Treatise on INVERTEBRATE PALEONTOLOGY *Moore, Editor* = (S) Echinodermata $1^{(1)}$ = *Geological Society of America*
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INVERTEBRATE PALEONTOLOGY

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Directed and Edited by
RAYMOND C. MOORE

Part S
ECHINODERMATA 1

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TREATISE ON INVERTEBRATE PALEONTOLOGY

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EDITORIAL PREFACE

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

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

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

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

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 zoölogical *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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Akademie der Wissenschaften, physikalische-mathematische Klasse, Abhandlungen. Berlin.

[K.] Akademie der Wissenschaften zu Wien, mathematische-naturwissenschaftliche Klasse, Denkschriften; Sitzungsberichte.

Akademiya Nauk SSSR, Institut Geologicheskikh Nauk, Trudy (Geologicheskaya Seriya). Moskva.

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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

By GEORGES UBAGHS

[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 èchinodermes BRUGUIÈRE, 1789; Radiaires èchinodermes 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,

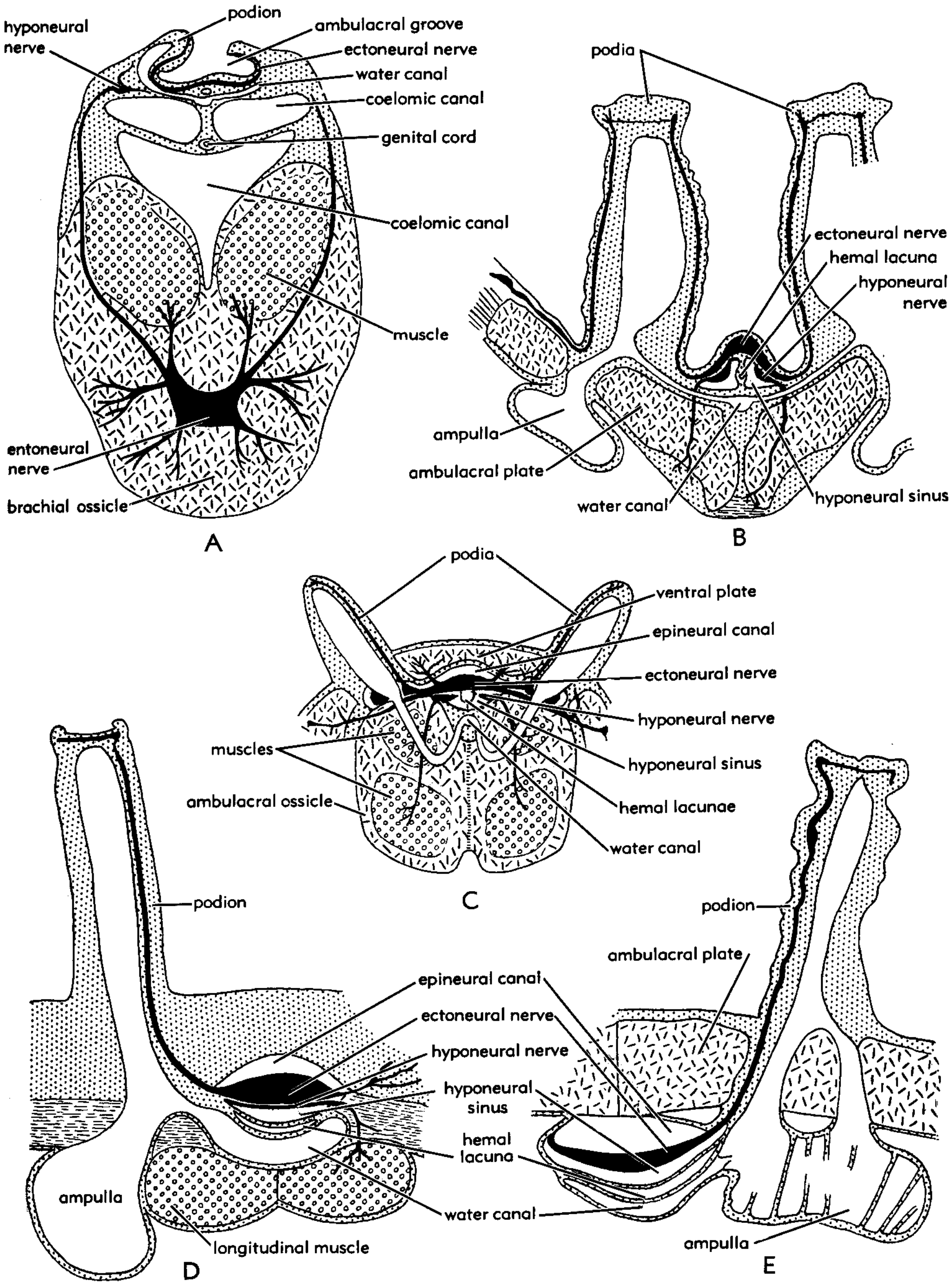

Fig. 1. Comparison of radial structures (sections of ambulacrum) in different echinoderm groups.——*A*. Crinoid.——*B*. Asteroid.——*C*. Ophiuroid.——*D*. Holothuroid.——*E*. Echinoid (Ubaghs, n).

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.

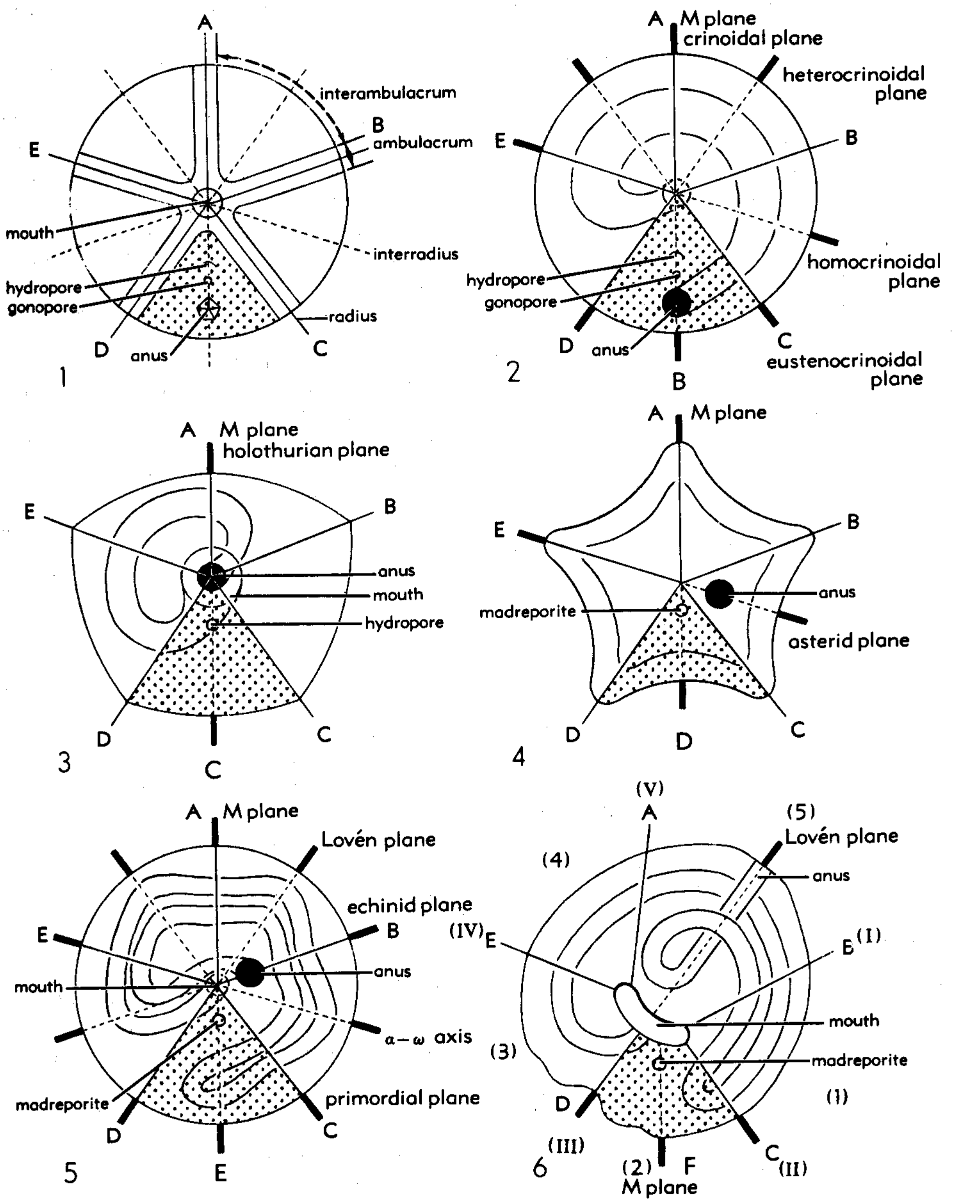

Fig. 2. Disposition of rays in relation to other structure in different echinoderm groups, all viewed from oral side (Ubaghs, n).——*1.* Orientation of generalized echinoderm according to nomenclature of rays proposed by P. H. Carpenter. ——*2-6.* Various planes of symmetry observed in *(2)* crinoids and 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

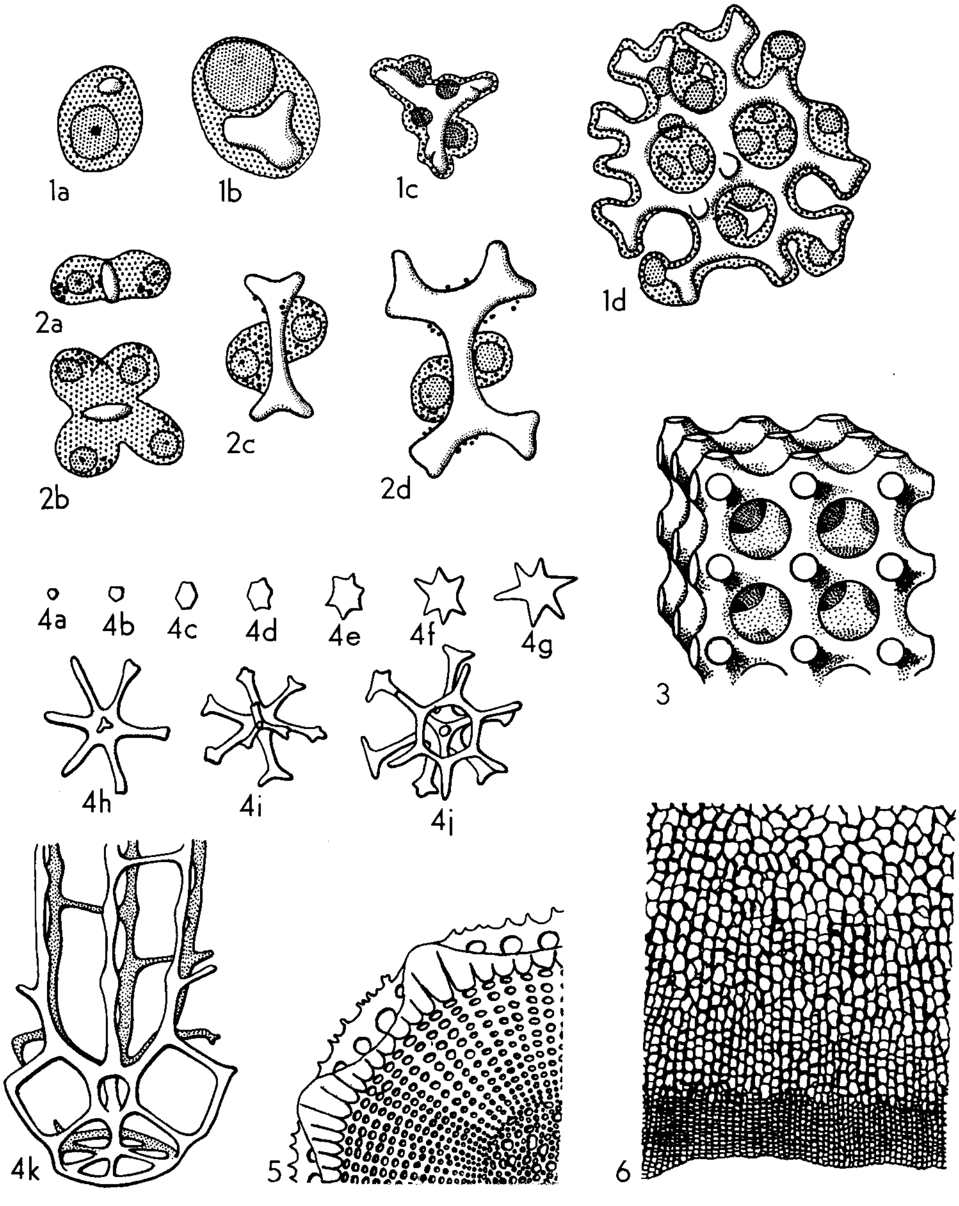

FIG. 3. Formation and biologic structure of echinoderm endoskeleton.——*1a-d.* Stages in development of plate of young ophiuroid, *Amphipholis squamata* (CHIAJE); *1a,b,* ×1,280; *1c,d,* ×640 (Woodland).——*2a-d.* Stages in development of ossicles of *Cucumaria* sp. (holothuroid), ×750 (Woodland).——*3.* 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-

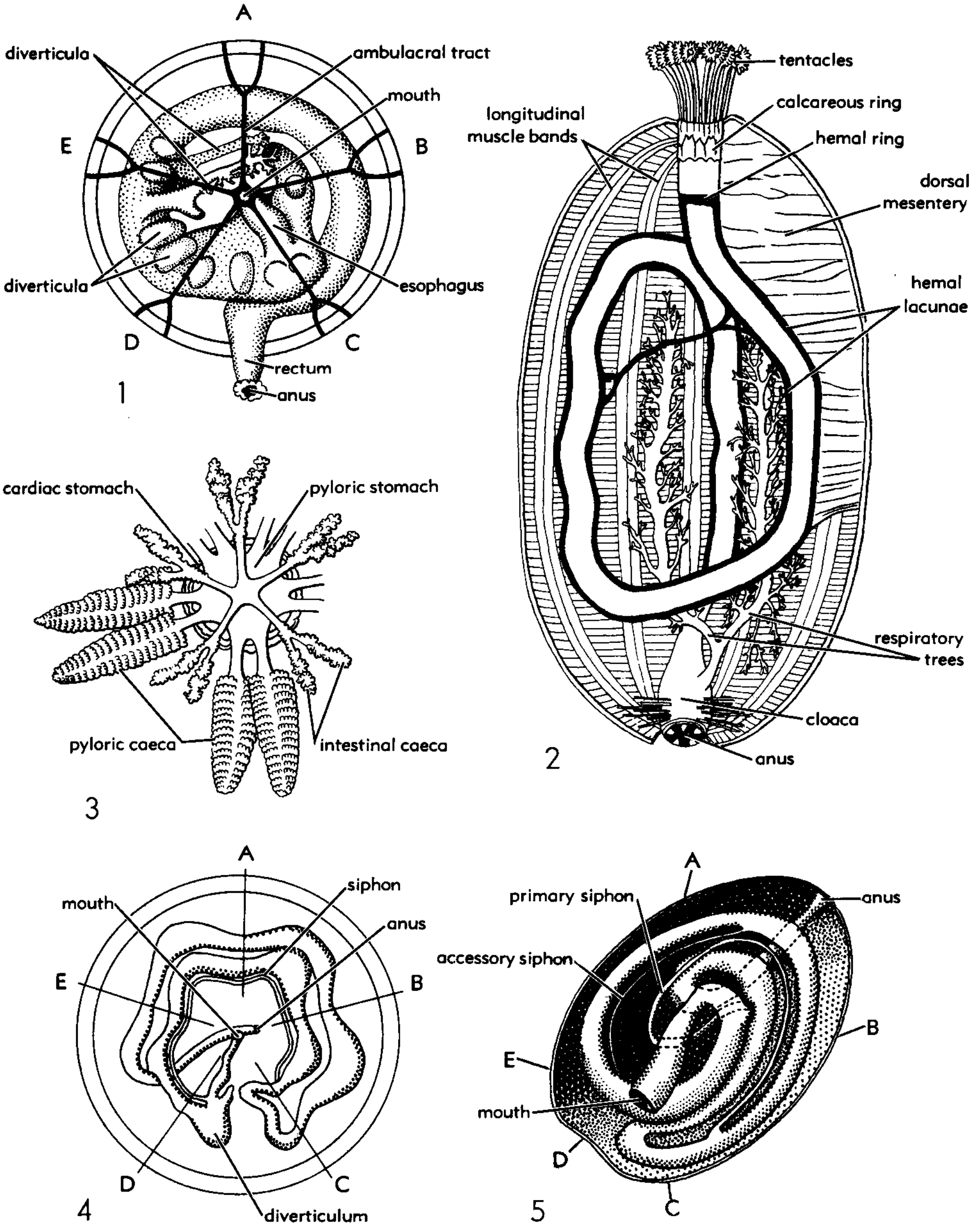

FIG. 4. Digestive systems of echinoderms.——*1.* Crinoid *(Antedon)*, showing many diverticula (Chadwick).——*2.* Holothuroid, with respiratory trees and hemal system (main lacunae, solid black) (Ludwig).——*3.* Asteroid *(Culcita)* (Hamann & Ludwig).——*4.* Regular echinoid *(Echinus)* (Cuénot).——*5.* Irregular 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.

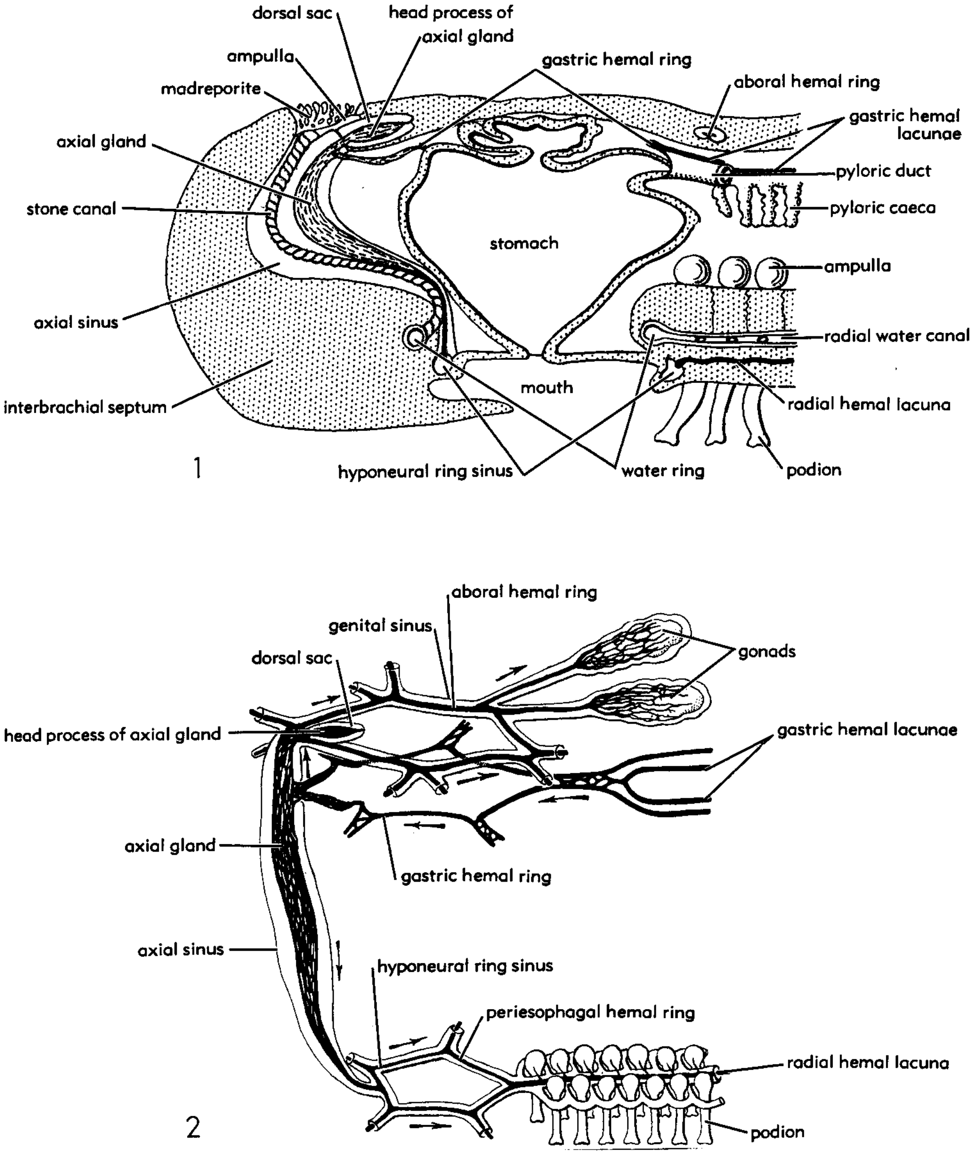

FIG. 5. Axial complex, hyponeural, and hemal systems in asteroid (Ubaghs, n).——*1.* Sagittal section through *CD* (left) interray and *A* ray (mod. from Cuénot).——*2.* Scheme of axial complex, hyponeural and hemal systems.

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

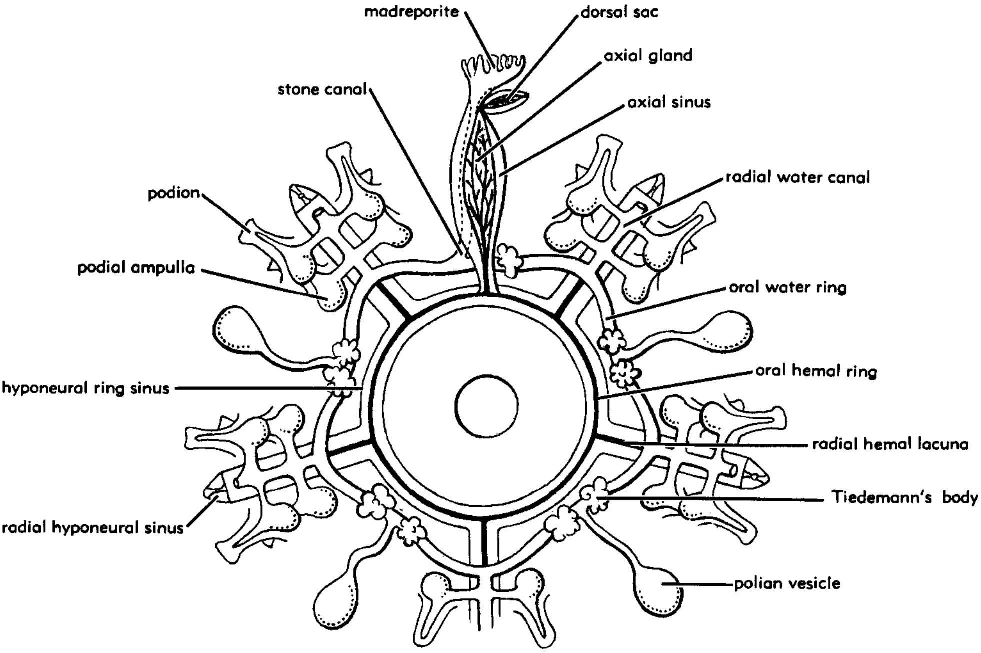

FIG. 6. Organization of water-vascular, hemal, and hyponeural-sinus systems in asteroid (diagram.) (Ubaghs, n).

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

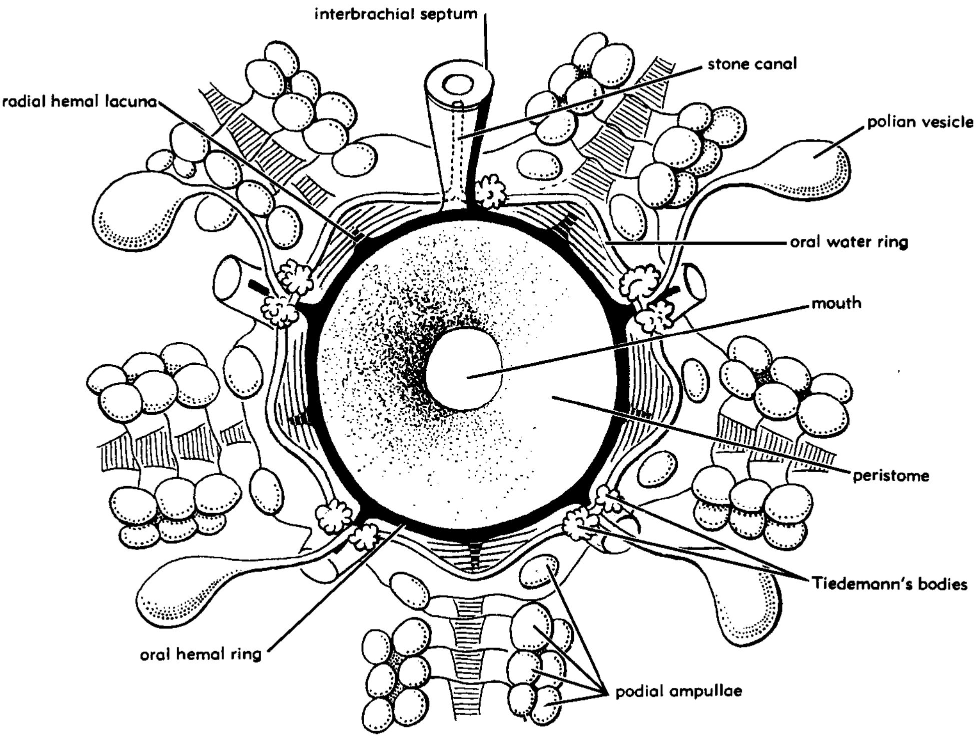

FIG. 7. Internal view of peristomial region of *Asterina gibbosa* (PENNANT) (asteroid), showing water-vascular and hemal systems, ×10 (Cuénot).

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-

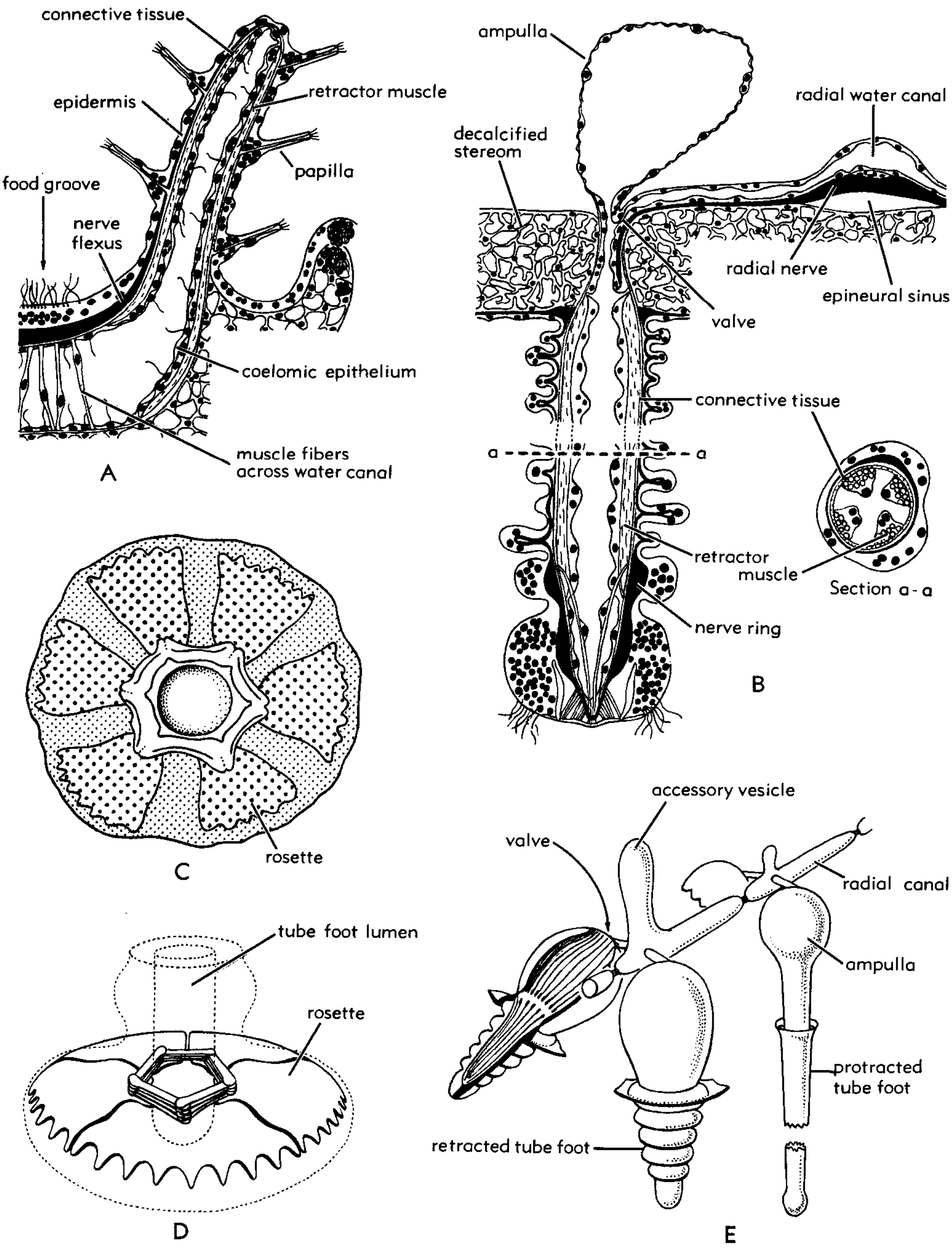

FIG. 8. Structure of tube feet.——*A*. Longitudinal section of tube foot of *Antedon bifida* (crinoid) (Nichols).——*B*. Longitudinal section of suckered tube foot and radial water canal of *Echinocyamus pusillus* (echinoid) (Nichols).——*C, D*. Structure and arrangement of skeletal elements in disc of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

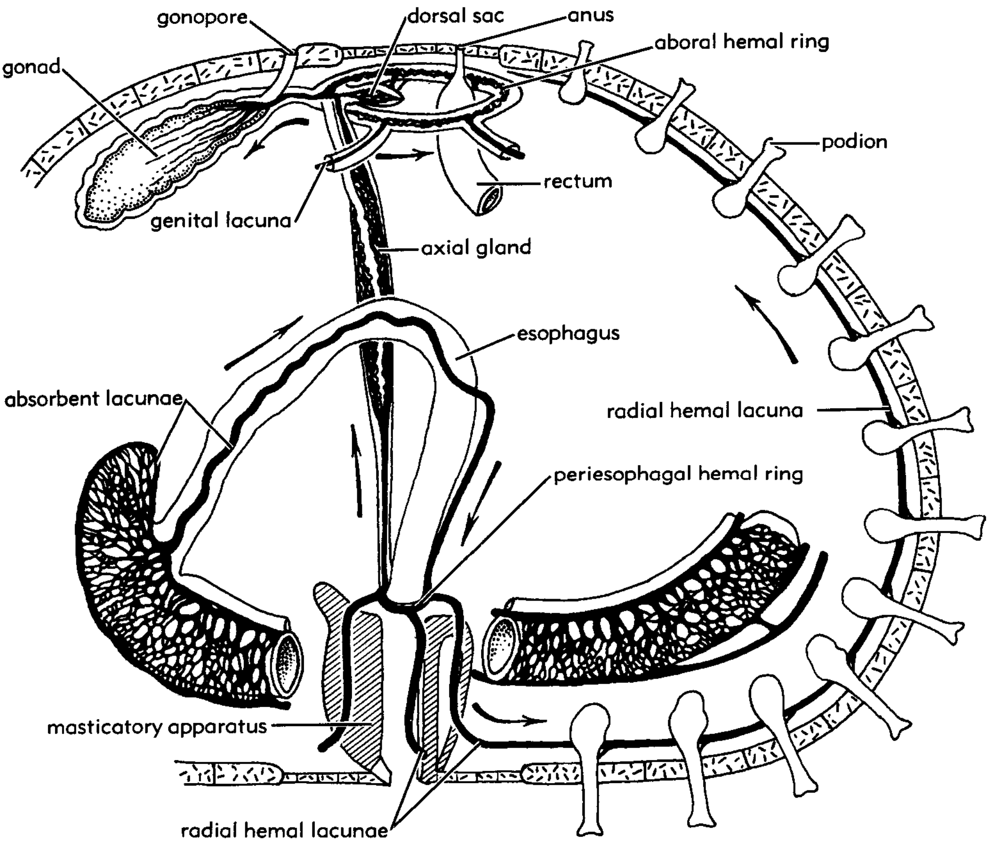

FIG. 9. Scheme of hemal system in regular echinoid (mod. from Cuénot).

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.]

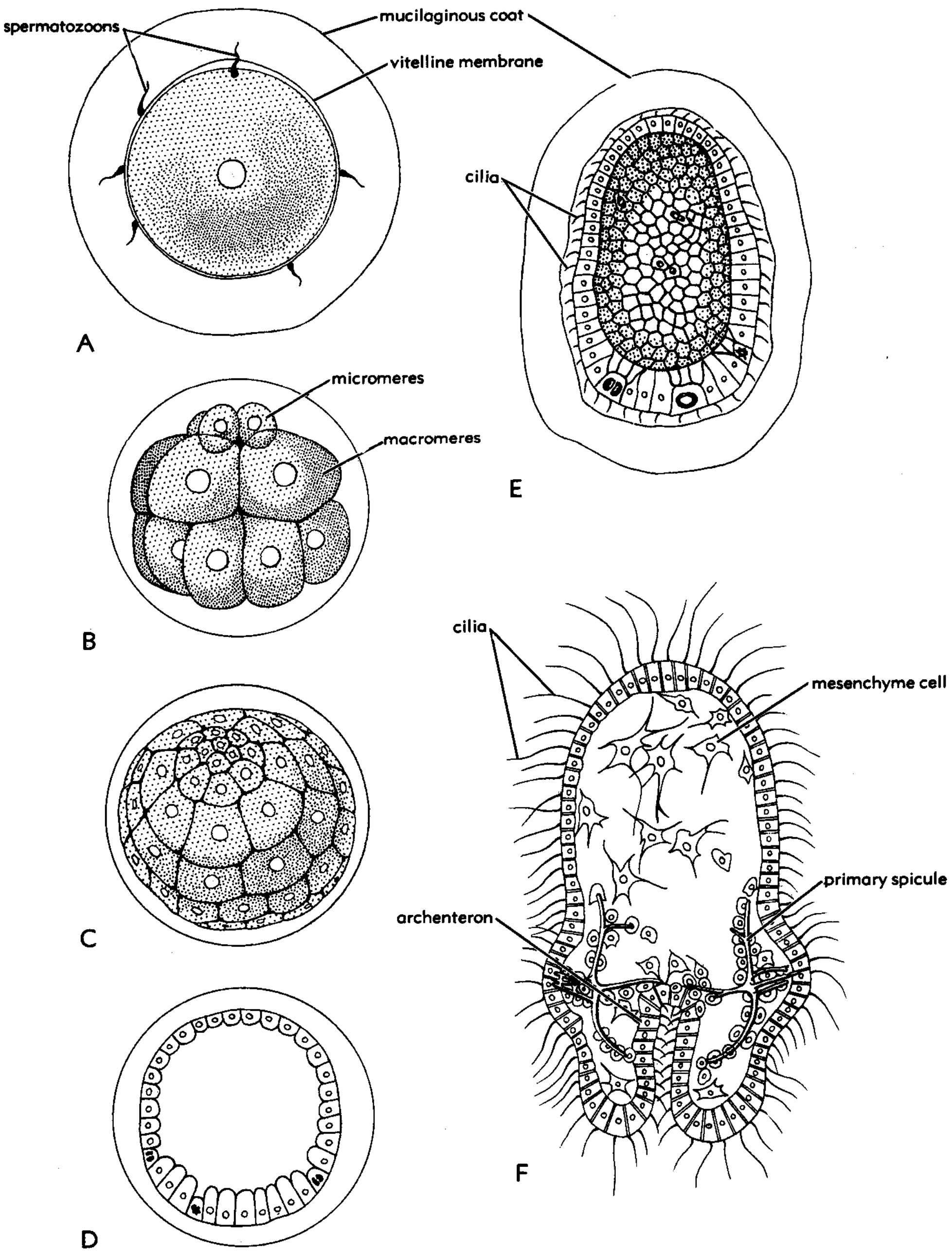

FIG. 10. Early ontogenetic stages of *Echinocyamus pusillus* (echinoid) (Théel).——*A*. Mature ovum at moment of impregnation, with one spermatozoon entering yolk and vitelline membrane beginning to separate, ×410.——*B*. Cleavage stage with 16 cells, ×400.——*C*. Later cleavage stage, at about three hours 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.

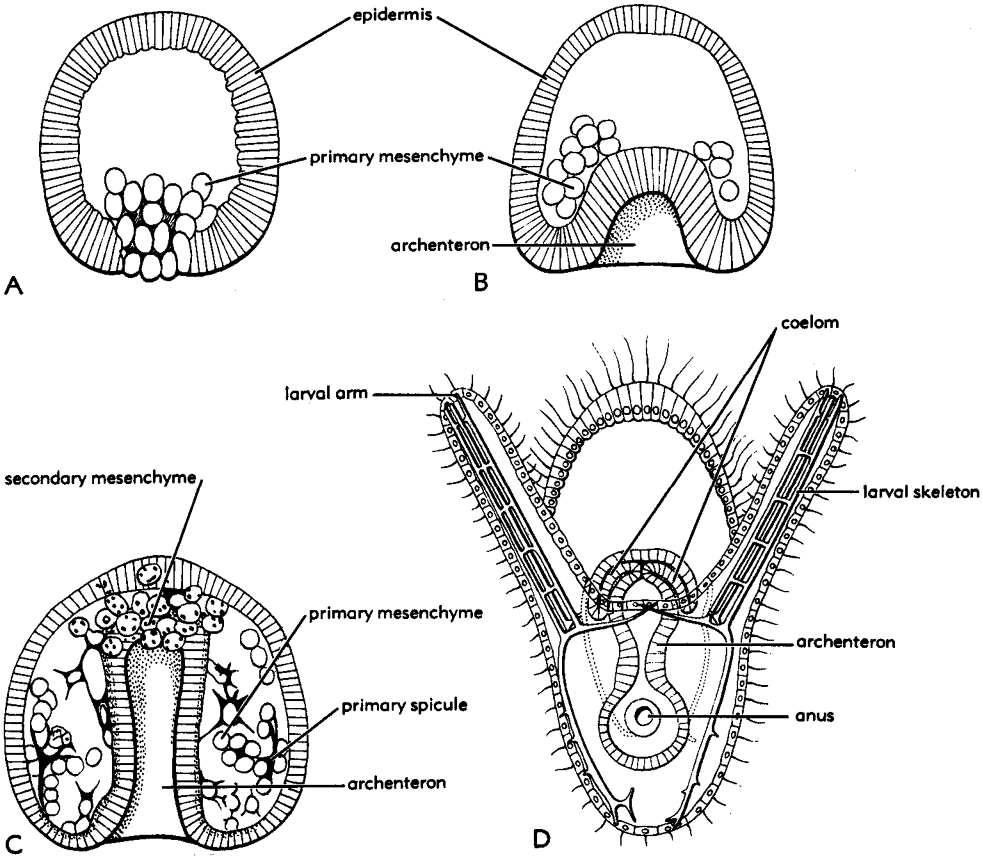

FIG. 11. Optical sections showing three stages *(A-C)* in formation of gastrula and mesenchyme of *Paracentrotus lividus* (echinoid) (Boveri); and young pluteus larva *(D)* of *Echinocyamus pusillus* (echinoid) showing formation of coeloms, ×270 (Théel).

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

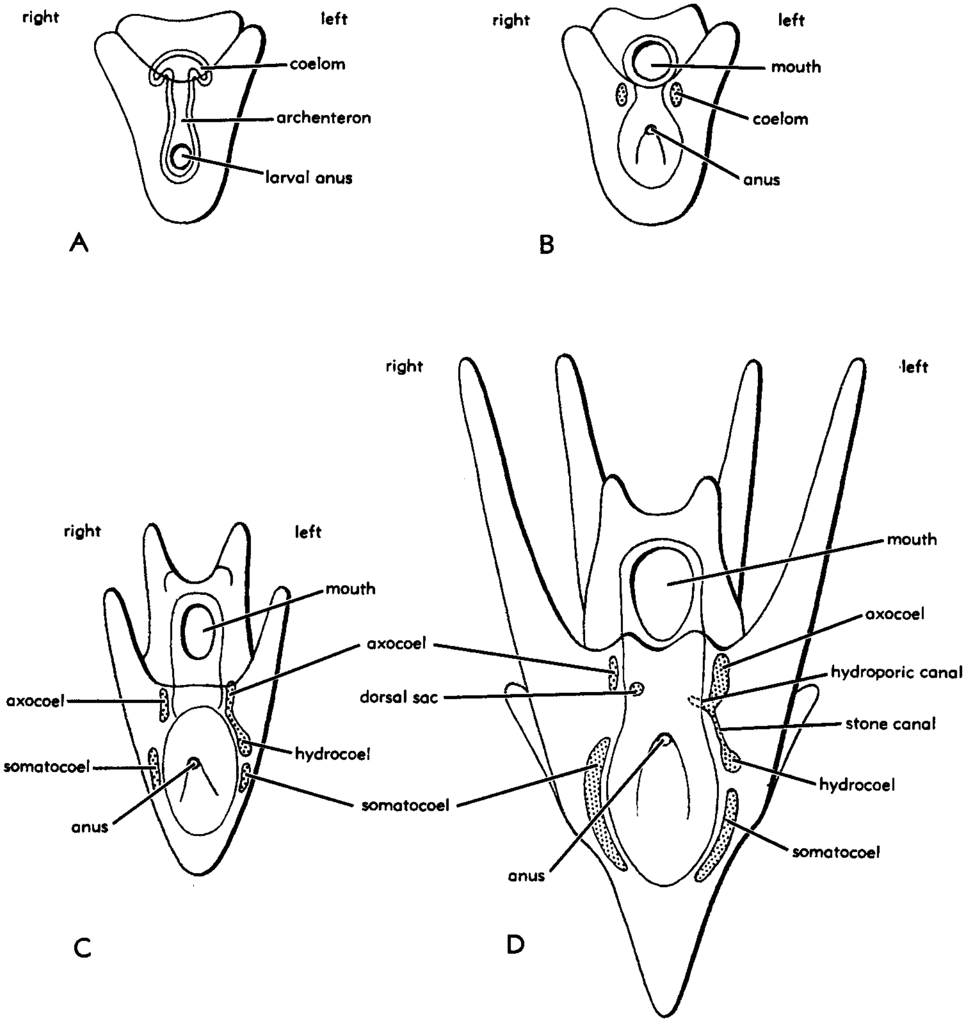

FIG. 12. Formation and first evolution of coeloms in echinoid larva (diagram.) (von Übisch).

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

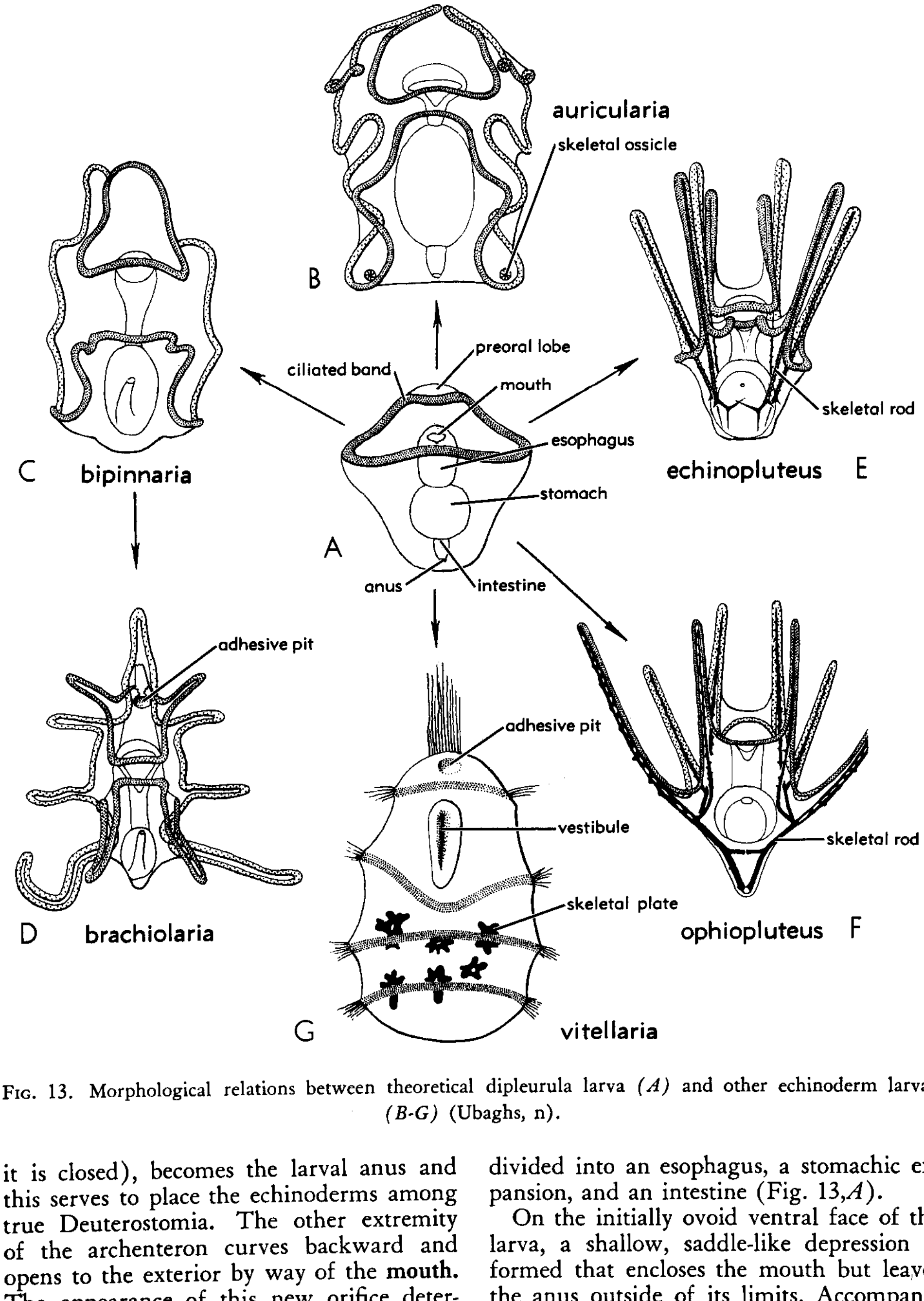

FIG. 13. Morphological relations between theoretical dipleurula larva *(A)* and other echinoderm larvae *(B-G)* (Ubaghs, n).

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-

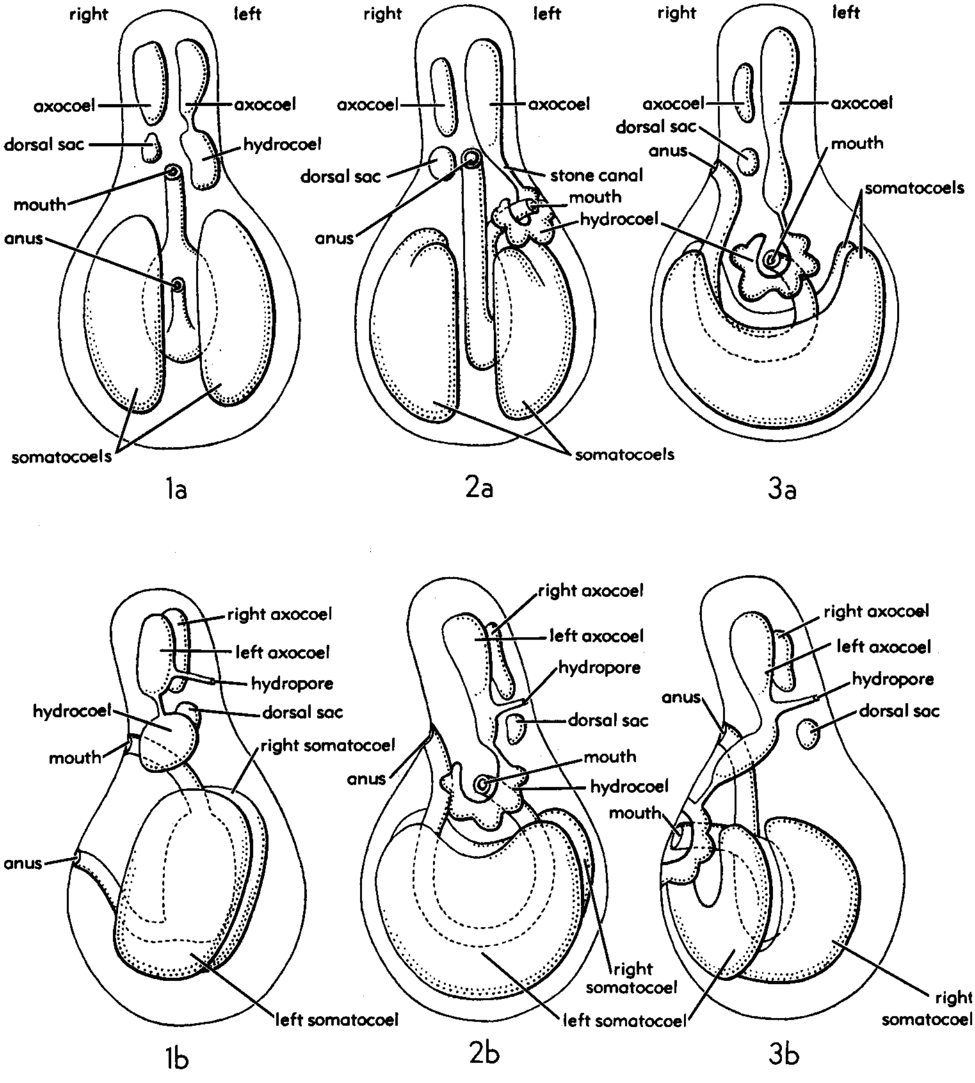

FIG. 14. First phases of metamorphosis in echinoderms (diagram.), upper row showing larvae from ventral side and lower row from left side.——*1a,b.* Initial symmetrical phase.——*2a,b.* Asymmetrical phase.——*3a,b.* Phase of secondary symmetry (Heider).

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-

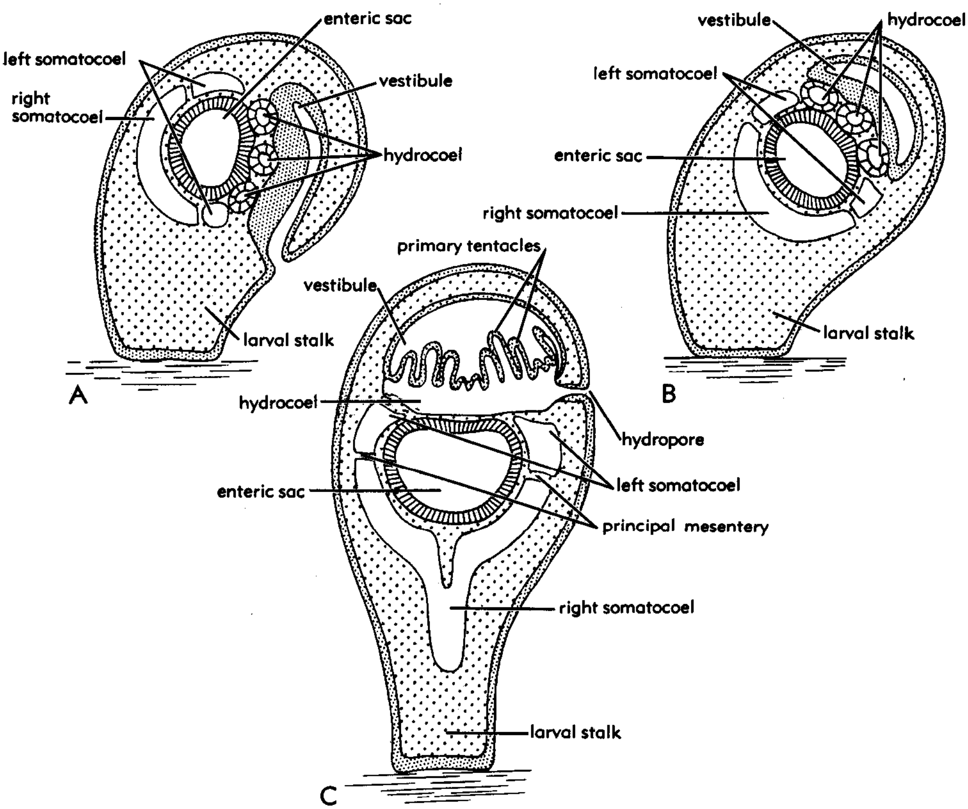

FIG. 15. Diagrammatic sections showing successive stages *(A-C)* of elevation among crinoids (mod. from Barrois).

