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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

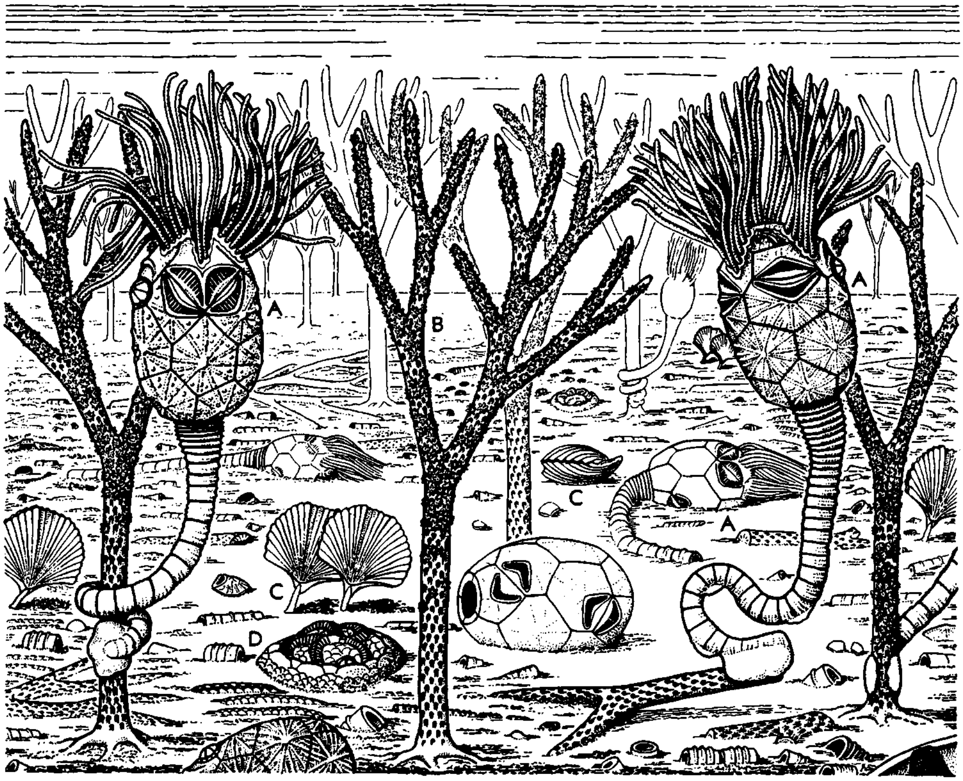


FIG. 32. Reconstruction of sea floor in southern Indiana during Richmond (Late Ordovician) time, showing *(A) Lepadocystis moorei* (MEEK), *(B)* ramose bryozoans, *(C)* small brachiopods, and *(D)* edrioasteroids in natural association (75).

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

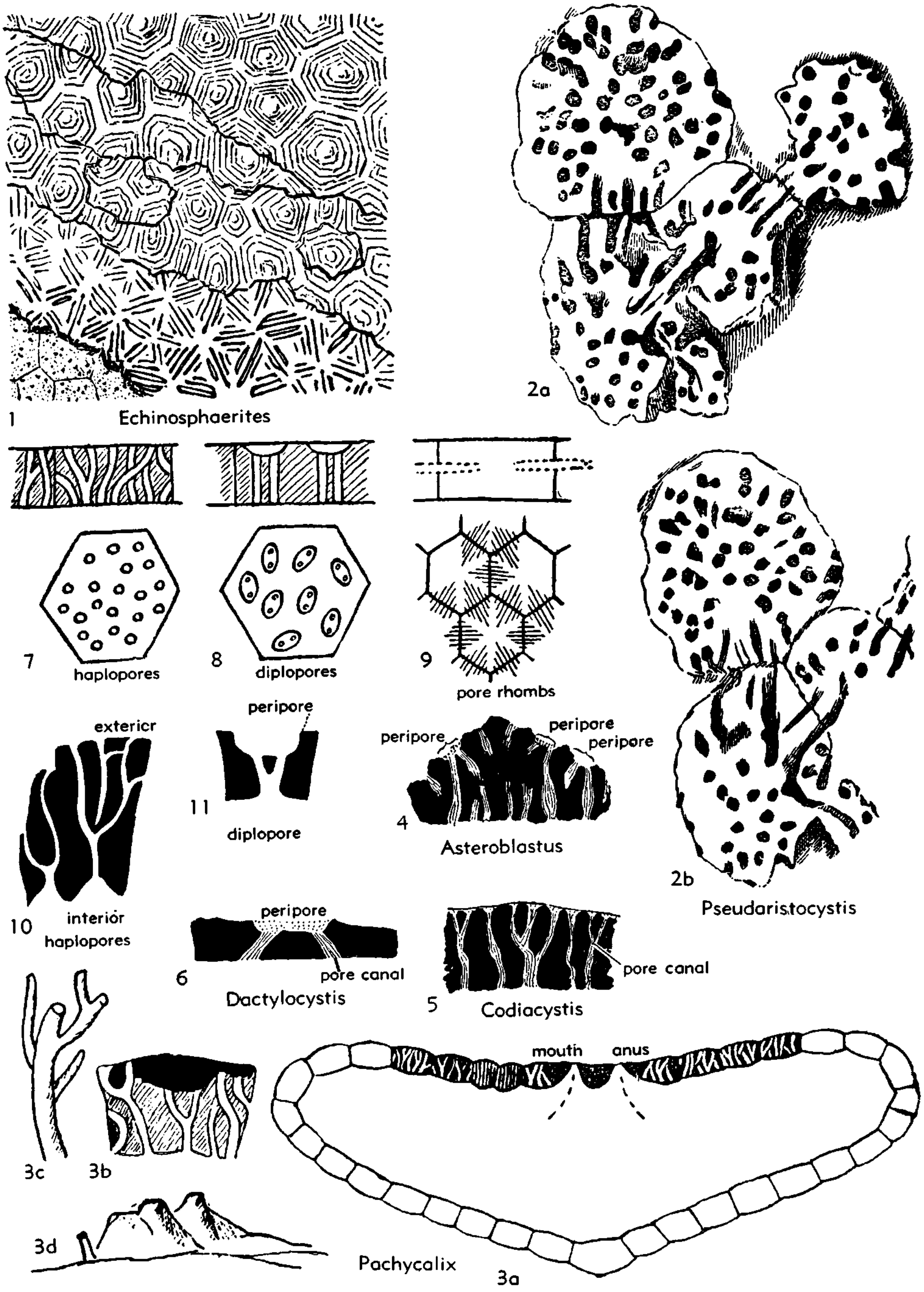
The diplopore type of thecal pores may well be older than pore rhombs, despite the reference by REGNÉLL (99) to "the fact that the Rhombifera appeared, as far as known, earlier than the Diploporita." The Middle Cambrian doubtful genera *Lapillocystites* and *Pilocystites* from Bohemia appear to be related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

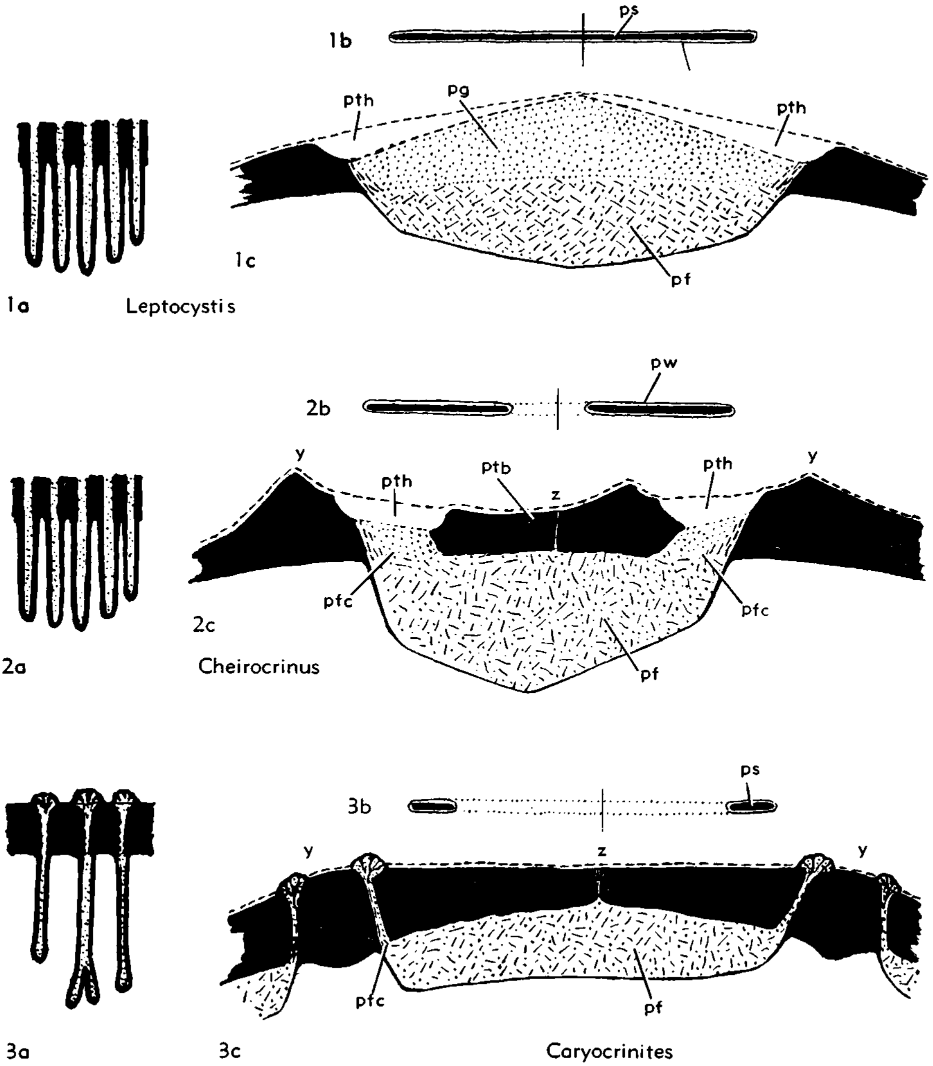


FIG. 34. Diagrammatic sections across pores *(1a, 2a, 3a)*, top views of pores *(1b, 2b, 3b)*, and sections along pores *(1c, 2c, 3c)* in selected cystoids.——*1. Leptocystis* (L.Ord.-L.Sil.), typical of conjunct pectinirhombs in Glyptocystitida.——*2. Cheirocrinus* (L.Ord.-U.Ord.), typical of disjunct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

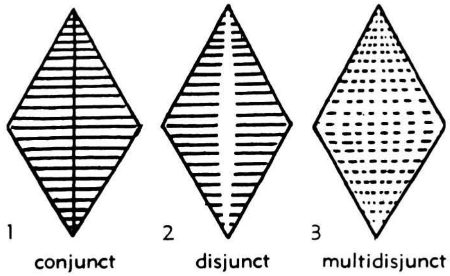


FIG. 35. Three principal types of pectinirhombs (12).

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

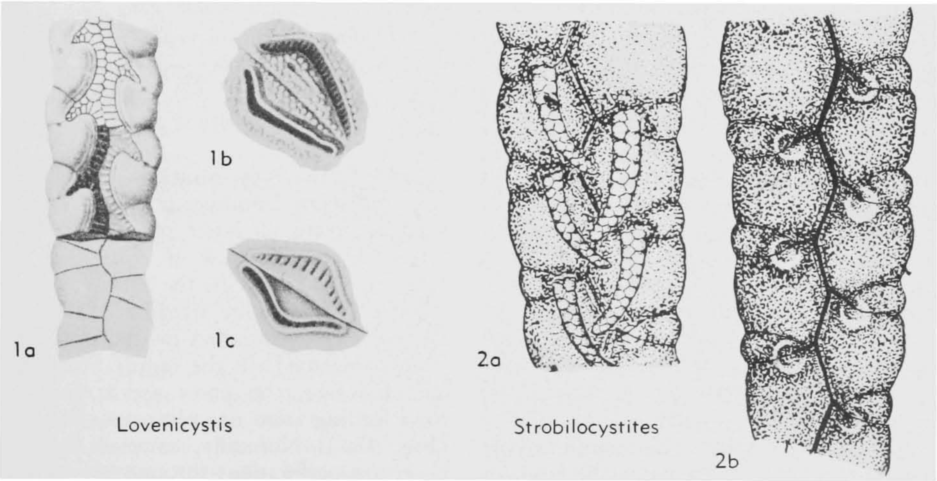


FIG. 36. Ambulacral and pore-rhomb structures of cystoids.——*1. Lovenicystis* (U.Sil.); *1a,* ambulacrum, covering plates in upper (proximal) section, flooring plates removed to show impressions on thecal plates in lower (distal) section; *1b,c,* examples of montidisjunct pectinirhombs (99).——*2. Strobilocystites*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

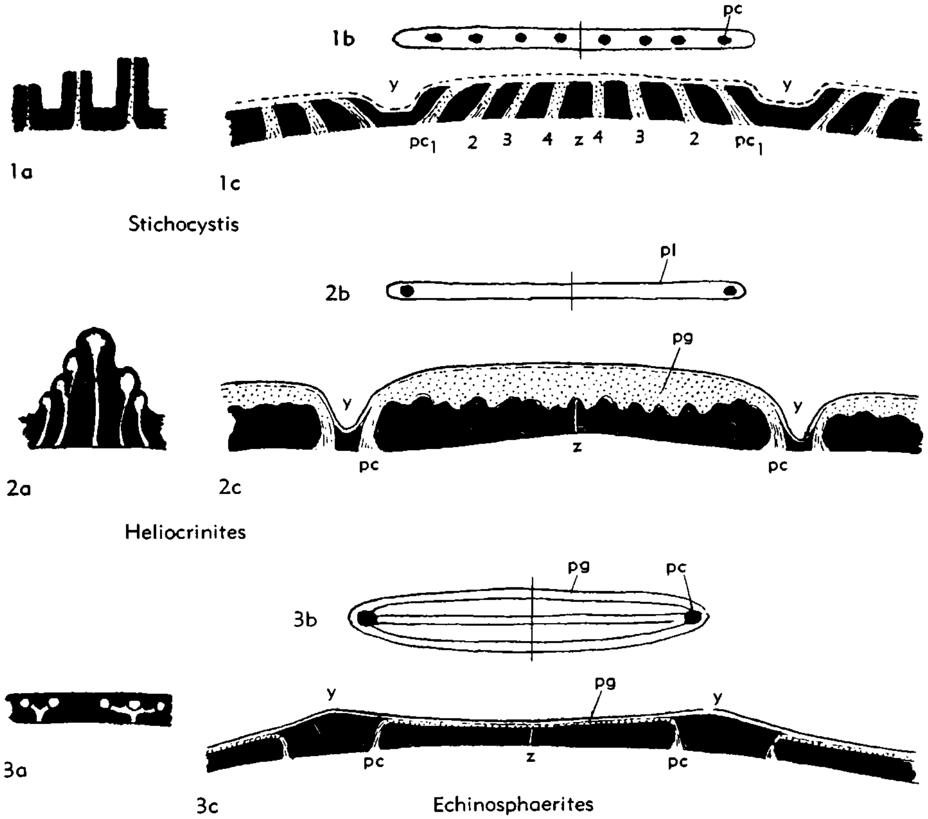


FIG. 37. Diagrammatic section across pores *(a)*, top view of a pore *(b)*, and section along a pore *(c)* in selected cystoids. ——*1. Stichocystis* (M.Ord.), typical of pore rhombs in Polycosmitida.——*2. Heliocrinites* (L.Ord.-U.Ord.), typical of simple tangential pore canals in Caryocystitida.——*3.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

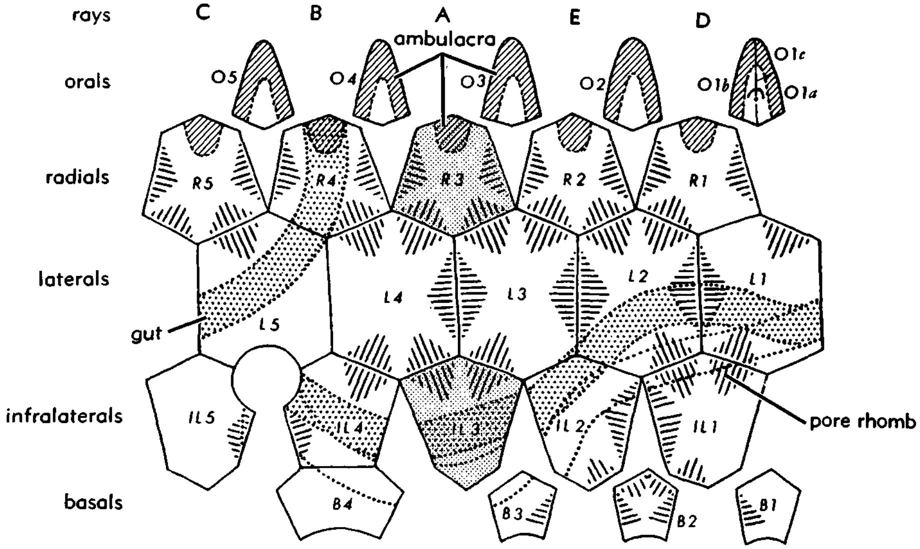


Fig. 38. Generalized plate diagram of a glyptocystitidan cystoid, with plate designations by Regnéll (adopted in the *Treatise*): *B,* basal; *IL,* infralateral; *L,* lateral; *O,* oral; *R,* radial. Ambulacra are indicated by oblique ruling on orals and radials. Pore rhombs are shown in all positions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

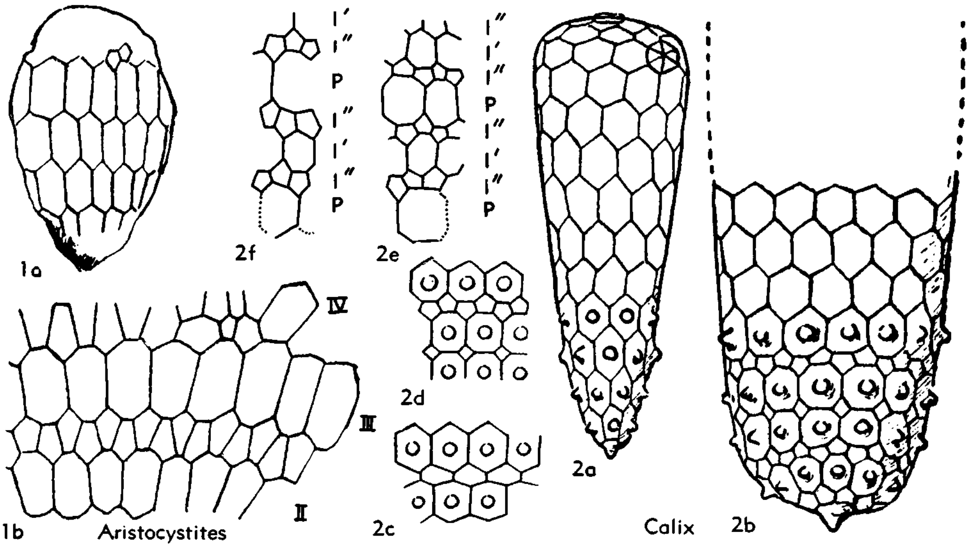


FIG. 39. Growth by interstitial addition of plates.——*1. Aristocystites bohemicus* BARRANDE (M.Ord.); *1a,* stage 1, in which plates are subequal, ×0.8; *1b,* stage 2, in which secondary plates have been inserted in circlets.——*2. Calix sedgwicki* ROUAULT (M.Ord.); *2a,* stage 1, ×1; *2b-d,* stage 2,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

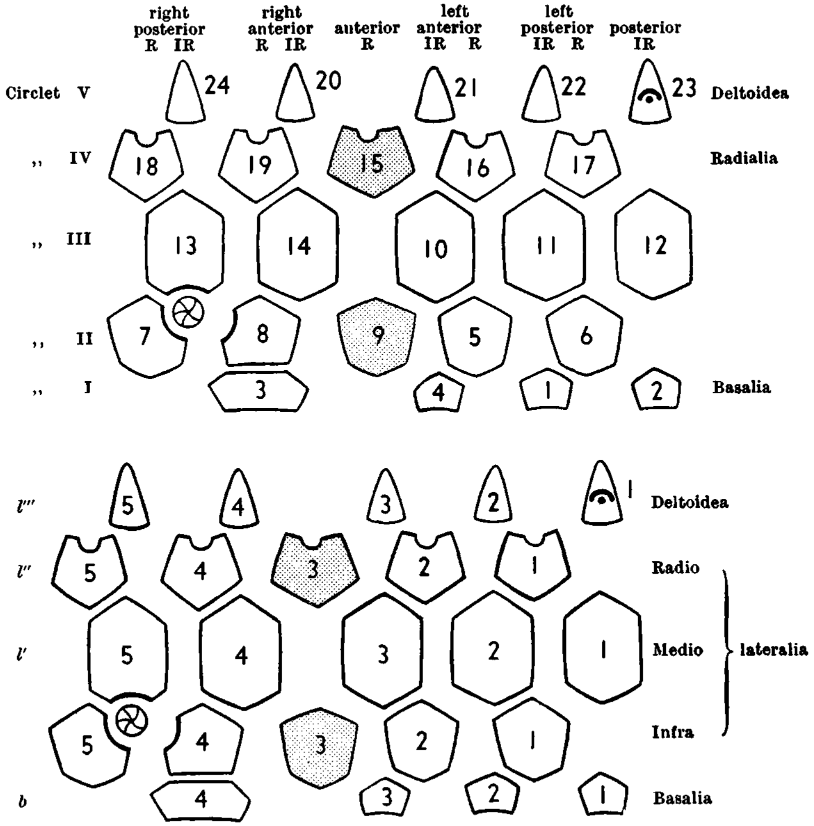


FIG. 40. Generalized plate diagrams of glyptocystitidan cystoids (plates of *A*-ray shaded), with designations by FORBES and BATHER (above) and by JAEKEL (below) (12).

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.

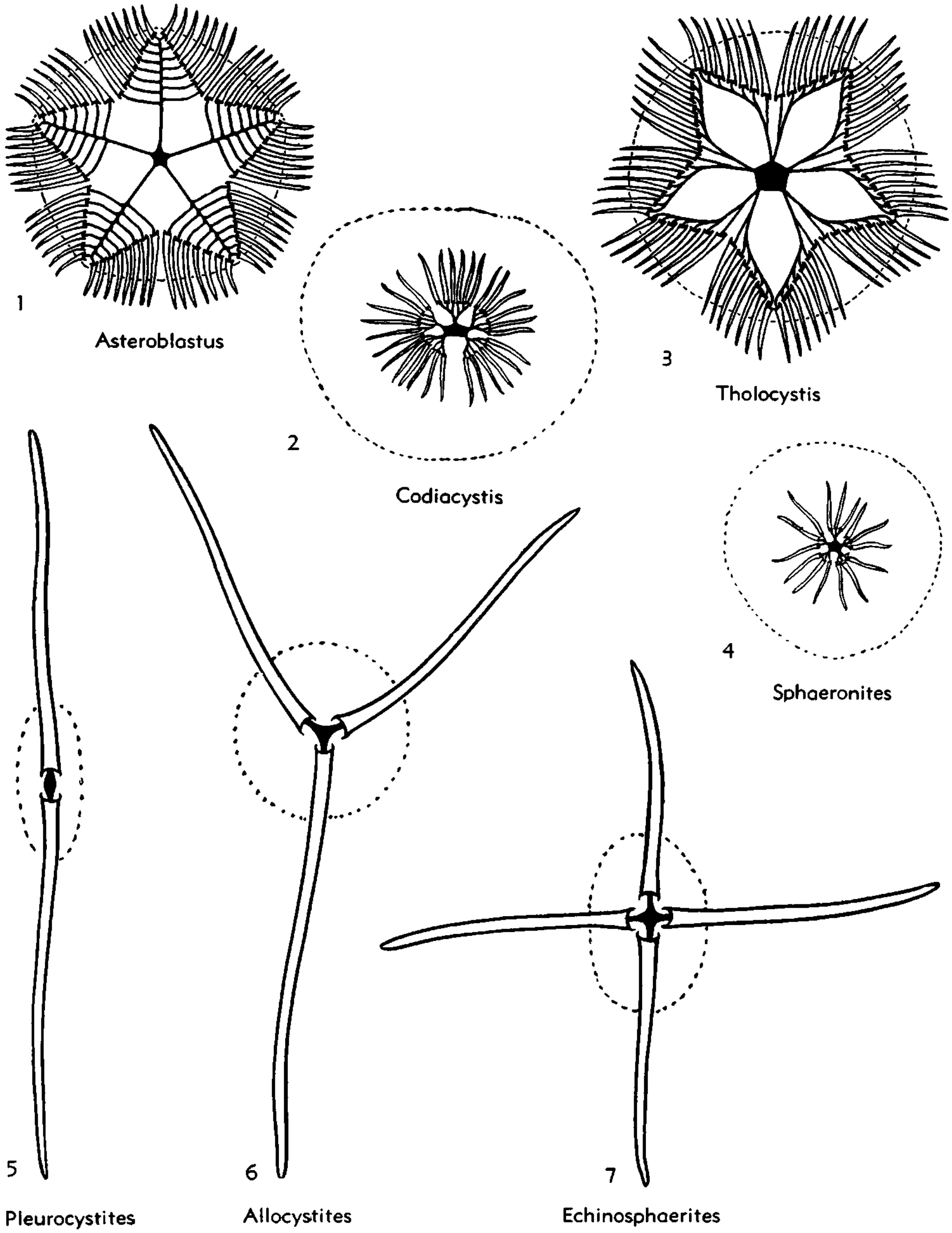


FIG. 41. Diagrammatic oral projections of ambulacral systems (69, Kesling, n).

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

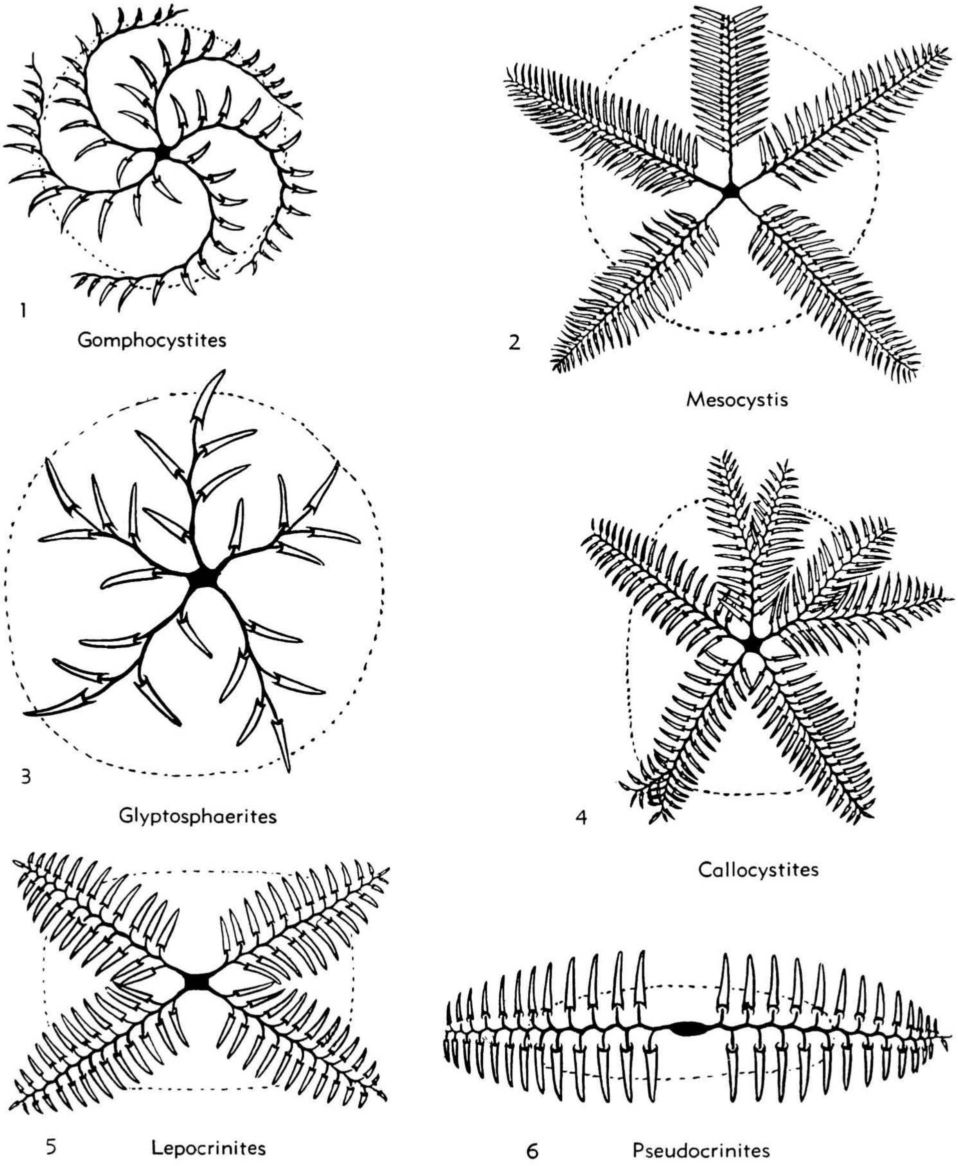


FIG. 42. Diagrammatic oral projections of ambulacral systems (69).

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

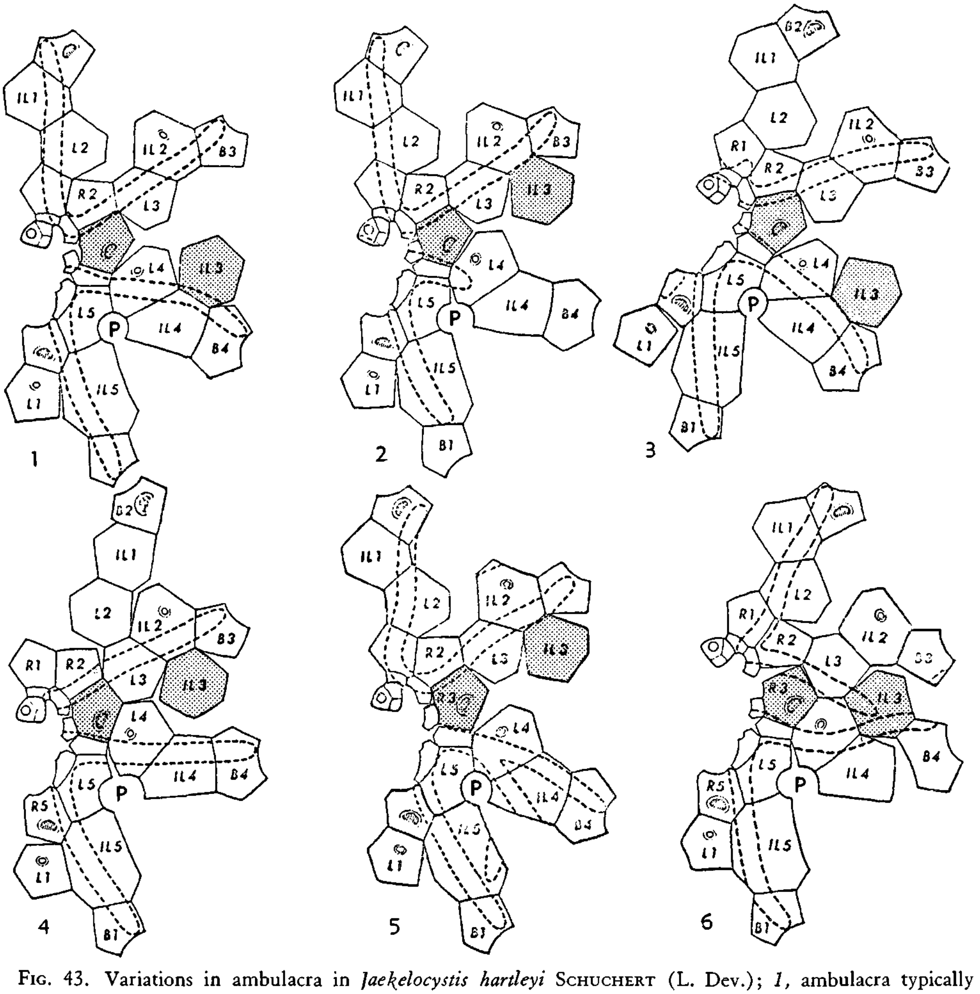


FIG. 43. Variations in ambulacra in *Jaekelocystis hartleyi* SCHUCHERT (L. Dev.); *1*, ambulacra typically developed; *2*, ambulacrum *IV (B)* short; *3*, ambulacrum *I (D)* deformed; *4*, ambulacrum *I (D)* aborted; *5*, ambulacrum *IV (B)* bifurcate; *6*, ambulacrum *II (E)* abutting on *IV (D)* (73).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

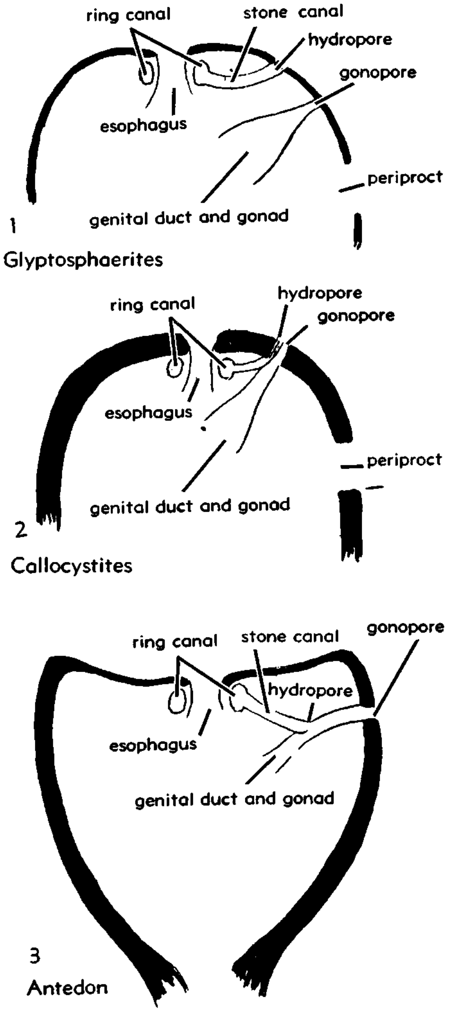


Fig. 44. Cross sections through peristome, hydropore, gonopore, and periproct.——*1,2.* Hypothetical reconstructions of *Glyptosphaerites* (L.Ord.-U.Ord.) and *Callocystites* (M.Sil.).——*3.* Young stage of *Antedon* (Rec.) (69).

