and antibrachial process. Usually with large antibrachial horn arising from right distal corner, its dimensions highly variable, but commonly subequal to arm; it may arise from obverse surface or distally; commonly very broad-based and almost lobelike; supplementary processes of similar dimensions may occur on distal left or laterally; antianal lobe may be extended in a process. All processes plated like theca, and containing extension of thecal cavity. Thecal plates large, angularly polygonal and nonimbricating in life; no striking differentiation in size or configuration of two faces; surface finely granular except on reverse face near anus, where plates are coarsely granular or pitted. Adbrachial plates rise as imbricating sheath about base of arm; left lateral adbrachial bearing complex tumescence which probably represents hydropore. Arm long, compressed and flexible; aboral suture ligamental; cover plates about half as wide as brachials; ambulacral groove narrow, cover plates standing at high angle over it and meeting adorally in zigzag, but in series with brachials to which they articulate; cover plate-brachial suture line sharply depressed; internally each cover plate grooved for its whole width. Anus may have been sphincterally closed and slitlike; its region on posterior surface crowded with very long and narrow periproct plates; anus floored by broad reverse lappet in which ovate subanal plate lies to one side of concentration of periproct plates. Stele long and differentiated. Proxistele tetramerous and anomalocystitoid, with many small polygonal integumentary plates in zone of flexible tissue between tetramere rings; best

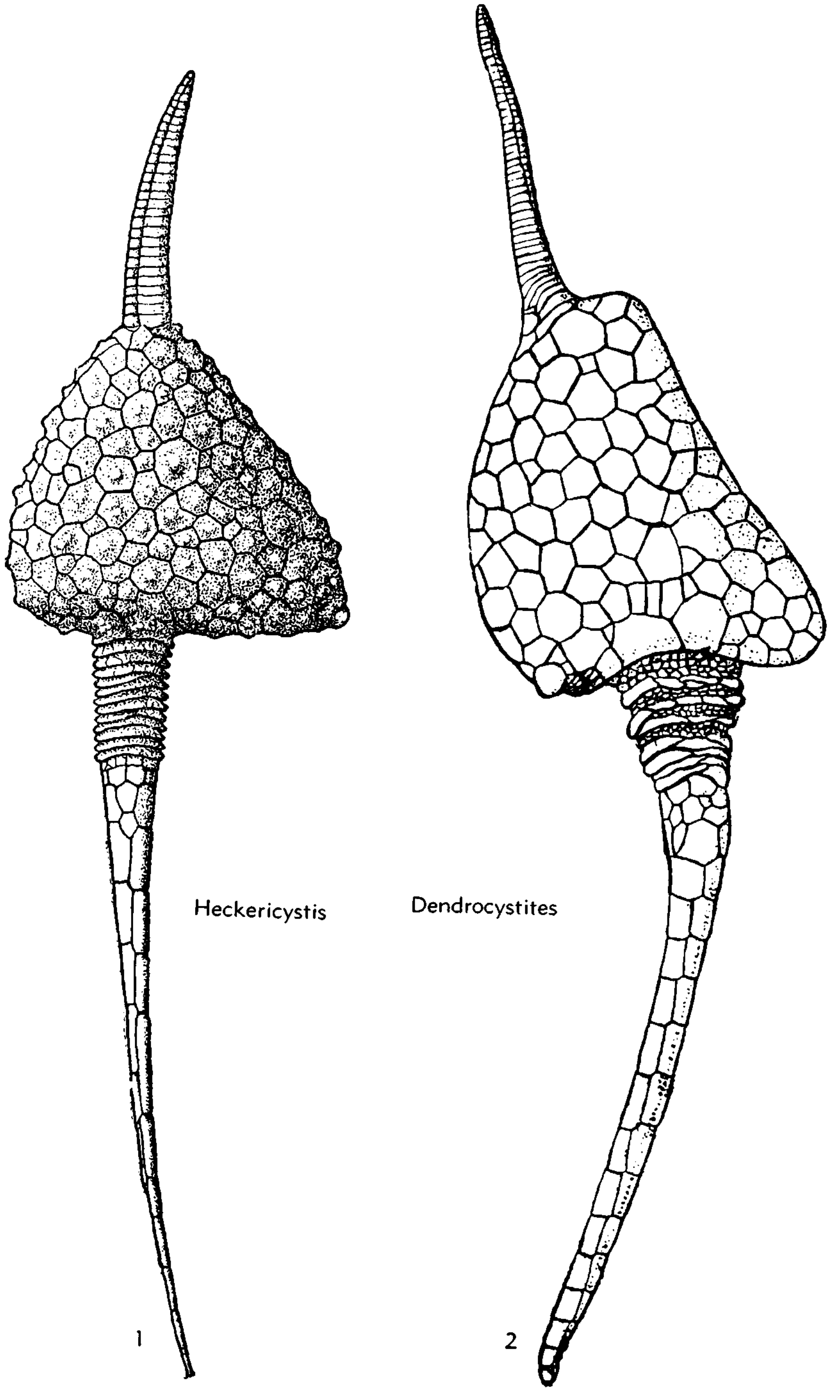

Fig. 384. Dendrocystitidae (p. S606, S608, S610, S613).

seen in specimens preserving inside view of tetrameres. Externally proxistele meres may be smooth, thin and almost scalelike, or very much thickened and complexly, radially rugose in completely unique manner. Mesistele reminiscent of *Minervaecystis,* with biseries of dististele correlating across mesistele with tetrameres in same manner as in that genus. Dististele very long and narrow, terete and composed of long dimeres proximally; these shift to alternating position distally; actual end of stele not seen. Dimere orientation obverse and reverse; suture in extensiplane. *U.Ord.,* Eu.(Scot.).

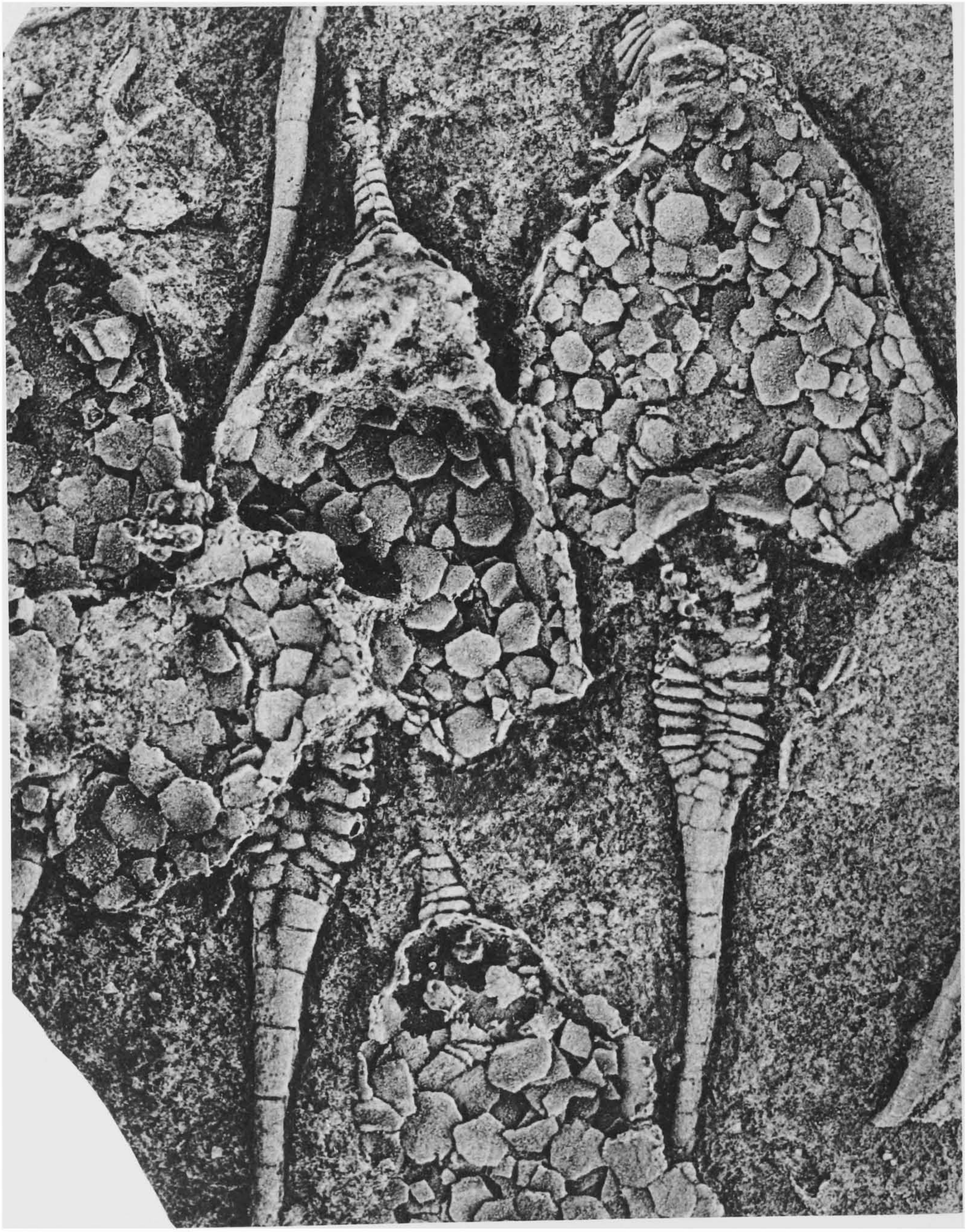

FIG. 385. *Dendrocystites barrandei* BATHER (Dendrocystitidae) (p. S606, S608, S610).

——FIG. 386, 387. **D. scoticus* (BATHER); 386, reverse face of BMNH E23700, fairly complete but with somewhat disarranged thecal plates, ×2.1 (Caster, n; drawing by E. A. Dalvé); 387, *1-6,* rubber molds of topotypes, all from BMNH; 387,*1,* reverse face showing usual imbrication of plates induced by compression during fossilization, with complete "antibrachial" horn, large hydropore pustule on right side of figure; arm slightly twisted so as to conceal aboral suture of brachial biseries (E23700), ×2.2; 387,*2,* reverse view showing proximal plates in tessellated life position (note granular ornament on these plates) imbricate periproct plates on posterior margin of anal lobe at right, hydropore pustule apparently with 2 pores, proximal stele unornamented (E5732), ×2.2; 387,*3,* arm detail, obverse view with adbrachials in place, hydropore pustule prominent (E5823), ×2; 387,*4,* reverse view of highly ornamented proxistele (note also many platelets inside lumen) (E5827), ×2.5; 387,*5,* reverse view of ornamented proxistele and interior surface of obverse tetrameres showing bourrelets (note axial rotation of keel in mesistele) (E5719), ×2.2; 387,*6,* reverse view of distal theca and arm (note biserial meeting of cover plates) (E5822), ×2 (all Caster, n). [See Fig. 376, 379.]