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

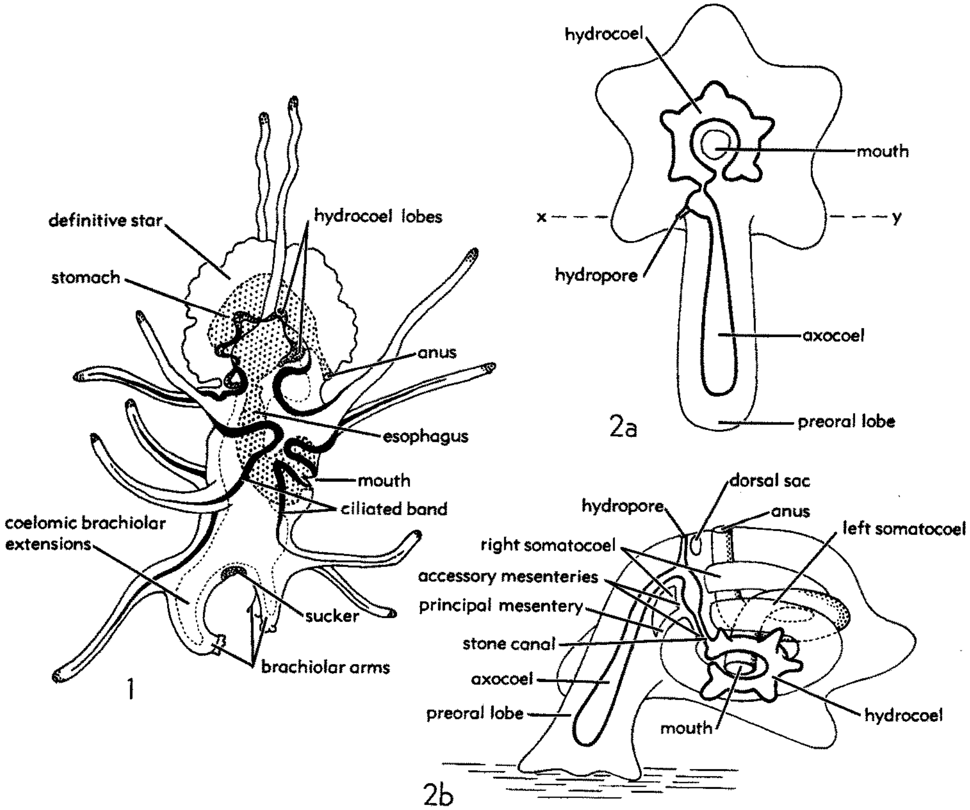

Fig. 16. Early stages in asteroid development.——*1.* Brachiolaria of *Asterias forbesi* in attached position, from left side, with definitive star formed from larval posterior region presenting its oral face to observer (Mead).——*2a,b.* Successive stages of flexion among asteroids, showing transverse 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

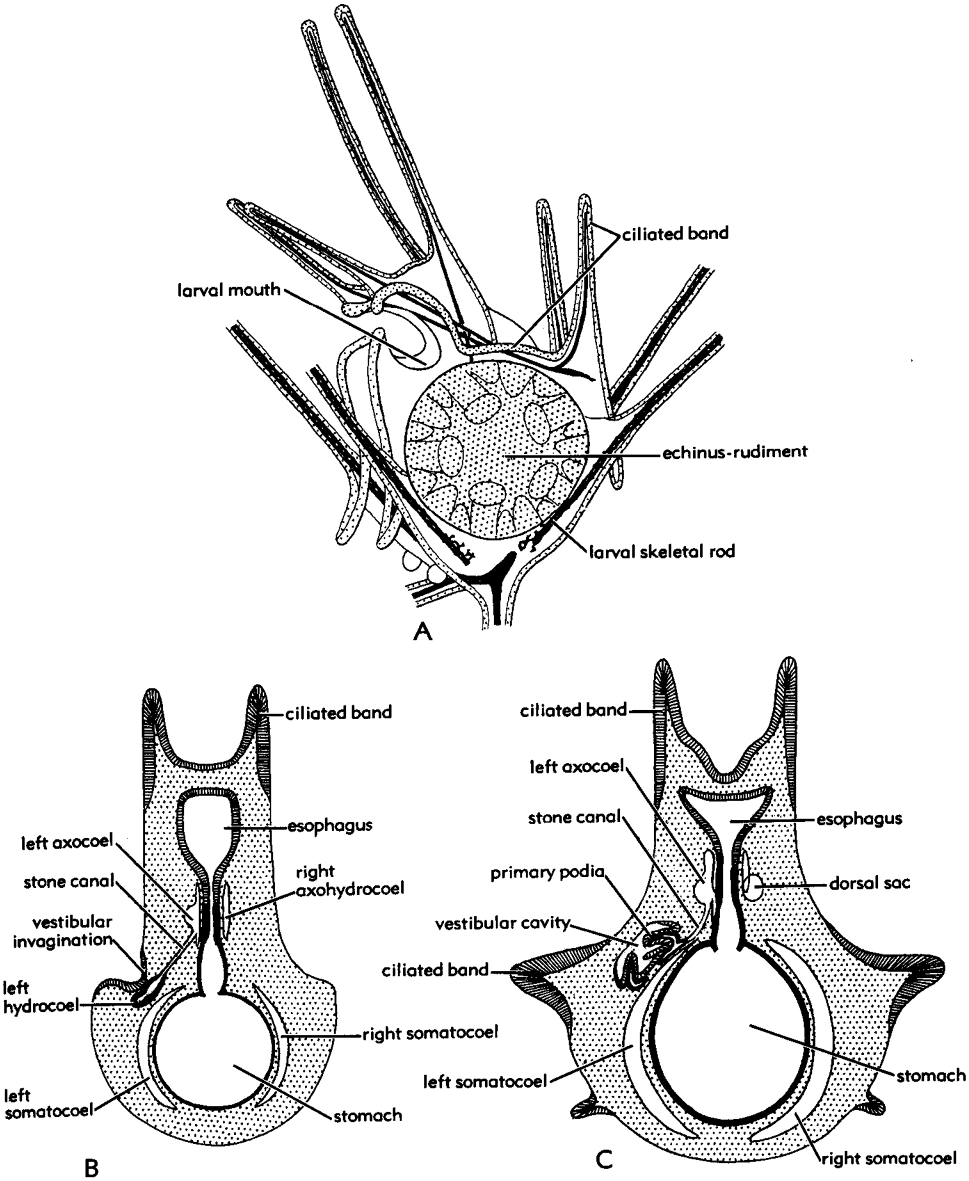

FIG. 17. Larval stages of echinoids.——*A*. Fully formed echinopluteus of *Arbacia punctulata* (LAMARCK) seen from left side, showing echinus rudiment (stippled area), ×100 (Gordon).——*B,C*. Diagrammatic frontal section through echinoplutei showing development of echinus rudiment on left side of larva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

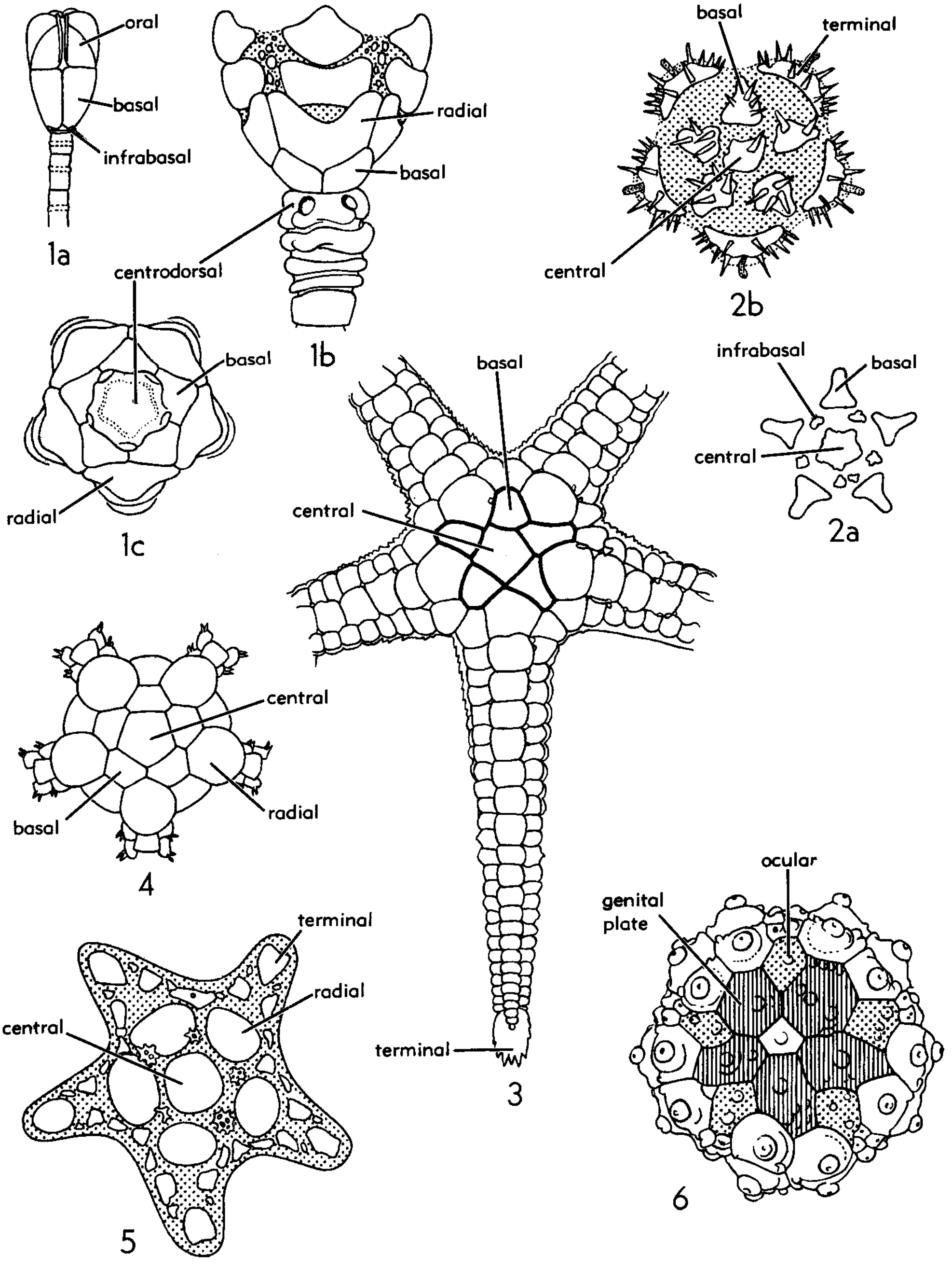

FIG. 18. Comparison of aboral endoskeletons of echinoderms.——*1. Promachocrinus kerguelensis* (crinoid); *1a,* very young larva, ×48 (Clark); *1b,c,* lateral and dorsal views of 2-year pentacrinoid stage, ×8 (Fell).——*2. Asterina* sp. (asteroid); *2a,b,* two stages, ×10 (Fell).——*3. Cnemidaster wyvillii* (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

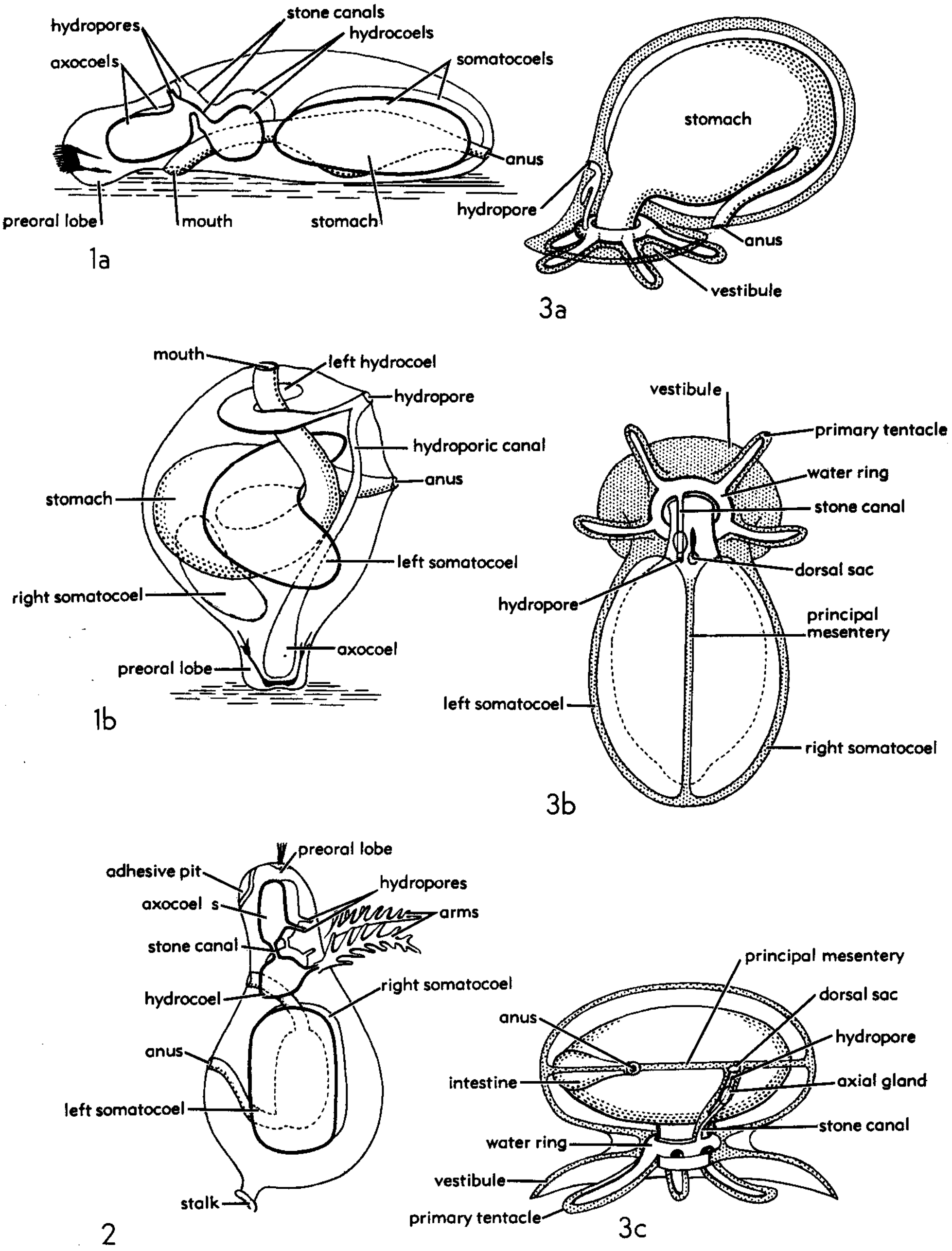

FIG. 19. Theoretical reconstructions of echinoderm ancestor.——*1*. Dipleurula ancestor; *1a,b,* from left side and after fixation (primitive pelmatozoic ancestor) (Bather).——*2*. Dipleurula ancestor (Heider).——*3*. Pentactaea ancestor; *3a-c,* from left side, dorsal view, and after torsion to radial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

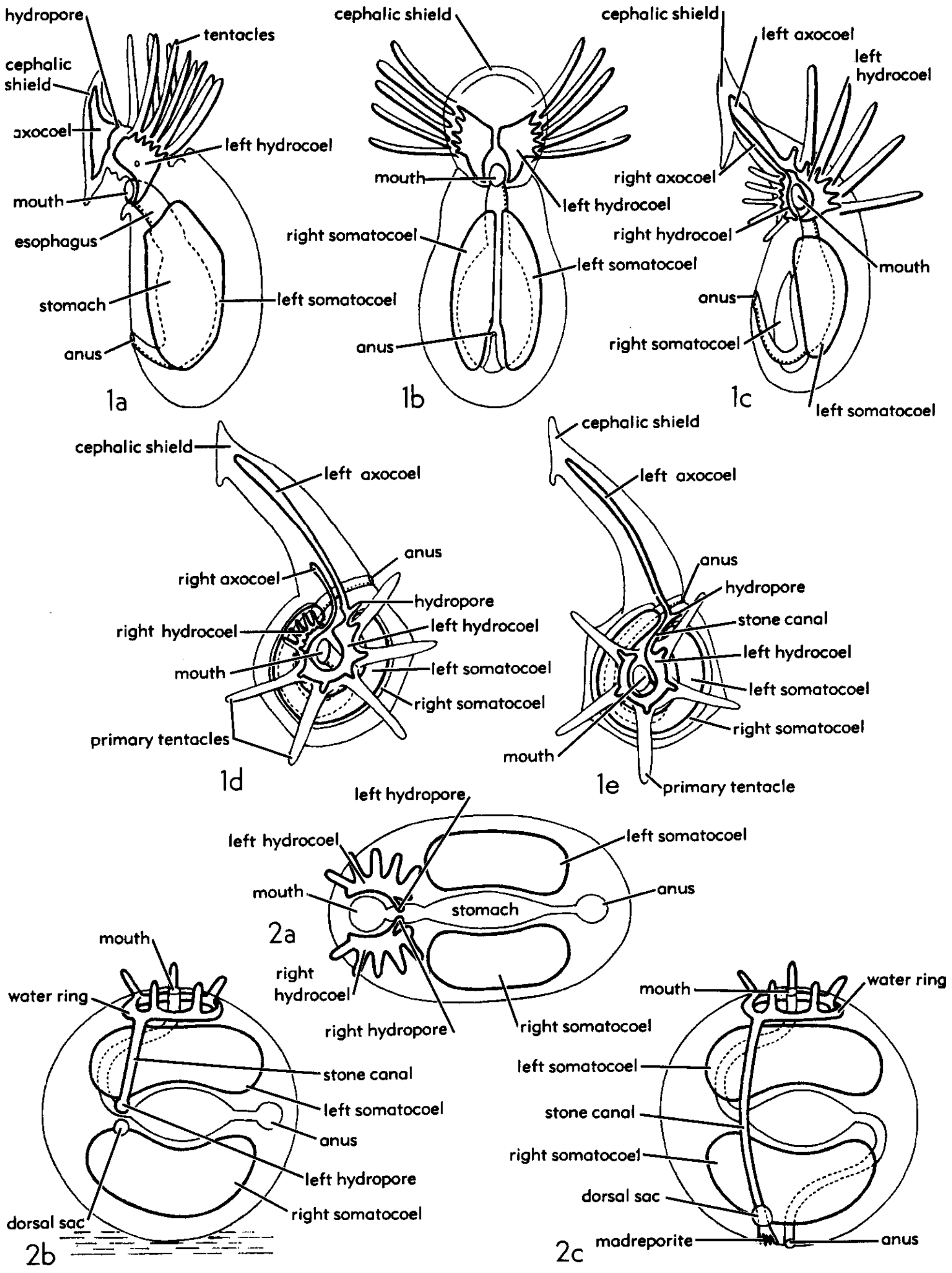

FIG. 20. Theoretical reconstructions of echinoderm ancestor (continued).——*1. Cephalodiscus*-like ancestor; *1a,b,* from left side and ventral view; *1c-e,* progressive stages in transformation to echinoderm, from left side (Grobben).——*2.* Echinoderm ancestor; *2a,* free-living bilateral form, ventral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

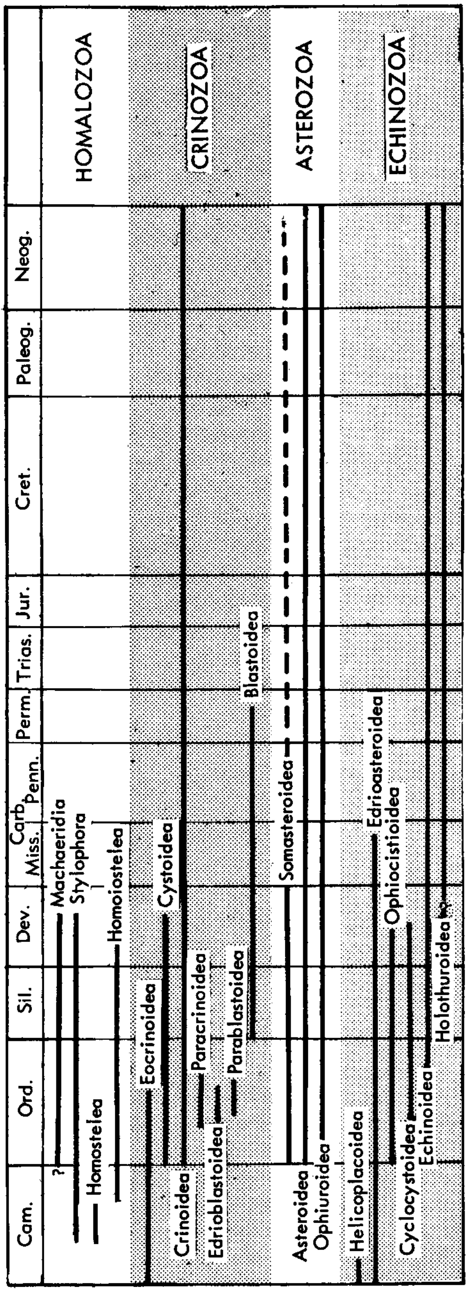

FIG. 21. Stratigraphic distribution of subphyla and class of Echinodermata (Ubaghs, n). [Added groups include the echinozoan class Camptostromatoidea (L. Cam.) and crinozoan class Lepidocystoidea (L. Cam.).]

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.**

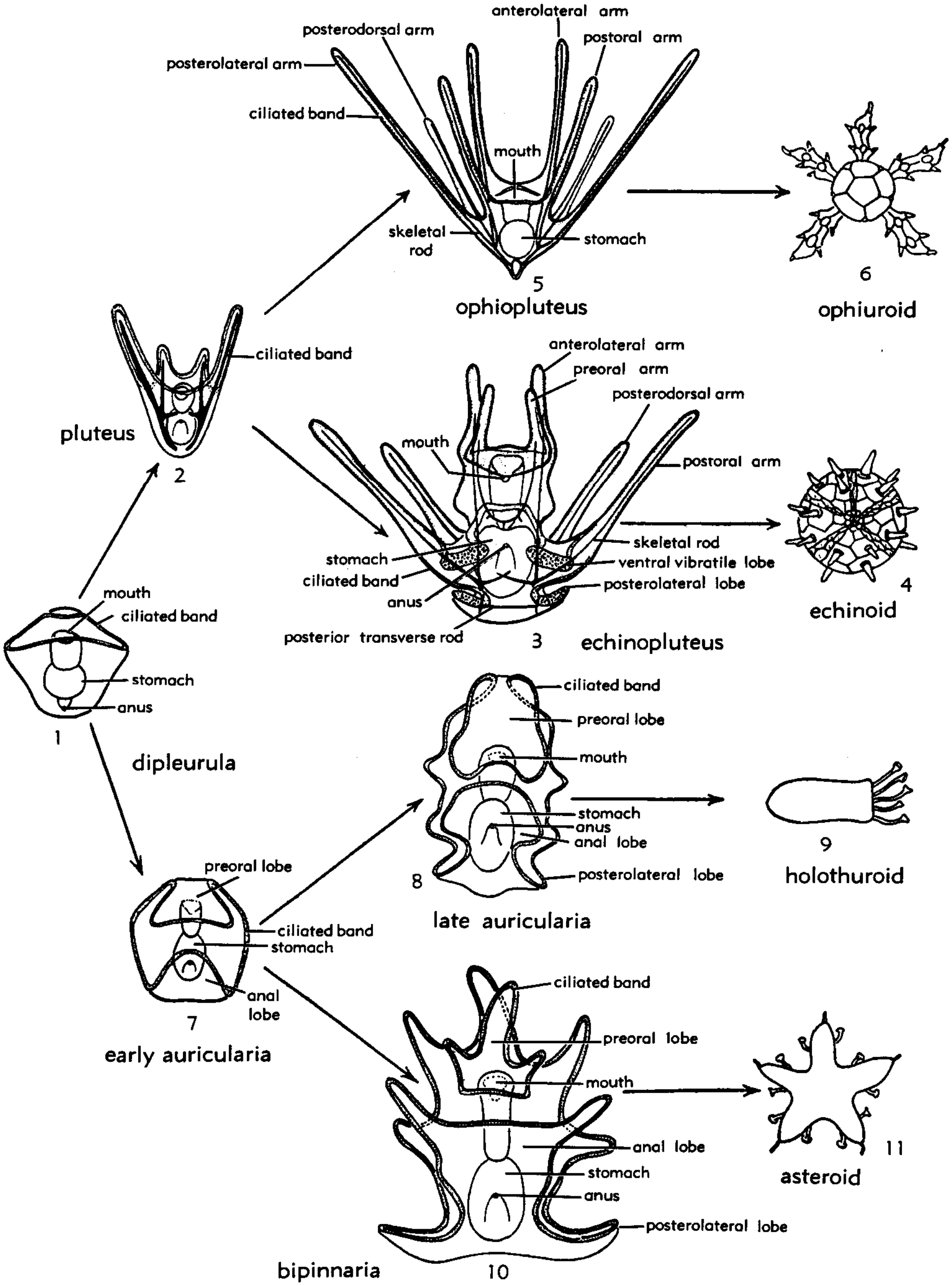

FIG. 22. General scheme illustrating relationships between bilaterally symmetrical larvae of echinoderms inferred from their morphology. *1*, Dipleurula; *2*, pluteus; *3*, echinopluteus, which metamorphoses into *4*, young echinoid; *5*, ophiopluteus, which metamorphoses into *6*, young ophiuroid; *7*,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

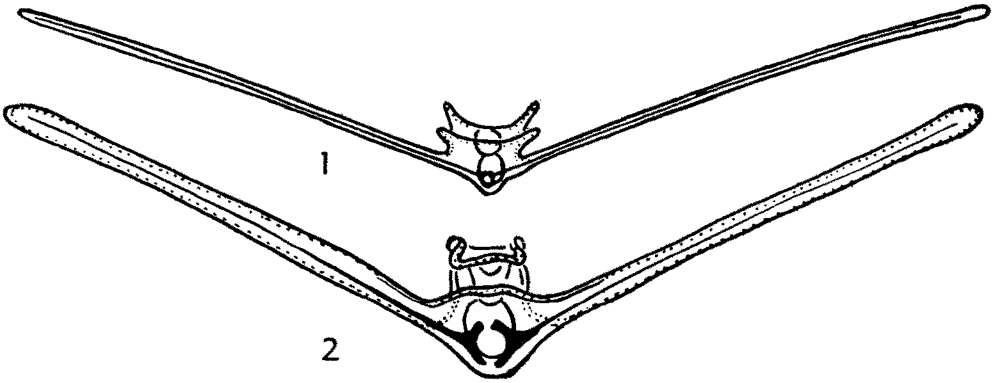

FIG. 23. Convergent larval forms. *1,* Ophiuroid, *Ophiothrix; 2,* echinoid, *Diadema* (8).

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.

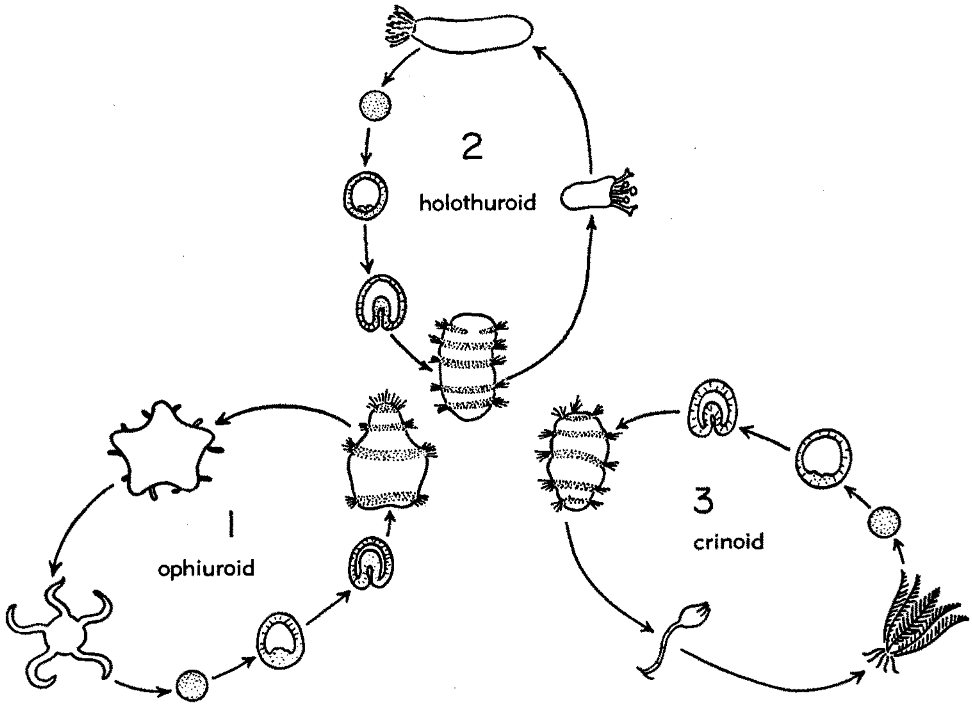

FIG. 24. Convergent patterns of development in unrelated echinoderms. *1*, Ophiuroid *(Ophioderma)*; *2*, holothuroid *(Cucumaria)*; *3*, crinoid *(Antedon)*. In each the larva is a banded vitellaria, which is a widely shared larval form now known to occur in three families of ophiuroids, most holothuroids,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

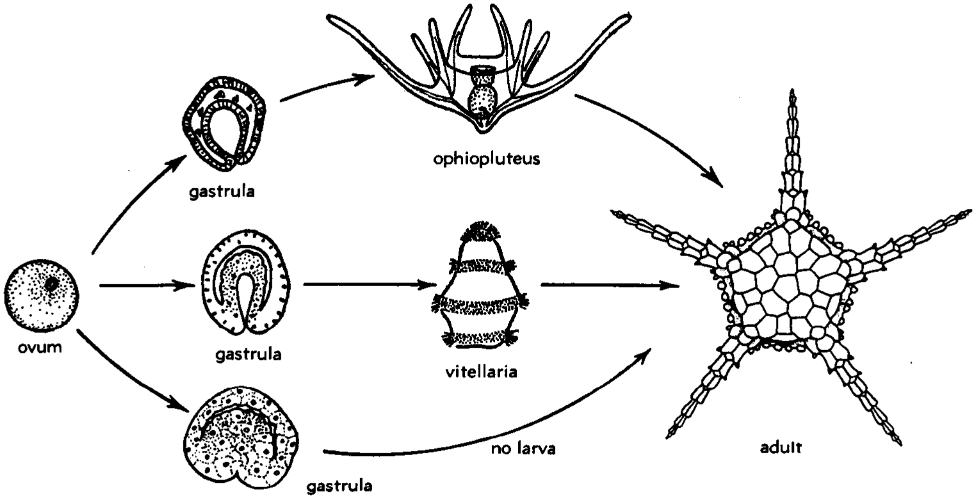

FIG. 25. Divergent patterns of development in ophiuroids. Above, with ophiopluteus larva, as in Ophiothricidae, some Amphiuridae, Ophiocomidae, and some Ophiuridae. Middle, with vitellaria larva, as in Ophiodermatidae, Ophionereidae, and some Ophiuridae. Below, with no larval form, as in Ophiomyxidae 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-

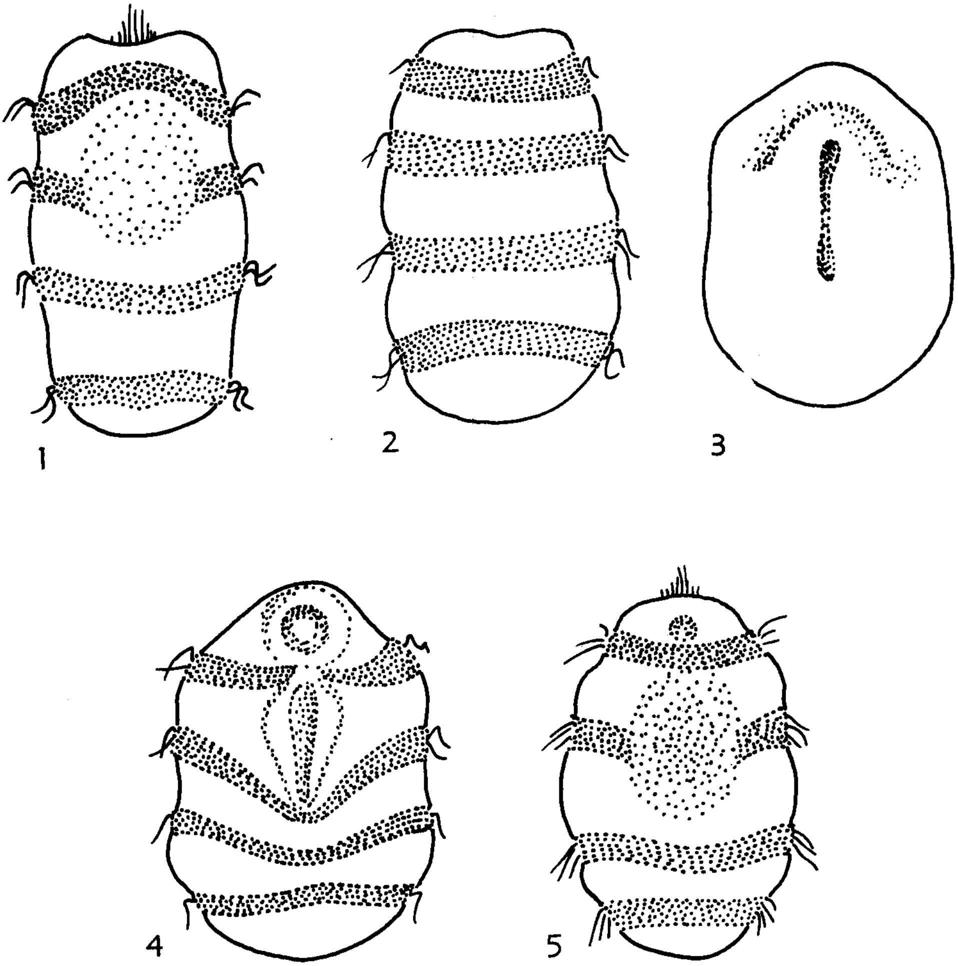

Fig. 26. Vitellaria larvae of comatulid crinoids.—*1. Tropiometra carinata* (Lamarck), Tropiometridae, ×160 (23).—*2. Heterometra savignyi* (J. Müller), Himerometridae, ×240 (28c).—*3. Notocrinus virilis* Mortensen, Notocrinidae, ×24 (28a).—*4. Isometra vivipara* Mortensen, Antedonidae, ×75 (23).—*5.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

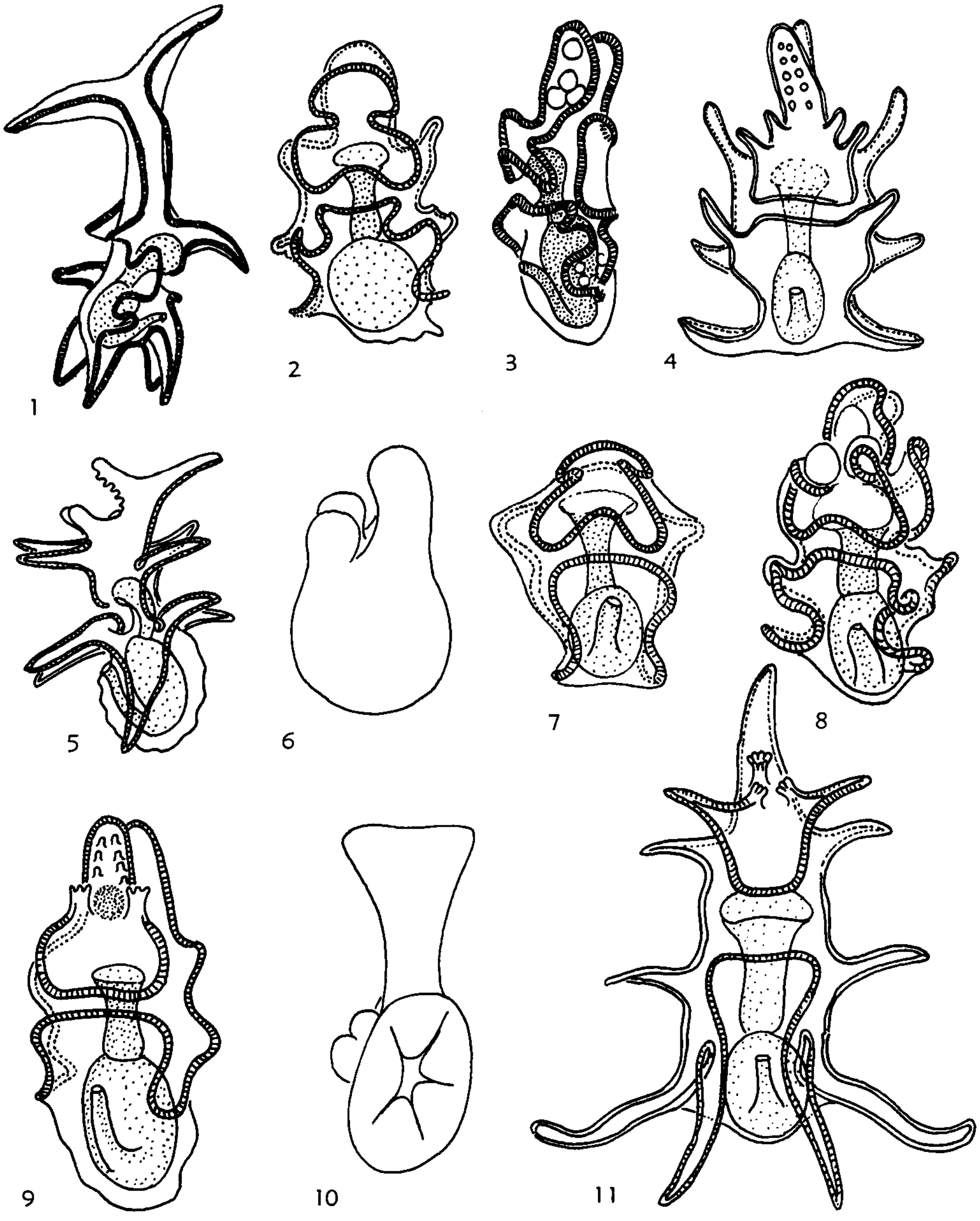

Fig. 27. Larvae of asteroids; bipinnariae *(1,2,7)* and brachiolariae *(3-6, 8-11)*.—*1. Luidia* sp. (*?sarsi* Düben & Koren), Platyasterida, Luidiidae, ×18 (15).—*2. Astropecten scoparius* Müller & Troschel, Paxillosina, Astropectinidae, ×48 (24).—*3. Archaster typicus* Müller & Troschel, Valvatina, 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*.

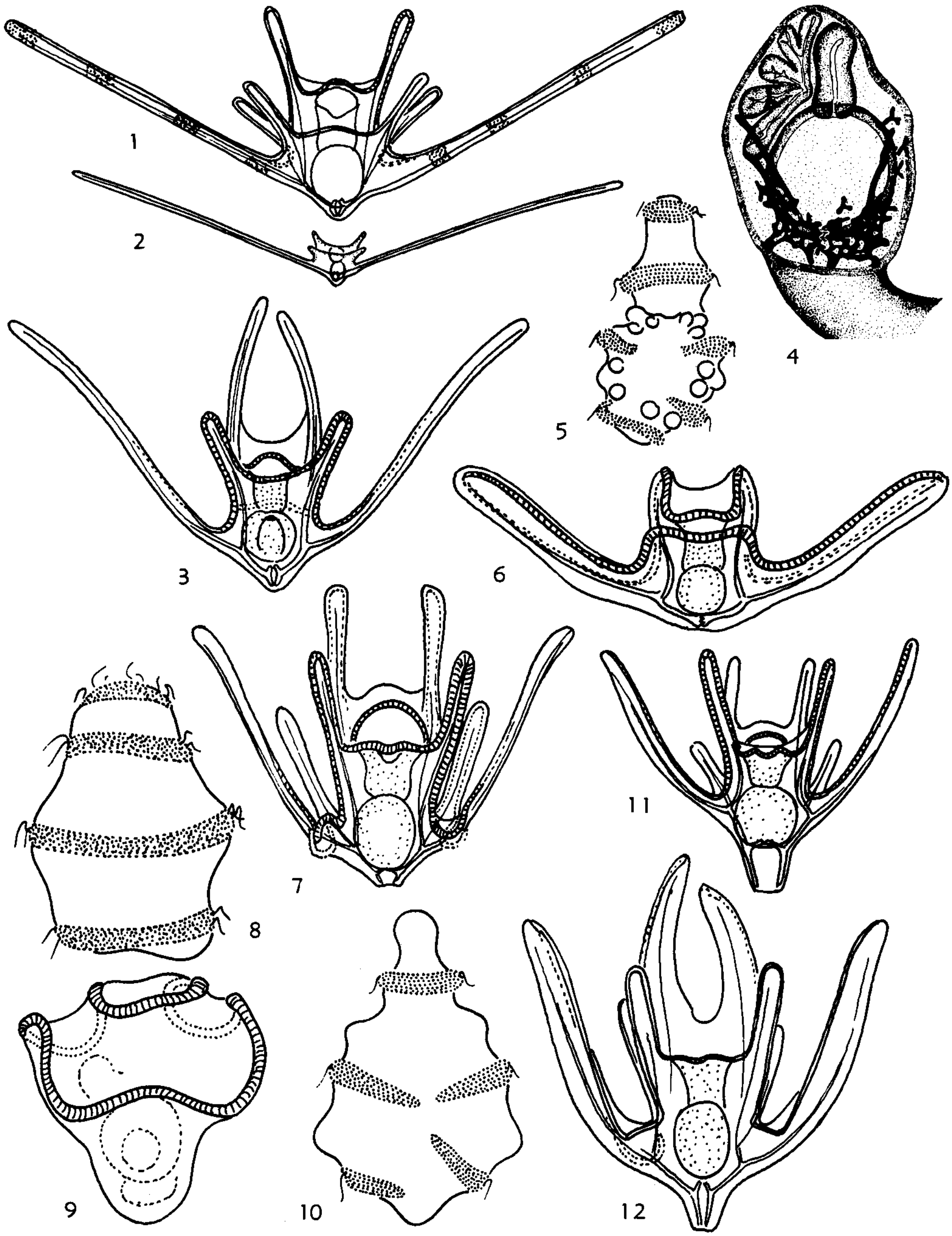

FIG. 28. Larvae of ophiuroids, ophioplutei *(1-4, 6,7,9,11,12)* and vitellariae *(5,8,10)*. All belong to order Ophiurida, larvae being unknown from other orders.—*1,2*. Ophiothricidae; *1, Ophiothrix savignyi* (MÜLLER & TROSCHEL), ×72 (28c); *2, Ophiothrix* sp., ×22 (24).—*3,4*, Amphiuridae; *3, Icalia 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-

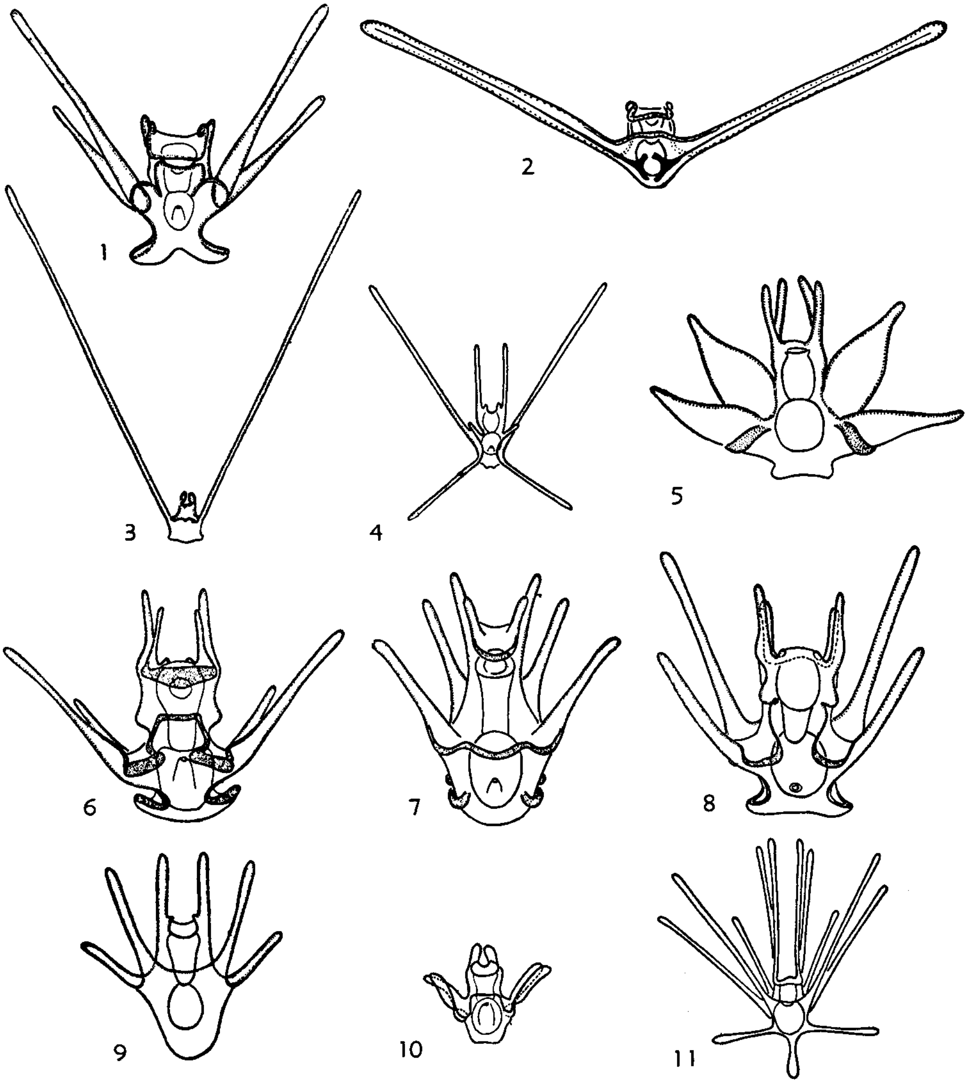

Fig. 29. Echinopluteus larvae of echinoids.—*1. Prionocidaris baculosa* (Lamarck), Cidaroida, Cidaridae, ×30 (28c).—*2. Diadema setosum* Gray, Diadematoida, Diadematidae, early larva, ×42 (28a).—*3.* Same, later stage (28b).—*4. Arbacia stellata* (Blainville), Arbacioida, Arbaciidae, ×24 (24).—*5. Mespilia 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-

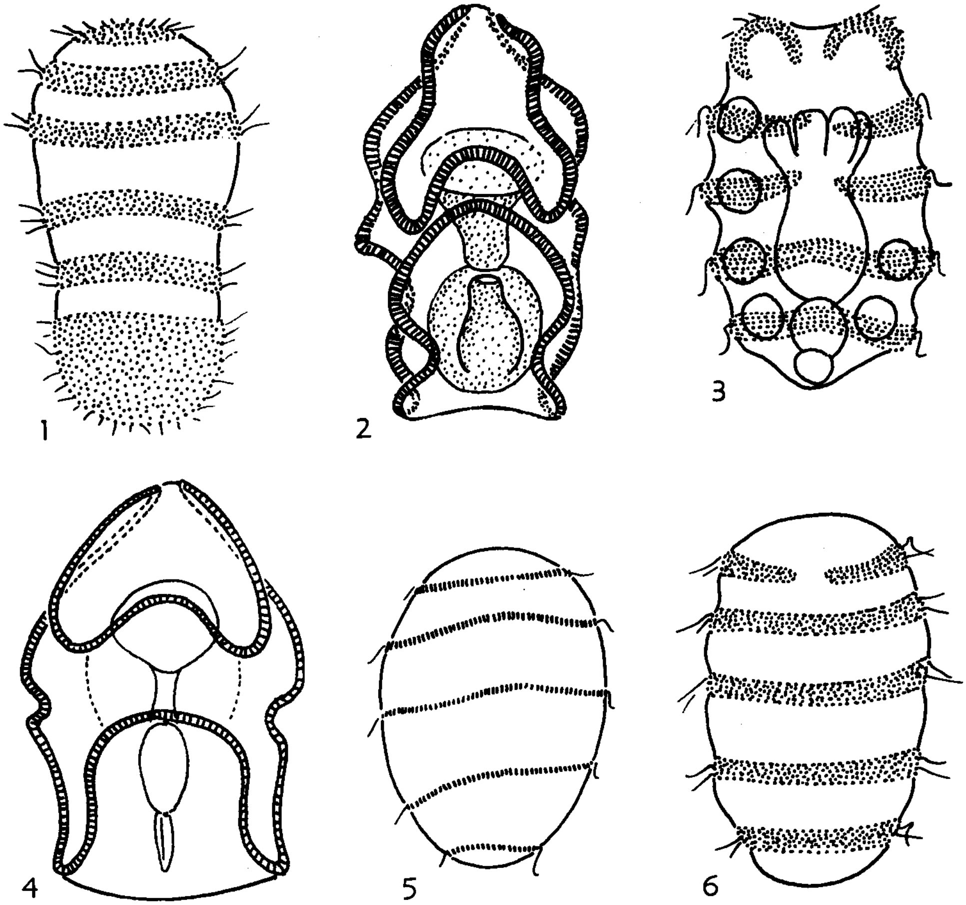

Fig. 30. Vitellaria larvae (doliolaria) *(1,3,5,6)*, and auricularia larvae *(2,4)* of holothuroids.—*1.* Dendrochirotida, *Cucumaria planci* von Marenzeller, Cucumariidae, ×135 (32).—*2.* Aspidochirotida, *Stichopus californiensis* (Stimpson), Stichopodidae, ×56 (24).—*3.* Aspidochirotida, *Holothuria 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 buski*. 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.

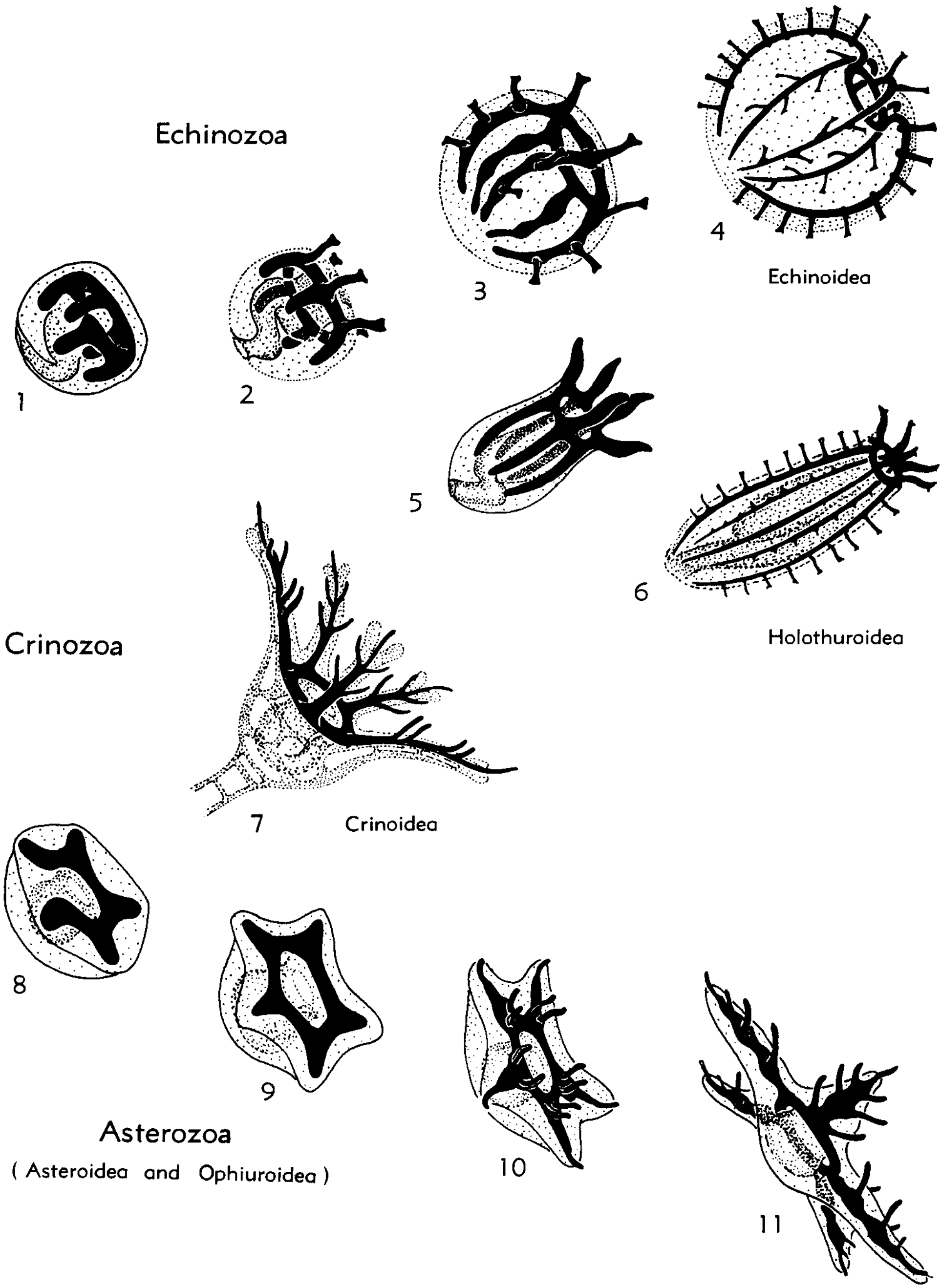

FIG. 31. Major patterns of growth gradients initiated by the hydrocoel during metamorphosis and immediately following it (hydrocoel shown in solid black). Echinozoa *(1-6)* display meridional patterns, whereas Crinozoa *(7)* and Asterozoa *(8-11)* exhibit divergent radial patterns (10) (Fell, n).

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

By ROBERT V. KESLING

[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

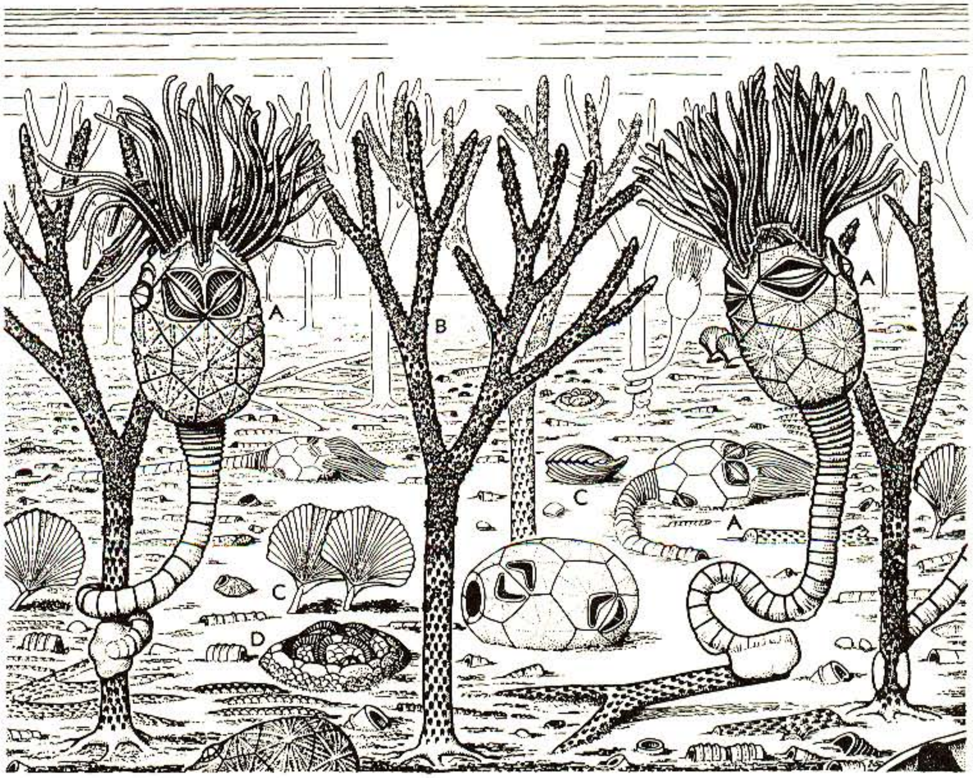


FIG. 32. Reconstruction of sea floor in southern Indiana during Richmond (Late Ordovician) time, showing *(A) Lepadocystis moorei* (MEEK), *(B)* ramose bryozoans, *(C)* small brachiopods, and *(D)* edrioasteroids in natural association (75).

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

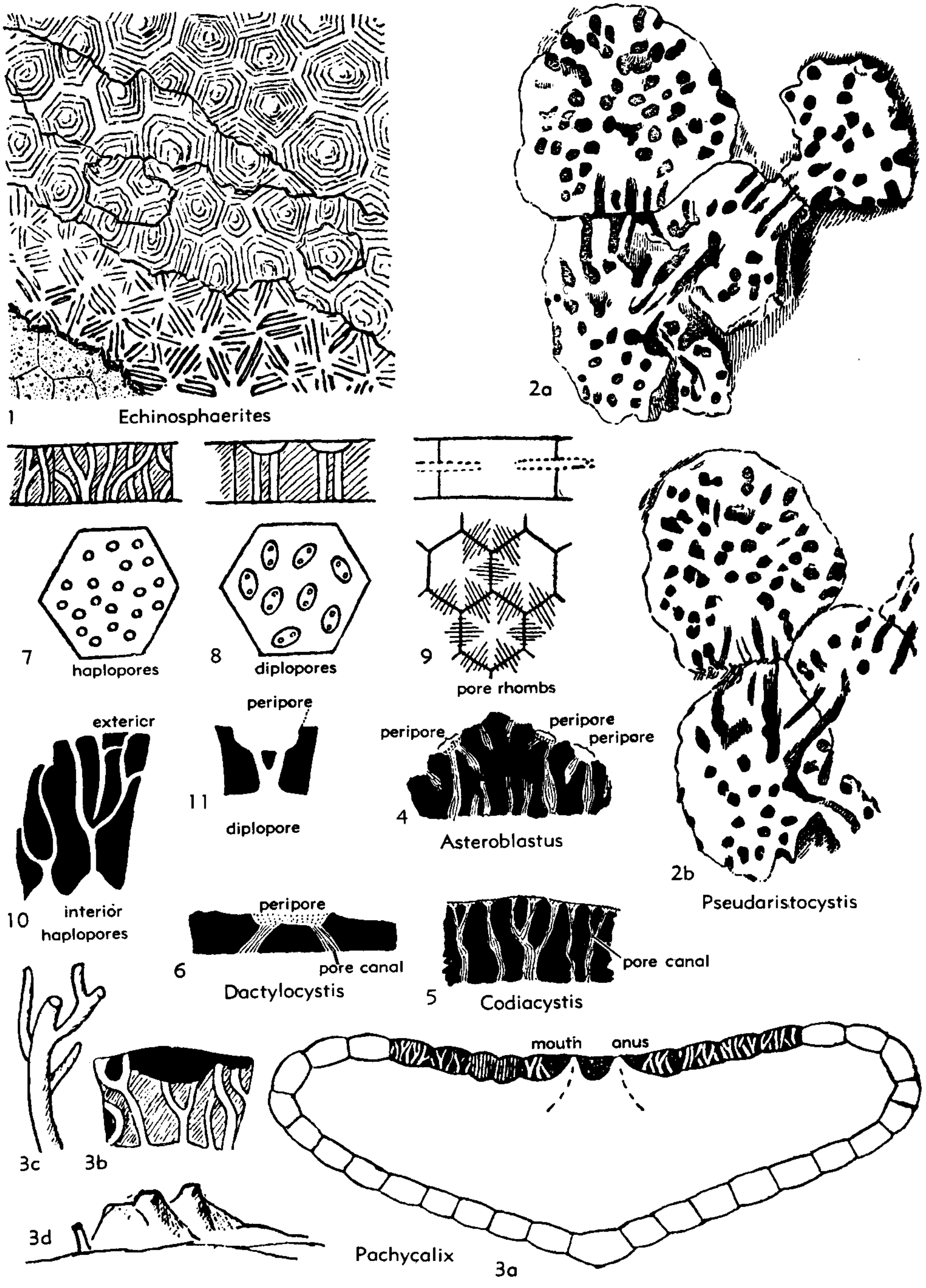
The diplopore type of thecal pores may well be older than pore rhombs, despite the reference by REGNÉLL (99) to "the fact that the Rhombifera appeared, as far as known, earlier than the Diploporita." The Middle Cambrian doubtful genera *Lapillocystites* and *Pilocystites* from Bohemia appear to be related 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.

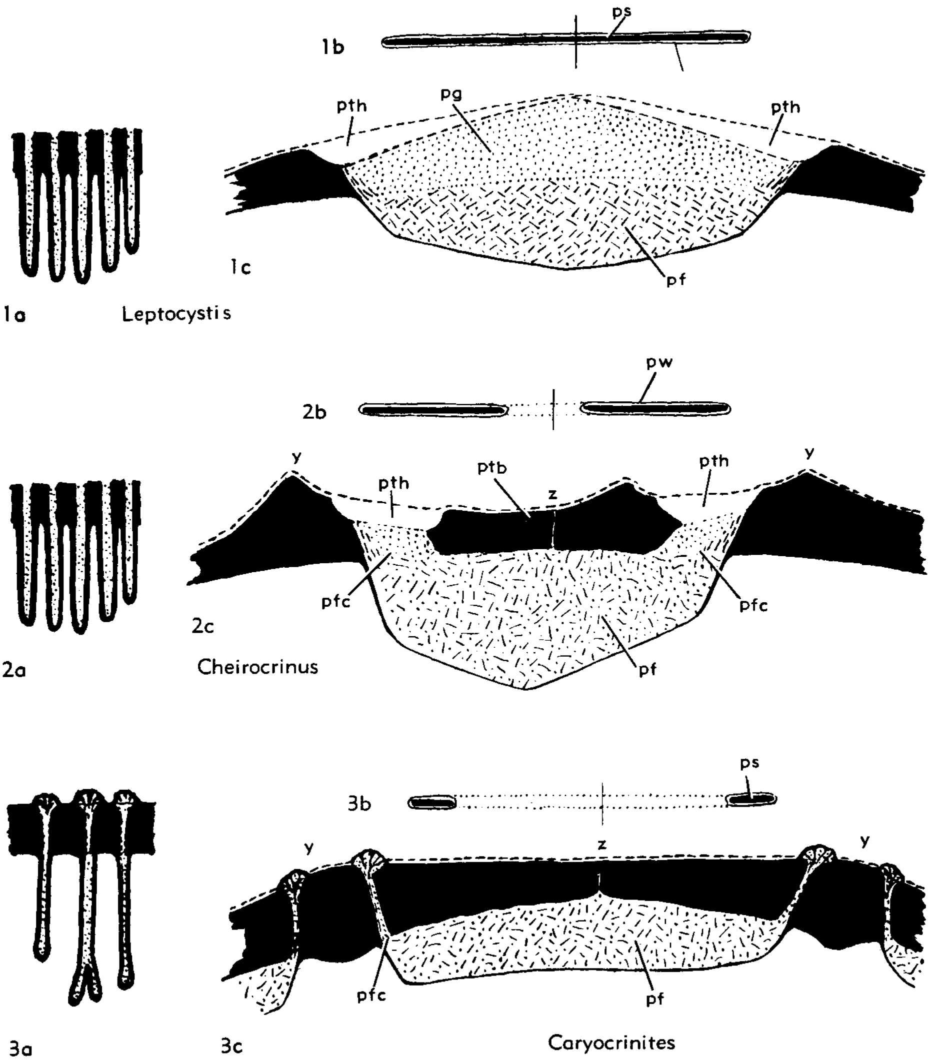


FIG. 34. Diagrammatic sections across pores *(1a, 2a, 3a)*, top views of pores *(1b, 2b, 3b)*, and sections along pores *(1c, 2c, 3c)* in selected cystoids.——*1. Leptocystis* (L.Ord.-L.Sil.), typical of conjunct pectinirhombs in Glyptocystitida.——*2. Cheirocrinus* (L.Ord.-U.Ord.), typical of disjunct 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-

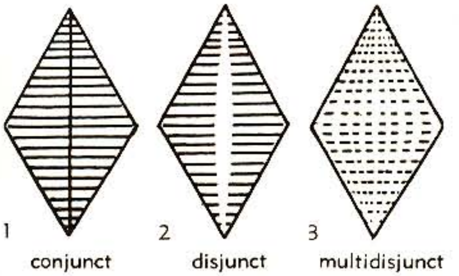


FIG. 35. Three principal types of pectinirhombs (12).

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

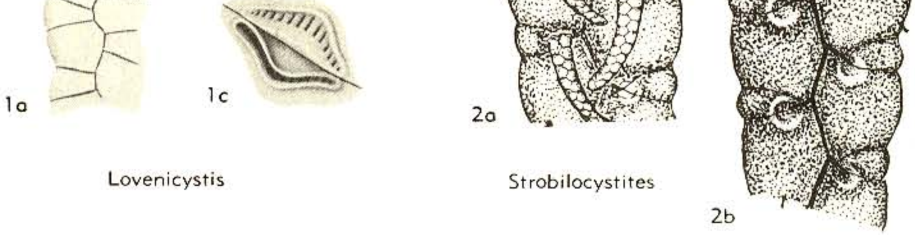


FIG. 36. Ambulacral and pore-rhomb structures of cystoids.——*1. Lovenicystis* (U.Sil.); *1a,* ambulacrum, covering plates in upper (proximal) section, flooring plates removed to show impressions on thecal plates in lower (distal) section; *1b,c,* examples of montidisjunct pectinirhombs (99).——*2. Strobilocystites* (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).