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

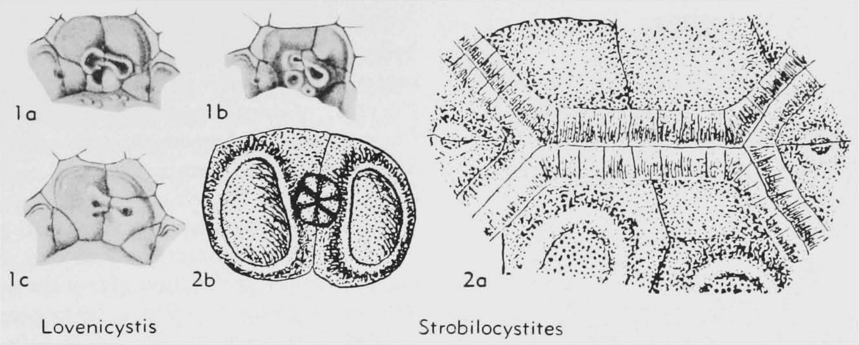


FIG. 45. Hydropore and gonopore features.——*1. Lovenicystis* (U.Sil.); *1a-c,* posterior sector or oral region showing various forms of hydropore and gonopore.——*2. Strobilocystites* (M.Dev.-U.Dev.); *2a,b,* peristome and bipartite hydropore and pyramid-closed gonopore (99, 120).

(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-

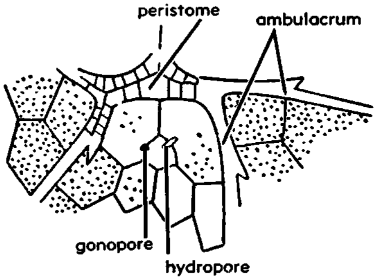


FIG. 46. *Protocrinites fragum* (EICHWALD) (L. Ord.). Diagrammatic plan of the posterior part of the oral region (146).

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.

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.

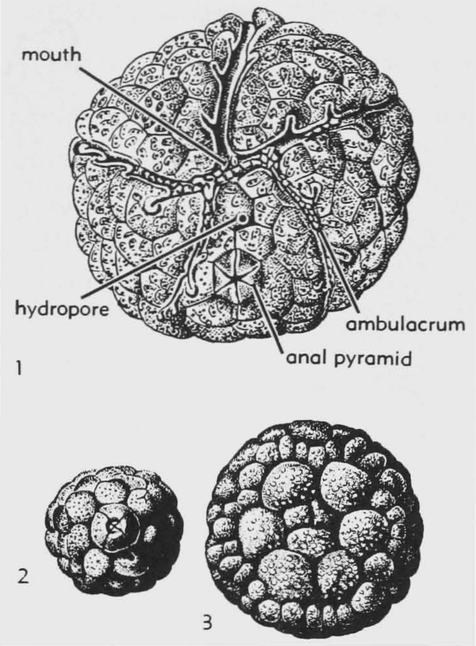
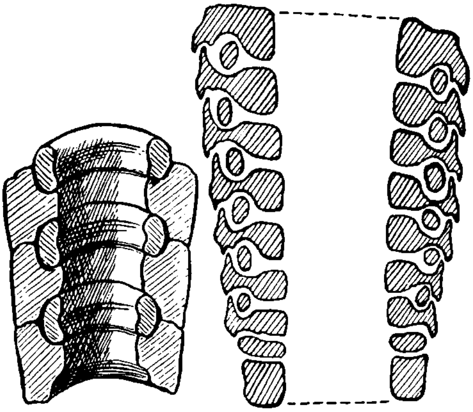


FIG. 47. *Protocrinites oviformis* EICHWALD (M. Ord.); *1,* oral view, ×1.5; *2,3,* aboral views of very young and adult individuals, showing ontogenetic changes in which traces of the cicatrix of columnar attachment are eradicated, ×1 (10).

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



1 Cheirocrinus 2 Strobilocystites

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-

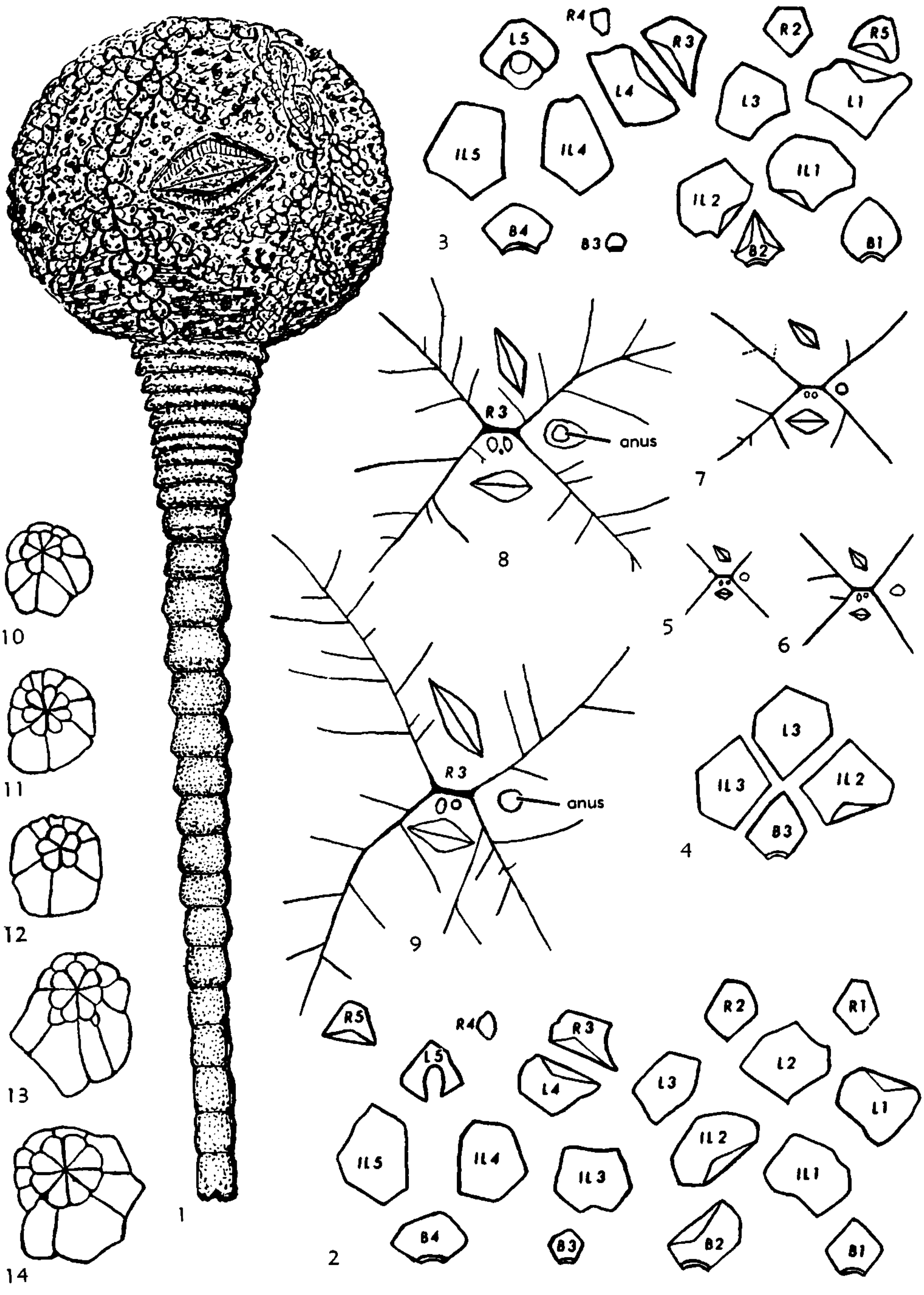


Fig. 49. Structures of *Strobilocystites* (M.Dev.-U.Dev.) and their variations.——*1. S. calvini* White (M. Dev.), restoration, ×2.——*2.* Diagram of plates in nearly average specimen, except that *B3* (4) is rather small (plates of *A*-ray shaded).——*3.* Diagram of plates of anomalous specimen in which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

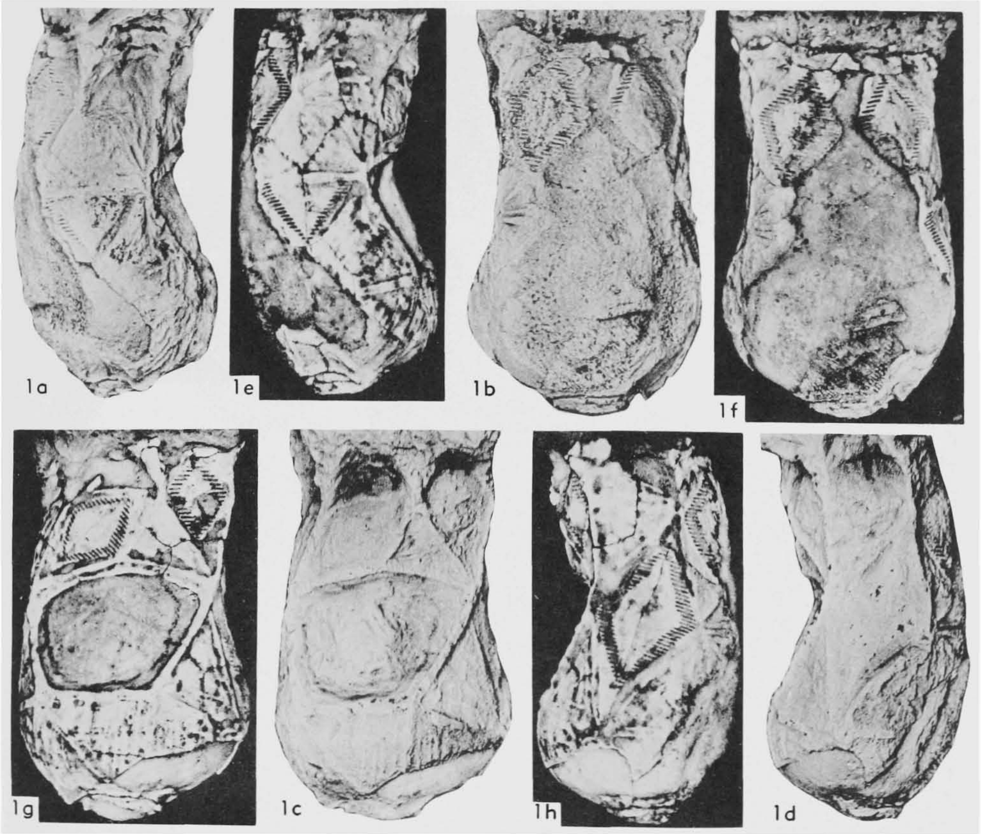


Fig. 50. Four views of a specimen coated with sublimated ammonium chloride and the same submersed in xylol, all photographed in high contrast. *Homocystites anatiformis* (Hall), M.Ord.(Trenton), Mich.; *1a-d,* four lat., ×2, coated; *1e-h,* same, submersed; only part of specimen shown in *1b* was exposed; 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

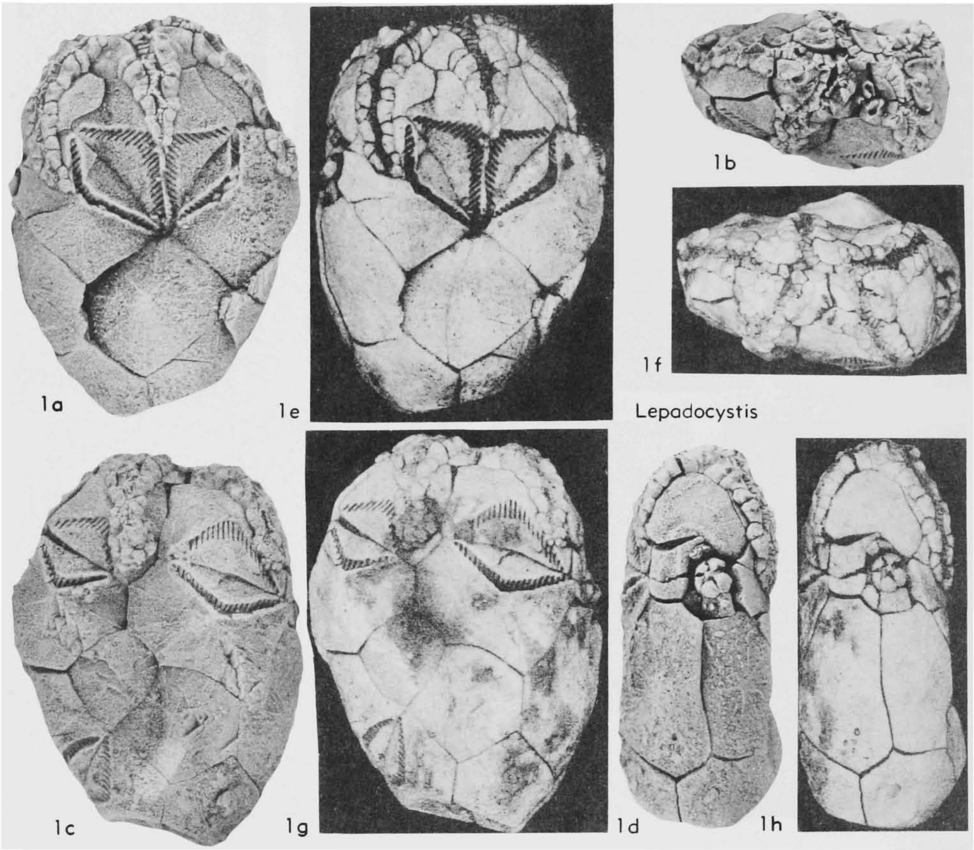


FIG. 51. Four views of a specimen coated with sublimated ammonium chloride and the same submersed in xylol, all photographed in low contrast. *Lepadocystis moorei* (MEEK), U.Ord.(Cincinnati.), Ind.; *1a-d,* lat. *(III),* oral, lat. (post) and lat. (anal), ×4, coated; *1e-h,* same submersed; this specimen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

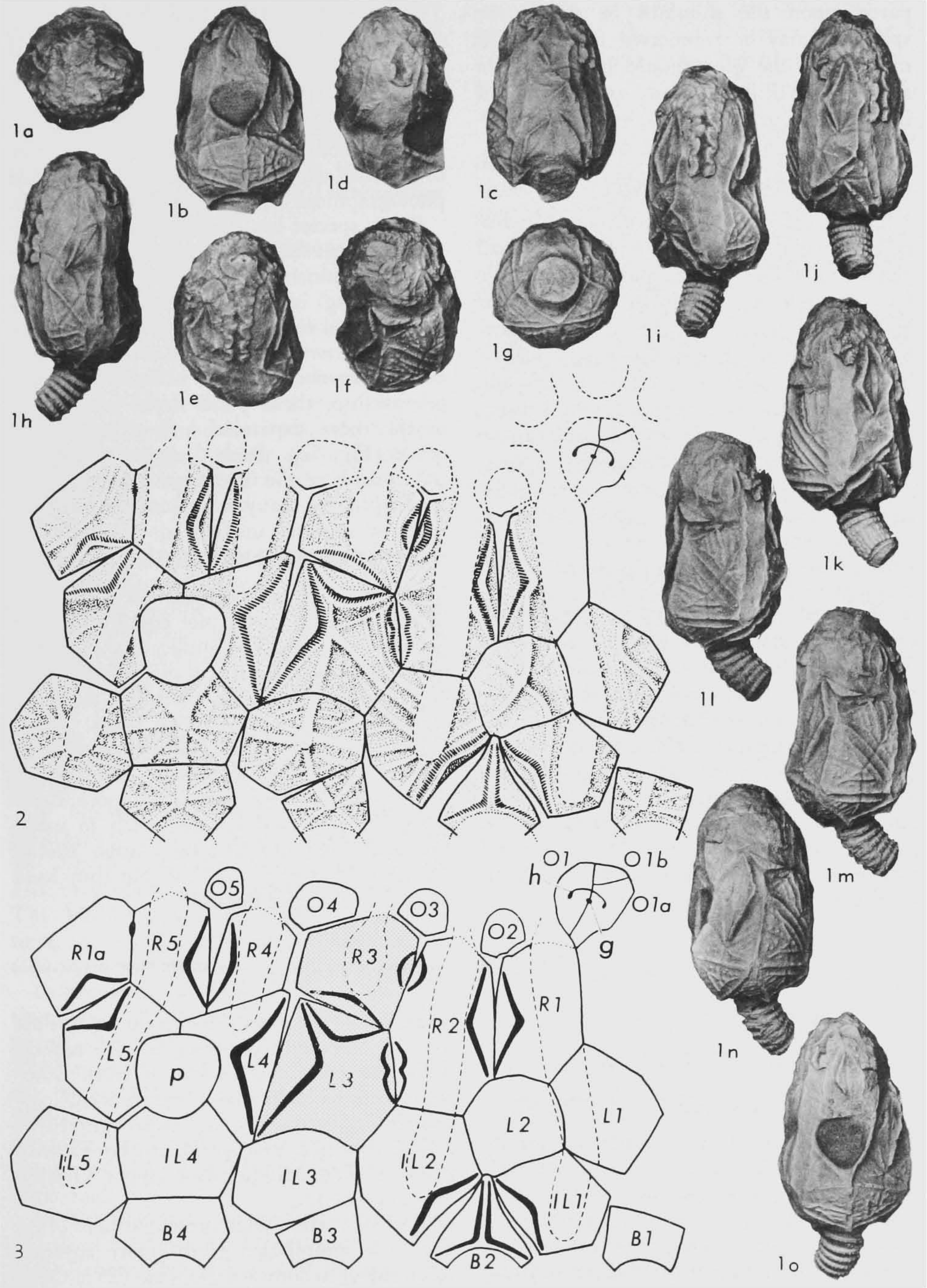


FIG. 52. *Glyptocystites ehlersi* KESLING, M.Ord.(Trenton.), Mich.; *1*, photographs, all ×1; *1a*, oral view; *1b,c*, aborally inclined views of interambulacra *4* and *1*; *1d-f*, orally inclined views of ambulacra *V (C)*, *I (D)*, and *III (A)*; *1g*, aboral view; *1h-o*, lateral views, *h* on interambulacrum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

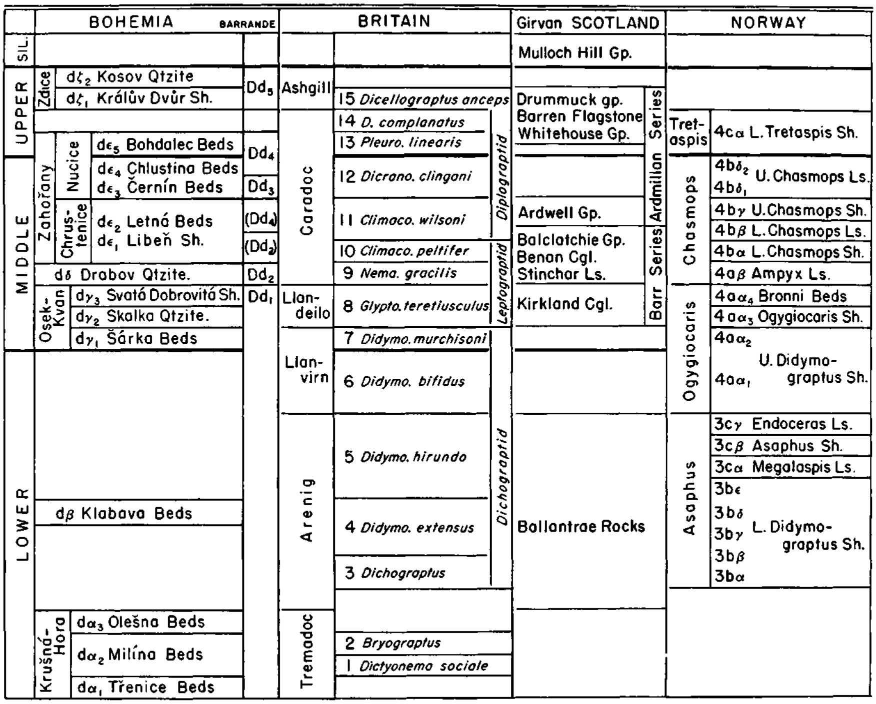


FIG. 53. Correlations of Ordovician formations in parts of Europe. Lower-Middle-Upper boundaries from THORSLUND (1960); other data from BOUČEK (1938), ÖPIK (1952), STØRMER (1953), REGNÉLL & HEDE (1960), and THORSLUND & JAANUSSON (1960).

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

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

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

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

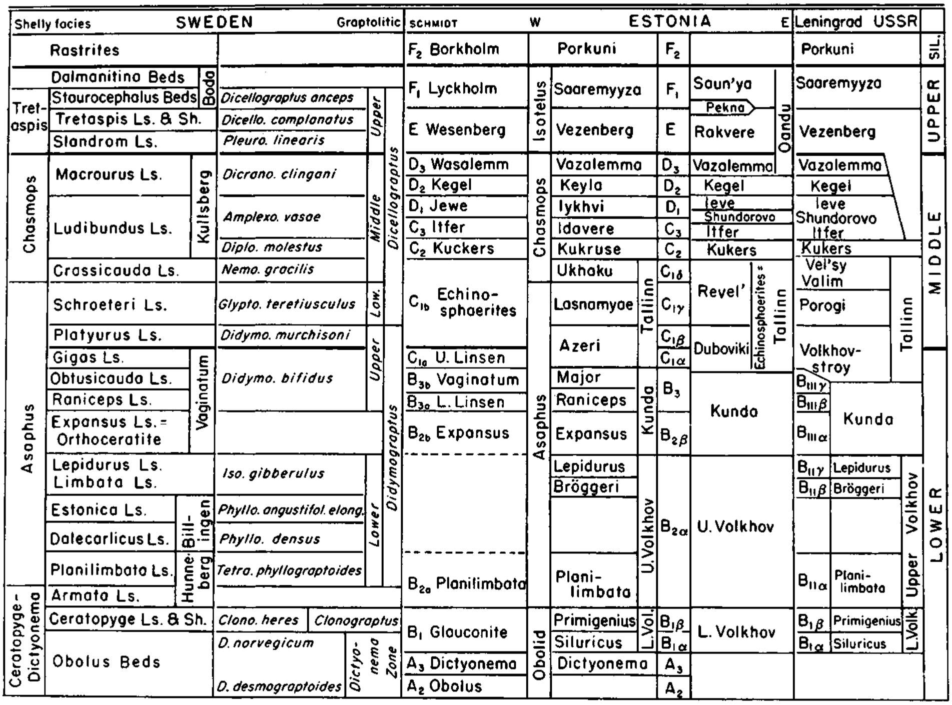


FIG. 53 *(Continued)*.

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

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

Lower Ordovician Cystoids

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

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

RHOMBIFERA

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

TABLE 1. *Number of Families of Cystoidea Known in Each Epoch.*
[Doubtful records not included.]

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

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

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

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

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

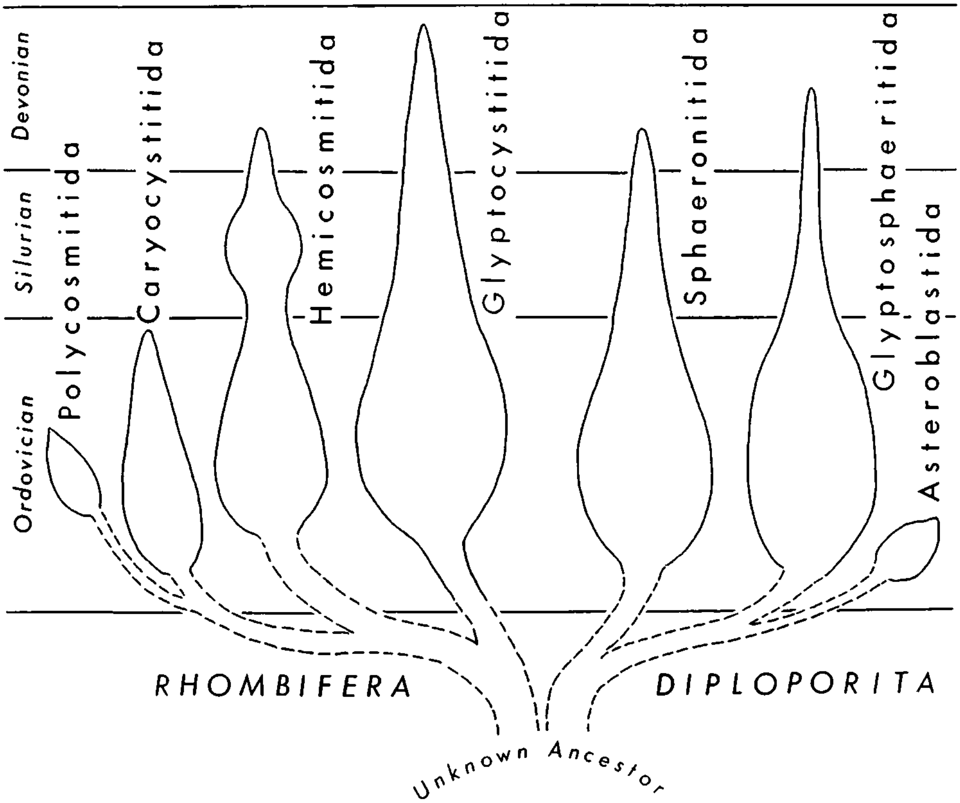


FIG. 54. Diagram representing stratigraphic distribution and inferred relationships of orders and superfamilies of Cystoidea (Kesling, n).

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

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

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

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

CARYOCYSTITIDA

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

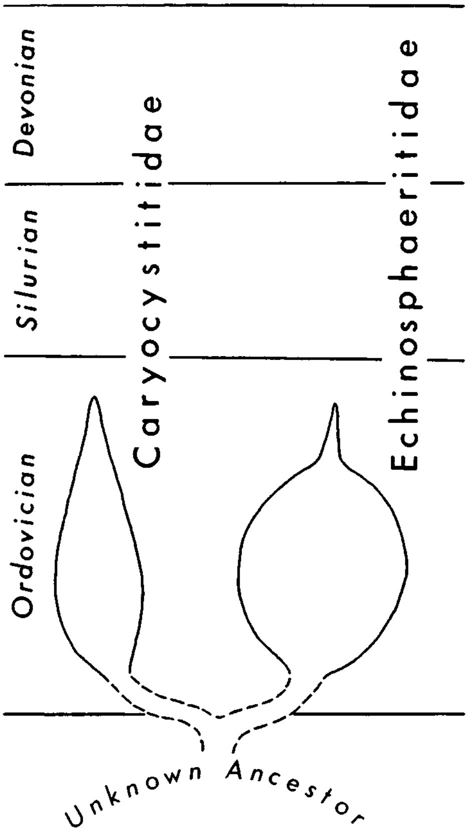


Fig. 55. Diagram representing stratigraphic distribution and inferred relationships of families of the Caryocystitida (Kesling, n).

HEMICOSMITIDA

The Hemicosmitida appear to be intermediate between the Glyptocystitida and

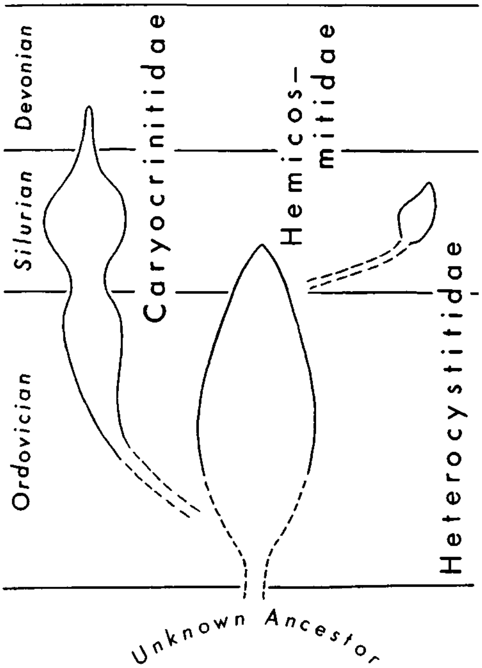


FIG. 56. Diagram representing stratigraphic distribution and inferred relationships of families of the Hemicosmitida (Kesling, n).

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-

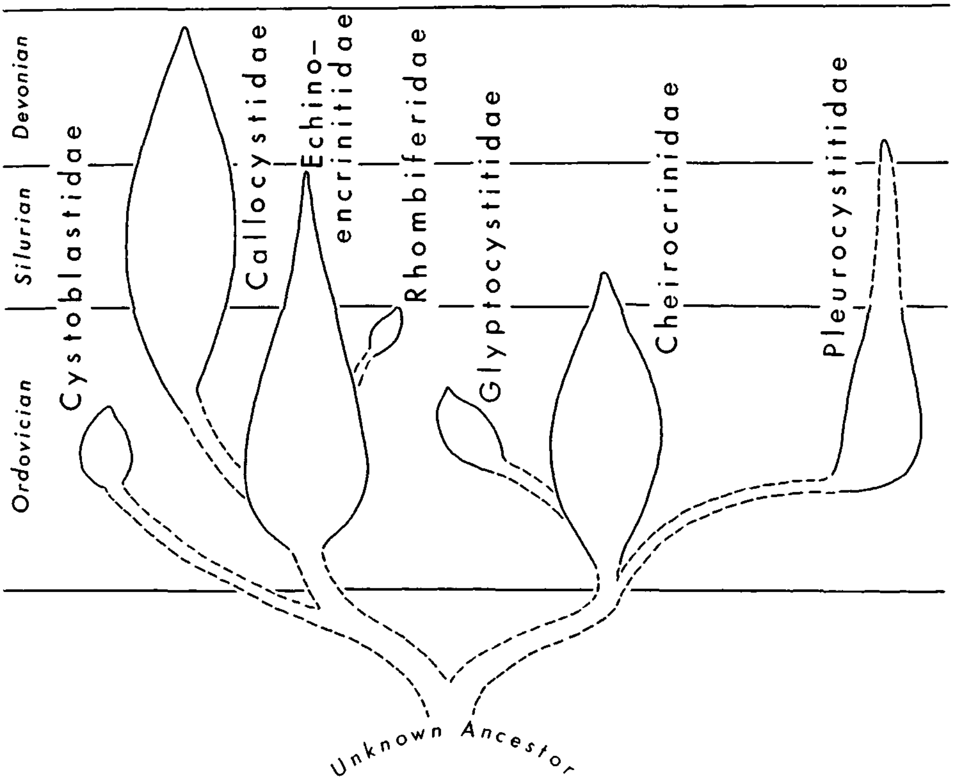


FIG. 57. Diagram representing stratigraphic distribution and inferred relationships of families of the Glyptocystitida (Kesling, n).

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-

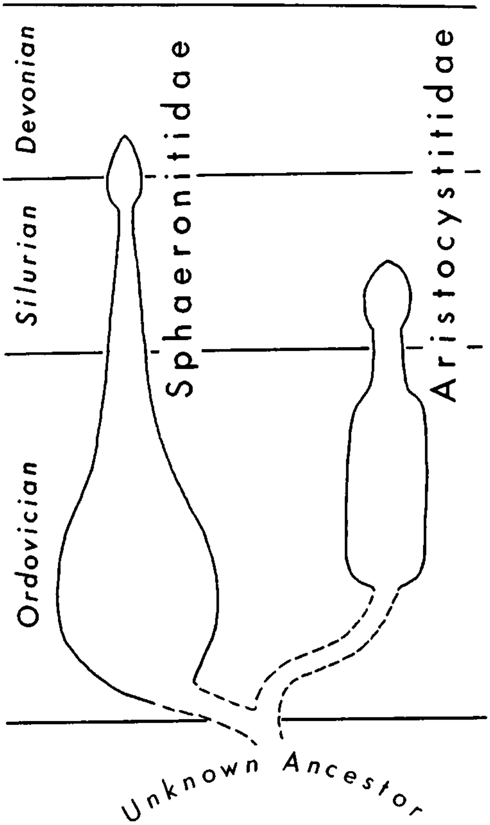


FIG. 58. Diagram representing stratigraphic distribution and inferred relationships of families of the Sphaeronitida (Kesling, n).