Heckericystis GILL & CASTER, 1960, p. 16 [**Dendrocystites kuckersiana* GEKKER [HECKER], 1940, p. 23; M]. Theca inflated, asymmetrically trigonal in profile; probably somewhat depressed, proximal subangular anal lobe; arm distal; anus at apex of anal lobe and apparently closed by or beneath prominent mammelon (or "sugarloaf plate"); thecal plates small and polygonal, each with central prominence; nothing known of facial or regional thecal differentiation. Arm biserial and moderately long; stele long and terete throughout, differentiated into 3 zones. Proxistele sheathed in many narrow elevated rings, probably tetramerous, but no sutures reported; intervening zones apparently integumentary; mesistele shown as composed of 3 circlets of polygonal platelets decreasing in number in each ring distally and suggesting transition from tetramerous to dimerous; dististele attenuate, sheathed in dimeres which are laterally opposed proximally, and obversely-reversely in distal region. *M.Ord. (Kuckers),* Est.——FIG. 384, *1.* **H. kuckersiana* (GEKKER) [HECKER], ×1.7 *(43).*

Dehmicystis CASTER, **new genus** [**Dendrocystites (Dendrocystoides?) globulus* DEHM, 1934, p. 20; M]. Spherically inflated (or moderately depressed), appearing circular when crushed; thinly plated, unornamented; anus large, circular and proximal, covered by large pyramid of elongate trigonal imbricating plates; some periproctal plates between anal pyramid and adanal thecal plates. Proxistele anomalocystitoid, very flexible; dististele long and dimerous. [GILL & CASTER (1960) tentatively assigned this species to *Rutroclypeus,* but further examination of the holotype reveals a large circular anal area, and strongly supports DEHM's original idea that the theca was inflated in life; hence the new assignment.] Only incomplete holotype known. *L.Dev. (Bundenbach),* Eu. (Ger.).——FIG. 388,*1,2.* **D. globulus* (DEHM); *1,* original figure, ×1.1 *(34)*; *2,* drawing from

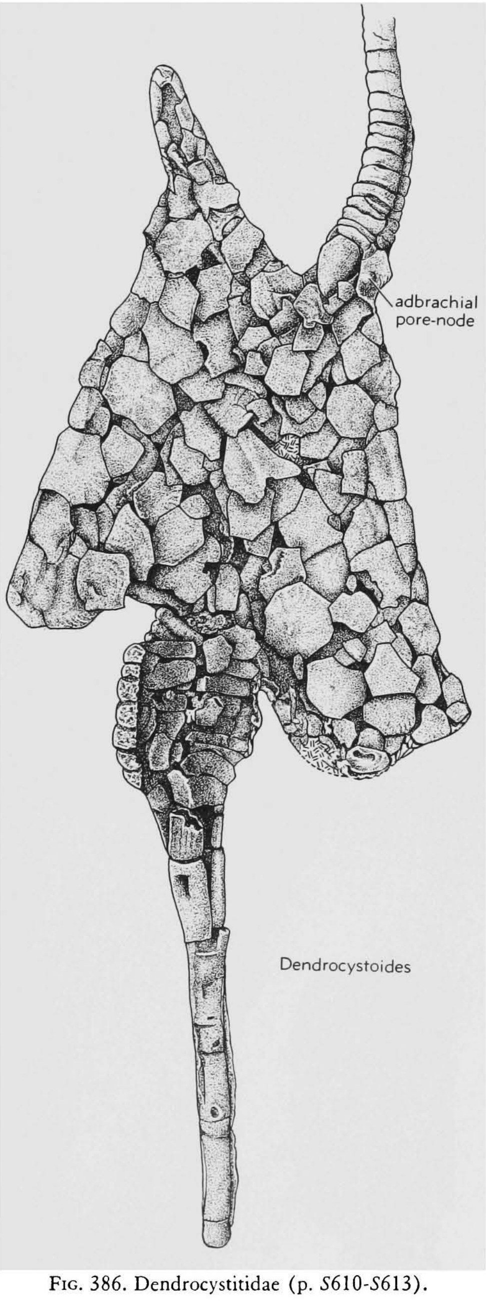

FIG. 386. Dendrocystitidae (p. *S*610-*S*613).

photograph of holotype and only known specimen (note anal pyramid), ×1.4 (Caster, n).

Family GIRVANICYSTIDAE Caster, new family

Solutans covered by relatively few large plates rigidly fused into two opposable faces united by flexible peripheral suture on extensiplane; prominent crest and spines on reverse face; proxistele anomalocystitoid, with many small platelets on proximal exterior of tetrameres. *U.Ord.*

Girvanicystis Caster, **new genus** [**G. batheri* Caster, **new species**; M]. Large, obliquely cordiform

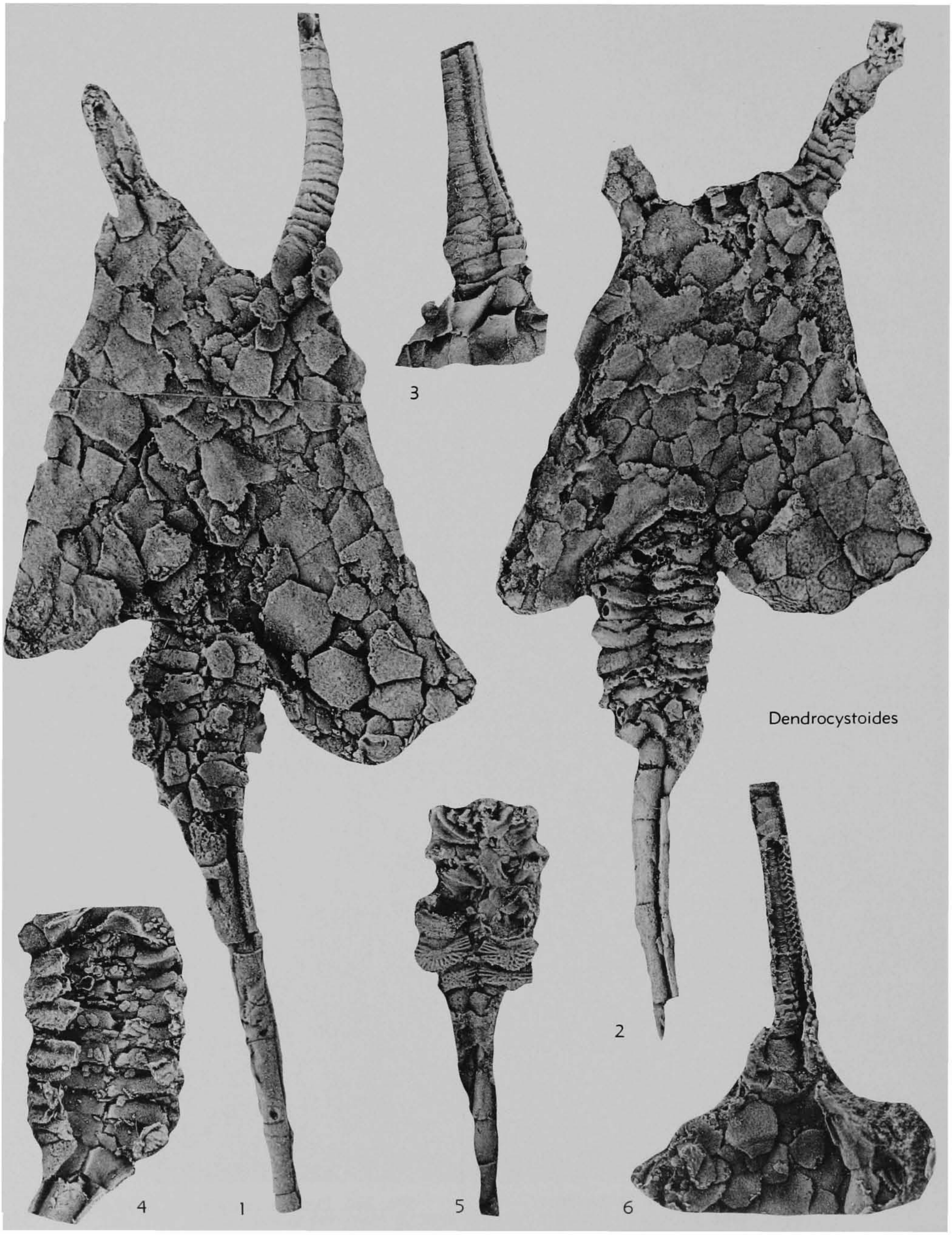

Fig. 387. Dendrocystitidae (p. S610-S613).

dendrocystitid, prominently and asymmetrically trilobate, with very large, unequal, rounded proximal lobes, anal one being larger; right anterolateral rounded lobe which extends well on distal side of level of arm insertion. Arm and anus on left side; anus well within reverse face of anal lobe; arm inserted on perimeteral suture between 2 thecal faces and essentially on thecal axis of balance. Deep rounded proximal re-entrant for insertion of stele. Thecal profile complex, but in general subplano-convex, obverse face being far less inflated than reverse one; marginally, except in immediate vicinity of arm base, both faces subplanate (perhaps slightly concavo-convex), in broad zone and apparently nearly in contact in life; obverse face apparently rose in broad axial arch, whereas reverse one shows distinct zones of tumescence: central area of anal lobe distended and bearing periproct with very high, asymmetric tumescence on distal side of this on left of thecal axis and extended to distal margin where it formed vertical distal wall of theca; beneath arm

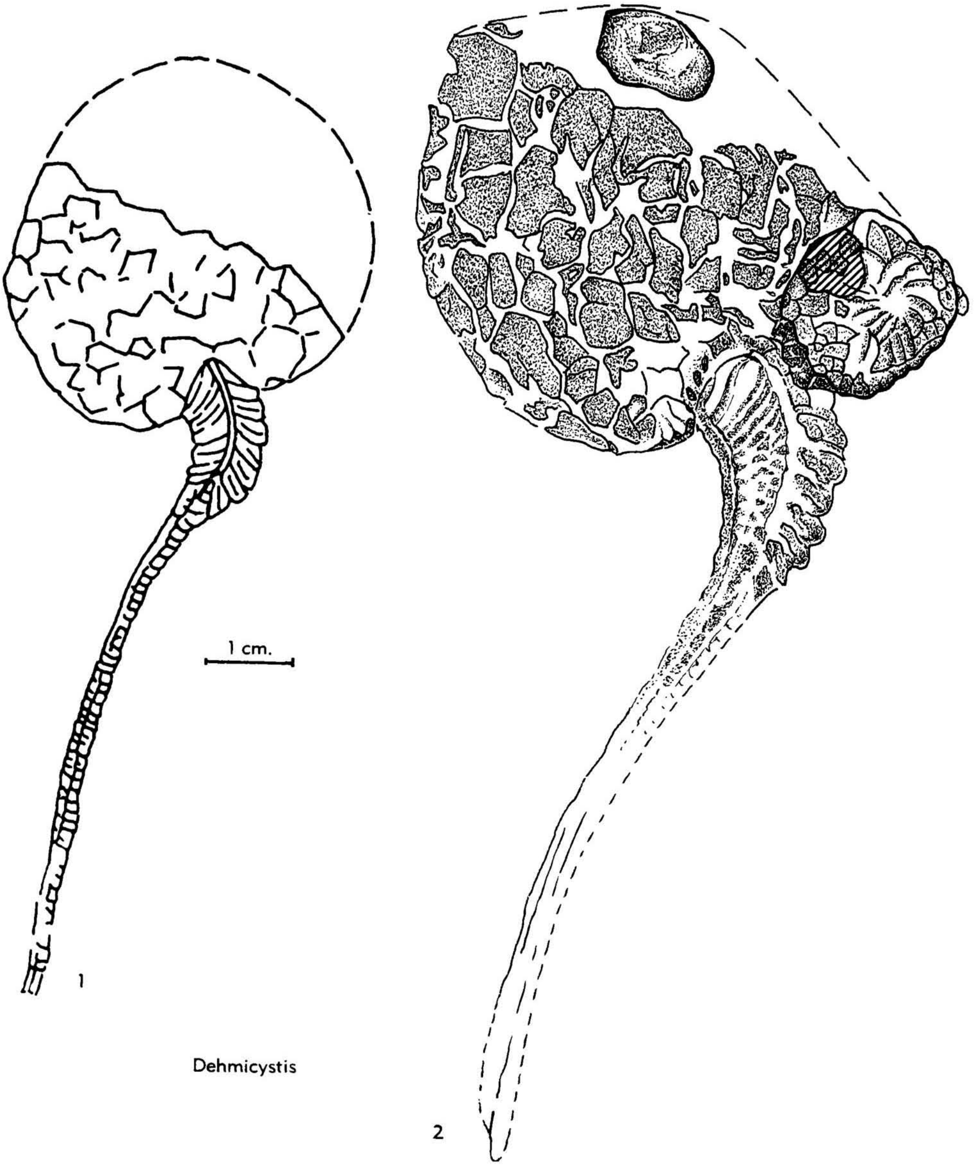

Fig. 388. Dendrocystitidae (p. S613).