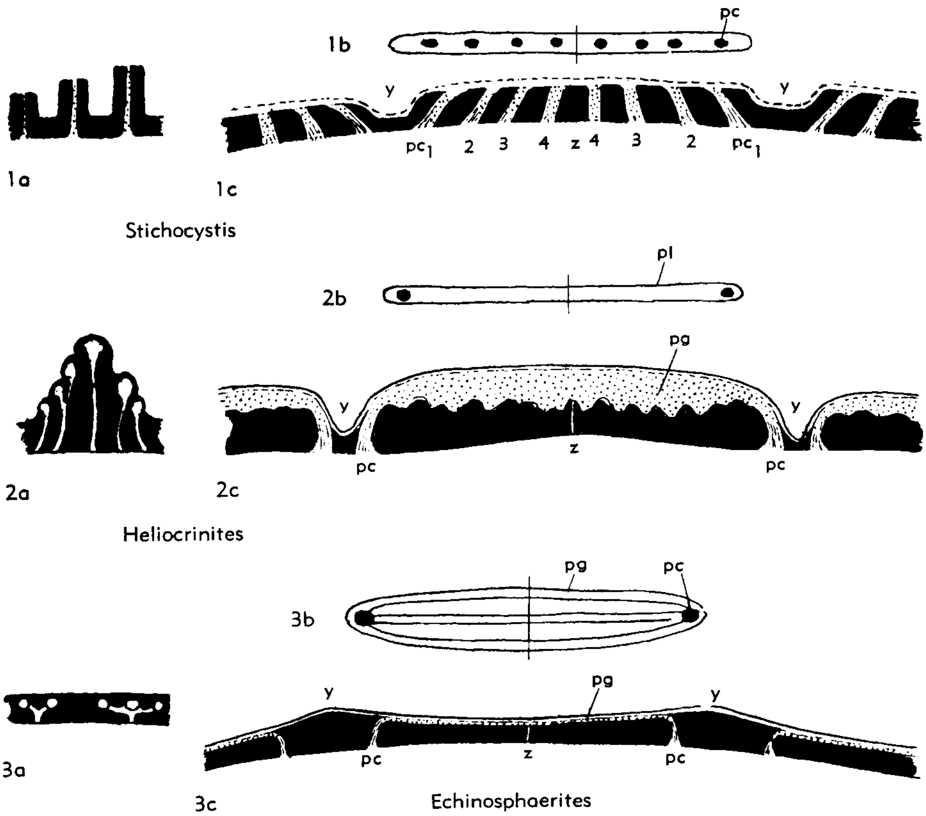


Fig. 37. Diagrammatic section across pores (*a*), top view of a pore (*b*), and section along a pore (*c*) in selected cystoids. ——*1. Stichocystis* (M.Ord.), typical of pore rhombs in Polycosmitida.——*2. Heliocrinites* (L.Ord.-U.Ord.), typical of simple tangential pore canals in Caryocystitida.——*3. 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

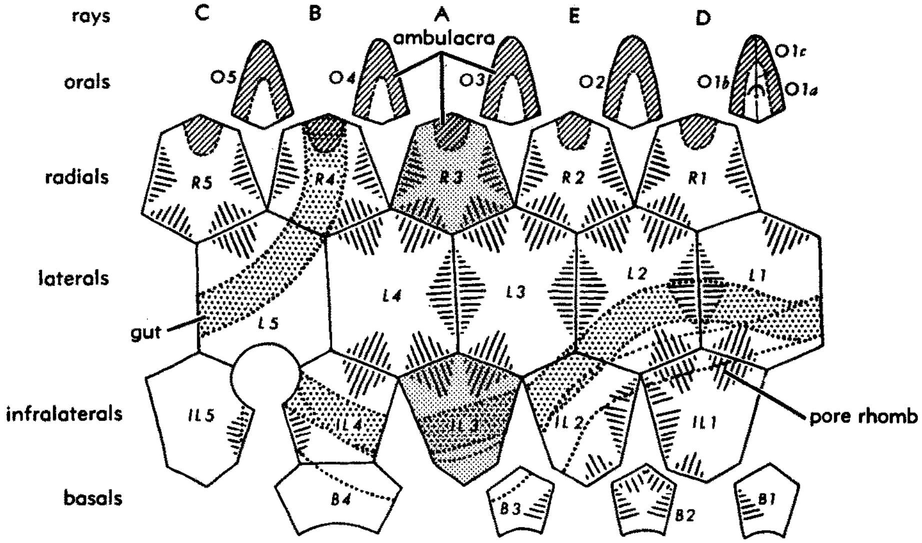


FIG. 38. Generalized plate diagram of a glyptocystitidan cystoid, with plate designations by REGNÉLL (adopted in the *Treatise*): *B*, basal; *IL*, infralateral; *L*, lateral; *O*, oral; *R*, radial. Ambulacra are indicated by oblique ruling on orals and radials. Pore rhombs are shown in all positions 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-*

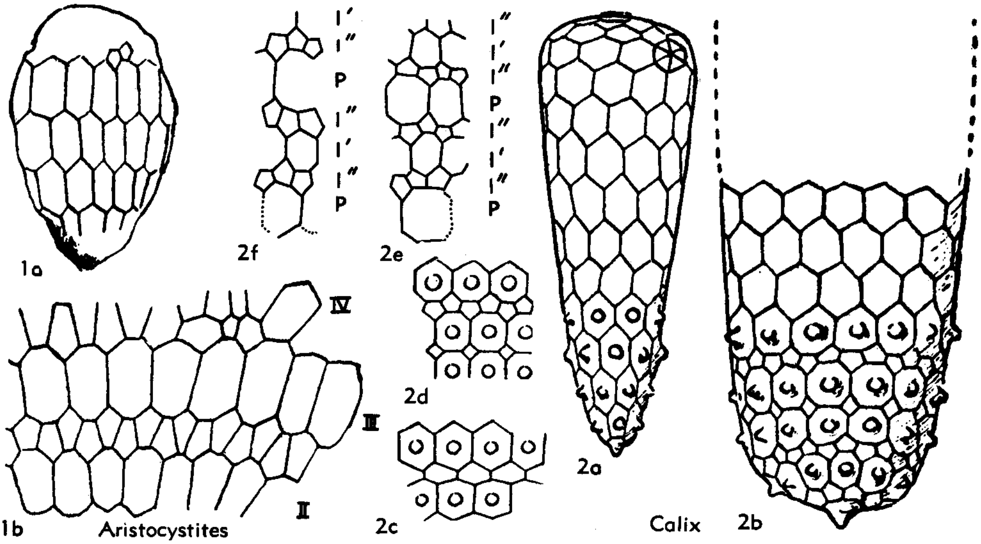


Fig. 39. Growth by interstitial addition of plates.——*1. Aristocystites bohemicus* Barrande (M.Ord.); *1a,* stage 1, in which plates are subequal, ×0.8; *1b,* stage 2, in which secondary plates have been inserted in circlets.——*2. Calix sedgwicki* Rouault (M.Ord.); *2a,* stage 1, ×1; *2b-d,* stage 2, 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

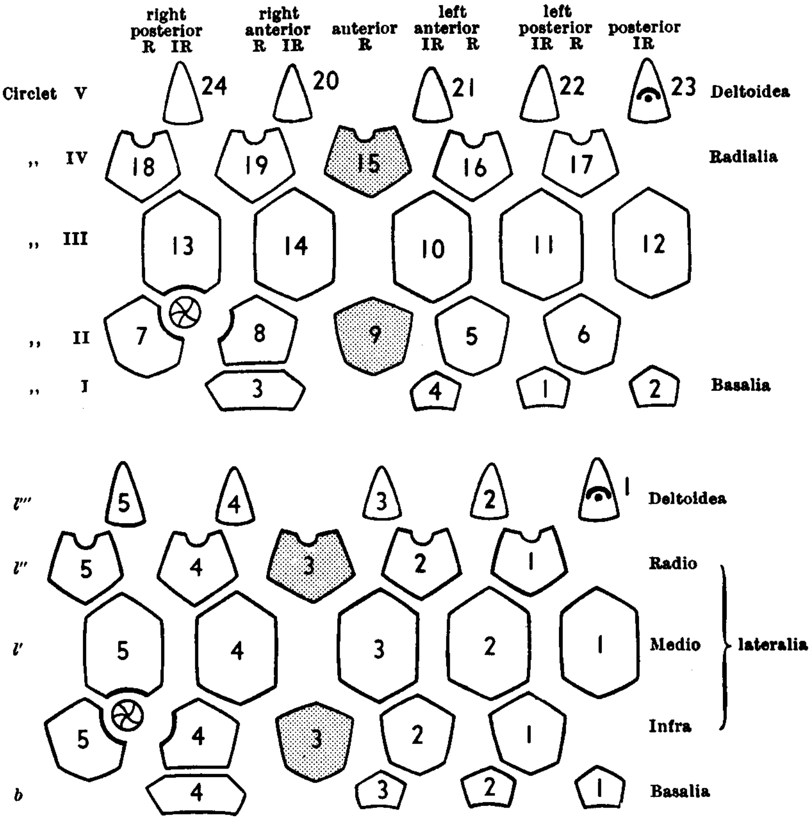


FIG. 40. Generalized plate diagrams of glyptocystitidan cystoids (plates of *A*-ray shaded), with designations by FORBES and BATHER (above) and by JAEKEL (below) (12).

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.

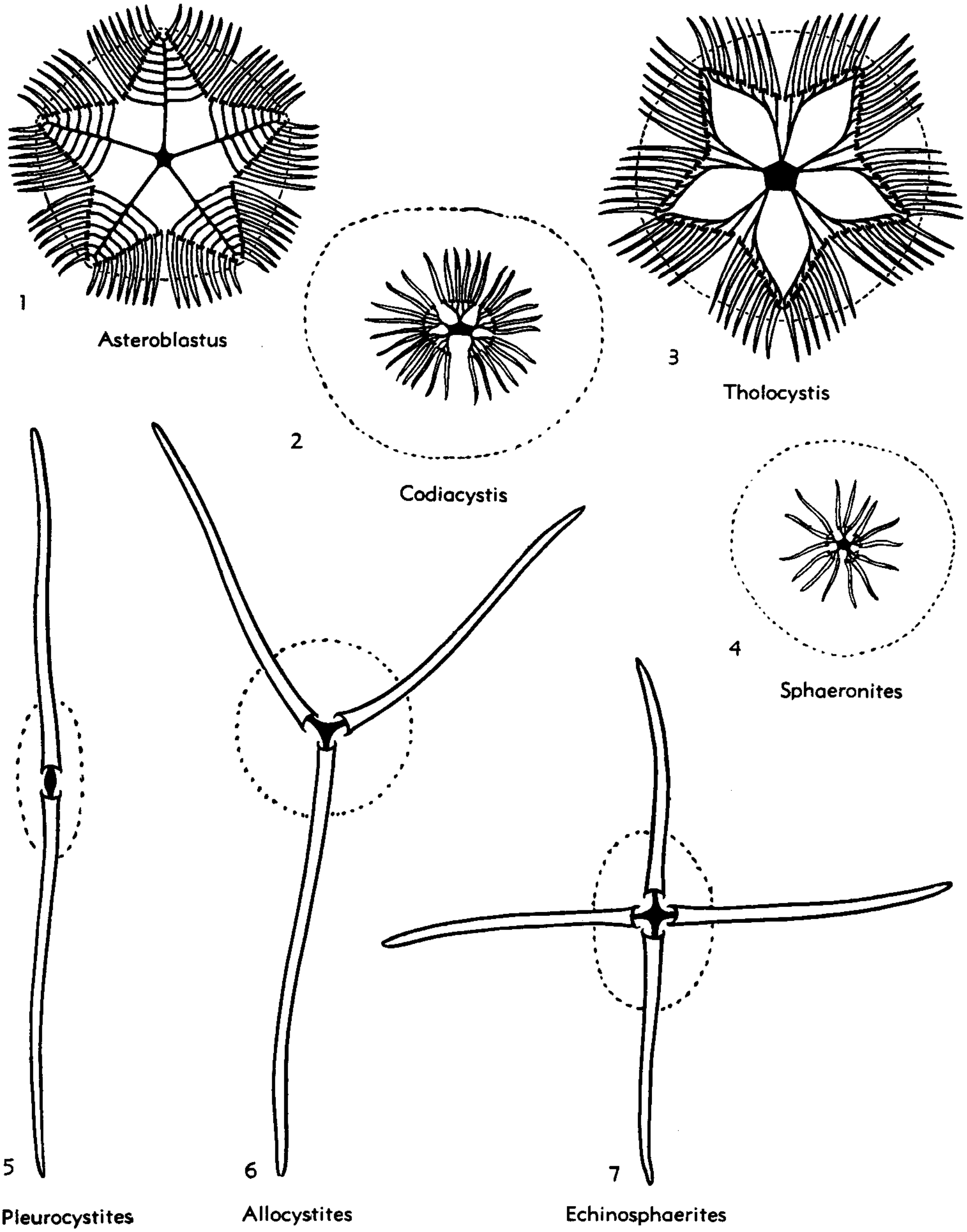


FIG. 41. Diagrammatic oral projections of ambulacral systems (69, Kesling, n).

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

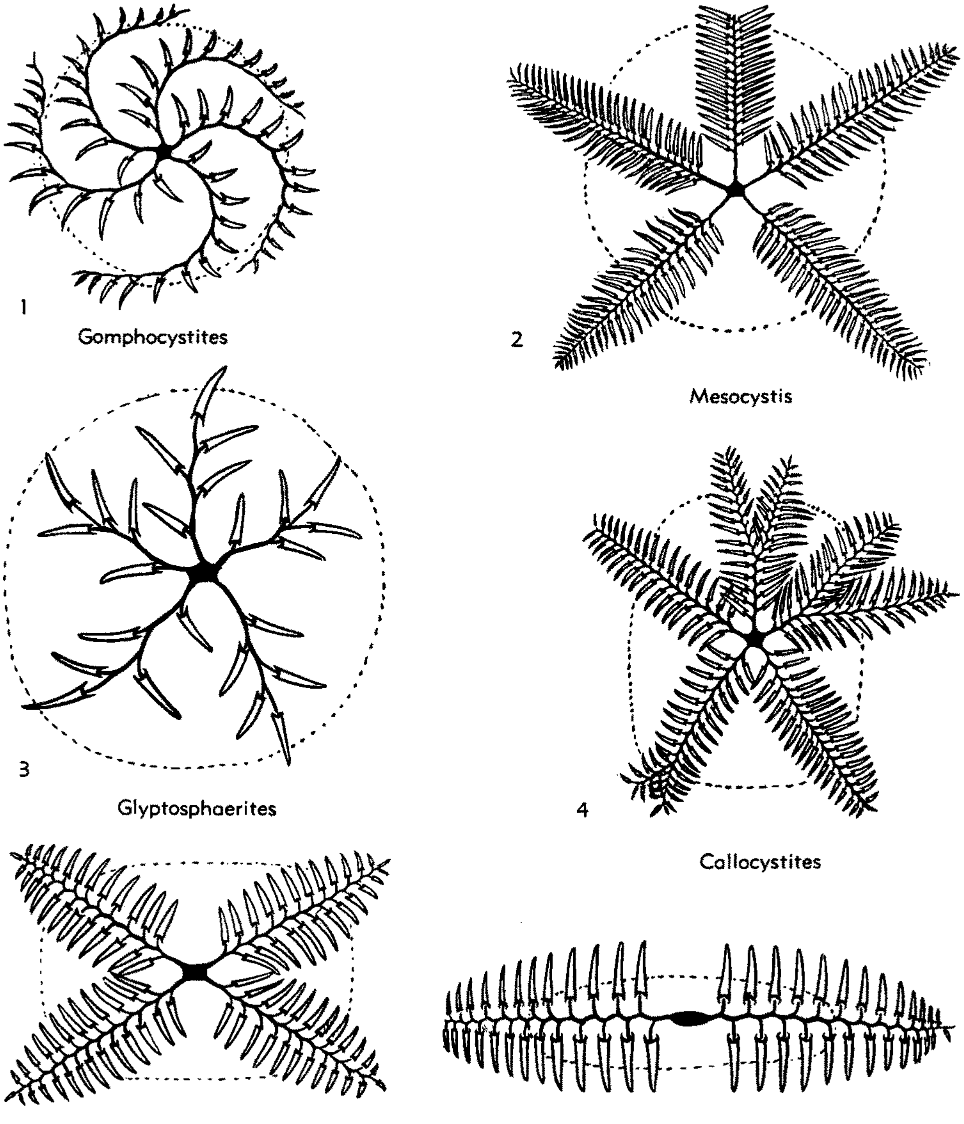


FIG. 42. Diagrammatic oral projections of ambulacral systems (69).

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

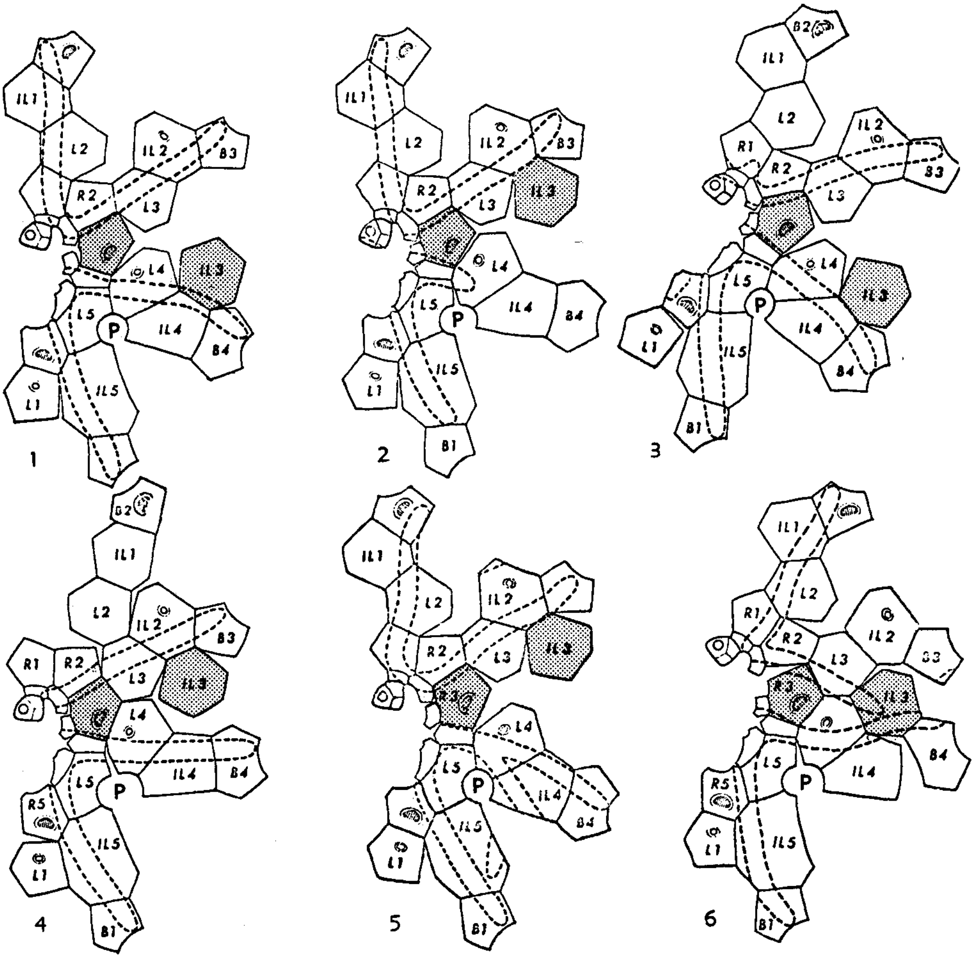


FIG. 43. Variations in ambulacra in *Jaekelocystis hartleyi* SCHUCHERT (L. Dev.); *1*, ambulacra typically developed; *2*, ambulacrum *IV (B)* short; *3*, ambulacrum *I (D)* deformed; *4*, ambulacrum *I (D)* aborted; *5*, ambulacrum *IV (B)* bifurcate; *6*, ambulacrum *II (E)* abutting on *IV (D)* (73).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

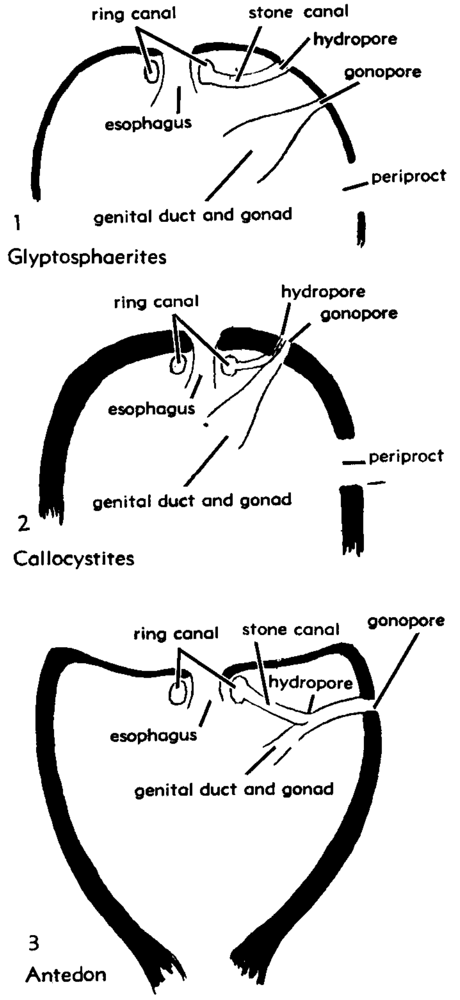


FIG. 44. Cross sections through peristome, hydropore, gonopore, and periproct.——*1,2.* Hypothetical reconstructions of *Glyptosphaerites* (L.Ord.-U.Ord.) and *Callocystites* (M.Sil.).——*3.* Young stage of *Antedon* (Rec.) (69).

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

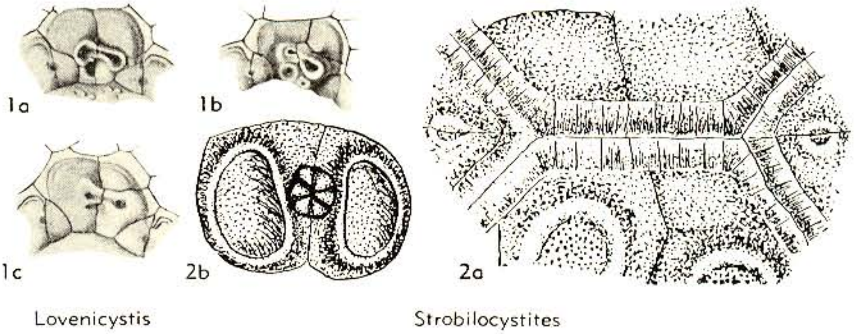


FIG. 45. Hydropore and gonopore features.——*1. Lovenicystis* (U.Sil.); *1a-c,* posterior sector or oral region showing various forms of hydropore and gonopore.——*2. Strobilocystites* (M.Dev.-U.Dev.); *2a,b,* peristome and bipartite hydropore and pyramid-closed gonopore (99, 120).

(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-

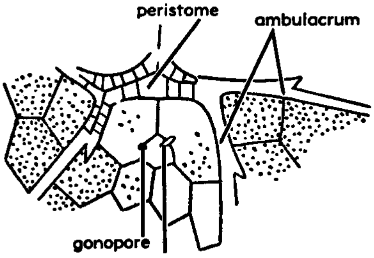


FIG. 46. *Protocrinites fragum* (EICHWALD) (L. Ord.). Diagrammatic plan of the posterior part of the oral region (146).

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.

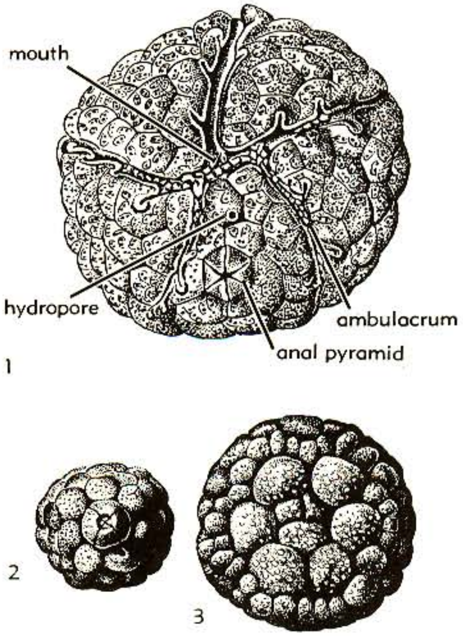


FIG. 47. *Protocrinites oviformis* EICHWALD (M. Ord.); *1*, oral view, ×1.5; *2,3*, aboral views of very young and adult individuals, showing ontogenetic changes in which traces of the cicatrix of columnar attachment are eradicated, ×1 (10).

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

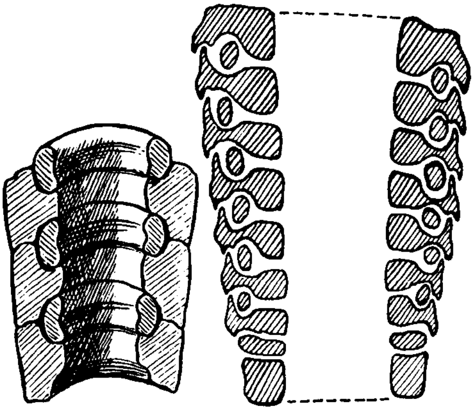


FIG. 48. Sections through proximal parts of the column, showing association of two alternating kinds of columnals.——*1. Cheirocrinus* (L.Ord.-U.Ord.).——*2. Strobilocystites* (M.Dev.-U.Dev.) (12, 120).

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-

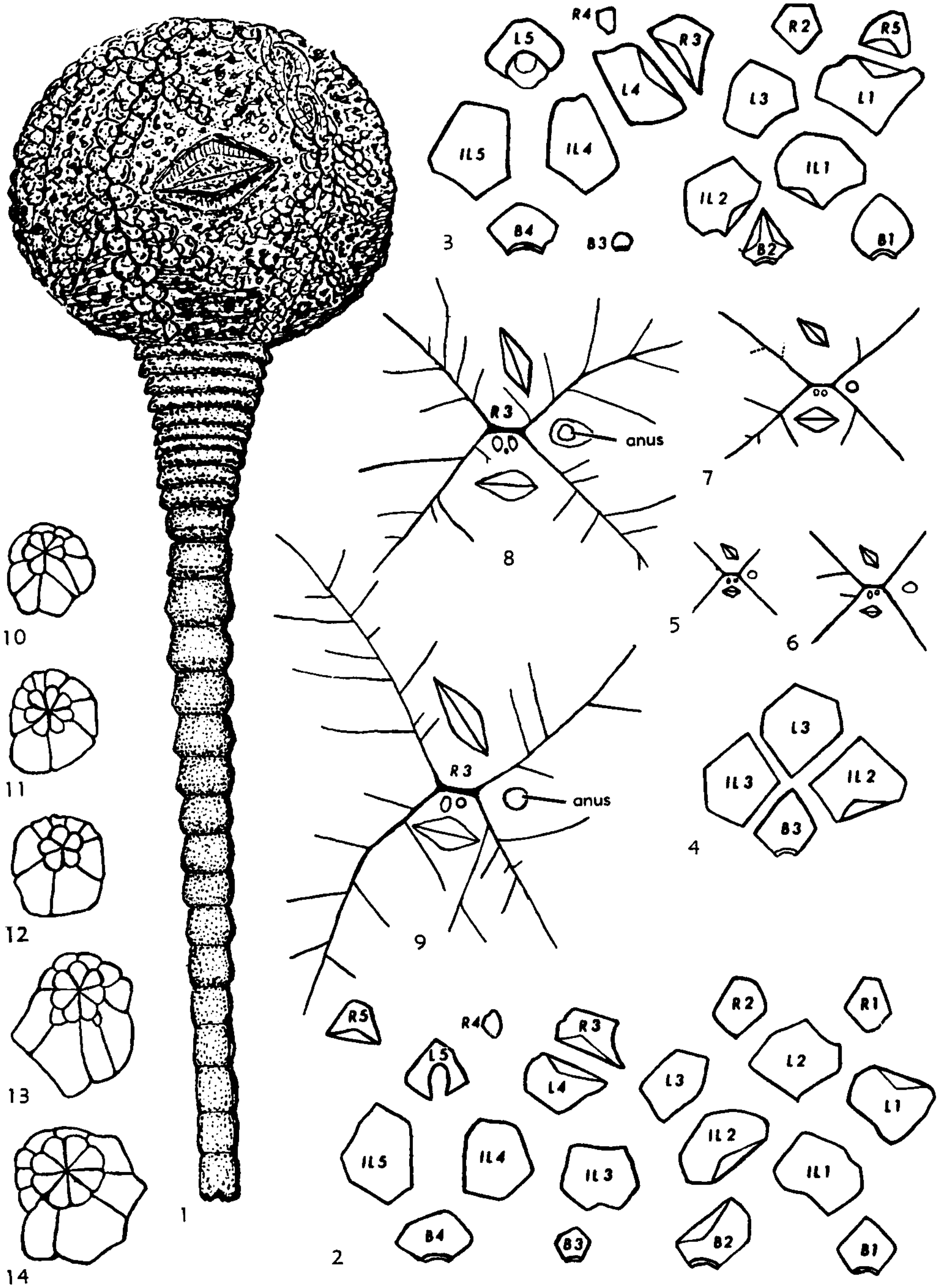


Fig. 49. Structures of *Strobilocystites* (M.Dev.-U.Dev.) and their variations.——*1. S. calvini* White (M. Dev.), restoration, ×2.——*2.* Diagram of plates in nearly average specimen, except that *B3* (4) is rather small (plates of *A*-ray shaded).——*3.* Diagram of plates of anomalous specimen in which *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-

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

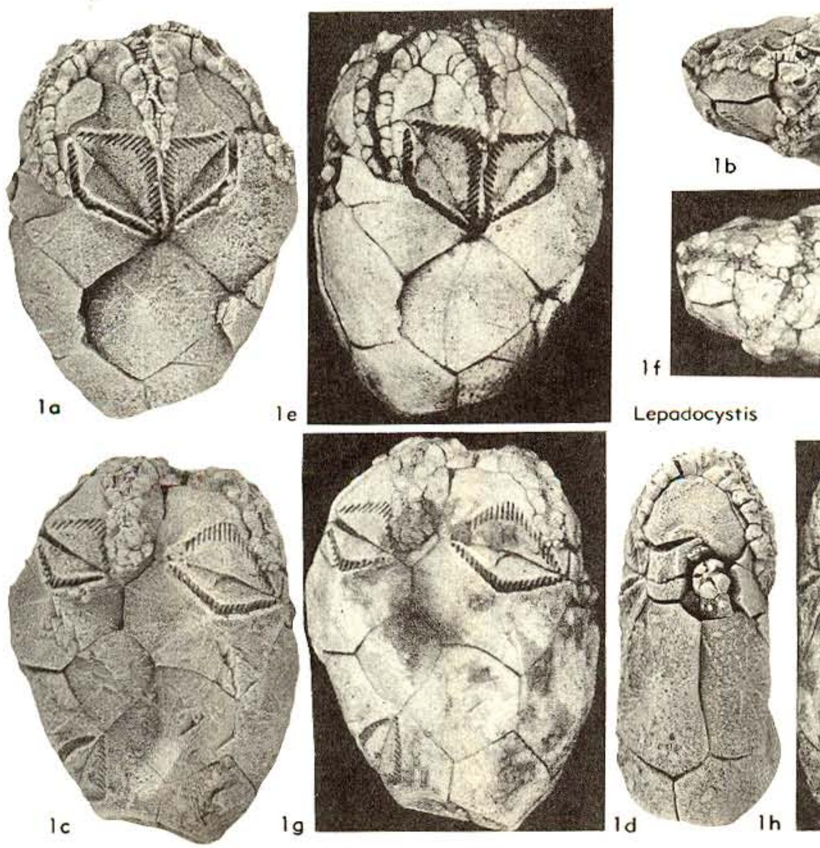


FIG. 51. Four views of a specimen coated with sublimated ammonium chloride and the same submersed in xylol, all photographed in low contrast. *Lepadocystis moorei* (MEEK), U.Ord.(Cincinnati.), Ind.; *1a-d*, lat. *(III)*, oral, lat. (post) and lat. (anal), ×4, coated; *1e-h*, same submersed; this specimen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

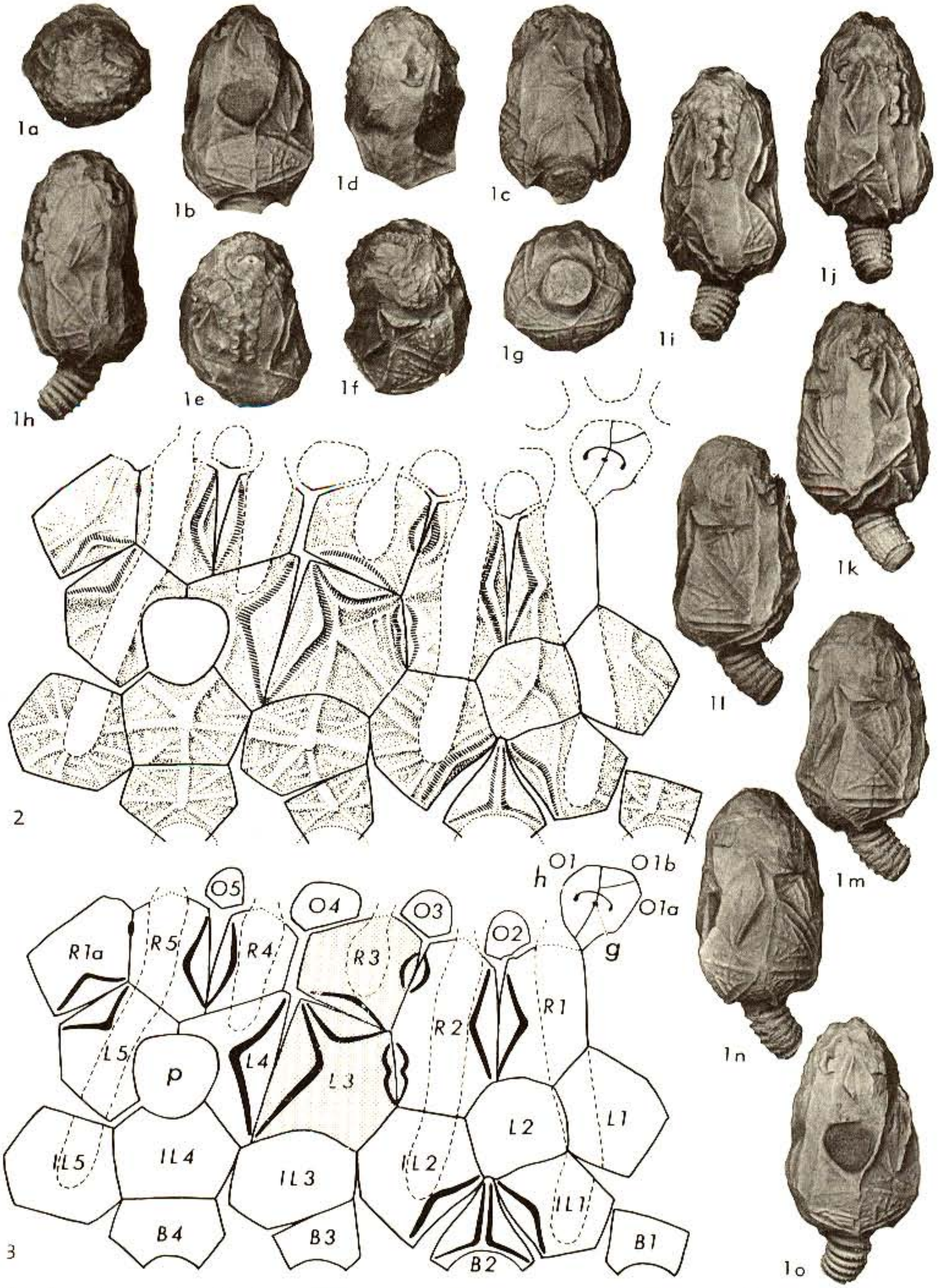


FIG. 52. *Glyptocystites ehlersi* KESLING, M.Ord.(Trenton.), Mich.; *1*, photographs, all ×1; *1a*, oral view; *1b,c*, aborally inclined views of interambulacra *4* and *1*; *1d-f*, orally inclined views of ambulacra *V (C)*, *I (D)*, and *III (A)*; *1g*, aboral view; *1h-o*, lateral views, *h* on interambulacrum *5* (posterior), *i on* ambulacrum *I (D)*, *j* on interambulacrum *1*, *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.

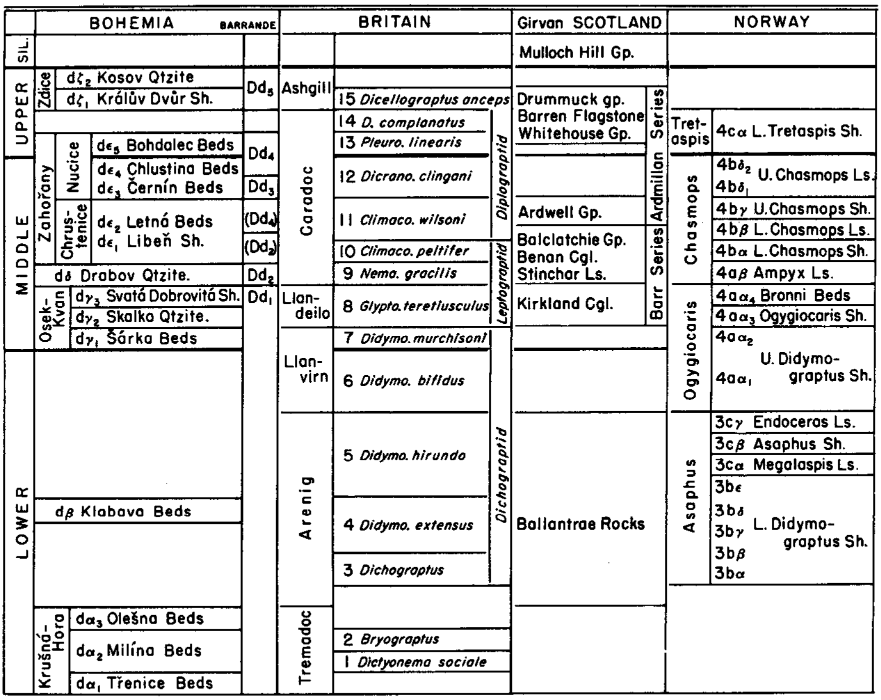


FIG. 53. Correlations of Ordovician formations in parts of Europe. Lower-Middle-Upper boundaries from THORSLUND (1960); other data from BOUČEK (1938), ÖPIK (1952), STØRMER (1953), REGNÉLL & HEDE (1960), and THORSLUND & JAANUSSON (1960).

Lowermost Ordovician outcrops in Bohemia, the Třenice Beds (dα_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 $C_I\beta$ 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

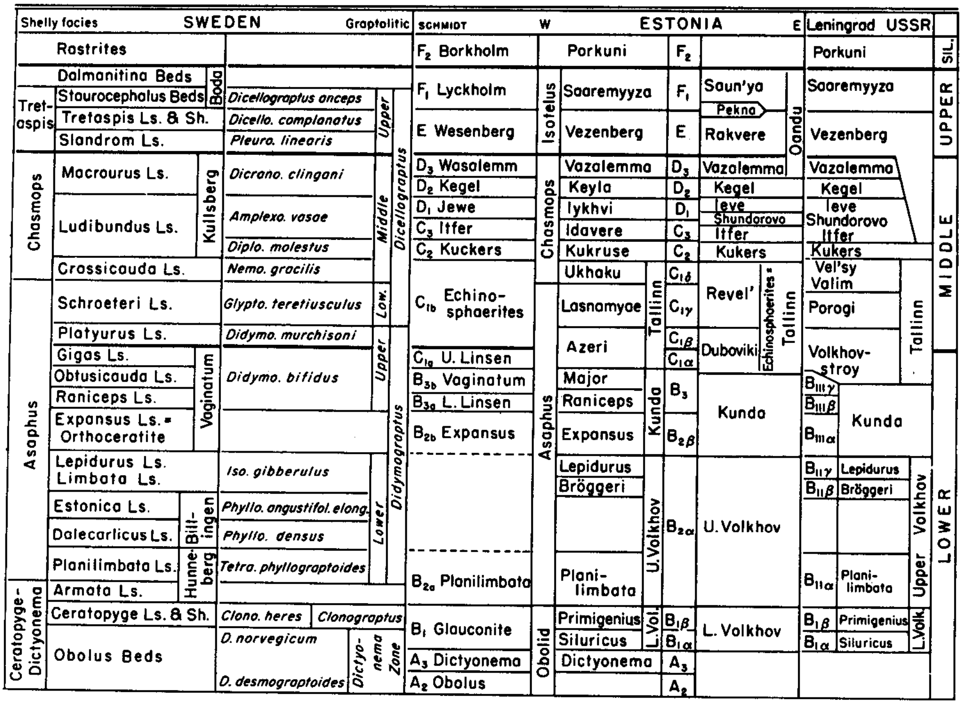


FIG. 53 *(Continued).*

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

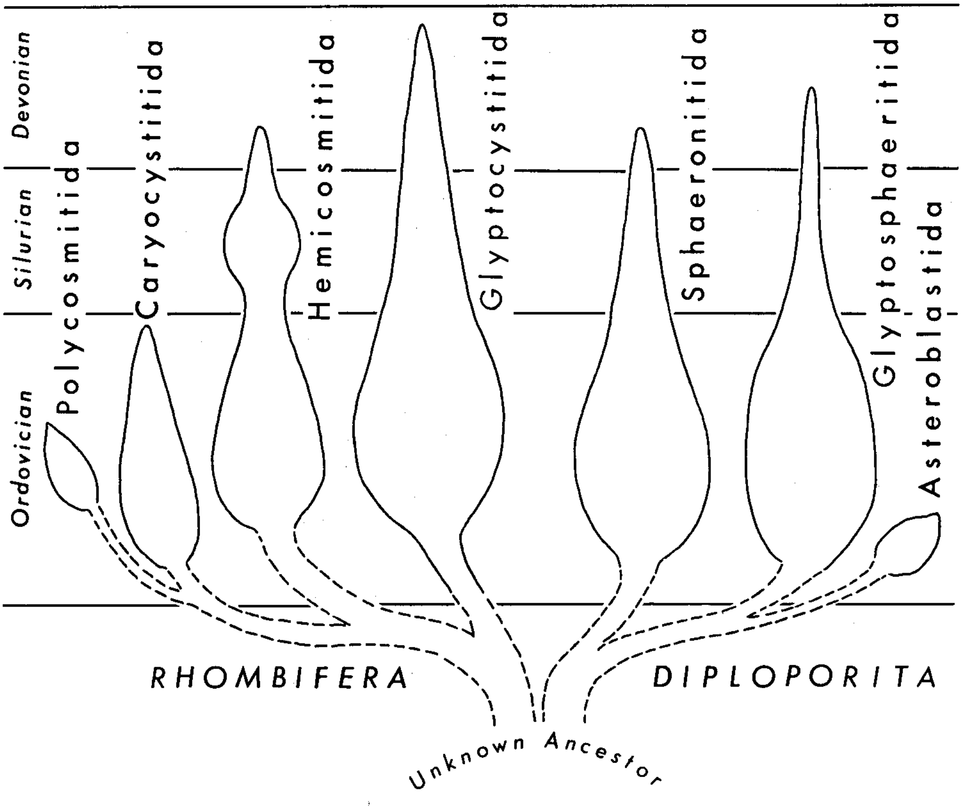


FIG. 54. Diagram representing stratigraphic distribution and inferred relationships of orders and superfamilies of Cystoidea (Kesling, n).

(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.

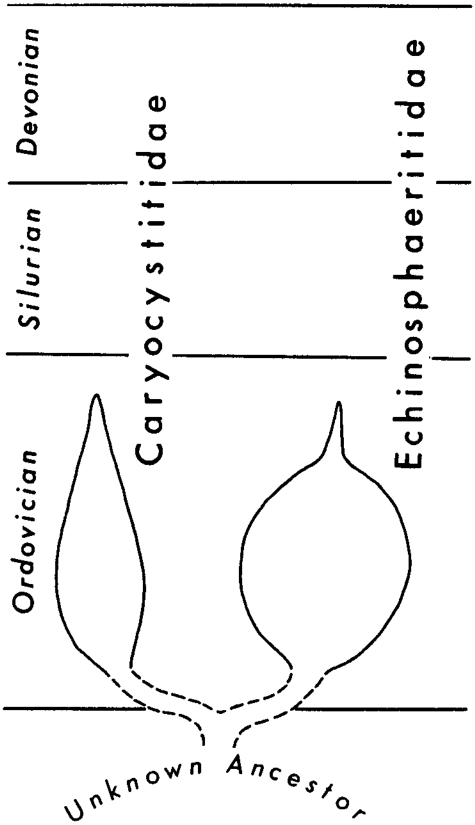


FIG. 55. Diagram representing stratigraphic distribution and inferred relationships of families of the Caryocystitida (Kesling, n).

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

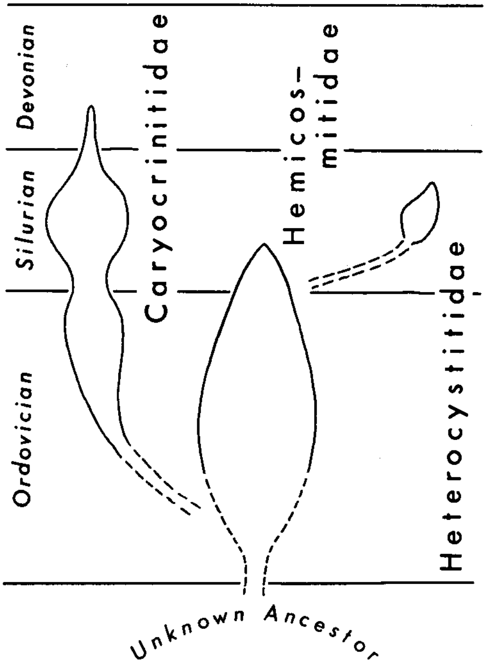


FIG. 56. Diagram representing stratigraphic distribution and inferred relationships of families of the Hemicosmitida (Kesling, n).

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-

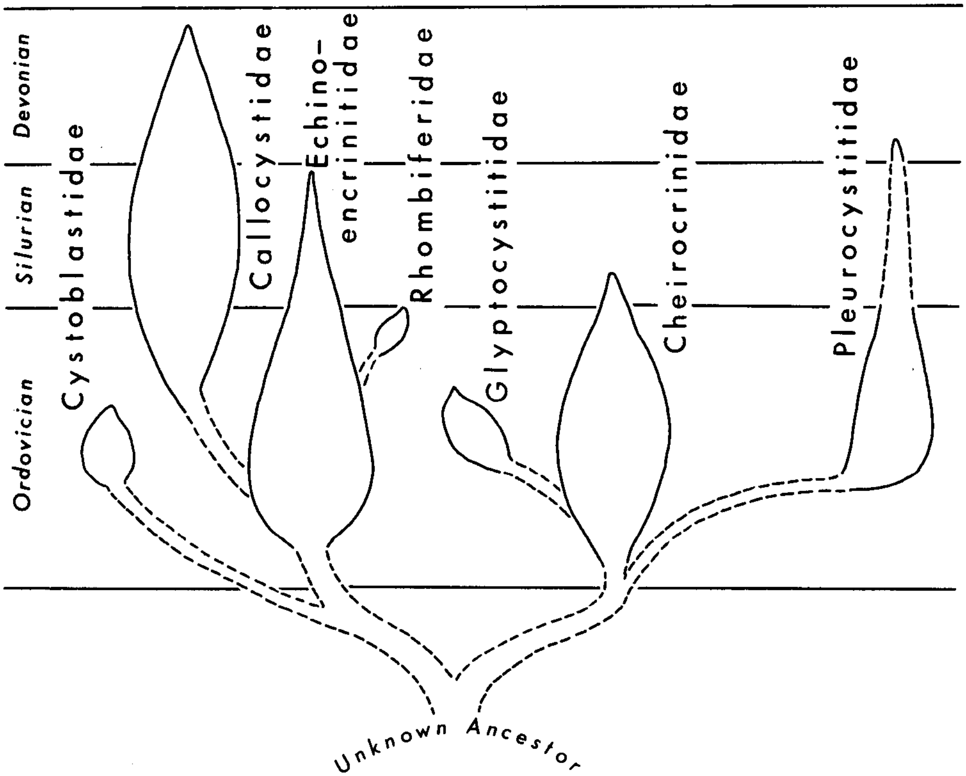


FIG. 57. Diagram representing stratigraphic distribution and inferred relationships of families of the Glyptocystitida (Kesling, n).

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-

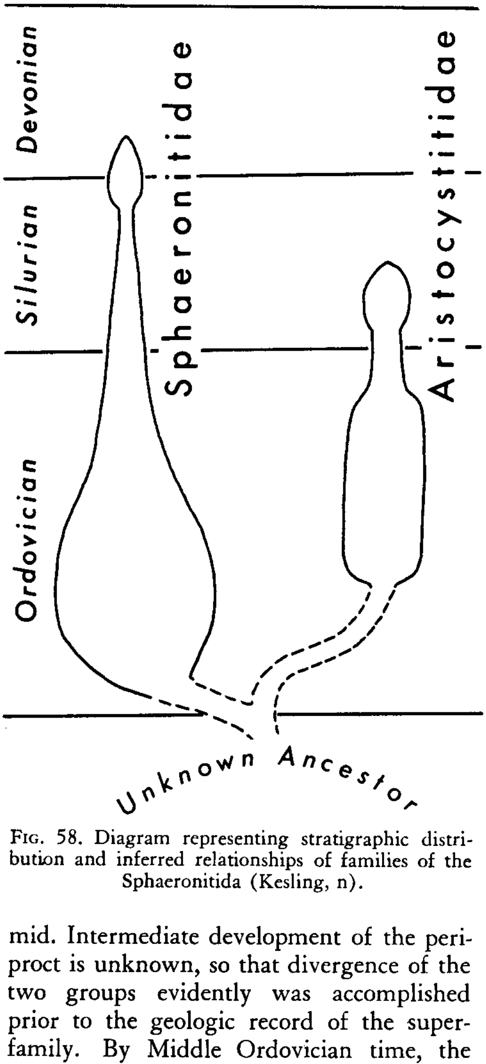


FIG. 58. Diagram representing stratigraphic distribution and inferred relationships of families of the Sphaeronitida (Kesling, n).

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-*

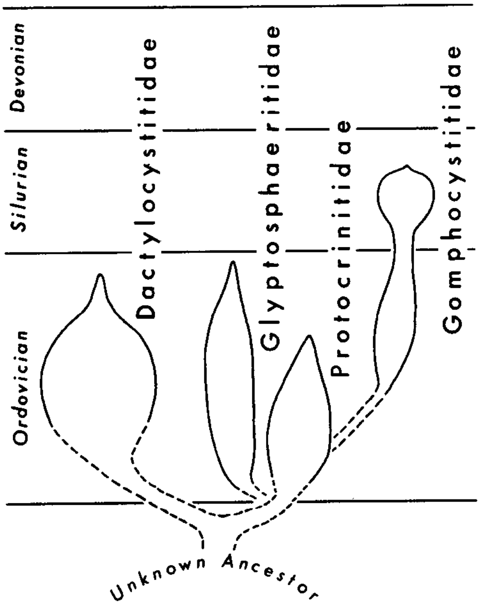


FIG. 59. Diagram representing stratigraphic distribution and inferred relationships of families of the Glyptosphaeritida (Kesling, n).

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 $B_{II\gamma}$ zone, which contains the oldest of the Asteroblastida, *Mesocystis pusirefskii* (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-

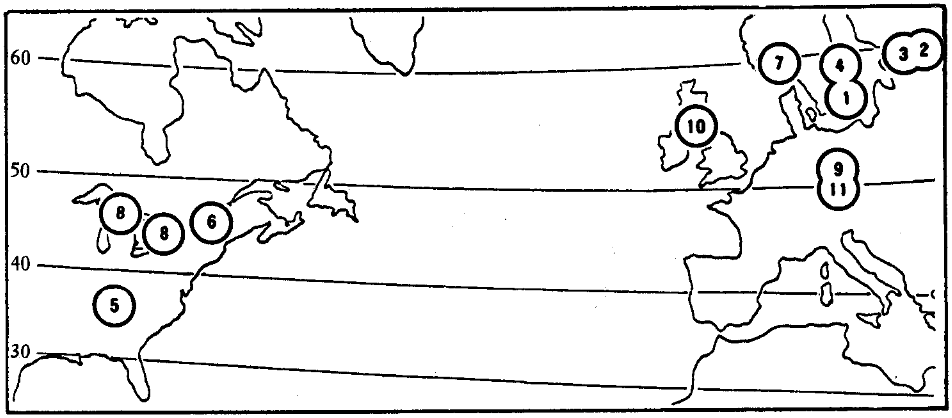


FIG. 60. Sequence and geographic distribution of cystoids of the family Cheirocrinidae.——*1. Cheirocrinus holmi,* L.Ord.*(Planilimbata),* Sweden(Öland).——*2. Leptocystis gigantea, Homocystites* spp., L.Ord. (B_2-B_3), USSR(Leningrad region).——*3. Cheirocrinus radiatus, C. ornatus,* etc., L.Ord.-U.Ord., 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

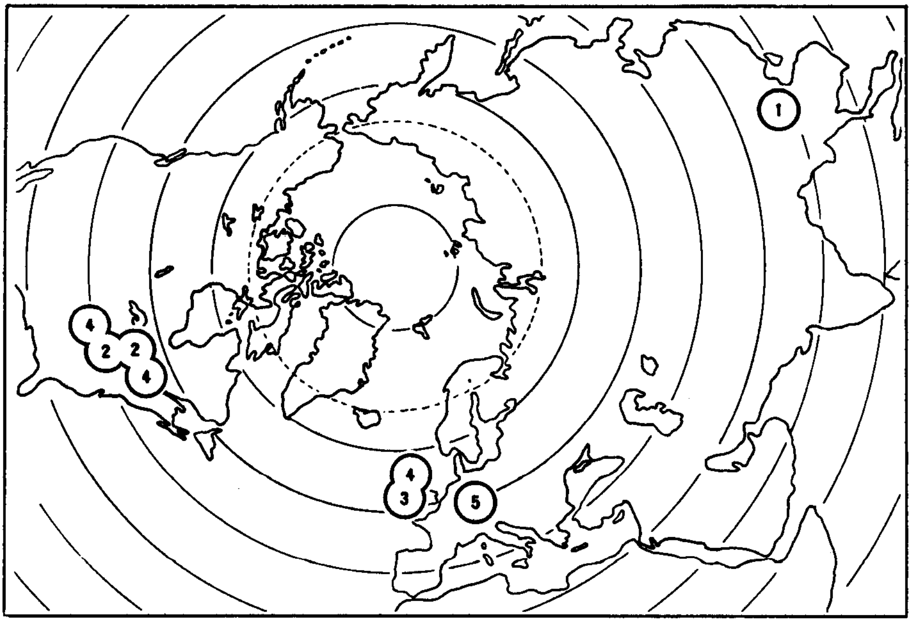


FIG. 61. Sequence and geographic distribution of cystoids of the family Pleurocystitidae.——*1. Pleurocystites bassleri*, M.Ord., China.——*2. P. elegans, P. filitextus, P. squamosus*, etc., *Amecystis*, M.Ord. (Trenton.), Can.(Que.-Ont.)-USA(Wis.-Minn.-Mich.-Ky.-N.Y.).——*3. P. anglicus, P. rugeri*, M.Ord. (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-

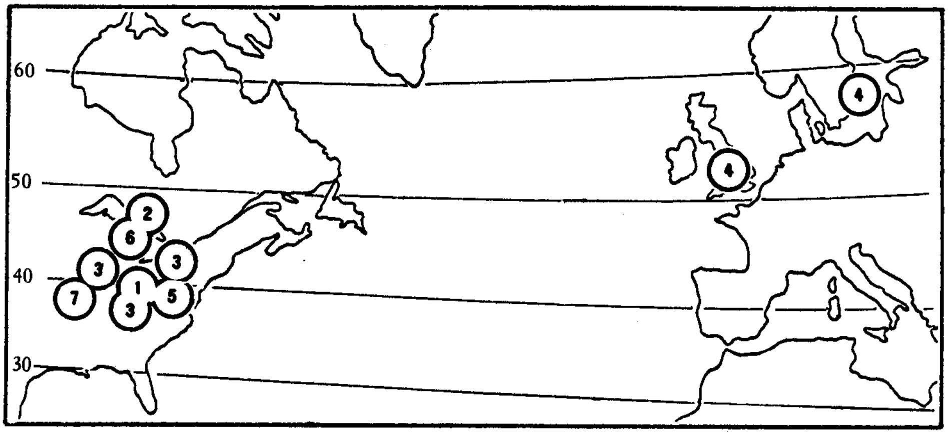


FIG. 62. Sequence and geographic distribution of cystoids of the family Callocystitidae.——*1. Lepadocystis,* U.Ord., USA(Ind.-Ohio).——*2. Brockocystis,* L.Sil., Can.(Ont.)-USA(Ohio).——*3. Apiocystites, Hallicystis, Tetracystis,* M.Sil.(Niagaran), Can.(Ont.)-USA(N.Y.-Wis.-Ill.-Tenn.).——*4. Apiocystites, 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

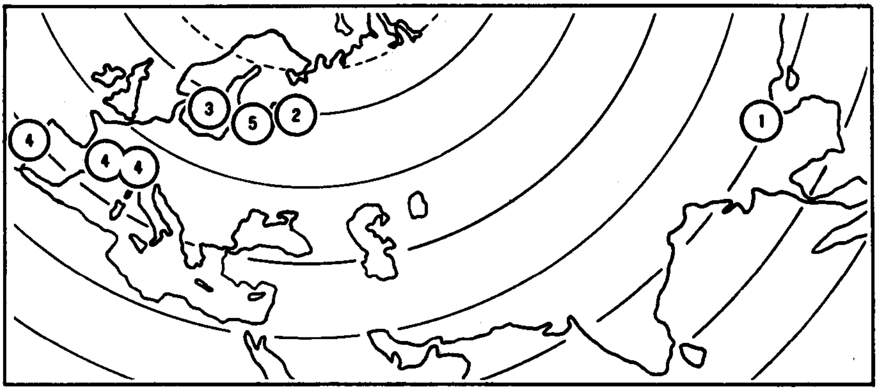


FIG. 63. Sequence and geographic distribution of cystoids of the family Hemicosmitidae.——*1. Hemicosmites jaekeli,* M.Ord., China.——*2. H. malum, H. oblongus,* M.Ord. ($C_1\beta$), Eu.(Baltic).——*3. H. oelandicus,* M.Ord.(L.*Chasmops*), Sweden.——*4. Corylocrinus elongatus, C. occidentalis, C. carnicus,* 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-

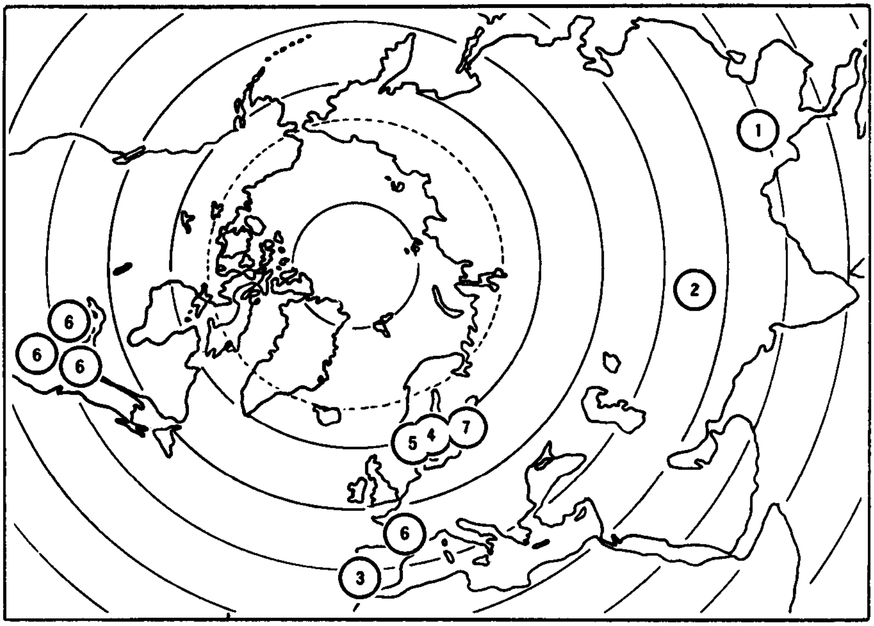


FIG. 64. Sequence and geographic distribution of cystoids of the genus *Caryocrinites*.——*1. C. aurorus, C. avellanus,* M.Ord.(Naugkangyi beds), Burma.——*2. C.* sp., M.Ord., Asia(Karakorum).——*3. C.* sp., M.Ord.(Llandeilo or Caradoc), Eu.(Port.).——*4. C. septentrionalis,* U.Ord., Sweden(Dalarna).——*5. 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*

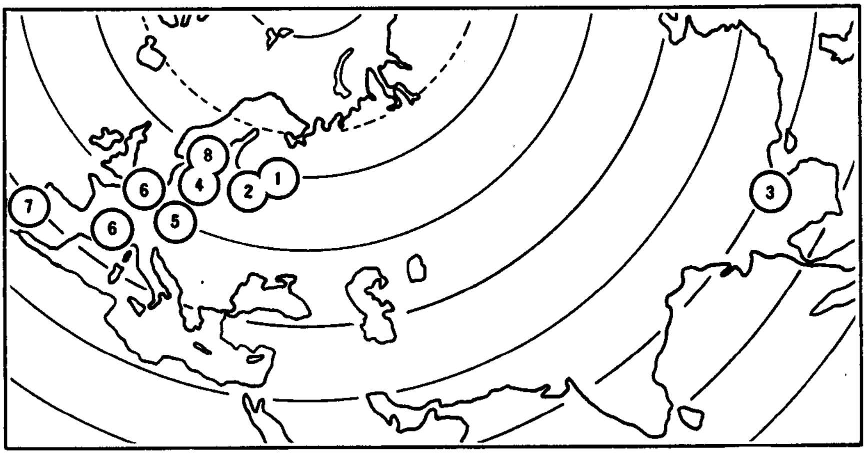


Fig. 65. Sequence and geographic distribution of cystoids of the genus *Heliocrinites*.——*1. H. echinoides,* L.Ord.(B_2), USSR(Leningrad region).——*2. H. radiatus,* L.Ord. (B_3), Eu.(Est.-Leningrad region).——*3.* H. *fiscellus, H. qualus, H. kweichouensis,* M.Ord., Burma-China(Yunnan-Kweichou).——*4. 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

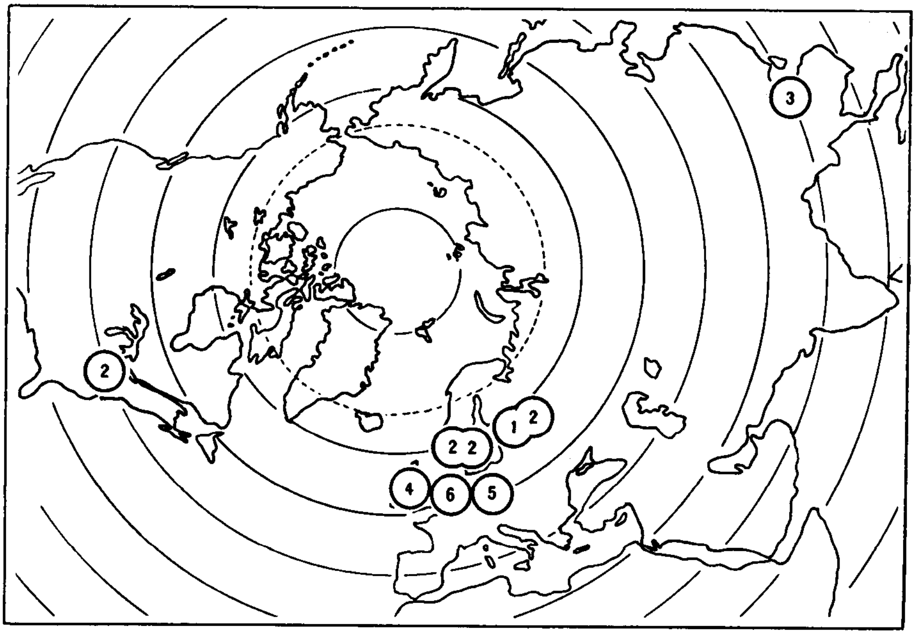


Fig. 66. Sequence and geographic distribution of cystoids of the genus *Echinosphaerites*.——*1*. *E.* sp., *E. ellipticus*, L.Ord.(B_2-B_3), Eu.(Est.).——*2*. *E. aurantium*, M.Ord., USA-Eu.(Sweden-Norway-Leningrad region).——*3*. *E. sinensis*, M.Ord., China.——*4*. *E. granulatus*, M.Ord.(Caradoc), Eire.——*5*. *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.