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-*

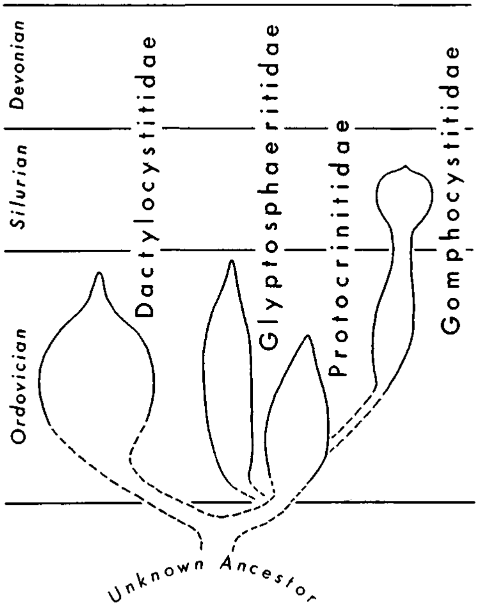


FIG. 59. Diagram representing stratigraphic distribution and inferred relationships of families of the Glyptosphaeritida (Kesling, n).

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-

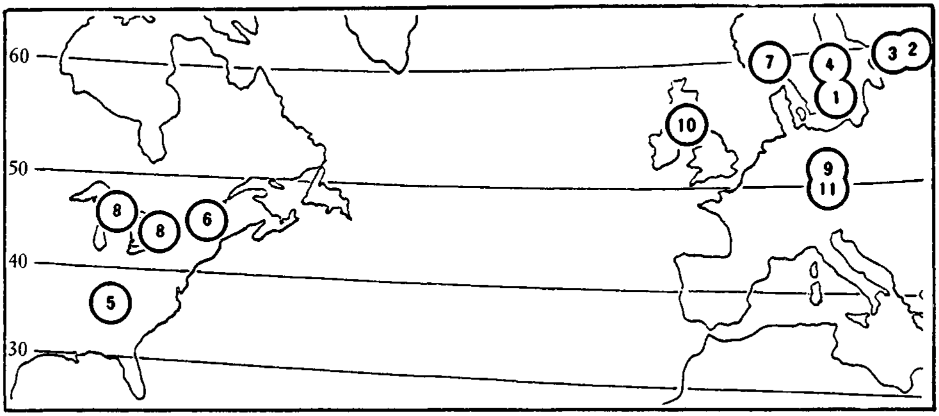


FIG. 60. Sequence and geographic distribution of cystoids of the family Cheirocrinidae.——*1. Cheirocrinus holmi,* L.Ord.*(Planilimbata),* Sweden(Öland).——*2. Leptocystis gigantea, Homocystites* spp., L.Ord. (B$_2$-B$_3$), USSR(Leningrad region).——*3. Cheirocrinus radiatus, C. ornatus,* etc., L.Ord.-U.Ord., 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

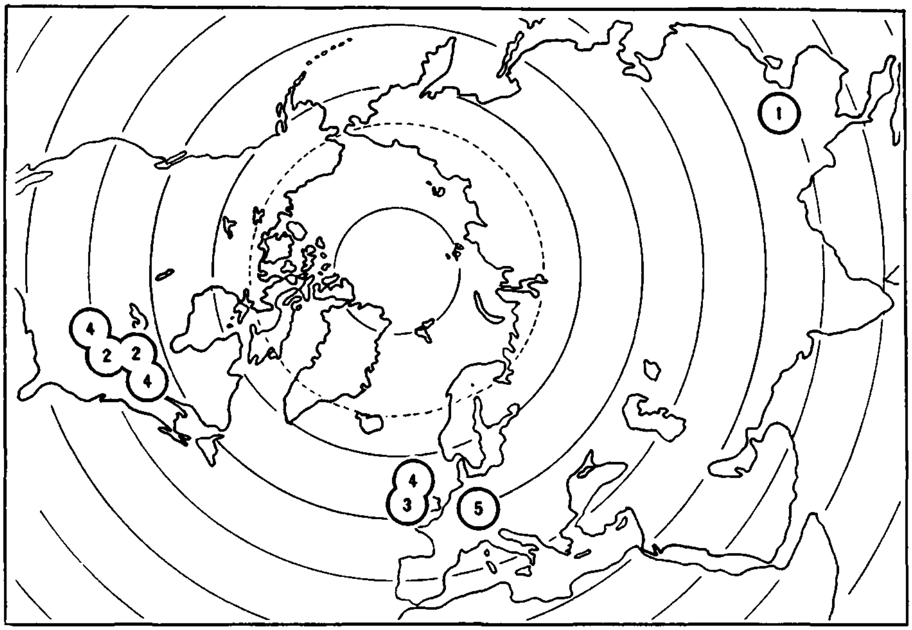


FIG. 61. Sequence and geographic distribution of cystoids of the family Pleurocystitidae.——*1. Pleurocystites bassleri,* M.Ord., China.——*2. P. elegans, P. filitextus, P. squamosus,* etc., *Amecystis,* M.Ord. (Trenton.), Can.(Que.-Ont.)-USA(Wis.-Minn.-Mich.-Ky.-N.Y.).——*3. P. anglicus, P. rugeri,* M.Ord. (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 ($3c\beta$), *Proctocystis monstruosa* Regnéll, from Sweden (*Expansus* Limestone), and *P. rossica* Regnéll, from Russia.

Glaphyrocystis occurs only in Estonia, *G. woehrmanni* Jaekel and *G. compressa* Jaekel, both being restricted to Upper Ordovician F_1. All Late Silurian echinoencrinitids are from England, in the Dudley Limestone: *Prunocystites baccatus* (Forbes), *P. fletcheri* Forbes, and *Schizocystis armata* Forbes.

The **Glyptocystitidae** are all North American, the five species of *Glyptocystites* occurring in Trenton rocks of Ontario, Quebec, and Michigan. The **Rhombiferidae** include only *Rhombifera bohemica* Barrande from Bohemia. No close relatives of the two families have been recognized.

The **Pleurocystitidae** (Fig. 61) may have begun with *Pleurocystites bassleri* Sun from the early Middle Ordovician of China; Regnéll (104) referred to it as "a somewhat doubtful species." Oklahoma has yielded *P. watkinsi* Strimple from the Middle Ordovician Bromide Formation. In late Middle Ordovician time in North America, *Pleurocystites* proliferated into numerous species recorded from Ontario, Quebec, Wisconsin, Minnesota, Michigan, Kentucky, and New York: *P. elegans* Billings, *P. exornatus* Billings, *P. filitextus* Billings, *P. squamosus* Billings, *P. robustus* Billings, *P. matutinus* (Ruedemann), and *P. mercerensis* Miller & Gurley. The genus continued to thrive on this continent in the Late Ordovician, with *P. anticostiensis* Billings, recorded on Anticosti Island and *P. beckeri* Foerste, *P. clermontensis* Foerste, *P. slocomi* Foerste, and *P. multistriatus* Ulrich & Kirk, from Iowa. The first emigrants to Europe were *P. anglicus* Jaekel, of Ireland, and *P. rugeri* Salter, of Wales, found in Caradoc strata. The species from the Craighead Limestone in Scotland were described by Bather (12), *P. foriolus, P. gibbus, P. procerus,* and *P. quadratus.* With these Late Ordovician species, *Pleurocystites* came to an end. The unique and perplexing *Amecystis laevis* (Raymond) occurs in Ontario and Michigan in the late Middle Ordovician Trenton rocks, with unknown ancestors or descendants. With no known Silurian forms, *Regulaecystis pleurocystoides* Dehm, from the Lower Devonian Hunsrück Slates, near Bundenbach, Germany, was unexpected, but insofar as known, closed the record of the family.

The **Cystoblastidae** include *Cystoblastus leuchtenbergi* Volborth from the Leningrad region (C_1), *C. kokeni* Jaekel, from Estonia (C_2), and *Hesperocystis deckeri* Sinclair, from Oklahoma (Bromide Formation, upper Chazy and lower Black River). Whether the American or Russian occurrences are earlier is open to question.

In the **Callocystitidae** (Fig. 62), the subfamily Apiocystitinae commence registry with *Lepadocystis moorei* (Meek), from Ohio and Indiana, in the Upper Ordovician Richmond beds. North America remained the stronghold of the subfamily until its extinction. The Early Silurian *Brockocystis* is known by *B. nodosaria* Foerste, from Ohio, and *B. huronensis* (Billings) and *B. tecumsethi* (Billings), from Ontario. *Hallicystis imago* (Hall) occurs in Wisconsin, Illinois, and Ohio in Middle Silurian Ni-

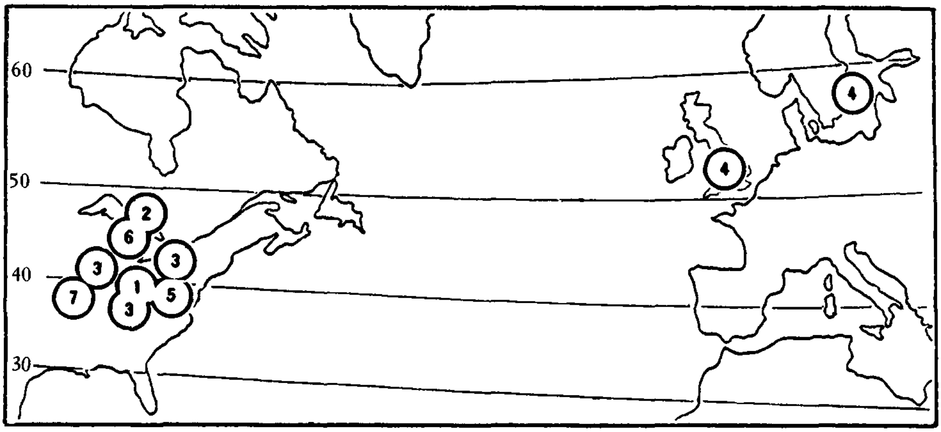


FIG. 62. Sequence and geographic distribution of cystoids of the family Callocystitidae.——*1. Lepadocystis,* U.Ord., USA(Ind.-Ohio).——*2. Brockocystis,* L.Sil., Can.(Ont.)-USA(Ohio).——*3. Apiocystites, Hallicystis, Tetracystis,* M.Sil.(Niagaran), Can.(Ont.)-USA(N.Y.-Wis.-Ill.-Tenn.).——*4. Apiocystites, Lovenicystis, Lepocrinites,* U.Sil., Eu.(Gotl.-Eng.).——*5. Jaekelocystis, Leptocrinites, Tetracystis,* L.Dev., USA (W.Va.-Md.).——*6. Lipsanocystis,* M.Dev., USA(Mich.).——*7. Strobilocystites,* M.Dev.-U.Dev., USA (Iowa) (Kesling, n).

agaran strata. Other Niagaran cystoids of the subfamily are *Apiocystites elegans* HALL, from New York and Ontario, and *Tetracystis fenestratus* (TROOST), from Tennessee. Early Devonian species include *Apiocystites anna* SAFFORD, from Tennessee, *Lepocrinites gebhardii* CONRAD, from New York, Maryland, and Virginia, and several species described by SCHUCHERT from West Virginia and Maryland: *Tetracystis chrysalis, Lepocrinites manlius, Jaekelocystis avellana, J. hartleyi,* and *J. papillata.* Michigan was the homeland of all described species of the Middle Devonian genus *Lipsanocystis.* In Iowa, *Strobilocystites calvini* WHITE, *S. polleyi* CALVIN, and *S. schucherti* THOMAS are reported from the upper Middle Devonian Cedar Valley Limestone, and the last-named species extends into the lower Upper Devonian Shell Rock Limestone. In Late Silurian time, the Apiocystitinae reached to Europe, with *Apiocystites pentrematoides* FORBES and *Lepocrinites oblongus* (FORBES), in England, and *Lovenicystis angelini* (JAEKEL), in Sweden. The invading stock did not become firmly entrenched, and no later European species have been found.

The subfamily Callocystitinae did not migrate beyond North America. *Callocystites canadensis* BILLINGS and *C. jewetti* (HALL) resided in New York and Ontario and *C. jewetti elongatus* FOERSTE in Ohio during the Middle Silurian. The contemporaneous *Coelocystis subglobosa* (HALL) was in Wisconsin, Illinois, and Ohio. Species of *Sphaerocystites* are limited to the Lower Devonian Keyser Formation, and are found in Pennsylvania, West Virginia, and Maryland.

The subfamily Staurocystinae reversed the route of the Apiocystitinae, developing first in Europe and emigrating to North America. In England, the Upper Silurian Dudley Limestone contains *Staurocystis quadrifasciata* (PEARCE), *Pseudocrinites bifasciatus* PEARCE, and *P. magnificus* FORBES. *Staurocystis* seems to have produced no more species; but *Pseudocrinites* reached its climax in North America during the Early Devonian, with seven species described by SCHUCHERT from the Keyser Formation in Pennsylvania, West Virginia, and Maryland.

The pattern of migrations is a little enigmatic. During Late Silurian time, England was receiving immigrants of the Apiocystitinae from North America at about the same time that it was dispatching emigrants of the Staurocystinae to North America. If currents were responsible for the spread of

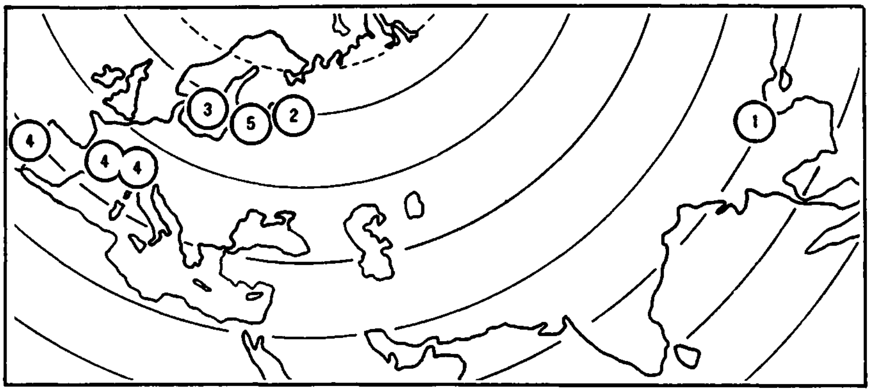


FIG. 63. Sequence and geographic distribution of cystoids of the family Hemicosmitidae.——*1. Hemicosmites jaekeli,* M.Ord., China.——*2. H. malum, H. oblongus,* M.Ord. ($C_1\beta$), Eu.(Baltic).——*3. H. oelandicus,* M.Ord.(L.*Chasmops*), Sweden.——*4. Corylocrinus elongatus, C. occidentalis, C. carnicus,* U.Ord., Eu.(Fr.-Port.-Carnic Alps).——*5. H. grandis, Tricosmites tricornis,* L.Sil.(F_2), Eu.(Est.) (Kesling, n).

cystoids, there was ample time in this epoch, of course, for reversals of direction.

HEMICOSMITIDA

The superfamily Hemicosmitida was dispersed throughout the northern hemisphere. In the **Hemicosmitidae** (Fig. 63), the genus *Hemicosmites* probably began in the Orient. The oldest described species may be *H. jaekeli* SUN, from China; nevertheless, it was nearly contemporaneous with some Baltic species, *H. malum* (PANDER) ($C_1\beta$) and *H. laevior* JAEKEL and *H. oblongus* (PANDER) (reported only as C_1). The last-named species has also been recorded from Wales. The exact age of *H. squamosus* FORBES, from Wales, has not been stated. *H. oelandicus* REGNÉLL occurs in Sweden in Lower *Chasmops* strata. Numerous species come from Estonia, including *H. altus* JAEKEL, *H. pulcherrimus* JAEKEL, and *H. pocillus* JAEKEL (D_1), *H. porosus* EICHWALD and *H. rudis* JAEKEL (D_3), *H. verrucosus* EICHWALD (F_1), and *H. grandis* JAEKEL (Lower Silurian, F_2), the youngest species found. *H. extraneus* EICHWALD has been discovered in Estonia and Russia (D_1 or D_3) and in Sweden (Kullsberg Limestone). The other two genera included in the Hemicosmitidae are restricted to Europe. *Corylocrinus* is represented in Upper Ordovician deposits of Russia, *C. olli* YAKOVLEV; France, *C. elongatus* JAEKEL and *C. europaeus* (QUENSTEDT); Portugal, *C. occidentalis* JAEKEL; and the Carnic Alps, *C. carnicus* BATHER. *Tricosmites* contains only the type species, *T. tricornis* (JAEKEL), from Estonia, where it occurs in the F_2 Borkholm Limestone with *Hemicosmites grandis* JAEKEL.

The second family of Hemicosmitida, the **Caryocrinitidae**, also seems to have originated in the Far East (Fig. 64). From the lower Middle Ordovician Naungkangyi Beds of northern Burma BATHER (11) described *Caryocrinites aurorus, C. avellanus,* and *C. turbo.* The Late Ordovician *C. septentrionalis* REGNÉLL is from Sweden. Other named species are all from Middle Silurian strata and, with one exception, from North America. Niagaran rocks of east-central United States and adjacent areas of Canada have yielded *C. milliganae* (MILLER & GURLEY), *C. gorbyi* (MILLER & GURLEY), and *C. indianensis* (MILLER), from Indiana; *C. persculptus* SPRINGER and *C. globosus* TROOST, from Tennessee; *C. missouriensis* (ROWLEY), from Missouri; and *C. ornatus* SAY, from Ontario, New York, Indiana, Iowa, and Wisconsin. The only other species known is from France, *C. ornatus europaeus* (QUENSTEDT). *Stribalocystites,* closely related to *Caryocrinites,* is exclusively North American. Middle Silurian species include *S. sphaeroidalis* (MILLER & GURLEY) and *S. tumidus* (MILLER), from Indiana, *S. bulbulus* (MILLER & GURLEY), from Tennessee, and *S. kentuckiensis* (MIL-

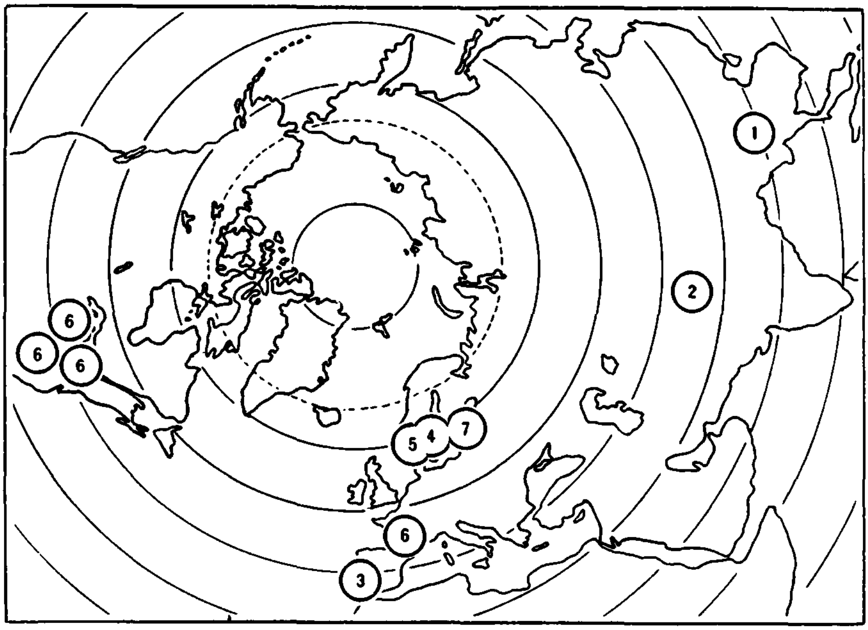


FIG. 64. Sequence and geographic distribution of cystoids of the genus *Caryocrinites.*——*1. C. aurorus, C. avellanus,* M.Ord.(Naugkangyi beds), Burma.——*2. C.* sp., M.Ord., Asia(Karakorum).——*3. C.* sp., M.Ord.(Llandeilo or Caradoc), Eu.(Port.).——*4. C. septentrionalis,* U.Ord., Sweden(Dalarna).——*5. C.* sp., L.Sil. (5b), Norway(Oslo).——*6. C. ornatus, C. milliganae, C. persculptus, C. ornatus europaeus,* M.Sil., Can.(Ont.)-USA(N.Y.-Ind.-Iowa-Wis.)-Eu.(Fr.).——*7. "C. ornatus"* of SCHMIDT (1858), U.Sil. (Wenlock, L.Oesel or Jaani beds), Eu.(Est.) (Kesling, n).

LER & GURLEY), from Kentucky. The last of the family is the Early Devonian *S. elongatus* (ROWLEY), from Missouri.

During the Late Ordovician, the Caryocrinitidae produced three short-lived genera, restricted stratigraphically to the epoch and geographically to western Europe. *Juglandocrinus crassus* KOENEN, *Oocystis major* DREYFUSS, and *O. vulgaris* DREYFUSS come from France; *Oocystis rugata* (FORBES), from Wales and England; and *Ptychocosmites sardinicus* JAEKEL, from Sardinia.

The family **Heterocystitidae** rests only on *Heterocystites armatus* HALL, from Niagaran rocks of New York.

POLYCOSMITIDA

In the superfamily Polycosmitida, only two species are involved, each the type of a genus that is type of a family. Both are Middle Ordovician, *Polycosmites bohemicus* JAEKEL, from Bohemia, and *Stichocystis geometrica* (ANGELIN), from Scandinavia and from drift in Germany. SUN (123) reported *Stichocystis* from China, as *S. geometrica* or a very similar species. The Chinese specimens are earliest Middle Ordovician, whereas the European are latest Middle Ordovician, supporting REGNÉLL'S (1948) contention that the genus migrated westward.

CARYOCYSTITIDA

The superfamily Caryocystitida achieved widespread distribution. The **Caryocystitidae** inhabited Asia and Europe. As recorded (Fig. 65), *Heliocrinites* began as *H. echinoides* (LEUCHTENBERG) in Russia (B_2). This species was followed by *H. radiatus* (EICHWALD) in Estonia and the Leningrad region (B_3). *H. granatum* (WAHLENBERG) from Sweden is said to be in the *"Orthoceras"* Limestone, presumably used in the broad sense for Lower and Middle Ordovician limestones. Early Middle Ordovician occurrences in the Orient are *H. fiscellus* (BATHER), *H. qualus* (BATHER), and *H. rugatus* (BATHER), in Burma, *H. subovalis*

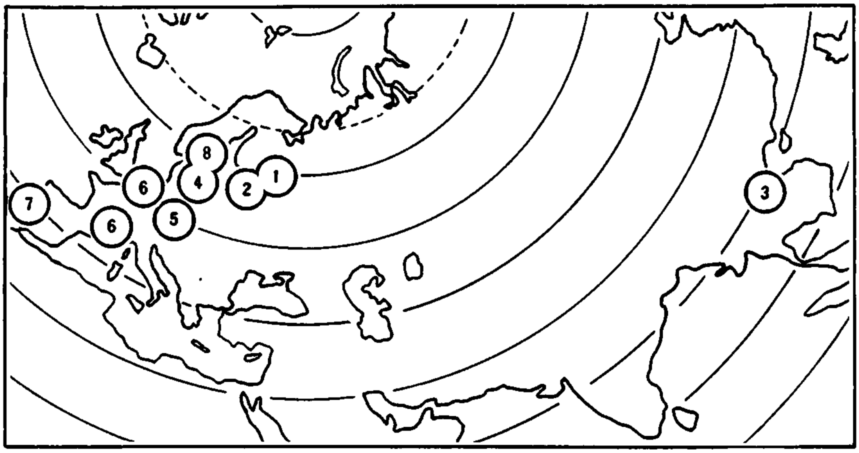


FIG. 65. Sequence and geographic distribution of cystoids of the genus *Heliocrinites*.——*1. H. echinoides*, L.Ord.(B_2), USSR(Leningrad region).——*2. H. radiatus*, L.Ord. (B_3), Eu.(Est.-Leningrad region).——*3.* H. *fiscellus, H. qualus, H. kweichouensis*, M.Ord., Burma-China(Yunnan-Kweichou).——*4. H. granatum, H. augustiporus, H. ovalis*, M.Ord.(L.*Chasmops*,) Sweden(Scania-Östergötl.-Jamtl.).——*5. H. confortatus*, M.Ord.-U.Ord.(Dd_4-Dd_5), Eu.(Czech.).——*6. H. rouvillei, H. malaisei*, U.Ord., Eu.(Fr.-Belg.).——*7. H. burdigalensis*, U.Ord., Eu.(Port.-Spain).——*8. H. stellatus, H. variabilis*, U.Ord., Sweden (Dalarna) (Kesling, n).

(Reed), in Yunnan, China, and *H. kweichouensis* (Sun), at Kweichou, China. At about the same time, the genus appeared in Estonia as *H. araneus* (von Schlotheim) in Estonia and Sweden (C_1) and *H. balticus* (Eichwald) in Estonia and Wales (C_2). The age of *H. ovum* (von Schlotheim) from near Reval, Estonia, is not given, but may be presumed to be about C_1. In Sweden, several species occur in the *Chasmops* series, *H. granatum* (Wahlenberg), *H. guttaeformis* Regnéll, *H. ovalis* (Angelin), *H. prominens* (Angelin), and *H. tenuistriatus* (Angelin). During the Late Ordovician, *Heliocrinites* continued in Sweden as *H. stellatus* Regnéll and *H. variabilis* Regnéll, and spread southward to Thuringia and Bohemia as *H. confortatus* (Barrande), to Belgium as *H. malaisei* Regnéll, to France as *H. rouvillei* (Koenen), and to Portugal as *H. burdigalensis* (Jaekel).

Caryocystites also has its earliest history centered in the Baltic and in China, but which area yielded the older fossils cannot be decided until greater stratigraphic accuracy is attained in correlation. *C. bicompressus* (Reed) comes from the Shih-tien Beds of China, *C. esthoniae* (Jaekel) from the C_2 of Estonia, and *C. laevis* Gekker from C strata of the Leningrad region. Elsewhere, *C. davisi* M'Coy occurs in Llandeilo rocks of Wales and England, *C. angelini* (Haeckel) in *Chasmops* beds of Sweden, and *C. lagenalis* Regnéll from the Swedish Kullsberg Limestone, which Regnéll (1945) regards as "Middle and (basal) Upper Ordovician." Bassler (1919) mentioned cystoid plates which he assigned to *Caryocystites* as abundant in his "*Caryocystites* bed" at the base of the Chambersburg Limestone in Pennsylvania and Maryland; no specifically determinable specimens have been described.

Other caryocystitid genera are from Middle and Upper Ordovician strata. *Orocystites helmhackeri* Barrande is found in Bohemia and Portugal (M.Ord.), *O. helmhackeri thuringae* (Jaekel) in Thuringia (M.Ord.), and *O.* sp. cf. *O. helmhackeri* in Belgium (U.Ord.). The inadequately described *Ulrichocystis eximia* Bassler is from Tennessee.

The **Echinosphaeritidae** are of particular interest because one species has been recognized in Europe and in North America. *Echinosphaerites ellipticus* Eichwald from Estonia (B_3) is the oldest known species of the family (Fig. 66). The famous *E. aurantium* (Gyllenhaal), including the

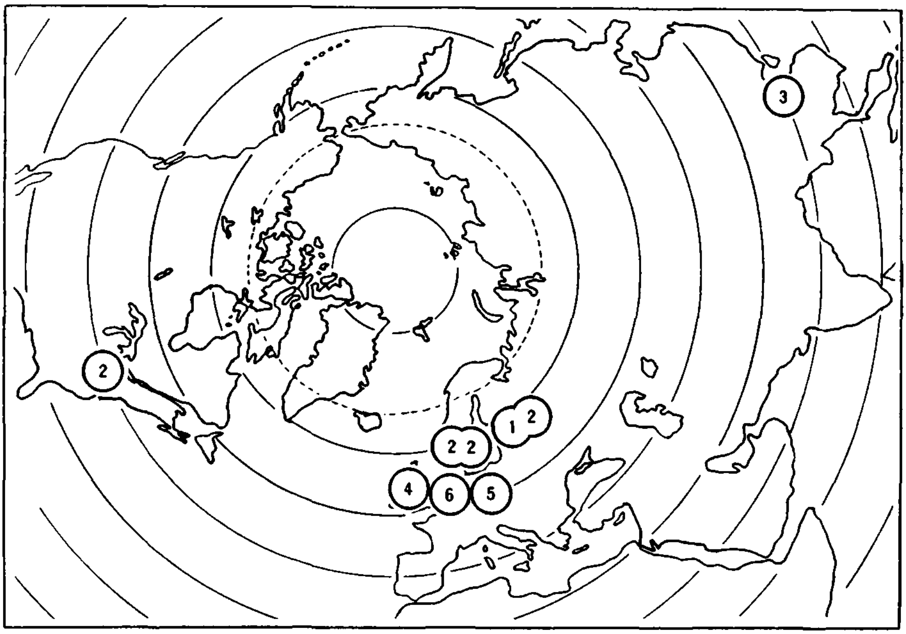


FIG. 66. Sequence and geographic distribution of cystoids of the genus *Echinosphaerites*.——*1. E.* sp., *E. ellipticus,* L.Ord.(B_2-B_3), Eu.(Est.).——*2. E. aurantium,* M.Ord., USA-Eu.(Sweden-Norway-Leningrad region).——*3. E. sinensis,* M.Ord., China.——*4. E. granulatus,* M.Ord.(Caradoc), Eire.——*5. E. barrandei,* M.Ord.(Dd_4), Eu.(Czech.).——*6. E. barrandei belgicus,* U.Ord.(Fauquez Sh.), Eu.(Belg.) (Kesling, n).

several subspecies and mutations erected, is present in Middle Ordovician deposits of the Leningrad region, Estonia, Sweden, Norway, Wales, and eastern United States (Pennsylvania, Virginia, and Tennessee). In the Baltic, this species ranges from C_{1b} to C_3. It bears a close resemblance to *E. sinensis* (REED) from China. *E. pogrebowi* GEKKER occurs in the Leningrad region (C_2). *E. grandis* JAEKEL, in Estonia and the Leningrad area, is perhaps from the C_2; in Sweden, it comes from the Kullsberg Limestone. From the C_3 of Estonia, two species were described by JAEKEL, *E. difformis* and *E. pirum*. In Ireland and Scotland, *E. granulatus* M'COY is found in the Caradoc Series. *E. barrandei* JAEKEL has been described from the Dd_4 of Bohemia and recognized in Norway, and *E. barrandei belgicus* JAEKEL, from the Upper Ordovician Fauquez Shales of Belgium. The age remains in doubt for *E. gyllenhahli* QUENSTEDT of Sweden and Russia, *E. globosus* JAEKEL, of Estonia, *E. globosus anglicus* JAEKEL, of Ireland, and *E. kloedeni* JAEKEL, from the drift of Estonia and northern Germany. *Arachnocystites infaustus* (BARRANDE) is from Bohemia (Dd_1-Dd_4).

DIPLOPORITA

Cystoids of the order Diploporita have been collected in southeastern Asia, Europe, northern Africa, and North America. The lack of finds in the southern hemisphere may be explained by absence of concerted collecting.

GLYPTOSPHAERITIDA

The superfamily Glyptosphaeritida may not have given rise to many species, but it spread over a considerable area. The family **Glyptosphaeritidae** contains only the type genus. One wishes to know whether *C. ferrigenus* (BARRANDE) from Bohemia (Dd_1) or *G. leuchtenbergi* (VOLBORTH) from the Baltic region (B_3 to C_{1b}) is older, but no conclusion is obtainable (Fig. 67). *G. suecicus* (ANGELIN) in Sweden is latest Middle Ordovician, and *G. mariae* JAEKEL in the drift of northern Germany is of unknown age.

The **Gomphocystitidae** began with *Pyrocystites orientalis* (Reed) in China. The genus has also been determined in Bohemia by Barrande, with *P. patulus* and *P. incertus* (D_1) and *P. pirum* (D_1 and D_4). No lineage leading to *Gomphocystites* has been discovered. *Gomphocystites* is a Middle Silurian genus, primarily North American. From Niagaran strata, *G. bownockeri* Foerste has been described from Ohio, *G. clavus* Hall from Wisconsin, *G. glans* Hall from Wisconsin and Illinois, *G. indianensis* Miller from Indiana, and *G. tenax* Hall from New York and Kentucky. This cystoid fauna has not been found in Michigan and Ontario. *"G.? californicus"* Stauffer, from the Kennett Formation in California, was thought to be Middle Devonian, but recent evaluations of stratigraphy place it in Middle Silurian. The only species outside North America is *G. gotlandicus* (Angelin) from the Högklint Limestone of Gotland. It is Middle Silurian, but its age relationship to the Niagaran species cannot be established.

The **Protocrinitidae** are widely dispersed (Fig. 68). *Protocrinites* begins its record with *P. fragum* (Eichwald) in the Baltic area (Vaginatum through Wasalemm). *P. sparsiporus* (Bather) occurs in Burma (Naungkangyi Beds). In Estonia, *P. oviformis* (Eichwald) is known from D_3 beds. Middle Ordovician protocrinitids from North America include *Eumorphocystis multiporata* Branson & Peck from Oklahoma and *Regnellicystis typicalis* Bassler from Virginia. The known species of *Fungocystites, F. rarissimus* and *F. solitarius,* were described from Bohemia by Barrande.