insertion reverse theca was bowed angularly and sharply. [Thecal surfaces appear to have been largely rigid in life, their contact sutural and integumentary; with obverse face narrower and shorter than reverse one, and with something of an opercular nature; both perimeters are thickened considerably and in such way that they articulated in pillbox manner with obverse margin lying within the reverse one and fitting into a smooth deep groove just inside the thickened margin of the reverse face.] Thecal plates extraordinarily large, those of reverse side being larger and (discounting periproct area) fewer than obverse. Tight fusion of plates of both faces manifest and breakage does not always seem to follow old suture lines. On right distal lateral side of reverse theca, just proximal of anterior lobe, several large plates fuse to form radially broadly pleated stellate plate of very large size; single large axial adsteleal plate present in both faces. Aside from the marginal thickenings of the 2 faces and surface granulation, scattered hollow excrescences are the only other "ornament"; several plates in the distal and right distal area of the obverse face each bear a high sharp or blunt broad-based spine; on the obverse proximal region the adsteleal and several other plates bear groups of small warts or tubercles. Anus in central area of reverse face of anal lobe, covered by broad, low circlet ("pyramid") of elongate, lunate, imbricating plates; this in turn is surrounded by circle of many relatively small polygonal plates, probably loosely articulated also in life, a periproct zone; the whole is set within a subcircular foramen through the large plates which firmly invest this part of the theca. Arm emerging on extensiplane and from facial suture, but with brachial orifice more excavated in vertical wall of obverse plates in distal region than in obverse "opercular" surface; apparently 4 large plates complete adbrachial series, those of obverse side sutured (not imbricated) and showing transverse marginal excavation to accommodate oral surface of arm; adbrachial margin flanged; near flange on left obverse adbrachial, tiny perforation with collared neck may represent hydropore. Proxistele tetramerous, anomalocystitoid, with imbrication of ring pairs on both obverse and reverse axial sutures; imbricate telescoping of rings sharply defined, each ring bearing circular median crest or flange and showing on distal postflange margin many small polygonal platelets, apparently originally embedded in investing integument (but no platelets have been observed inside proxistele). Mesistele showing usual dendrocystitoid transition from tetramerous to dimerous condition, exhibits slight median reverse keel and passes into dististele within short distance; dimeres are opposite there for most of length and are sutured in extensiplane; disistele relatively stout and long. *U.Ord.*, Scot. ——FIG. 389, 390. **G. batheri*; 389, reverse face of holotype, presumably upwardly oriented in life (note adbrachial spinous hydropore) (BMNH, Gray Coll., 28473), ×3.4; 390, obverse face of paratype (obverse plates coarsely stippled, interior of reverse plates finely so) (note flanged hydropore with radii on interior of adbrachial plate which bears spine in surface) (BMNH, Begg. Coll., E5791), ×3.1 (all Caster, n). [See Fig. 373, 374.]

Family RUTROCLYPEIDAE Gill & Caster, 1960

[Rutroclypeidae GILL & CASTER, 1960, p. 22]

Solutans with nummuloidally depressed thecae, with or without prominent lobation, covered by many small polygonal plates which may be smooth, centrally umbonate, or prominently spinose; arm nearly axial, emerging from obverse face, no other facial differentiation; proxistele anomalocystitoid, dististele dimerous, with suture in symmetry plane. *L.Dev.*

Rutroclypeus WITHER, 1933, p. 18[1] [*emend.* GILL & CASTER, 1960, p. 30] [**R. junori*; M]. Thecal outline circular, nummuloidally depressed, giving impressions of polyplated (commonly hexagonally) sphere which has been pressed into nummuloidal mold; lobation may develop *(R. withersi)*; thecal margins vertical, coinlike, with plates and sutures falling as they may without any evident adjustment to form, plates small and usually bearing umbo, boss, or elongate solid spine in type species (although holotype is sparsely spinose). Juveniles show relatively fewer, larger, and less spiny plates than adults and they are more fusiform in outline, as well as possibly less depressed. Plate increment in *R. withersi* (possibly mainly on its lobations) is by exaggerated rosetting (see *Dendrocystites sedgwicki*) and hundreds of tiny platelets appear around larger primary plates, each with miniscule spine, thus creating appearance recalling miliary spines about bosses of echinoids. [These zones of small plates seem to have been flexibly joined and may be a form of facial differentiation. The spines may extend onto the proxistele, one to a plate, and apparently only on the obverse face; a single median proximal one on the mesistele has been noted.] Adult arm short and inserted distally to left of axis and within obverse disc; no adbrachial thecal plate differentiation noted, but some evidence indicates that at least one adoral plate bears swollen hydropore tumescence like that of Dendrocystitidae. Juvenile arm proportionately shorter and broader than in adults and axially inserted or nearly so. Anus unknown but must be marginal (slight marginal swelling adjacent to stele may mark spot). Stele long and differentiated; proxistele tetramerous, triangular

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[1] Originally described as a xiphosuran arthropod.

in outline, and flatly anomalocystitoid (more inflated in juveniles); mesistele very short and conical, its plating recording transition from proximal tetramerous to distal dimerous arrangement (see *Minervaecystis*); dististele long and narrow, becoming spatulate distally in some specimens, with dimeres opposite apparently throughout its length and somewhat depressed, suture is in symmetry plane. *L.Dev.,* Australia(Victoria).——FIG. 391,*1*. **R. junori;* diagrammatic sketch of holotype,

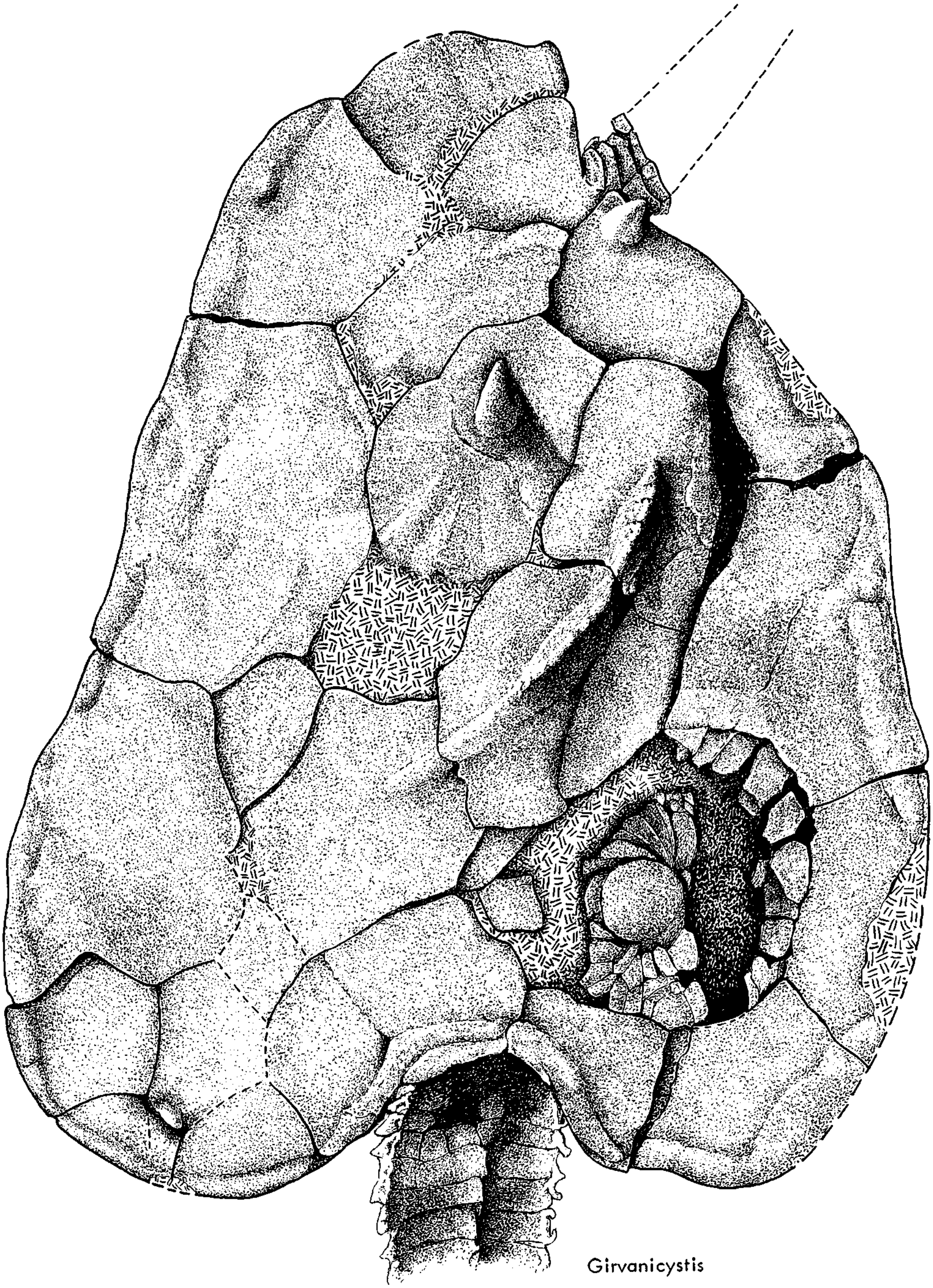

FIG. 389. Girvanicystidae (p. *S*614-*S*616).