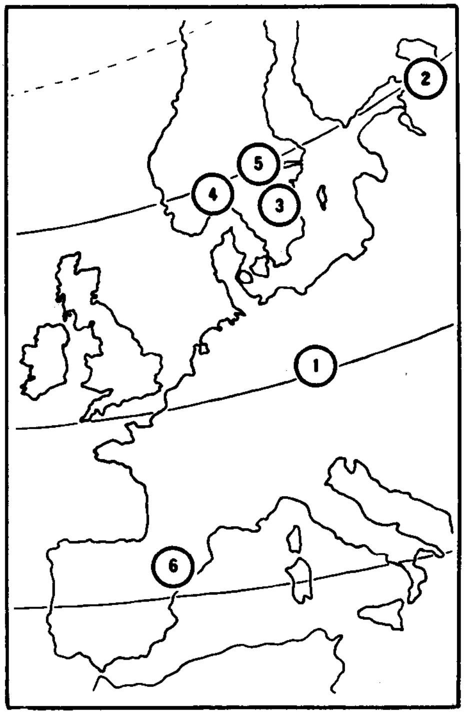


Fig. 67. Sequence and geographic distribution of cystoids of the genus *Glyptosphaerites.*——*1. G. ferrigenus,* Ord. (Dd$_1$), Eu. (Czech.).——*2. G. leuchtenbergi,* L.Ord. (B$_3$-C$_1$), Eu. (Baltic).——*3. G. leuchtenbergi,* M.Ord. (*Platyurus* Ls.), Eu. (Sweden).——*4. G.* sp., M.Ord.(*Chasmops* Ls.), 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 *Sphæronites.*

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-

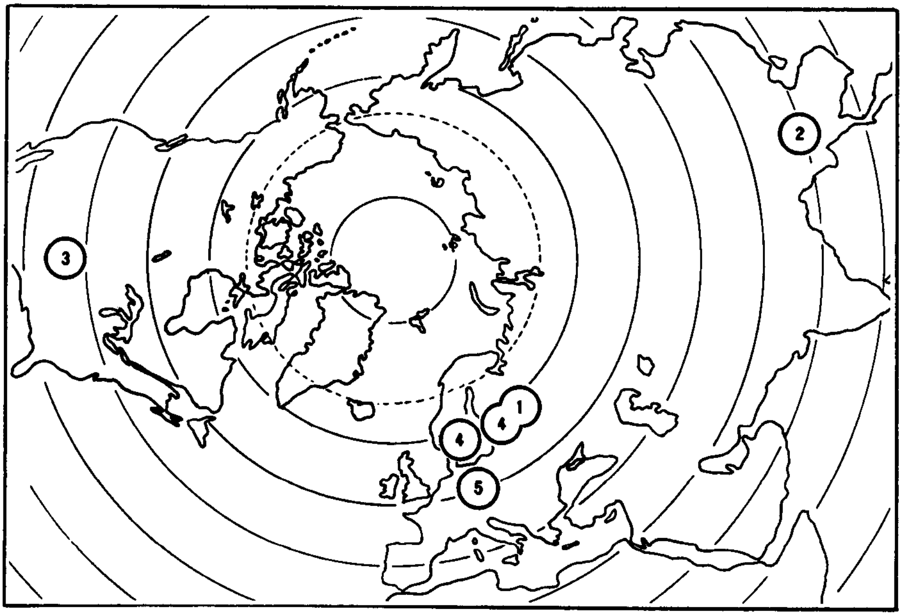


FIG. 68. Sequence and geographic distribution of cystoids of the family Protocrinitidae.——*1. Protocrinites fragum,* L.Ord.(*Vaginatum* beds or C_1), Eu.(USSR).——*2. P. sparsiporus,* M.Ord.(Naungkangyi beds), Burma.——*3. Eumorphocystis,* M.Ord.(Bromide), USA(Okla.).——*4. P. oviformis, P. fragum,* M.Ord. (D_3), Eu.(USSR-Est.-Scand.-Ger.).——*5. Fungocystites,* M.Ord.(Dd_4), Eu.(Czech.) (Kesling, n).

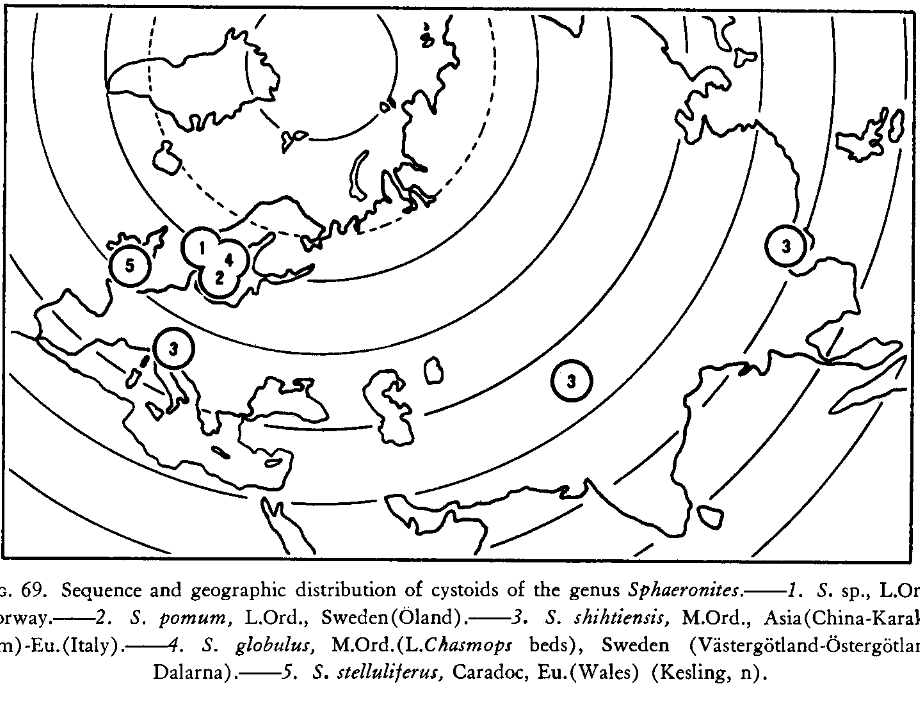


FIG. 69. Sequence and geographic distribution of cystoids of the genus *Sphaeronites.*——*1. S.* sp., L.Ord., Norway.——*2. S. pomum,* L.Ord., Sweden(Öland).——*3. S. shihtiensis,* M.Ord., Asia(China-Karakorum)-Eu.(Italy).——*4. S. globulus,* M.Ord.(L.*Chasmops* beds), Sweden (Västergötland-Östergötland-Dalarna).——*5. 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.

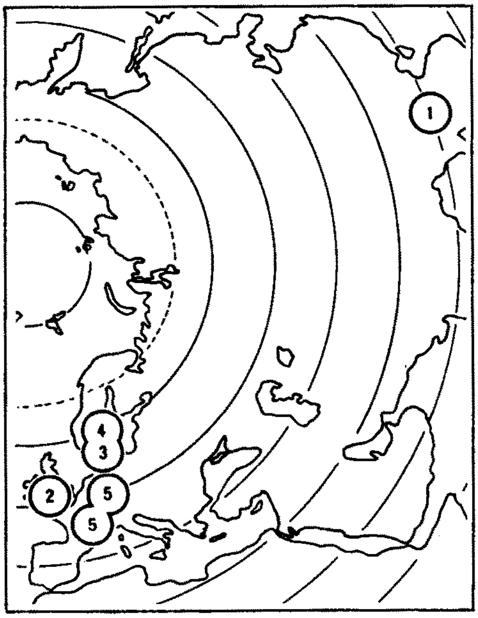


Fig. 70. Sequence and geographic distribution of cystoids of *Eucystis* and related genera.——*1.* "*Eucystis* cf. *raripuncta*" of Reed (1917), M.Ord., China.——*2. E. litchi*, Caradoc, Eu.(Wales).——*3. E. quadrangularis, E.* sp., U.Ord.(L.Boda beds). Sweden(Scania).——*4. E. raripuncta, E. angelini, E. 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 supra-generic 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

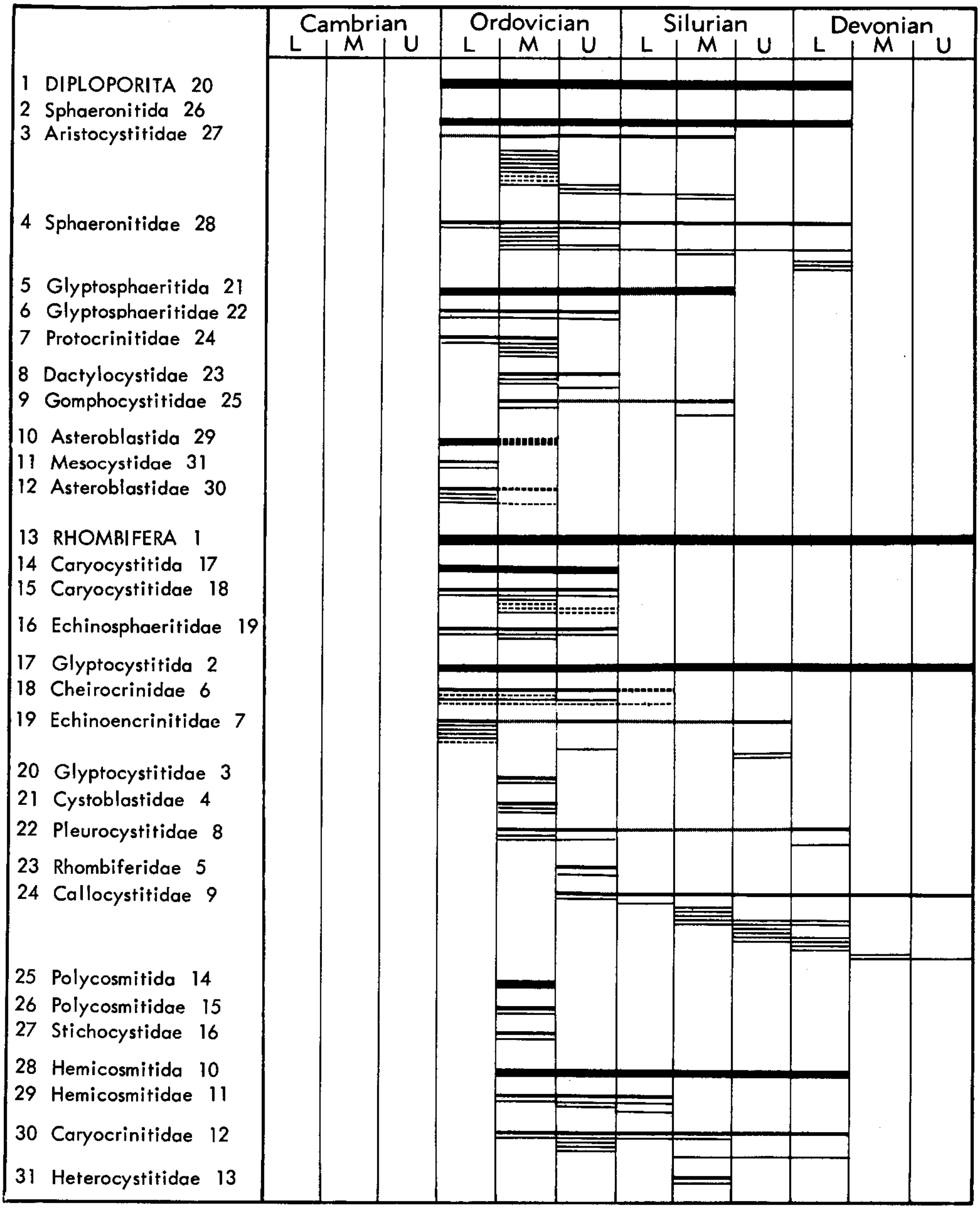


FIG. 71. Stratigraphic distribution of suprageneric cystoid taxa; geologic periods indicated only to epoch. The numbers following the names of taxa indicate systematic placement as given in the preceding tabular outline of cystoid classification. Also, an alphabetical list of taxa is accompanied by index 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 Diploporita, 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. *S*164. 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. *S*167.

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).

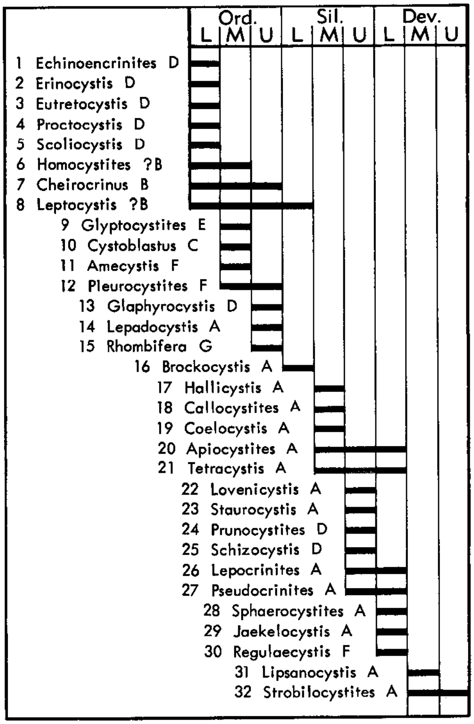


FIG. 72. Stratigraphic distribution of genera belonging to the superfamily Glyptocystitida. Classification of the genera in families is indicated by letter symbols: A—Callocystitidae, B—Cheirocrinidae, C—Cystoblastidae, D—Echinoencrinitidae, E—Glyptocystitidae, F—Pleurocystitidae, G—Rhombiferidae. The 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
Apiocystites—20
Brockocystis—16
Callocystites—18
Cheirocrinus—7
Coelocystis—19
Cystoblastus—10
Echinoencrinites—1
Erinocystis—2
Eutretocystis—3
Glaphyrocystis—13
Glyptocystites—9
Hallicystis—17
Homocystites—6
Jaekelocystis—29
Lepocrinites—26
Leptocystis—8
Lipsanocystis—31
Lepadocystis—14
Lovenicystis—22
Pleurocystites—12
Proctocystis—4
Prunocystites—24
Pseudocrinites—27
Regulaecystis—30
Rhombifera—15
Schizocystis—25
Scoliocystis—5
Sphaerocystites—28
Staurocystis—23
Strobilocystites—32
Tetracystis—21

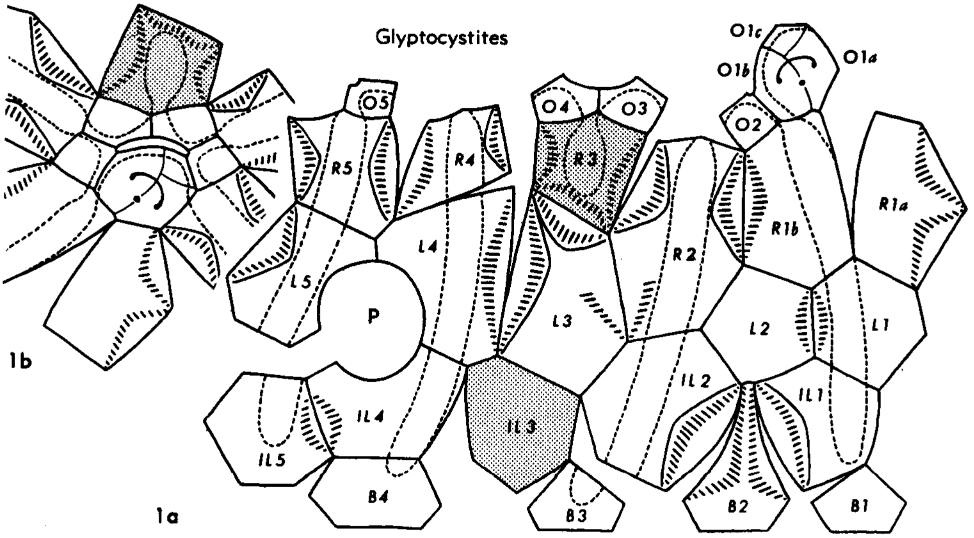


Fig. 73. Glyptocystitidae (p. *S*169-*S*170). [Plate designations as in Figure 38.]

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

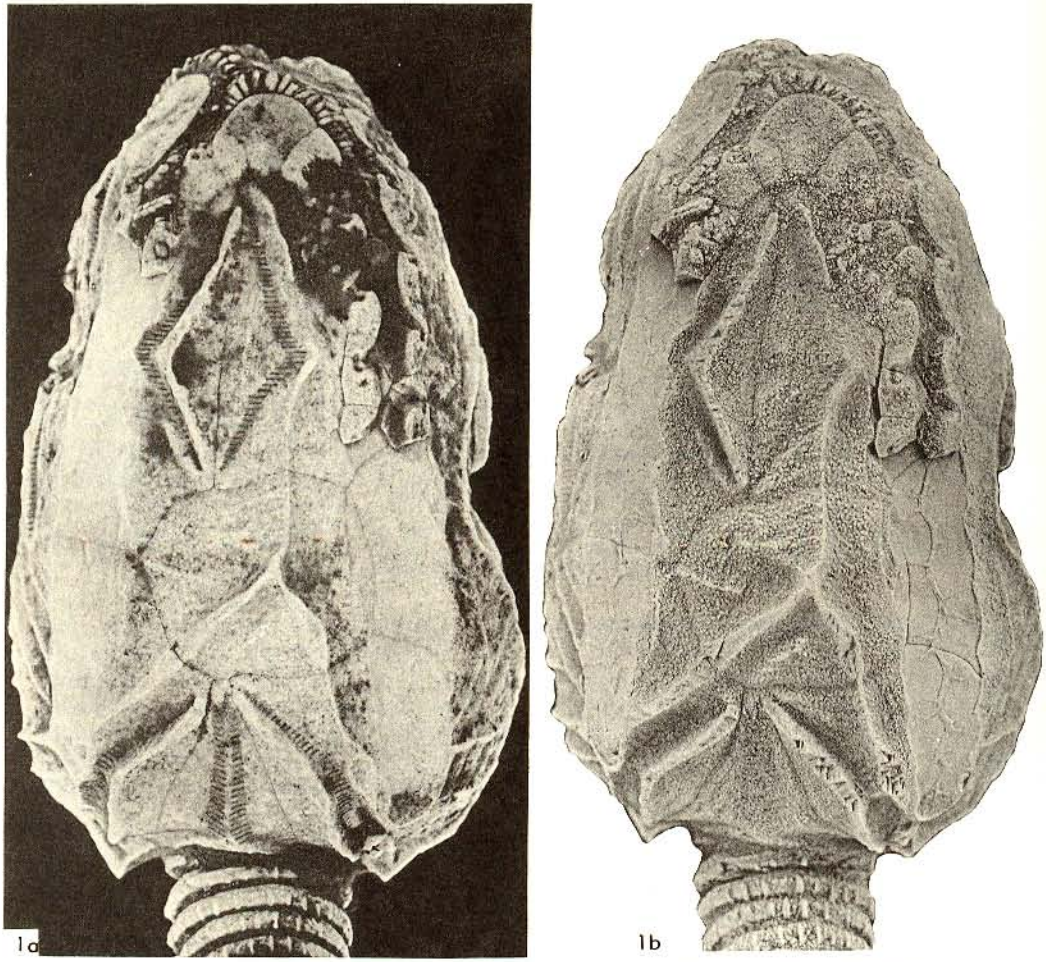
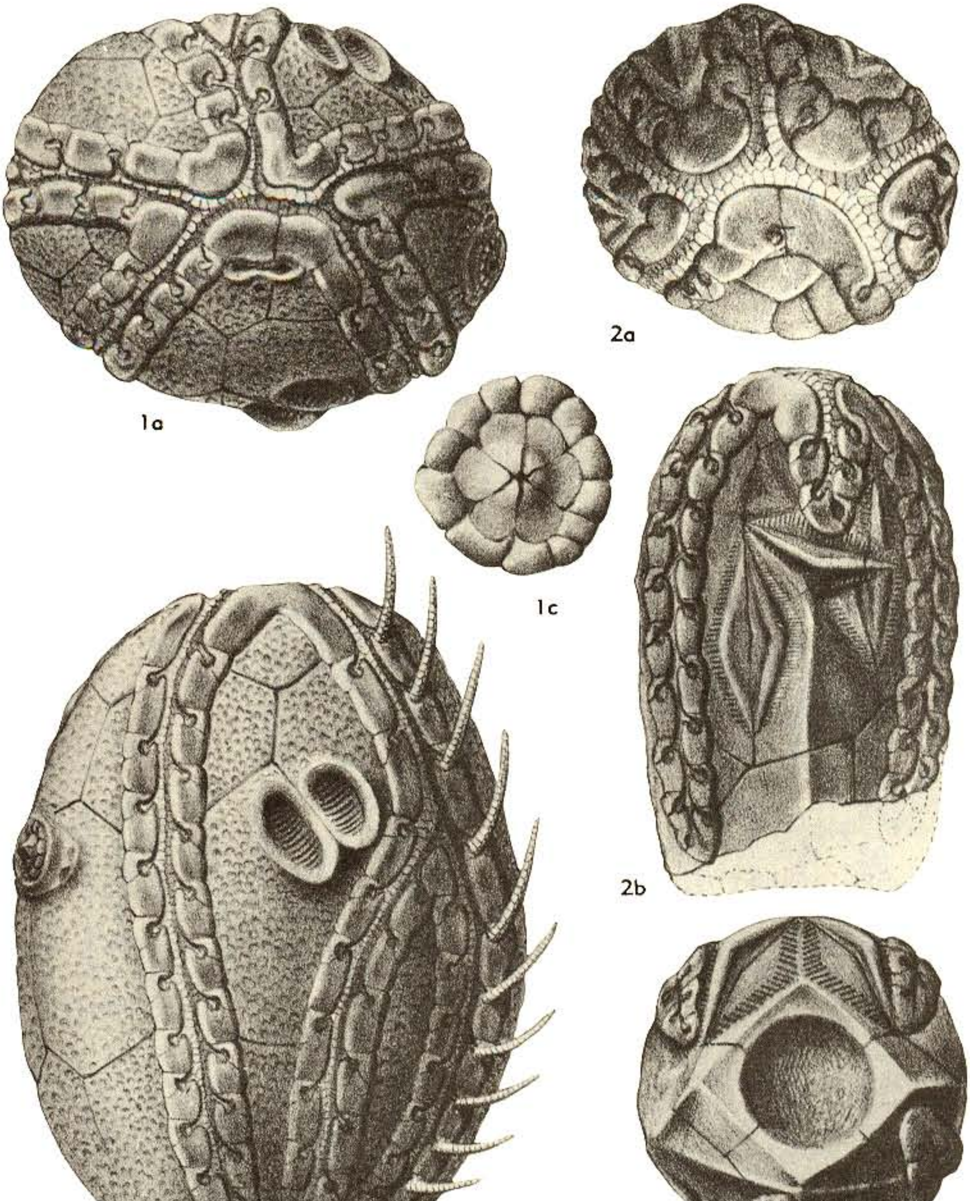


FIG. 74. Glyptocystitidae (p. *S*169-*S*170).——*1. Glyptocystites ehlersi* Kesling, M.Ord., USA(Mich.); *1a,b*, lat. view (*L2* near center, below rhomb), coated with ammonium chloride and submersed in xylol, ×3.75 *(73)*.

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. S169-S170; S199-S201).

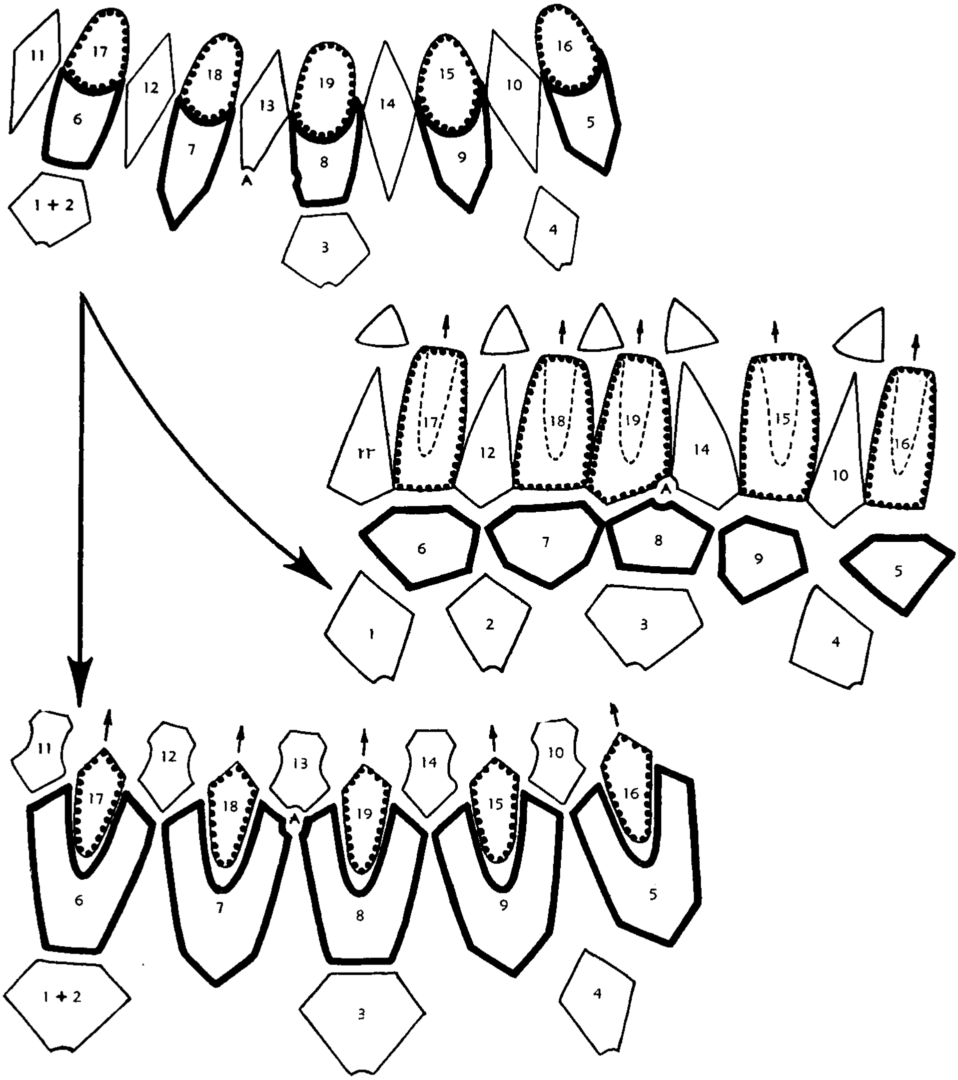


FIG. 76. Hypothetical derivation of cystoids and blastoids from a common ancestor as suggested by MOORE (1954); *1,* "hypothetical evolutionary derivative of a pre-*Cystoblastus* type"; *2, Cystoblastus; 3,* typical eublastoid with lancet plates identified as rhombiferan RR, deltoids as rhombiferan LL, 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,*

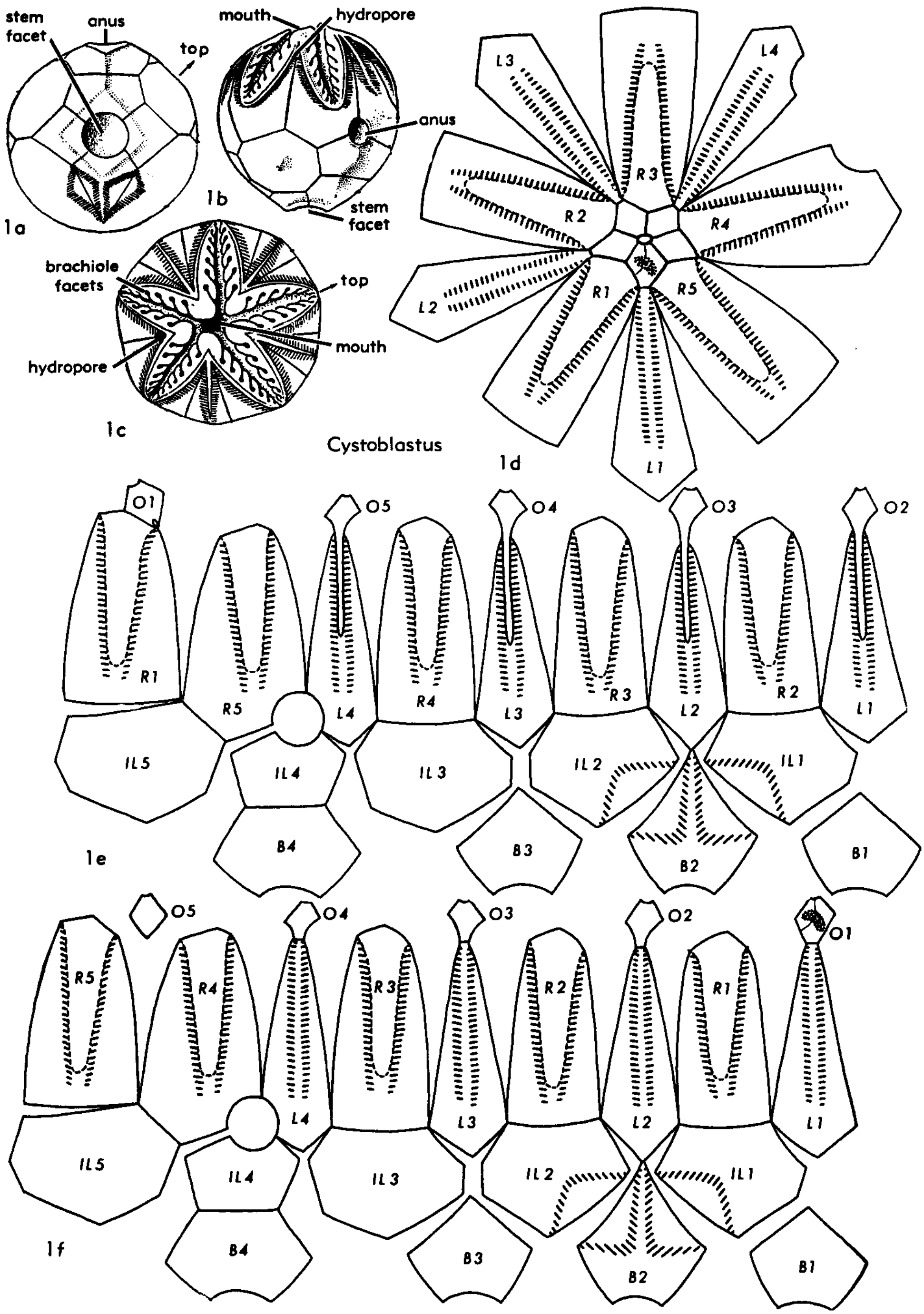


FIG. 77. Morphology of *Cystoblastus*.——*1*. **C. leuchtenbergi* VOLBORTH, M.Ord., Eu.(USSR); *1a-c*, aboral, lat., oral views of theca, ×4 (10); *1d*, oral region (diagram. reconstr.) (Kesling, n); *1e*, plate diagram to accord with VOLBORTH's original description (Kesling, n).——*1f*. *C. kokeni* JAEKEL, 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).

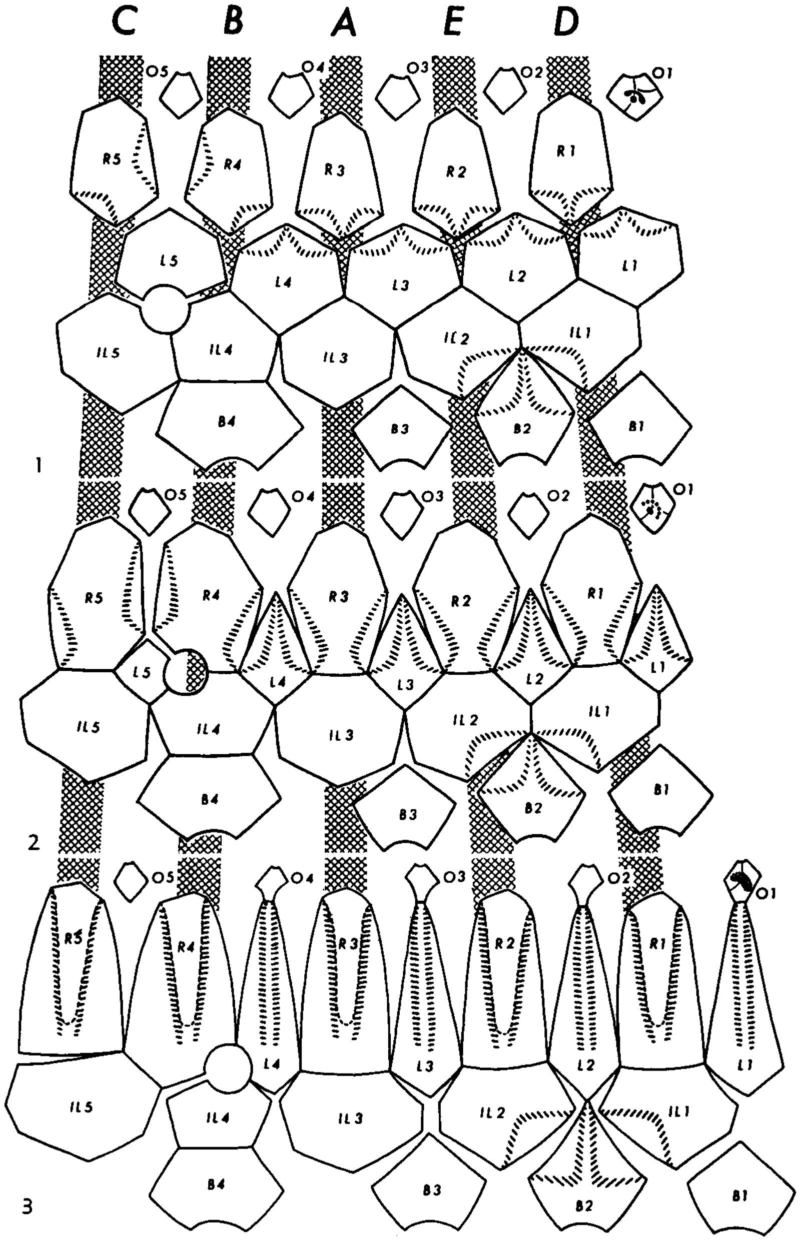


Fig. 78. Hypothetical derivation of *Cystoblastus (3)* from a generalized glyptocystitidan ancestor *(1)* with an intermediate stage (2). As shown, the evolution is supposed to have involved (1) diminution and disappearance of *L5*, (2) insertion of *RR* between *ILL* to rest atop corresponding *LL*, (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.]

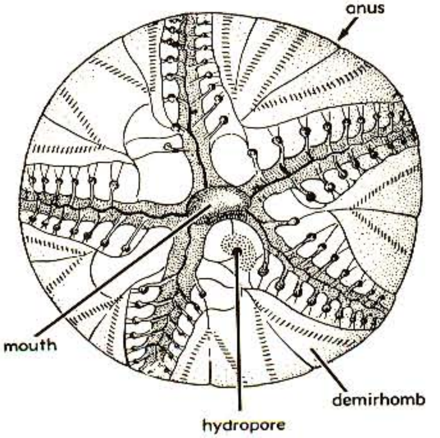


FIG. 79. Cystoblastidae (p. *S*171-*S*176). *Cystoblastus kokeni* JAEKEL, M.Ord., Eu.(Est.); oral view (reconstr.), ca. ×2 (Cuénot, 1953, from Yakovlev).

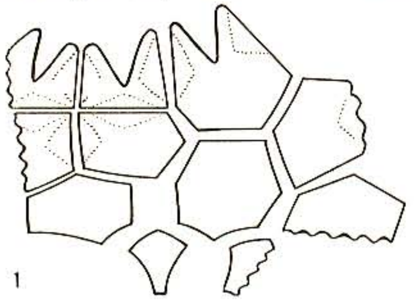


FIG. 80. Cystoblastidae (p. *S*177).——*1. *Hesperocystis deckeri* SINCLAIR, M.Ord., USA(Okla.); plate diagram of preserved part of holotype*(117)*.

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-

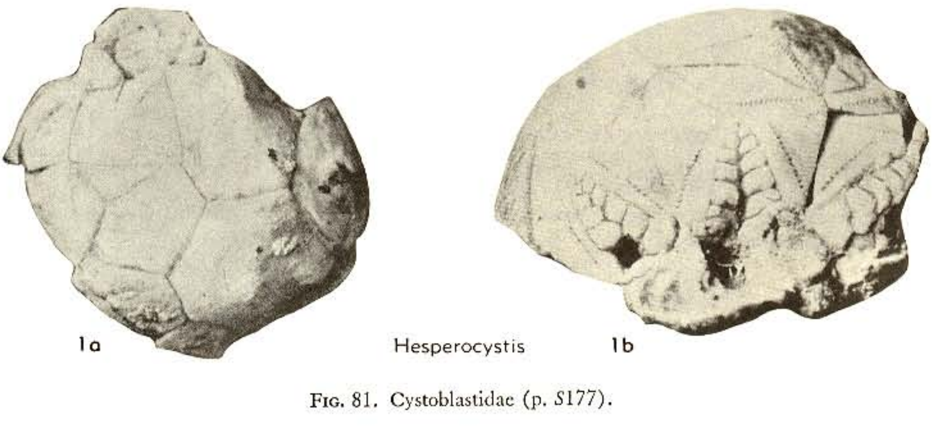


FIG. 81. Cystoblastidae (p. *S*177).

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

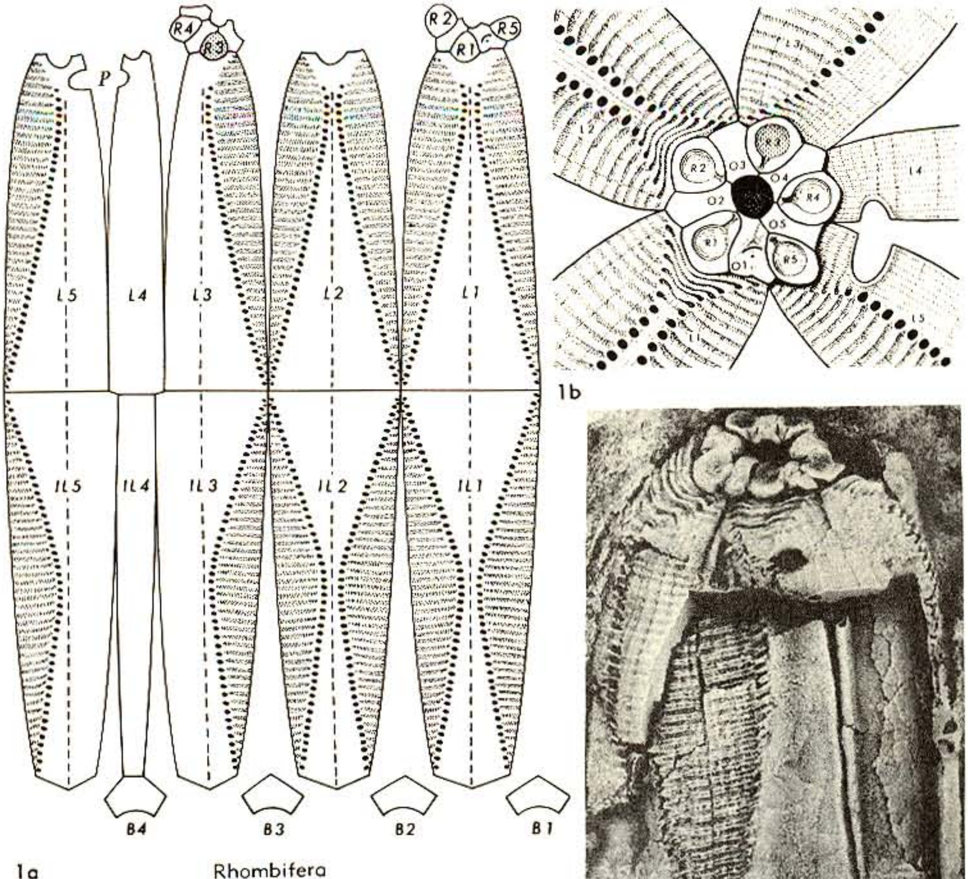


FIG. 82. Rhombiferidae (p. S178-S179).——*1.* **Rhombifera bohemica* BARRANDE, U.Ord., Eu.(Czech.); *1a*, plate diagram, ×2; *1b*, oral region, ×4; *1c*, latex cast showing part of interior on opposite side of theca, ×4 *(74)*. [Plate designations as in Figure 38.]

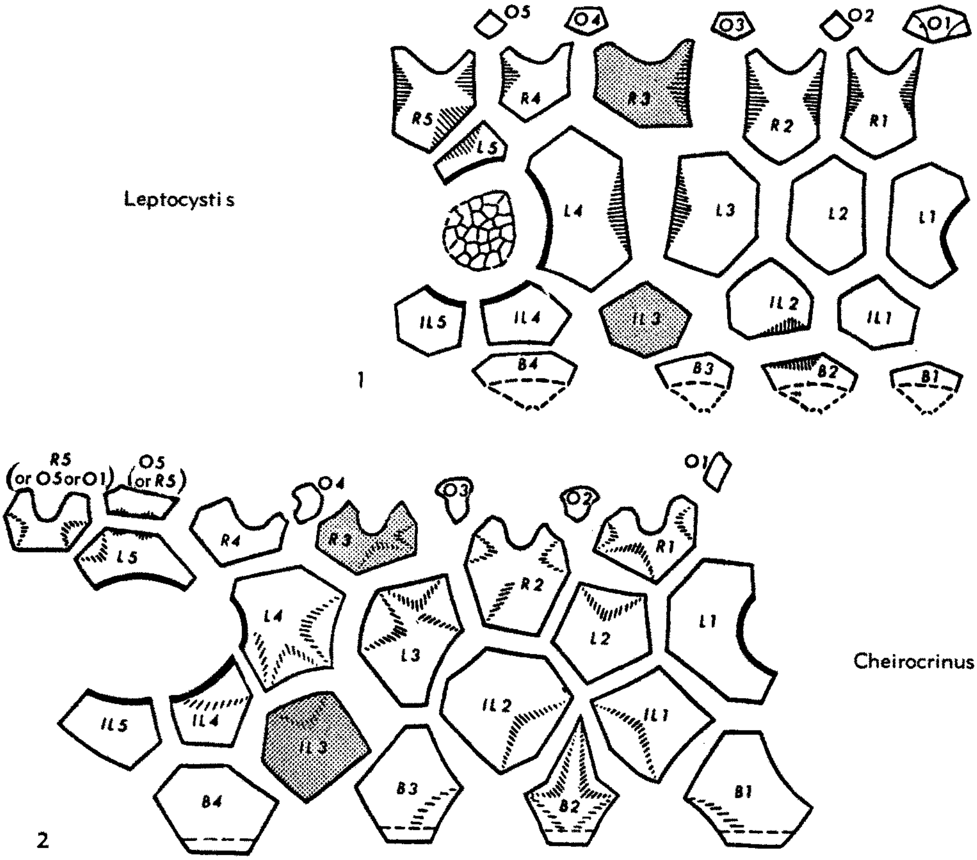


FIG. 83. Cheirocrinidae (p. *S*182-*S*184).——*1. Leptocystis constricta* (BATHER), U.Ord., Scot.; plate diagram *(12)*.——2. **Cheirocrinus penniger* (EICHWALD), L.Ord., Eu.(Est.); plate diagram *(12)*. [Plate designations as in Figure 38.]

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*

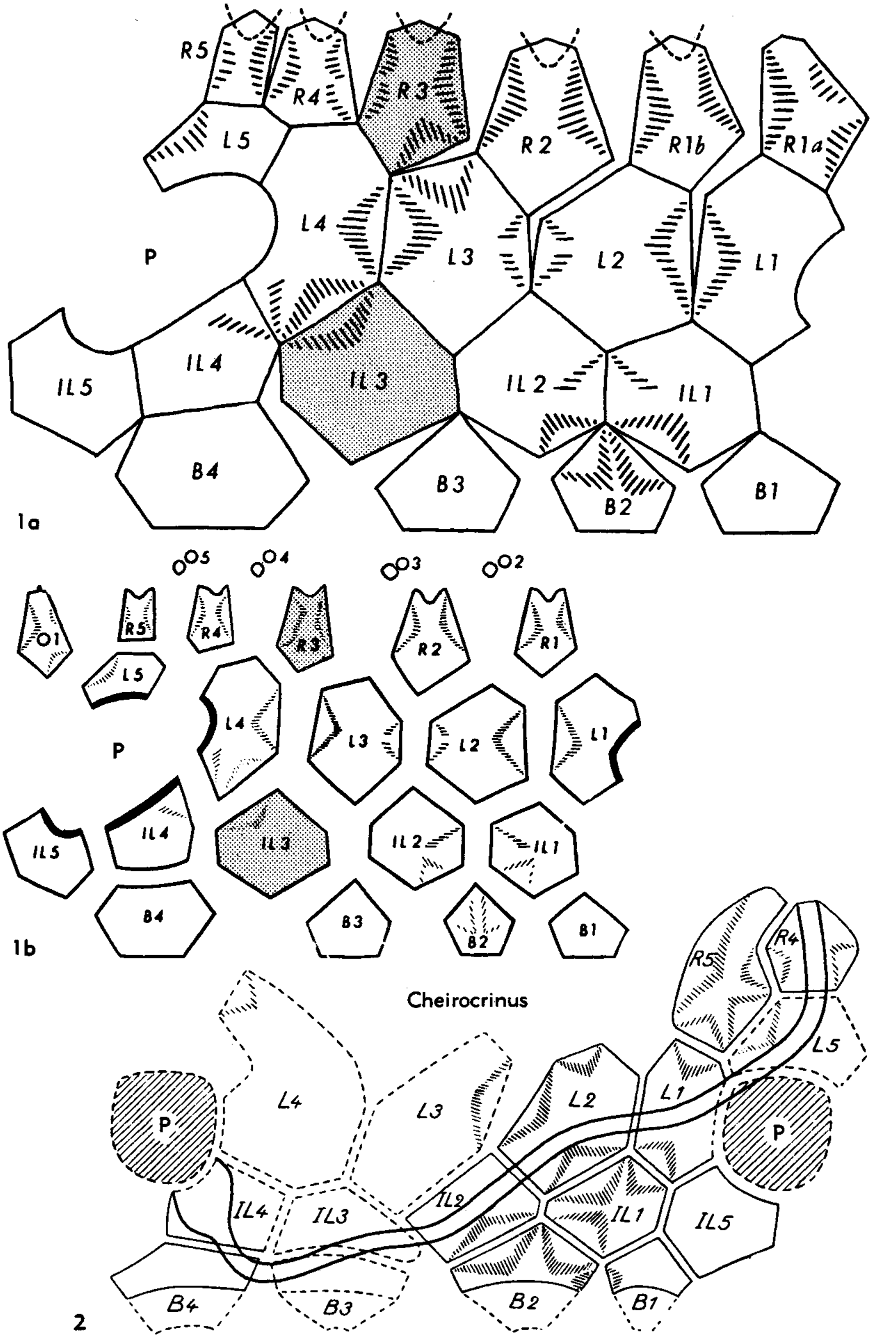


FIG. 84. Cheirocrinidae. Plate diagrams, plates of *A*-ray shaded, designations of plates as in Figure 38 (p. *S*182).

(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.

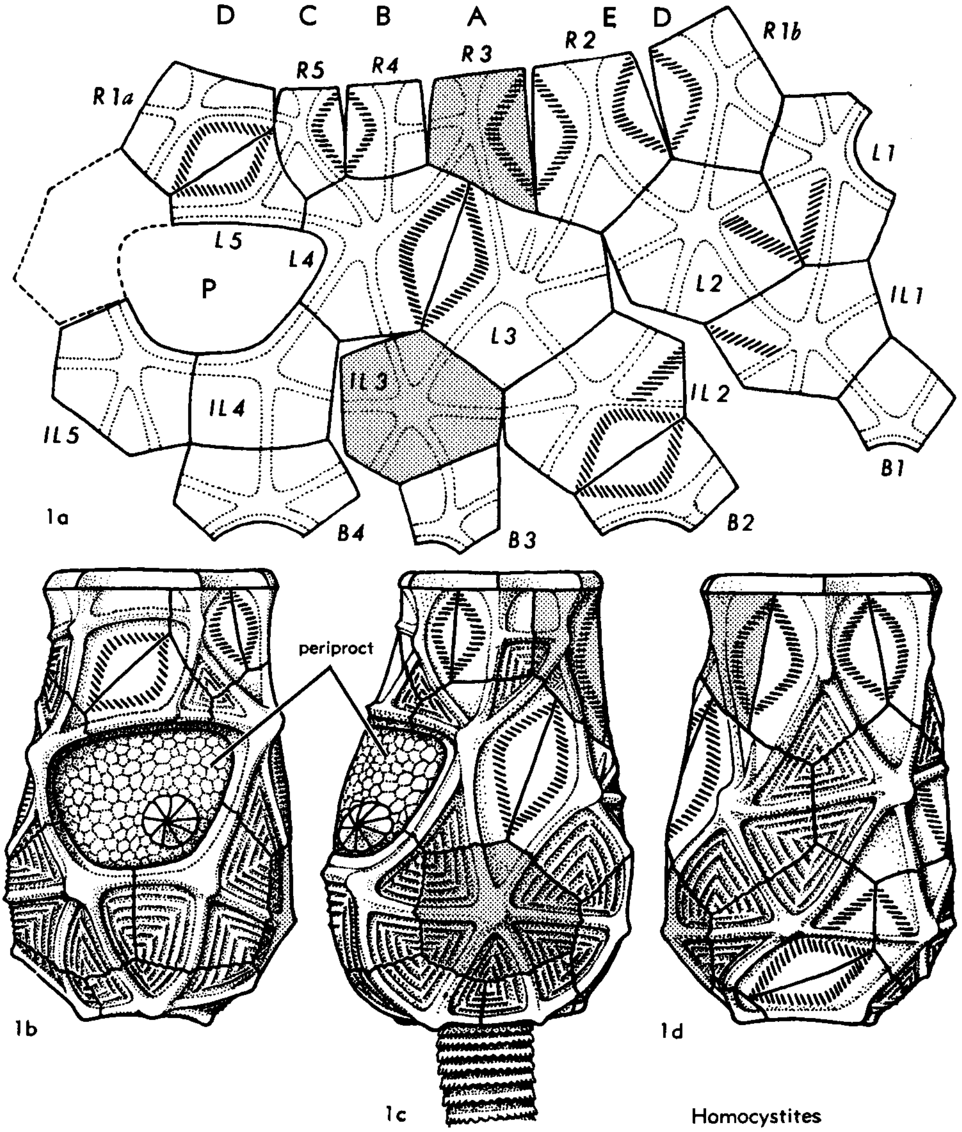


FIG. 85. Cheirocrinidae (p. S182-S184).——*1. Homocystites anatiformis* (HALL), M.Ord., USA(Mich.); *1a*, plate diagram; *1b-d*, reconstructions of theca in lateral views, ca. 2.5 *(74)*. [Plate designations as in Figure 38, inferred rays of Carpenter system indicated by capital letters at top.]

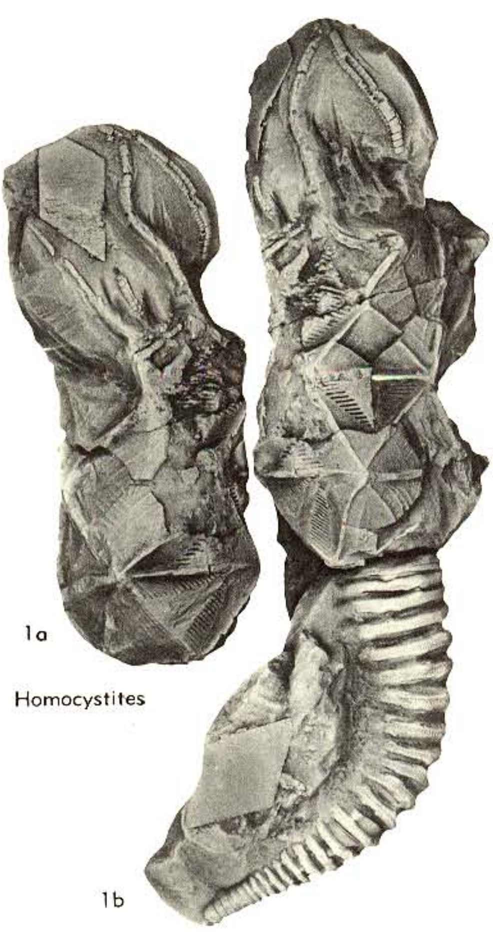


FIG. 86. Cheirocrinidae (p. S183-S184).

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(3cβ), 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

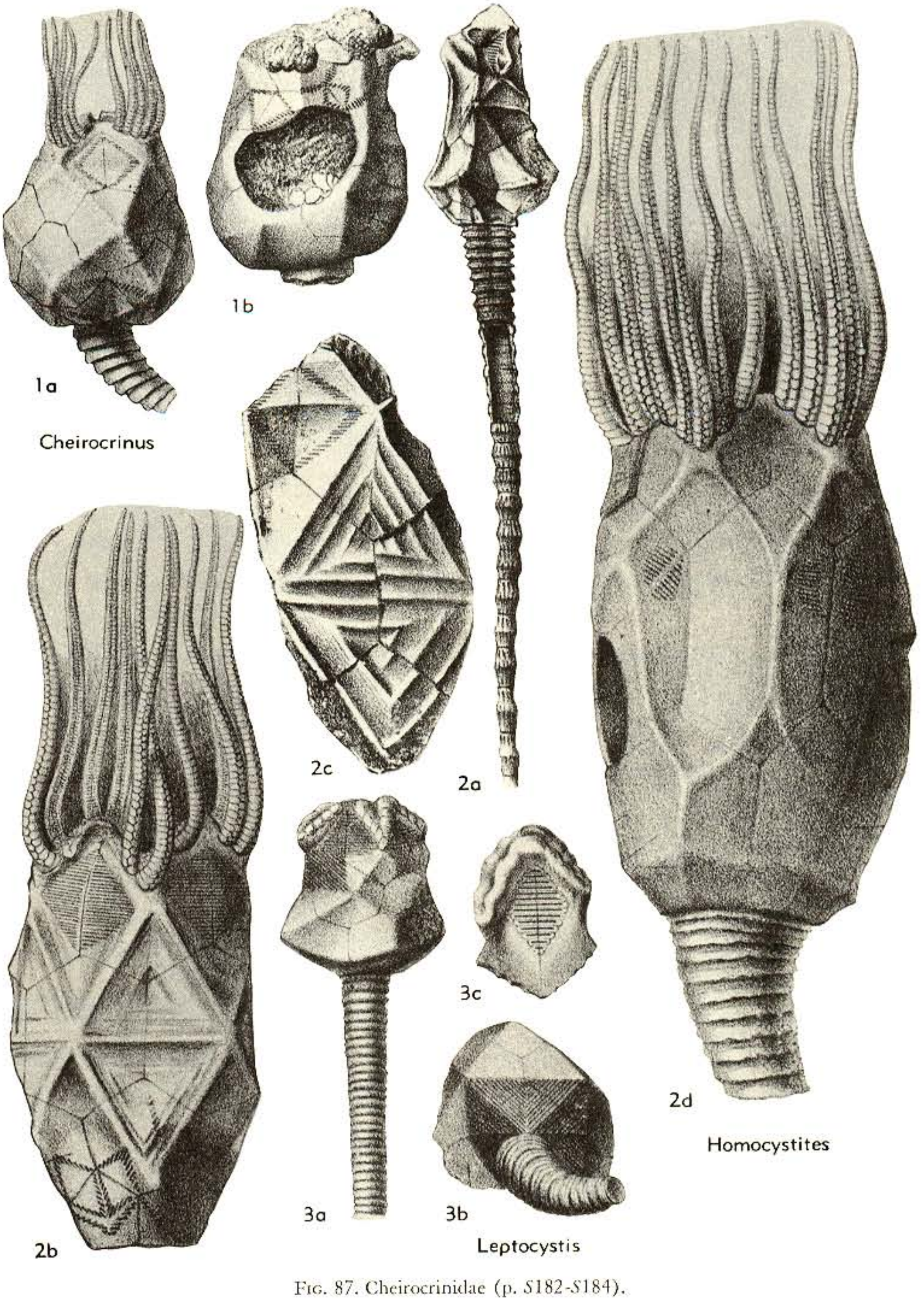


FIG. 87. Cheirocrinidae (p. S182-S184).

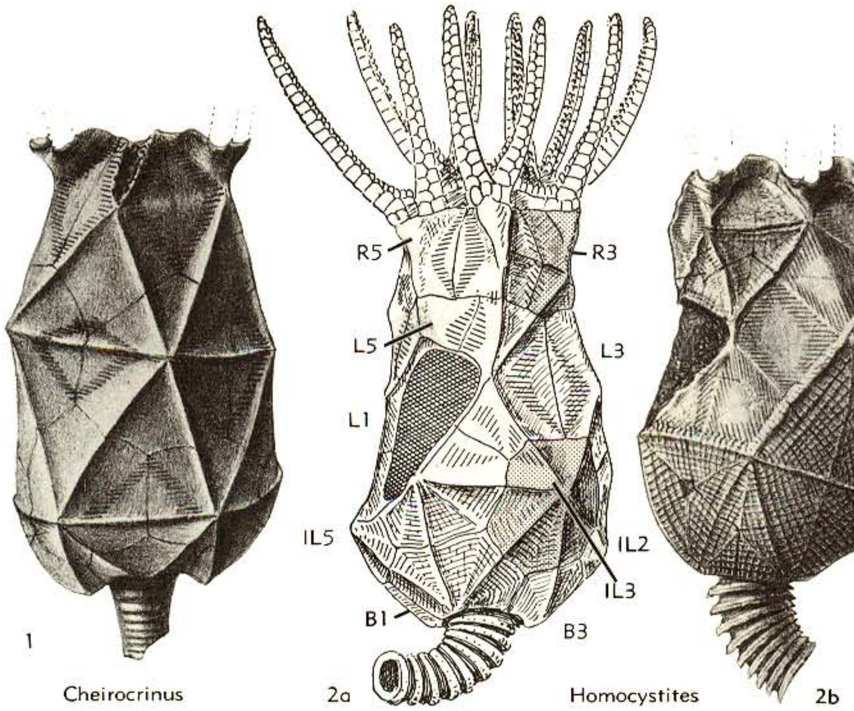


FIG. 88. Cheirocrinidae, plates of *A*-ray shaded (p. *S*182-*S*184). [Plate designations in *2a* are as given in Figure 38.]