The family **Dactylocystidae** is based on very unusual but very rare cystoids from Estonia: *Dactylocystis schmidti* Jaekel (D_1), *Estonocystis antropoffi* Jaekel (D_1), and *Revalocystis mickwitzi* Jaekel (E).

SPHAERONITIDA

Cystoids of the superfamily Sphaeronitida are found in many places in the northern hemisphere, but they are especially characteristic of central and southern Europe. In fact, Termier & Termier (127) called this area the "province à Amphorides" because of the predominance of the Aristocystitidae.

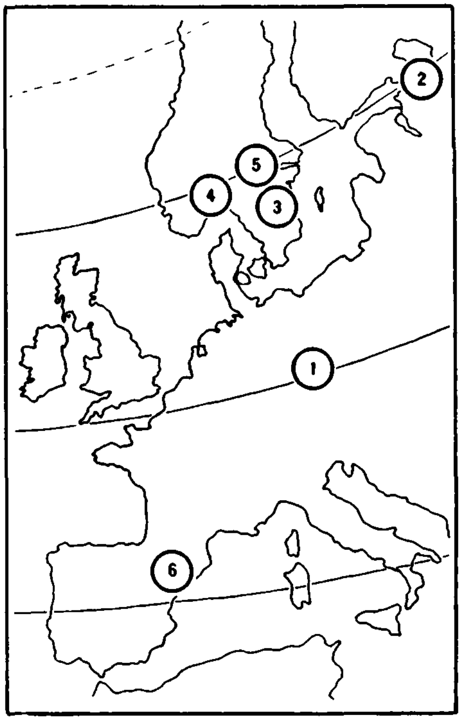


Fig. 67. Sequence and geographic distribution of cystoids of the genus *Glyptosphaerites.*——*1. G. ferrigenus,* Ord. (Dd_1), Eu. (Czech.).——*2. G. leuchtenbergi,* L.Ord. (B_3-C_1), Eu. (Baltic).——*3. G. leuchtenbergi,* M.Ord. (*Platyurus* Ls.), Eu. (Sweden).——*4. G.* sp., M.Ord.(*Chasmops* Ls.), Norway(Oslo region).——*5. G. suecicus,* M.Ord. (*Macrourus* Ls.), Sweden(Dalarna).——*6. G. leuchtenbergi hispanicus,* U.Ord., Eu.(Spain) (Kesling, n).

The family **Sphaeronitidae** contains some genera that became diverse and left an ample record and some that are understood only from a few specimens. Generic boundaries are not sharply drawn, adding to the difficulty of searching out the geographic extent of a particular genus.

Insofar as known, the ancestor of the family is the earliest Ordovician *Paleosphaeronites* from Bohemia. It is closely related to the slightly younger *Sphaeronites.*

For much of its content, *Sphaeronites* is taxonomically bound to the fate of the genera poorly established by Haeckel (58), *Pomosphaera, Pomonites,* and *Pomocystis.* These are here suppressed, and *Sphaeronites* is acknowledged as one of the senior syn-

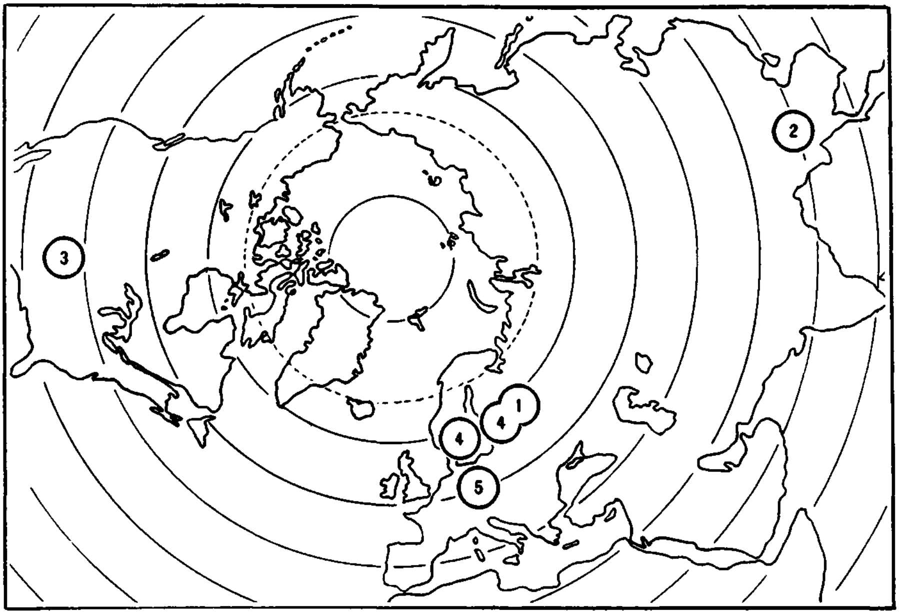


FIG. 68. Sequence and geographic distribution of cystoids of the family Protocrinitidae.——*1. Protocrinites fragum,* L.Ord.(*Vaginatum* beds or C_1), Eu.(USSR).——*2. P. sparsiporus,* M.Ord.(Naungkangyi beds), Burma.——*3. Eumorphocystis,* M.Ord.(Bromide), USA(Okla.).——*4. P. oviformis, P. fragum,* M.Ord.(D_3),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

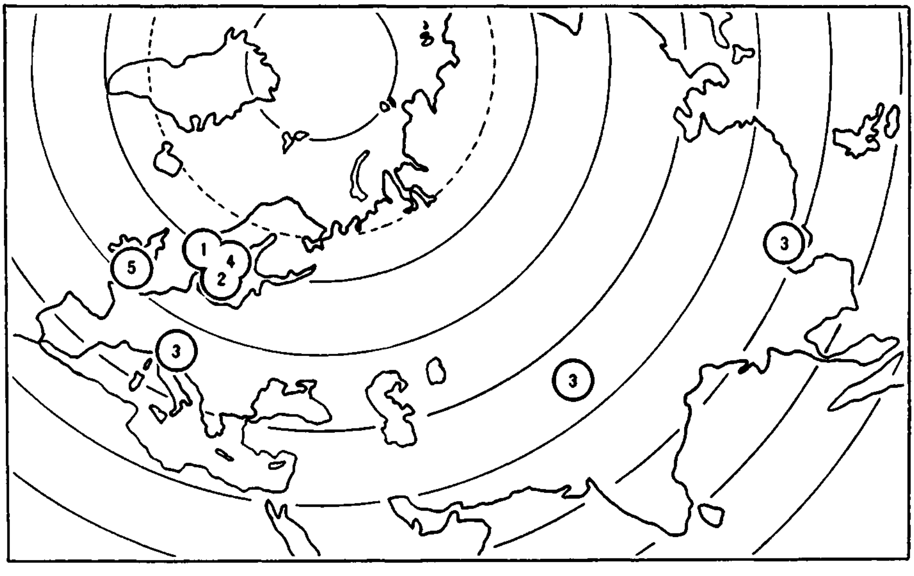


FIG. 69. Sequence and geographic distribution of cystoids of the genus *Sphaeronites.*——*1. S.* sp., L.Ord., Norway.——*2. S. pomum,* L.Ord., Sweden(Öland).——*3. S. shihtiensis,* M.Ord., Asia(China-Karakorum)-Eu.(Italy).——*4. S. globulus,* M.Ord.(L.*Chasmops* beds), Sweden (Västergötland-Östergötland-Dalarna).——*5.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

onyms involved. Its oldest occurrence (Fig. 69) is in the 3cβ of Norway (100). The prolific *S. pomum* (Gyllenhaal) is found in the *Asaphus* Limestone of Sweden in strata equivalent to the 3cβ. *S. shihtienensis* (Reed) is an eastward extension of the genus during early Middle Ordovician, being recorded in Yunnan, China, and the central Asian Karakorum region. In Sweden, the genus continued as *S. globulus* (Angelin) in the Lower *Chasmops.* The westernmost extent is in Wales, where *S. stelluliferus* Salter is found in Caradoc beds and *S. punctatus* Forbes and *S. pyriformis* (Forbes) are found in the Ashgillian Rhiwlas Limestone. The stratigraphic position of *S. dalecarlicus* (Angelin) in Sweden, *S. pentactaeus* (Haeckel) in Scandinavia, and *S. tesselatus* Phillips in England is not known. The closely related *Haplosphaeronis* makes its debut in the Shihtien Beds of southeastern China as *H. lobifera* (Reed). In Sweden, *H. oblonga* (Angelin) is known from lower *Chasmops* strata. Regnéll (101) gave the Swedish range of *Haplosphaeronis* as at least from Kullsberg to Boda (Fig. 53). From Norway comes the Middle Ordovician *H. kiaeri* Jaekel and *H. kiaeri norvegica* Jaekel and from Belgium the Late Ordovician *H. proiciens* Regnéll.

Eucystis lacks clear separation from certain Early Devonian cystoids, which could be interpreted as species either of the genus in a broad sense or of strongly similar genera derived from *Eucystis.* The latter disposition is followed in the *Treatise.* The oldest species known was described from Yunnan, China, as *E.* sp. cf. *E. raripuncta* Reed (98), from the early Middle Ordovician Shihtien Beds (Fig. 70). The species probably is not *E. raripuncta* Angelin, which occurs in the Boda Limestone of Sweden. *E. litchi* (Forbes) from Wales (Caradoc) was said by Regnéll (100) to be atypical of *Eucystis.* In addition to *E. raripuncta,* the Boda Limestone of Sweden has yielded *E. angelini* Regnéll, *E. acuminata* Regnéll, and *E. quadrangularis* Regnéll. The Lower Devonian of Germany, France, Bohemia, and Morocco contains cystoids of the late *Eucystis* complex. *E. hercynica* Jaekel from Germany is retained provisionally in *Eucystis.* *Carpocystites soyei* Oehlert from France and *Proteocystites flavus* Barrande, *P. barrandenus* (Haeckel), and *Bulbocystis mira* Ružička from Bohemia are tentatively placed in their respective genera.

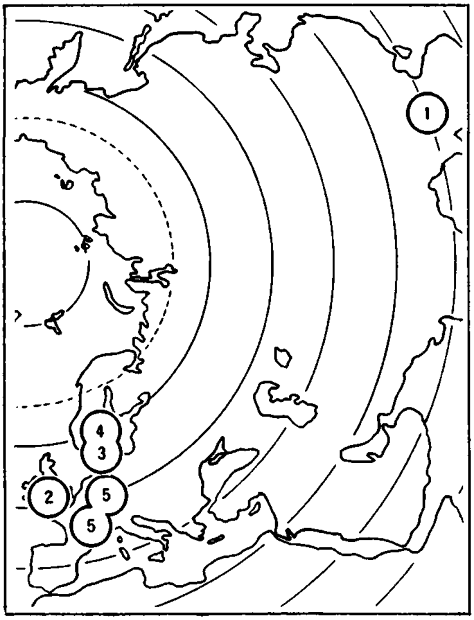


Fig. 70. Sequence and geographic distribution of cystoids of *Eucystis* and related genera.——*1.* "*Eucystis* cf. *raripuncta*" of Reed (1917), M.Ord., China.——*2. E. litchi,* Caradoc, Eu.(Wales).——*3. E. quadrangularis, E.* sp., U.Ord.(L.Boda beds). Sweden(Scania).——*4. E. raripuncta, E. angelini, E. acuminata,* U.Ord.(U.Boda beds), Sweden (Dalarna).——*5. E. hercynica, Carpocystites soyei, Proteocystites flavus, P. barrandenus, Bulbocystis mira,* L.Dev., Eu.(Ger.-Czech.-Fr.) (Kesling, n).

Tholocystis kolihai Chauvel from France does not have clear affinities with any other described cystoid of the Sphaeronitidae.

Bohemia produced all the known species of *Archegocystis* and *Codiacystis. A. desideratus* Barrande has the distinction of being the oldest (Dd_1) Bohemian sphaeronitid. In the Chrustenitz region, Barrande (3) described an amazing number of species of *Codiacystis* from Dd_4 beds, under the original assignment to *Aristocystites (C. potens, C. sculptus)* and to *Craterina (C. absens, applanata, bohemica, consobrina, docens, embryo, excavata, excavata intermedia, idealis, infundibulum, modica, oneta, simulans, surgens,* and *tecta).* These species have never been subjected to revision; they appear to be excessive.

Allocystites hammelli S. A. MILLER from Indiana is notable for being the only Silurian cystoid of the Sphaeronitidae. It is not particularly well described or well represented.

In the **Aristocystitidae,** the generic boundaries are even more diffuse than in the Sphaeronitidae. The antiquity of the family seems to lie in the Early Ordovician species from China, *Sinocystis loczyi* REED, *S. yunnanensis* REED, *S. mansuyi* (REED), and *Aristocystites sinicus* (SUN); and from Burma, *Pseudaristocystis dagon* (BATHER). *Sinocystis* reached Morocco in Llandeilo time as *S. segaudi* TERMIER & TERMIER. Two species of *Aristocystites* have also been described from Morocco, *A. gigas* TERMIER & TERMIER, from Llandeilo strata, and *A. regularis* TERMIER & TERMIER, from Caradoc strata. Other species were found in Bohemia (Dd_4) by BARRANDE, *A. bohemicus, A. desideratus,* and *A. rudis.*

Calix is another genus associated with the so-called *Aristocystites* fauna. In France, it is represented by the Middle Ordovician *C. sedgwicki* ROUAULT and *C. rouaulti* CHAUVEL and by the Late Ordovician *C. lebesconti* CHAUVEL. *Pachycalix halli* (ROUAULT) occurs in the Middle Ordovician of Brittany, and *P. pachytheca* TERMIER & TERMIER in the Caradocian of Morocco. The somewhat doubtful *Lepidocalix pulchrum* TERMIER & TERMIER has been found in Algeria (M.Ord.). The unique *Campylostoma grandis* DREYFUSS was obtained from Upper Ordovician beds in France. The Dd_4 in Bohemia contains, in addition to the species of *Aristocystites, Amphoracystis irregularis* (BARRANDE), *Hippocystis subcylindrica* (BARRANDE), and the questionable *Baculocystites simplex* BARRANDE.

The Middle Silurian fauna of east-central North America seems to be the culmination of a lineage that began with *Holocystites ovalis* (ANGELIN) in Sweden during the Late Ordovician. It contains *Holocystites* and *Trematocystis,* the former beset by a multiplicity of species names. For specimens from Indiana, S. A. MILLER alone created species for localities, *H. indianensis* and *madisonensis*; for shape and ornamentation of theca, *H. adipatus, amplus, baculus, canneus, commodus, elegans, globosus, ornatissimus, ornatus, papulosus, parvulus, parvus, perlongus, plenus, pustulosus, rotundus, scitulus, subovatus, subrotundus, tumidus, turbinatus,* and *ventricosus*; and for acquaintances, *benedicti, brauni, colletti, dyeri, faberi, gorbyi, spangleri, wetherbyi,* and *wykoffi.* One suspects that MILLER was overzealous in discrimination. Other species are known from Wisconsin, Illinois, Ohio, and Tennessee, including *Holocystites abnormis* HALL, *H. affinis* MILLER & FABER, *H. cylindricus* (HALL), *H. greenvillensis* FOERSTE, *H. gyrinus* MILLER & GURLEY, *H. scutellatus* HALL, *H. sphaericus* WINCHELL & MARCY, *H. sphaeroidalis* MILLER & GURLEY, *H. splendens* MILLER & GURLEY, and *H. winchelli* HALL. This extensive list is evidence of the abundance of these cystoids in Niagaran rocks of the United States. The closely allied *Trematocystis,* from the same strata and geographic locale, contains *T. subglobosa* (MILLER) and *T. hammelli* (MILLER); it may be found to have one or more additional species from MILLER's replete set.

ASTEROBLASTIDA

The superfamily Asteroblastida lived in Early Ordovician time in the Baltic provinces. *Mesocystis pusirefskii* (HOFFMAN) is the oldest. The other species are *Asteroblastus foveolatus* (EICHWALD), *A. regularis* JAEKEL, *A. sublaevis* JAEKEL, *A. volborthi* SCHMIDT, *Asterocystis globulus* JAEKEL, *A. tuberculatus* (SCHMIDT), *Metasterocystis micropelta* JAEKEL, and *Mesocystis jaekeli* YAKOVLEV. Fragmentary specimens from Morocco identified by TERMIER & TERMIER (126) as *Asteroblastus* were said to come from Llandeilo strata. The stratigraphic accuracy is not known.

MIGRATIONS

The whole undertaking of establishing migration routes is fraught with uncertainties. All taxonomic determinations are not accurate, and correlations are not reliable. Even some geographic occurrences have been cited incorrectly. As REGNÉLL (105) stated, "To be sure, it is no easy task to recognize the individual threads in this entangled web . . . the pictures of palaeobiogeographic features in remote times which we endeavour to envisage are poor in details, on account of scanty information."

To simplify the geographic factor, five areas can be designated which have had distinctive cystoid faunas—(1) Burma and adjacent parts of China, (2) Scandinavia and the eastern Baltic region, (3) central and southern Europe and the Mediterranean region, (4) the British Isles, and (5) eastern North America. These areas are particularly prominent during the Ordovician, the time of maximum diversity and distribution of the cystoids.

Regnéll (101), from a detailed study of the succession of cystoids, concluded that many of the significant faunal elements came from the Far East or that they originated in the Arctic and spread to both the Far East and to Europe. The picture of cystoid migration that emerges in the light of the Ordovician correlations adopted in this section of the *Treatise* in part substantiates, in part deviates from that which he depicted.

From inspection of the known ranges of the families (Fig. 71), it is apparent that the late Early Ordovician and early Middle Ordovician were times when specialized stocks evolved; they were also times when old lineages spread into new territories. Hence, this interval is one of extreme importance in unraveling the origins of the suprageneric taxa and their prime routes of dispersal.

Much of the available information on the sequence of recorded first appearances of various taxa in the five principal regions is summarized in Table 5. This is a compilation of the cystoid distribution in time and space insofar as known. In analyzing these data, one must not lose sight of the small percentage of sediments of a particular age that are exposed, the lack of persistent collecting from many outcrops, and the possibility that many key species lived in small populations.

Nevertheless, in the examples selected in Table 5, eight taxa made their appearance in the Baltic region, six in the China-Burma region, one in North America, and none in the British Isles or southern Europe. Thus, two centers emerge as significant. Many of the Early and Middle Ordovician migrations appear to have been interchanges between these two centers.

Several taxa originated in the Baltic during the late part of Early Ordovician and spread to Burma and China during the early part of Middle Ordovician: *Heliocrinites* (Fig. 65), *Echinosphaerites* (Fig. 66), *Protocrinites* (Fig. 68), and *Sphaeronites* (Fig. 69). On the other hand, some taxa developed in the Far East during the early part of Middle Ordovician and quickly migrated westward to the Baltic region: *Haplosphaeronis, Eucystis* (Fig. 70), *Stichocystis,* and possibly *Caryocrinites* (Fig. 64). A plausible explanation of this pattern was suggested by Regnéll (100), that the evolutionary center may not have been at either the Baltic or Far East occurrences of cystoids, but situated instead in the Arctic Sea, whence the faunal elements dispersed, some arriving first in the Baltic and others arriving first in the Far East.

The families Cheirocrinidae and Asteroblastidae are exceptions among the cystoids appearing first in the Baltic during Early Ordovician. Neither reached Burma or China. The Cheirocrinidae (Fig. 60) extended to North America and southern Europe during the Middle Ordovician, and the Asteroblastidae seem to have spread to the Mediterranean region at that time. Conversely, the Pleurocystitidae (Fig. 61) begin their record in China, if Sun's (124) identification is correct, and spread to North America (Middle Ordovician), to Britain (Late Ordovician), and to Germany (Early Devonian), but never reached the Baltic region.

Some of the occurrences are interrupted, and little can be inferred about intermediate locales. This applies to *Holocystites* from the Baltic (U.Ord.) to North America (M. Sil.). The Echinoencrinitidae have no representation during the Middle Ordovician or Early and Middle Silurian, the Sphaeronitidae and Caryocrinitidae during Early or Late Silurian, or the Pleurocystitidae during all of the Silurian.

The supposed Scottish-Hungarian barrier separating the Baltic region from the "province à Amphorides" may have been an influence in guiding cystoid migrations. For example, *Heliocrinites* (Fig. 65) and *Echinosphaerites* (Fig. 66), which have a considerable fossil record, seem to have gone from the Baltic to Britain before extending to Bohemia. The same route may have been followed later by *Caryocrinites* (Fig. 64), which has a record in the Baltic in

TABLE 5. *Sequence and Time of Recorded Appearances in Various Regions of Selected Families and Genera of Cystoids.*

[Where considerable doubt exists as to which of two occurrences is the older, both are assigned the same sequence number. Where the occurrence itself is dubious, the entry is followed by a question mark.]

	North America	British Isles	Baltic	Southern Europe	China-Burma
Cheirocrinidae					
Cheirocrinus		6 U.Ord.	1 L.Ord.		
Homocystites	4 M.Ord.		3 L.Ord.	5 M.Ord.	
Leptocystis		6 U.Ord.	2 L.Ord.	7 L.Sil.	
Echinoencrinitidae					
Echinoencrinites			1 L.Ord.		
Glaphyrocystis			2 U.Ord.		
Prunocystites		3 U.Sil.			
Pleurocystitidae					
Pleurocystites	2 M.Ord.	3 U.Ord.			1 M.Ord.?
Amecystis	2 M.Ord.				
Regulaecystis				4 L.Dev.*	
Callocystitidae					
Apiocystitinae					
Lepadocystis	1 U.Ord.				
Brockocystis	2 L.Sil.				
Hallicystis	3 M.Sil.				
Tetracystis	3 M.Sil.				
Apiocystites	3 M.Sil.	4 U.Sil.			
Lovenicystis			4 U.Sil.		
Lepocrinites	5 L.Dev.	4 U.Sil.			
Jaekelocystis	5 L.Dev.				
Lipsanocystis	6 M.Dev.				
Strobilocystites	7 M.Dev.				
Callocystitinae					
Callocystites	3 M.Sil.				
Coelocystis	3 M.Sil.				
Sphaerocystites	5 L.Dev.				
Staurocystinae					
Staurocystis		4 U.Sil.			
Pseudocrinites	5 L.Dev.	4 U.Sil.			
Hemicosmitidae					
Hemicosmites		2 M.Ord.	1 M.Ord.		1 M.Ord.
Corylocrinus			3 U.Ord.	3 U.Ord.	
Tricosmites			4 L.Sil.		
Caryocrinitidae					
Caryocrinites	4 M.Sil.	3 U.Ord.	2 M.Ord.?	4 M.Sil.	1 M.Ord.
Juglandocrinus				3 U.Ord.	
Oocystis		3 U.Ord.		3 U.Ord.	
Ptychosmites				3 U.Ord.	
Stribalocystites	4 M.Sil.				
Polycosmitidae					
Polycosmites				2 M.Ord.	
Stichocystis			3 M.Ord.		1 M.Ord.
Caryocystitidae					
Heliocrinites		3 M.Ord.	1 L.Ord.	4 U.Ord.	2 M.Ord.
Caryocystites	3 M.Ord.?	3 M.Ord.	3 M.Ord.		2 M.Ord.
Orocystites			3 M.Ord.	3 M.Ord.	
Echinosphaeritidae					
Echinosphaerites	3 M.Ord.	4 M.Ord.	1 L.Ord.	5 M.Ord.	2 M.Ord.
Arachnocystites				2 M.Ord.	
Gomphocystitidae					
Pyrocystites				2 M.Ord.	1 M.Ord.
Gomphocystites	3 M. Sil.		3 M.Sil.		
Protocrinitidae					
Protocrinites			1 L.Ord.		2 M.Ord.
Eumorphocystis	3 M.Ord.				
Fungocystites				4 M.Ord.	

TABLE 5 *(continued)*

	North America	British Isles	Baltic	Southern Europe	China-Burma
Sphaeronites		3 M.Ord.	1 L.Ord.		2 M.Ord.
Haplosphaeronis			2 M.Ord.		1 M.Ord.
Eucystis		3 M.Ord.?	2 M.Ord.	4 L.Dev.	1 M.Ord.
Holocystites	2 M.Sil.		1 U.Ord.		
Asteroblastus			1 L.Ord.	2 M.Ord.?	

*Germany

Middle Ordovician, Britain in Late Ordovician, and France in Middle Silurian.

Within the subfamily Apiocystitinae, *Apiocystites* occurs first in the Middle Silurian rocks of the United States and then in the Upper Silurian rocks of Britain, but *Lepocrinites* appears first in the Upper Silurian of Britain and extended to America in Early Devonian time. In this migration, *Lepocrinites* was joined by *Pseudocrinites*. Only during Late Silurian did callocystitids send out emigrants from North America. The easternmost extent of this minor wave was Sweden.

Despite these invasions and extensions, the regions produced distinctive faunas. The Middle Ordovician cystoids of North America are dominated by *Pleurocystites* and *Homocystites*. The fauna of this age in the Baltic consists primarily of *Heliocrinites, Echinosphaerites,* and *Caryocystites,* although other cystoids are present. The Early and Middle Ordovician faunas of Estonia contain many rare genera. The majority of Ordovician cystoids in central and southern Europe are Aristocystitidae. The Silurian cystoids of North America are mostly *Holocystites, Caryocrinites,* and Callocystitidae. Other examples could be cited.

In summary, the cystoids evolved as distinctive faunas, probably because each population was closely attuned to the ecological factors in a particular province. Only rarely did a species develop a range of tolerance sufficient to thrive over a broad intercontinental area.

CLASSIFICATION

INTRODUCTION

Taxonomy of cystoids has not followed a consistent trend. For the class as a whole, additions and deletions have been piecemeal and have lacked universal acceptance, despite the comprehensive works of JAEKEL (69, 71) and BATHER (10). Major contributions have been sporadic, and very few changes have been made in recent years.

From new discoveries of fossil cystoids, through the years, new genera were made known and accommodated into the suprageneric framework. From sharper discrimination, sometimes astute and sometimes picayune, additional genera have been created by splitting the old. For the most part, attempts to assess the genera, even within a superfamily, have been perfunctory. Many authors have been reluctant to eliminate genera; this criticism may apply to the *Treatise,* wherein several genera of dubious taxonomic value have been retained because time was insufficient to locate and evaluate types of the assigned species, particularly of cystoids described in the previous century.

The long-dominant concept of Cystoidea including any and all pelmatozoans not definitely classed as crinoids led to an amalgamation of echinoderms having such diverse morphology that they fell far short of constituting a definable class. The Cystoidea attained its present state by major excisions. Removal and diagnosis of the Edrioasteroidea were early accomplished by BILLINGS (20) and confirmed by the major contribution of JAEKEL (69) and BATHER (9, 10). This was followed by separation of the Carpoidea by JAEKEL (70), the Eocrinoidea by JAEKEL (71), the Paracrinoidea by REGNÉLL (99), and the Edrioblastoidea by FAY (45). Not all workers have accepted these efforts to reduce the Cystoidea.

The position of the Blastoidea is still debated. Rather firm positions for including and for excluding them from the Cystoidea have been taken in the past decade. In the *Treatise,* the Blastoidea are classed as a separate taxon.

To identify the echinoderms that have appeared in literature as cystoids but are here classified otherwise, a list is offered of "Echinoderms Formerly Included in Cystoidea."

Some of the problems of classification have been of a nomenclatural nature. An especially perplexing area of concern is the publication by Haeckel (58) of genera based on previous accounts, *nomina nuda,* and hypothetical genera. This creation of names for possible cystoids that could have developed on theoretical grounds, coupled with his general unreliability for according authorship of species, makes it difficult to do justice to his work. Nearly all of his genera are extremely weakly founded, but one must decide if they are recognizable at all and whether they were even based on specimens. Lists are presented herein of Junior Synonyms, Nomina Nuda, Preoccupied Names, and Unrecognizable Genera.

DEVELOPMENT OF CLASSIFICATION

The cystoids *Sphaeronites pomum* and *Echinosphaerites aurantium* are so abundant in the *Asaphus* and *Chasmops* Limestones of Sweden, respectively, that some exposures yield a wealth of these spherical fossils, which are closely packed in certain strata. Linné (79) mentioned them as *"Crystall-äplen"* and Wallerius (140) as *"Spat-klot,"* both authors expressing the current belief that such crystal-apples and lime-balls were of inorganic origin.

EARLY WORK

The brilliant, pioneer work of Johan Abraham Gyllenhaal, a Swedish miner, was published in the journal of the Royal Swedish Academy of Science (Kgl. Vetenskap Academiens Handlingar) in 1772 (56). (His name was misspelled as Gyllenhahl at the heading of the paper, and has been so cited many times.) In it he illustrated these two common species and named them *Echinus pomum* and *E. aurantium,* regarding them as sea urchins "of the genus *Echinus,* or its nearest relatives" (translated from the title by Regnéll (99), who presented annotations and commentary on the work). He correctly interpreted the peristome and periproct in *Sphaeronites pomum,* but identified the periproct as the peristome and the gonopore as the periproct in *Echinosphaerites aurantium.* The significant contribution was Gyllenhaal's recognition of these objects not only as organic but also as representing echinoderms.

Whereas several additions of genera were published in the succeeding 70 years, only two bear much taxonomic interest in that the idea of cystoid relationship to echinoids was changed. Thomas Say (112) described *Caryocrinites* from North America as a crinoid, and Hisinger (66) stated that cystoids were intermediate between "Encrinites" (crinoids) and "Echinites" (echinoids) because they were provided with a stem (column) and yet displayed similarities to sea urchins.

In 1846, Leopold von Buch (31) published a paper that he had read earlier, in which he recognized for the first time the independence of the cystoids from other echinoderms. He called them *"Cystideen."*

MÜLLER

The most important attempt at classification, however, was that of Johann Müller (90). He devised an outline of classification which was not completed with taxonomic names until years after his time.

Cystoid Taxa with Index Numbers for Sequence Given on Figure 71

Aristocystitidae—3
Asteroblastida—10
Asteroblastidae—12
Callocystitidae—24
Caryocrinitidae—30
Caryocystitida—14
Caryocystitidae—15
Cheirocrinidae—18
Cystoblastidae—21
Dactylocystidae—8
DIPLOPORITA—1
Echinoencrinitidae—19
Echinosphaeritidae—16
Glyptocystitida—17
Glyptocystitidae—20
Glyptosphaeritida—5
Glyptosphaeritidae—6
Gomphocystitidae—9
Hemicosmitida—28
Hemicosmitidae—29
Heterocystitidae—31
Mesocystidae—11
Pleurocystitidae—22
Polycosmitida—25
Polycosmitidae—26
Protocrinitidae—7
RHOMBIFERA—13
Rhombiferidae—23
Sphaeronitida—2
Sphaeronitidae—4
Stichocystidae—27

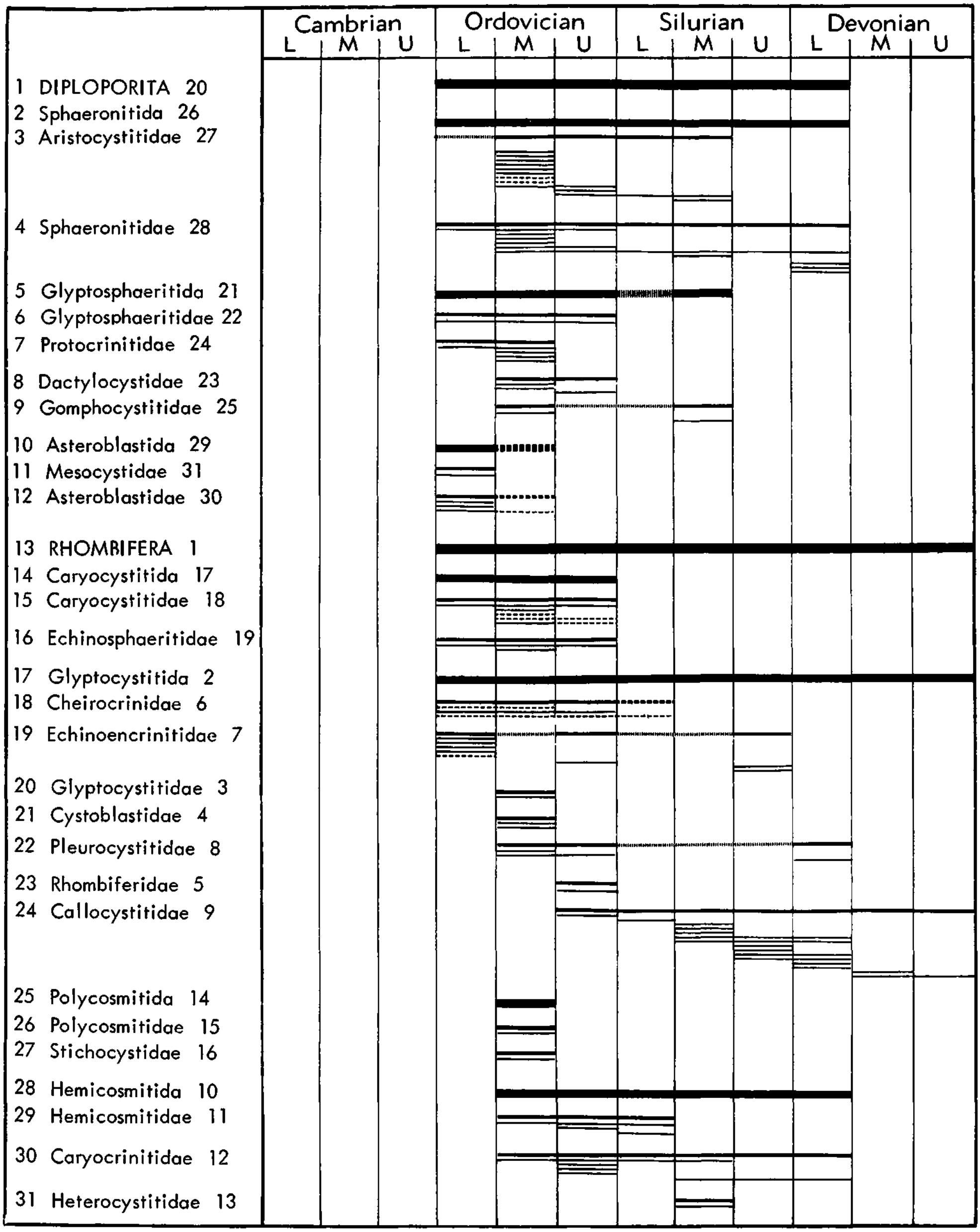


FIG. 71. Stratigraphic distribution of suprageneric cystoid taxa; geologic periods indicated only to epoch. The numbers following the names of taxa indicate systematic placement as given in the preceding tabular outline of cystoid classification. Also, an alphabetical list of taxa is accompanied by index numbers referring to the serially arranged numbers that precede the names of taxa on the diagram; this facilitates location of any selected family as plotted with respect to stratigraphic occurrence. [Range of orders (capital letters) and superfamilies indicated by heavy black lines, that of families by intermediate-weight lines, and individual genera by thinnest lines.]