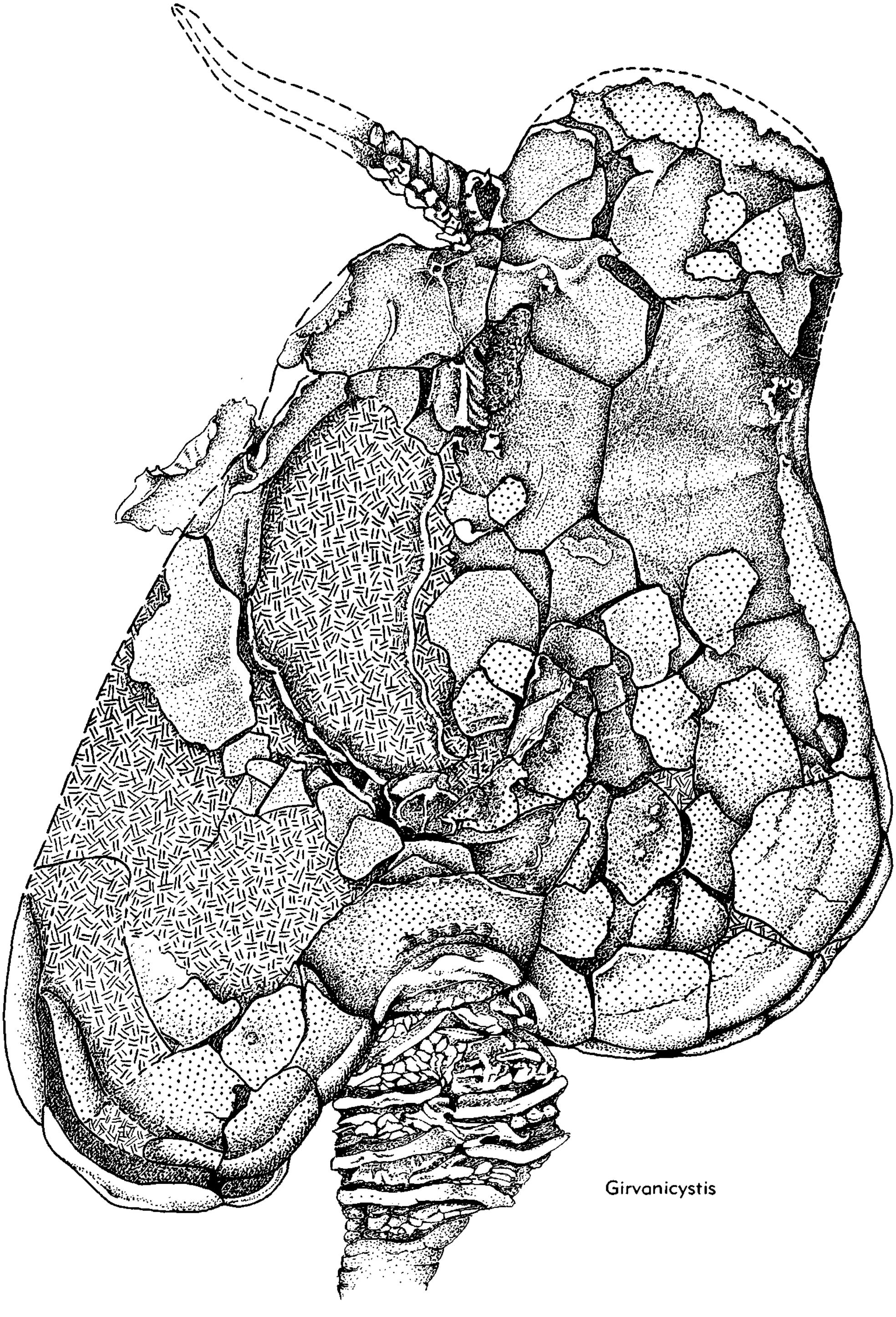

FIG. 390. Girvanicystidae (p. S614-S616).

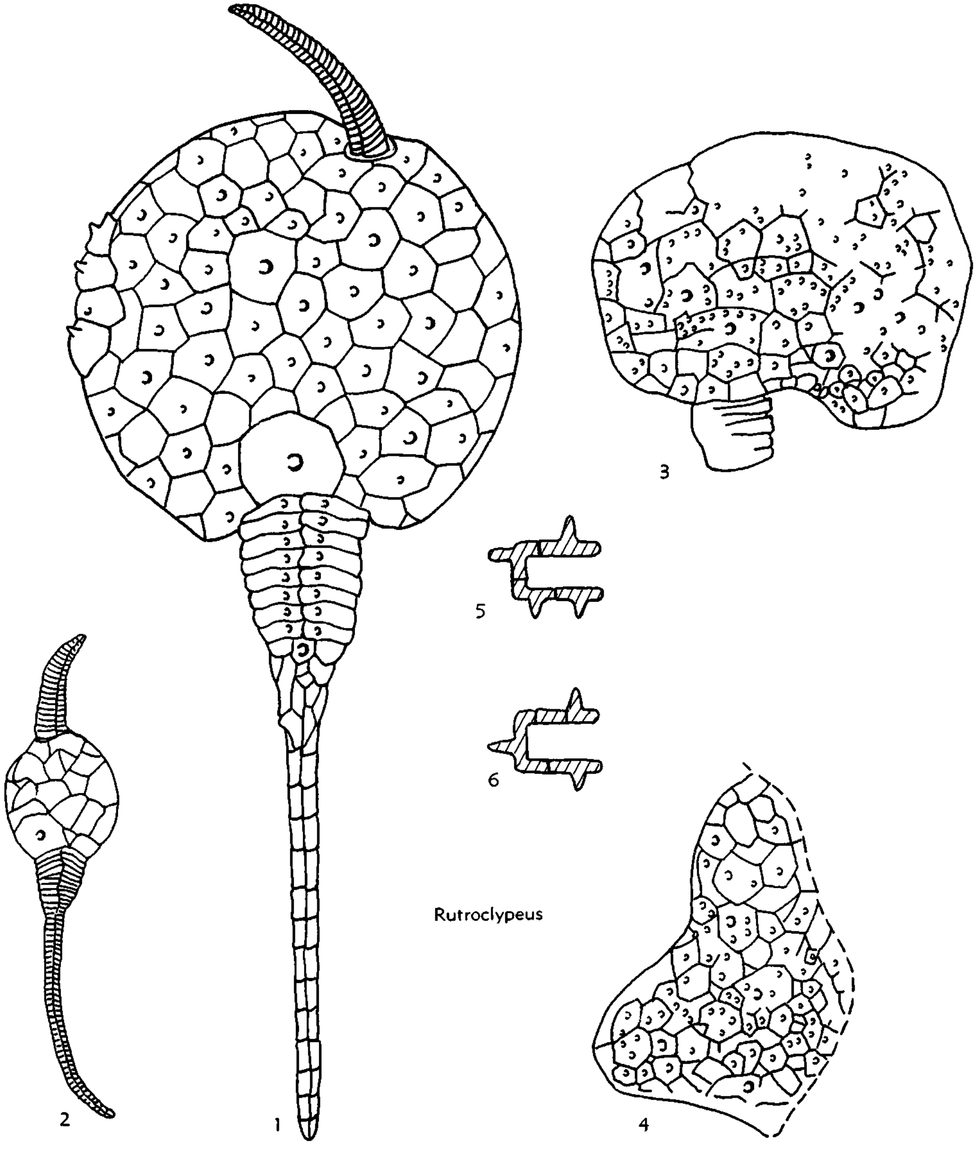

Fig. 391. Rutroclypeidae (p. *S*616-*S*617, *S*619).

×1.7 (Caster, n).——Fig. 391,*2*. *R. victoriae* Gill & Caster, somewhat crushed juvenile specimen showing its relatively few larger plates and large arm, ×1.7 (Caster, n).——Fig. 391,*3-6*. *R. withersi* Gill & Caster; *3,* specimen showing thecal lobation (?anal) and miliary granules, ×1.7; *4,* partial theca (holotype) with pronounced (?anal) lobe, ×1.7; *5,6,* diagrammatic cross sections of thecal periphery showing nummuloidal geniculation of plates, enl. (all Caster, n).——Fig. 392. *R. wilḳinsi* Gill & Caster; stereoscopic views of antanal side of theca showing spines on all of its plates but none on proxistele, ×1.8 *(43).*

Family SYRINGOCRINIDAE Parsley & Caster, 1965

[Syringocrinidae Parsley & Caster, 1965, p. 115]

Elongate, ovoid, rigid and inflated theca; facially differentiated, convexi-planate (or inferiorly concave), covered mainly by few

FIG. 392. **Rutroclypeus wilkinsi* GILL & CASTER (Rutroclypeidae) (p. S616-S617, S619).

large plates, few large infracentrals, many small, flexibly joined supracentrals in ovoid area, and possibly partially surrounded by larger supracentrals; anus unknown. Arm long, terete, emerging from distal left margin of theca. Stele axially differentiated; proxistele anomalocystitoid, inflated; mesistele long, petiolate to lanceolate dististele; proximal mesistele unit an annulus; remaining surface with three series of plates, two of which are in series with dististele biseries and third in median position, composed of distally diminishing series of long plates; dististele biserial, becoming nearly dimerous at end with suture in extensiplane, along which considerable compression forms finlike structure, reverse dististele plates keeled and spinose. *M.Ord.*

Syringocrinus BILLINGS, 1859, p. 65 [**S. paradoxicus*; M]. Characters of family. [The pseudostylocone of the mesistele and proximal dististele is an especially typical feature. Restorations (Fig. 393) depict all available information on this genus.] *M.Ord.*, Can.(Ont.).——FIG. 393,*1*. *S. sinclairi* PARSLEY & CASTER; restorations based on type specimens; *1a*, obverse face with cross sections of stele indicated in life orientation, ×3.8; *1b*, reverse face, ×3.8 *(69)*.——FIG. 393,*2*. **S. paradoxicus*; views of holotype; *2a*, BATHER's (1913) drawing of stele as known to him, ×1.9; *2b*, present condition after bit of preparation, ×1.9 *(43)*.

Family IOWACYSTIDAE Gill & Caster, 1960

[Iowacystidae GILL & CASTER, 1960, p. 20]

Trigonal, much-depressed solutes with advanced differentiation of thecal plates, including rigid frame of marginal plates and characteristic supracentral and infracentral plates; arm on distal right side of obverse face; anus marginal at proximal left corner, closed by bivalved boss. Stele somewhat depressed, with short tetramerous proxistele which is narrowly annular, inconspicuous mesistele, and dominantly biserial (not dimerous) disistele with suture in symmetry plane. *U.Ord.*

Iowacystis THOMAS & LADD, 1926, p. 6 [**I. sagittaria*; M]. (Diagnosis based on restudy of type materials by PARSLEY & CASTER, 1965.) Thecal outline in form of isosceles triangle, with rigid marginal framework and high facial differentiation; facial surfaces parallel, one with few rigidly united large infracentrals, highly ornamented, and other with many large supracentrals which are flexibly joined together and also highly ornamented; single large median adsteleal plate on