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*

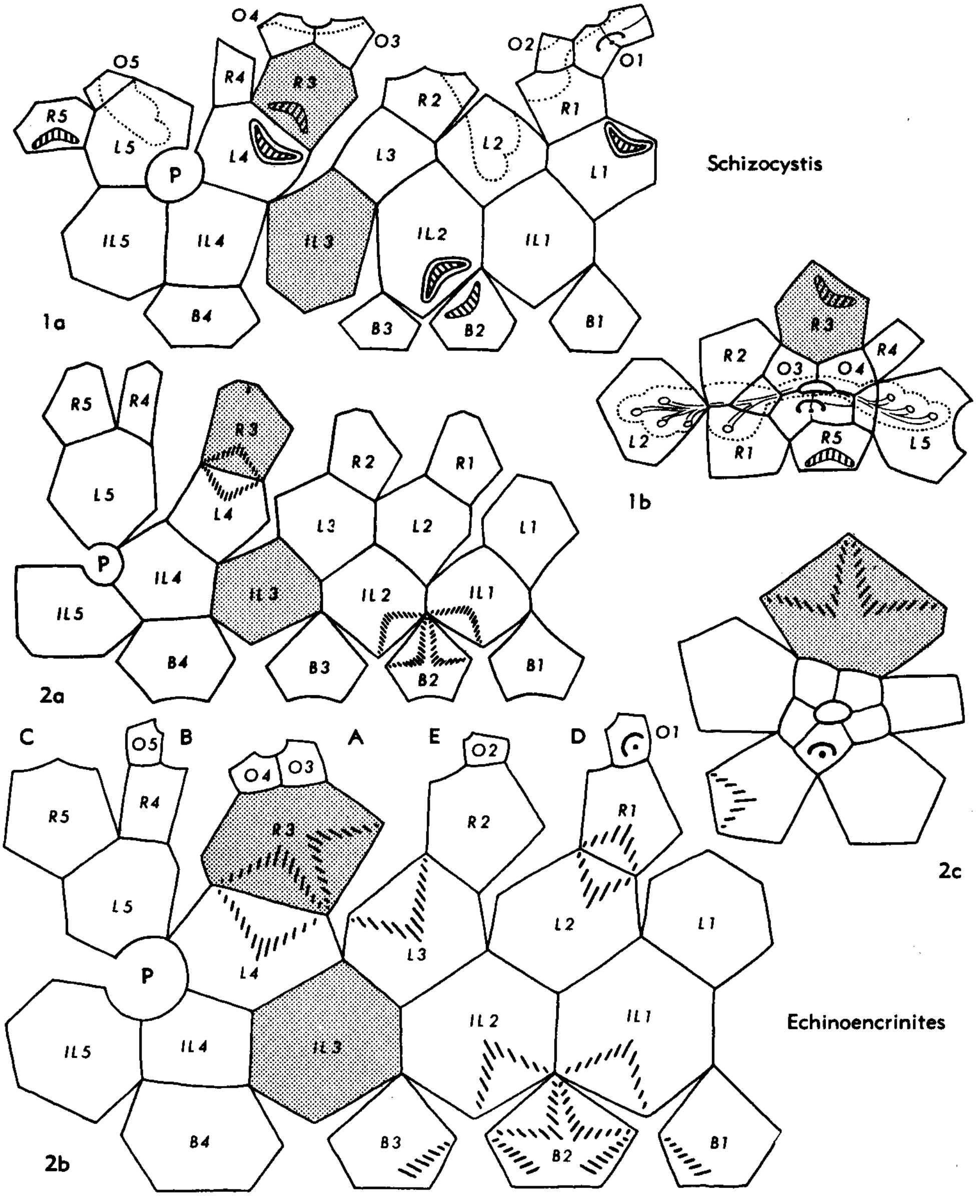


FIG. 89. Echinoencrinitidae. Plate diagrams, *A*-ray plates shaded, plate designations as in Figure 38 (p. *S*187-*S*189, *S*191).

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

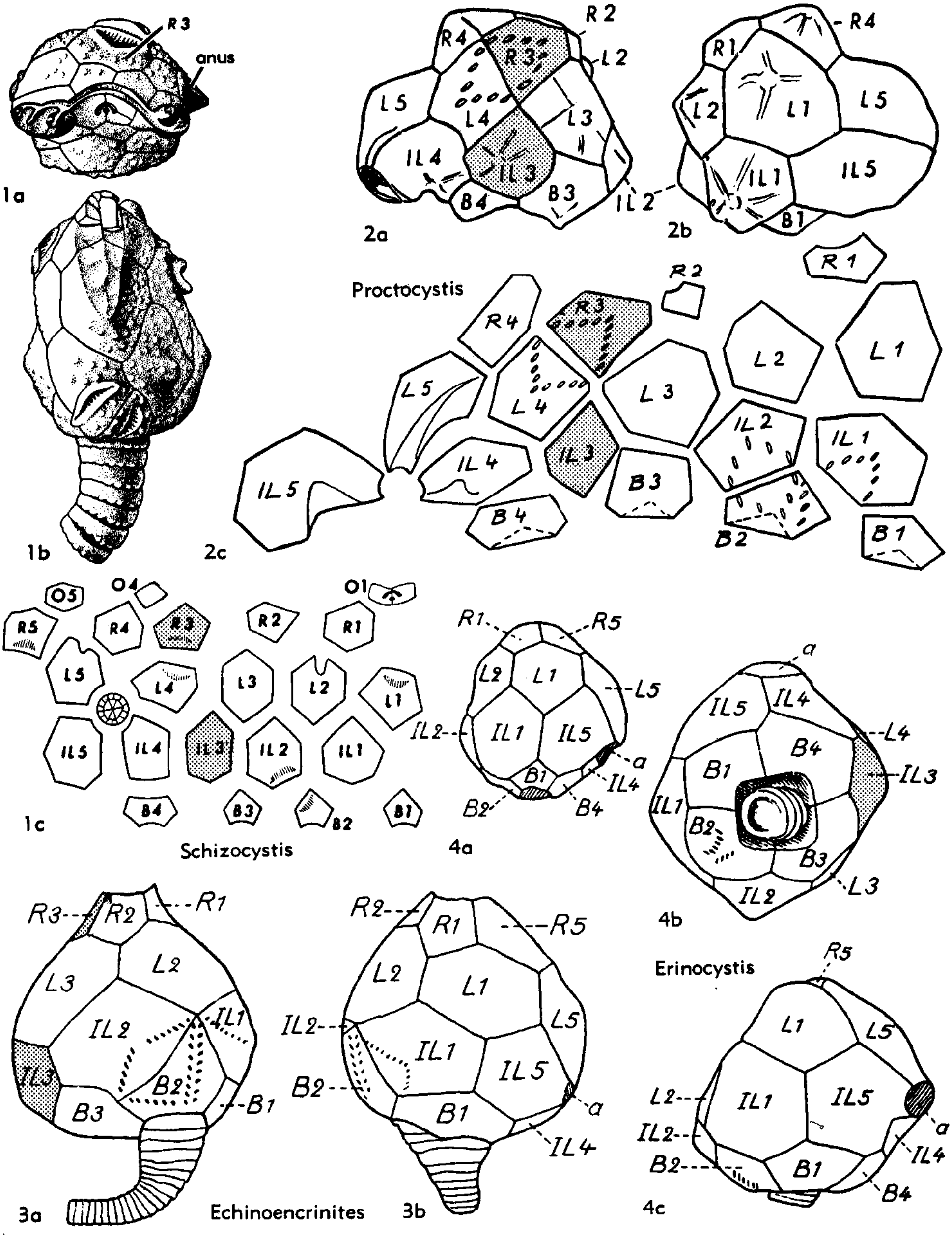


Fig. 90. Echinoencrinitidae, plates of *A*-ray shaded, plate designations as in Figure 38 (p. *S*187-*S*189, *S*191).

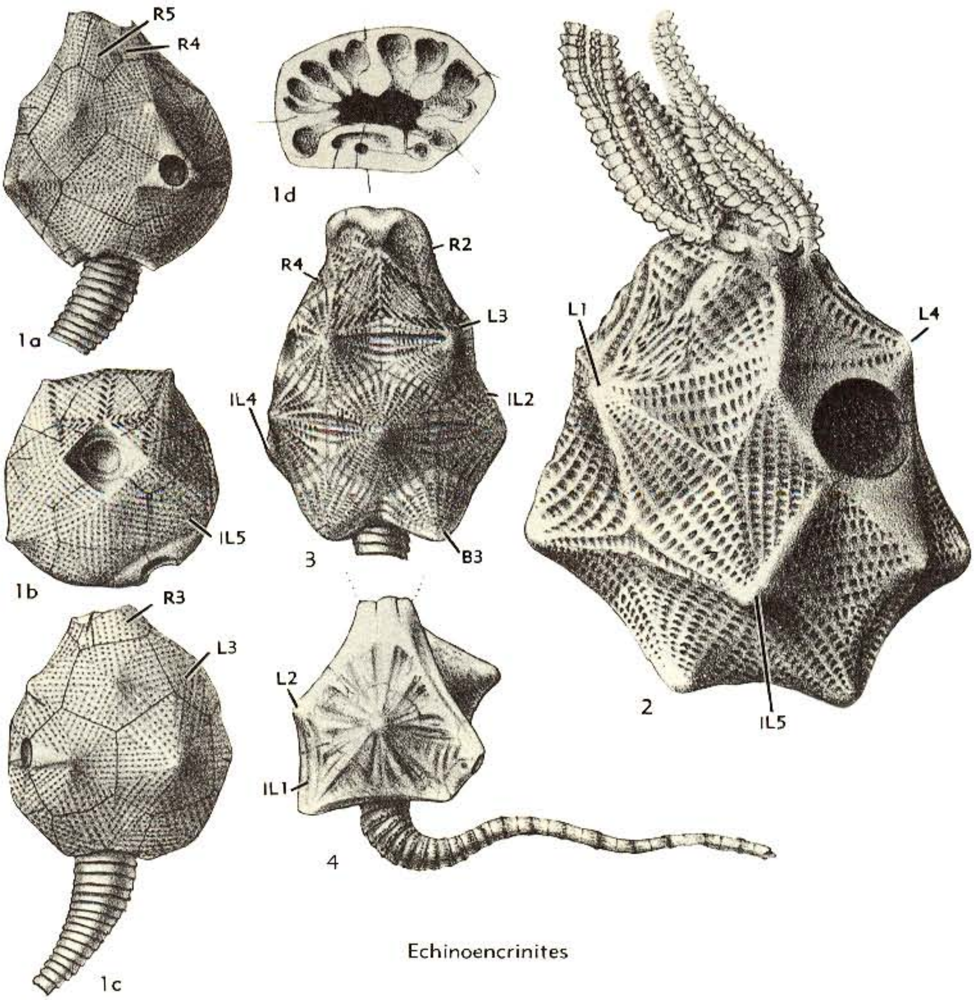


FIG. 91. Echinoencrinitidae, all L.Ord., USSR (Leningrad region), plate designations as in Figure 38 (p. *S*187-*S*189).

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

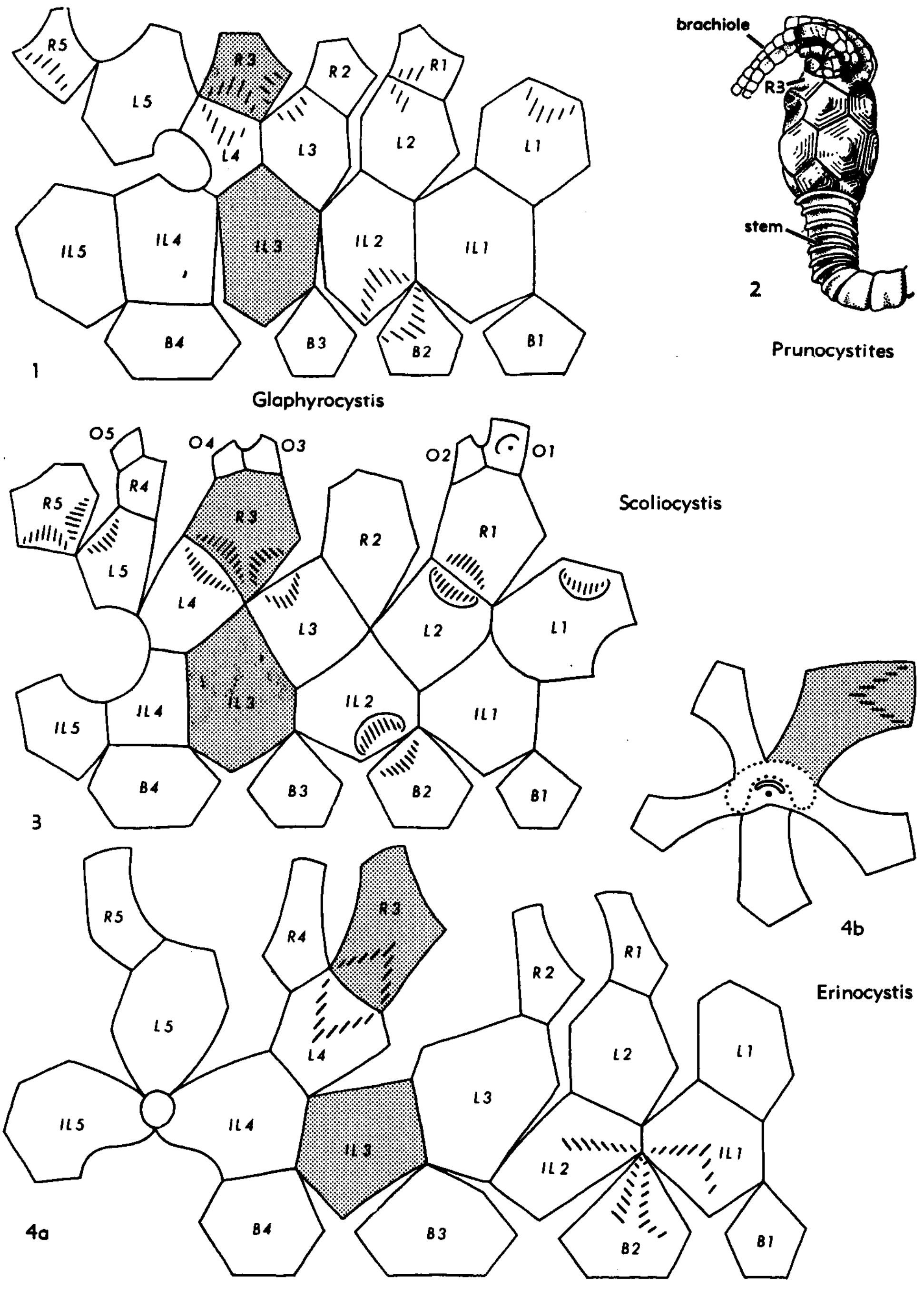
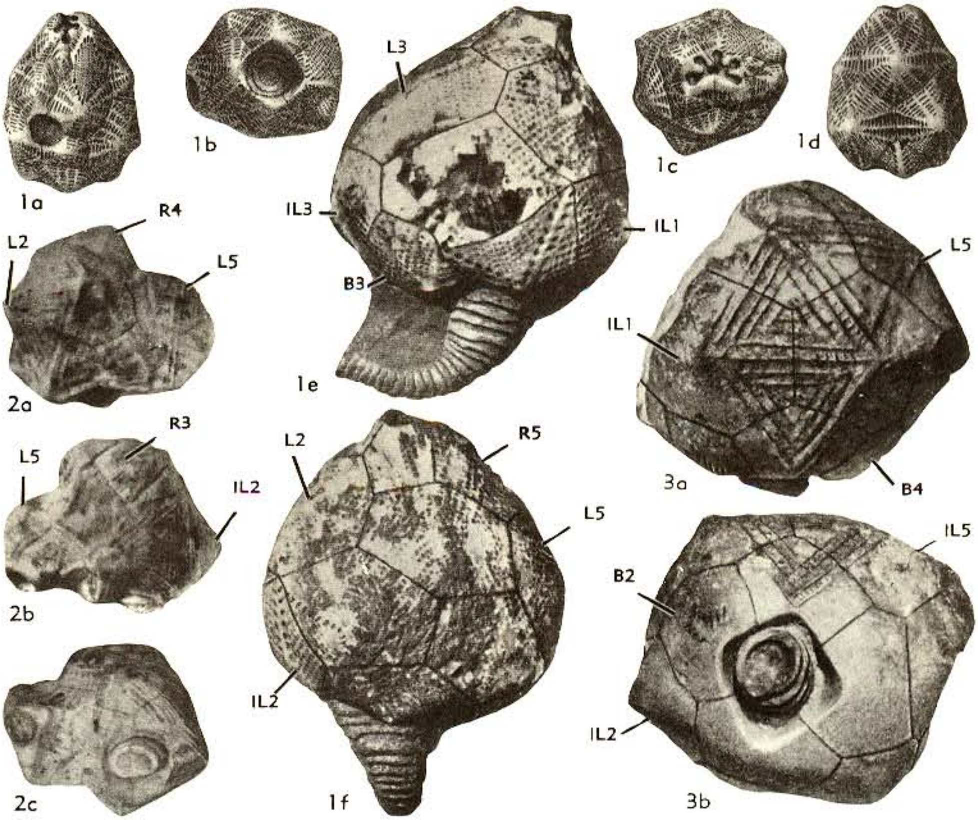


Fig. 92. Echinoencrinitidae. Plate diagrams, plates of *A*-ray shaded, plate designations as in Figure 38 (p. *S*189-*S*192).



Proctocystis Echinoencrinites Erinocystis

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

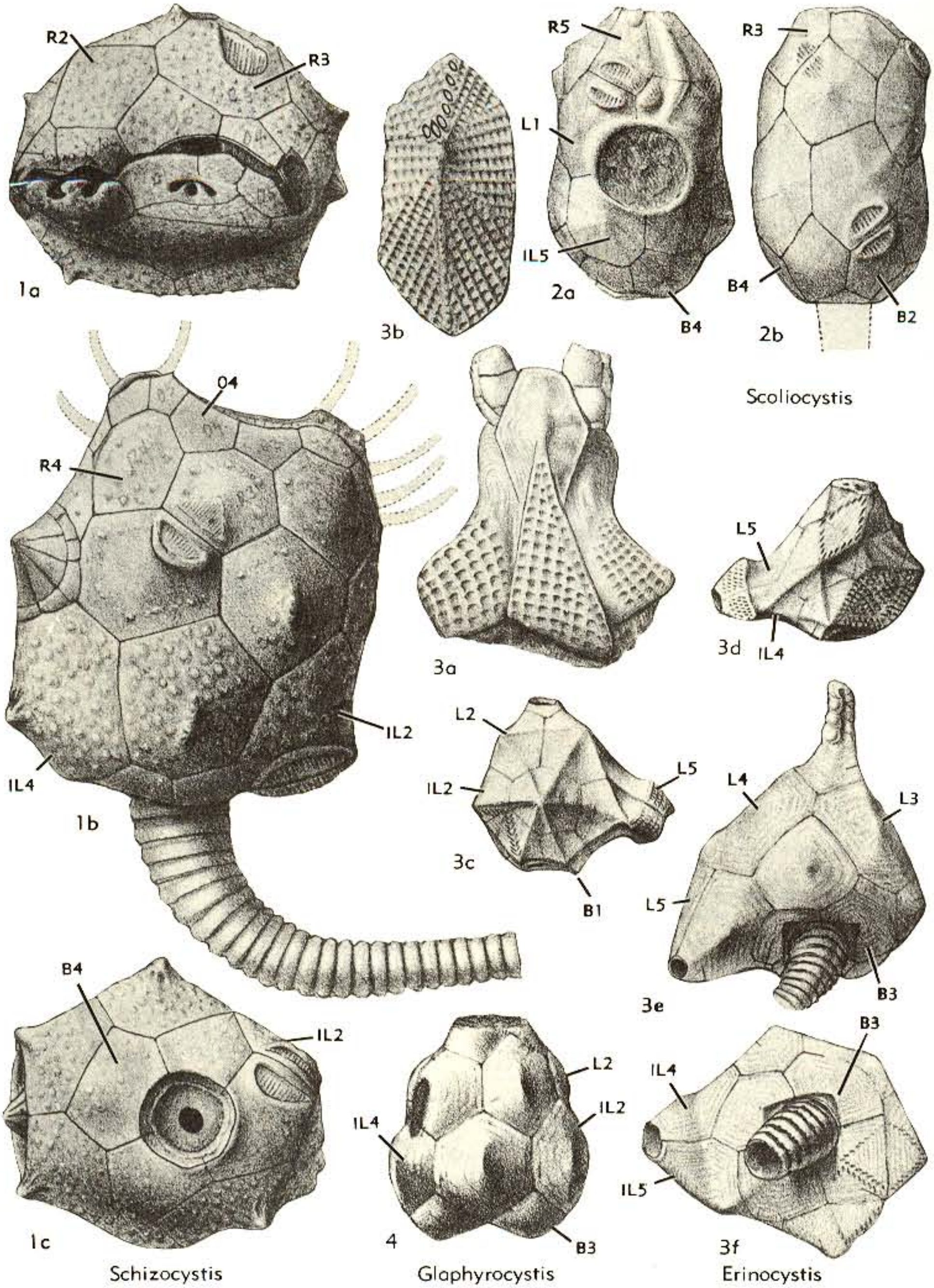


FIG. 94. Echinoencrinitidae (p. S189-S192). [Plate designations as in Figure 38.]

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).

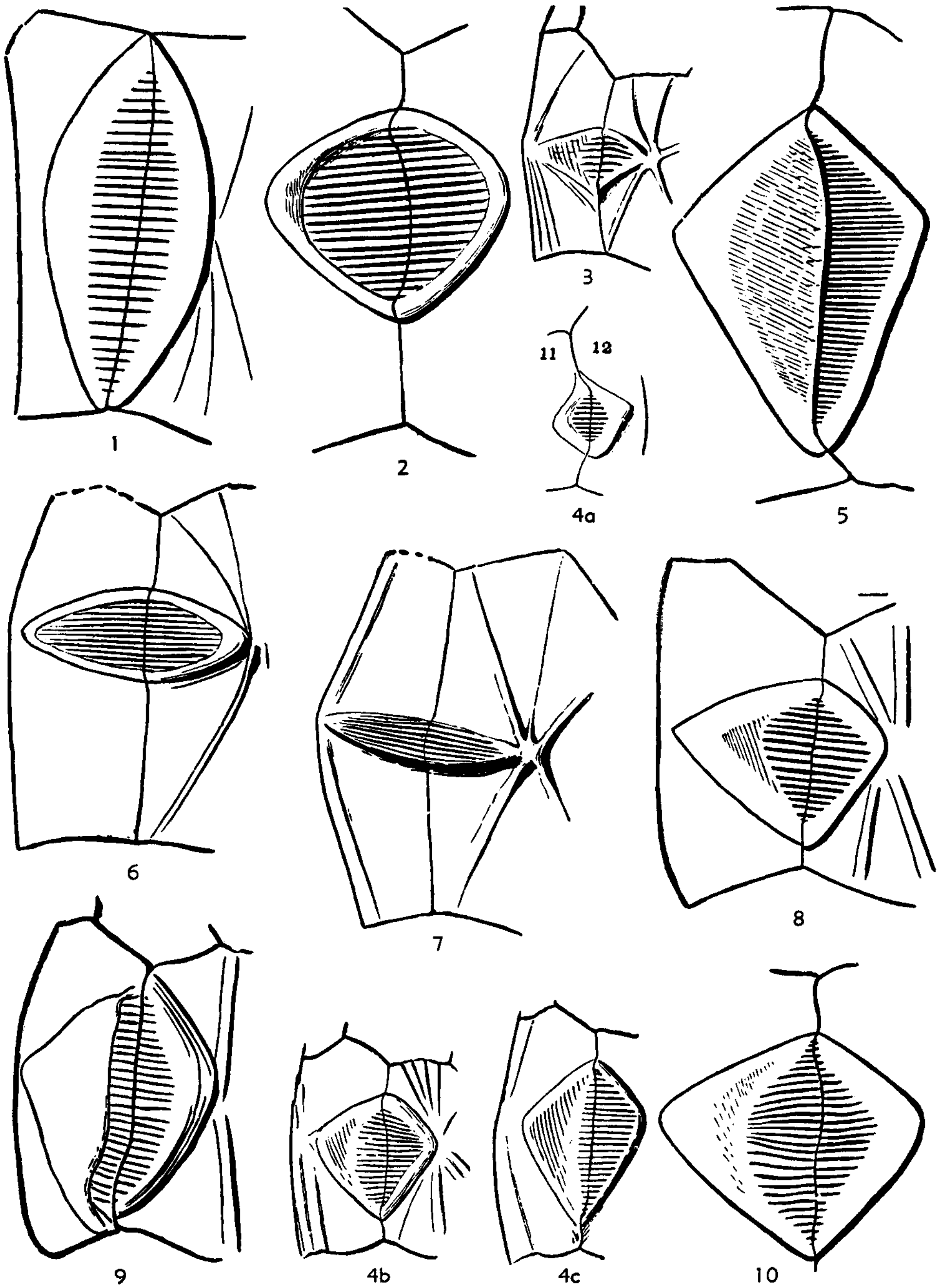


Fig. 95. Pleurocystitidae (p. *S*194-*S*199).——*1-10. Pleurocystites,* M.Ord.-U.Ord.; pectinirhomb *L1/L2* in various species, all ×5 *(12).*

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*.

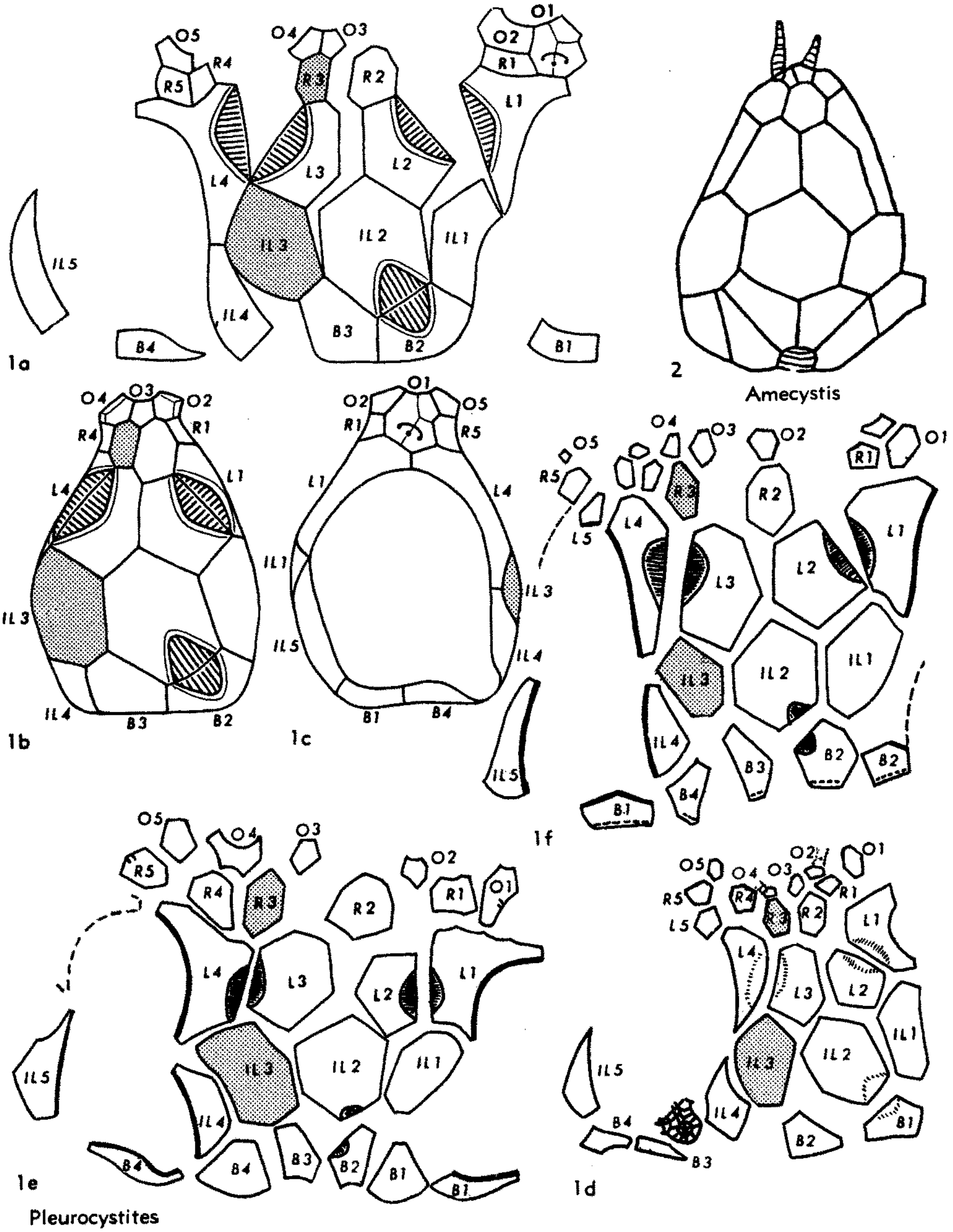


FIG. 96. Pleurocystitidae, plates of *A*-ray shaded (p. S194-S199). [Plate designations as in Figure 38.]

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

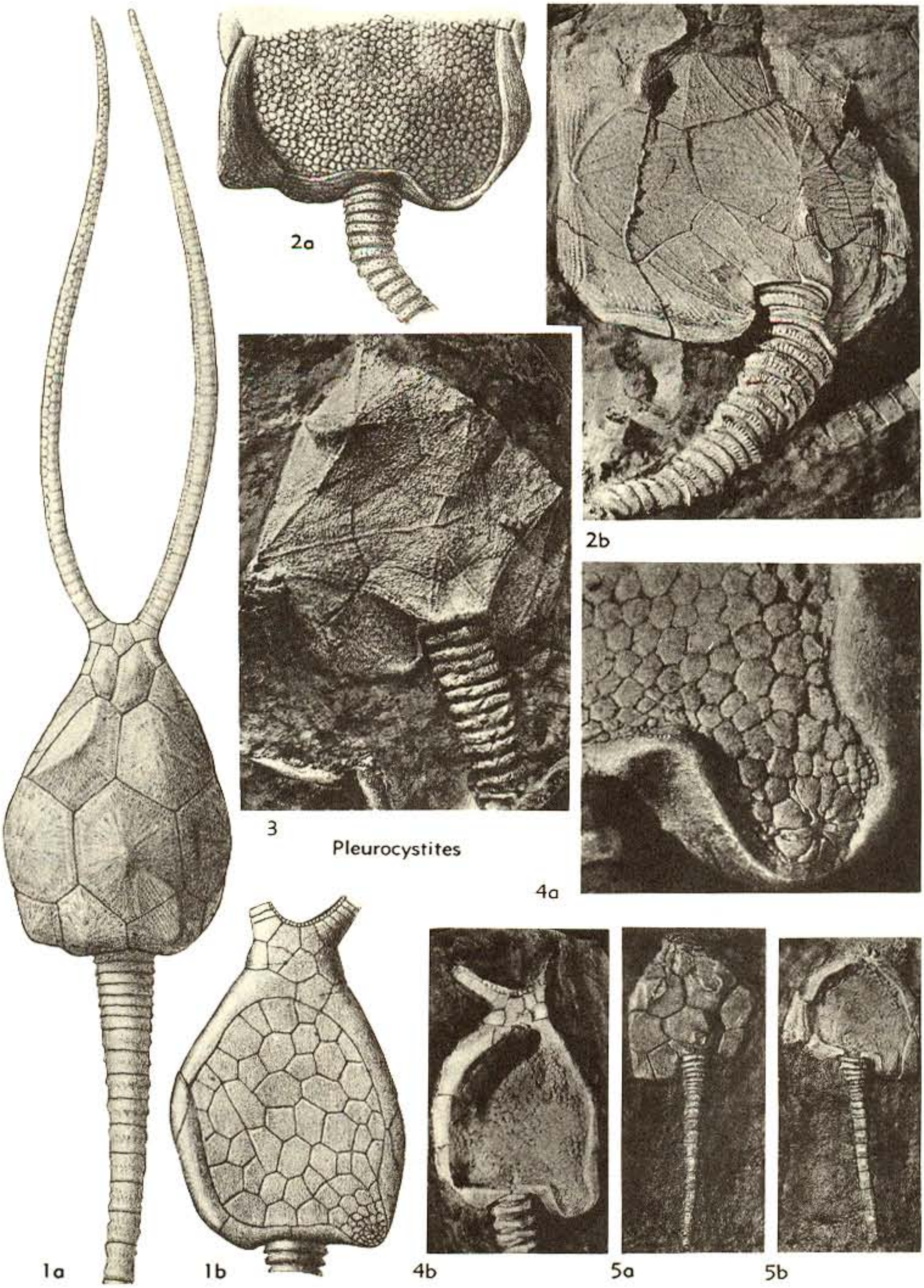


FIG. 97. Pleurocystitidae (p. S194-S199).

(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,

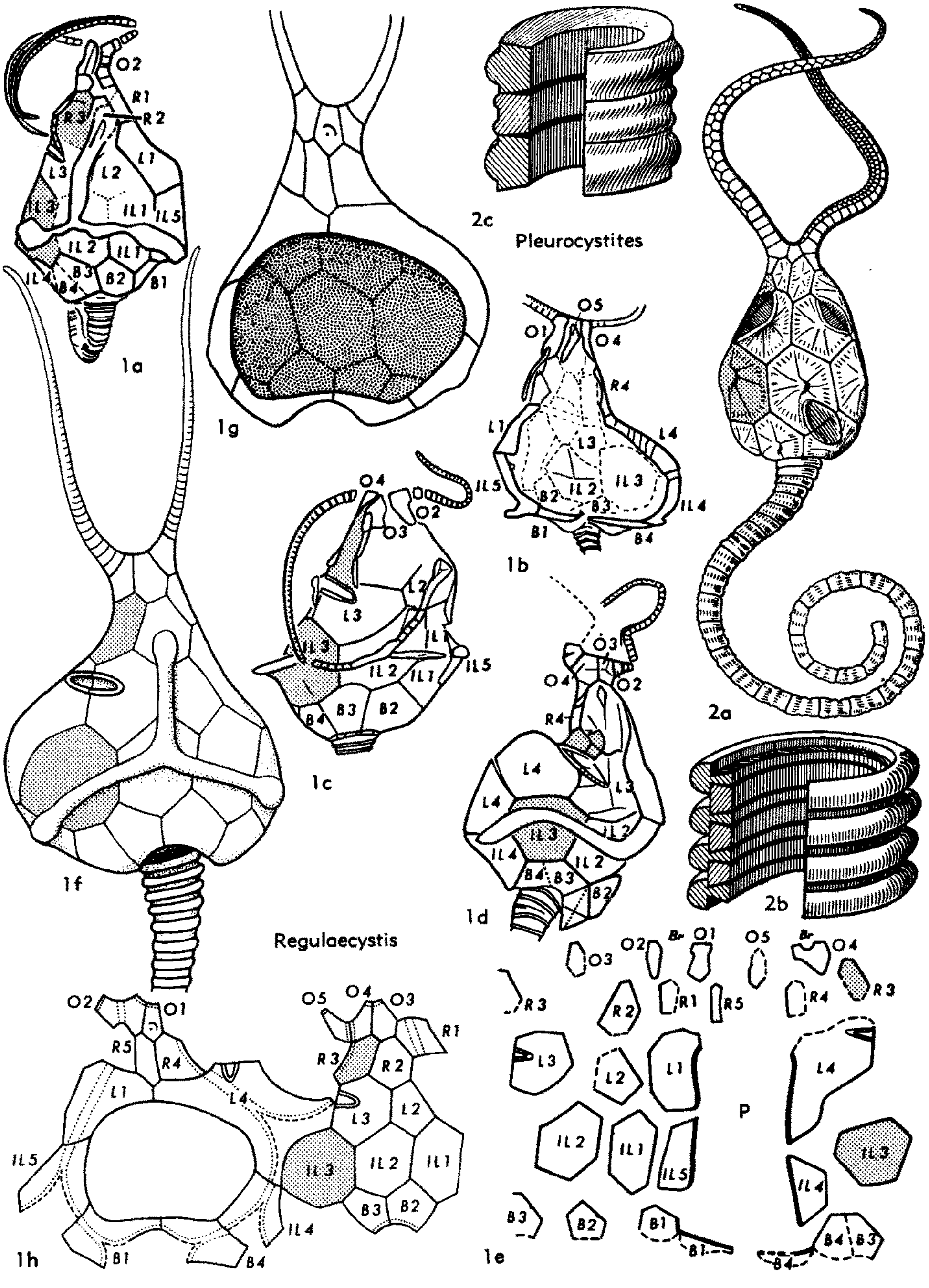


FIG. 98. Pleurocystitidae, plates of *A*-ray shaded (p. *S*194-*S*199). [Plate designations as in Figure 38.]

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.*

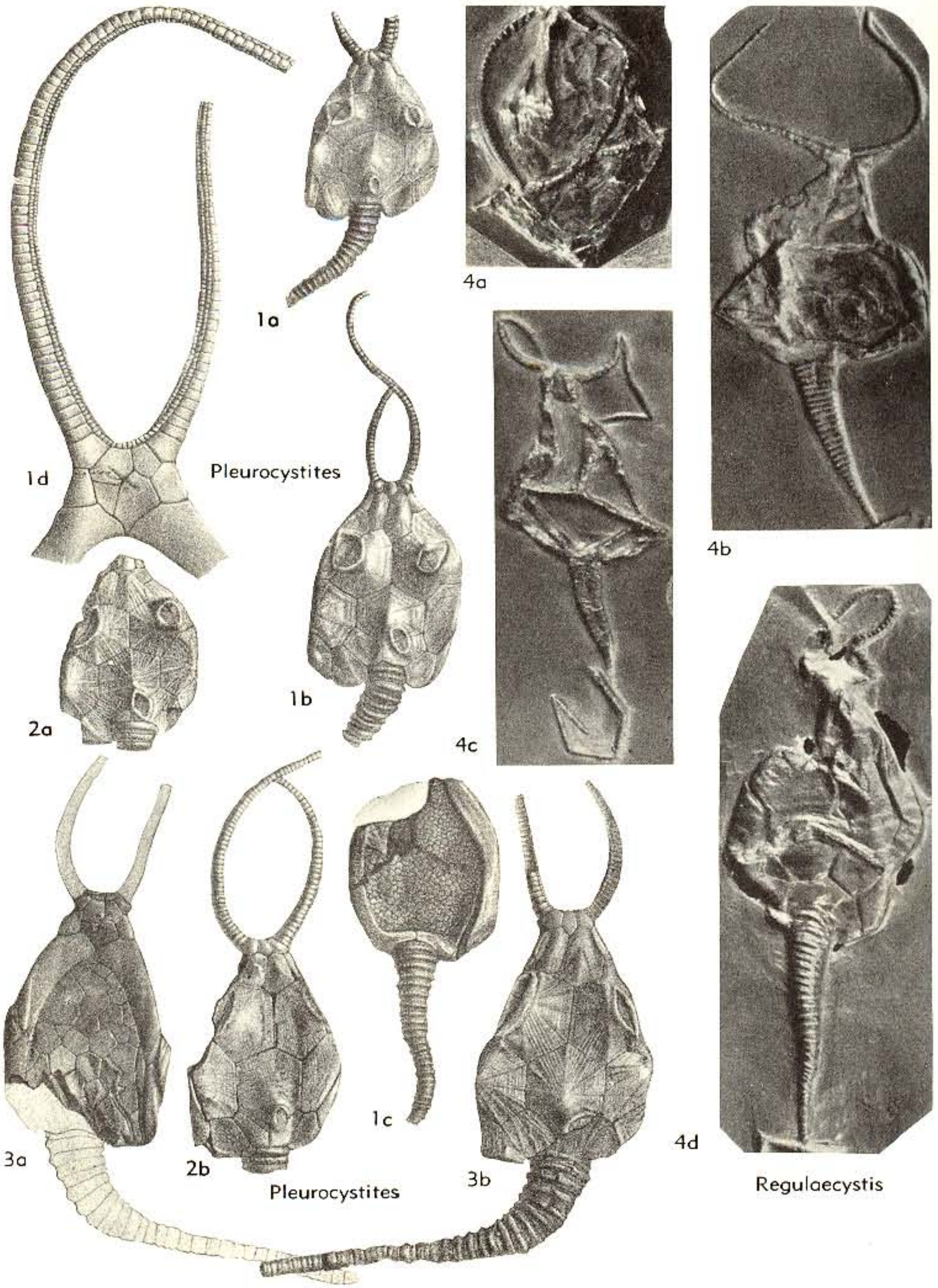


Fig. 99. Pleurocystitidae (p. S194-S199).

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

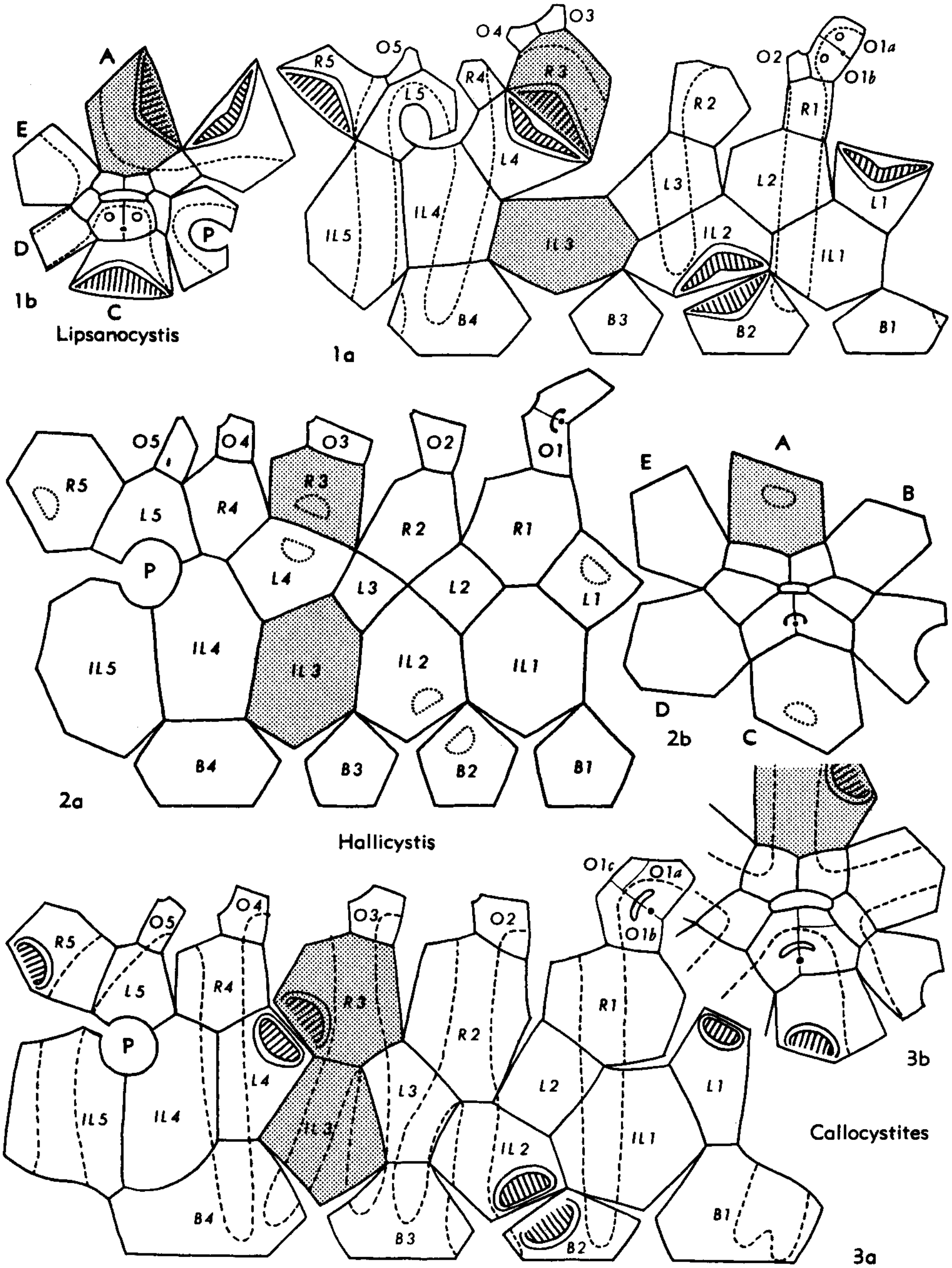


Fig. 100. Callocystitidae, Callocystitinae *(3)*, Apiocystitinae, *(1,2)*, plates of *A*-ray shaded (p. *S*199-*S*201, *S*209, *S*212-*S*213). [Plate designations as in Figure 38.]

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-

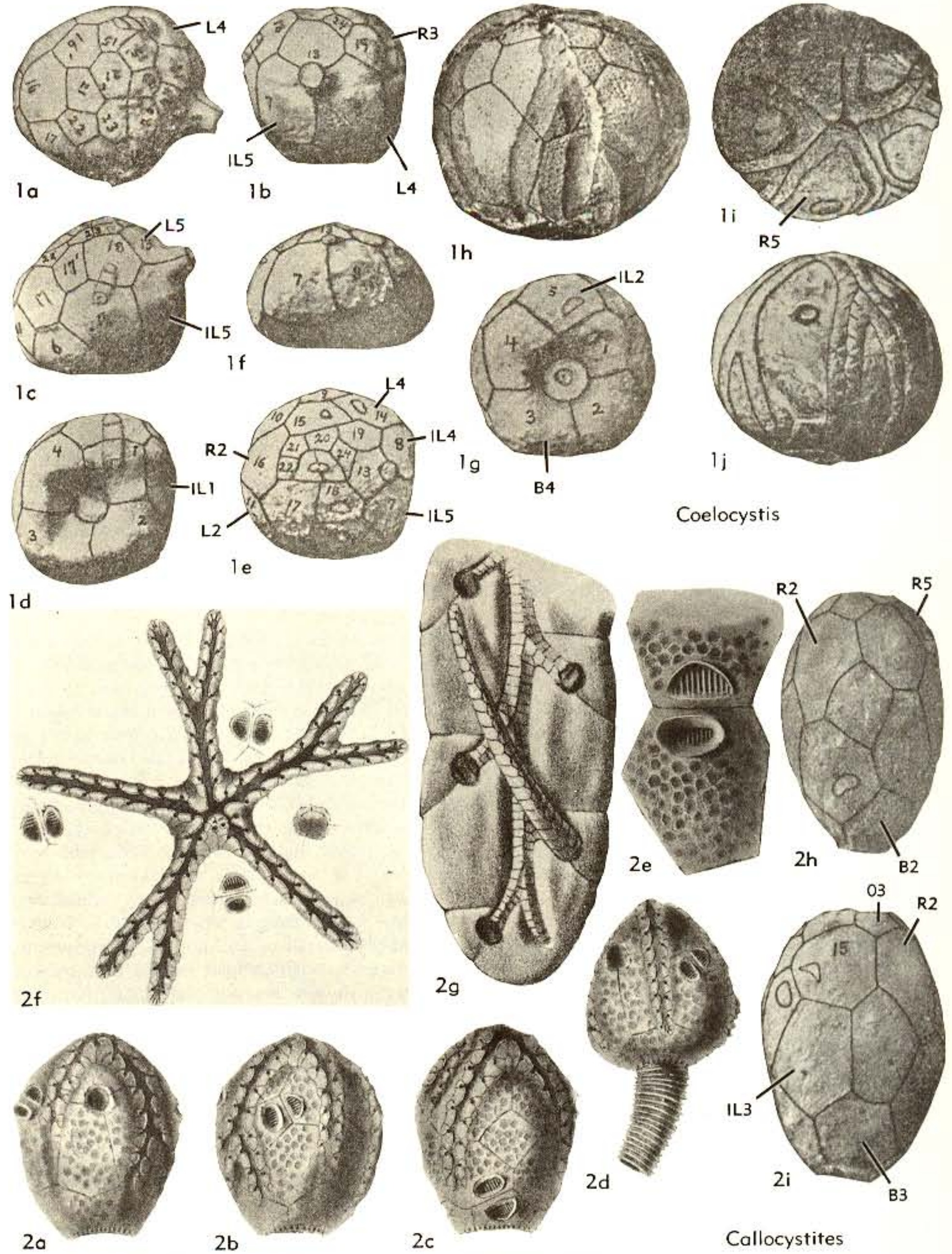


Fig. 101. Callocystitidae, Callocystitinae (p. S199-S202). [Plate designations as in Figure 38.]

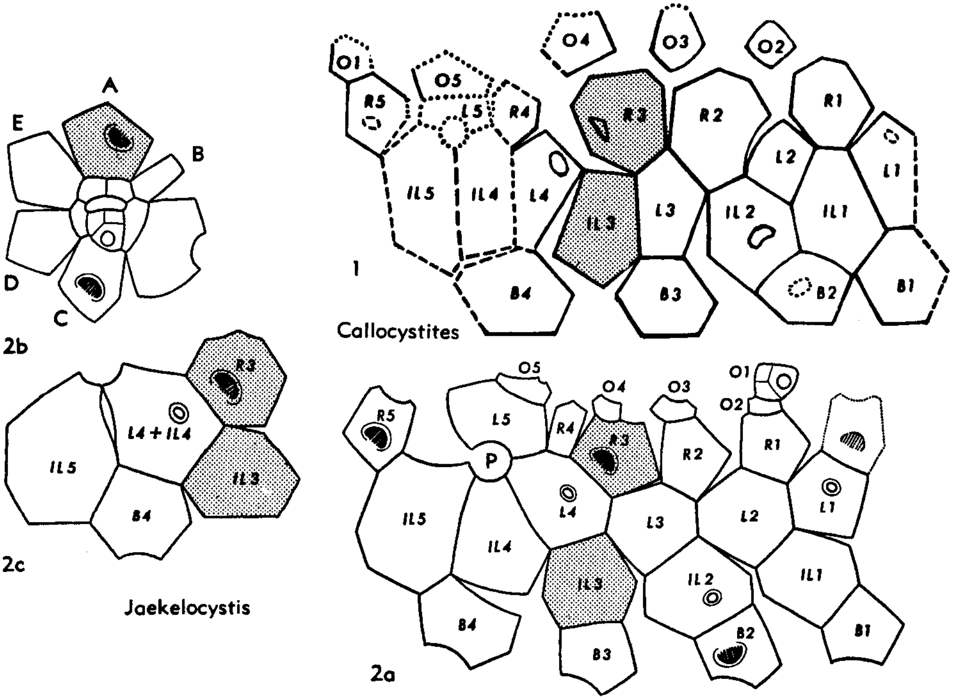


FIG. 102. Callocystitidae, Callocystitinae *(1)*, Apiocystitinae *(2)*, plate diagrams, plates of *A*-ray shaded (p. *S*199-*S*201, S209). [Plate designations as in Figure 38, Carpenter letter symbols for rays in *2b*.]

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

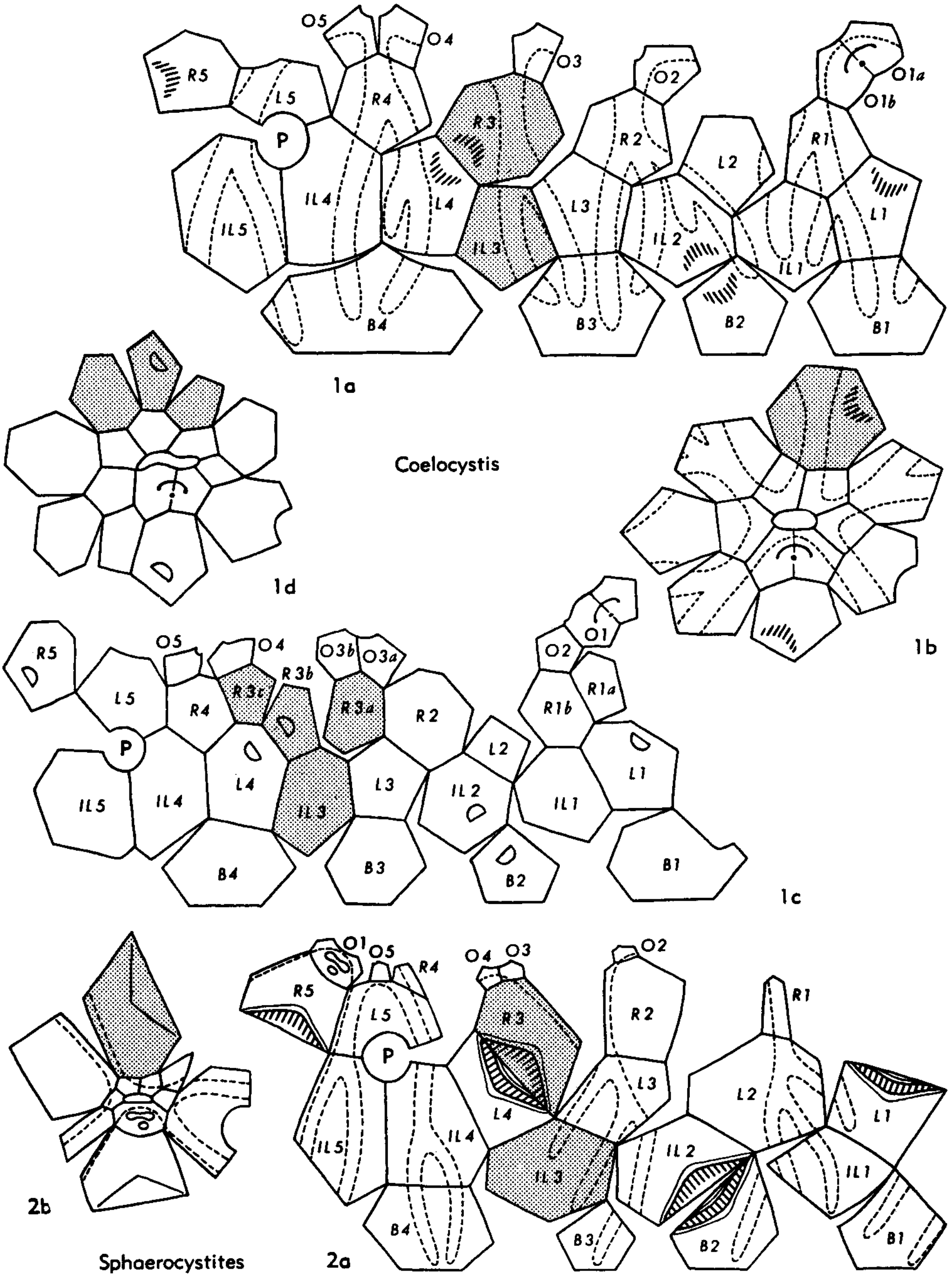


FIG. 103. Callocystitidae, Callocystitinae. Plate diagrams, plates of *A*-ray shaded (p. S201-S203). [Plate designations as in Figure 38.]

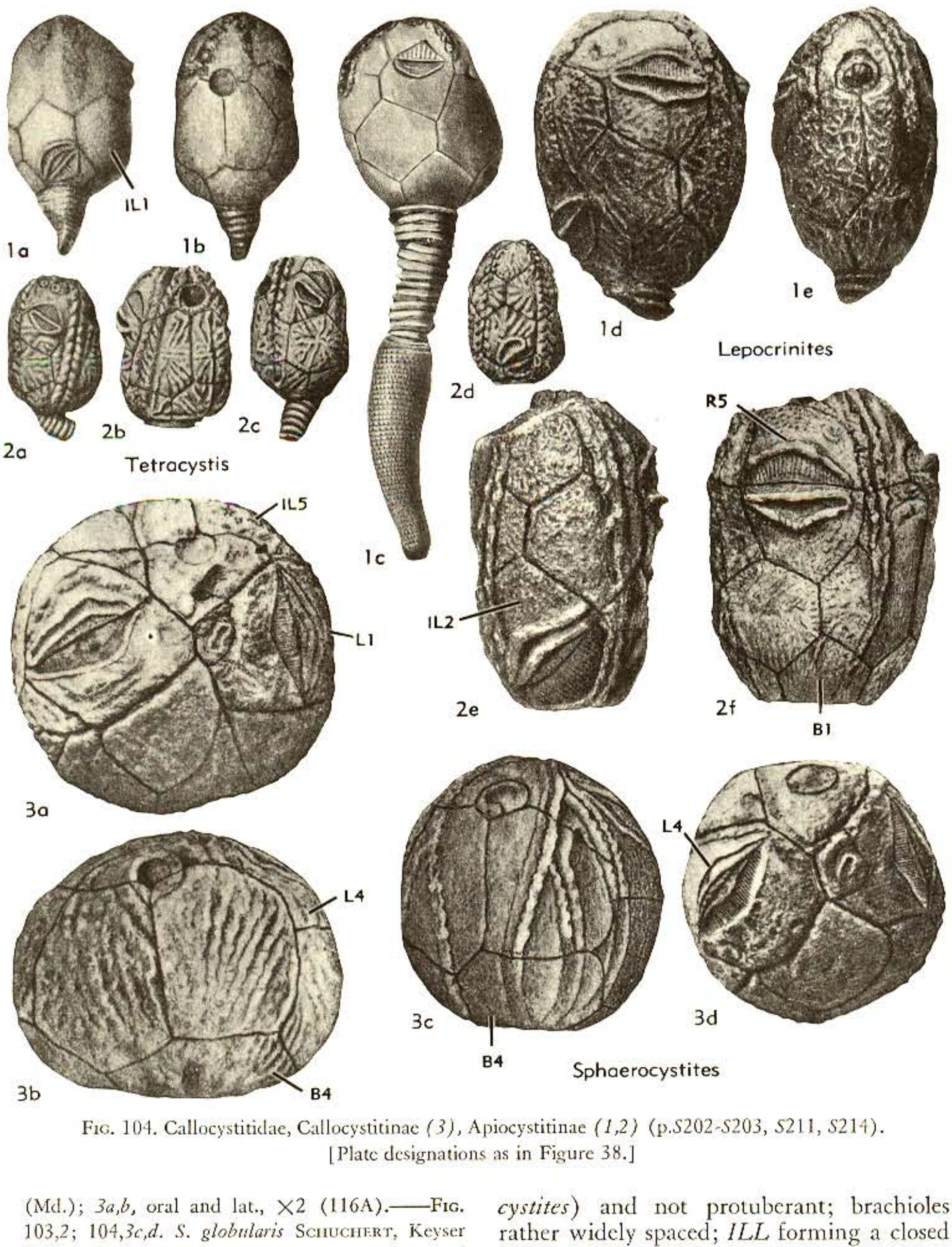


Fig. 104. Callocystitidae, Callocystitinae *(3),* Apiocystitinae *(1,2)* (p.S202-S203, S211, S214). [Plate designations as in Figure 38.]

(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

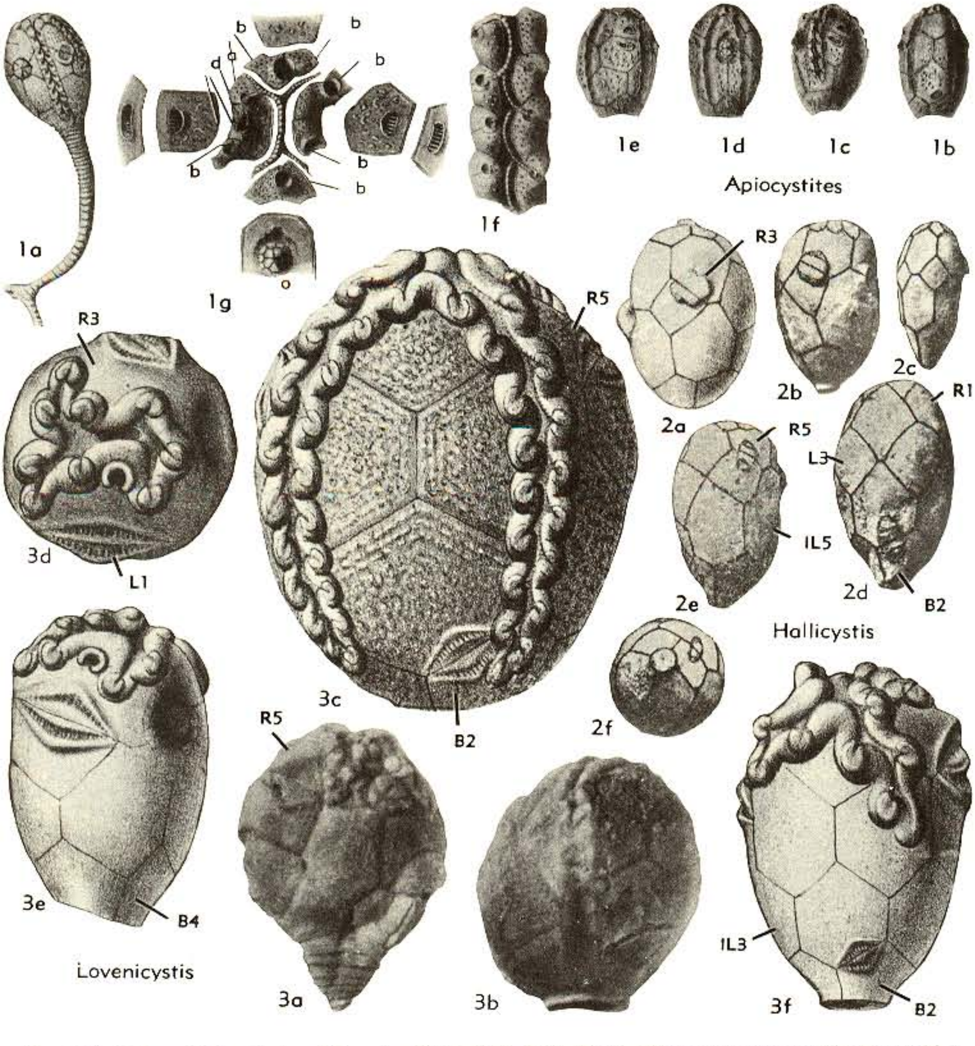


FIG. 105. Callocystitidae, Apiocystitinae (p. *S206*, *S209*, *S212*-*S214*). [Plate designations as in Figure 38.]