He divided cystoids into two groups, those with *"Doppelporen,"* which were restricted to individual plates, and those with *"Porenrauten."* The first he called the *"Diploporiten"* and the second he left unnamed. In the following summary of his outline, the present taxa are indicated in brackets.

Classification of Cystoids by Müller

1. Cystoids with pore rhombs [Rhombifera].
    - a. Rhombs without external openings for the pores, *Hemicosmites, Caryocrinites* [Hemicosmitida].
    - b. Pores linked by an outer rod [actually a pore canal beneath epitheca], *Caryocystites* [Caryocystitida, Caryocystitidae in part].
    - c. Pores linked by several outer rods [actually multiple pore canals beneath epitheca], *Echinosphaerites* [Caryocystitida, Echinosphaeritidae in part].
    - d. With few pore rhombs, *Echinoencrinites, Pseudocrinites, Apiocystites, Prunocystites* [Glyptocystitida].
2. Cystoids with double pores, which occur on the same plate (Diploporiten), *Sphaeronites, Protocrinites, Glyptosphaerites* [Diploporita].

Müller's worthy system, which with additions and slight emendation serves as the order-superfamily classification now in use, was not readily accepted for nearly a half century.

EICHWALD

The next contribution to taxonomy was by E. von Eichwald (44), who sought to formalize his concepts of the cystoids. He created four "orders," written as family names, which he assigned to the Crinoidea. Of these, his Rhombiporitidae was said to contain *Cheirocrinus* and *Gonocrinus* [=*Echinoencrinites*], and corresponds to the Glyptocystitida of the Rhombifera. His Diploporitidae is the order Diploporita. His order Taxiporitidae is an admixture of Rhombifera and Crinoidea; it contained the cystoids *Heliocrinites, Caryocystites,* and *Echinosphaerites* [Caryocystitida] and *Hemicosmites* [Hemicosmitida]. His last order, the Aporitidae, contained only the eocrinoid *Cryptocrinites.*

Classification of Cystoidea by Eichwald, 1860 (44)

[As orders of Crinoidea]

Order Diploporitidae *(Sphaeronites, Protocrinus, Glyptosphaerites)*
Order Taxiporitidae *(Echinosphaerites, Caryocystites, Heliocrinus, Hemicosmites, Cyclocrinus)*
Order Rhombiporitidae *(Gonocrinus, Cheirocrinus)*
Order Aporitidae *(Cryptocrinus)*

QUENSTEDT

A simple division was proposed by F. A. Quenstedt (96) in which he divided cystoids into the "Serti" and the "Tricati." The first contained few and mostly large plates, to which he assigned *Caryocrinites, Hemicosmites,* and an "entire host of Rhombocystiden" (here translated); hence it corresponds to the Glyptocystitida and Hemicosmitida of the Rhombifera. The second, which Quenstedt admitted contained essentially different forms, contained *Echinosphaerites* of the Rhombifera and various genera of the Diploporita.

ANGELIN

N. P. Angelin (1) divided the cystoids into three groups. His Apora was so named because the pore canals were obscured in *Echinosphaerites* and *Caryocystites* [now included in the Caryocystitida]; he added *"Megacystis"* [=*Holocystites*], apparently because pores were not discerned on the steinkerns. His Gemellipora (twin-pores) corresponds to the Diploporita. His last group, Pedicellata, contained *Glyptocystites* and *Lepocrinites* (under other names), and hence is equivalent to the Glyptocystitida, insofar as one may judge from the content rather than the name.

Classification of Cystoidea by Angelin, 1878 (1)

Apora *(Echinosphaera, Caryocystis, Megacystis)*
Gemellipora *(Sphaeronis, Glyptosphaera)*
Pedicellata *(Glyptocystis, Lepadocrinus)*

ZITTEL

Karl A. von Zittel (147) used a tripartite division, each part of which he ascribed to J. Müller. The group Aporitidae were carpoids, edrioasteroids, and eocrinoids. The Diploporitidae included the Diploporita. The Rhombiferi were subdivided according to Müller's classification, although some carpoids, eocrinoids, crinoids, and a blastoid were included along with cystoids. The Rhombiferi appeared for the first time in the stem form of the Rhombifera.

Classification of Cystoidea by Zittel, 1879 (147)

Group Aporitidae J. MÜLLER
Group Diploporitidae J. MÜLLER
Group Rhombiferi J. MÜLLER

BARRANDE

JOACHIM BARRANDE (3), in his monumental work on cystoids of Bohemia, divided the Cystoidea according to their supposed number of thecal openings. Many of his determinations of openings were in error. He did not, however, formally declare these divisions to be taxa, and he may perhaps have regarded them merely as a utilitarian aid in identification.

NEUMAYR

MELCHIOR NEUMAYR (91) proposed a classification of "groups" (written informally as families with *-iden* termination) and "orders" (written with a subfamilial *-inen* termination). It is important not for the overall treatment, but for the first appearance of the stems from which Sphaeronitidae, Aristocystitidae, Echinosphaeritidae, and Pleurocystitidae were derived.

Classification of Cystoidea by Neumayr, 1889 (91)

- Group Sphaeronitiden
    - Order Sphaeronitinen
    - Order Aristocystinen
    - Order Mesitinen
- Group Echinosphaeritiden
- Group Pleurocystiden

MILLER

S. A. MILLER (85) published a list of 12 families, the first 11 in alphabetical order and the last called "Family uncertain." By present standards, seven of the families contained noncystoid echinoderms. MILLER's work did establish the families Caryocrinitidae and Gomphocystitidae.

Classification of Cystoidea in Families by S. A. Miller, 1889 (85)

Amygdalocystidae
Anomalocystidae
Caryocrinidae
Comarocystidae
Echinocystidae
Eocystidae
Gomphocystidae
Holocystidae
Hybocystidae
Lepadocrinidae
Platycystidae
Family Uncertain

STEINMANN

G. STEINMANN (121) expressed taxonomically the conviction held by several workers in that century that cystoids were intermediate forms giving rise to other echinoderms. In the following key, his Eucystoidea contains both Rhombifera and Diplorita, his Cystechinoidea was created for one cystoid and one echinoid, his Cystasteroidea for an edrioasteroid, and his Cystocrinoidea for a unit of the Glyptocystitida, a unit of the Hemicosmitida, and a crinoid.

Classification of Cystoidea by Steinmann, 1890 (121)

A. No sharp border present between upper and lower sides of theca. No distinct free arms, instead mostly developed as ambulacral grooves or fields.
  a. Plates either numerous and irregular or less numerous and arranged in various circlets like those in crinoids, *Glyptosphaerites, Echinosphaerites, Lepocrinites* .... Eucystoidea
  b. Part of thecal plates arranged in meridional rows, *Cystocidaris, Mesites* .... Cystechinoidea
B. Upper and lower sides of theca different; several free arms developed like those of crinoids.
  a. Theca flat, with 5 arms fused onto a disc, *Agelacrinus* .... Cystasteroidea
  b. Theca beaker-shaped; free arms at junction of upper and lower sides, *Echinoencrinites, Caryocrinites, Porocrinus* .... Cystocrinoidea

BERNARD

BERNARD (17) included the cystoids in his "groupe des Eucystidés," which he divided into six families. He introduced the Glyptosphaeritidae and Callocystitidae, although their definitions would scarcely suffice in modern taxonomy. The former included, in addition to *Glyptosphaerites, Protocrinites* of the Protocrinitidae, *Proteocystites* of the Sphaeronitidae, and an eocrinoid; it was based on the presence of diplopores, small brachioles, and ambulacral grooves. Apart from the Eucystidés, BERNARD placed *Cystoblastus* and *Asteroblastus* as transitional to the blastoids; he also listed "Cystocrinoides," supposedly intermediate between cystoids and crinoids, but containing an eocrinoid and two crinoids as listed genera.

Classification of Cystoidea (Cystidés) in Families by Bernard, 1895 (17)

Aristocystidés
Échinosphaeritidés
Glyptosphaeritidés
Caryocrinidés
Callocystidés
Pleurocystidés

HAECKEL

The work of E. Haeckel (58), notorious for serious misconceptions and factual errors and liberally supplied with hypothetical genera, introduced a classification that divided the majority of cystoids into those with numerous plates and those with few. It is remembered, however, for the introduction of the Amphoridea, an assemblage of cystoids, eocrinoids, paracrinoids, and carpoids that found favor with certain subsequent authors and long delayed trimming the cystoids to a definite taxon. The families and their divisions (presumably subfamilies) added little to classification.

Classification of Cystoidea by Haeckel, 1896 (58)

- Class Amphoridea
  - Family Eocystida—hypothetical.
  - Family Anomocystida or Pleurocystida—*Pleurocystites* and carpoids.
  - Family Aristocystida or Holocystida—diploporites, rhombiferans, and carpoids.
  - Family Palaeocystida or Archaeocystida—cystoids, carpoids, and crinoids.
- Order Microplacta or Eucystidea—numerous thecal plates, irregularly arranged.
  - Family Pomocystida (Sphaeronitida, Proteocystida).
  - Family Fungocystida (Glyptosphaerida, Malocystida).
  - Family Agelacystida (Hemicystida, Asterocystida).
  - Family Ascocystida—forms transitional to holothurians.
- Order Megaplacta or Parcystidea—few thecal plates, regularly arranged.
  - Family Callocystida (Acanthocystida, Apiocystida, Pseudocrinida).
  - Family Glyptocystida (Hexalacystida, Sycocystida).

KOKEN

Also in 1896, Koken (78) presented a key to the cystoids in his "Leitfossilien." Because he based his primary division on the extent of the ambulacra, the Diploporita and Rhombifera appear in each of the two major groups.

Classification of Cystoidea by Koken, 1896 (78)

A. Brachiata—brachioles near the mouth.
  1. Numerous thecal plates,
     - With diplopores: *Holocystites, Sphaeronites.*
     - With pore rhombs: *Echinosphaerites, Caryocystites.*
  2. Few thecal plates, arranged in circlets,
     - With simple pores: *Cryptocrinites, Hypocrinus* (eocrinoid, crinoid).
     - With numerous pore rhombs: *Caryocrinites, Hemicosmites.*
     - With few pore rhombs: *Echinoencrinites.*

B. Abrachiata—long ambulacra radiating from the mouth.
  1. Numerous thecal plates,
     - With pores absent: *Agelacrinites* (edrioasteroid).
     - With diplopores: *Mesites, Protocrinites, Glyptosphaerites.*
  2. Few thecal plates,
     - With numerous pore rhombs: *Glyptocystites.*
     - With few pore rhombs: *Lepocrinites, Callocystites.*

BATHER AND JAEKEL

It was a coincidence that the two most influential, penetrating, substantial classifications were in preparation simultaneously but independently, by Bather (9) and by Jaekel (69), and both appeared in the same year, 1899. It is an even more astonishing coincidence that the two classifications agreed on nearly all major divisions.

Both authors recognized the order Rhombifera and Diploporita with many of the same families. Both used families Glyptocystitidae, Callocystitidae, Caryocrinitidae, Echinosphaeritidae, Glyptosphaeritidae, Gomphocystitidae, Sphaeronitidae, Aristocystitidae, and Mesocystidae, in various spellings and taxa.

The main difference between Bather (9) and Jaekel (69) lies in the inclusion by the former of the order Amphoridea (for the Aristocystitidae and carpoids) and the order Aporita (for some eocrinoids). Although they both put *Dactylocystis* and *Protocrinites* into one family, Bather called it Protocrinidae and Jaekel called it Dactylocystidae; actually, the two genera are representative of separate families. Although both put *Rhombifera* and *Tiaracrinus* into one family, Bather called it Tiaracrinidae and Jaekel called it Tetracystidae; actually, *Rhombifera* is the type of a cystoid family and *Tiaracrinus* is a crinoid. Bather's subfamily Echinoencrininae of the Glyptocystidae is approximately equal to Jaekel's family Scoliocystidae. Hence, for the most part, even the differences are those of taxonomic names rather than content.

Bather's classification appeared slightly earlier than Jaekel's, and has priority. Bather introduced the following taxa (with variant spellings and ranks): Glyptocystitidae, Echinoencrinitidae, Mesocystidae, and Protocrinitidae. Jaekel introduced Cheirocrinidae, Cystoblastidae, and Dactylocystidae.

Classification of Cystoidea (Called Cystidea) by Bather, 1899 (9)

Order Amphoridea
  Aristocystidae
  Dendrocystidae
  Anomalocystidae
Order Rhombifera
  Echinosphaeridae
  Macrocystellidae
  Tiaracrinidae
  Malocystidae
  Glyptocystidae
    Echinoencrininae
    Callocystinae
    Glyptocystinae
  Caryocrinidae
Order Aporita
  Cryptocrinidae
Order Diploporita
  Sphaeronidae
  Glyptosphaeridae
  Protocrinidae
  Mesocystidae
  Gomphocystidae

Classification of Cystoidea by Jaekel, 1899 (69)

Order Dichoporita
  Regularia
    Chirocrinidae
    Cystoblastidae nov.
    Pleurocystidae
    Scoliocystidae nov.
    Callocystidae Bernard
      Glyptocystinae
      Apiocystinae
      Staurocystinae
      Callocystinae
  Irregularia
    Caryocrinidae nov.
    Echinosphaeridae nov.
    ?Tetracystidae nov.
Order Diploporita
  Mesocystidae
  Sphaeronidae
  Aristocystidae nov.
  Gomphocystidae nov.
  Glyptosphaeridae
  Dactylocystidae

Bather's (10) treatment of the Cystoidea in Lankester's *A Treatise on Zoology* was published in 1900, after he had the opportunity to examine Jaekel's (69) classification briefly. For intent and purpose, however, Bather followed his taxonomy of the previous year. He added the family Eocystidae to the Amphoridea and the family Comarocystidae to the Rhombifera. Therewith, he emphasized an important distinction between his system and that of Jaekel; we may note that Bather's concept of the cystoids was very broad, including the carpoids and other pelmatozoans, whereas Jaekel's concept was more restricted, approaching the modern content of the class.

Classification of Cystoidea (Called Cystidea) by Bather, 1900 (10)

Order Amphoridea
  Aristocystidae
  Dendrocystidae
  Eocystidae
  Anomalocystidae
Order Rhombifera
  Echinosphaeridae
  Comarocystidae
  Macrocystellidae
  Tiaracrinidae
  Malocystidae
  Glyptocystidae
    Echinoencrininae
    Callocystinae
    Glyptocystinae
  Caryocrinidae
Order Aporita
  Cryptocrinidae
Order Diploporita
  Sphaeronidae
  Glyptosphaeridae
  Protocrinidae
  Mesocystidae
  Gomphocystidae

Also in 1900, a classification of cystoids appeared in the Zittel textbook (translation by Eastman). It took no cognizance of the significant changes introduced by Bather (9) and Jaekel (69).

Classification of Cystoidea in Families by Zittel-Eastman, 1900

Aristocystidae
Sphaeronitidae
Camarocystidae
Echinosphaeritidae
Cryptocrinidae
Caryocrinidae
Anomalocystidae
Callocystidae
Agelacrinidae

Jaekel (70) formally set up the class Carpoidea, which he had used the year previously as a *nomen nudum*; the current concept of these echinoderms, however, includes only the Heterostelea of Jaekel. Then, Bather (11, in Reed) defended his classification, including the Amphoridea, and presented it once again, with slight modification, in 1913.

The classification closest to the one in the *Treatise* was published by Jaekel in 1918 (71). The families Hemicosmitidae, Heterocystitidae, Polycosmitidae, Stichocystidae, and Caryocystitidae came into being. Jaekel's subclasses Dichoporita and Diploporita are the orders Rhombifera and Diploporita recognized here. His orders and suborders were strangely named and used in the sense of superfamilies. In this important contribution, the blastoids were included as a subclass of the cystoids, in the same rank as "Dichoporita" and Diploporita; this close affinity of cystoids and blastoids was to become a point of taxonomic controversy. It should be mentioned that Jaekel at the same time refined his definition of Carpoidea and set up the Eocrinoidea, which he made a subclass of the Crinoidea.

Classification of Cystoidea by Jaekel, 1918 (71)

- Subclass Dichoporita
  - Order Regularia
    - Chirocrinidae
    - Cystoblastidae
    - Scoliocystidae
    - Pleurocystidae
    - Callocystidae
      - Glyptocystinae
      - Schizocystinae
      - Apiocystinae
      - Staurocystinae
      - Callocystinae
  - Order Irregularia
    - Suborder Hemicosmites, nov.
      - Hemicosmitidae
      - Caryocrinidae
      - Heterocystidae
    - Suborder Polycosmites, nov.
      - Polycosmitidae
      - Stichocystidae
    - Suborder Caryocystites, nov.
      - Caryocystidae
      - Echinosphaeridae
  - Order Tetracystida
  - Order ?Pentacystida
- Subclass Diploporita
  - Order Asterocystida
    - Asterocystidae
    - Mesocystidae
  - Order Seriolata
    - Estonocystidae, nov.
    - Protocrinidae
    - Glyptosphaeridae
    - Gomphocystidae
  - Order Sphaeronita
    - Sphaeronidae
    - Aristocystidae
- Subclass Blastoidea
  - *"Vorform: Cystoblastus"*
  - *"Aberrante Versuchsform* (Parablastida)"
    - Blastocystidae
  - Order Radiolata
    - Suborder Spiraculata
      - Troostoblastidae
      - Pentremitidae
      - Nucleoblastidae
        - *"Anhang: Eleutherocrinus"*
      - Granatoblastidae
        - *"Anhang: Pentephyllum, Zygocrinus"*
    - Suborder Fissiculata
      - Orophocrinidae
      - Codasteridae
  - Order Coronata
    - Stephanoblastidae

BROILI

In the Zittel-Broili textbook (21), the Cystoidea were divided into three orders corresponding to edrioasteroids, carpoids, and cystoids in the sense used here. The last was called the Hydrophoridea.

Classification of Cystoidea in Zittel-Broili (21)

- Order Thecoidea Jaekel (Edrioasteroidea Billings, *emend.* Bather)
  - Edrioasteridae Jaekel
  - Steganoblastidae
  - Cyathocystidae
  - Agelacrinidae Hall (*emend.* Jaekel)
- Order Carpoidea Jaekel (Amphoridea Bather)
  - Anomalocystidae H. Woodward (Heterostelea Jaekel)
- Order Hydrophoridea Zittel
  - Suborder Rhombifera Zittel, *emend.* Bather (Dichoporita Jaekel)
    - Echinosphaeritidae Neumayr

Caryocrinidae Jaekel
Macrocystellidae Bather
Chirocrinidae Jaekel
Scoliocystidae Jaekel
Pleurocystidae Miller & Gurley (*emend.* Jaekel)
Callocystidae Bernard
Cystoblastidae Jaekel
Suborder Diploporita
  Aristocystidae Neumayr (*emend.* Jaekel)
  Sphaeronidae Jaekel (Pomocystae Haeckel)
  Gomphocystidae Jaekel
  Glyptosphaeridae Jaekel
  Protocrinidae Bather (Dactylocystidae Jaekel)
  Mesocystidae Jaekel

Bather (15) in his last published classification, in the *Encyclopaedia Britannica,* 14th ed., abandoned the Amphoridea and treated the Cystoidea and Blastoidea as distinct but closely related.

BASSLER

Bassler (5) in the "Pelmatozoa Palaeozoica" for the *Fossilium Catalogus,* and Bassler & Moodey (7) in *Bibliographic and Faunal Index of Paleozoic Pelmatozoan Echinoderms* turned back taxonomy to the 1900 concepts of Bather, enlarging somewhat on the unwieldy Amphoridea and altering the Rhombifera and Diploporita to a degree, but nevertheless reviving a general system that Jaekel (71) had condemned and Bather (15) had come to abandon.

Classification of Cystoidea by Bassler & Moodey, 1943 (7)

Order Amphoridea Haeckel
  Eocystitidae Bassler (Eocystidae Bather)
  Aristocystitidae Bassler (Aristocystidae Neumayr)
  Anomalocystitidae Bassler (Anomalocystidae Meek)
  Dendrocystitidae Bassler (Dendrocystidae Bather)
  Cothurnocystidae Bather
  Malocystitidae Bassler (Malocystidae Bather)
  Comarocystitidae Bassler (Comarocystidae Bather)
Order Rhombifera Zittel
  Echinosphaeritidae Neumayr (Echinosphaeridae Jaekel)
  Caryocrinitidae Bassler (Caryocrinidae Bernard)
  Callocystitidae Bassler (Callocystidae Bernard)
  Cheirocrinidae Jaekel
  Pleurocystitidae Bassler (Pleurocystidae Jaekel)
  Echinoencrinitidae Phleger (Echinoencrinidae Bather)
  Cryptocrinitidae Bassler (Cryptocrinidae Zittel)
  Macrocystellidae Bather
Order Diploporita Zittel
  Sphaeronitidae Neumayr (Sphaeronidae of authors)
  Glyptosphaeritidae Bassler (Glyptosphaeridae Jaekel)
  Protocrinitidae Bassler (Protocrinidae Bather)
  Gomphocystitidae Bassler (Gomphocystidae Jaekel)
  Eumorphocystidae Branson & Peck

Regnéll (99) criticized Bassler (5) and Bassler & Moodey (7) for their classification, and elected to follow Jaekel (71) in including the blastoids in the Cystoidea. He also corrected some of the taxonomic names of earlier authors, and presented a general critique of noncrinoid Pelmatozoa. Regnéll set up the Paracrinoidea to receive certain forms that had been assigned by some to the cystoids.

Moore (89) gave a summary of Pelmatozoa, and stated that "the relegation of blastoids to rank as a subclass of the cystoids, as recently proposed by Regnéll (99), is a backward step which is not accepted." Regnéll (104) rebutted Moore's contention by saying, "Now, the way of classification is a purely technical question and a matter of personal judgement and taste." He then referred to previous interpretations of *Cystoblastus, Asteroblastus,* and *Tholocystis* as possible intermediate forms between the cystoids (in a restricted sense) and the blastoids.

Other papers could be discussed here; but these above have treated the Cystoidea as an entity, whereas many lesser contributions have been concerned with only a part of the class.

CLASSIFICATION ADOPTED IN TREATISE

GENERAL DISCUSSION

The classification adopted here differs in some respects from any previously presented. Except for the inclusion of the Blastoidea, Jaekel's (71) diagnoses were mostly sound and his criteria clearly stated, insofar as suprageneric taxa were concerned. Unfortunately, the generic content of each taxon was not complete, and generic distinctions were sketchy or omitted.

No single morphological character will suffice to differentiate all the families. Criteria employed for the families in one superfamily are not applicable to those in another superfamily. To judge from the morphological extremes included therein, some superfamilies are taxonomically more discrete than others. Similarly, some families are composed of very diverse genera, whereas others contain closely similar genera. Monofamilial superfamilies and monogeneric families serve to emphasize the inadequacy of the fossil record. Our knowledge of the Callocystitidae, probably the best understood of families, appears to have been the result of fortuitous availability of good specimens rather than innate qualities of the cystoids concerned.

Inasmuch as cystoids became extinct in the mid-Paleozoic, their physiology, specific variation, and diagnostic features must be inferred, in many cases from an insufficient sample of the population. The criteria based on the fossils are undoubtedly artificial to some degree. Nevertheless, the separation of the two orders on the basis of the thecal pores has been granted wide acceptance. As it has subsequently developed, the choices of names for them have priority but little else in their favor.

The Rhombifera have thecal pores extending from one plate to another, but not all genera exhibit rhombic arrangements. And the Diploporita have thecal pores confined to individual plates, but not all genera have these developed as diplopores. Both orders contain some cystoids with very regular disposition of thecal plates and some with irregular. The number of thecal pores varies greatly in each order. Some Rhombifera and some Diploporita have no column in the adult.

Criteria for dividing the Rhombifera into superfamilies are not the same as those for dividing the Diploporita. The four superfamilies of the Rhombifera are differentiated by the sort of thecal pores and the regularity of the thecal plates. The three superfamilies of the Diploporita are distinguished by the development of the ambulacral system and, to a lesser degree, by the nature of the column and the distribution of thecal pores.

Within superfamilies, the families are defined on various characters, such as number and arrangement of thecal plates, shape of theca, size of periproct, development of ambulacra, number of brachioles, number and location of rhombs or diplopores, and development of column.

Although the effort may be somewhat discretionary, the Systematic Descriptions contains in the Cystoidea a key to all families and in each family a key to the firmly established genera. These should prove useful to the beginning student and may be valuable to the advanced worker in gauging the validity of the current classification and in formulating additional emendations. The keys constitute a compendium of the taxonomy adopted in the *Treatise.*

ORDER RHOMBIFERA

The Rhombifera are a group of cystoids in which the thecal pores extend from one plate to another, being normally shared equally by the two plates. Most cystoids of the order have the pores, called dichopores, aligned in rhombs, but the Polycosmitidae are an exception. The Rhombifera were clearly separated from the Diploporita when the fossil record starts in the Lower Ordovician (Fig. 54), so that a previous long history may be inferred. The order reached its maximum diversity in Middle Ordovician, but continued to produce new genera throughout the Silurian and much of the Devonian. The last surviving cystoid was the rhombiferan *Strobilocystites* from the Upper Devonian of Iowa.

The basis for differentiating superfamilies was indicated long ago by MÜLLER (90). It is rather remarkable that, among the relatively few cystoids known in his time, he had representation of the different superfamilies, and that he was discerning enough to discover the key character. Subsequently, taxonomic names were devised to fit the categories set up by MÜLLER.

SUPERFAMILY GLYPTOCYSTITIDA

The thecal pores of the Glyptocystitida are pore rhombs, typically developed as pectinirhombs. In all the pores are open to the outside, but some have pores that are subcircular, rather than parallel slits, so that the rhombs do not fit the textbook concepts of pectinirhombs.

In addition to the form of the pores, the Glyptocystitida have thecae composed of 24 basic plates (although rare exceptions are found in which one or more plates may be bipartite or tripartite). These plates are disposed more or less in circlets of four basals *(BB),* five infralaterals *(ILL),* five laterals *(LL),* five radials *(RR),* and five orals or deltoids *(OO).* Because of the constant number of the thecal plates, species and genera can be compared in greater detail than those of other superfamilies.

The Glyptocystitida are divisible into two groups (Fig. 57), one characterized by large periprocts containing numerous plates in addition to the anal pyramid and another distinguished by small periprocts containing not more than a single circlet of auxiliary plates around the anal pyramid. The first group includes the Pleurocystitidae, Cheirocrinidae, and Glyptocystitidae. Of these, the Pleurocystitidae is distinctive for having a strongly compressed theca, extremely large periproct, and few pore rhombs. The Cheirocrinidae can be differentiated from the Glyptocystitidae by their shorter ambulacra and fewer brachioles.

The second group, with small subcircular periprocts, includes the Echinoencrinitidae, Callocystitidae, Cystoblastidae, and Rhombiferidae. The first two both have subovate thecae, but can readily be distinguished by shortness of the ambulacra and (in most) the protuberant nature of the periproct region in the Echinoencrinitidae. The Cystoblastidae have a pentremite shape that cannot be confused with that of any other Rhombifera; the theca bears such resemblance to a pentremite blastoid that Jaekel (68, 69, 71) repeatedly emphasized the derivation of the Blastoidea from this family of cystoids. The Rhombiferidae contains only the type genus, *Rhombifera,* which also has a unique shape; the spindle-like theca is futher conspicuous in having the laterals set directly atop the infralaterals with the radials reduced to small plates alternating with the orals, an arrangement not met with in any other cystoid.

SUPERFAMILY HEMICOSMITIDA

The cystoids of the Hemicosmitida exhibit a degree of regularity in the plate pattern, although not as prominent as that in the Glyptocystitida. The chief character lies in the nature of the rhombs, which are numerous and internally like pectinirhombs, but have the pores covered by epitheca. The Hemicosmitida bear close resemblances to crinoids, some more than others, in form of the column and organization of the theca. This similarity is interpreted here as convergence, rather than indicative of close genetic affinity.

The division into families (Fig. 56) is not as sharply defined as in other superfamilies. The Heterocystitidae are readily identified by the 10 plates in the circlet above the basals, as contrasted with the six in the Hemicosmitidae and Caryocrinitidae. Insofar as *Hemicosmites* and *Caryocrinites* are concerned, the differences are clear; in the latter, the brachioles lie at the borders of a "tegmen" formed by modified covering plates, which roof over the ambulacral grooves. The other genera of the same families, however, are not so definitely of one or the other type; the "tegmen" of some is much reduced and the ambulacra rather closely set, so that classification becomes a matter of preference. As a result, the contents of the Hemicosmitidae and Caryocrinitidae in the *Treatise* do not conform in all respects to any previously presented. The taxonomic treatment of these cystoids offers fertile ground for further investigation.

SUPERFAMILY POLYCOSMITIDA

Of all superfamilies of the Rhombifera, the Polycosmitida is the one least known because of the scarcity of complete specimens and well-preserved structures. The thecal pores are the openings of inclined canals, disposed symmetrically with respect to plate sutures but not connected by preserved inside or outside tangential pore canals. Pore rhombs are numerous and apparently present on all sides of thecal plates.

In the Polycosmitidae the pores are arranged in rows that outline rhombic areas, whereas in the Stichocystidae they are irregularly placed within sectors of the plates so as to fill the rhombic areas. *Polycosmites,* the only genus of its family, is known only from isolated plates. If complete thecae are found, perhaps other criteria may enter into the familial diagnoses.

The pore structure, on which this superfamily is based, seems to be intermediate between that of the Hemicosmitida and that of the Caryocystitida. The paleontological record, however, does not suffice to warrant phylogenetic conclusions.

SUPERFAMILY CARYOCYSTITIDA

In the Caryocystitida, the ends of the dichopores open to the interior of the theca and the tangential canals linking paired pores lie beneath a layer of epitheca. Pairs of pores may be linked by a single tangential canal (simple) or by more than one (compound). Where the epitheca is not preserved, the tangential canals display a superficial resemblance to the pore slits in conjunct pectinirhombs of the Glyptocystitida, although they are more numerous and are underlain by stereotheca.

Two families (Fig.55) are distinguished by the number of thecal plates, the Caryocystitidae with 30 to 120 plates and the Echinosphaeritidae with 200 to more than 800. Other differences are not so incisive. In the Caryocystitidae, the epitheca is seldom preserved and presumably was thinner or more incompletely calcified than that of the Echinosphaeritidae, but this has not been proved; the theca is elongate in many genera, but some are ovate and approach the spherical shape of the Echinosphaeritidae; also, the plates tend to be arranged in circlets and to be disposed in alternating position, as opposed to the irregular pattern of the tiny plates in the other family.

ORDER DIPLOPORITA

The Diploporita are a group of cystoids in which the thecal pores are nearly all confined to individual plates. Commonly, these pores are paired as diplopores, but in some genera the canals are irregular, do not divide in two, and are called haplopores. It is unsafe to assert that diplopores or haplopores are the ancestral form of cystoid pores, for the record is too fragmentary to support either contention.

Certain incompletely preserved fossils from the Middle Cambrian of Bohemia may belong to the Diploporita, and they are assigned with question in the *Treatise*. Unquestionable Diploporita are present in Lower Ordovician deposits. The order extends into the Lower Devonian. Like the Rhombifera, the order attained maximum diversity in the Ordovician.

The three superfamilies (Fig. 54) are classified by form of the ambulacra, which are very short in the Sphaeronitida, long in the Glyptosphaeritida, and intermediate and quite regular in the Asteroblastida. Other superfamilial characters are the shape of the theca, distribution of the thecal pores, and development of the column.

SUPERFAMILY GLYPTOSPHAERITIDA

Genera of the Glyptosphaeritida (Fig. 59) have long ambulacra, variously developed in the families. The theca varies in shape from irregular and saclike to ovate or globular with a high degree of symmetry. Pores are present as diplopores, typically with peripores highly developed, invariably found in the ambulacra-bearing plates and in some cystoids on the interambulacral areas as well.