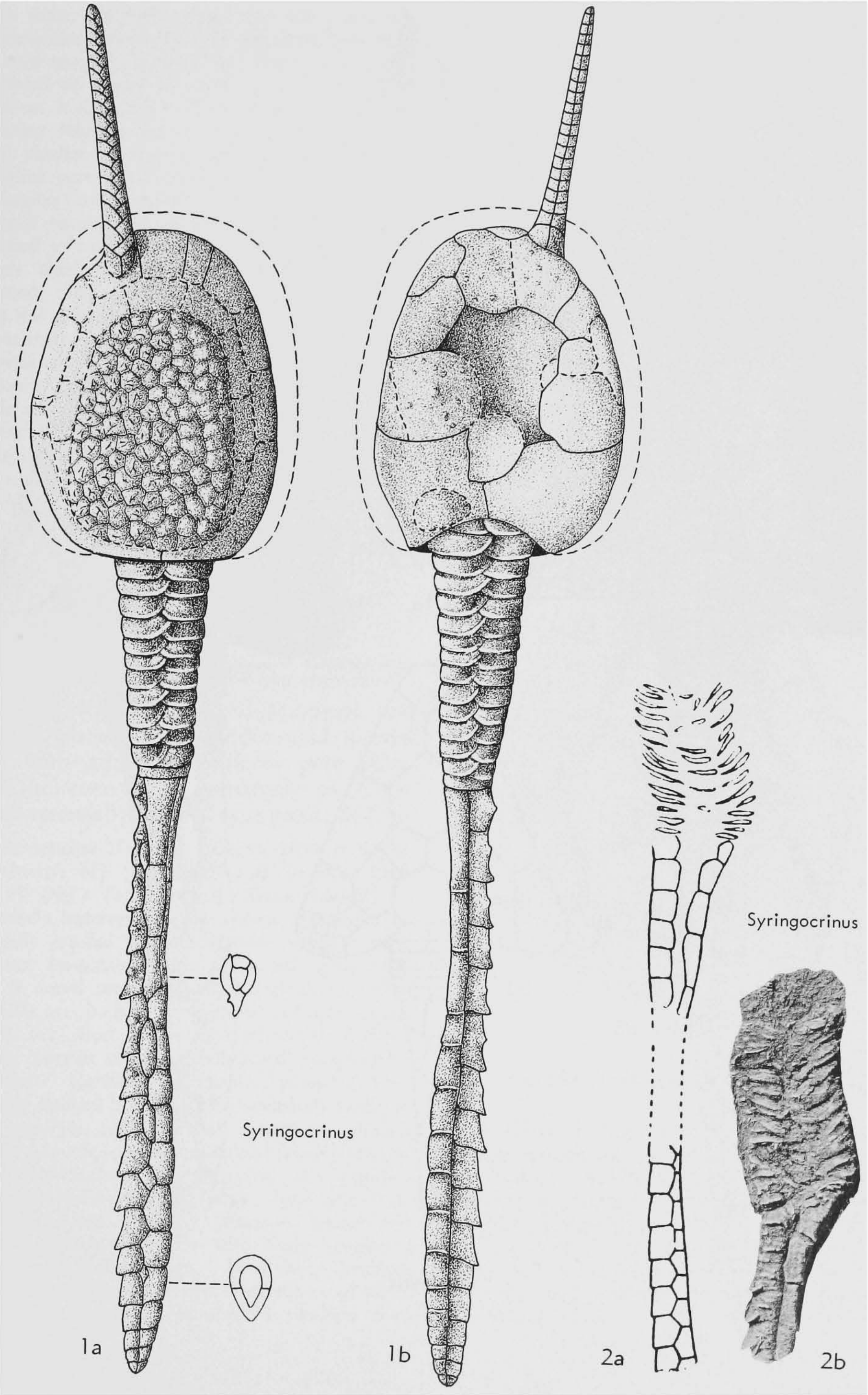

FIG. 393. Syringocrinidae (p. S620).

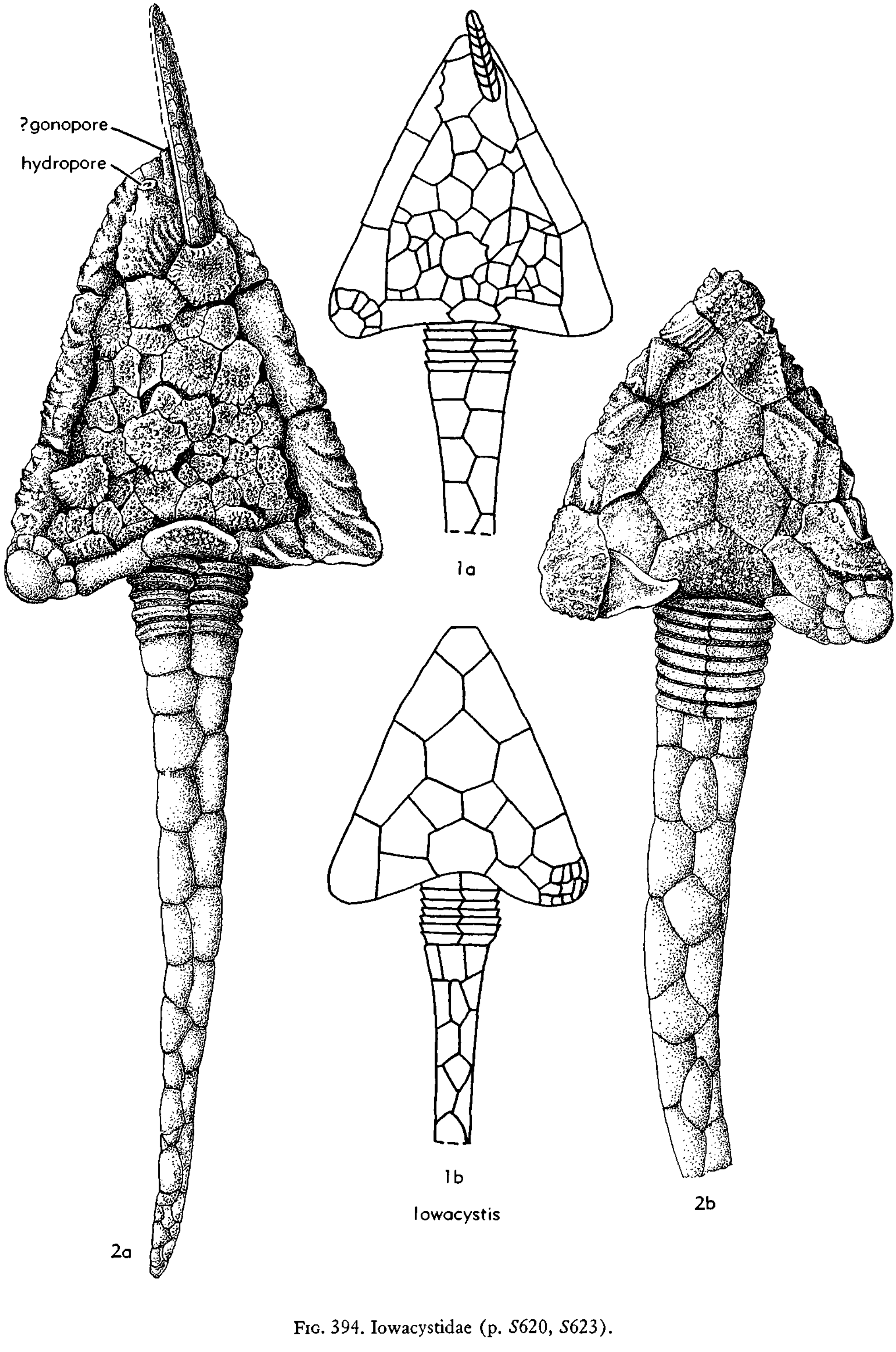

FIG. 394. Iowacystidae (p. *S*620, *S*623).

each face, also with adanal and adbrachial differentiation; anus closed by bivalved boss of 2 quarter-spheres parting in extensiplane, surrounded by circlet of small quadrilateral plates and on reverse side with 3 large adanal plates, creating lobelike aspect; left adoral plate bearing phialine hydropore aperture, with smaller phialine pore distally from it (?gonopore). Arm emerging from right distal supracentrals and located on sutural complex between 4 plates excavated to form brachial orifice; arm terete, relatively short and narrow. Stele somewhat depressed, thick and stubby, axially differentiated but less so than in most homoiosteles, with 5 or 6 carinate tetrameres; mesistele visible only on reverse side, where 1st 2 pairs of biseries of distal plates are separated by large median plates; dististele with several more such inserts discontinuous along reverse surface; mesistele and dististele merging on obverse side, dististele biserial (not dimeral) with suture in symmetry plane. *U.Ord.*, USA(Iowa).——Fig. 394. **I. sagittaria*; *1a,b,* obverse and reverse faces, ×1.7 *(84)*; *2a,b,* same, based on restudy of types, ×2.5, ×2.25 *(69)*.

Family BELEMNOCYSTITIDAE
Parsley, new family

[Family diagnosis and revised diagnosis of *Belemnocystites* furnished by Ronald L. Parsley, University of Cincinnati]

Solutes with regularized marginal and somatic plates; single nonterminal biserial arm with adjacent coniform pore plate. Stele holomerous or apparently so. Characters essentially those of type genus. *M.Ord.*

Belemnocystites Miller & Gurley, 1894, p. 6 [**B. wetherbyi*; M] [=*Belemnocystis* Bather, 1900, p. 51 (obj.) *(nom. van.)*]. Theca suboval, depressedly biconvex in cross section; depression especially marked in somatic areas, with 11 regularized marginals, 5 ventral somatic plates, and *ca.* 6 dorsal somatic plates, marginals extending equally over both faces. Single biserial arm appears to be very short, extending anteriorly from dorsal distal somatic area; left adbrachial plate bearing coniform aperture, presumably hydropore. Stele deeply inserted into theca, not extensively anchored to proximal adsteleals, but mainly to adjacent large somatic plates; proxistele undifferentiated and apparently holomerous (*ca.* 15 ?annular) segments with very large lumen; distal stele structure unknown. Granular prosopon, poorly preserved, plates apparently with fairly prominent concentric growth rings. Anus not identified, probably lateral, in proximal left corner of theca. [This genus bears a number of common traits with *Iowacystis* (e.g., configuration, location and interrelationship of the arm and pore plate, unusual somatic biconvexity of the theca, and similar nature and symmetry of the ventral somatic plates, including what appears to be an azygous adanal plate).] *M.Ord.*, USA(Ky.).——Fig. 395,*1*. **B. wetherbyi*; *1a,b,* obverse and reverse faces, based on holotype, ×3 (Parsley, n). [?=*Myeinocystites* Strimple, 1953.]

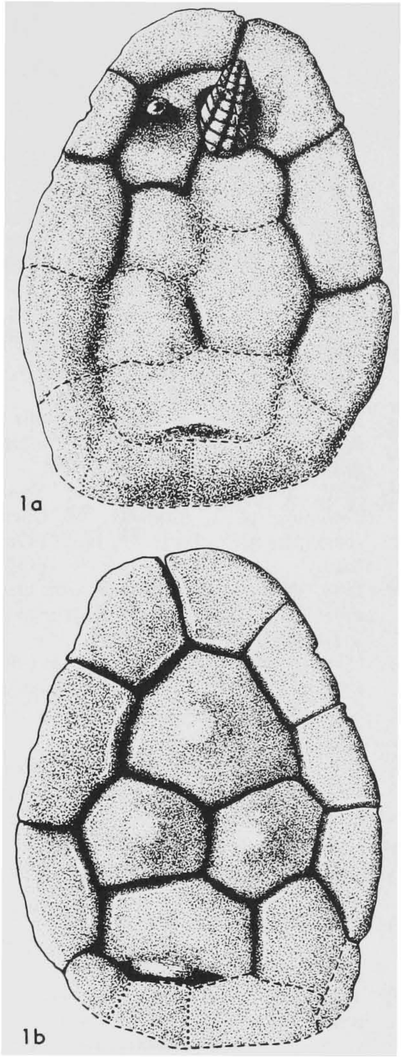

Fig. 395. Belemnocystitidae (p. S623).