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

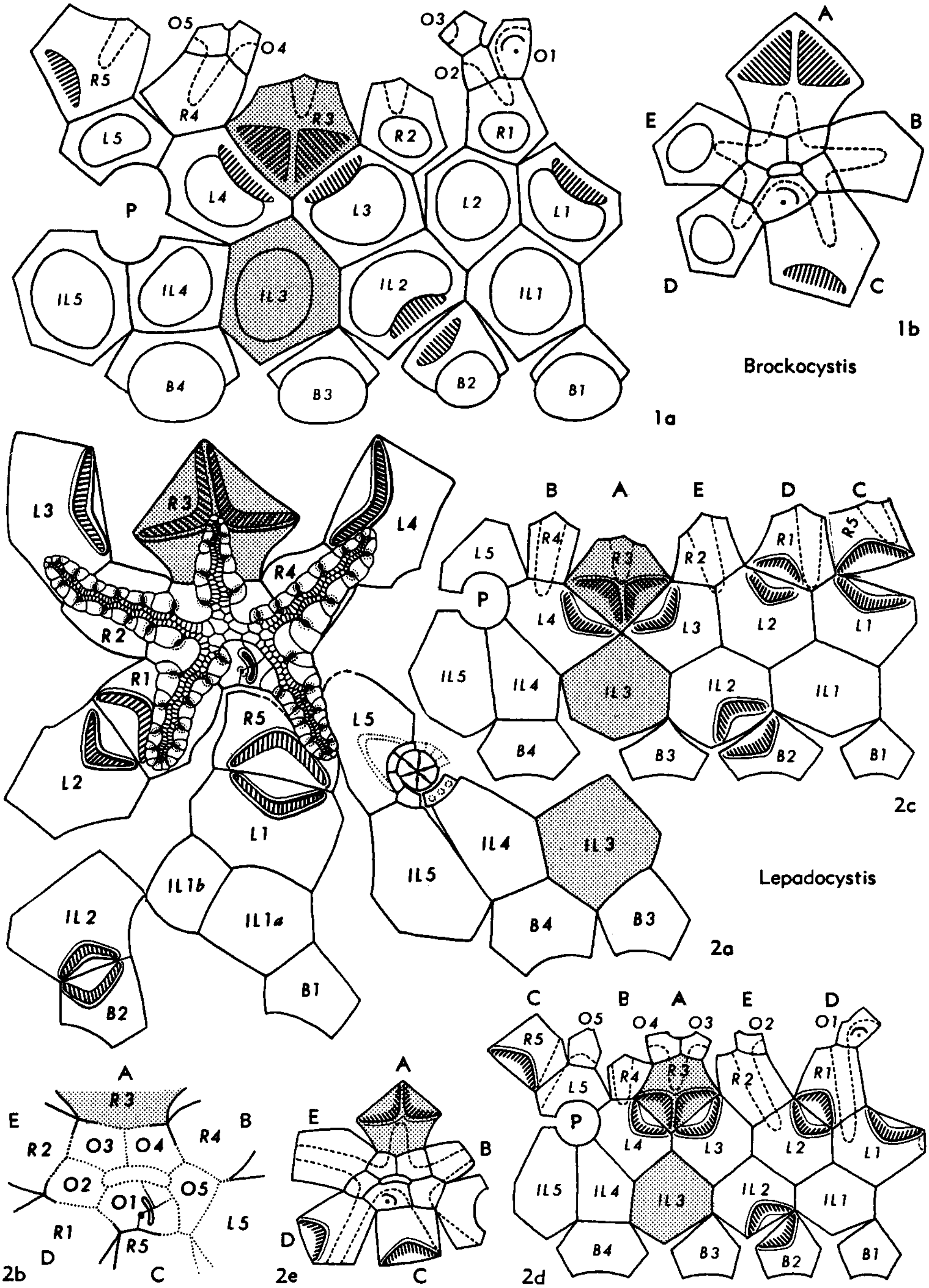


Fig. 106. Callocystitidae, Apiocystitinae, plates of *A*-ray shaded (p. *S206-S211*). [Plate designations as in Figure 38.]

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.);

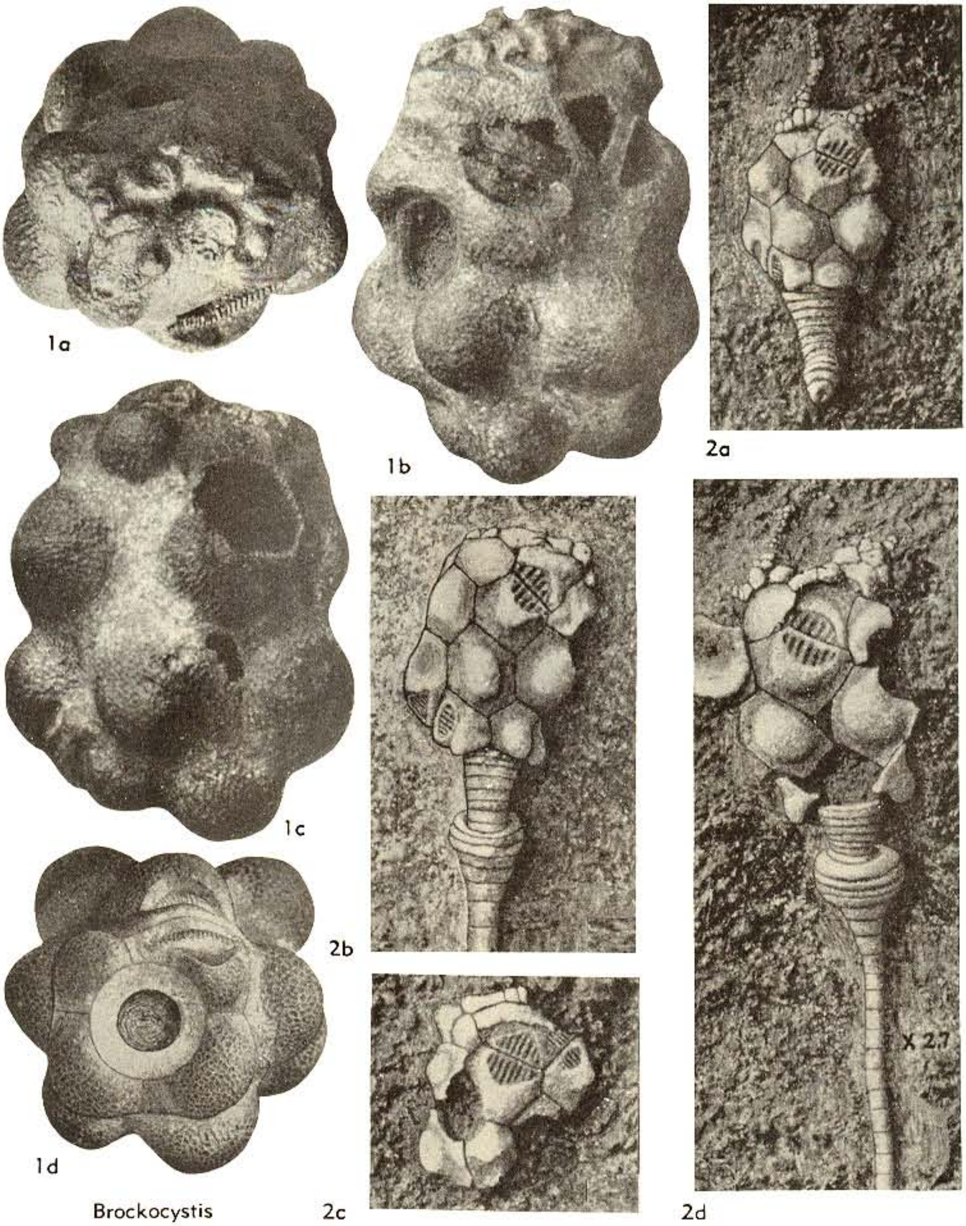


FIG. 107. Callocystitidae, Apiocystitinae (p. S206-S209).

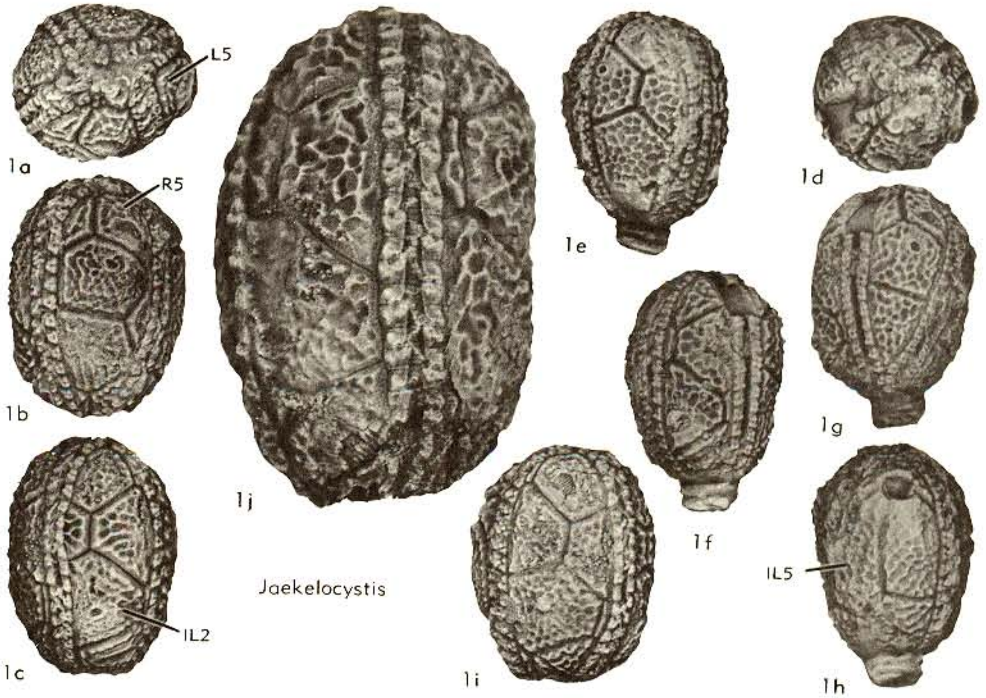


FIG. 108. Callocystitidae, Apiocystitinae (p. *S*209). [Plate designations as in Figure 38.]

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

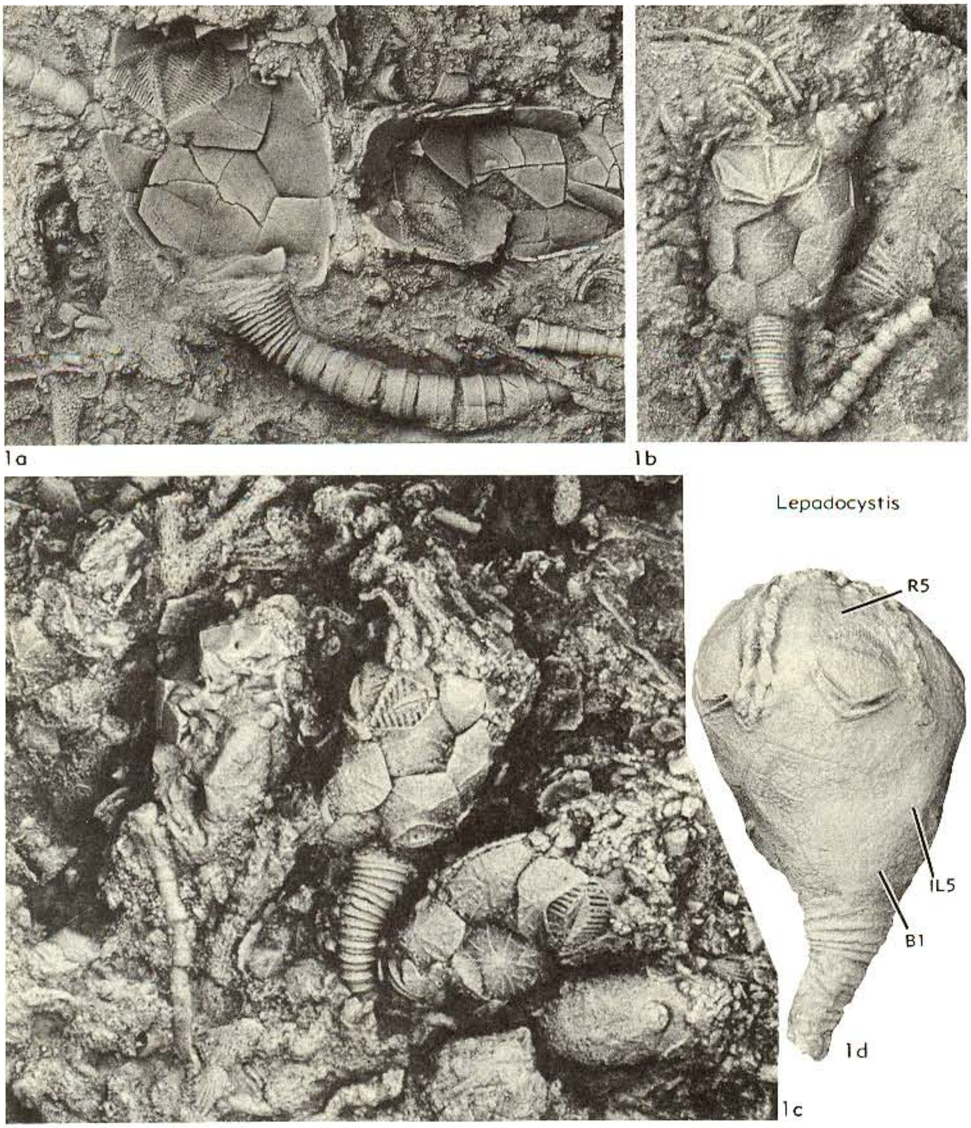


FIG. 109. Callocystitidae, Apiocystitinae (p. *S210-S211*).

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

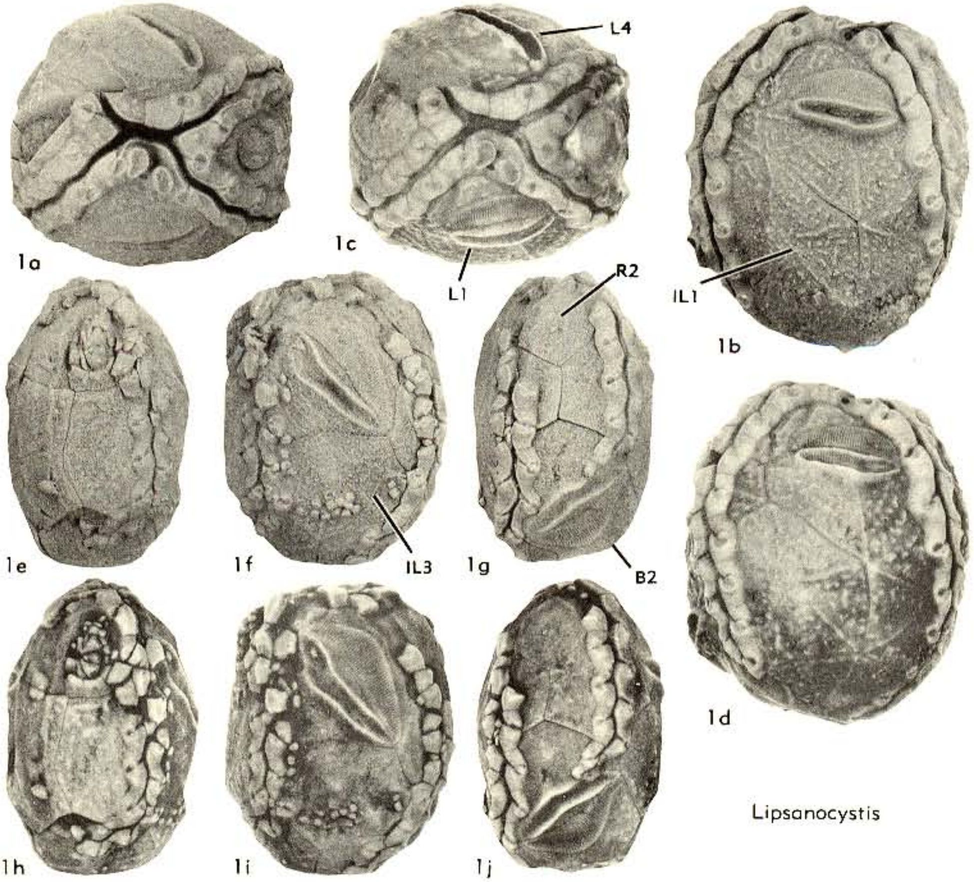


Fig. 110. Callocystitidae, Apiocystitinae (p. *S212-S213*). [Plate designations as in Figure 38.]

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,

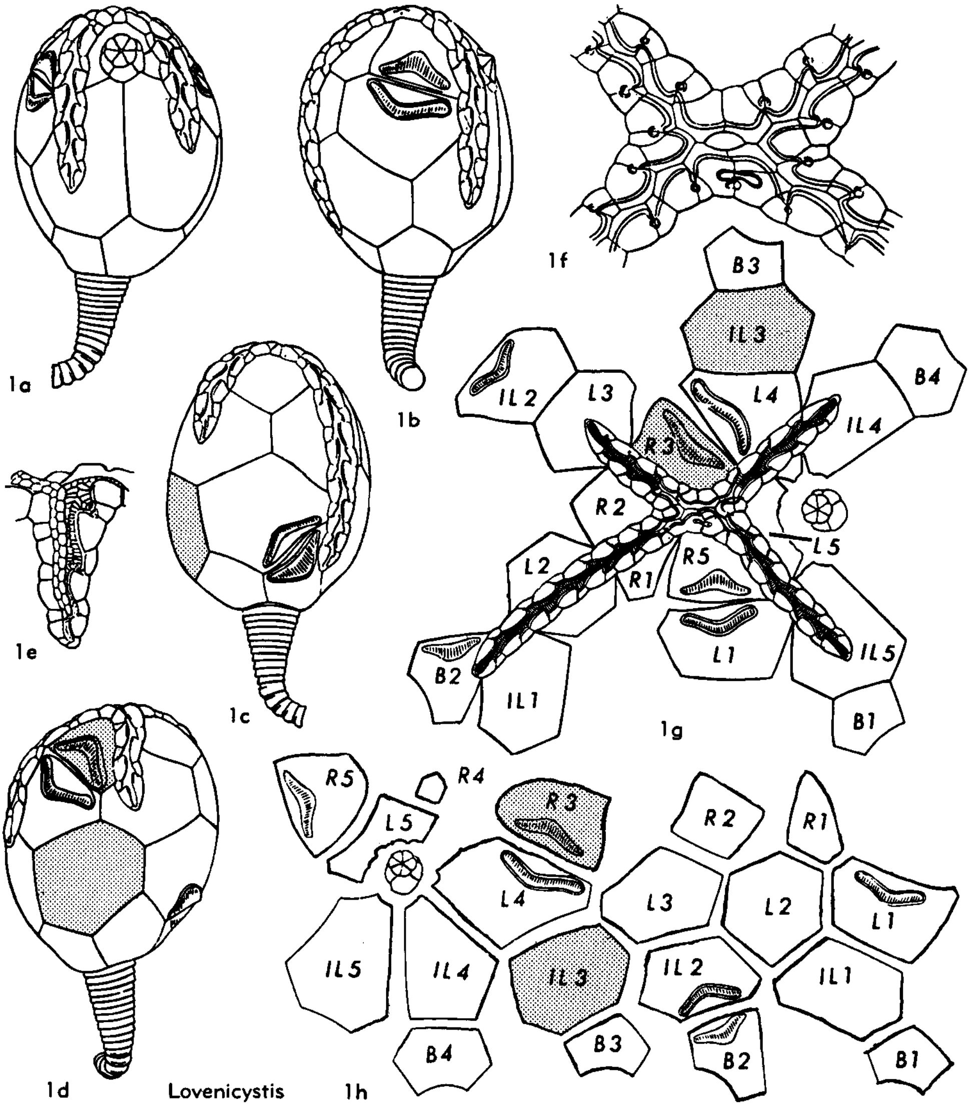


FIG. 111. Callocystitidae, Apiocystitinae. Lateral views (reconstr.) and plate diagrams; plates of *A*-ray shaded (p. *S*213-*S*214). [Plate designations as in Figure 38.]

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;*

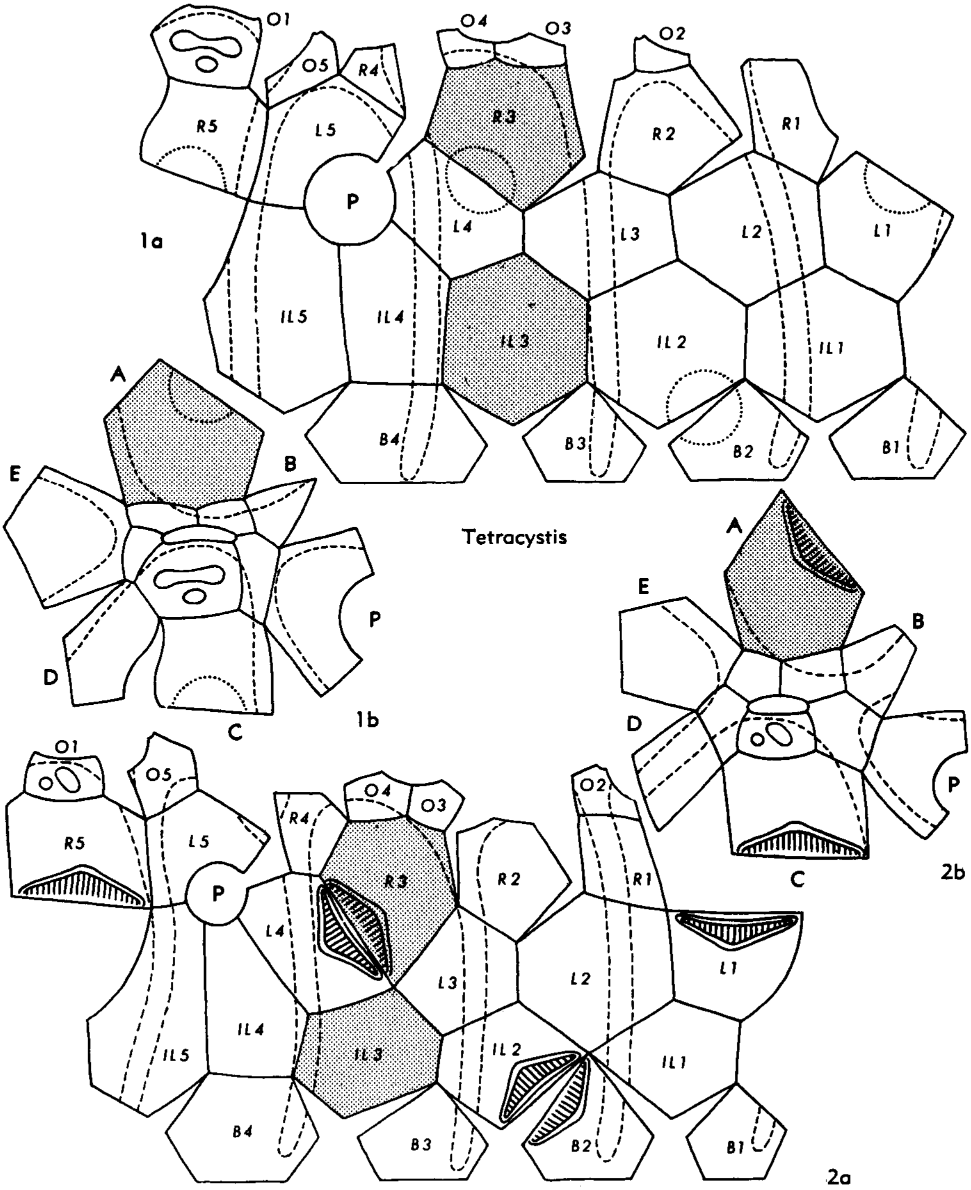


FIG. 112. Callocystitidae, Apiocystitinae. Plate diagrams, plates of *A*-ray shaded (p. *S*214). [Plate designations as in Figure 38, Carpenter letter symbols for rays in *1b,d*.]

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*.]

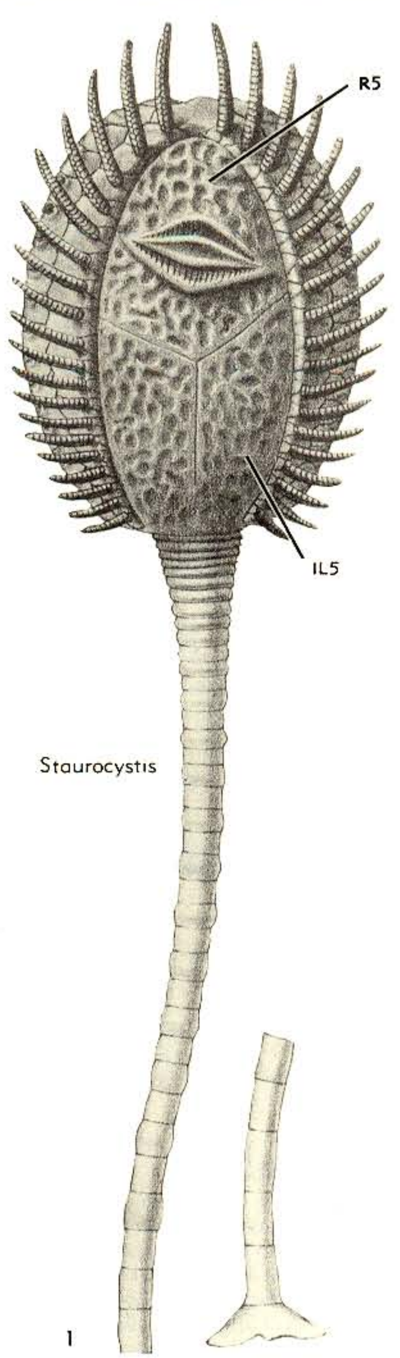


Fig. 113. Callocystitidae, Staurocystinae (p. *S*217-*S*218). [Plate designations as in Figure 38.]

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).

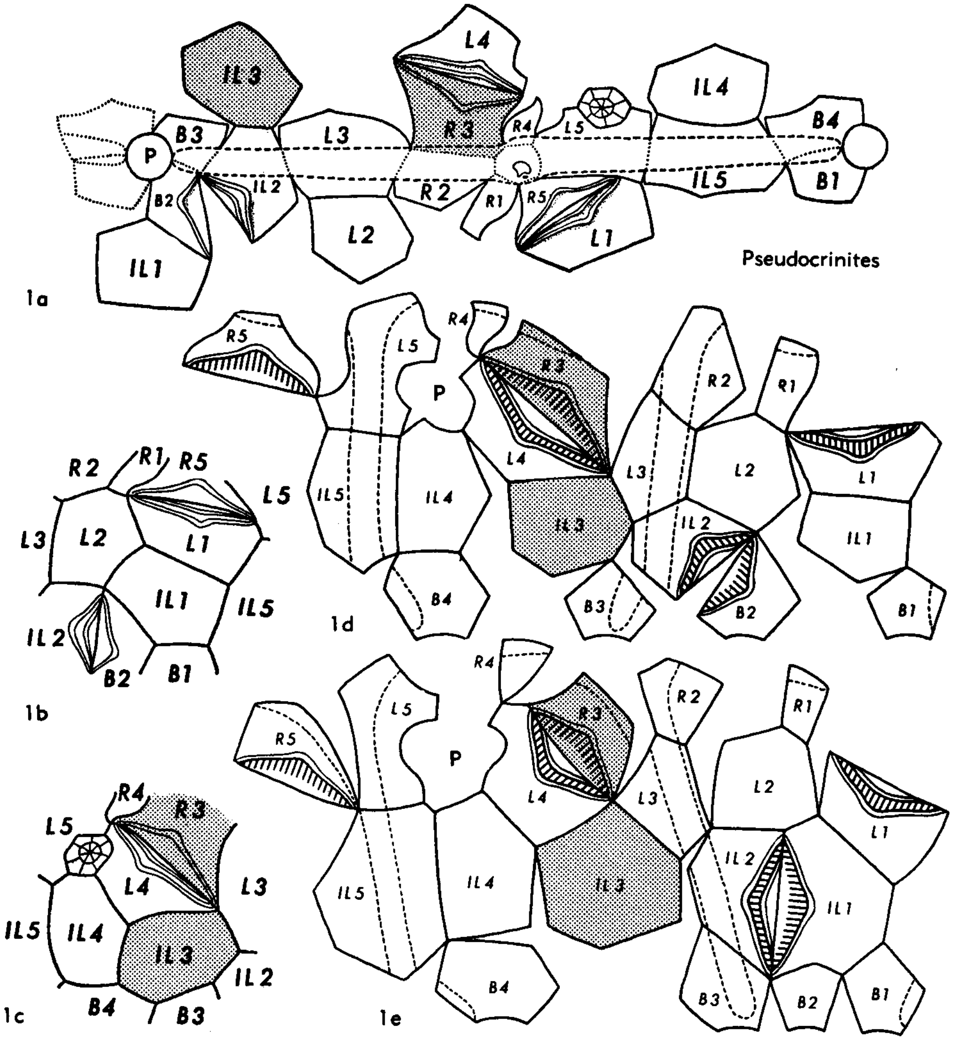


FIG. 114. Callocystitidae, Staurocystinae. Plate diagrams, plates of *A*-ray shaded (p. *S*218). [Plate designations as in Figure 38.]

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

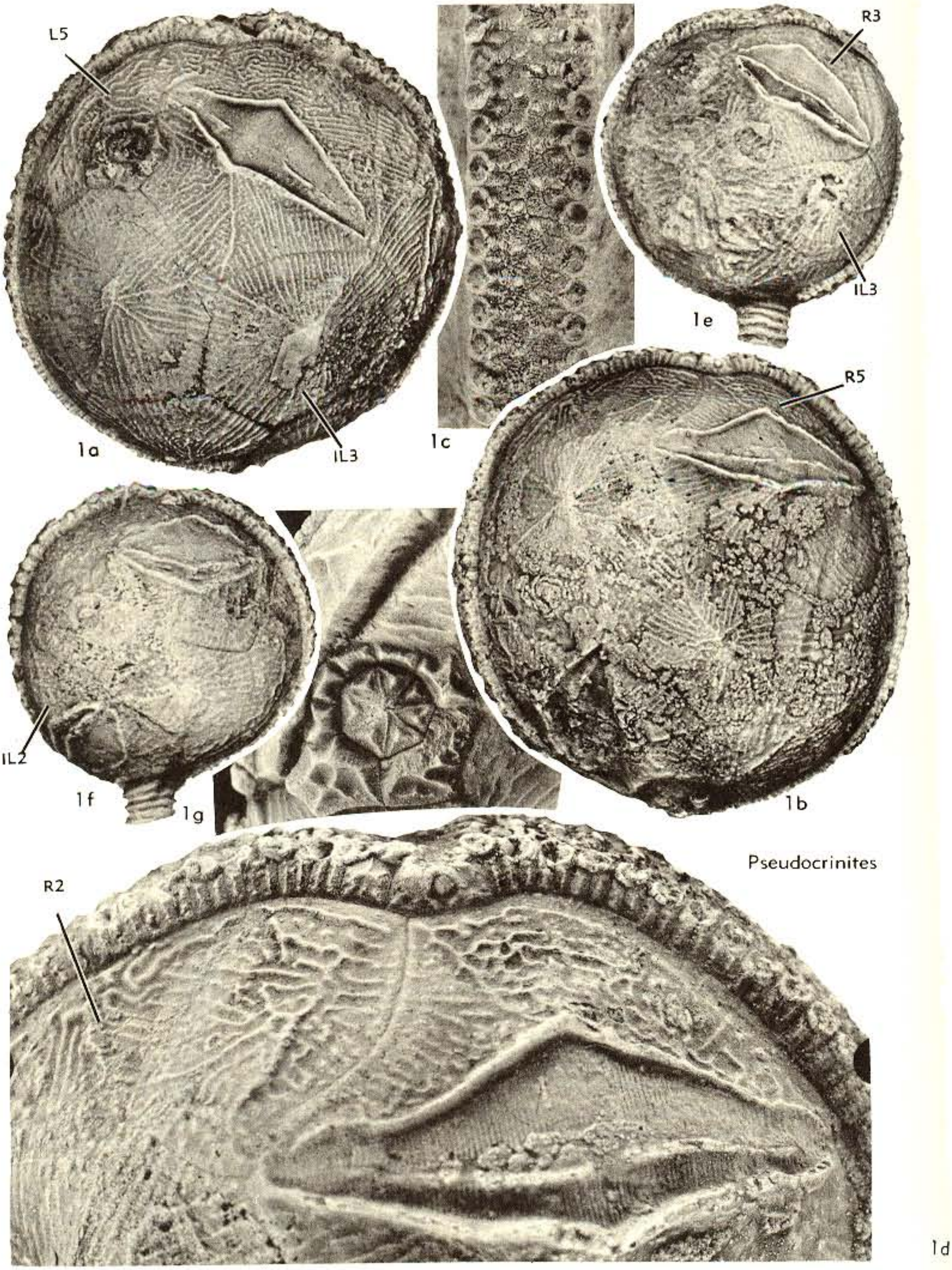


Fig. 115. Callocystitidae, Staurocystinae (p. *S*218). [Plate designations as in Figure 38.]

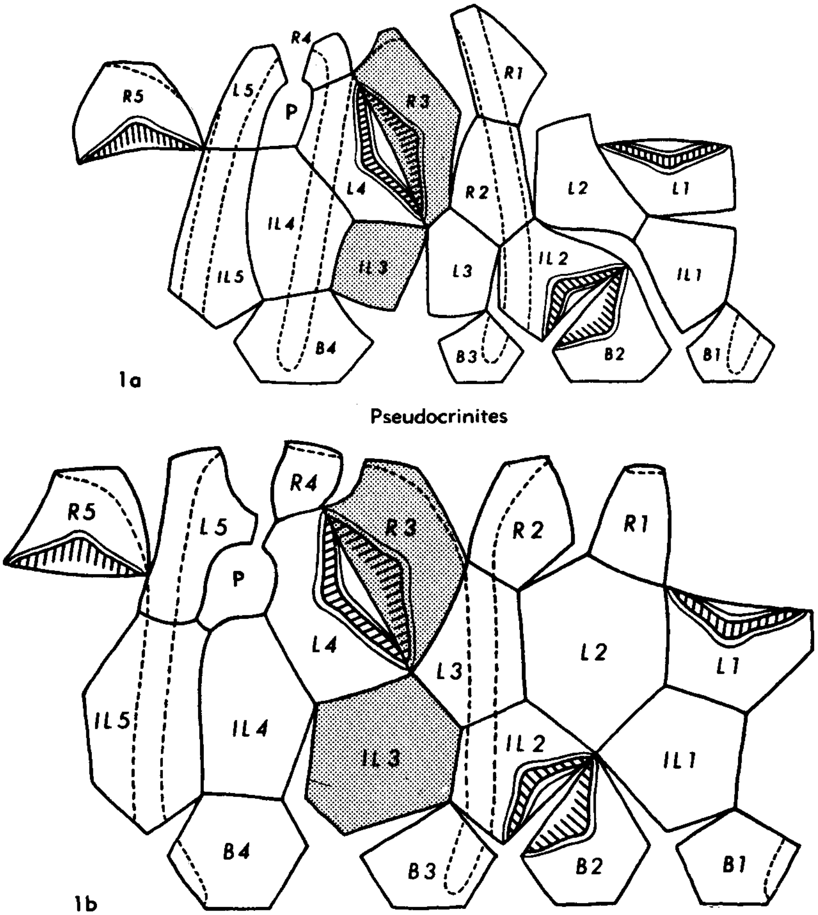


FIG. 116. Callocystitidae, Staurocystinae. Plate diagrams, plates of *A*-ray shaded (p. *S*217-*S*218). [Plate designations as in Figure 38.]

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

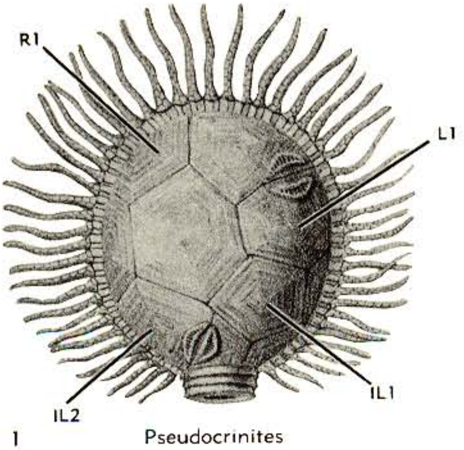


FIG. 117. Callocystitidae, Staurocystinae (p. S217-S218). [Plate designations as in Figure 38.]

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).

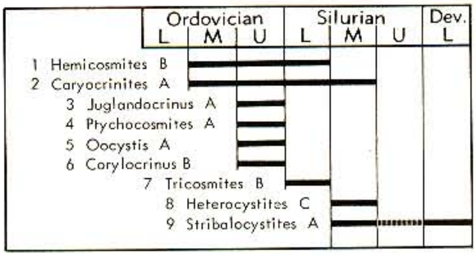


FIG. 118. Stratigraphic distribution of genera belonging to the superfamily Hemicosmitida. Classification of the genera in families is indicated by letter symbols: A—Caryocrinitidae, B—Hemicosmitidae, C—Heterocystitidae. The following alphabetical list of genera furnishes cross reference to the serially 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,*

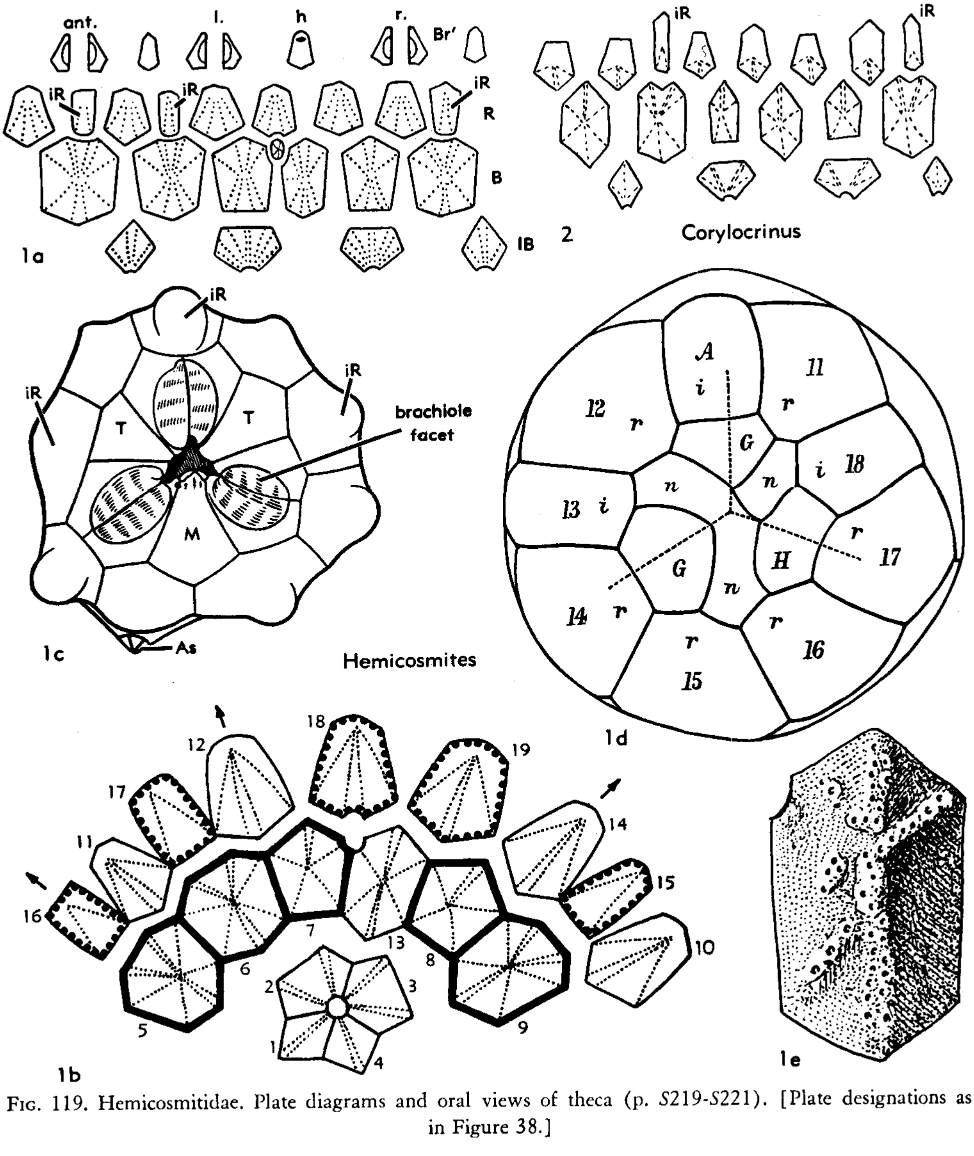


Fig. 119. Hemicosmitidae. Plate diagrams and oral views of theca (p. S219-S221). [Plate designations as in Figure 38.]

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

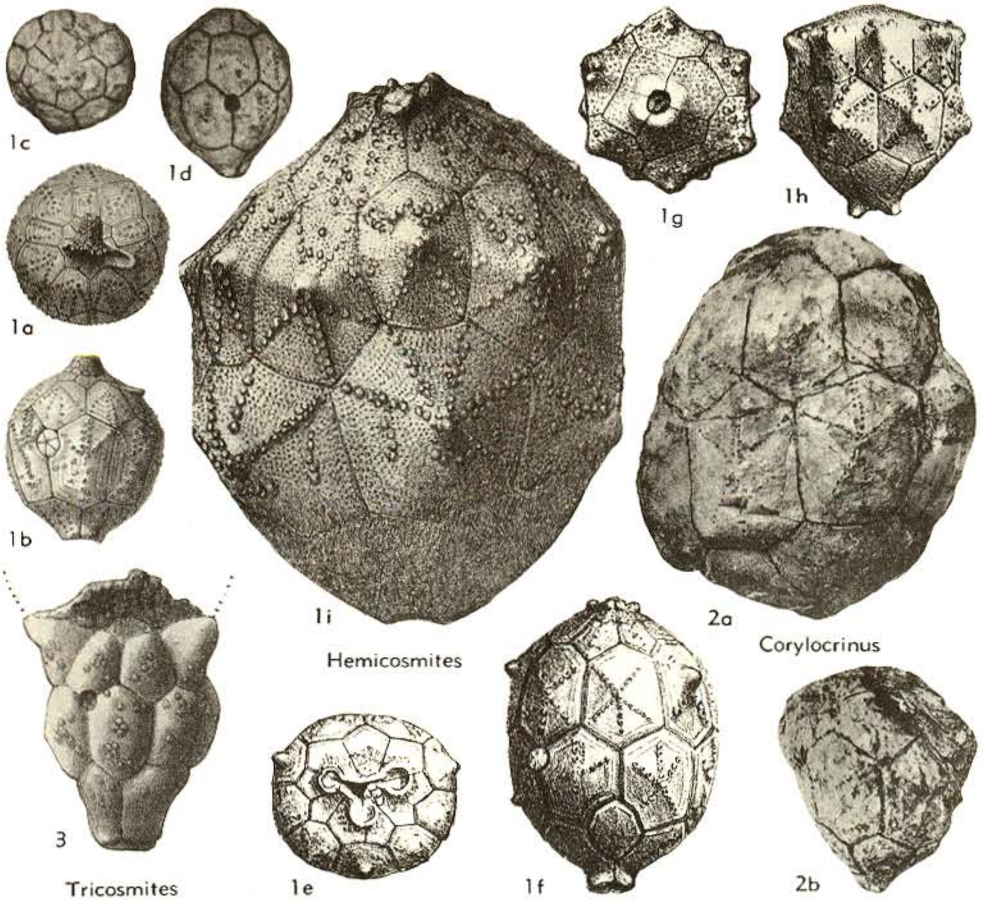


FIG. 120. Hemicosmitidae (p. *S*219-*S*221).

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

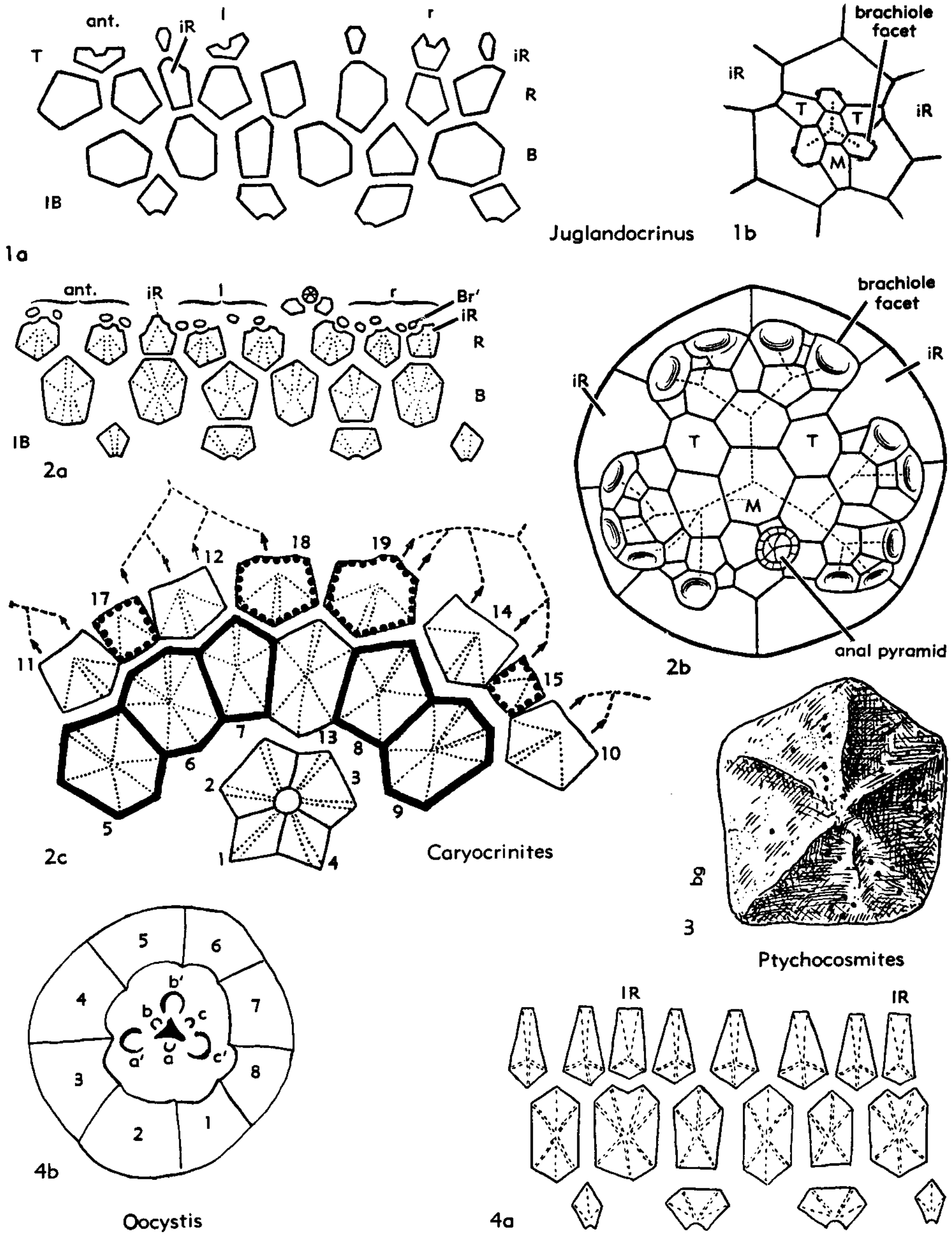


FIG. 121. Caryocrinitidae. Plate diagrams and oral views of theca (p. S223-S225).

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

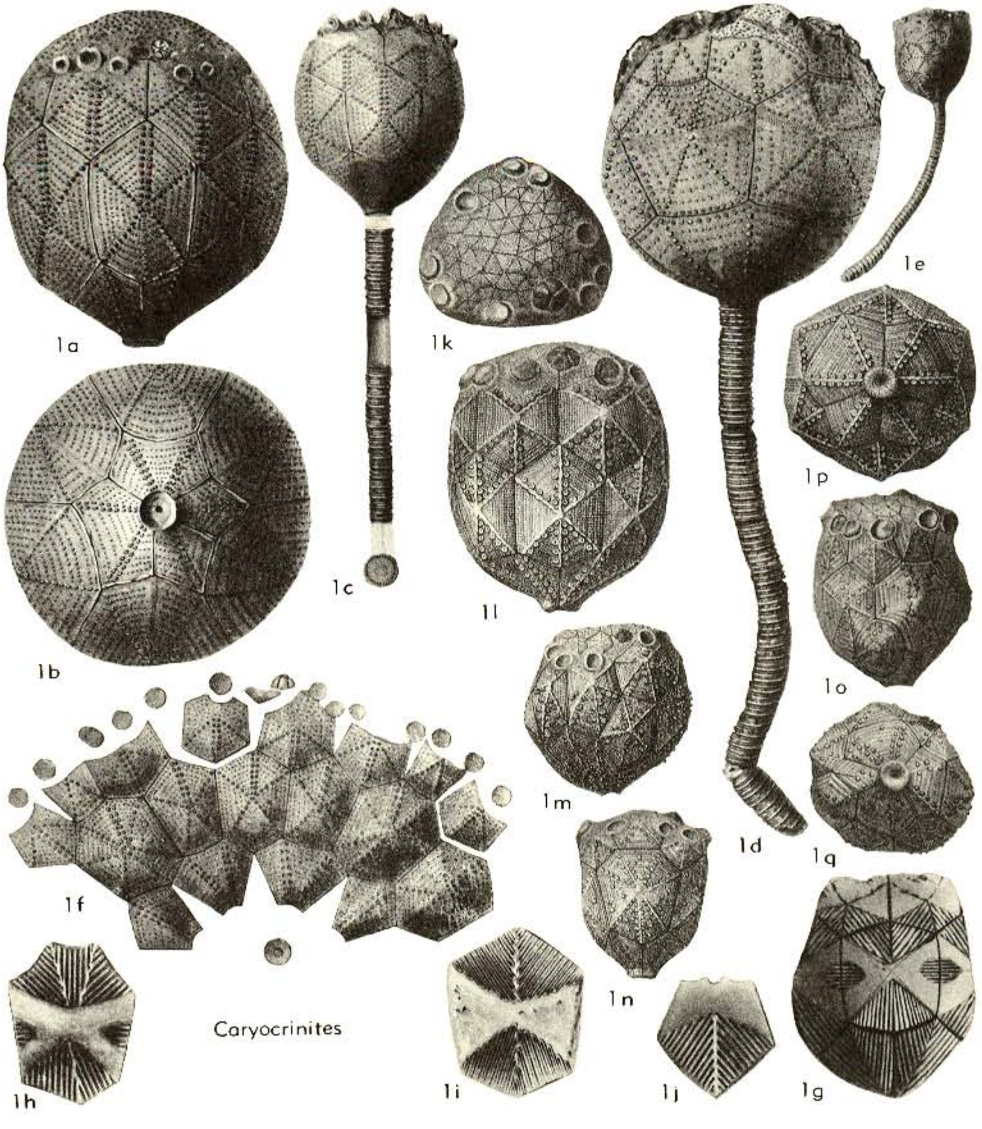


FIG. 122. Caryocrinitidae (p. *S*223-*S*225).

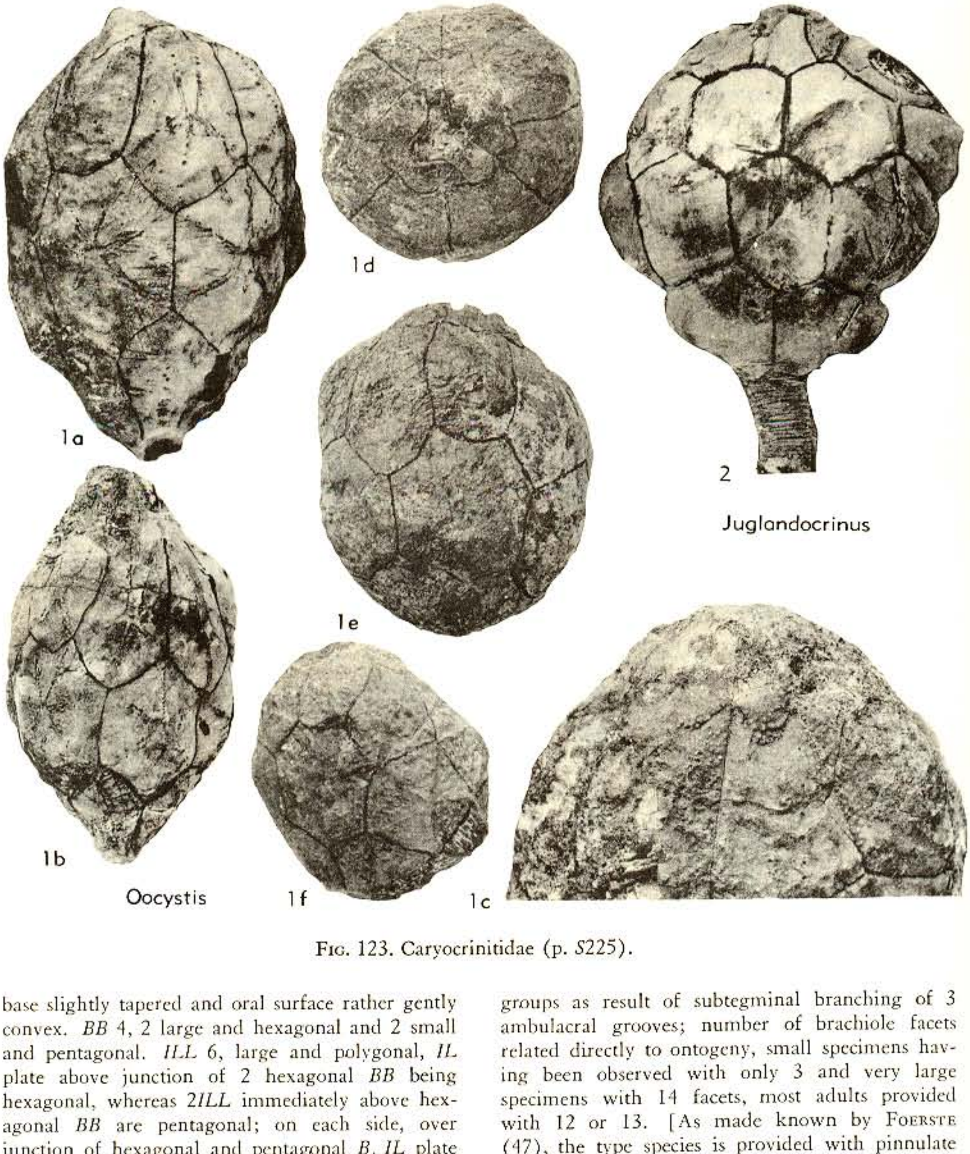


FIG. 123. Caryocrinitidae (p. *S*225).

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 2*ILL* 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).

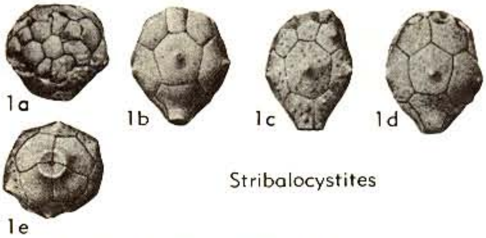


Fig. 124. Caryocrinitidae (p. *S225-S226*).

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

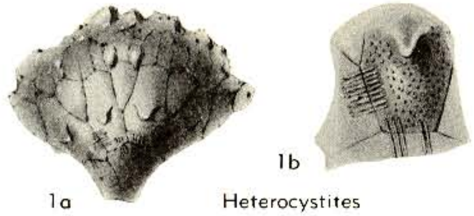


FIG. 125. Heterocystitidae (p. *S226-S227*).

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

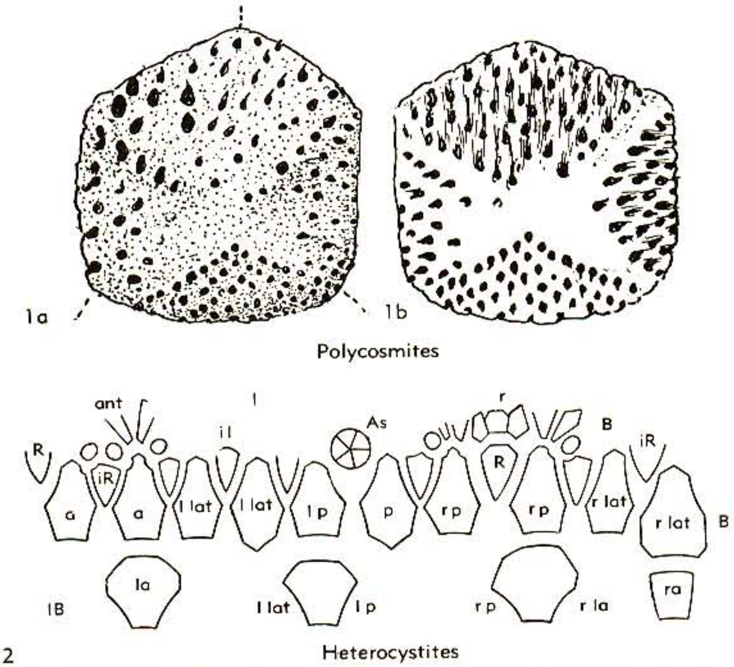


FIG. 126. Polycosmitidae *(1)*; Heterocystitidae *(2)*. Plates and plate diagram (p. *S226-S227*).

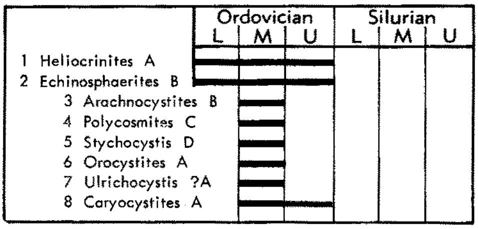


FIG. 127. Stratigraphic distribution of genera belonging to the superfamilies Polycosmitida and Caryocystitida. Classification of the genera in families is indicated by letter symbols: A—Caryocystitidae, B—Echinosphaeritidae, C—Polycosmitidae, D—Stichocystidae. The following alphabetical list of genera 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.*

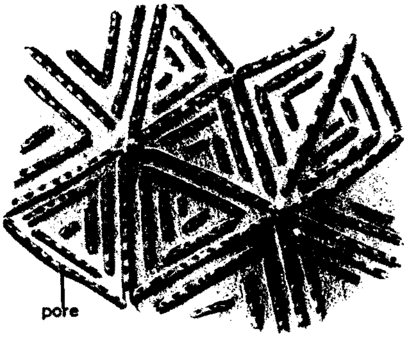
Polycosmites JAEKEL, 1918, p. 98 [**P. bohemicus*; OD]. Theca including at least some polygonal plates penetrated by simple pores distributed in rhombic sectors but not arranged in long rows. *M.Ord.*, Eu.(Boh.).——FIG. 126,*1*. **P. bohemicus*; *1a,b*, thecal plate ext. and int. (71).

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.

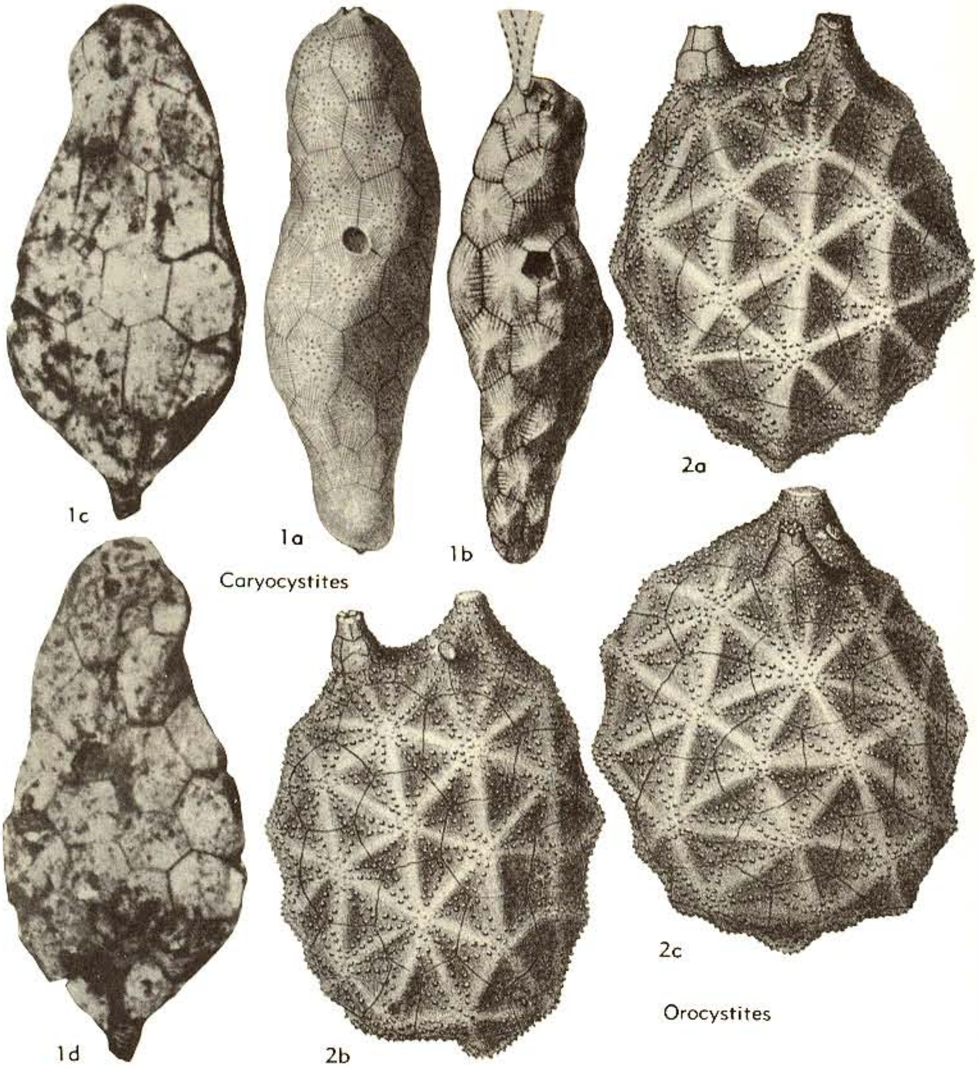


FIG. 129. Caryocystitidae (p. *S229*, *S231*).