Ambulacra are spiral in the Gomphocystitidae, long, straight, and regularly provided with short lateral branches in the Dactylocystidae, long and zigzag, with regularly alternating branches in the Protocrinitidae, and long, irregularly branched in the Glyptosphaeritidae. The Glyptosphaeritidae also have an apple-shaped theca, anchored by a short, small column; except for the peristomial covering plates, these cystoids show weak expression of symmetry. The Gomphocystitidae, shaped like an inverted pear, have no true column, although the theca is aborally prolonged as a stemlike section. The Protocrinitidae and Dactylocystidae have a high degree of pentameral symmetry, especially the latter; both have the ambulacra resting on special alternating thecal plates known as adambulacrals. Primary distinction lies in the distribution of diplopores, which occur in interambulacral and ambulacral plates in the Protocrinitidae, but are restricted to the adambulacrals in the Dactylocystidae. In addition, the main ambulacral grooves in the latter are very straight, and the bordering adambulacral plates are regularly shaped and distinctly different from the interambulacral plates.

SUPERFAMILY SPHAERONITIDA

The brachioles are closely set around the peristome in representatives of the Sphaeronitida so that the ambulacra, if any can be distinguished, are quite short. Most of the cystoids are attached by the base of the theca, at least as adults, and show no trace of a column. Thecal pores are developed either as diplopores or as haplopores.

The two families (Fig. 58) are separated on the basis of the ambulacra. In the Sphaeronitidae, the ambulacra branch directly from the corners of the peristome, in characteristic patterns for the genera; in the Aristocystitidae, however, no extensions of any kind are known for the food grooves, and the brachiole facets are set adjacent to the peristome. Whereas the Sphaeronitidae are rather similar in form, the Aristocystitidae contain a heterogeneous assemblage showing extremes not only in shape of the theca but also in kinds of thecal pores. Many of the genera are poorly known. Any key to the established genera is highly artificial at this time.

The inconsistent order Amphoridea, conceived by Haeckel (58) to embrace markedly dissimilar echinoderms, including some of his imaginary genera, met with obstacles to acceptance from the start. The association of the Aristocystitidae with carpoids, eocrinoids, and paracrinoids was unnatural, so that Jaekel (69) was fully justified in removing so-called amphorideans to the Diploporita. From time to time, Bather (10-13) defended the Amphoridea, but at last dropped the group in his final (15) classification of the cystoids. Nevertheless, Bassler & Moodey (7) retained it in their compilation of Paleozoic Pelmatozoa. Regnéll (99) stoutly denied the desirability for such a "fatal" taxon, and it seems to have been suppressed effectively.

SUPERFAMILY ASTEROBLASTIDA

Cystoids placed in the Asteroblastida have in common a bud- or pentremite-shaped theca, small column, straight ambulacra, diplopores confined to interambulacral plates, and a high degree of pentameral symmetry. The superfamily is of particular interest because some authors have proposed that it contains the ancestral form of the blastoids. Undoubtedly, the thecal shape and strong symmetry convey an impression of a blastoid lacking only the hydrospires. This particularly applies to *Asteroblastus,* just as it did to *Cystoblastus* among the Rhombifera. As early as 1874, Schmidt (114) concluded that *Asteroblastus* was a transitional form. Bergounioux (16) included the genus in his chapter of the *Traité de Zoologie* on the blastoids. Wanner (1951) thought that, if blastoids did originate from known cystoids, only the Asteroblastidae contained the required structures. On the other hand, Jaekel (71) was quite as firmly convinced that the Blastoidea descended from *Cystoblastus.*

In the Asteroblastidae, the ambulacra are broad, the brachioles relatively few, and the thecal plates organized comparable to those in the Glyptocystitida. In direct contrast, in the Mesocystidae, the ambulacra are very narrow, the brachioles numerous (as many as 1,000), and the thecal plates exceptionally numerous, tiny, and irregularly disposed. Insofar as known, both families are present in Early Ordovician, and the Cystoblastidae may have lived on into Middle Ordovician time.

SUMMARY OF CHARACTERS

The main characters of the orders and superfamilies of cystoids recognized in the *Treatise* are summarized in Table 6 on p. S164. Certain other characters are used in diagnoses of superfamilies in one order but not in the other. These appear in the Key to Orders, Superfamilies, Families, and Subfamilies on p. S167.

ECHINODERMS FORMERLY INCLUDED IN CYSTOIDEA

Acanthocystites Barrande, 1887 [=*Acanthocystis* Bather, 1889 (*nom. van. pro Acanthocystites* Barrande, 1887), *non* Carter, 1863, *nec* Haeckel, 1887 (*nom. null. pro Acanthocyrtis* Haeckel, 1881), *nec* Haeckel, 1896 (*nom. nud.*)] .... Eocrinoidea

Achradocystites Volborth, 1870 [=*Achradocystis* Haeckel, 1896 (*nom. van.*)] .. Paracrinoidea

Amygdalocystites Billings, 1854 [=*Amygdalocystis* Carpenter, 1891 (*nom. van.*); *Ottawacystites* Wilson, 1946] .... Paracrinoidea

Anatiferocystis Chauvel, 1941 .... Stylophora

Anomalocystites Hall, 1859 [=*Anomalocystis* Bather, 1889 (*nom. van.*); *Anomocystis* Haeckel, 1896 (*nom. null. pro Anomalocystites* Hall)] .... Stylophora

Table 6. *Characters of Cystoid Orders and Superfamilies*

Order	Rhombifera				Diploporita		
Superfamily	Glypto-cystitida	Hemicos-mitida	Polycos-mitida	Caryo-cystitida	Glypto-sphaer-itida	Sphaer-onitida	Astero-blastida
Thecal plate arrangement	Regular	Regular	Irregular	Irregular	Irregular	Irregular	Some regular
Kind of pores	Pectini-rhombs, pores open	Inner tan-gential canals, pores covered	No inner or outer tangenti-al canals calcified	Subepi-thecal tangential canals, pores inside	Diplo-pores, dispersed or ambul-acral	Diplo-pores or haplo-pores, dispersed	Diplopores on special interamb-ulacral plates
Number of pore units	Few in most	Many	Numerous	Very numerous	Numerous	Numerous	Relatively few
Column	Present, normally flared at theca	Present, much like crinoid column	Weakly developed	Weakly developed, absent in some	Small, absent in some	Absent	Present, weakly developed

Anomocystis Jaekel, 1918 [*non* Haeckel, 1896 (*nom. null. pro Anomalocystites* Hall, 1859)] .... Stylophora

Archaeocystites Barrande, 1887 [=*Archaeocystis* Haeckel, 1896 (*nom. van.*)] ?Eocrinoidea

Ascocystites Barrande, 1887 [=*Ascocrinus* Barrande, 1887, *non* Tromelin & Lebesconte, 1876 (*nom. nud.*); *Ascocystis* Bather, 1889 (*nom. van.*)] .... Eocrinoidea

Astrocystites Whiteaves, 1897 ...... Edrioblastoidea

Ateleocystites Billings, 1858 [=*Ateleocystis* Lindström, 1888; *Atelecystis* Bather, 1889 (*nom. null.*); *Atelocystis* Haeckel, 1896 (*nom. null.*)] .... Stylophora

Balanocystites Barrande, 1887 [=*Balanocystis* Haeckel, 1896 (*nom. van.*)] .... Stylophora

Batherocystis Bassler, 1950 .... Eocrinoidea

Belemnocystites Miller & Gurley, 1894 [=*Belemnocystis* Bather, 1900 (*nom. van.*); *Myeinocystites* Strimple, 1953] ...... Homoiostelea

Billingsocystis Bassler, 1950 .... Paracrinoidea

Bockia Gekker, 1938 .... Eocrinoidea

Canadocystis Jaekel, 1900 [=*Sigmacystis* Hudson, 1911] .... Paracrinoidea

Cardiocystites Barrande, 1887 [=*Cardiocystis* Haeckel, 1896 (*nom. van.*)] .... Eocrinoidea

Ceratocystis Jaekel, 1900 .... Stylophora

Cigara Barrande, 1887 .... Eocrinoidea

Columbocystis Bassler, 1950 .... Eocrinoidea

Comarocystites Billings, 1854 [=*Comarocystis* Carpenter, 1891 (*nom. van.*)] ...... Paracrinoidea

Cothurnocystis Bather, 1913 .... Stylophora

Crinocystites Hall, 1867 [=*Crinocystis* Haeckel, 1896 (*nom. van.*)] .... Crinoidea

Cryptocrinites von Buch, 1840 [=*Cryptocrinus* Geinitz, 1846 (*nom. van.*)] .... Eocrinoidea

Cyclocystoides Billings & Salter, 1858 .... Cyclocystoidea

Decacystis Gislén, 1927 .... Homostelea

Dendrocystites Barrande, 1887 [=*Dendrocystis* Bather, 1889 (*nom. van.*)] .... Homoiostelea

Dendrocystoides Jaekel, 1918 .... Homoiostelea

Enoploura Wetherby, 1879 [=*Enopleura* Springer, 1913 (*nom. van.*)] .... Stylophora

Eocystites Billings, 1868 [=*Eocystis* Bather, 1900 (*nom. van.*) *non* Haeckel, 1896 (*gen. hypoth.*)] .... Eocrinoidea

Foerstecystis Bassler, 1950 Eocrinoidea

Gogia Walcott, 1917 .... Eocrinoidea

Gyrocystis Jaekel, 1918 .... Homostelea

Iowacystis Thomas & Ladd, 1926 ...... Homoiostelea

Kirkocystis Bassler, 1950 .... Stylophora

Lagynocystis Jaekel, 1918 .... Stylophora

Lapillocystites Barrande, 1887 .... Eocrinoidea

Larites de Gregorio .... Unrecognizable

Lepidocystis Foerste, 1938 .... Lepidocystoidea

Lichenoides Barrande, 1846 [=*Lichenocystis* Haeckel, 1896 (*nom. van.*)] .... Eocrinoidea

Lingulocystis Thoral, 1935 .... Eocrinoidea

Lodanella Kayser, 1885 .... Crinoidea

Lysocystites S. A. Miller, 1889 [*nom. subst. pro Echinocystites* Hall, 1865, *non* Thomson, 1861] [=*Lysocystis* Bather, 1897 (*nom. van.*); *Echinocystis* Haeckel, 1896 (*nom. van. pro Echinocystites* Hall), *non* Gregory, 1897 (*nom. van. pro Echinocystites* Thomson); *Aethocystites* S. A. Miller, 1892; *Aethocystis* Bather, 1900 (*nom. van.*)] .... Eocrinoidea

Macrocystella Callaway, 1877 .... Eocrinoidea

Malocystites Billings (in Chapman), 1857 [=*Malocystis* Carpenter, 1891 (*nom. van.*)] .... Paracrinoidea

Mimocystites Barrande, 1887 [=*Mimocystis* Carpenter, 1891 (*nom. van.*)] .... Eocrinoidea

Mitrocystites Barrande, 1887 [=*Mitrocystis* Bather, 1889 [*nom. van.*] .... Stylophora

Narrawayella Foerste, 1920 .... Cyclocystoidea

Neocystites Barrande, 1887 [=*Neocystis*

Bather, 1889 *(nom. van.)*] .... Probably a root
Palaeocystites Billings, 1858 .... Eocrinoidea
Peltocystis Thoral, 1935 .... Stylophora
Phyllocystis Thoral, 1935 .... Stylophora
Pilocystites Barrande, 1887 .... Eocrinoidea
Placocystella Rennie, 1936 .... Stylophora
Placocystites de Koninck, 1869 [=*Placocystis* Haeckel, 1896 *(nom. van.)*] .... Stylophora
Platycystites S. A. Miller, 1889 [=*Platycystis* Bather, 1900 *(nom. van.), non* Léger, 1892] .... Paracrinoidea
Polyptychella Jaekel, 1918 .... Eocrinoidea
Protocystites Hicks, 1872 [*non* Salter, 1865 *(nom. nud.)*; =*Protocystis* Bather, 1900 *(nom. van.), non* Wallich, 1862] .. ?Eocrinoidea
Rhenocystis Dehm, 1932 .... Stylophora
Rhipidocystis Jaekel, 1901 .... Eocrinoidea
Savagella Foerste, 1920 .... Cyclocystoidea
Schuchertocystis Bassler, 1950 .... Paracrinoidea
Sinclairocystis Bassler, 1950 .... Paracrinoidea
Springerocystis Bassler, 1950 .... Eocrinoidea
Staurosoma Barrande, 1887 .... Crinoidea
Syringocrinus Billings, 1859 .... Homoiostelea
Tiaracrinus Schultze, 1867 .... Crinoidea
Trachelocrinus Ulbich, 1929 .... ?Eocrinoidea
Trochocystites de Verneuil & Barrande, 1860 [*non* Barrande, 1859 *(nom. nud.)*; =*Trigonocystis* Haeckel, 1896; *Trochocystis* Haeckel, 1896 *(nom. van.)*] .... Homostelea
Trochocystoides Jaekel, 1918 .... Homostelea
Wellerocystis Foerste, 1920 .... Paracrinoidea

JUNIOR SYNONYMS

Aethocystites S. A. Miller, 1892 [=*Lysocystites* S. A. Miller, 1889] .... Eocrinoidea
Amorphocystites Jaekel, 1896 = *Caryocystites* von Buch, 1846
Anthocystis Haeckel, 1896 = *Callocystites* Hall, 1852
Citrocystis Haeckel, 1896 = *Echinosphaerites* Wahlenberg, 1818
Crystallocystis Haeckel, 1896 = *Echinosphaerites* Wahlenberg, 1818
Dagoncystis Chauvel, 1941 (obj.) = *Pseudaristocystis* Sun, 1936
Deutocystites Barrande, 1887 = *Echinosphaerites* Wahlenberg, 1818
Dipleurocystis Jaekel, 1918 = *Pleurocystites* Billings, 1854
Dorycystites Kloucek, 1917 = *Calix* Rouault, 1851
Ennaecystis Haeckel, 1896 = *Caryocrinites* Say, 1825
Eocrinus Jaekel, 1918 [=*Gogia* Walcott, 1917] .... Eocrinoidea
Gonocrinites Eichwald, 1840 = *Echinoencrinites* von Meyer, 1826
Heliopirum Haeckel, 1896 = *Heliocrinites* Eichwald, 1840
Hexalacystis Haeckel, 1896 = *Hemicosmites* von Buch, 1840
Leucophthalmus Koenig, 1825 = *Echinosphaerites* Wahlenberg, 1818
Meekocystis Jaekel, 1899 = *Lepadocystis* Carpenter, 1891
Megacystites Hall, 1865 = *Holocystites* Hall, 1864
Ovocystis Reed, 1917 = *Sinocystis* Reed, 1917
Palmacystis Haeckel, 1896 = *Eucystis* Angelin, 1878
Phacocystis Haeckel, 1896 (obj.) = *Pseudocrinites* Pearce, 1842
Sycocystites von Buch, 1846 = *Echinoencrinites* von Meyer, 1826
Trimerocystis Schuchert, 1904 = *Pseudocrinites* Pearce, 1842
Trinemacystis Haeckel, 1896 = *Echinosphaerites* Wahlenberg, 1818

NOMINA NUDA

Genera which clearly lack description, notes, or illustration are designated as *nom. nud.*; genera which are described and founded on hypothetical species based on nonexistent fossils are designated as *gen. hypoth.* The latter are creations of Haeckel, 1896.

Amphoraea Haeckel, 1896 *(gen. hypoth.)*
Anthocystites Bernard, 1893 *(nom. nud.)*
Archaeocystis Haeckel, 1896 *(gen. hypoth.)*
Ascocrinus Tromelin & Lebesconte, 1876 *(nom. nud.)*
Chilocystis Perner, 1911 *(nom. nud.)*
Eocystis Haeckel, 1896 [*gen. hypoth.*; *non* Bather, 1900 (*nom. van. pro Eocystites* Billings, 1868)]
Lagarocystis Jaekel, 1899 *(nom. nud.)*
Microcystites Ulrich, 1880 *(nom. nud.)*
Palamphora Haeckel, 1896 *(gen. hypoth.)*
Pentactaea Haeckel, 1896 *(gen. hypoth.)*
Pomonites Haeckel, 1896 *(gen. hypoth.)*
Proteroblastus Jaekel, 1895 *(nom. nud.)*
Protocystites Salter, 1865 *(nom. nud.)*
Psolocystis Haeckel, 1896 *(gen. hypoth.)*
Stephanamphora Haeckel, 1896 *(gen. hypoth.)*
Thuriocystis Haeckel, 1896 [*nom. nud.* (Jena Zeitschr.); *gen. hypoth.* (Festschr. Gegenb.)]
Trochocystites Barrande, 1859 *(nom. nud.)*

PREOCCUPIED NAMES

Craterina Barrande, 1887 (*non* Bory, 1826, *nec* Curtis, 1826, *nec* Gruber, 1884) = *Codiacystis* Jaekel, 1899
Mesites Hoffman, 1866 (*non* Schoenherr, 1838, *nec* Geoffroy, 1838, *nec* Jenyns, 1842, *nec* Ludwig, 1893) = *Mesocystis* Bather, 1898

UNRECOGNIZABLE GENERA

Pomocystis Haeckel, 1896 (probably = *Haplosphaeronis* Jaekel, 1926)
Pomosphaera Haeckel, 1896 (probably = *Haplosphaeronis* Jaekel, 1926)

SUMMARY OF CLASSIFICATION AND STRATIGRAPHIC DISTRIBUTION

The tabular outline of classification that follows is accompanied by statement of the stratigraphic range of each taxon as reported and interpreted into terms of Lower, Middle, and Upper parts of periods in accordance with the correlations given in Fig. 53. The bracketed index numbers preceding each taxon are for cross reference to and from the stratigraphic-distribution diagram (Fig. 71); the first of the two numbers are in sequence in the tabular outline and follow the names of the taxa in the diagram, whereas the second numbers are in sequence in the diagram. The numbers in parentheses before the range of each taxon refer to the number of genera; the first indicates well-established genera and the second (if required) the total genera recorded in the *Treatise*.

Genera are plotted on stratigraphic-distribution diagrams in the sections of the systematic descriptions devoted to the various families. These compilations are interpreted into parts of periods in accordance with correlations on p. *S*128-*S*129, as are those for the suprageneric taxa. It is hoped that this summary, like those for other fossil groups in the *Treatise*, will be useful for various purposes.

Suprageneric Taxa of Cystoidea

Cystoidea *(class)* (81, 87). *L.Ord.-U.Dev.* (Fig. 71)
(1-13) Rhombifera *(order)* (46, 51). *L.Ord.-U.Dev.* (Fig. 71).
(2-17) Glyptocystitida *(superfamily)* (30, 33). *L.Ord.-U.Dev.* (Fig. 54, 81)
(3-20) Glyptocystitidae (1). *M.Ord.* (Fig. 57, 81)
(4-21) Cystoblastidae (2). *M.Ord.* (Fig. 57, 81)
(5-23) Rhombiferidae (1). *U.Ord.* (Fig. 57, 81)
(6-18) Cheirocrinidae (1, 3). *L.Ord-L.Sil.* (Fig. 57, 81)
(7-19) Echinoencrinitidae (7, 8). *L.Ord.-U.Sil.* (Fig. 57, 81)
(8-22) Pleurocystitidae (3). *M.Ord.-L.Dev.* (Fig. 57, 81)
(9-24) Callocystitidae (15). *U.Ord.-U.Dev.* (Fig. 57, 81)
(10-28) Hemicosmitida *(superfamily)* (9). *M.Ord.-L.Dev.* (Fig. 54, 116)
(11-29) Hemicosmitidae (3). *M.Ord.-L.Sil.* (Fig. 56, 116)
(12-30) Caryocrinitidae (5). *M.Ord.-L.Dev.* (Fig. 56, 116)
(13-31) Heterocystitidae (1). *M.Sil.* (Fig. 56, 116)
(14-25) Polycosmitida *(superfamily)* (2). *M.Ord.* (Fig. 54, 125)
(15-26) Polycosmitidae (1). *M.Ord.* (Fig. 125)
(16-27) Stichocystidae (1). *M.Ord.* (Fig. 125)
(17-14) Caryocystitida *(superfamily)* (5, 6). *L.Ord.-U.Ord.* (Fig. 54, 125)
(18-15) Caryocystitidae (3, 4). *L.Ord.-U.Ord.* (Fig. 55, 125)
(19-16) Echinosphaeritidae (2). *L.Ord.-U.Ord.* (Fig. 55, 125)
(20-1) Diploporita *(order)* (35, 37). *L.Ord.-L.Dev.* (Fig. 71)
(21-5) Glyptosphaeritida *(superfamily)* (10). *L.Ord.-M.Sil.* (Fig. 54, 131)
(22-6) Glyptosphaeritidae (1). *L.Ord.-U.Ord.* (Fig. 59, 131)
(23-8) Dactylocystidae (3). *M.Ord.-U.Ord.* (Fig. 59, 131)
(24-7) Protocrinitidae (4). *L.Ord.-M.Ord.* (Fig. 59, 131)
(25-9) Gomphocystitidae (2). *M.Ord.-M.Sil.* (Fig. 59, 131)
(26-2) Sphaeronitida *(superfamily)* (21, 23). *L.Ord.-L.Dev.* (Fig. 54, 139)
(27-3) Aristocystitidae (10, 12). *M.Ord.-M.Sil.* (Fig. 58, 139)
(28-4) Sphaeronitidae (11). *L.Ord.-L.Dev.* (Fig. 58, 139)
(29-10) Asteroblastida *(superfamily)* (4). *L.Ord., ?M.Ord.* (Fig. 54)
(30-12) Asteroblastidae (3). *L.Ord., ?M.Ord.* (Fig. 71)
(31-11) Mesocystidae (1). *L.Ord.* (Fig. 71)

SYSTEMATIC DESCRIPTIONS

Class CYSTOIDEA von Buch, 1846

[*nom. correct.* Nicholson, 1879 (*pro* Cystideen von Buch, 1846)] [=Cystideae Forbes, 1848; Cystidea Hall, 1847; Cystoidia DeLage & Hérouard, 1903; Hydrophoridea Zittel, 1903]

Calcareous plates around body constituting theca that extends to mouth, not differentiated into dorsal calyx and ventral tegmen; thecal plates penetrated from within theca by pores, either perforating plates or terminating subepithecally, never provided with inward radial structures like hydrospires. Ambulacra recumbent on surface of theca and, with possible exception of *Cystoblastus,* exothecal, only openings being those of ambulacral or food grooves leading to mouth; flooring plates, if present, biserially arranged. Brachioles composed of biserial plates, groove covered by tiny biserial plates, unbranched except in *Caryocrinites,* in which brachioles are developed as arms (biserially plated) bearing pinnules (biserially plated). Column present in most forms, in some shed early in ontogeny, in a few perhaps never developed. *L.Ord.-U. Dev.*

To the name of this class could be appended numerous emendations, altering its content by enlargements, restrictions, and revisions, so as to approach the form here considered definitive. The foremost emendations are those of BATHER in 1899 (9), who published the first comprehensive classification and review; JAEKEL (69), who abandoned the Aporita and Amphoridea and omitted the Carpoidea, formally defined by him later (70); BATHER (10), who gave extensive treatment of the cystoids in a textbook that strongly influenced the concept of the class for many years; JAEKEL (70), who published a full classification of the cystoids with formal separation of the Eocrinoidea; BATHER (15) in a review and revision of the class in the *Encyclopaedia Britannica;* and REGNÉLL (99), who excised the Paracrinoidea and revised the Pelmatozoa. To the list of emendations could be added those of other authors, who shaped parts of the class into definitive form: NEUMAYR (91), S. A. MILLER (85), BERNARD (17), BATHER (11, 12), BROILI-ZITTEL (27), BASSLER (5), and BASSLER & MOODEY (7). With all these emendations to which the Cystoidea have been subjected, the class, as herein conceived, nevertheless differs in minor points from any previously published. In general, it is treated much as by JAEKEL in 1918 (71) but without inclusion of the Blastoidea.

The stratigraphic distribution of supra-generic groups of cystoids is shown in Figure 71.

Key to Cystoid Orders, Superfamilies, Families, and Subfamilies

1. Thecal pores developed as rhombs, with units extending across sutures .... *Order* RHOMBIFERA, 2

   Thecal pores developed as units normally contained within plates, commonly as diplopores, rarely extending across sutures .... *Order* DIPLOPORITA, 14

2. Theca composed of 4 *BB*, 5 *ILL*, 5 *LL*, 5 *RR*, and 5 *OO* (with rare exceptions); rhombs as distinct pectinirhombs on particular sutures, outer surface with well exposed slits *Superfamily* GLYPTOCYSTITIDA, 3

   Theca composed of 4 *BB*, 6 to 10 *LL*, 8 or more *LL*, several *RR*; rhombs with inner side of strong folds or laminae perpendicular to sutures, outer side of pores (covered by stereom or epitheca) each surrounded by a rim (or divided into 2 or more smaller pores) .... *Superfamily* HEMICOSMITIDA, 10

   Theca composed of numerous, irregularly arranged plates; pore rhombs on all sides of thecal plates, pores inclined and not connected by inside or outside calcareous tubes .... *Superfamily* POLYCOSMITIDA, 12

   Theca composed of numerous, irregularly arranged plates; pores connected by outer covered tubes *Superfamily* CARYOCYSTITIDA, 13

3. Periproct large, containing numerous plates 4

   Periproct small, anal pyramid surrounded by not more than one circlet of auxiliary plates 6

4. Theca strongly compressed, periproct comprising most of one side of theca, 3 rhombs or less .... *Family* Pleurocystitidae

   Theca ovate, periproct much smaller than one side of theca, numerous rhombs 5

5. Ambulacra short, limited to crown of theca, brachioles relatively few .... *Family* Cheirocrinidae

   Ambulacra long, extending down over theca, brachioles numerous .... *Family* Glyptocystitidae

6. Theca shaped like a pentremite or bud, with marked pentameral symmetry; ambulacra very large, tapering, tongue-shaped; rhombs numerous .... *Family* Cystoblastidae

   Theca ovate, spindle-shaped, globular, or biconvex, but not pentremite-shaped; ambulacra not broad and tongue-shaped; rhombs not very numerous, in many reduced to 3 7

7. Ambulacra short, restricted to crown of theca 8

   Ambulacra long, extending down over theca; periproct never produced .... *Family* Callocystitidae, 9

8. Theca with shape of quadrate spindle; *ILL* and *LL* comprising sides of theca, *RR*

and *OO* alternating small plates in circlet at crown; 3 long vertical rhombs on *LL* set directly above 3 long rhombs on *ILL*; periproct small .... *Family* Rhombiferidae

Theca ovate to subglobular; *RR* large; periproct typically produced .... *Family* Echinoencrinitidae

9. Theca ovate or globular; 4 or 5 divided ambulacra; brachioles small, widely spaced; *LL* intercalated deeply into *ILL* circlet, as many as 3 *LL* in contact with *BB* .... *Subfamily* Callocystitinae

Theca ovate or biconvex; 2 to 4 undivided, strongly protuberant ambulacra; brachioles very numerous, closely spaced; plate circlets variously modified by shape of theca .... *Subfamily* Staurocystinae

Theca ovate; 4 or 5 undivided (except in *Strobilocystites*) ambulacra not protuberant; brachioles relatively widely spaced; *ILL* forming closed circlet .... *Subfamily* Apiocystitinae

10. Ten *ILL* in circlet above *BB* .... *Family* Heterocystitidae

No more than 6 *ILL* in circlet above *BB* .. 11

11. Brachioles few, clustered at top with very short ambulacral grooves; periproct lateral .... *Family* Hemicosmitidae

Brachioles at lateral borders of covering plates (so-called "tegmen"), which forms roof over ambulacral grooves; periproct at upper border of theca .... *Family* Caryocrinitidae

12. Pores not arranged in rows .... *Family* Polycosmitidae

Pores in radial rows ...... *Family* Stichocystidae

13. Theca ovate or elongate; 30 to about 120 plates, tending to be arranged in circlets, alternating; epitheca seldom preserved .... *Family* Caryocystitidae

Theca bullet-shaped or spheroidal; 200 to more than 800 tiny irregularly polygonal plates; epitheca preserved in many specimens as smooth, concentrically striped layer .... *Family* Echinosphaeritidae

14. Theca ovate, saclike, pear-shaped, or globular; ambulacra radial, extending over theca, with alternating lateral branches (single or in groups) to brachioles; most forms stemmed, few becoming free as adults; diplopores restricted to ambulacral plates or spread out over rest of theca .... *Superfamily* GLYPTOSPHAERITIDA 15

Theca with one of several shapes, ovate to conical, with one or other end expanded in some; ambulacra with brachioles concentrated near mouth, not extending over theca; most attached by base of theca; pores irregularly distributed over theca .... *Superfamily* SPHAERONITIDA 16

Theca bud-shaped or bullet-shaped with flat base; ambulacra straight, pentamerally arranged, distally resting on *RR*; stemmed; diplopores only on interambulacral plates .... *Superfamily* ASTEROBLASTIDA 17

15. Theca apple-shaped; stem short; ambulacral grooves long, twisted or zigzag, with few irregularly alternating brachioles, ends may branch to several brachioles; pores in many forms radially disposed, in some concentrated in upper parts of plates .... *Family* Glyptosphaeritidae

Theca saclike, bullet-shaped, or ovate; stemmed as young, but may be free as adult; ambulacral grooves very long, slightly zigzag, with regularly alternating branches leading to brachioles, may extend to aboral end; pores distributed over both ambulacral and interambulacral plates .... *Family* Protocrinitidae

Theca ovate to pear-shaped; stemmed or free; ambulacra long, straight, brachioles at ends of short, very regularly alternating branches, so that those of each ambulacrum are arranged in 2 straight rows; brachiole-bearing plates regularly alternating, bearing diplopores; interambulacral plates irregularly arranged, without diplopores .... *Family* Dactylocystidae

Theca shaped like inverted pear; no special columnar section known; ambulacra spiral, branches (if present) from only one side; brachioles unknown; diplopores distributed over theca .... *Family* Gomphocystitidae

16. Ambulacral grooves distinctly branched immediately from peristome; numerous brachioles in each radius .... *Family* Sphaeronitidae

No extensions of any kind known in food grooves; at most, one brachiole in each radius, number may be reduced to 2, no brachioles or attachment known for some forms .... *Family* Aristocystitidae

17. Theca bud-shaped; ambulacra broad, leaflike; brachioles relatively few; 4 *BB*, 6 *ILL*, other plates in circlets, and several additional intervening plates .... *Family* Asteroblastidae

Theca bullet-shaped, base rather flat; ambulacra very narrow, long, straight; numerous brachioles; plates small, exceptionally numerous .... *Family* Mesocystidae

Order RHOMBIFERA Zittel, 1879

[*nom. correct.* BATHER, 1899 (*pro* Rhombiferi ZITTEL, 1879)] [=Rhombiporitidae+Taxiporitidae EICHWALD, 1860; Dichoporita JAEKEL, 1899]

Thecal pores developed as dichopores, arranged in rhombs in which each unit or dichopore is shared by 2 adjacent plates. *L.Ord.-U.Dev.*

The structure of the rhombs varies in the order and serves as the character by which the four superfamilies can be differentiated. The number of rhombs also varies, from very few in most of the Glyptocystitida to very numerous in the Caryocystitida.

The thecal plates are regularly arranged in the cystoids included in the Glyptocystitida and Hemicosmitida, but not in the Polycosmitida and Caryocystitida. A column is present in most of the Rhombifera, but is absent in some of the Caryocystitida.

Insofar as known, the Rhombifera includes the last surviving cystoids.

Superfamily GLYPTOCYSTITIDA Bather, 1899

[*nom. transl.* REGNÉLL, 1945, p. 68 (*ex* Glyptocystidae BATHER, 1899, p. 920)] [=Regularia JAEKEL, 1899, p. 193; superfamily Glyptocystidea BATHER, 1913, p. 433]

Theca in most genera composed of four *BB*, five *ILL*, five *LL*, five *RR*, and five *OO*, although plate *O1* is tripartite in many genera and *R1* is bipartite in some; a few anomalous plate divisions known to occur in some specimens. Rhombs developed as distinct pectinirhombs, most as full rhombs and a few as demirhombs, with well-exposed pores or slits. Column present, in most forms with expanded, flexible proximal part. *L.Ord.-U.Dev.*

Within this superfamily certain trends are well demonstrated. First, the number of rhombs tends to be reduced to three: *B2/IL2*, *L1/R5*, and *L4/R3*. In the strongly modified Pleurocystitidae, the rhombs *L3/L4*, *L1/L2*, and *B2/IL2* show persistence in that order. Second, the periproct tends to show specialization; in the Pleurocystitidae and to a lesser degree in the Glyptocystitidae and Cheirocrinidae, it is enlarged and filled with numerous small plates (periproctals) in addition to the anal pyramid; in the Echinoencrinitidae it tends to be prolonged and protuberant, but with a small opening. Third, the pore rhombs become specialized, whereby one of the halves is surrounded by a rim (e.g., *Pseudocrinites, Lovenicystis*) or even reduced to a small circular opening with a tubular border (e.g., *Jaekelocystis*). Fourth, the hydropore changes from an elongate slit bisected by a suture through *O1* to two separate openings (e.g., *Lipsanocystis, Strobilocystites*) or even reduced to one large sievelike opening, perhaps combined with the gonopore (e.g., *Jaekelocystis*). On the other hand, there is no consistent progression with regard to ornamentation of plates or size of theca.