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ADDENDUM

CAMPTOSTROMATOIDS

By J. Wyatt Durham

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Class CAMPTOSTROMATOIDEA Durham, 1966

[*nom. correct.* Durham, herein (*pro* Camptostromoidea Durham, 1966, p. 1219)]

Free-living, apparently medusaeform radially symmetrical echinoderms; body wall heavily plated and containing several different types of ossicles; mouth and anus at opposite poles, with no elongation along this axis; sutural pores abundant on oral and external lateral surfaces but absent from region of aboral pole; detailed organization uncertain but presumably radial; arms radail, plated, attached to periphery of test; seemingly no calcareous ring. *L.Cam.(Olenellus Zone).*

The genus *Camptostroma,* for which this class has been established, was originally (ref. *1*) described by Ruedemann *(4)* as a probable floating "tubularian hydrozoan." Subsequently Kieslinger *(3)* included it in the Scyphozoa, an assignment that was followed by Harrington & Moore *(2)* in part F of the *Treatise on Invertebrate Paleontology.* Careful examination of the type and other original material (all external molds) suggested that *C. roddyi* was an echinoderm (a possibility recognized by Ruedemann). Fortunately, a recently discovered specimen retains the original calcite plates, the cleavage and reticulate microstructure of which confirm assignment to

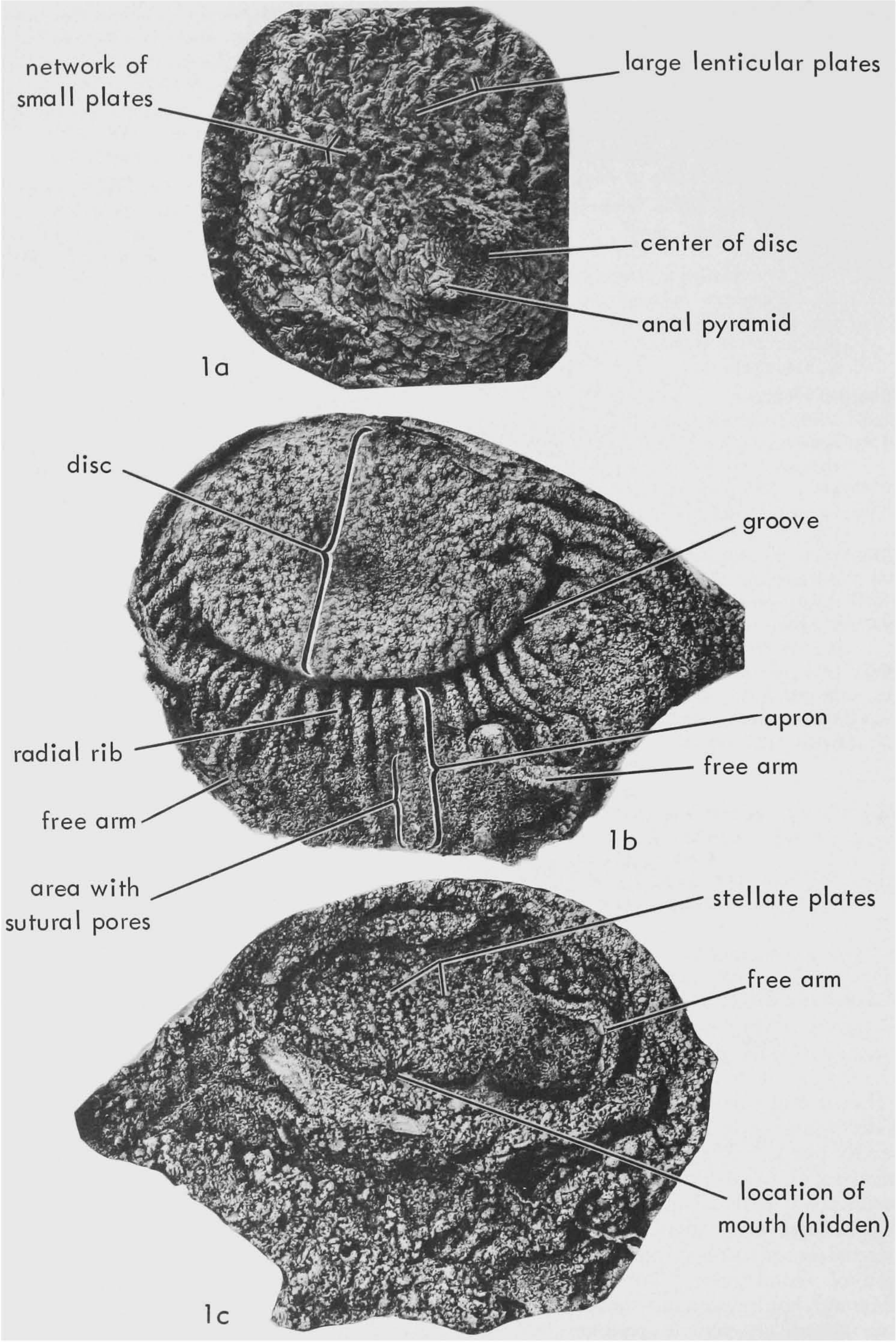

Fig. 396. Camptostromatidae (p. S630).

the echinoderms. *C. roddyi,* the type species (other species referred to *Camptostroma* do not appear to be congeneric), occurs in shales of the Lower Cambrian Kinzers Formation of Pennsylvania, in the same strata that contain lepidocystoids. About 15 specimens of *C. roddyi* have been found, but none are as complete as the type and some are very poor. Disassociated plates apparently referable to *Camptostroma* are abundant in some limestones associated with the shales.

Some details of the organization and structure of the test of *Camptostroma roddyi* have not been resolved, but it appears to have been medusaeform in shape, with a centrally domed aboral surface and a peripheral radially ridged apron with a few marginal free arms, and with the oral surface concave. Except immediately around the peristome, sutural pores are abundant on the oral surface and extend onto the upper margin of the peripheral apron. On the oral surface (but not on the peripheral apron) the small plates with sutural pores are arranged around larger stellately ridged plates. On the upper surface of the distal margin of the peripheral apron is an area of uniformly small plates, deeply incised for sutural pores. Proximally the poriferous area merges into a nonporiferous, strongly ribbed area built of small plates. Centrally the aboral domed disc is built of large flat lenticular plates imbedded in a network of numerous small plates. When the surface is contracted the flat plates are more or less overlapped by the meshwork of small plates, but when expanded these plates are the most conspicuous elements of this surface. A conspicuous raised structure considered to be an anal pyramid is present, slightly off center, on the aboral surface of some specimens. It appears to be composed of about seven elongate plates. The peripheral free arms are incompletely preserved on the available specimens but were relatively slender and had large plates on the aboral surface. Their length appears to have been sufficient to reach to the mouth. The number of arms is uncertain but seems to have been between four and eight. The central domed area is set off from the peripheral apron by a well-marked groove on the type and some other individuals, but there is a possibility that this groove may be an artifact of burial. The peristomial area, although surrounded by plates of several types, in contrast to other areas of the test, seems to be composed largely of flattened lenticular plates without sutural pores.

None of the plates of the test are firmly sutured to one another, and away from the peristomial region the plates seem to have been distributed through a thick body wall much as in many holothurians. Presumably the tissues would have decayed rapidly after death, the plates becoming disassociated and scattered easily. No evidence of a pentaradiate symmetry is recognizable, but the numerous radial ridges surrounding the aboral disc indicate a well-defined radial symmetry. On a nonleached specimen more than 40 of these ridges were observed, but on the holotype (although marginally incomplete) there appear to have been about 60. Another specimen seems to have had at least 50 ridges.

It is suggested that the sutural pores contained tube feet more or less similar to those of modern echinoderms and that they were connected by an internal radial plexus of the water-vascular system. Presumably the tube feet served primarily for respiration, but they probably also were utilized in food gathering or transport of food toward the mouth. The few slender arms do not suggest that they were used for locomotion—probably they were primarily food-gathering organs. The mouth seems to have been relatively small, so that food was probably of small particle size. No madreporite or genital aperture has been recognized, but the plates are so numerous and often so disarranged in detail that it would be easy to overlook these features.

The mode of life of *Camptostroma* is somewhat uncertain, but in view of the apparent medusaeform body it is suggested that it was probably pelagic or bathypelagic. It may have been comparable to the pelagic holothurian *Pelagothuria* or bathypelagic types such as *Benthodytes* and *Galatheathuria.* A comparison might also be made with the free-living comatulid crinoids, but the body structure is not at all comparable to that of the crinoids. The camptostromoid test, built of several different types of ossicles in intimate relationship, is suggestive of that of some holothurians, especially

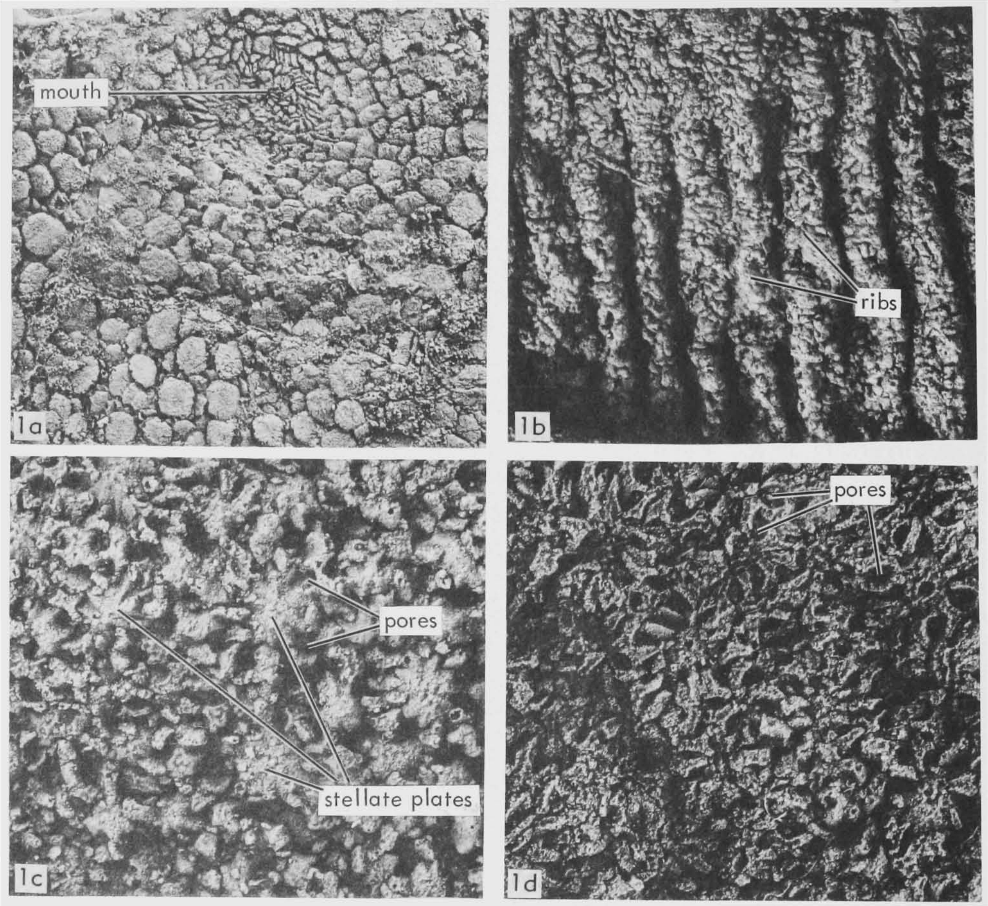

FIG. 397. Camptostromatidae (p. S630).

members of the Dactylochirotida and Dendrochirotida. However, the presence of peripheral arms that are heavily plated (adoral plated arms known in the Devonian holothurian *Palaeocucumaria*, 5) instead of adoral nonplated arms, the apparent lack of pentaradiate or bilateral symmetry, and the absence of elongation along the oral-aboral axis distinguish camptostromatoids from holothurians. Further, although the densely plated test of *Camptostroma* makes recognition of a calcareous ring difficult, no evidence of one was observed and it is assumed that it was absent. Grossly, the camptostromatoids might be compared with the ophiocistioids, but the lack of firmly sutured plates and the multiple types of ossicles in the wall of the test readily differentiate the camptostromatoids.

Family CAMPTOSTROMATIDAE
Durham, new family

Characters of class. *L.Cam.(Olenellus Zone).*

Camptostroma RUEDEMANN, 1933, p. 5 [**C. roddyi*; OD]. Test medusaeform, with few heavily plated peripheral arms; anus on aboral surface near center, with well-developed pyramid; most areas of wall composed of several types of ossicles; sutural pores on oral surface and upper distal margin of peripheral apron. *L.Cam.(Olenellus Zone)*, USA (Pa.).——FIG. 396-397. **C. roddyi*; 396,*1a*, part of aboral disc, ×2.5; 396,*1b-c*, aboral, oral views of same individual, ×1.4; *397,1a*, adoral region, ×5; 397,*1b*, ribbed area of apron, ×5; 397,*1c*, detail of mid-oral surface, ×10; 397,*1d*, detail of aboral surface of distal portion of apron, ×10 (P. M. Kier, n).