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

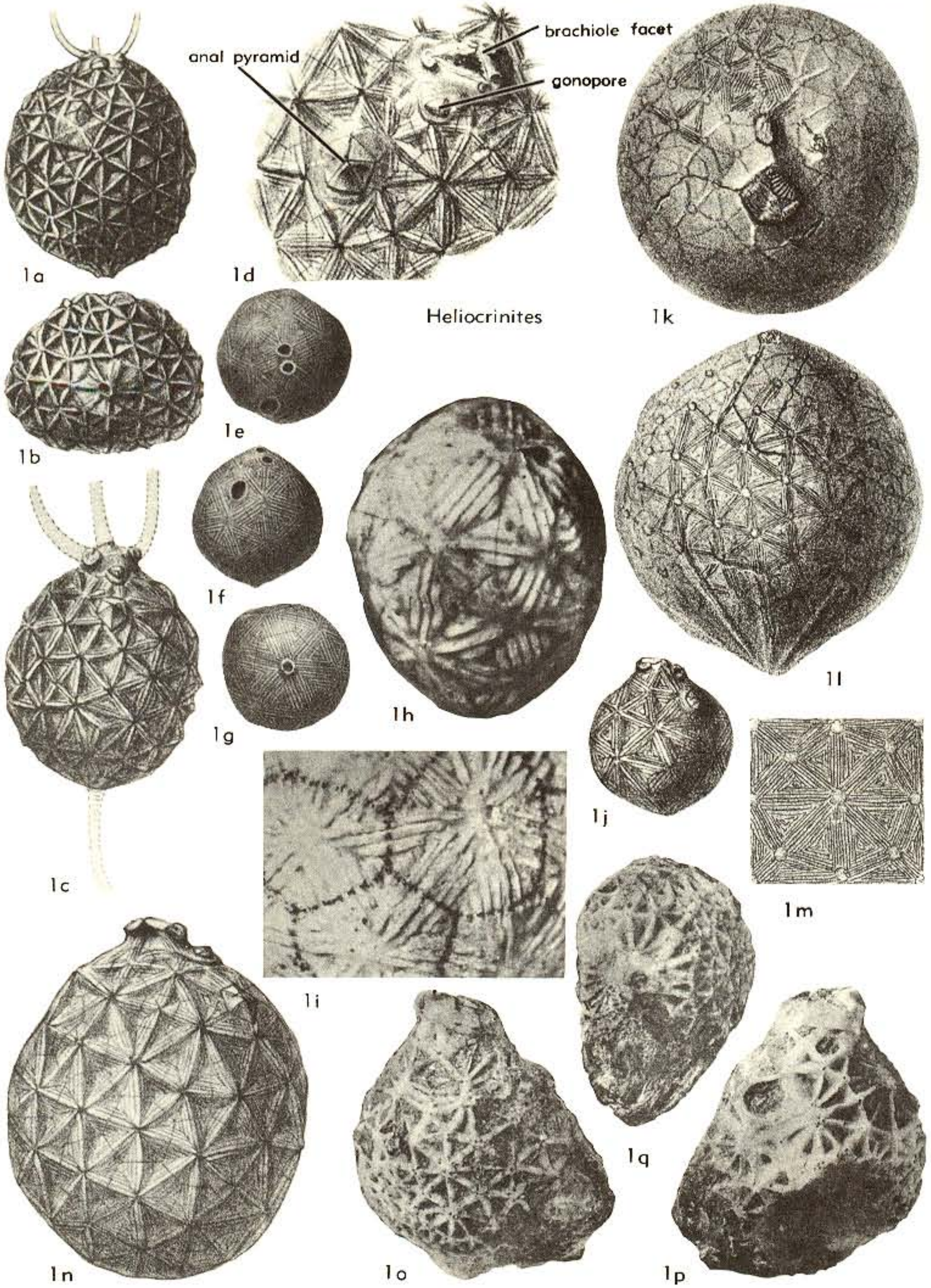


FIG. 130. Caryocystitidae (p. S229-S230).

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$_1$, 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).

1

Ulrichocystis

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

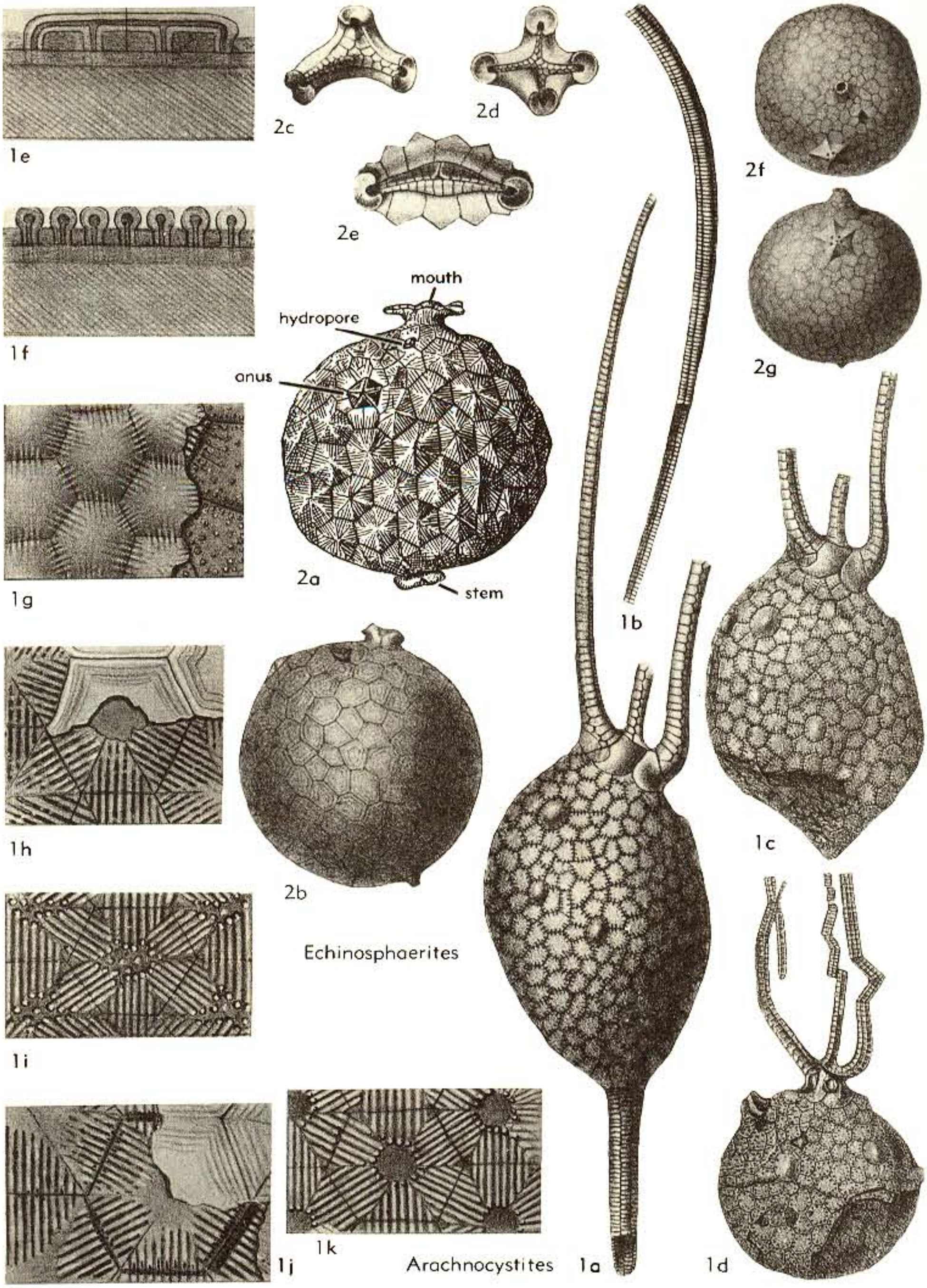


FIG. 132. Echinosphaeritidae (p. S233).

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., X1 (10); *2b*, reconstr., X1 (69); *2c-e*, oral regions, 3 specimens, showing different numbers of brachiole facets, enl. (69); *2f,g*, oral and lat., X1 (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., X1; *1b*, long section of column, X1 (69); *1c,d*, lat., 2 specimens, X1; *1e,f*, enlarged sections along and through pore canals; *1g-k*, enlarged parts of thecal plates in various stages of exfoliation (3).

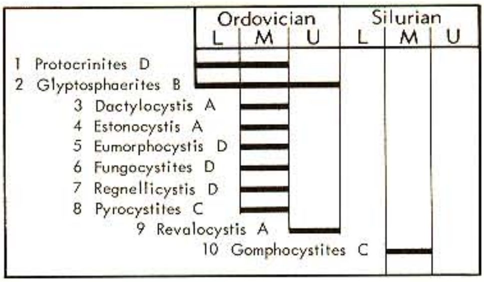


FIG. 133. Stratigraphic distribution of genera belonging to the superfamily Glyptosphaeritida. Classification of the genera in families is indicated by letter symbols: A—Dactylocystidae, B—Glyptosphaeritidae, C—Gomphocystitidae, D—Protocrinitidae. The following alphabetical list of genera furnishes cross 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.

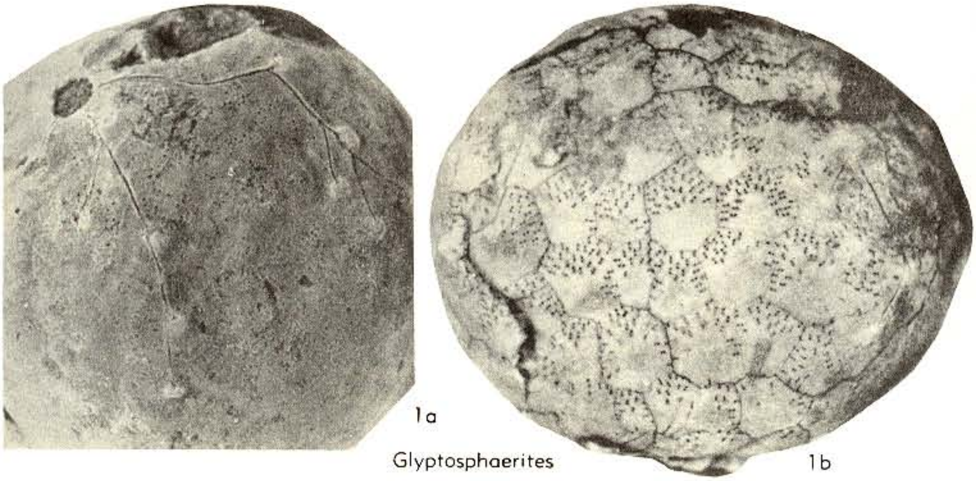


FIG. 134. Glyptosphaeritidae (p. S235).

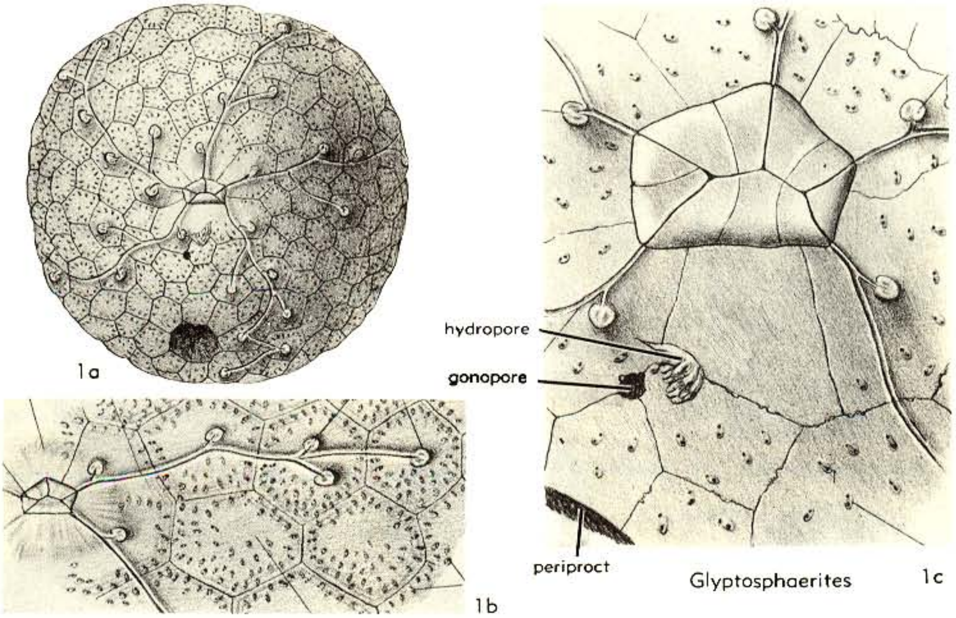


FIG. 135. Glyptosphaeritidae (p. *S*235).

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

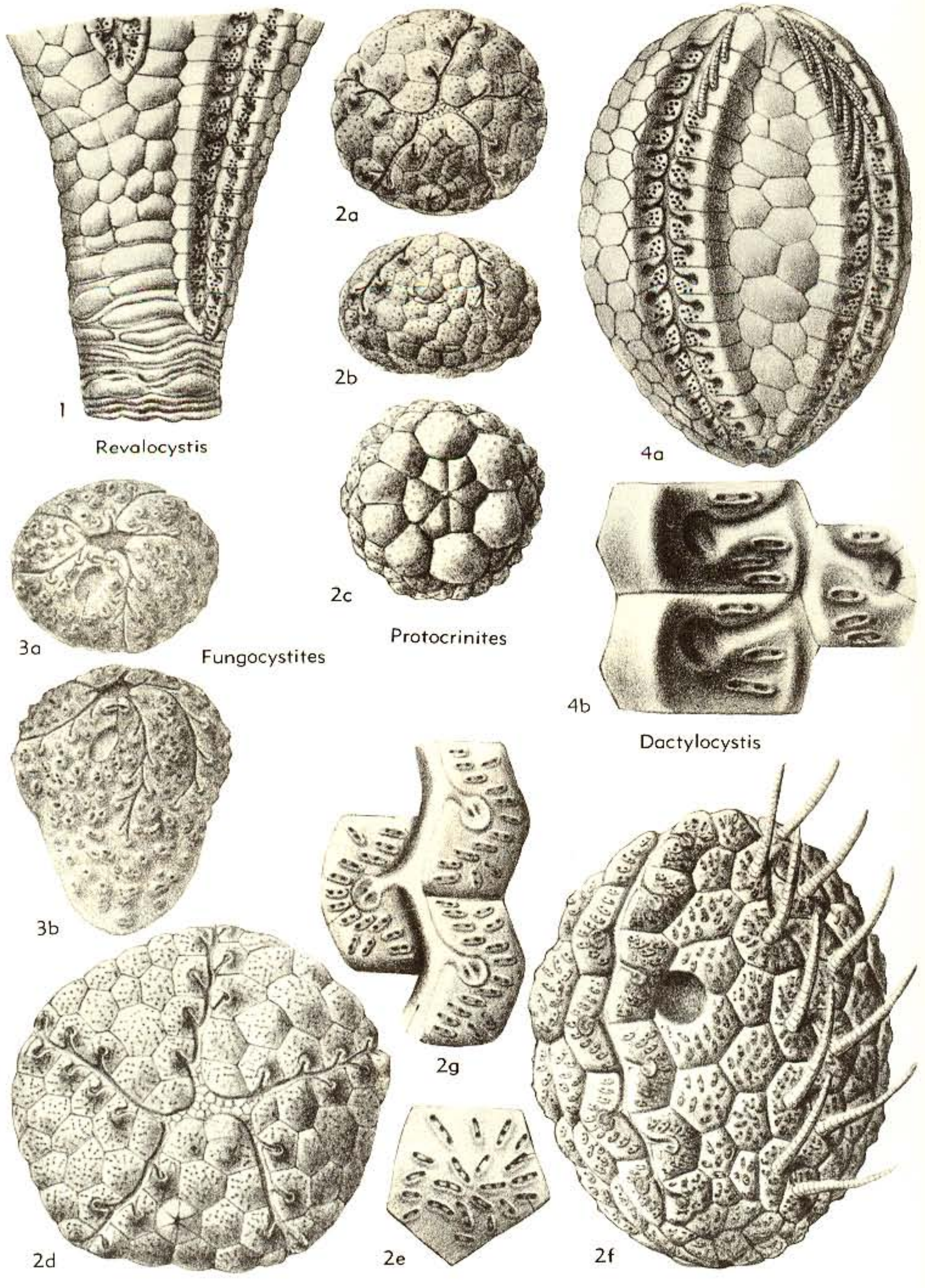


Fig. 136. Dactylocystidae *(1,4)*; Protocrinitidae *(2,3)* (p. S237–S240).

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.]

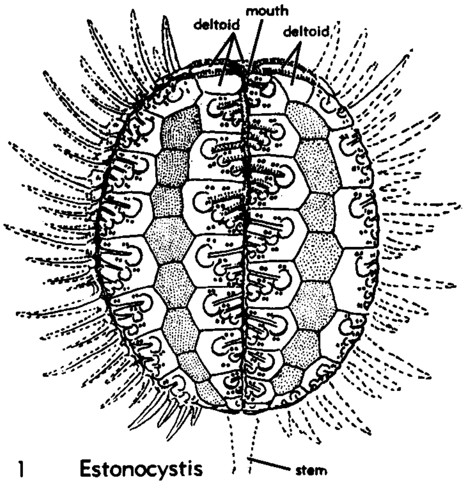


Fig. 137. Dactylocystidae (p. *S*237).

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-

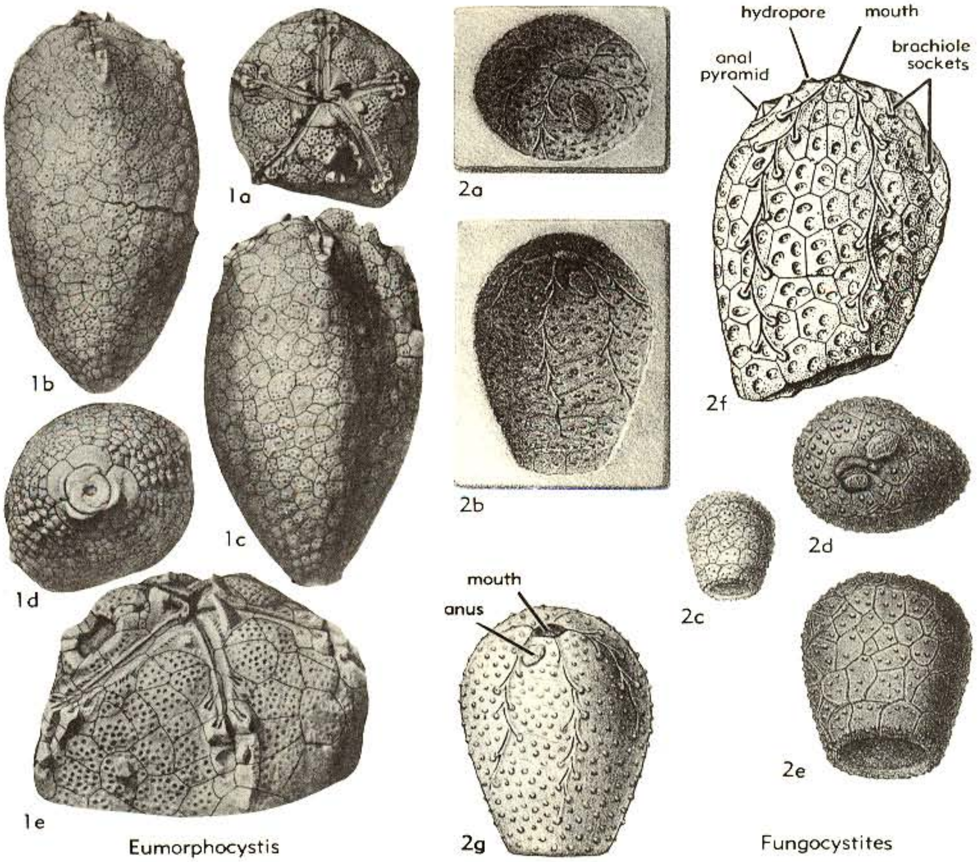


FIG. 138. Protocrinitidae (p. *S*239-*S*240).

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

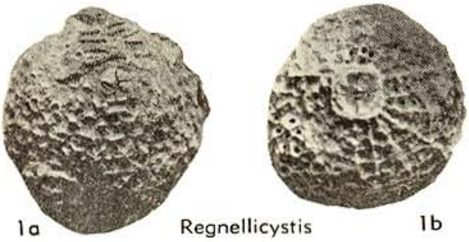


FIG. 139. Protocrinitidae (p. S240).

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*, Dd_1; *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

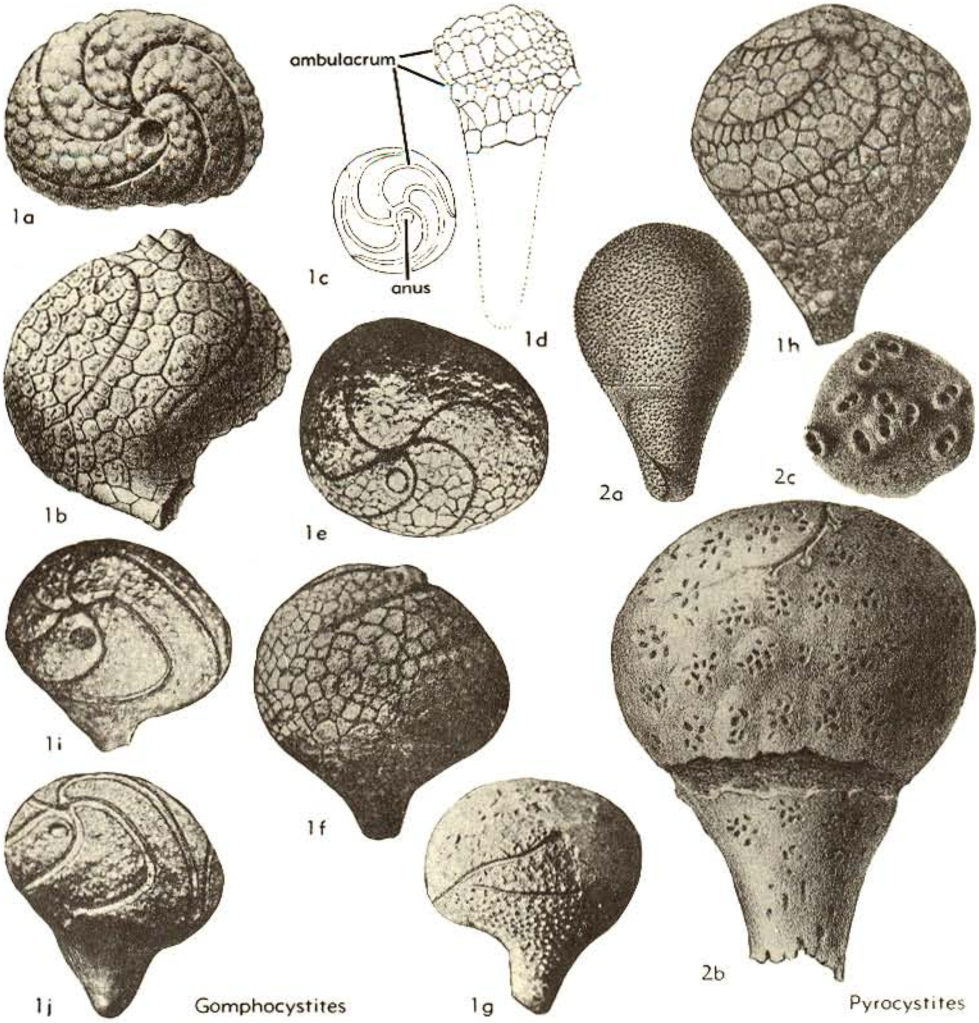


FIG. 140. Gomphocystitidae (p. S240).

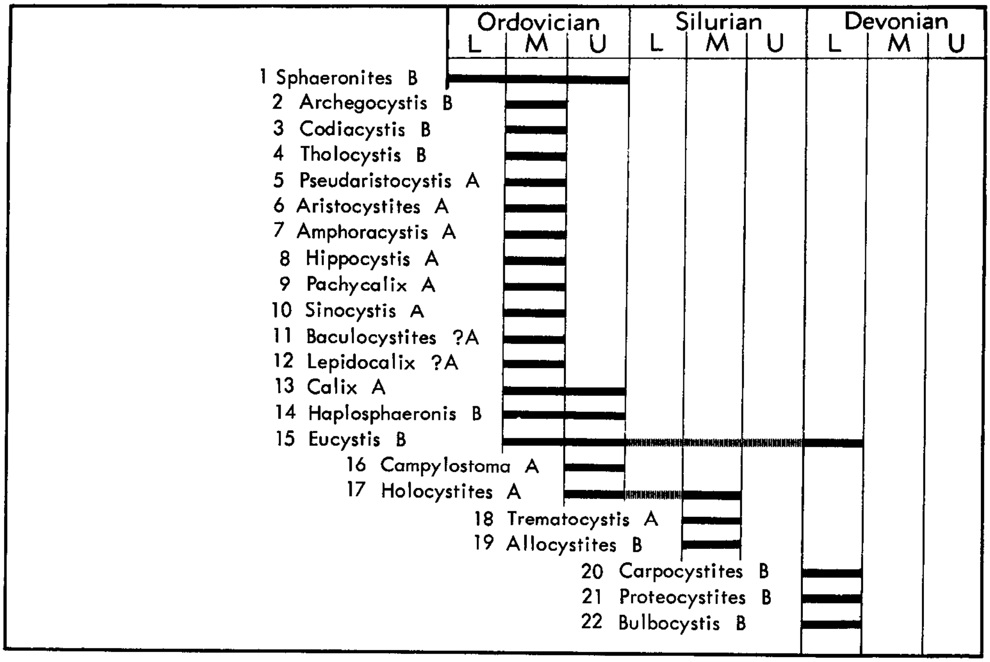


FIG. 141. Stratigraphic distribution of genera belonging to the superfamily Sphaeronitida. Classification of the genera in families is indicated by letter symbols: A—Aristocystitidae, B—Sphaeronitidae. The following alphabetical list of genera furnishes cross reference to the serially arranged numbers 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

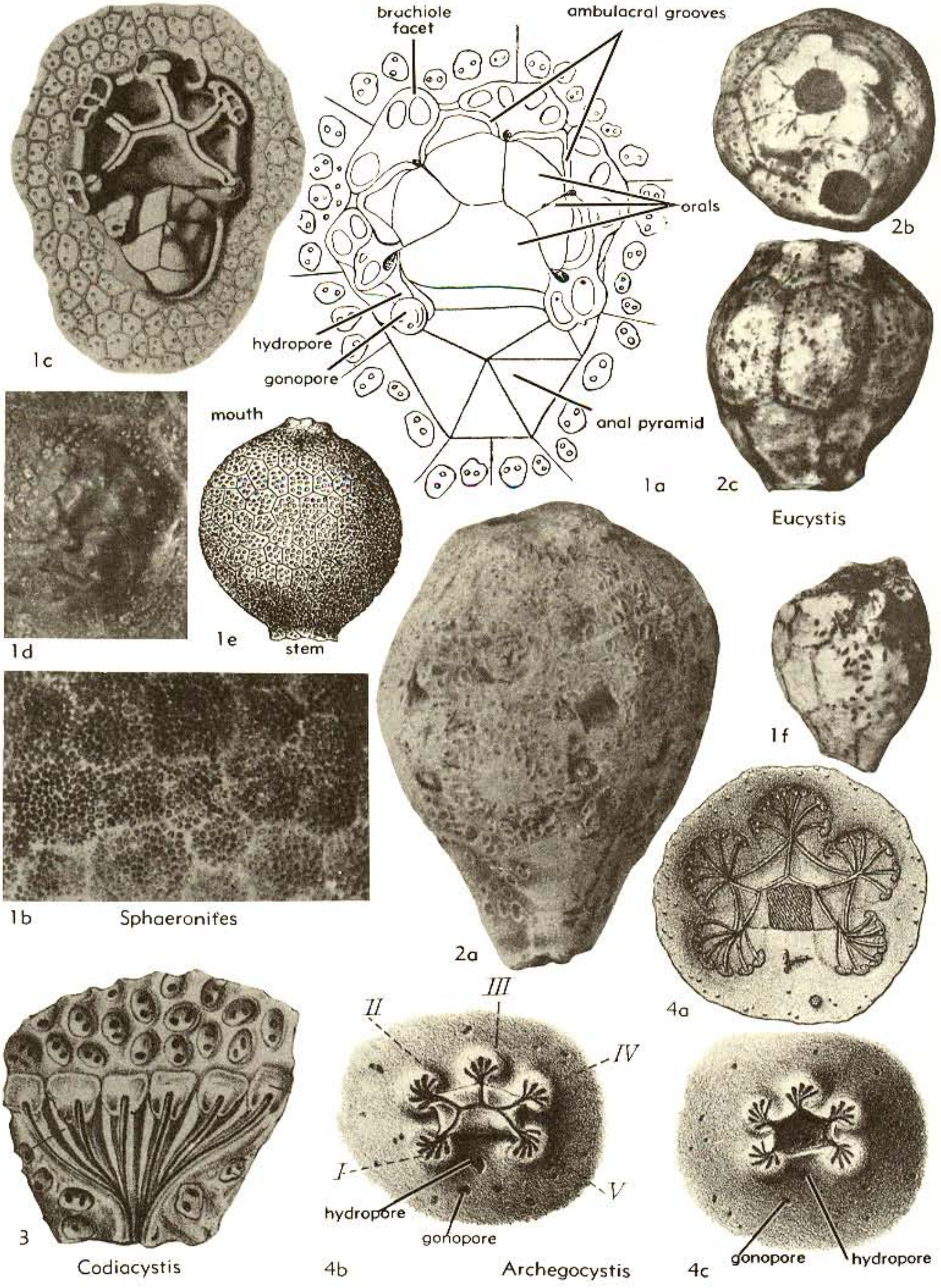


FIG. 142. Sphaeronitidae (p. S243, S245, S247).

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*

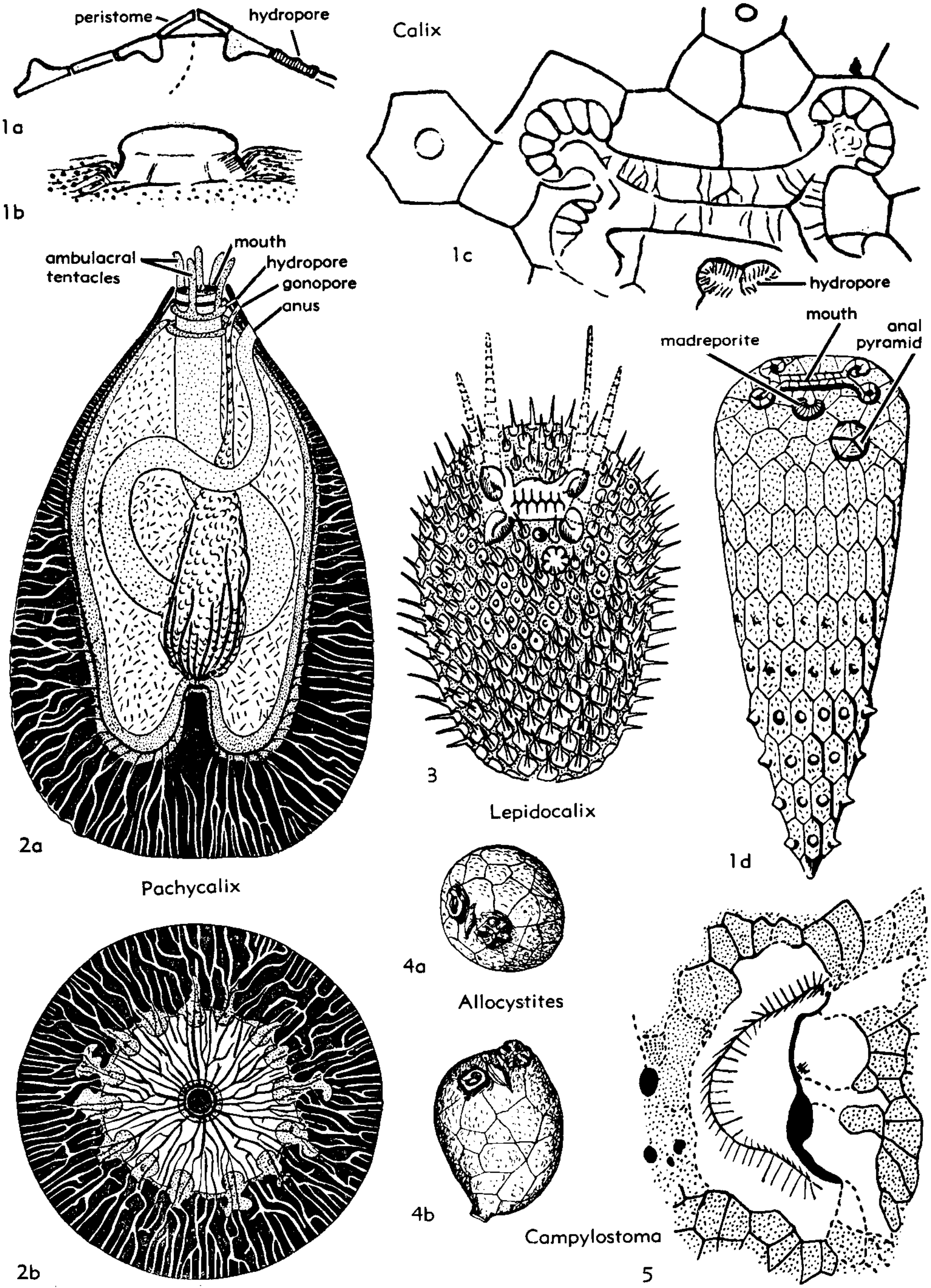


FIG. 143. Aristocystitidae *(1-3,5)*; Sphaeronitidae *(4)* (p. S243, S254-S256).

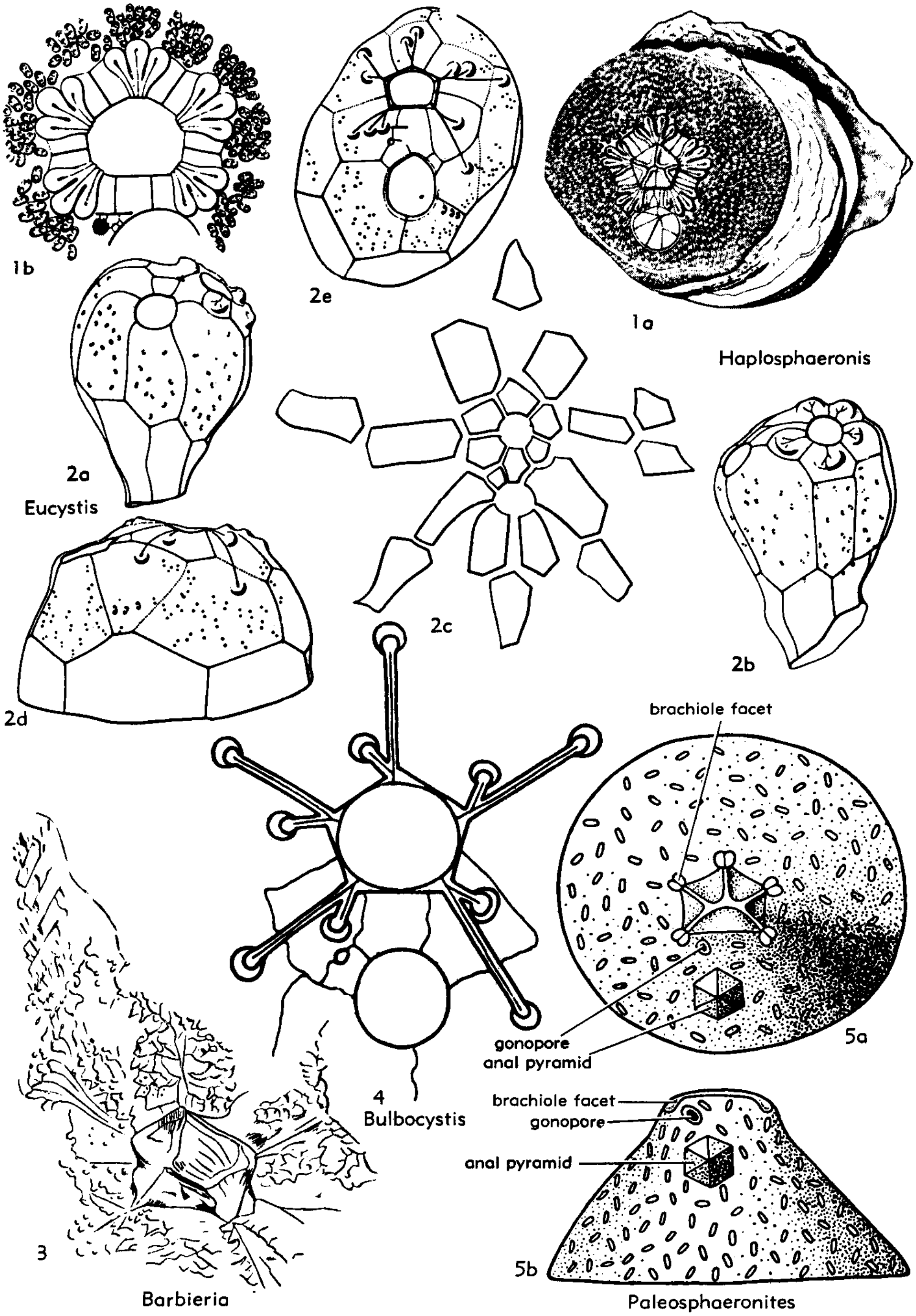


FIG. 144. Sphaeronitidae (p. S243, S247-S248).

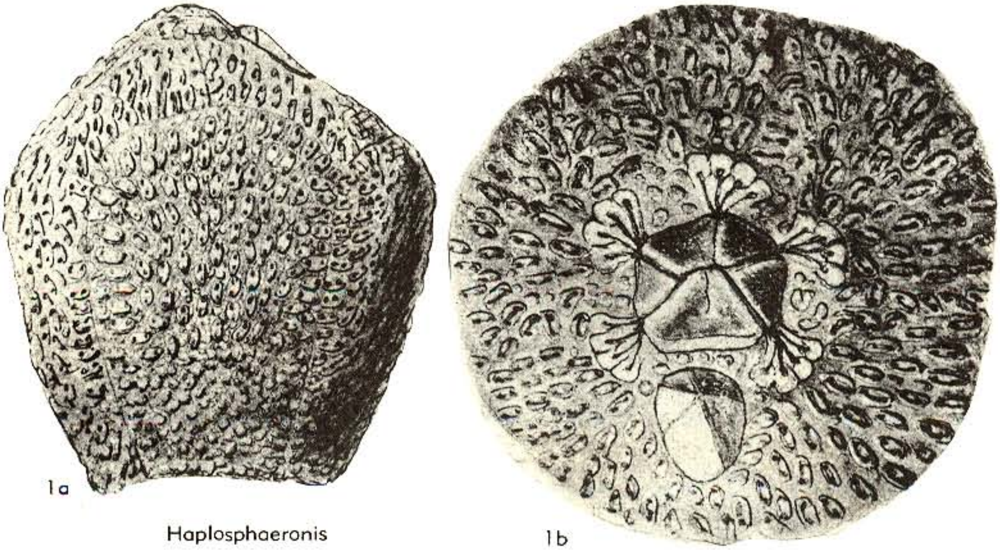


FIG. 145. Sphaeronitidae (p. *S*247-*S*248).

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. kiaeri;* 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.

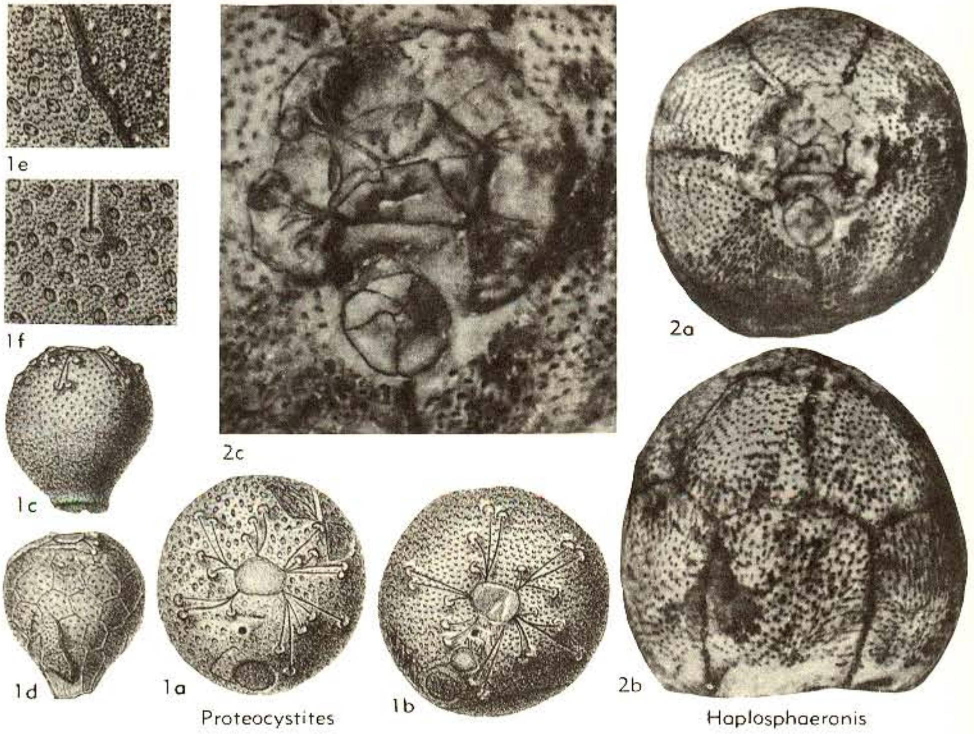


Fig. 146. Sphaeronitidae (p. *S*247-*S*249).

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

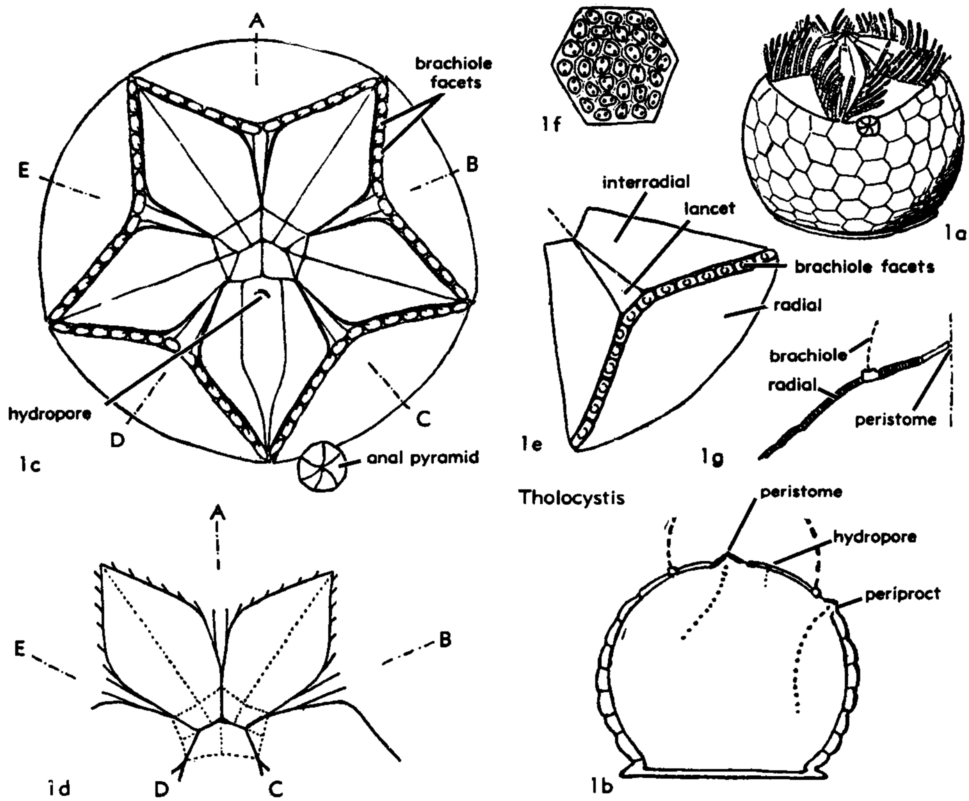


FIG. 147. Sphaeronitidae (p. S249-S250).——*1.* **Tholocystis ķolihai* CHAUVEL, M.Ord., France; *1a,b,* posterior (*CD* interray) view of theca (reconstr.) and hypothetical cross section through peristome, ×2; *1c-e,* diagrammatic analyses of ambulacral field, ambulacral branching, and sector of ambulacral 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. ķolihai;* 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.

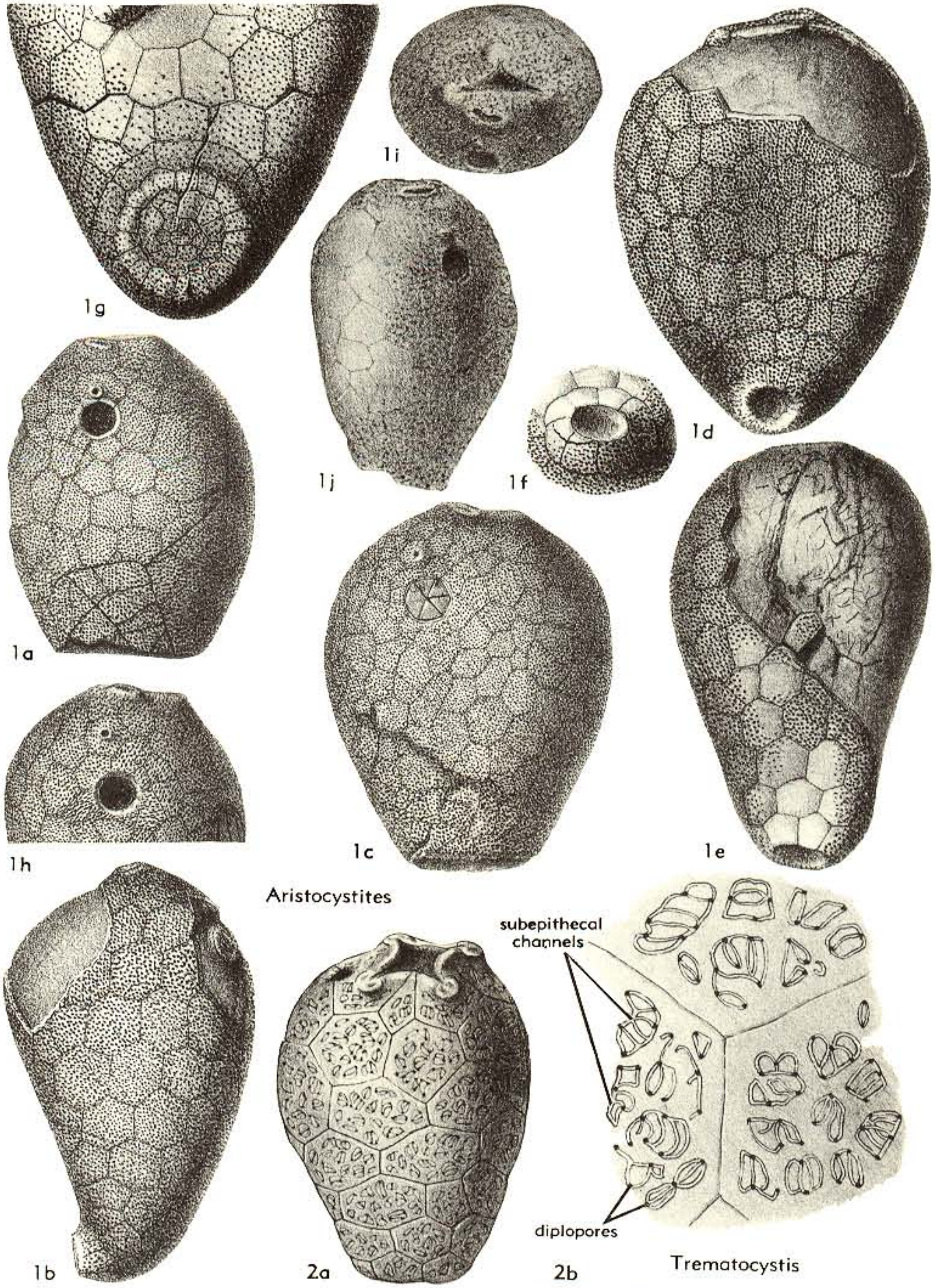


FIG. 148. Aristocystitidae (p. *S*252-*S*253, *S*258).

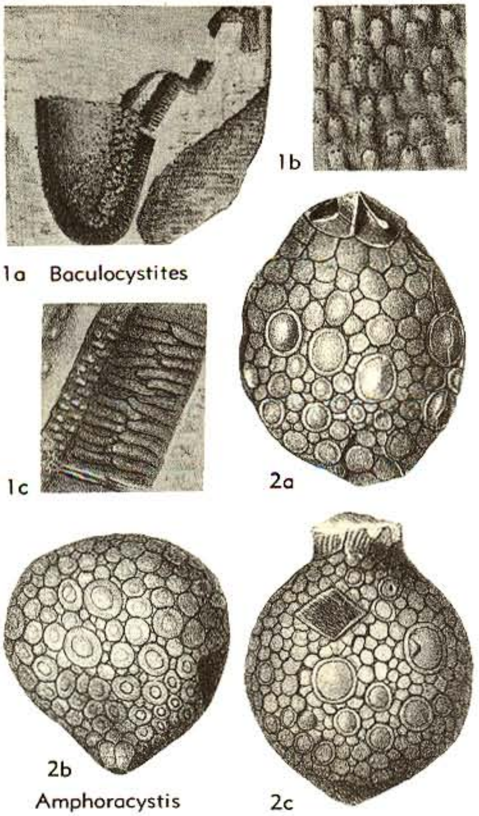


FIG. 149. Aristocystitidae (p. S253-S254).

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-*

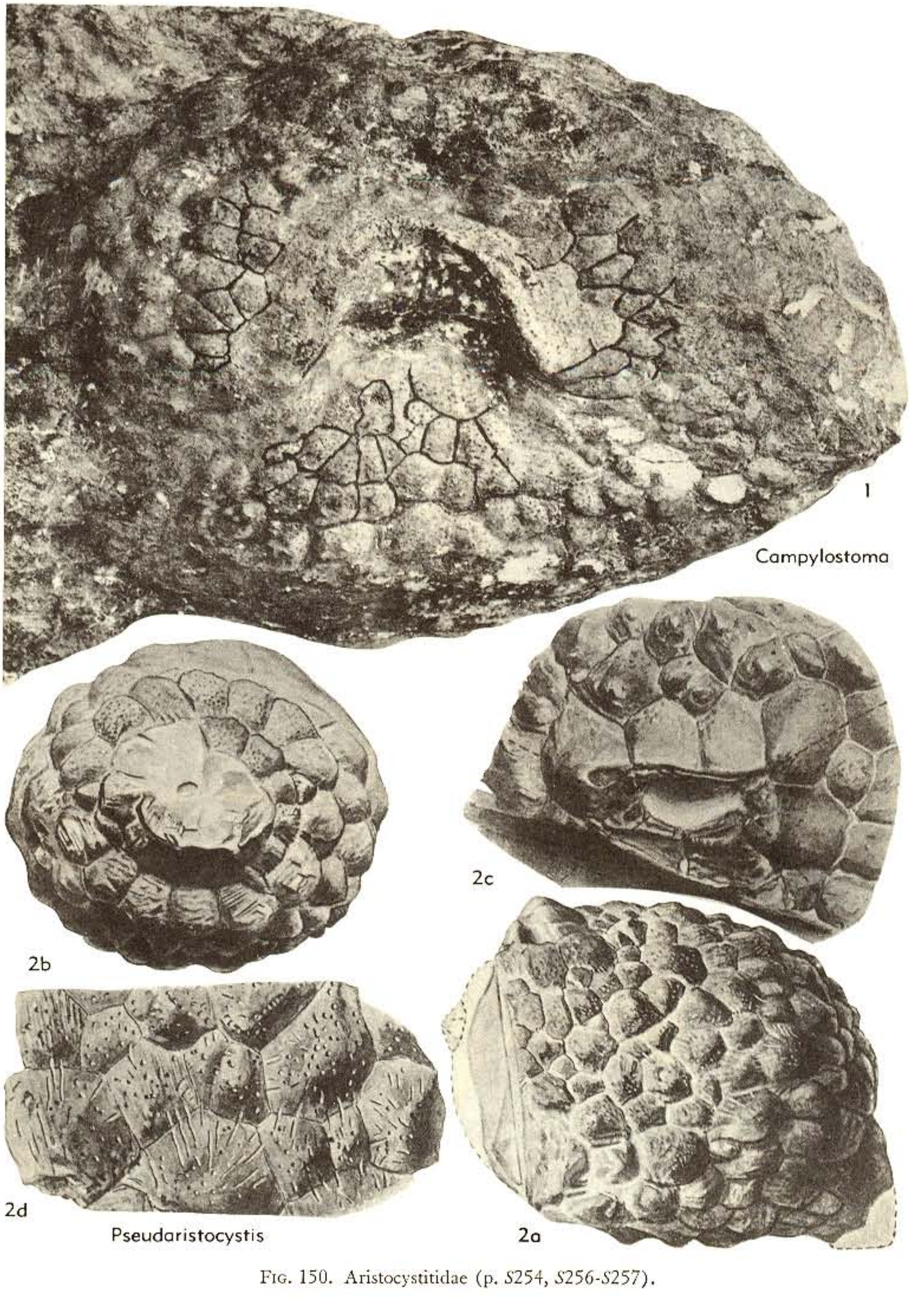


FIG. 150. Aristocystitidae (p. S254, S256-S257).

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*

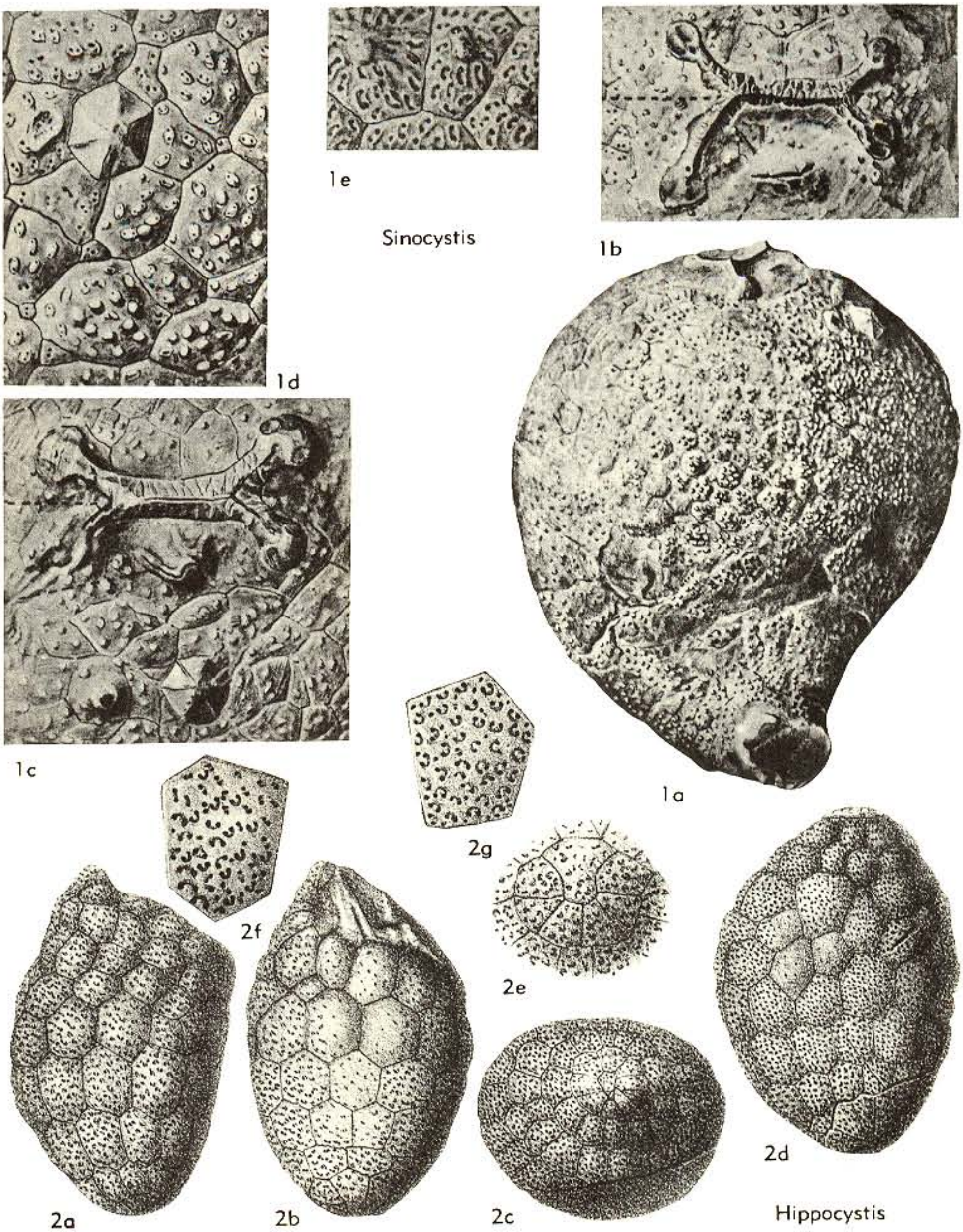


FIG. 151. Aristocystitidae (p. *S*254, *S*257-*S*258).

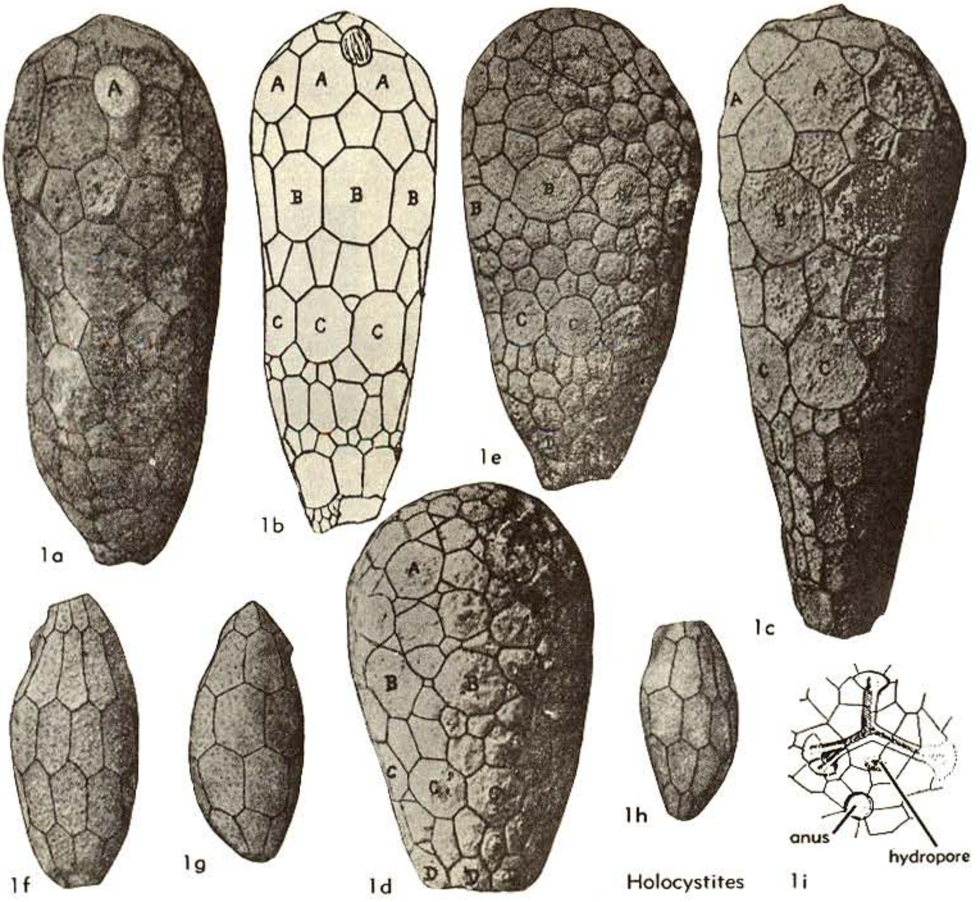


Fig. 152. Aristocystitidae (p. S254).