Because the plates occur with regularity, they can be compared readily from one genus to another. As a result, this superfamily is best known and understood. It also has, perhaps, the longest range, definitely so if the Cambrian Aristocystitidae are discounted as unsubstantiated cystoids; at any rate, this superfamily contains the last surviving cystoids known, from the Upper Devonian of Iowa.

The stratigraphic distribution of genera belonging to the Glyptocystitida is shown in Figure 72.

Family GLYPTOCYSTITIDAE Bather, 1899

[*nom. correct.* KESLING, herein (*pro* Glyptocystidae BATHER, 1899, p. 920)]

Theca more or less ovate, not compressed. Periproct large, containing numerous plates in addition to anal pyramid, but not comprising most of one side of theca. Pore rhombs numerous. Ambulacra long, extending down over theca ("recumbent"), provided with numerous short alternating branches to brachiole facets; one or more ambulacra extending to *BB* in adults. *M. Ord.*

This family is known only from North America. The species include the type, *G. multiporus* BILLINGS, and the more recently described *G. batheri* SINCLAIR, *G. grandis* SINCLAIR, *G. regnelli* SINCLAIR, and *G. ehlersi* KESLING. Aside from the circumstance that ambulacrum IV is much shorter in *G. regnelli* and *G. ehlersi* than in the other species, there seems no grouping that would serve a useful taxonomic purpose. The family, therefore, remains monogeneric.

Glyptocystites BILLINGS, 1854, p. 215 [**G. multiporus*; OD] [=*Glyptocystis* BATHER, 1900, p. 64 (*nom. van.*)]. Theca elongate ovate or subpyriform, with *BB* somewhat indented for junction with the column. Rhombs numerous, one-half of each normally bordered by rim ("monti-disjunct"), 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).

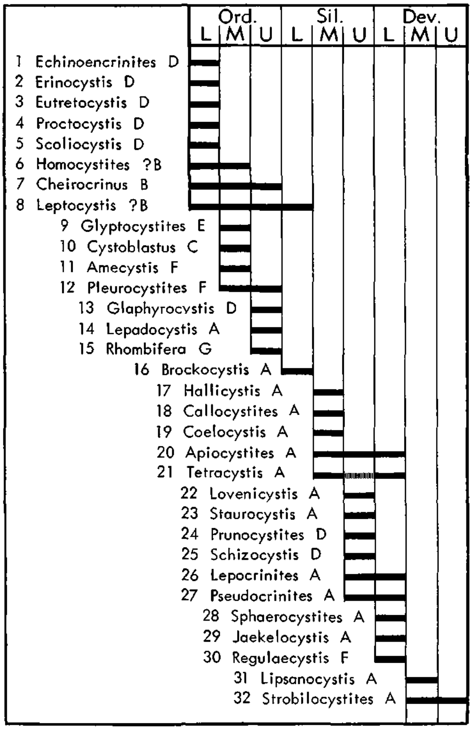


Fig. 72. Stratigraphic distribution of genera belonging to the superfamily Glyptocystitida. Classification of the genera in families is indicated by letter symbols: A—Callocystitidae, B—Cheirocrinidae, C—Cystoblastidae, D—Echinoencrinitidae, E—Glyptocystitidae, F—Pleurocystitidae, G—Rhombiferidae. The 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

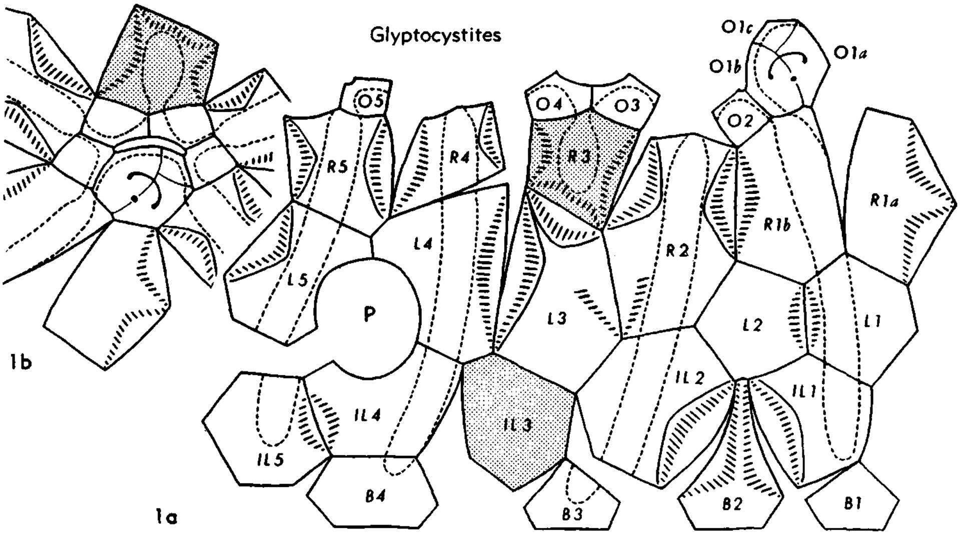


FIG. 73. Glyptocystitidae (p. *S*169-*S*170). [Plate designations as in Figure 38.]

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

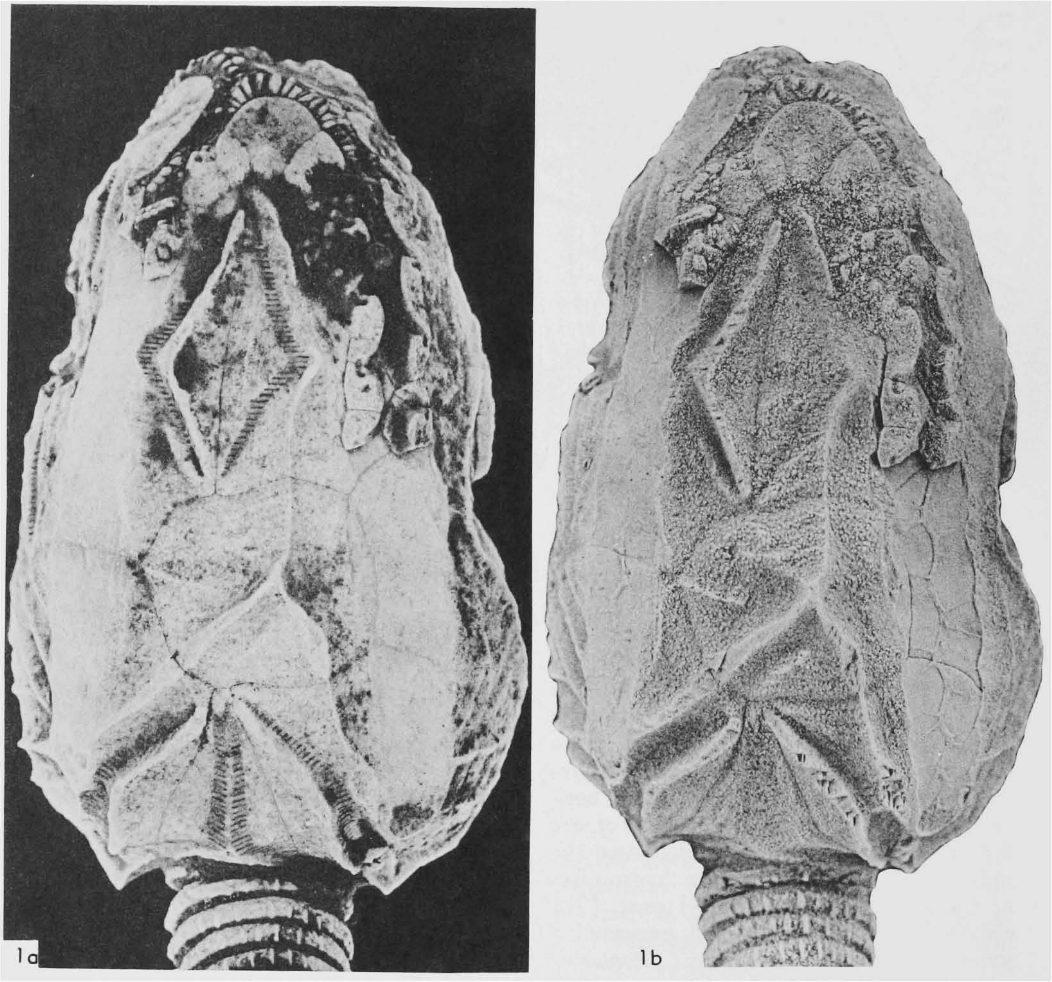
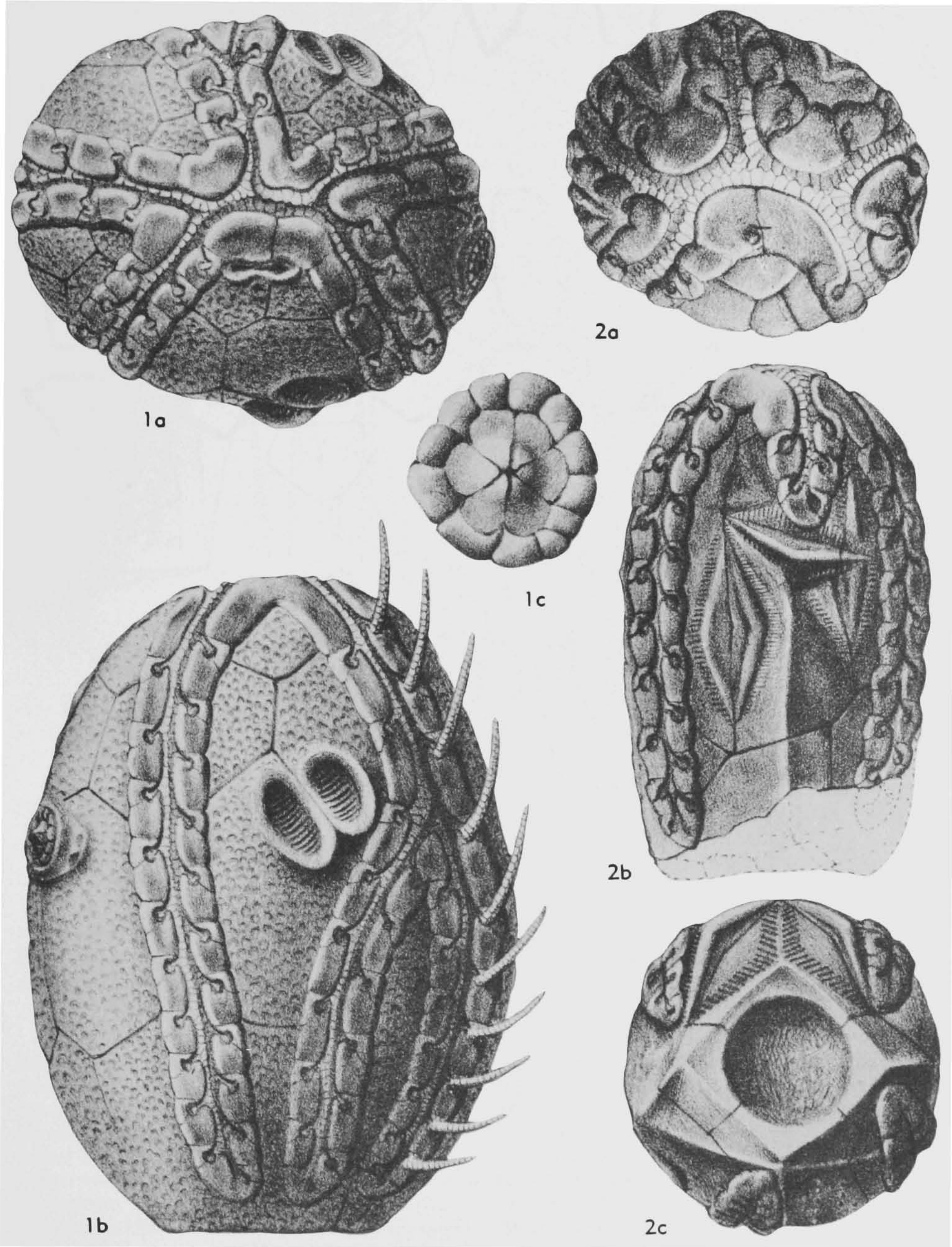


FIG. 74. Glyptocystitidae (p. S169-S170).——*1. Glyptocystites ehlersi* KESLING, M.Ord., USA(Mich.); *1a,b,* lat. view (*L2* near center, below rhomb), coated with ammonium chloride and submersed in xylol, ×3.75 *(73).*

of their length, obtusely at junction with *OO*. It appears dubious that *RR* could be forked plates, as originally described and shown in most figures, for it would necessarily follow that ambulacra in this genus are not superficial but integral parts of the theca, with no thecal plates on which to rest; this would be such a drastic departure from cystoid morphology that *Cystoblastus* might well be removed to form another class. Four *LL* kite-shaped, acutely acuminate adorally and obtusely acuminate aborally. *OO* subequal, small; one oral in type species said to have perforation at its distal corner, hydropore, situated at head of *R4/R5* suture; all other orals apparently with long narrow extensions down onto *LL* below. Two full rhombs on *B2* and adjacent *ILL*; 2 long demi-rhombs on each radial, shared with plates on either side; pore slits numerous, from 550 to about 1,800 listed. Periproct round, rather small, shared about equally by *IL4*, *L4*, and *R4*. Ambulacra tongue-shaped, with numerous alternating brachiole facets (about 60 and about 200 in the two known species). Plate designations in the type species present a dilemma, and no solution is entirely satisfactory or consistent with other cystoids. JAEKEL (69), in his elaborate discussion of the genus, showed *L1* at right of *R1* in his Fig. 42 and at left of it in his Fig. 43; he also confessed to bewilderment at position of the hydropore reported by VOLBORTH (1867), and said that he had been unable to find such a structure in his specimens. If the hydropore is present where stated, then by analogy with other cystoids it should lie between *R1* and *R5*, whereby

R5 would be the radial bordering the periproct; but the rhomb-bearing basal should by analogy *B2* and the subhexagonal basal *B4,* the lateral above *B2* should be *L2,* the radial between *L1* and *L2* should be *R1,* and the radial bordering the periproct would be *R4.* In one plate diagram, the *RR* are designated with reference to the hydropore as commonly figured in the type species and other plates with reference to the basal rhombs; in the other, the *RR* are designated with



Callocystites **Glyptocystites**

FIG. 75. Callocystitidae; Glyptocystitidae (p. *S*169-*S*170; *S*199-*S*201).

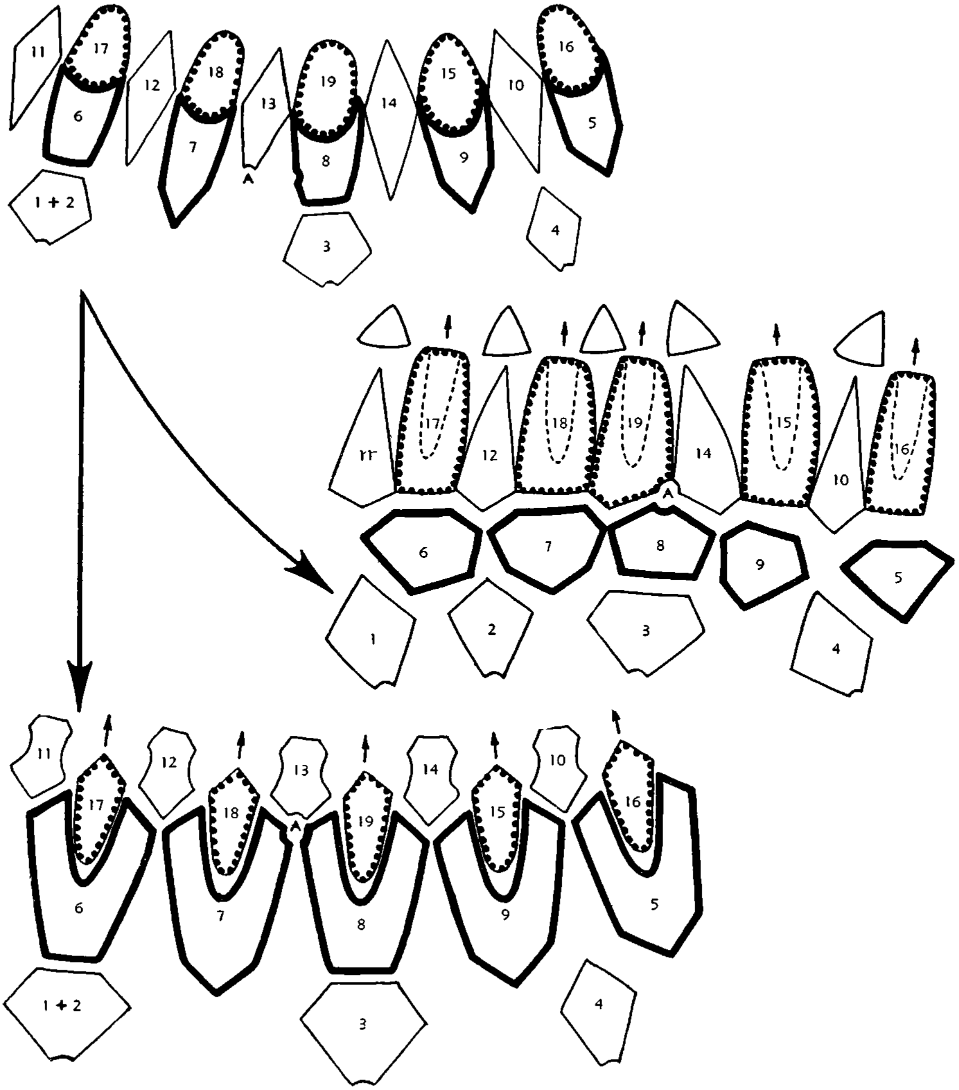


FIG. 76. Hypothetical derivation of cystoids and blastoids from a common ancestor as suggested by MOORE (1954); *1*, “hypothetical evolutionary derivative of a pre-*Cystoblastus* type”; *2*, *Cystoblastus; 3,* typical eublastoid with lancet plates identified as rhombiferan RR, deltoids as rhombiferan LL, and radials as rhombiferan *ILL* (89).

reference to other plates, so that they are directly adoral to corresponding *ILL*, and the reported position of the hydropore is assumed to be erroneous, as indicated by YAKOVLEV. One might suspect that VOLBORTH erred in his interpretation or description; his type specimen was already lost when JAEKEL made his study in 1899. YAKOVLEV (143-146) discovered a different situation in *Cystoblastus kokeni* JAEKEL, one which agrees with the arrangement in other cystoids of the Glyptocystitida. He found the hydropore and gonopore to be in the normal posiiton with respect to the basal pore rhombs, the missing *L* to be *L4*, and the periproct to be in the interambulacrum between III and IV. The hydropore in this species is a group of perforations forming a sieve structure more or less to the right of the small round gonopore. *M.Ord.*, Eu.(Est.-USSR).——FIG. 76. Relationship of *Cystoblastus* to blastoids (Kesling, n).——FIG. 77,*1*. **C. leuchtenbergi*, USSR; *1a-c*,

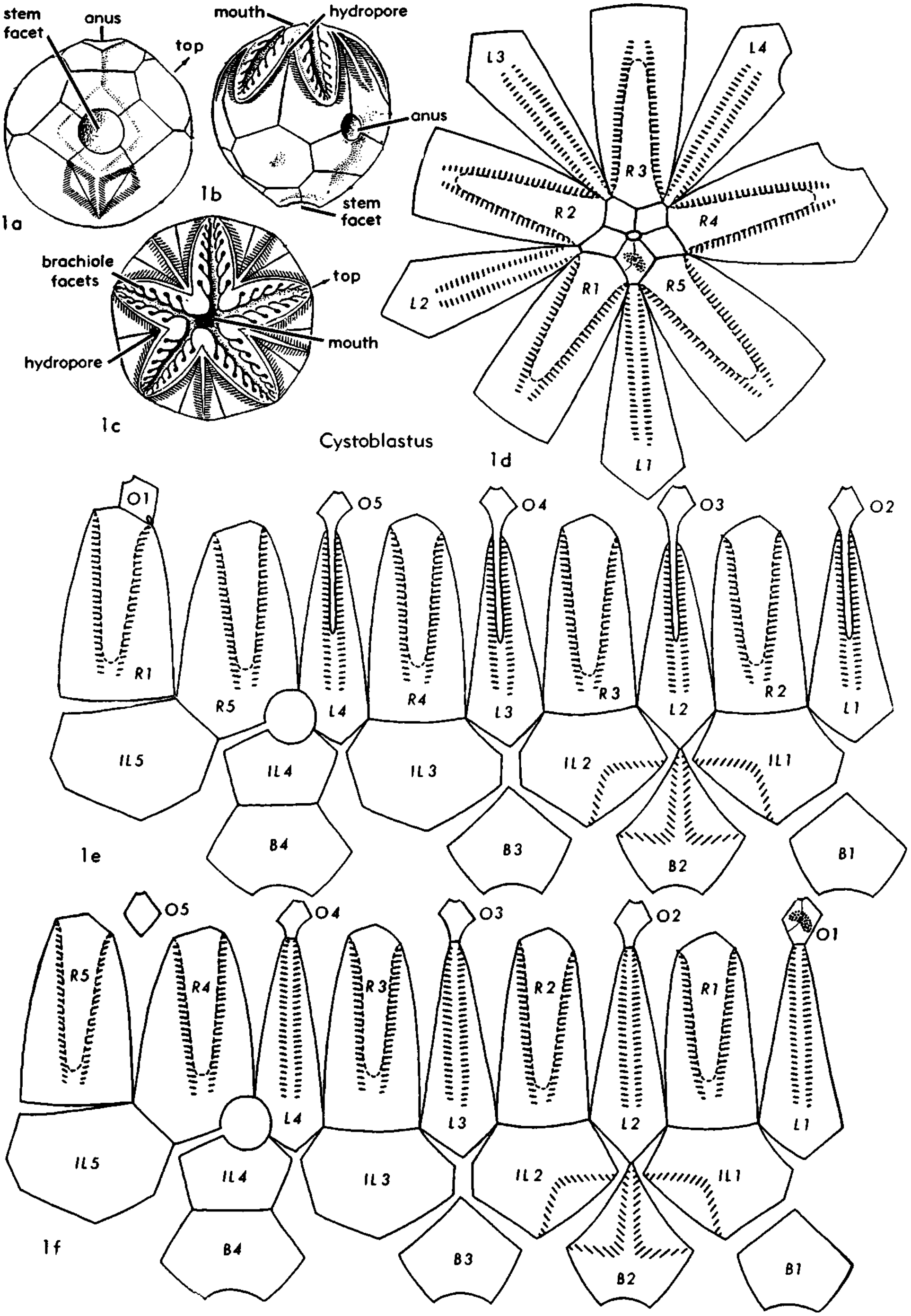


FIG. 77. Morphology of *Cystoblastus.*——*1.* **C. leuchtenbergi* VOLBORTH, M.Ord., Eu.(USSR); *1a-c,* aboral, lat., oral views of theca, ×4 (10); *1d,* oral region (diagram. reconstr.) (Kesling, n); *1e,* plate diagram to accord with VOLBORTH's original description (Kesling, n).——*1f. C. kokeni* JAEKEL, M.Ord., Eu. (Est. diagram); plate diagram interpreted in accordance with YAKOVLEV's description (Kesling, n). [Plate designations as in Figure 38.]

aboral, lat., oral views, ×4 (10); *1d,* oral region (diagram. reconstr.) (Kesling, n); *1e,f,* plate diagrams interpreted according to VOLBORTH's original description and according to YAKOVLEV's description of *C. ḳoḳeni* (Kesling, n).——FIG. 79. *C. ḳoḳeni* JAEKEL, Kuckers (C_2), Est.; oral view (reconstr.), approx. ×2 (Cuénot, 1953, after Yakovlev).

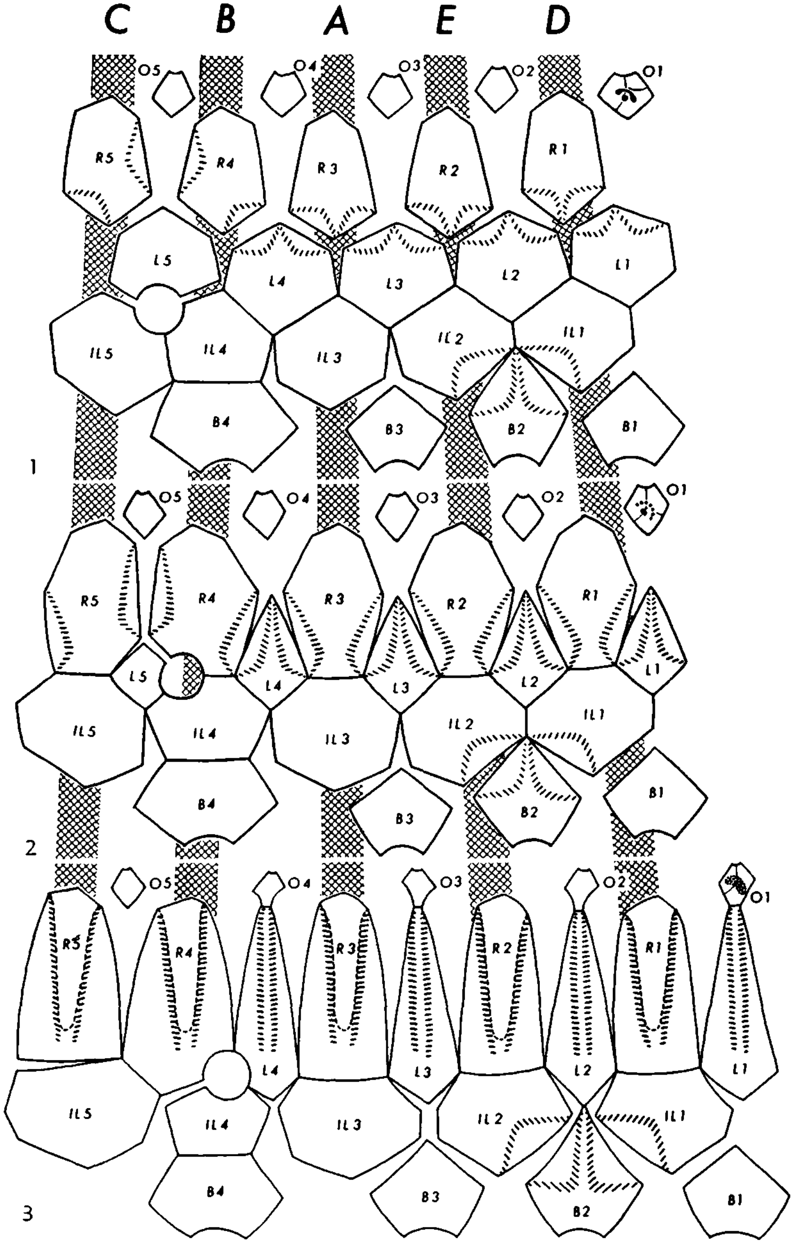


FIG. 78. Hypothetical derivation of *Cystoblastus (3)* from a generalized glyptocystitidan ancestor *(1)* with an intermediate stage (2). As shown, the evolution is supposed to have involved (1) diminution and disappearance of *L5,* (2) insertion of *RR* between *ILL* to rest atop corresponding *LL,* (3) shift of periproct from *IL5-L5-IL4* position to *IL4-R4-L4,* (4) elongation of *L1-L4* suture, and (5) modification of hydropore from simple slit to perforated area (Kesling, n). [Plate designations as in Figure 38.]

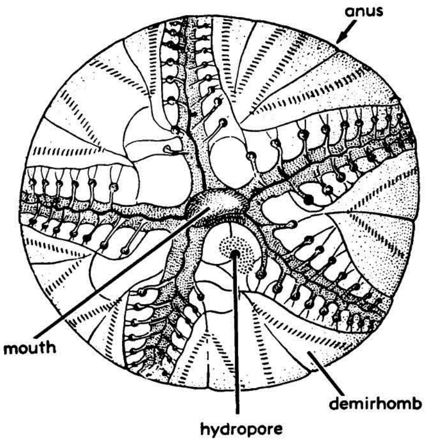


FIG. 79. Cystoblastidae (p. *S*171-*S*176). *Cystoblastus kokeni* JAEKEL, M.Ord., Eu.(Est.); oral view (reconstr.), ca. ×2 (Cuénot, 1953, from Yakovlev).

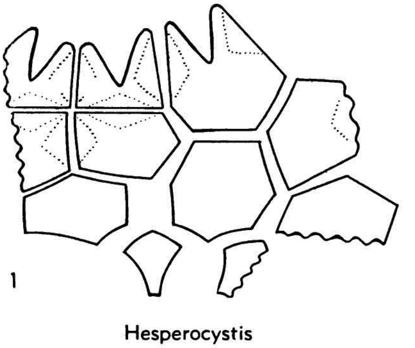


FIG. 80. Cystoblastidae (p. *S*177).——*1.* **Hesperocystis deckeri* SINCLAIR, M.Ord., USA(Okla.); plate diagram of preserved part of holotype*(117)*.

Hesperocystis SINCLAIR, 1945, p. 709 [**H. deckeri*; OD]. Theca known only from fragment preserving a few plates, which from description and figures I account as *B3*, *IL2*, *IL3*, *L3*, *R1*, *R2*, and parts of *B2*, *IL1*, *L2*, *L4*, and *R3*. No part of periproct or hydropore recorded, making orientation difficult. The 2 *BB,* from their position away from the periproct, cannot include *B4*; the left one is near center of known thecal area, and considered to be *B3*. Strangely, there is no basal rhomb; insofar as known, rhombs begin at the *LL* level; full rhombs are present as follows: *L2/?L1*, *L3/L4*, *L3/R2*, *L4/R3*, *R1/?R5*, and *R1/R2*; 3 demirhombs, one at each end of the *R2/R3* suture. *IL1*, *IL2*, and *IL3* in a continuous row; *L2* separated from *L3* by *R1/IL2* suture; *R1*, *R2*, and *R3* in a continuous row; *L3*, *L4*, *R2*, and *R3* with their right-angle corners meeting to form a +; *R1* considerably larger than other 2 *RR*. Ambulacra broad, like those of *Cystoblastus,* probably extending halfway down *RR*. [The pentremite shape of the known specimen, coupled with the broad ambulacra and rhomb-bearing *RR,* indicates a probably secure association with *Cystoblastus*.] *M.Ord.,* USA(Okla.).——FIG. 80,*1*; 81,*1*. **H. deckeri*; 80,*1*, plate diagram of holotype, only known specimen; 81,*1*, lat. and oral, holotype, ×1.5 (117).

Family RHOMBIFERIDAE Kesling, 1962

[Rhombiferidae KESLING, 1962, p. 281]

Theca extremely elongate, spindle-shaped, consisting of five *OO*, five *RR*, five *LL*, at least four *ILL* (presumably five), and probably four *BB*. Rhombs developed only between *ILL* and between *LL,* unusually large. *RR* reduced to small plates alternating with *OO* and with them forming slightly elevated ring, corona-like, around peristome. Brachioles erect, attached to facets that nearly fill *RR* plates. *U.Ord*.

As pointed out by KESLING (74), no lineage is known that indicates even faintly the relationship of the bizarre cystoid known as *Rhombifera*. The vertical align-

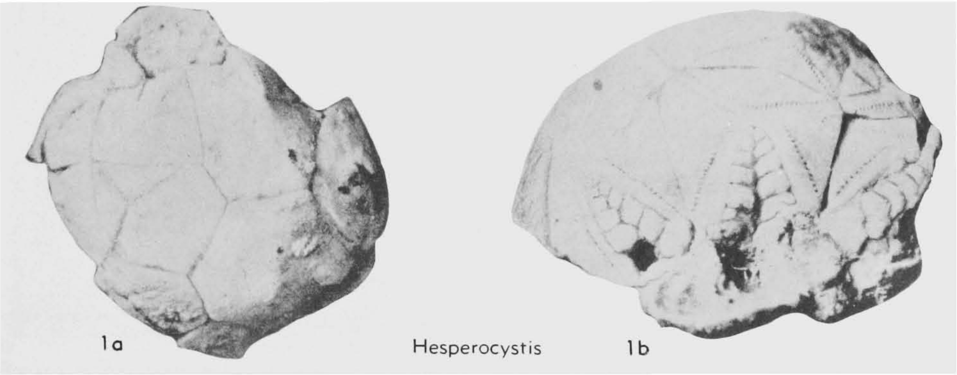


FIG. 81. Cystoblastidae (p. *S*177).

ment of *ILL* and *LL* is unique, as is the extreme reduction of *RR*. The presence and nature of pore rhombs are sufficient to assign it to the order Rhombifera, superfamily Glyptocystitida.