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LEPIDOCYSTOIDS

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Class LEPIDOCYSTOIDEA Durham, new class

Free-living, placoid echinoderms with differentiated oral and aboral surfaces; oral surface with numerous small plates with sutural pores, free biserial arms, and anal aperture; character of oral aperture unknown; aboral surface with numerous imbricating plates originating at apex of surface; anus marginal on oral surface, with well-developed anal pyramid; arms grooved, with cover plates, arranged in concentric circlets on oral surface, oldest outermost, resting on flat basal plates; arms presumably for feeding; organs in sutural pores presumably respiratory. *L.Cam.(Olenellus Zone).*

This group of echinoderms is known from a few more or less crushed specimens from the Kinzers Formation of Pennsylvania, where they occur in the same strata as medusaeform camptostromatoids. Most individuals seem referable to the single described species, *Lepidocystis wanneri* Foerste (1). Two specimens have three circlets of arms, probably with five arms to a circlet (no specimen has a complete circlet of arms; it is possible that there might be only four). Arms of each circlet are aligned along radii from the presumed central location of the mouth. One smaller specimen (Fig. 398,*1b*), preserved partly in the round (either immature or else representing another species), seems to have only a single circlet of free arms (but draped along the side of the test during burial). The basal plates of the outermost arms are adjacent to the margin of the aboral imbricating plates, but the bases of the inner arms are set in the midst of the small, marginally incised plates of the oral surface. There is one cover plate to each segment of the arm, with the distal margin of the cover plate serrate and slightly overlapping the proximal margin of the next. The oral surface is covered with small, relatively thick plates, with three or four deep marginal grooves for sutural pores (one to each face). These pores are very numerous and the oral surface must have been densely covered with the organs that extended through them. It is assumed that these organs were respiratory in function and connected by an internal plexus of the water-vascular system.

No feature recognizable as a mouth has been observed, but it seems probable that this was centrally located on the oral surface. It is uncertain how food was transported from the arms: food particles may have been transferred to the mouth by the arms themselves; they may have been moved from the base of the arms to a central mouth by ciliary action; or there may have been subvective channels from the arms. A well-developed anal pyramid built of numerous plates is situated marginally on the oral surface midway between two of the outermost arms. Two specimens indicate that the elongated portion of the test covered with imbricating plates was more or less conical and that the oral surface was arched. The presence of presumed respiratory organs in the sutural pores on the oral surface suggests that *Lepidocystis* lived up-

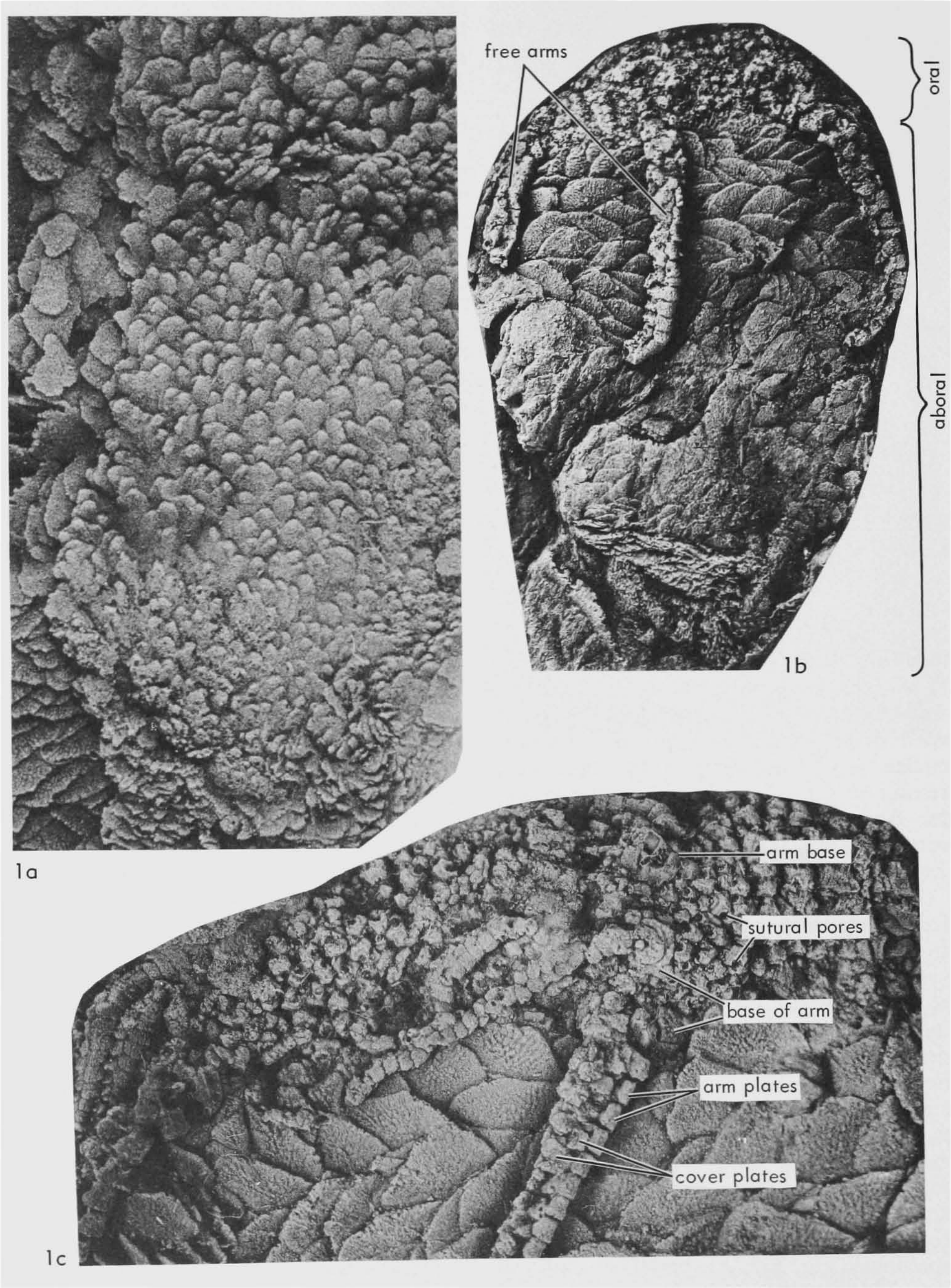

FIG. 398. Lepidocystidae (p. S634).

right on the sea floor with the apical portion of the aboral surface imbedded in sediment (Fig. 399).

The lepidocystoids differ from eocrinoids by restriction of the sutural pore-bearing area to the interbrachial oral surface, the presence of imbricating plates on the aboral surface, the circlets of arms on the oral surface, and the mode of attachment of the arms. They differ from most edrioasteroids, cystoids, and helicoplacoids by the presence of sutural pores, and from camptostromatoids by the possession of only a single type of plate in any area, as well as the position of the anus on the oral surface. They differ from the edrioasteroid *Stromatocystites,* which has sutural pores on the oral surface, by the presence of free arms.

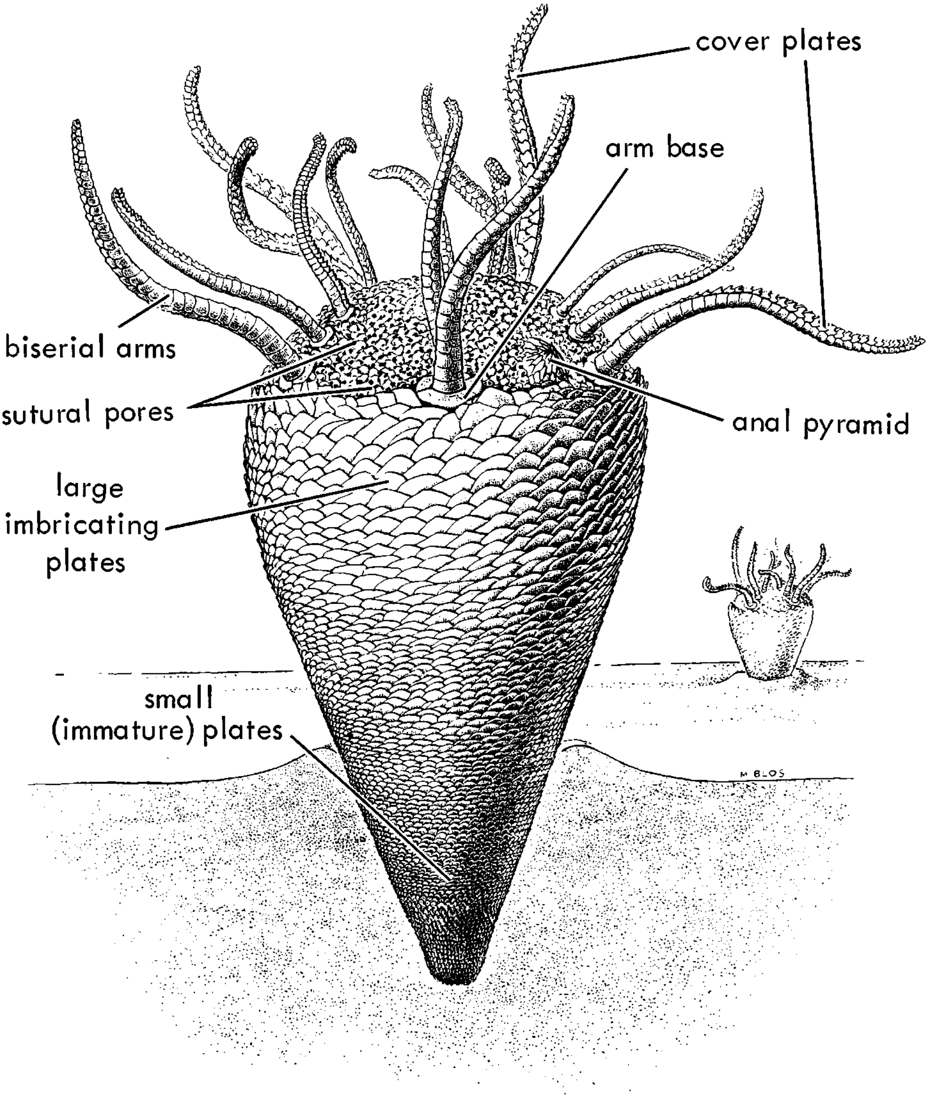

FIG. 399. Lepidocystidae (p. S634).

Family LEPIDOCYSTIDAE Durham, new family

Characters of class. *L.Cam.(Olenellus Zone).*

Lepidocystis FOERSTE, 1938, p. 212 [**L. wanneri*; M]. Aboral surface of test conical, built of numerous scalelike imbricating plates, those of oral surface small, heavy, deeply incised by single large sutural pore on each side; anus at margin of oral surface, with well-developed anal pyramid. *L.Cam.(Olenellus Zone),* USA(Pa.).——FIG. 398-399. **L. wanneri*; 398,*1a,* detail of small adapical plates, ×8.5; 398,*1b,* small individual with free arms draped along side of test, ×3.1; 398,*1c,* part of oral surface of specimen with 3 circlets of arms, ×4; 399, restoration showing probable mode of life, approx. ×1.5 (Durham, n).

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CYMBIONITES AND PERIDIONITES—UNCLASSIFIED MIDDLE CAMBRIAN ECHINODERMS

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INTRODUCTION

Cymbionites and *Peridionites* are nominal genera proposed in 1941 by WHITEHOUSE (ref. *11*) on the basis of fossils found in lowermost Middle Cambrian strata (Zone of *Xystridura*) of Queensland, Australia. Specimens of the first-mentioned form were obtained in abundance from the basal 40 feet of the zone and less numerous representatives of the second in a bed of limestone approximately 24 feet higher in the section.