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

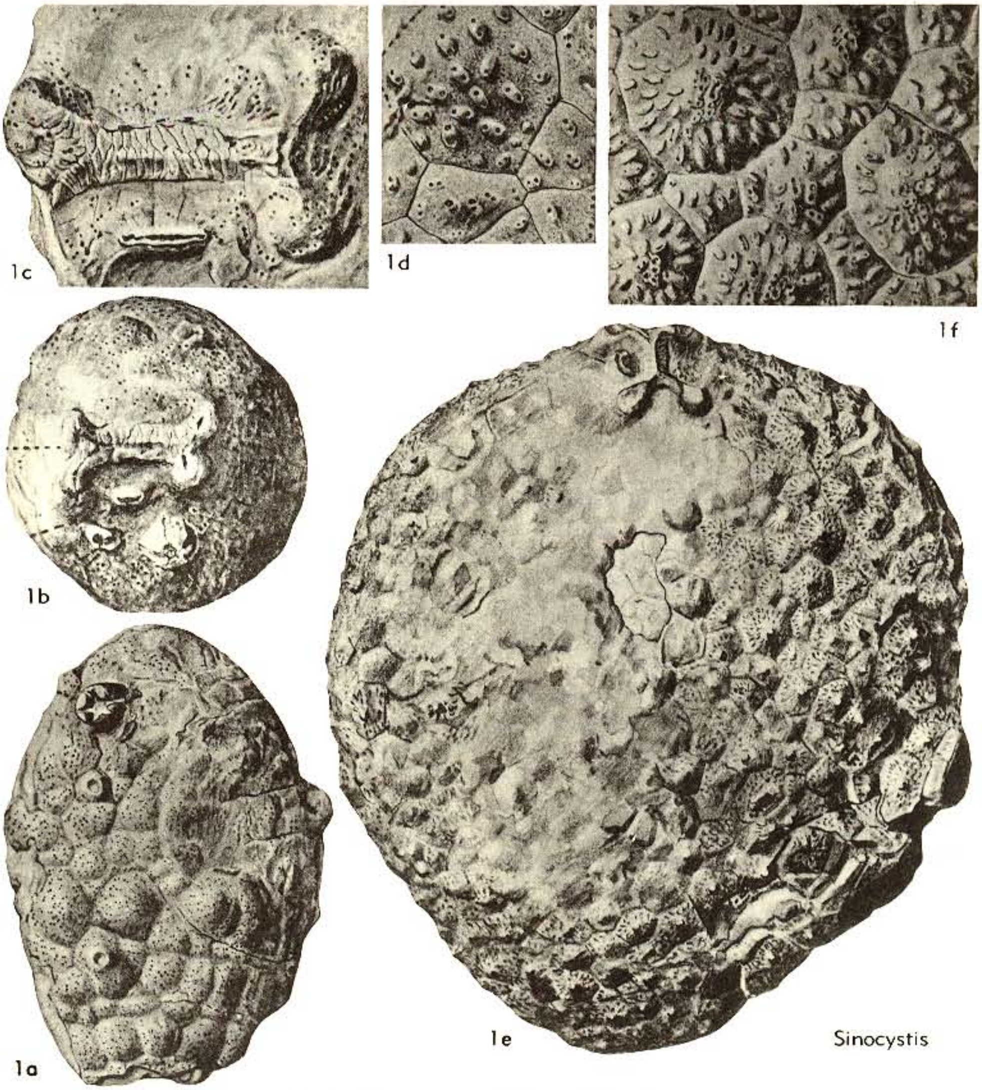


Fig. 153. Aristocystitidae (p. *S257-S258*).

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,*

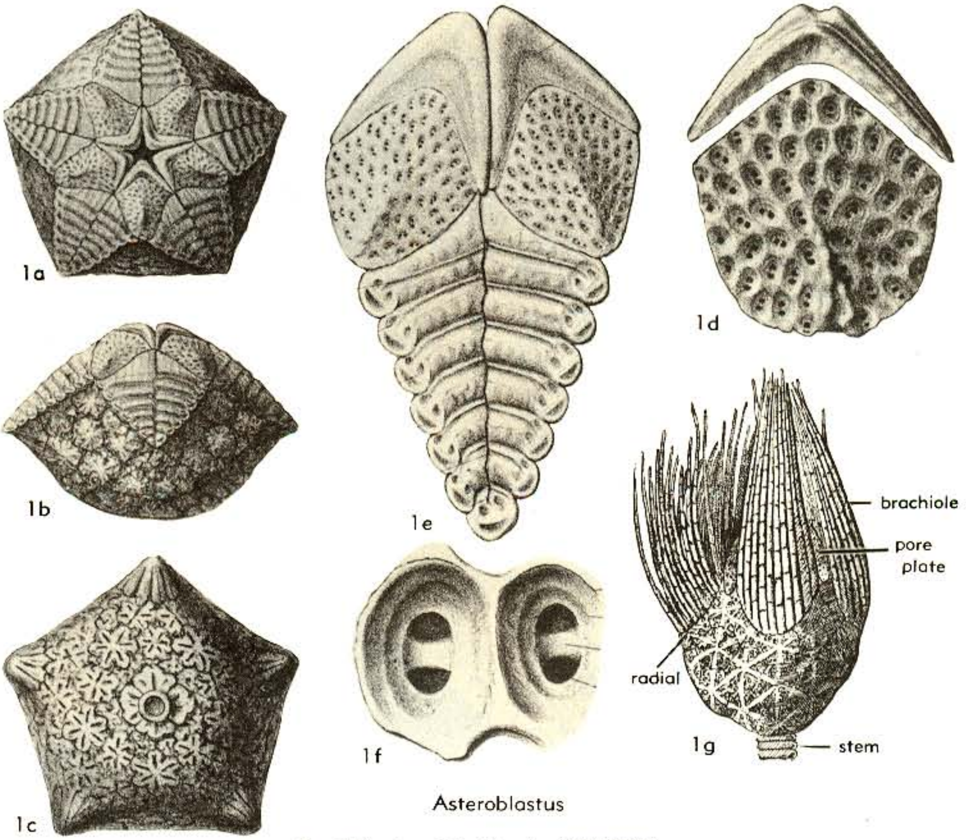


FIG. 154. Asteroblastidae (p. *S*258-*S*259).

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,

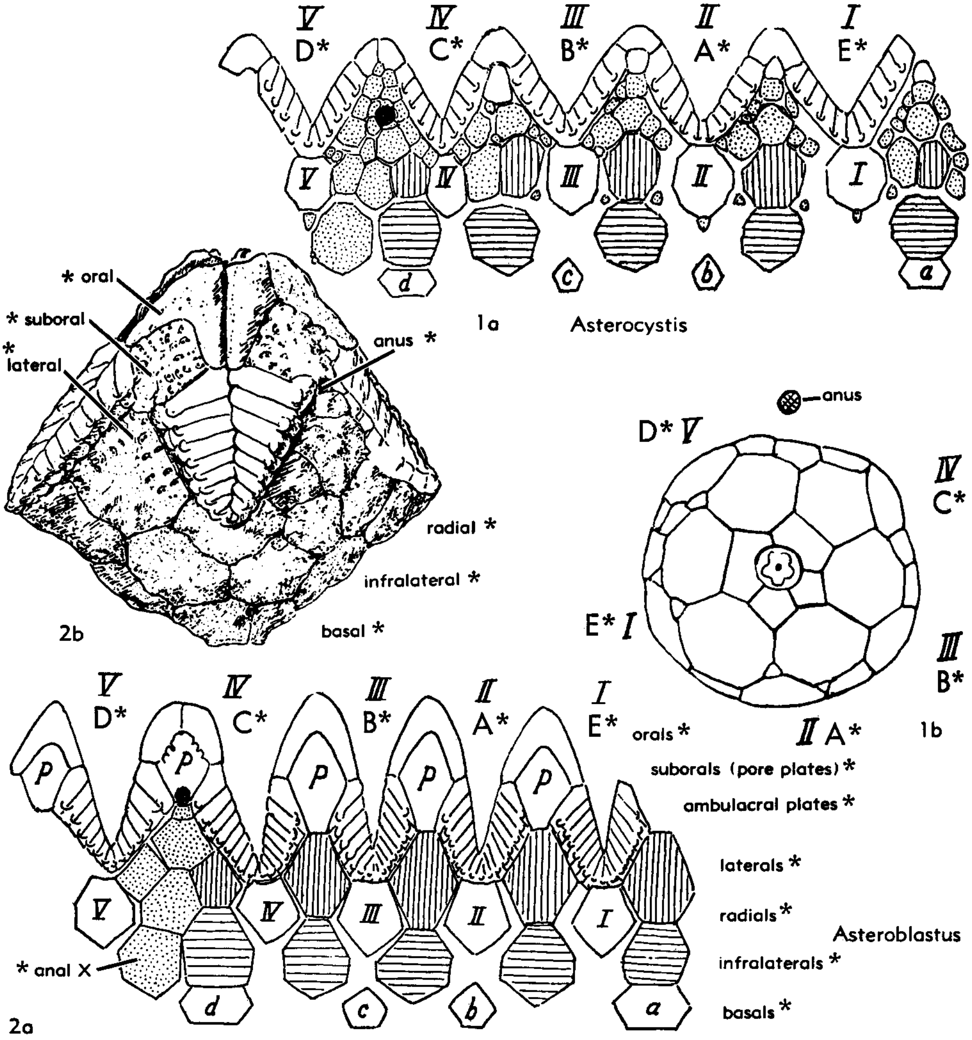


Fig. 155. Designations of plates and rays in Asteroblastidae, given by Jaekel and identifications of them (marked by asterisks) judged by Kesling to be appropriate (Kesling, n).

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*

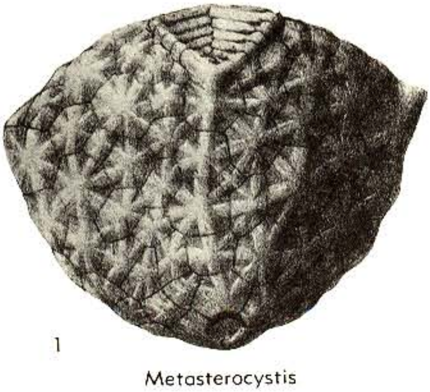


Fig. 156. Asteroblastidae (p. *S259-S260*).

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).

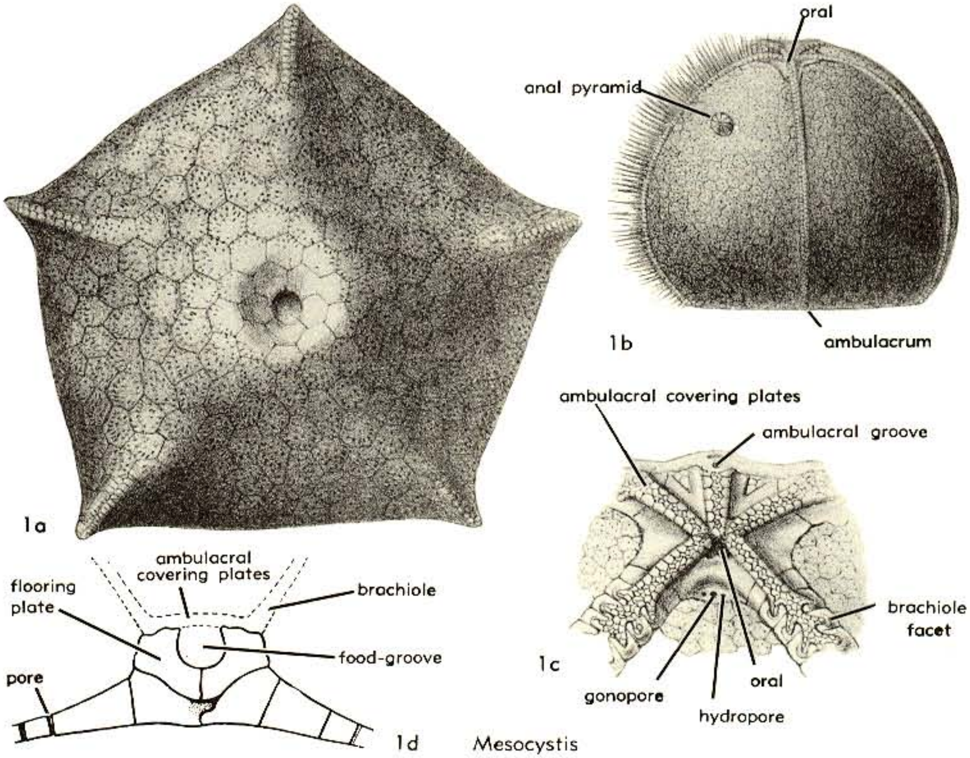


Fig. 157. Mesocystidae (p. *S260-S261*).

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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.

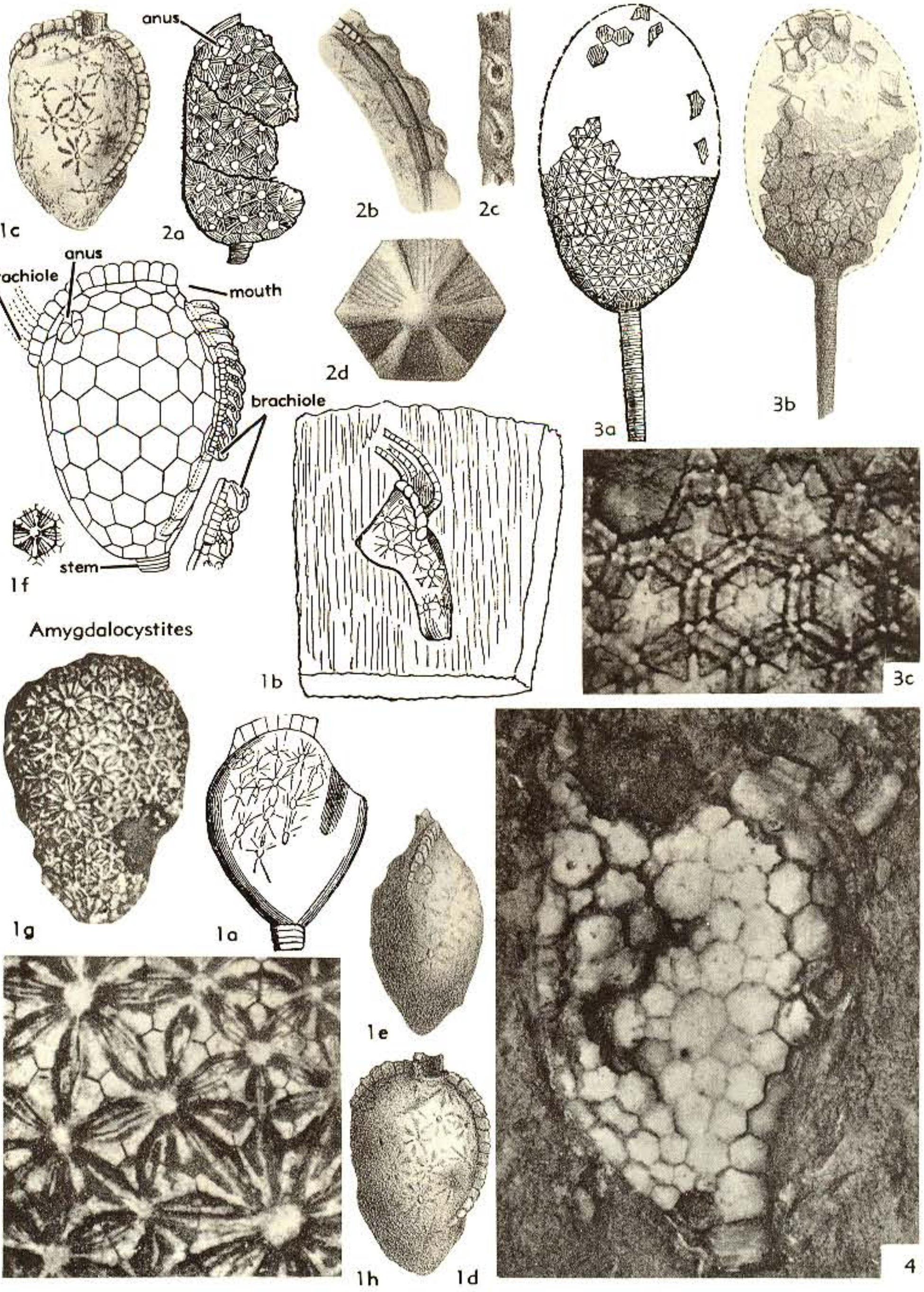


FIG. 158. Morphological features of Paracrinoidea illustrated by *Amygdalocystites*, all Middle Ordovician from Ontario; *1*, **A. florealis* BILLINGS; *2*, *A. tenuistriatus* BILLINGS; *3*, *A. radiatus* BILLINGS; *4*, *A. laevis* W. R. BILLINGS.

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.

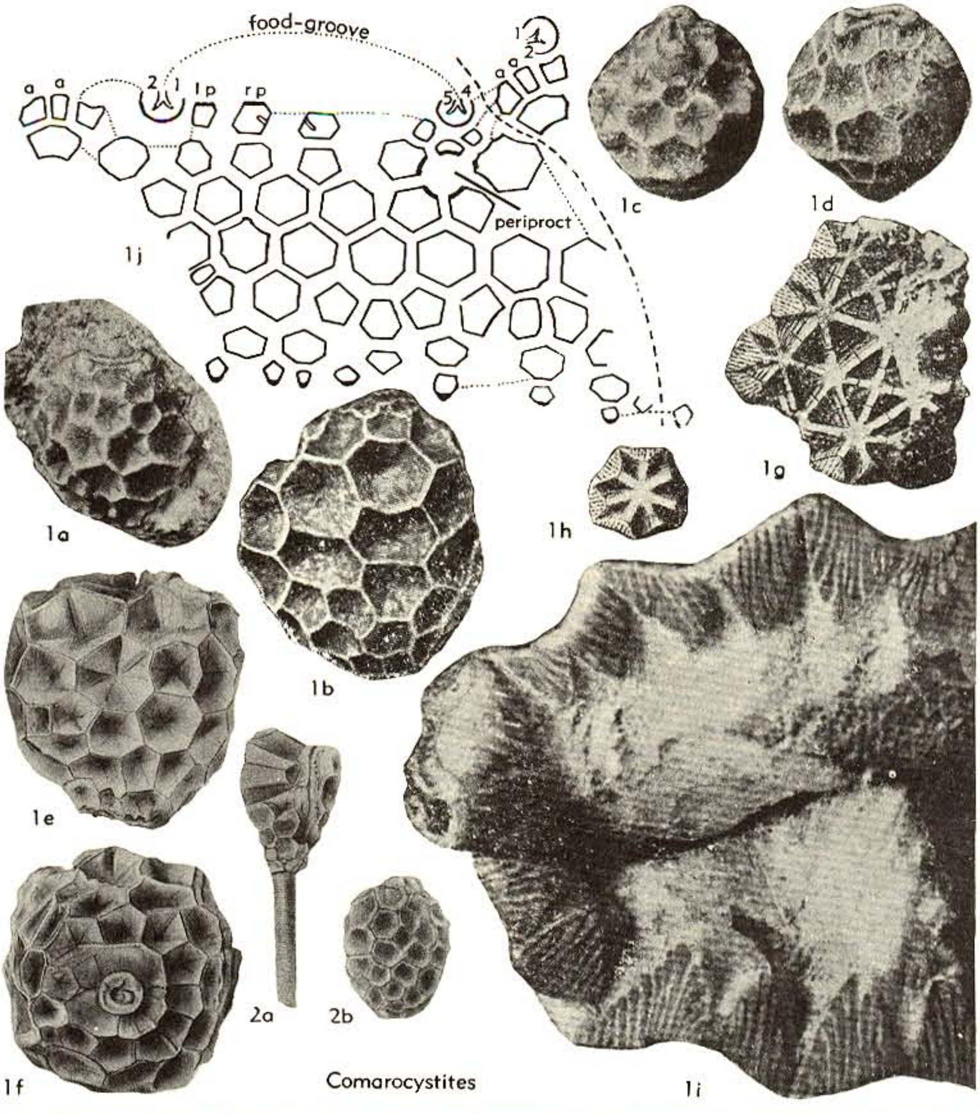


FIG. 159. Morphological features of Paracrinoidea illustrated by *Comarocystites,* all Middle Ordovician of Missouri; *1, C. shumardi* MEEK & WORTHEN; *2, C. obconicus* MEEK & WORTHEN.

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*

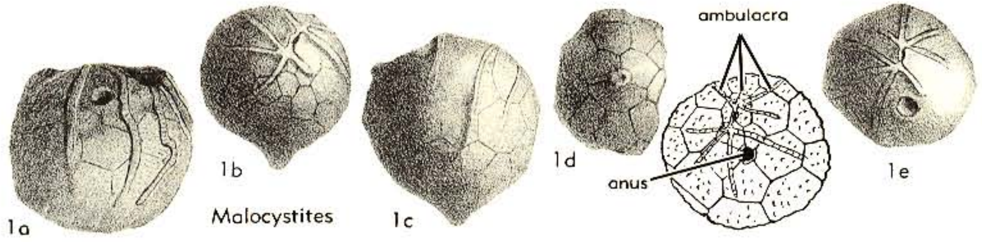


FIG. 160. Varicata (Malocystitidae) (p. S278).

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

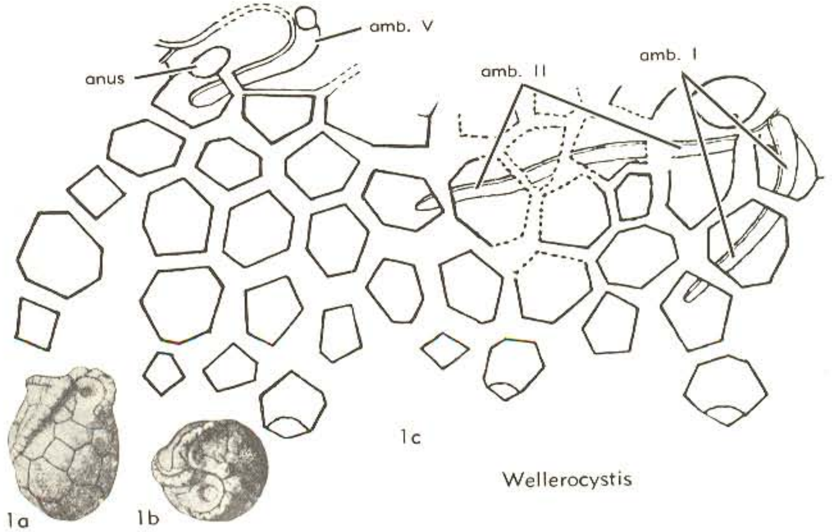


FIG. 161. Varicata (Malocystitidae) (p. S278).

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

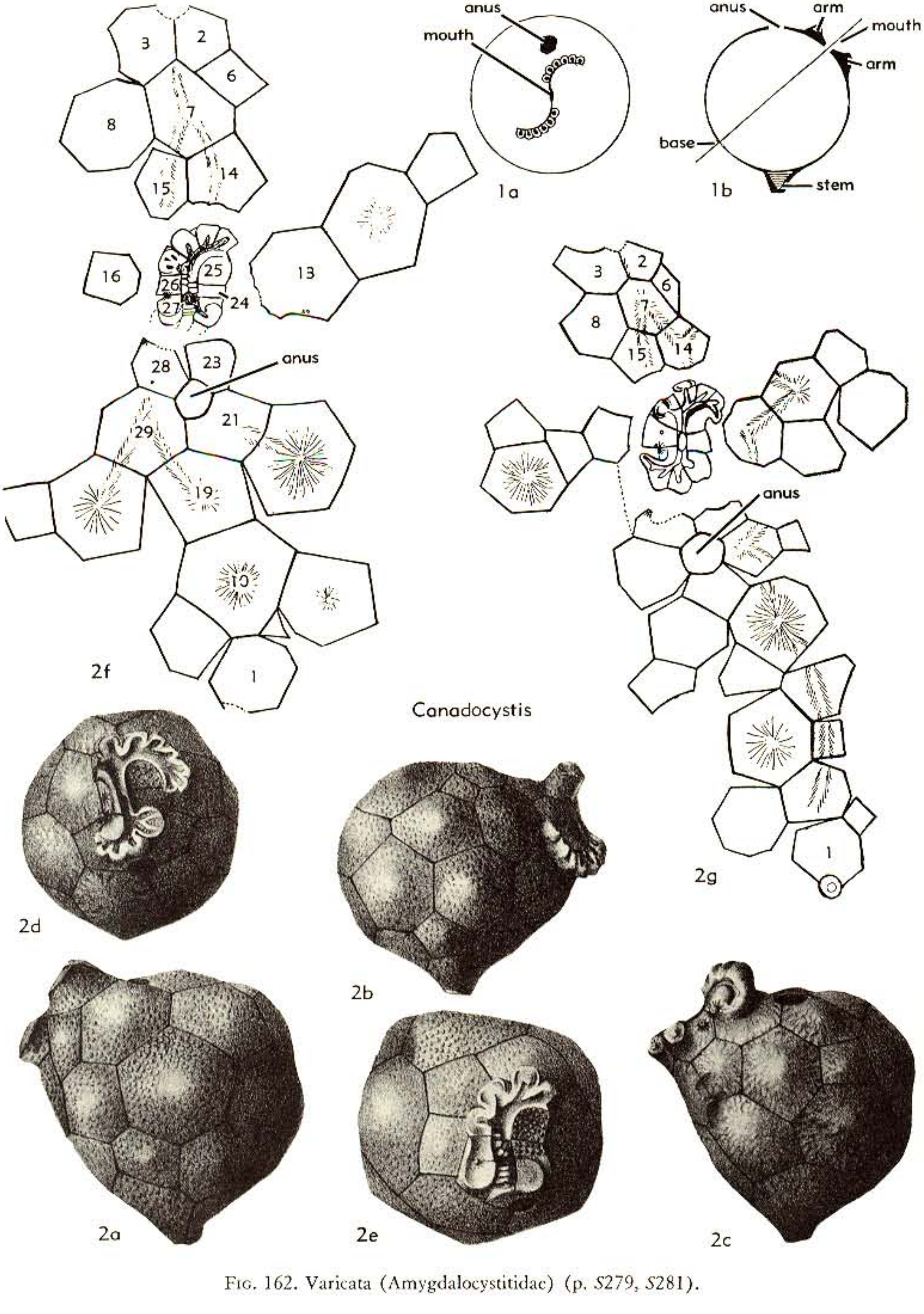
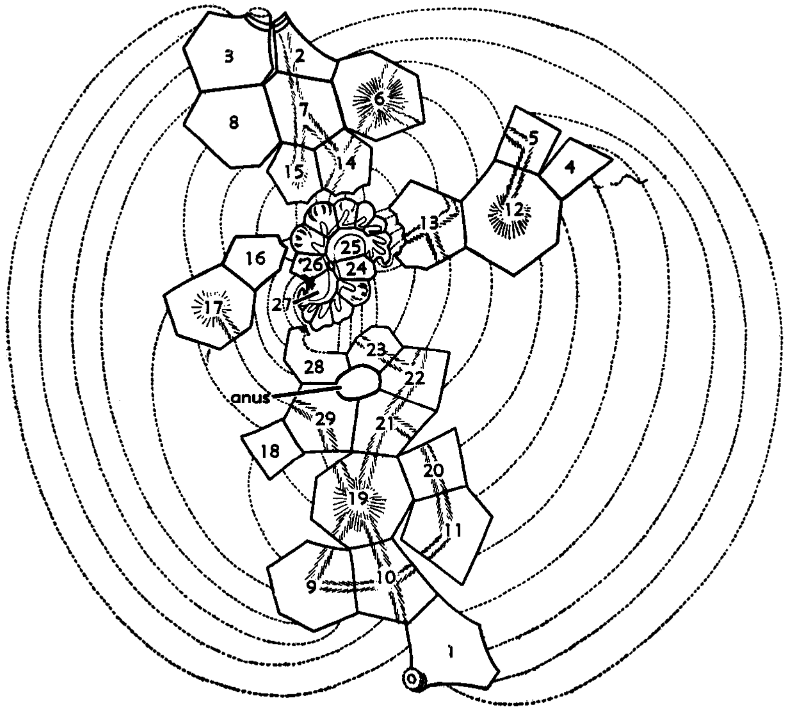


FIG. 162. Varicata (Amygdalocystitidae) (p. *S*279, *S*281).



1 Canadocystis

FIG. 163. Varicata (Amygdalocystitidae) (p. S279, S281).

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, ×4 (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

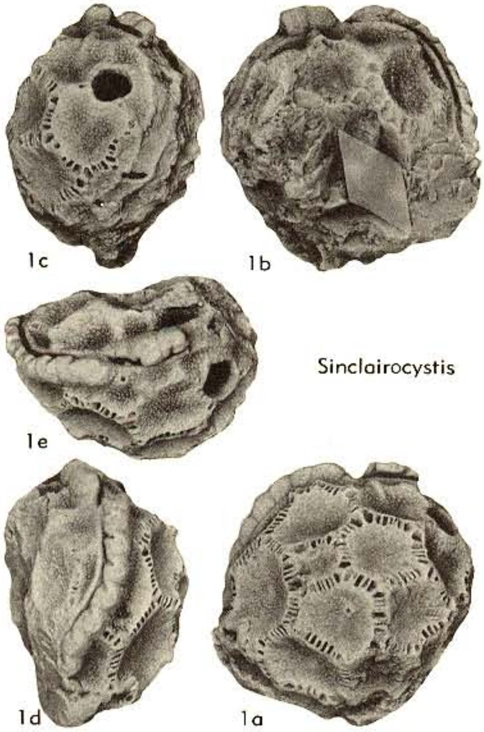


FIG. 164. Varicata (Amygdalocystitidae) (p. S281-S282).

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-

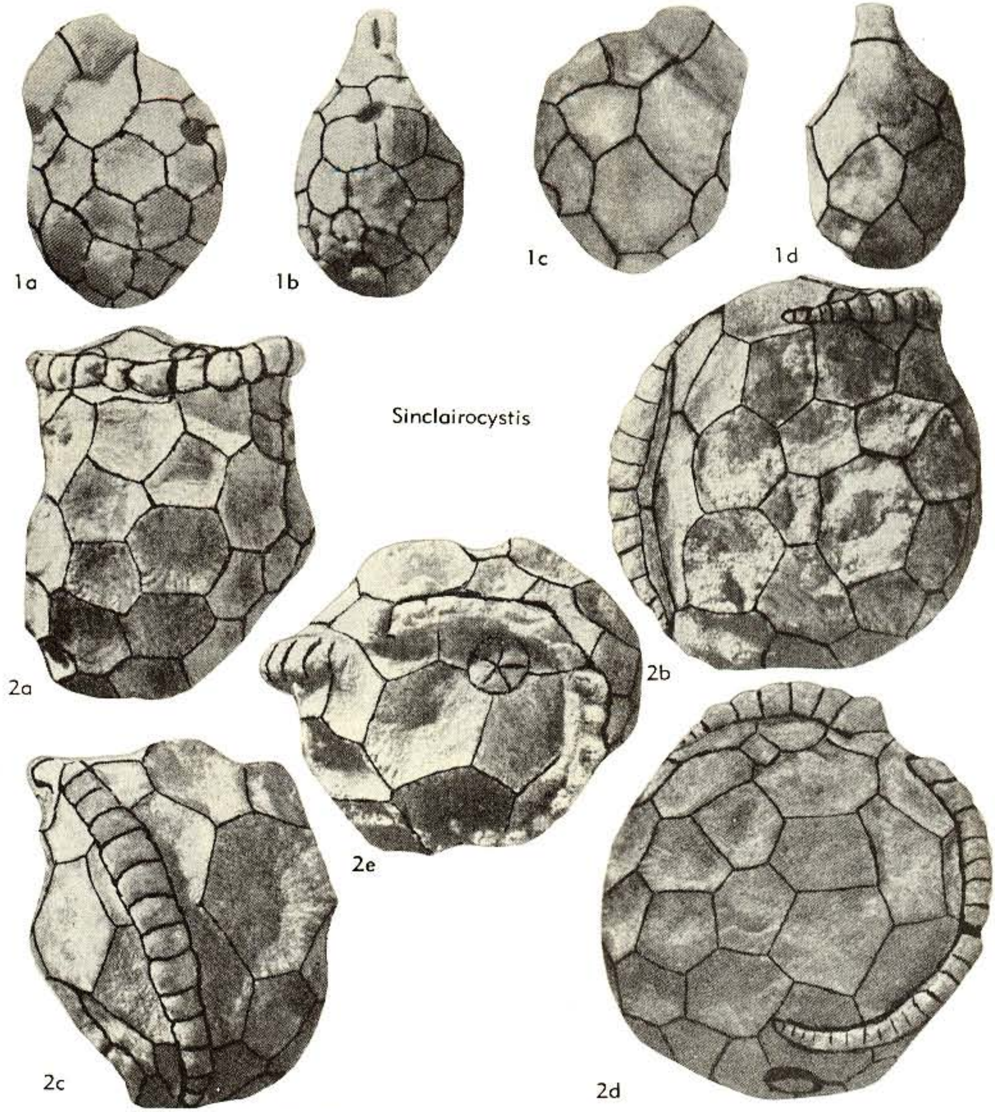


Fig. 165. Varicata (Amygdalocystitidae) (p. S281-S282).

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

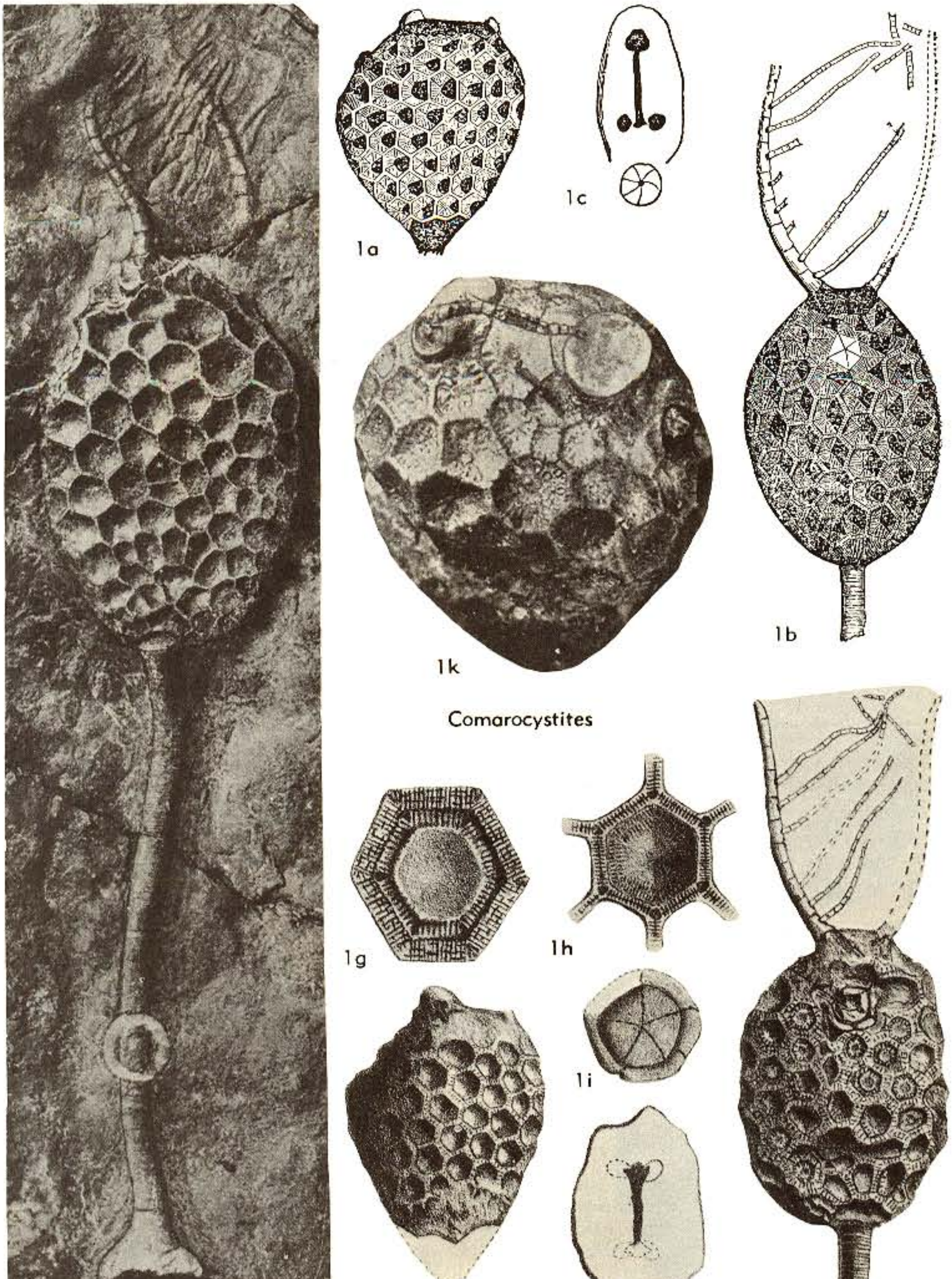


Fig. 166. Brachiata (Comarocystitidae) (p. S282-S287).

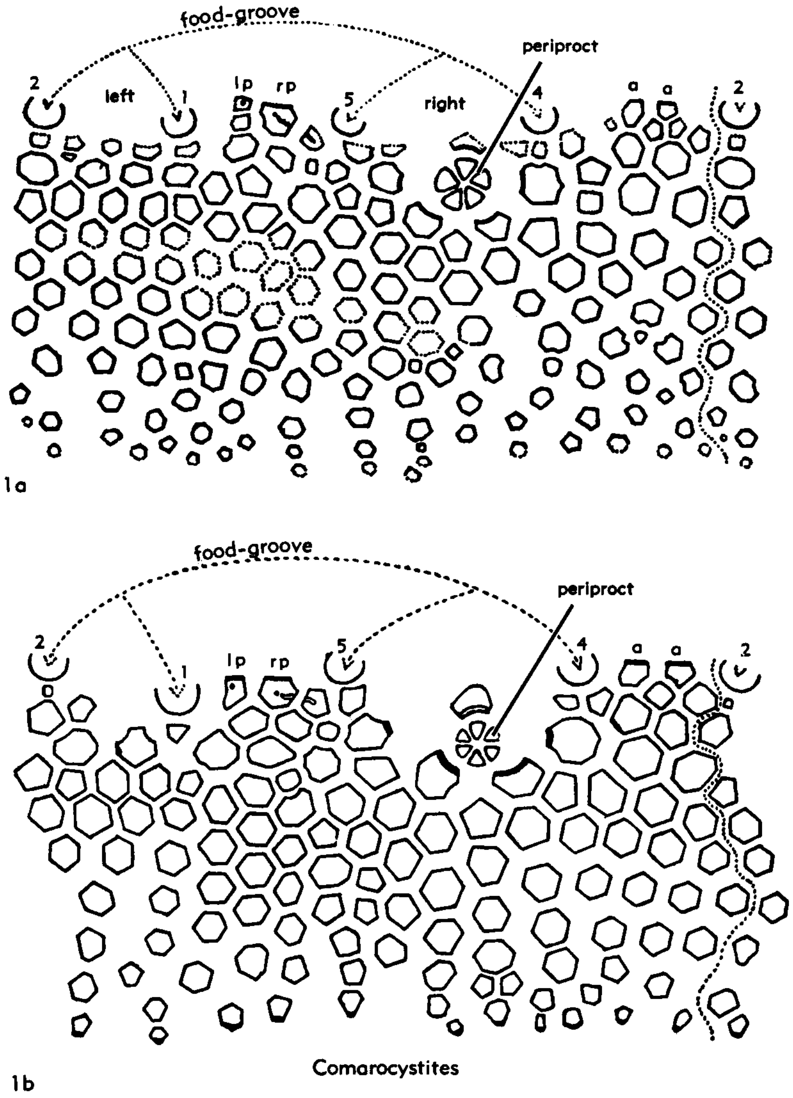


FIG. 167. Brachiata (Comarocystitidae; two plate diagrams) (p. S282-S287).

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

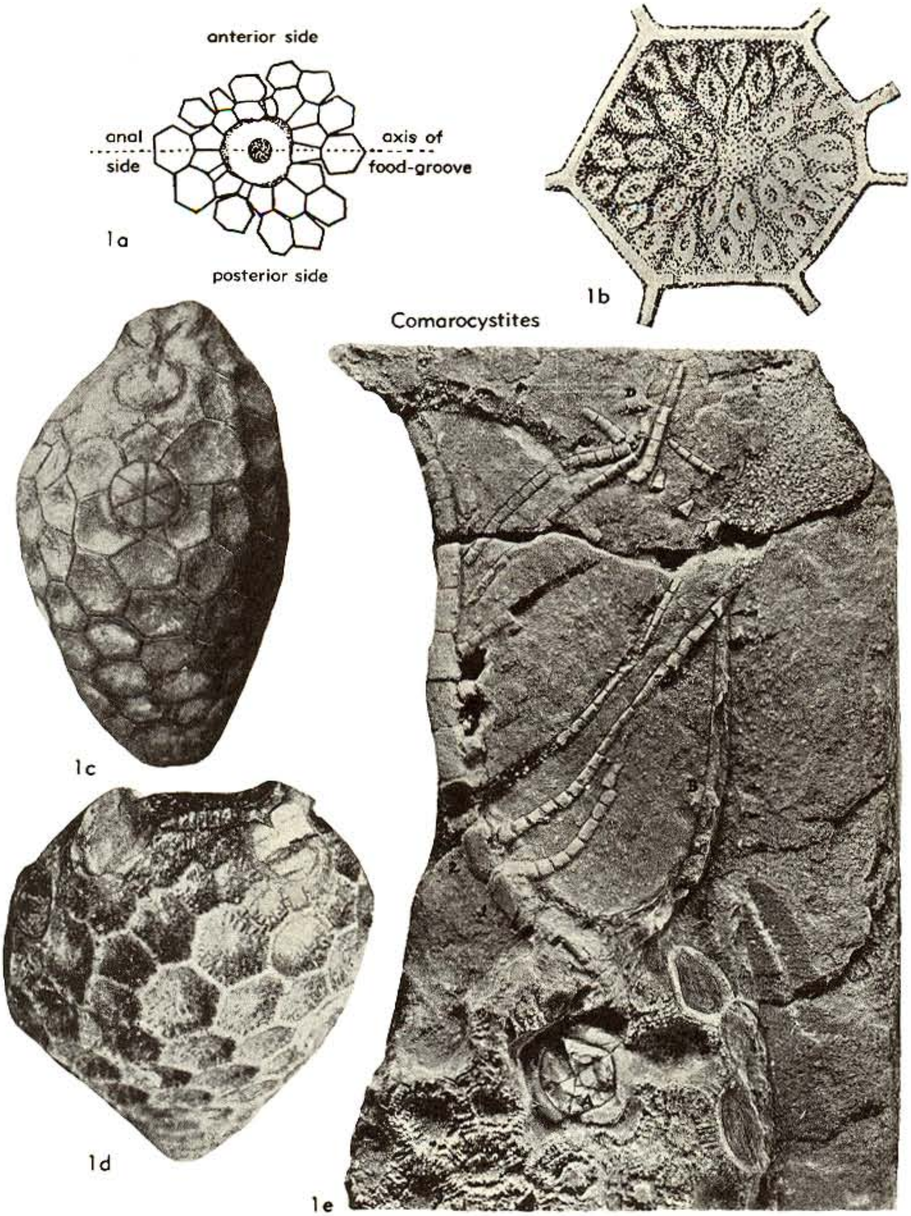


Fig. 168. Brachiata (Comarocystitidae) (p. S282-S287).

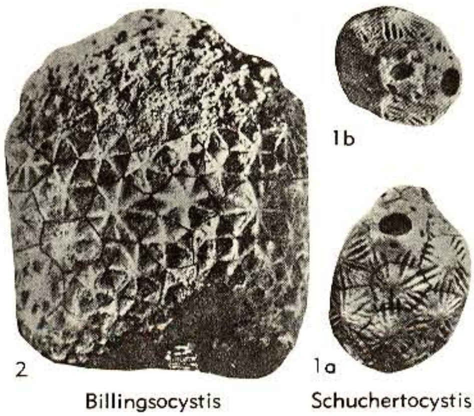


FIG. 169. Brachiata (Comarocystitidae) (p. *S*287-*S*288).

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.

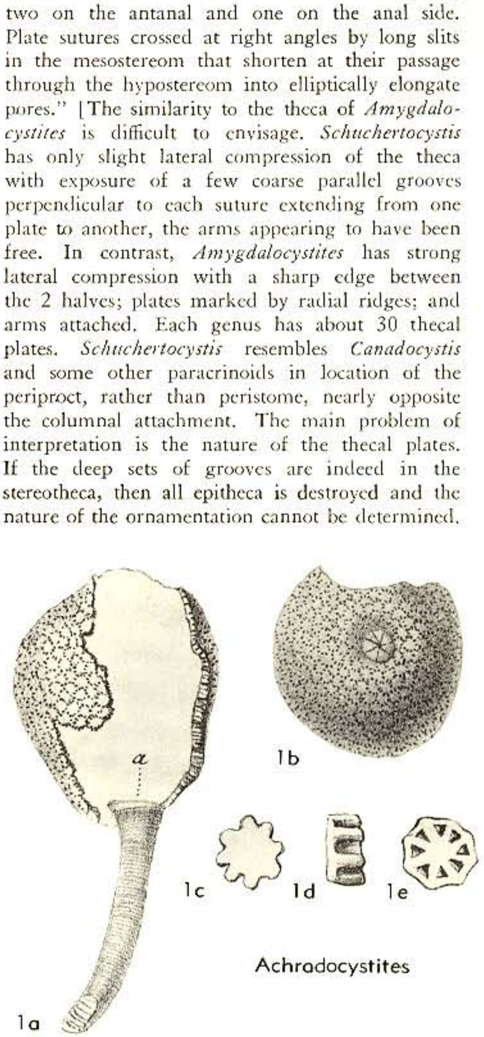


FIG. 170. Class, Order, and Family Uncertain (p. *S*288).

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).

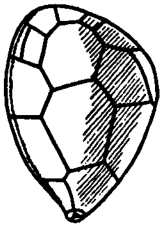


FIG. 171. Class, Order, and Family Uncertain (p. S288).

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

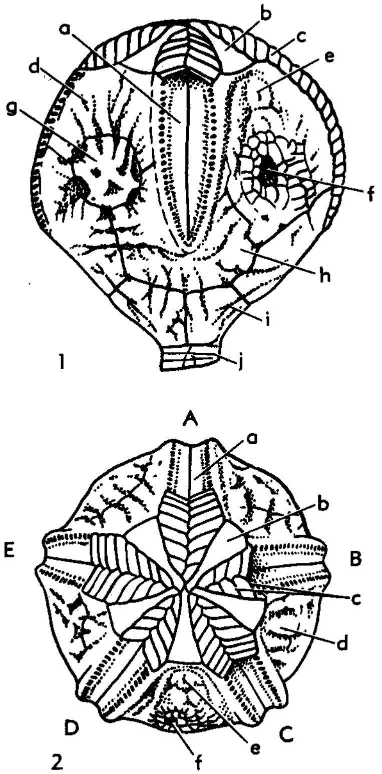

FIG. 172. Morphological features of edrioblastoids—oral *(1)* and *D*-ray *(2)* views of theca of **Astrocystites ottawaensis*, ×2 (reconstr.) (1). [Explanation: *a*, part of ambulacrum with cover plates removed, showing marginal rows of pores in floor plates; *b*, oral plate; *c*, cover plates; *d*, deltoid; *e*, ?hydropore; *f*, anal orifice; *g*, infradeltoid; *h*, radial; *i*, basal; *j*, column.]

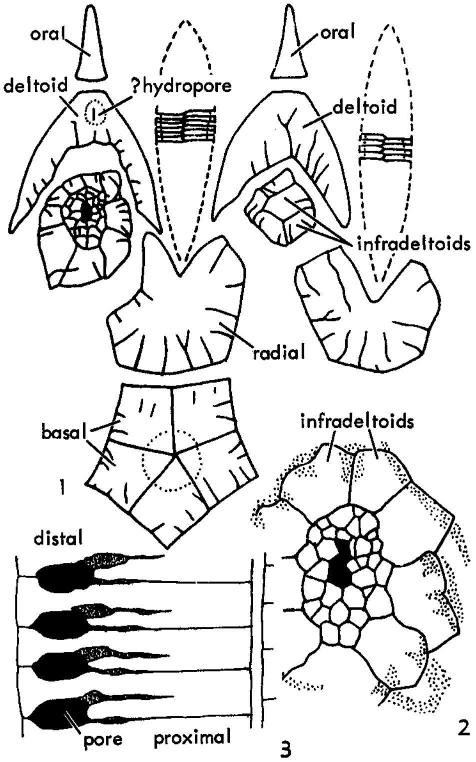

Fig. 173. Morphological features of edrioblastoids—*_Astrocystites ottawaensis_.——*1.* Partial plate layout, ×2.5 (based on Hudson, 4).——*2.* Plates surrounding anal orifice, ×5 (based on Hudson, 4).——*3.* Part of ambulacral floor showing marginal pores with depressions on plates extending toward perradial 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.*

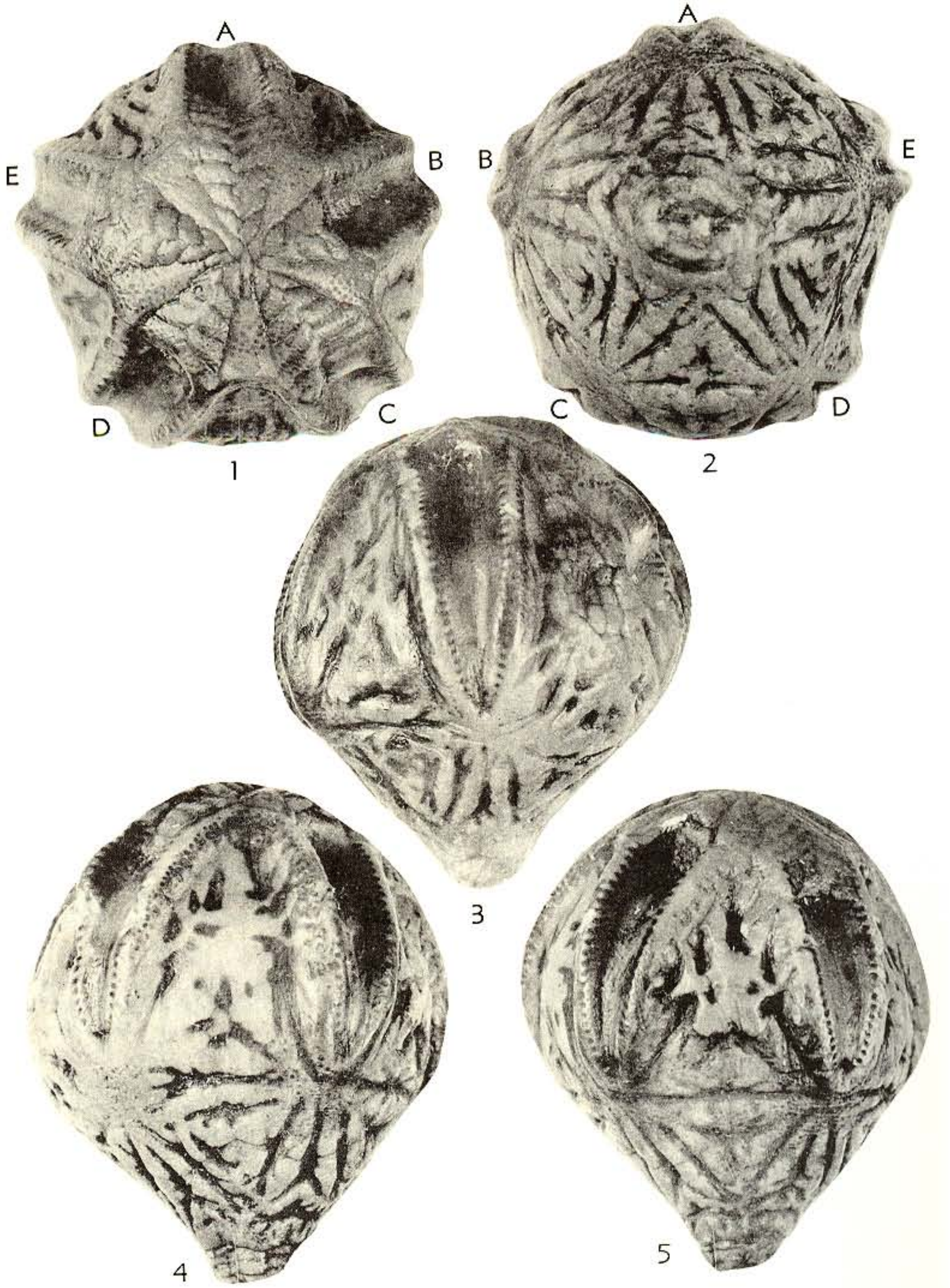

FIG. 174. Astrocystitidae (**Astrocystites ottawaensis*) (p. S292).

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.

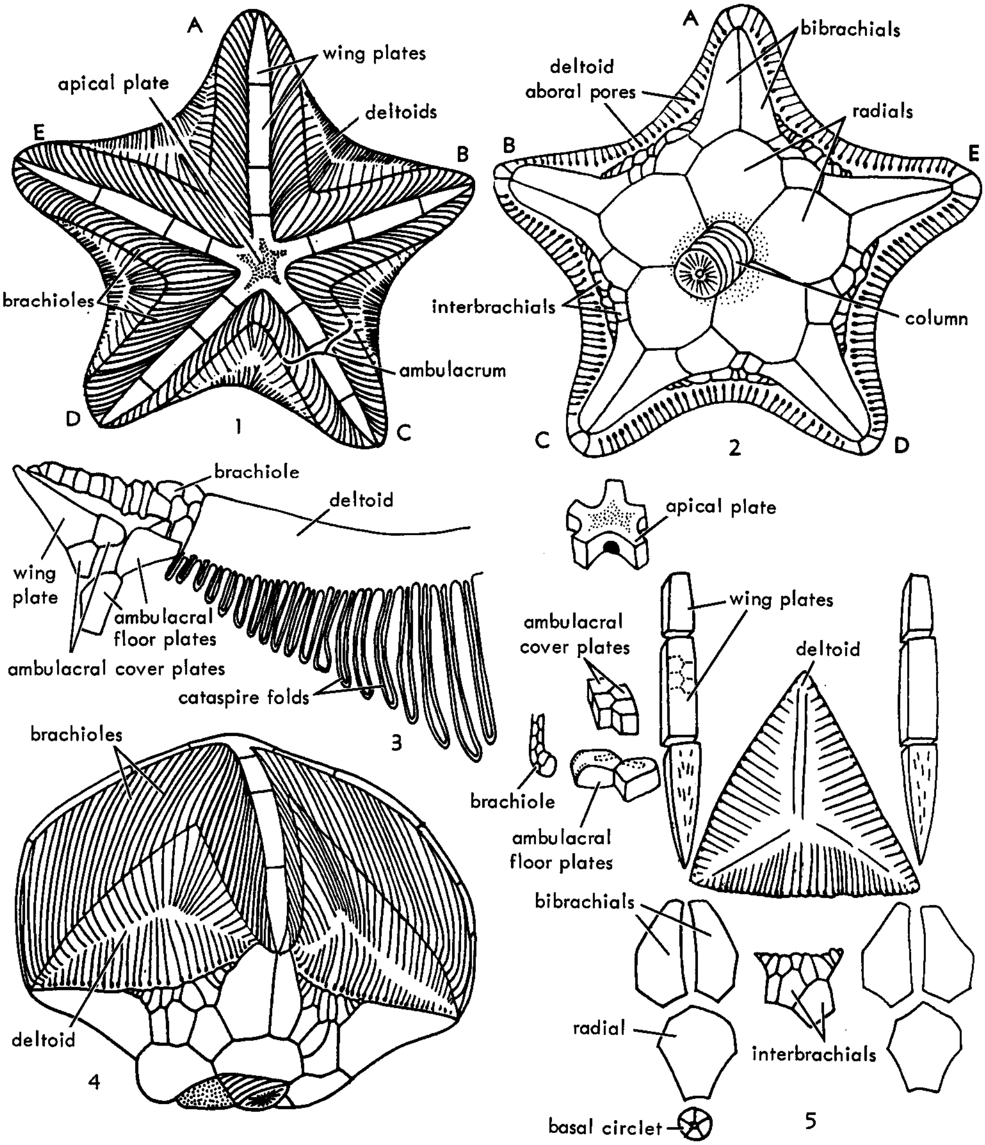

FIG. 175. Morphological features of parablastoids.——**Blastoidocrinus carchariaedens* (all Fay, n).——*1,2*. Oral and aboral view of theca, ×2.4.——*3*. Cross section of part of deltoid and ambulacrum showing cataspires, ×8.——*4*. *D*-ray view of theca, ×2.4.——*5*. Partial layout of plates, ×2.4.

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.*

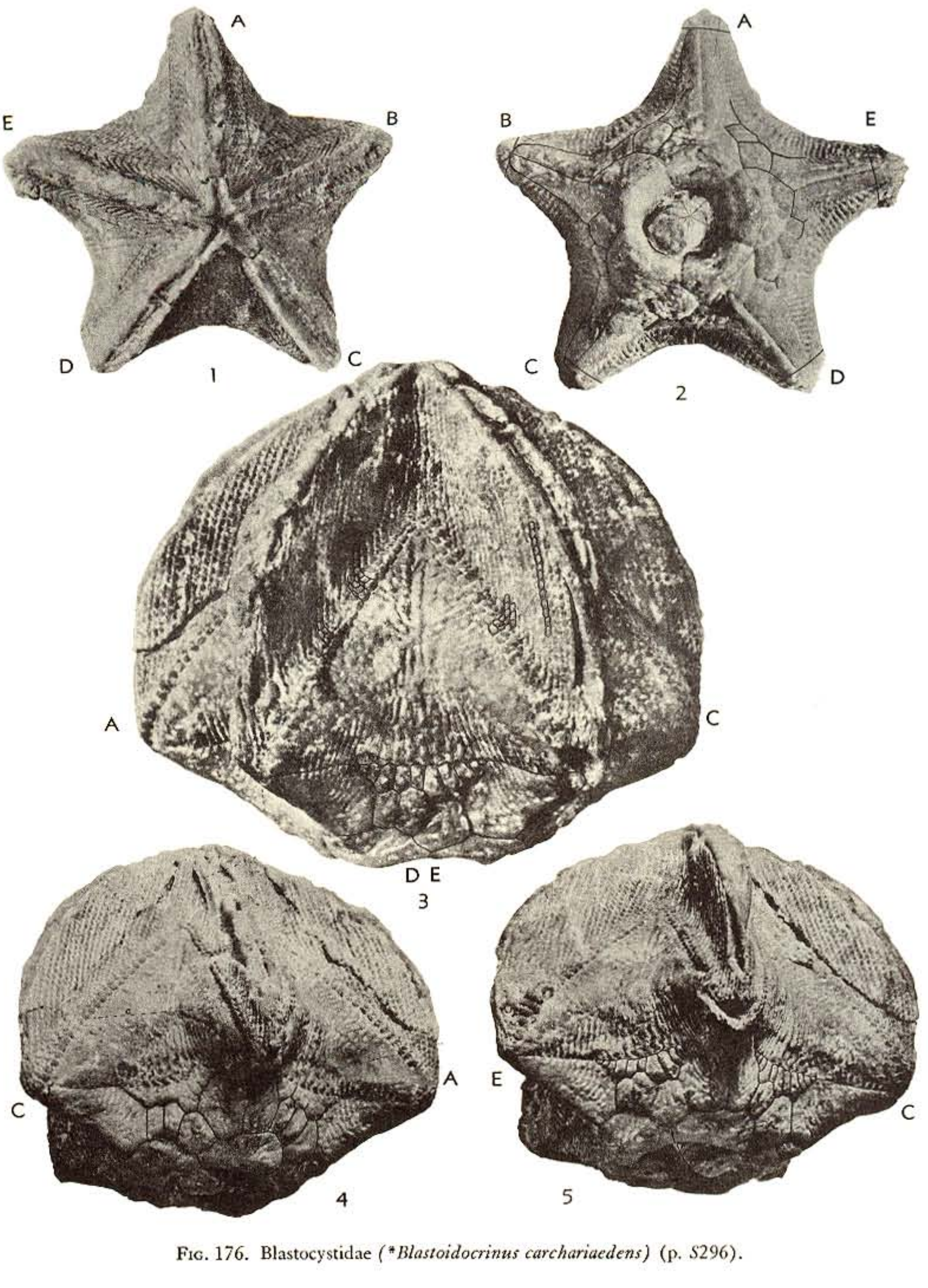

FIG. 176. Blastocystidae (**Blastoidocrinus carchariaedens*) (p. S296).

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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