For the purpose of classifying these two genera, both of which are monotypic, WHITEHOUSE introduced new families named Cymbionitidae and Peridionitidae, which respectively were assigned to the new classes Cycloidea and Cyamoidea, and both were placed in a new subphylum of the Echinodermata named Haplozoa.

DESCRIPTION

Each of the two fossil forms displays a thick calcareous skeleton comprised of a few plates disposed around a median crateriform depression. The animals are judged to have been free-living on the sea bottom, for no trace of fixed attachment has been observed.

The remains of *Cymbionites* consist of a hemispherical or thimble-shaped body with average diameter of 12 mm. (Fig. 400,*1a*). Less commonly the fossils are barrel- or saucer-like. Typically they are composed of five tightly joined massive plates of wedge-shaped form, with sutures discernible only on weathered specimens. The median depression, variable in depth, possesses fluted sides. A transverse section through the bottom of the depression commonly shows the presence of a tiny central plate additional to the five main ones and surrounded by them in manner that entirely conceals the small central plate in view of the exterior. The festooned edge of the calyx bears a minute peripheral groove.

The skeleton of *Peridionites* resembles a biconvex half-lens having almost perfect semicircular outline in side view and an elliptical shape in apical view (Fig. 400, *2a-e*). The fossils are diminutive in size, with maximum diameter mostly less than 10 mm. Biradial in form, they are composed of five massive calcareous plates—a median apical one adjoined by two large terminal plates and two smaller mediolateral plates located on opposite sides of a moderately deep central cavity which is

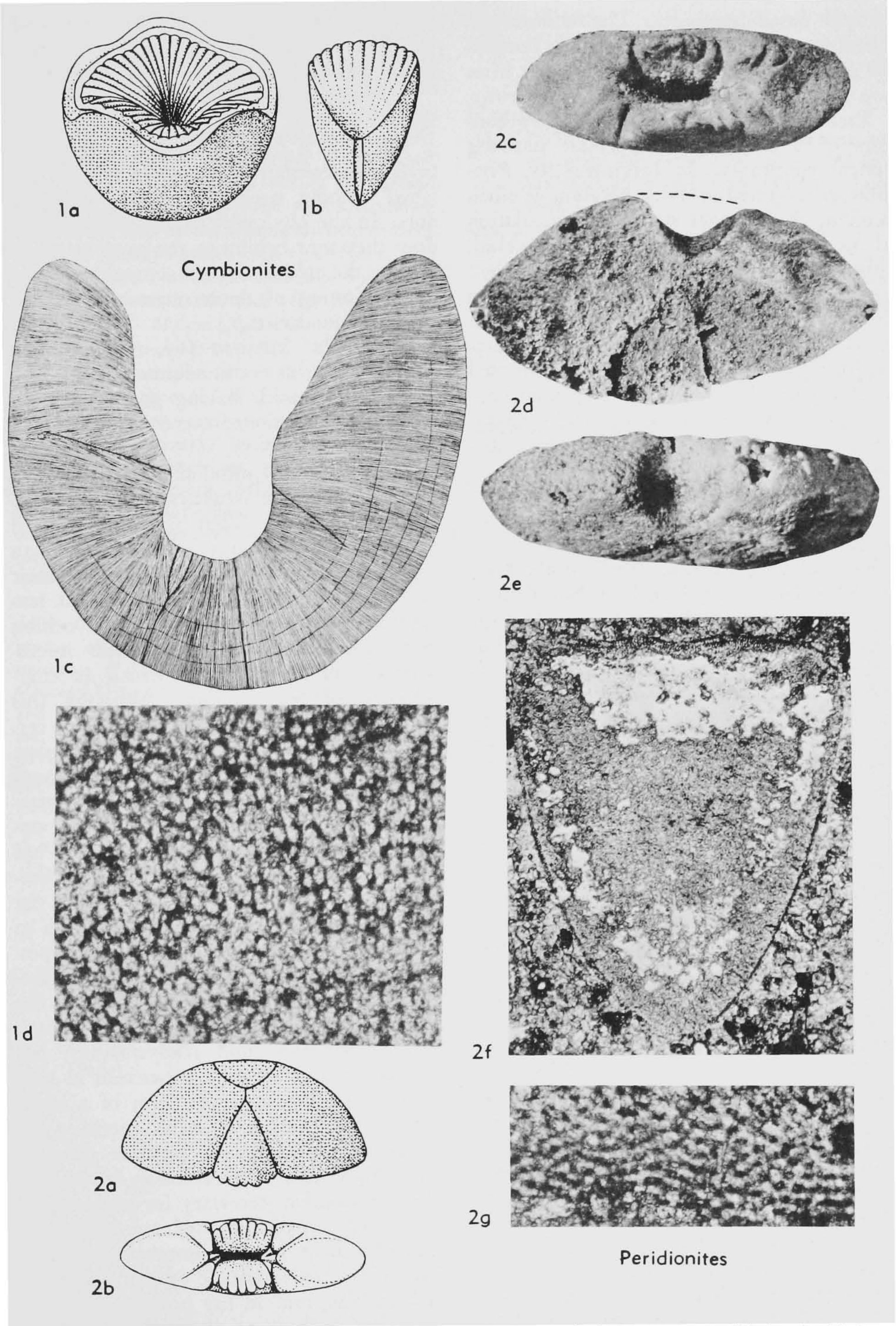

FIG. 400. **Cymbionites craticula* WHITEHOUSE *(1)*; **Peridionites navicula* WHITEHOUSE *(2)* (unclassified M.Cam. echinoderms) (p. *S*637).

radially fluted internally. The truncate abapical face of each terminal plate is marked by three shallow depressions set off from one another by diverging narrow furrows.

Each plate in both of these genera consists of a single calcite crystal showing optical continuity. In specimens of *Peridionites* subjected to dolomitization or silicification, the original stereomic reticulation of the plates generally cannot be observed, although it may be visible locally in small patches of the surface (Fig. 605,*2f,g*). On the other hand, the reticular microstructure of plates belonging to *Cymbionites* commonly is very evident. They are composed of close-packed "but intermittently impinging" prismatic fibers with a calcite network optically continuous with the fibers between them (Fig. 400,*1c,d*).

INTERPRETATIONS

These two genera of fossils have been interpreted in extraordinarily different ways.

1) In the view of WHITEHOUSE *(11)* both forms are echinoderms. *Peridionites* is considered to be the dorsal skeleton of a bilaterally symmetrical five-segmented organism which corresponds morphologically to the dipleurula stage in larval development of echinoderms. *Cymbionites* is judged to be the aboral skeleton of an essentially radiate organism equivalent to the pentactula stage in ontogeny of eleutherozoic echinoderms. Asteroids, ophiuroids, and echinoids are thought to be derivatives of the Cycloidea (class represented solely by the genus *Cymbionites* as now known), and those in their turn are supposed to come from the Cyamoidea (class represented only by *Peridionites* among yet discovered fossils). The Cyamoidea are interpreted as ancestral also to the Homalozoa ("Carpoidea" and Machaeridia) in one line and to the Pelmatozoa [Crinozoa] (Cystoidea, Blastoidea, Edrioasteroidea, Crinoidea) in another line. These concepts have been accepted by some *(7)* but rejected by most workers *(1-3, 5, 6, 8, 9)*.

2) According to GISLÉN *(2)* (as well as TERMIER & TERMIER, 9), *Cymbionites* is an echinoderm provisionally interpretable as a cystoid with only the basal part of the theca calcified. *Peridionites,* however, is not an echinoderm but possibly a ctenophore modified for benthonic existence like the modern *Platyctenida* and distinguished by having a calcareous skeleton.

3) Neither of the two discussed fossils is an echinoderm, in the opinion of CUÉNOT & TÉTRY *(1)*. Instead, both are considered to be representatives of phyla which vanished without producing known descendants. In the phylogeny of the animal kingdom they may belong in the great gap separating the cnidarians and ctenophores from the beginning of deuterostomians marked by the echinoderms.

4) Finally, SCHMIDT *(6),* who accepted both genera as echinoderms, interpreted them as eocrinoids having greatly reduced thecae that functioned merely as stabilizing structures.

The temerity of some of these hypotheses contrasts with the weakness of evidence in support of them. That *Cymbionites* and *Peridionites* are truly echinoderms can hardly be doubted, for not only are their plates composed of single crystals but reasonably well-preserved specimens exhibit unequivocal traces of honeycomb microstructure of the stereom which is characteristic of the phylum. Although this much is established, nothing more is certain. Do the fossils constitute complete skeletons, as their morphology and manner of preservation (including lack of associated fragments) seem to indicate, or, oppositely, are they incomplete remains? What was the nature of soft parts originally associated with the skeletons? How may the remains be oriented correctly in relation to morphology of the organisms? Such questions presently are unanswerable. *Cymbionites*—but not *Peridionites*—suggests the basal part of the theca of such crinozoans as *Parorthocrinus* and *Rhopalocystis,* but the resemblance is quite superficial in that it relates only to external form of a small part of the body *(10),* thus meriting no serious consideration of possible relationships. Inasmuch as these fossils fail to provide information necessary for understanding of the organization of animals represented by them, it seems improper to assign them either to extant or extinct classes of echinoderms, and in my opinion not even to recognize them as distinct families. Beyond statement of what can be observed, all is speculation.

SYSTEMATIC DESCRIPTIONS

Cymbionites WHITEHOUSE, 1941, p. 9 [**C. craticula*; M]. Echinodermal remains consisting of calcareous dome-shaped bodies composed typically of 5 equal curved plates of thick wedge-shaped form, firmly joined together laterally and apically as cuplike structure with fluted wall surrounding more or less deep central depression; stereom composed of closely packed prismatic fibers with calcite meshwork in optical continuity with fibers occurring between them; each plate consisting of single crystal. *M.Cam.(Xystridura Zone),* Australia(Queensl.).——FIG. 400,*1*. **C. craticulata*; *1a,b,* oblique lat. view of complete specimen and single isolated plate, ×3 *(11)*; *1c,* long. (vertical) sec. showing sutures and growth lines, ×7 *(11)*; *1d,* tang. sec. showing honeycomb structure of stereom, ×120 (Ubaghs, n).

Peridionites WHITEHOUSE, 1941, p. 5 [**P. navicula*; M]. Echinodermal remains comprising calcareous dome-shaped bodies which are laterally compressed and biradial in form, composed of 5 plates including single apical plate, 2 large end plates, and 2 somewhat smaller mediolateral plates bordering narrow deep central fossa; each plate comprising single crystal with originally reticulate stereom. *M.Cam.(Xystridura Zone),* Australia (Queensl.).——FIG. 400,*2*. **P. navicula; 2a,b,* lat. and truncate faces, ×5 *(11)*; *2c-e,* truncate, lat., and apical faces (*2d,e,* holotype, with apical plate lacking), ×5.6 (Queensland Univ. photographs, n); *2f,* long. (vertical) sec. of end plate showing preserved remnant of honeycomb stereom structure on upper edge, ×15 (Ubaghs, n); *2g,* tang. thin sec. showing stereom reticulation, ×120 (Ubaghs, n).

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INDEX

Italicized names in the following index are considered to be invalid; those printed in roman type, including morphological terms, are accepted as valid. Suprafamilial names are distinguished by the use of full capitals and authors' names are set in small capitals with an initial large capital. Page references having chief importance are in boldface type (as **S332**).