Rhombifera Barrande, 1867, p. 175 [**R. bohemica*; OD]. Theca shaped like a quadrate spindle, or bipyramidal, with adoral and aboral halves resembling high, square, truncated pyramids attached base to base; each face somewhat convex. Corona-like ring around mouth formed of slightly elevated alternating *OO* and *RR*. Periproct near mouth, directed upward with its aboral side extended outward, transverse subelliptical opening formed by deep indentation in *L3* and shallow one in *L4*. *BB* probably very small, to judge from steinkerns of thecae. *ILL* and *LL* large, with each of *LL* set above corresponding *ILL* and aligned with it; except for eccentric periproct, a plane of symmetry through *IL4* and *L4* and *IL1*/*IL2* and and *L1*/*L2* sutures; *IL4* and *L4* narrow vertical strips along one face of theca, and other *ILL* and *LL* each angled to form edges of quadrate spindle. Six large rhombs, each set along vertical suture: 3 full rhombs *IL1*/*IL2*, *IL1*/*IL5*, and *IL2*/*IL3*, and 3 demirhombs *L1*/*L2*, *L1*/*L5*, and *L2*/*L3*, rhombs filling most of each face of theca, provided with numerous oval pores. Brachiole facets subcircular, large, one on each *R* and filling most

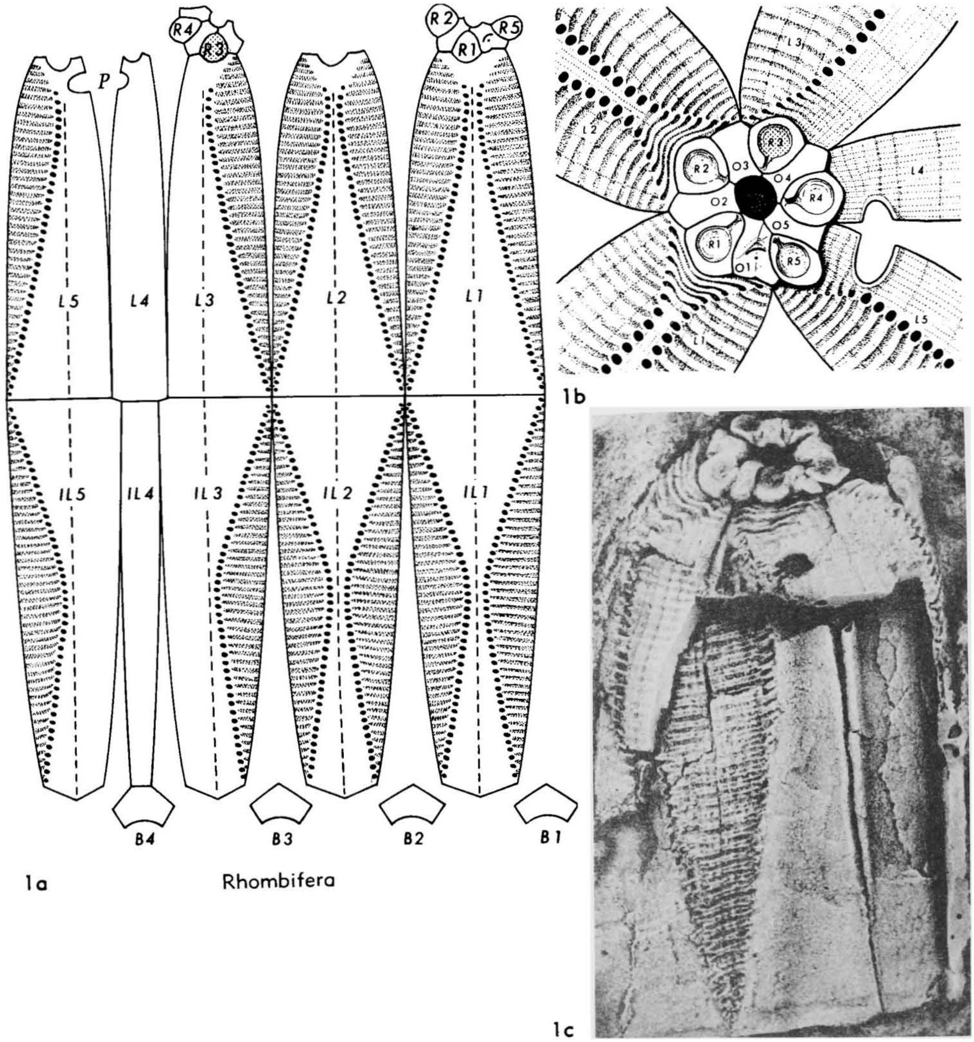


Fig. 82. Rhombiferidae (p. S178-S179).——1. **Rhombifera bohemica* Barrande, U.Ord., Eu.(Czech.); *1a*, plate diagram, ×2; *1b*, oral region, ×4; *1c*, latex cast showing part of interior on opposite side of theca, ×4 *(74)*. [Plate designations as in Figure 38.]

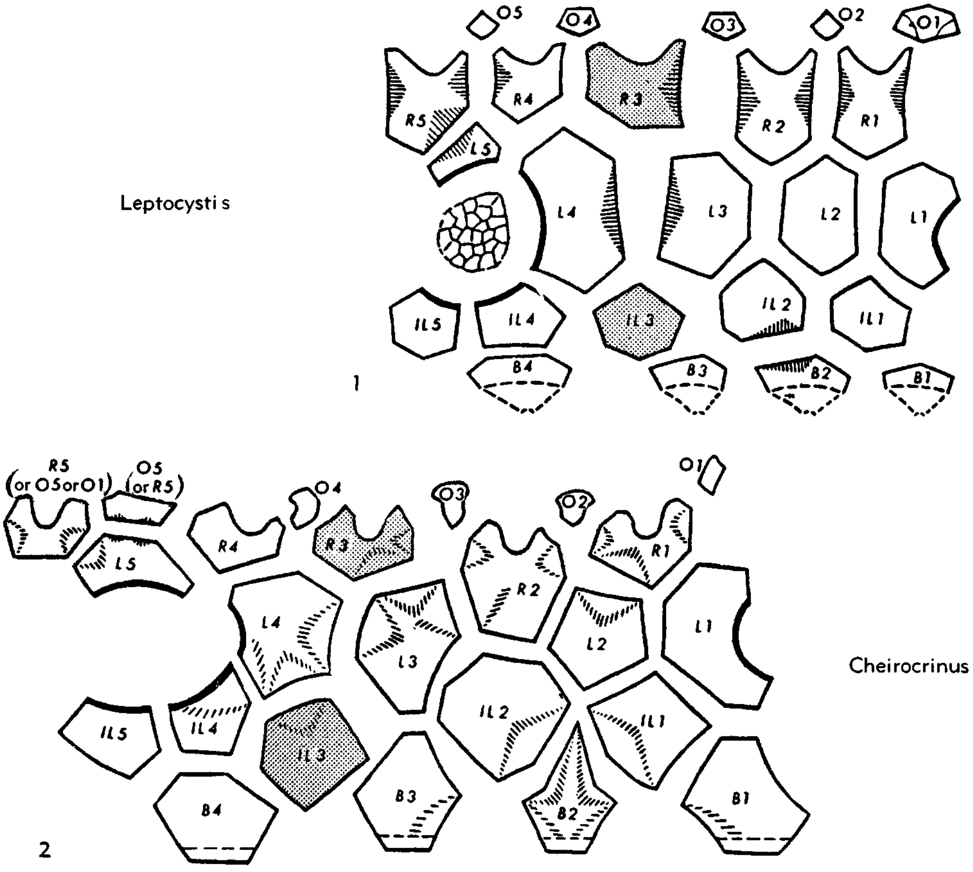


Fig. 83. Cheirocrinidae (p. S182-S184).——*1. Leptocystis constricta* (Bather), U.Ord., Scot.; plate diagram *(12)*.——2. **Cheirocrinus penniger* (Eichwald), L.Ord., Eu.(Est.); plate diagram *(12)*. [Plate designations as in Figure 38.]

of plate. Hydropore and possibly gonopore on *O1*, each small. *U.Ord.*, Eu.(Czech.).——Fig. 82,*1*. **R. bohemica*; *1a*, plate diagram, ×2; *1b*, oral region, ×4; *1c*, latex cast showing part of interior on opposite side of theca, ×4 (73).

Family CHEIROCRINIDAE Jaekel, 1899

[*nom. correct.* Bather, 1913, p. 434 (*pro* Chirocrinidae Jaekel, 1899, p. 212)]

Theca irregularly ovate, *BB* indented to accommodate junction with column. Plates of each row may form complete circlets, or *ILL* may be interrupted by aboral displacement of *L2* or *L3*, or both, or *LL* by insertion of *R2* between *L2* and *L3*; *R1* represented by two plates in many species, so that circlet of *RR* contains six plates. Periproct large, containing numerous small platelets in addition to anal pyramid. Ambulacra short, radiating from peristome atop flat or slightly arched oral region, which more or less truncates theca, each bordered by few brachioles; ambulacra never extending far, if at all, onto *RR*. Pectinirhombs numerous, developed as full rhombs or as demirhombs, conjunct or disjunct, ranging from eight to more, commonly 15 or more; rhombs *B2/IL2*, *L3/L4*, *L5/R1a*, *R1b/R2*, and *R2/R3* present on most, if not all, species; many species with rhomb *B2/IL1*, and some with rhombs between all *RR* (Fig. 83, 84). *L.Ord.-L.Sil.*

Most workers recognize only one genus, *Cheirocrinus*. Jaekel (69) explained his reasons for creating *Leptocystis*, but later (71) ignored it completely. The genus *Homocystites* was placed in synonymy with

Cheirocrinus shortly after its erection by BARRANDE (3) and kept there. Some grounds, however, support recognition of a genus including cystoids like *Homocystites alter* BARRANDE, as distinguished from those like *Cheirocrinus penniger*

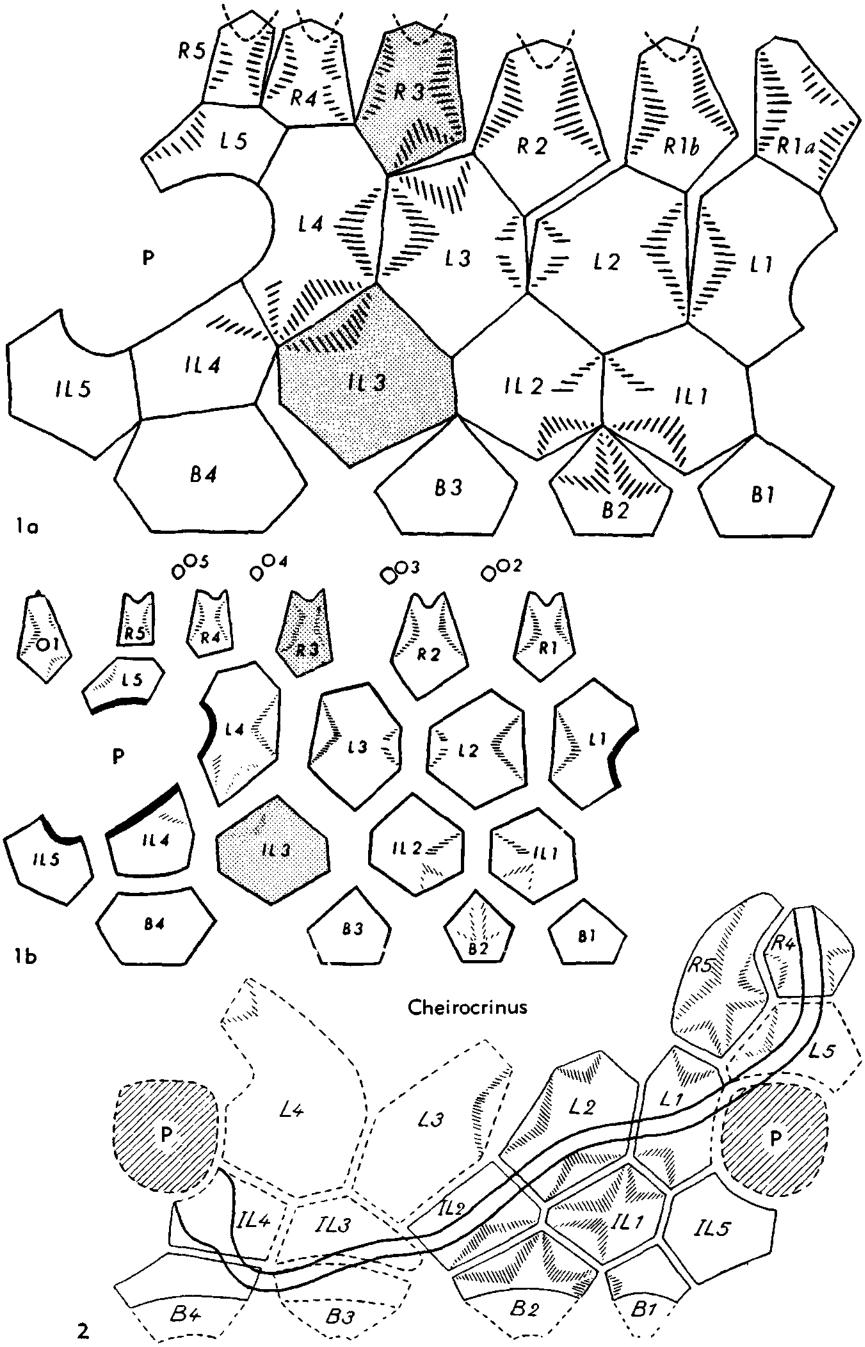


FIG. 84. Cheirocrinidae. Plate diagrams, plates of *A*-ray shaded, designations of plates as in Figure 38 (p. S182).

(Eichwald). Jaekel (69) divided the species having demirhombs into three groups: (1) those with only *"Spannleisten"* (ridges from centers of plates to each of the sides), (2) those with both *"Spannleisten"* and parallel *"Nebenleisten"* (ridges perpendicular to sides of plates), and (3) those with *"Gitterskulptur"* (reticulation of ridges and growth lines). Of these groups, the type species of *Cheirocrinus* represents the first and that of *Homocystites* the more highly ornamented second. Here *Homocystites* is expanded to include the third group also, which is obviously closely related to the second. It seems preferable to explain the kinds of cystoids associated with each genus than to lump all together without any recognition.

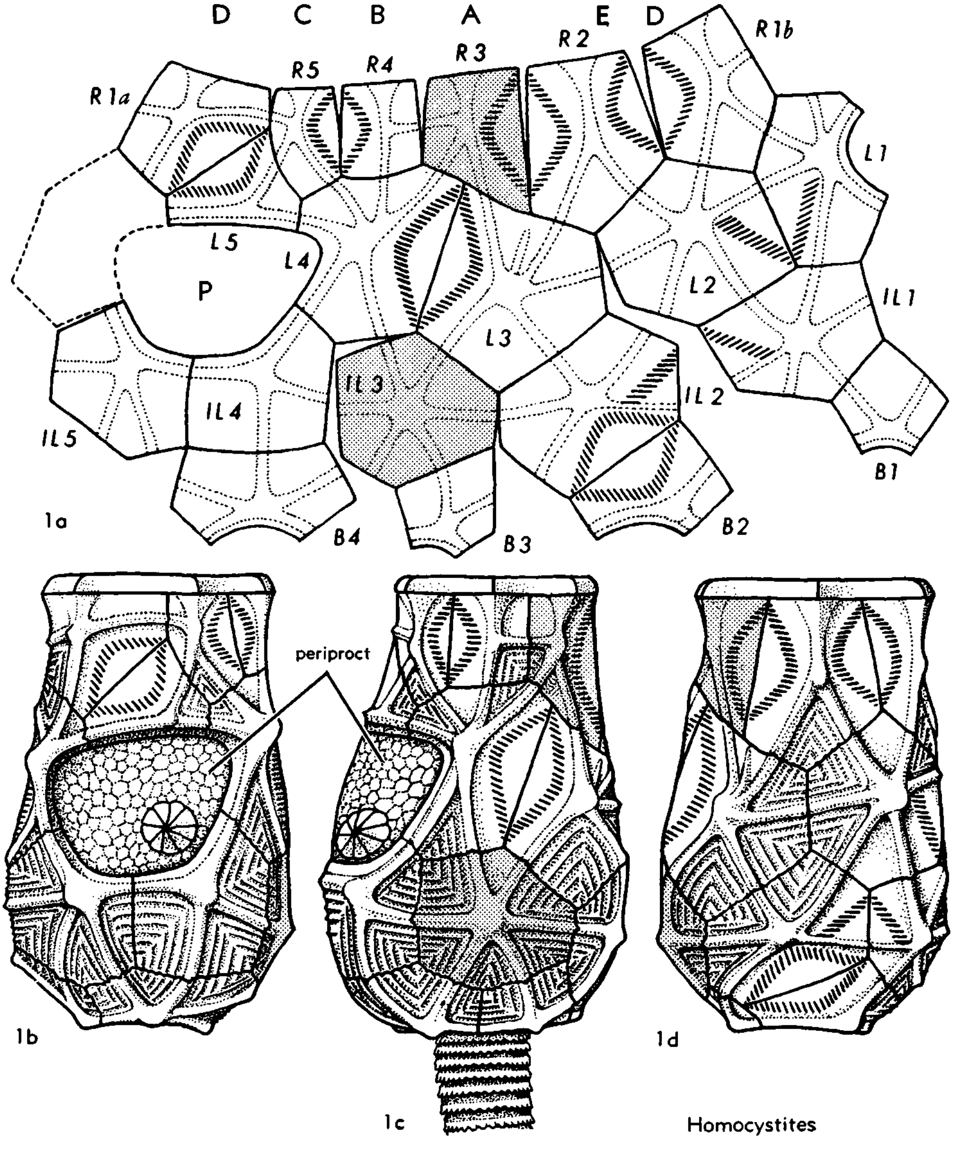


Fig. 85. Cheirocrinidae (p. S182-S184).——*1. Homocystites anatiformis* (Hall), M.Ord., USA(Mich.); *1a*, plate diagram; *1b-d*, reconstructions of theca in lateral views, ca. 2.5 *(74)*. [Plate designations as in Figure 38, inferred rays of Carpenter system indicated by capital letters at top.]

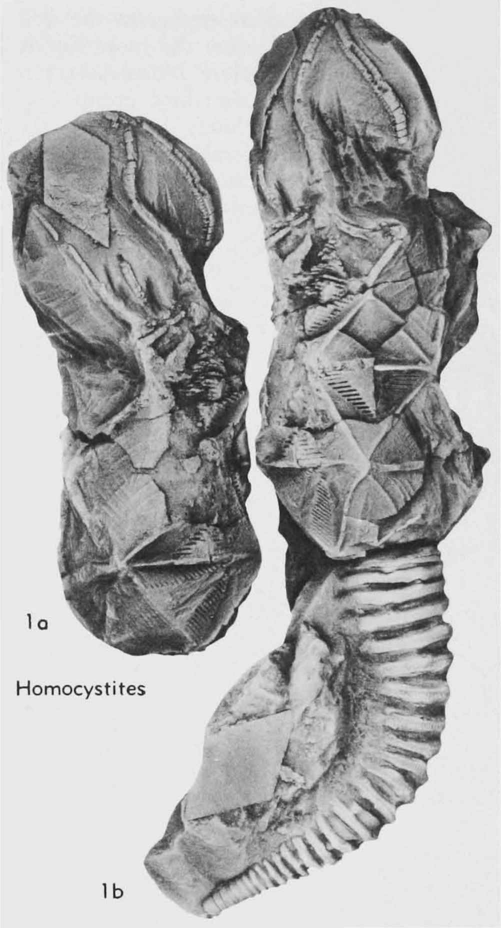


FIG. 86. Cheirocrinidae (p. S183-S184).

The crux of the taxonomic problem is whether to accredit the characters originally attributed to each genus as restrictive or to interpret and revise the description to accord with observations of the type species. Thus, JAEKEL (69) noted in *Leptocystis tertius* an association of conjunct rhombs and proximal columnals that did not appear to be telescoped but all of subequal size. In the species described by BATHER (12) as *Cheirocrinus constrictus,* however, conjunct rhombs are associated with strongly modified proximal columnals. I am inclined to regard the nature of the rhombs as significant, for the fact that the column is unknown in many specimens, if for no other reason.

Thus, to *Cheirocrinus* would be assigned *C. radiatus* JAEKEL, *C. volborthi* (SCHMIDT), *C. penniger* (EICHWALD), *C. granulatus* JAEKEL, *C. leuchtenbergi* (ANGELIN), *C. nodosus* JAEKEL, and probably the incompletely known *C. interruptus* JAEKEL and *C. ornatus* EICHWALD; to *Homocystites, H. alter* BARRANDE, *H. anatiformis* (HALL), *H. insignis* (JAEKEL), *H. forbesi* (BILLINGS), *H. sculptus* (SCHMIDT), *H. degener* (JAEKEL), *H. striatus* (JAEKEL), *H. angulatus* (WOOD), and *H. walcotti* (JAEKEL); and to *Leptocystis, L. tertius* (BARRANDE), *L. atavus* (JAEKEL), *L. giganteus* (LEUCHTENBERG), and *L. constrictus* (BATHER).

Key to Genera of Cheirocrinidae

1. Pectinirhombs developed as conjunct rhombs, at least on the base .... *Leptocystis*
   Pectinirhombs developed as disjunct or multidisjunct rhombs 2
2. Theca ornamented only by ridges radiating from centers to sides of plates, forming a large network of triangles ...... *Cheirocrinus*
   Theca ornamented by both large radiating ridges from centers to sides of plates and parallel lateral ridges, forming concentric triangles with the former; lateral ridges may be interrupted by growth lines to make a reticulate sculpture ...... *Homocystites*

Cheirocrinus EICHWALD, 1856, p. 123 [*non* SALTER in MURCHISON, 1859, *nec* HALL, 1860] [**Cyathocrinus penniger* EICHWALD, 1842, p. 78; OD] [=*Chirocrinus* HAECKEL, 1896, p. 402 *(nom. van.), non* ANGELIN, 1878 *(nom. van. pro Cheirocrinus* SALTER, *non* EICHWALD)]. Pectinirhombs normally including some demirhombs as well as full rhombs, in many species varying greatly in size and shape. Thecal plates ornamented only by ridges radiating from centers to each of sides, in some forms with gentle slopes to sides and not with sharply defined boundaries. Most, perhaps all, species with 2 half-rhombs on *B2* and at least 3 rhombs shared by *RR.* Brachioles confined to crown of theca, along the sides of the ambulacra, which are short and never branch. Hydropore and gonopore, insofar as known, bisected by suture through plate *O1.* Columnals appearing to be telescoped, perhaps all columns in proximal part composed of outer columnals flexibly held by interlocking inner columnals. Periproct large. *L. Ord. - U. Ord.,* USSR - Est. - Scand. - Belg.-Scot. ——FIG. 83,*2*; 87,*1*. **C. penniger* (EICHWALD), L.Ord., Eu.(Est.); 83,*2,* plate diagram (12); 87,*1a,b,* lat., two thecae, ×1 (69).——FIG. 84, *1a,b*; 88,*1*. *C. radiatus* (JAEKEL), L.Ord.(Kunda, B_3), Eu.(USSR); 84,*1a,b,* plate diagrams (Kesling, n, after 12, 69); 88,*1,* lat. view, *L2* near center, ×2 (69).——FIG. 84,*2*. *C. hyperboreus* REGNÉLL, L.Ord($3c\beta$), Norway; diagram of known plates with heavy lines indicating inferred course of the gut (100). [See also Fig. 34,*2*, 48,*1*.]

?**Homocystites** Barrande, 1887, p. 160 [**H. alter*; OD] [=*Homocystis* Bather, 1889, p. 269 *(nom. van.)*]. General shape and plate arrangement like that of *Cheirocrinus,* of which some consider this genus to be a junior synonym. Rhombs highly developed, demirhombs commonly in form of

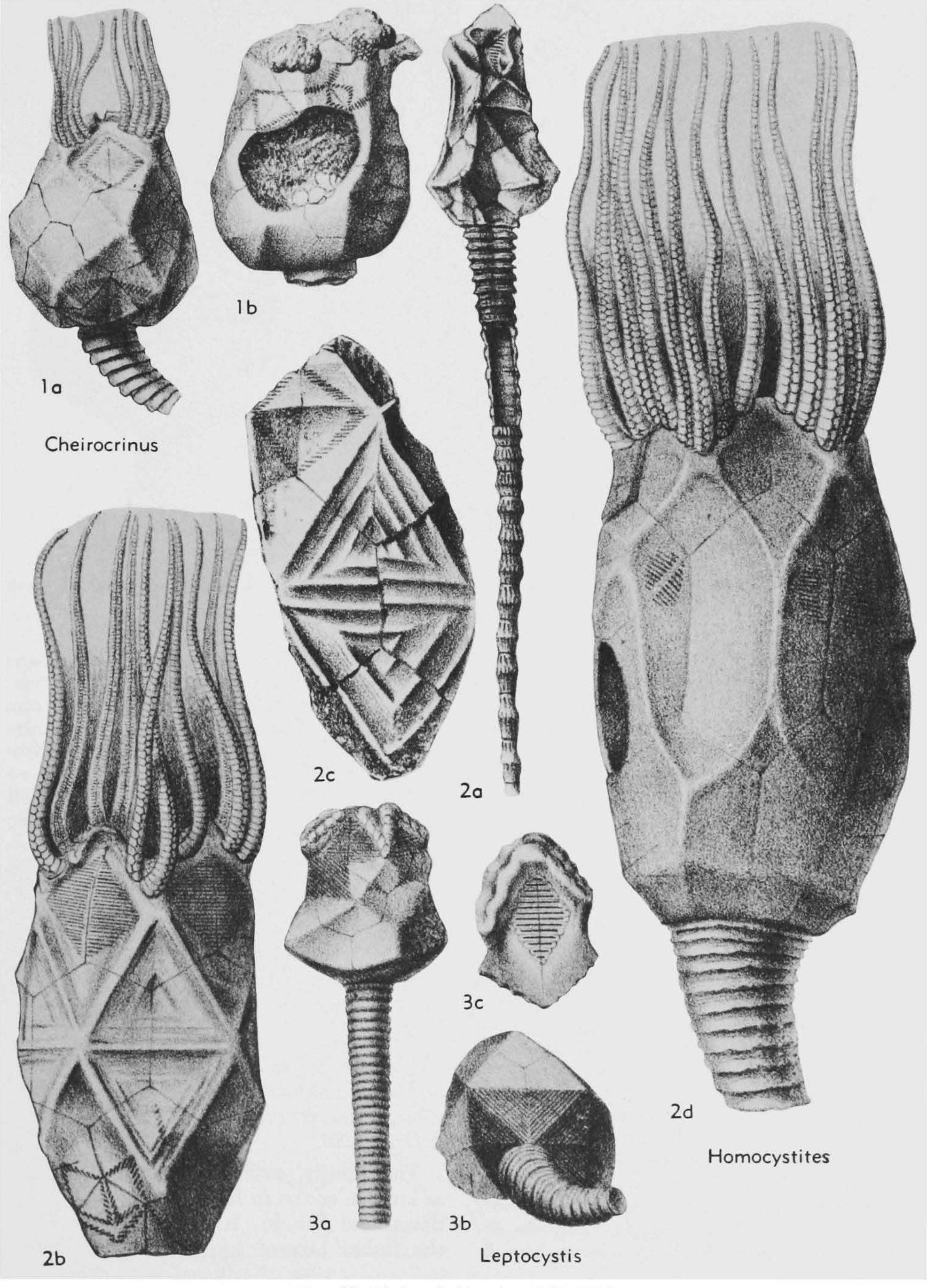


Fig. 87. Cheirocrinidae (p. S182-S184).

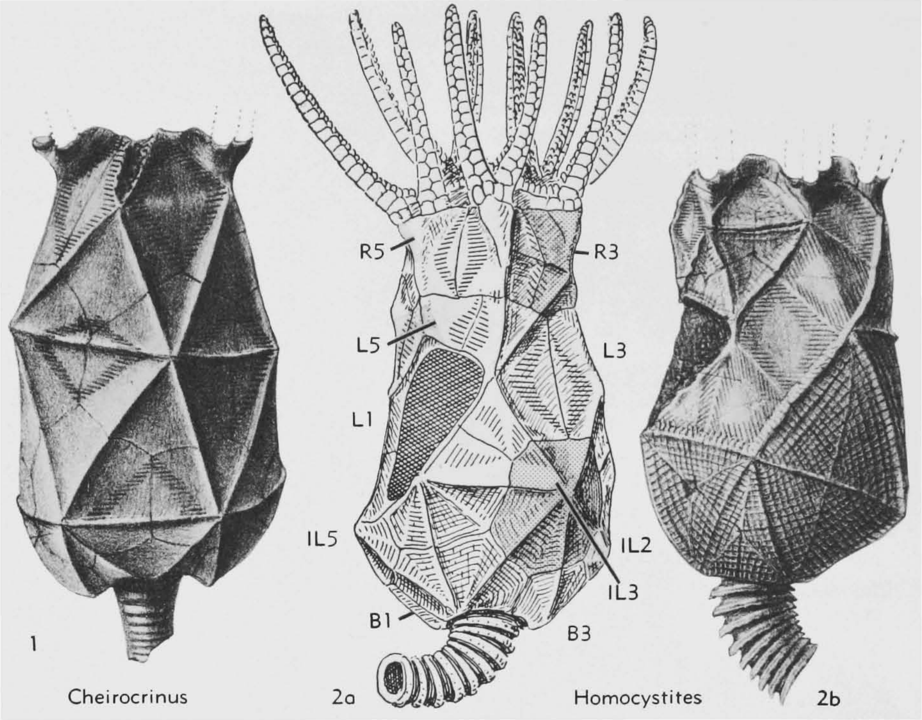


FIG. 88. Cheirocrinidae, plates of *A*-ray shaded (p. *S*182-*S*184). [Plate designations in *2a* are as given in Figure 38.]

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*

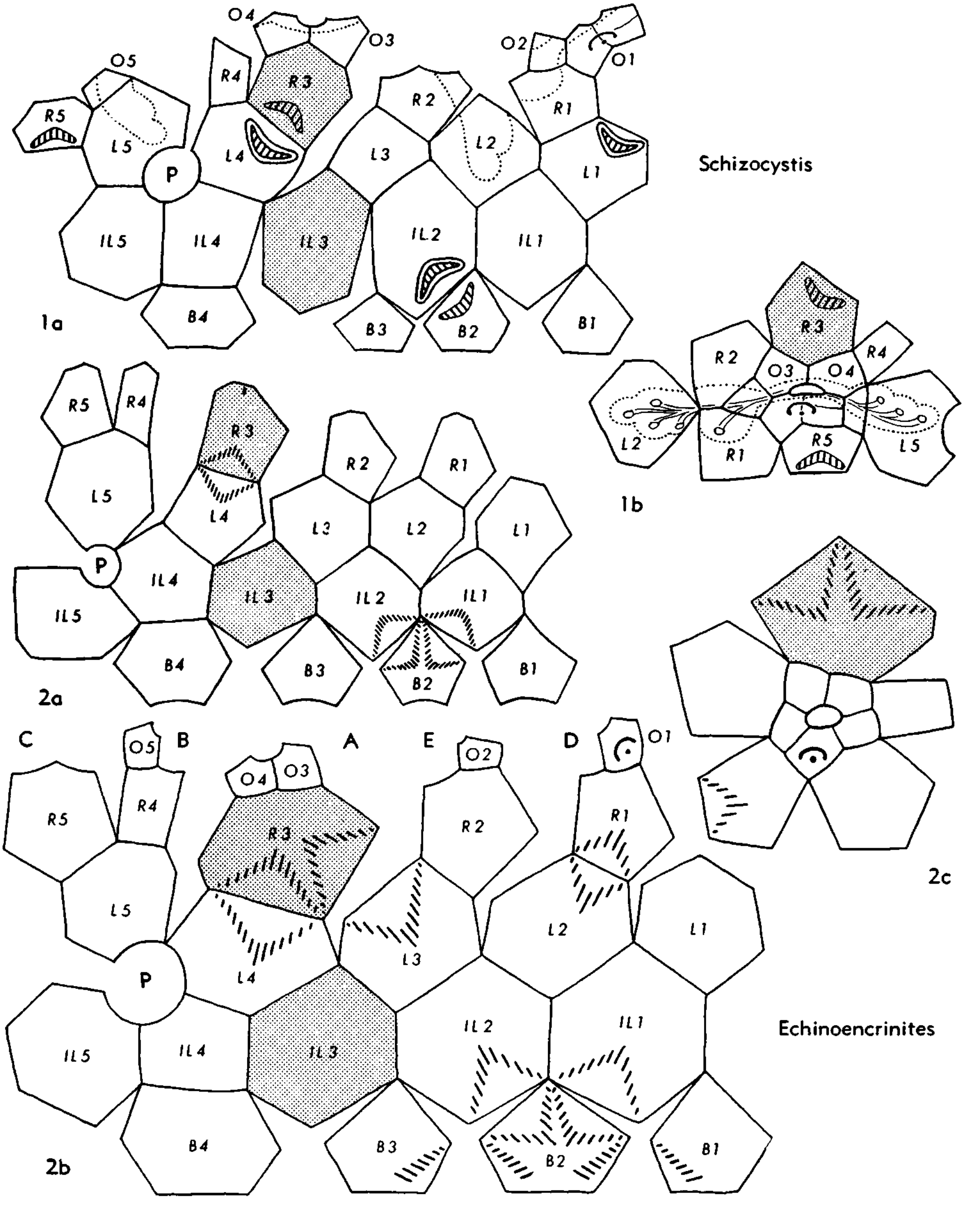


FIG. 89. Echinoencrinitidae. Plate diagrams, *A*-ray plates shaded, plate designations as in Figure 38 (p. *S*187-*S*189, *S*191).

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

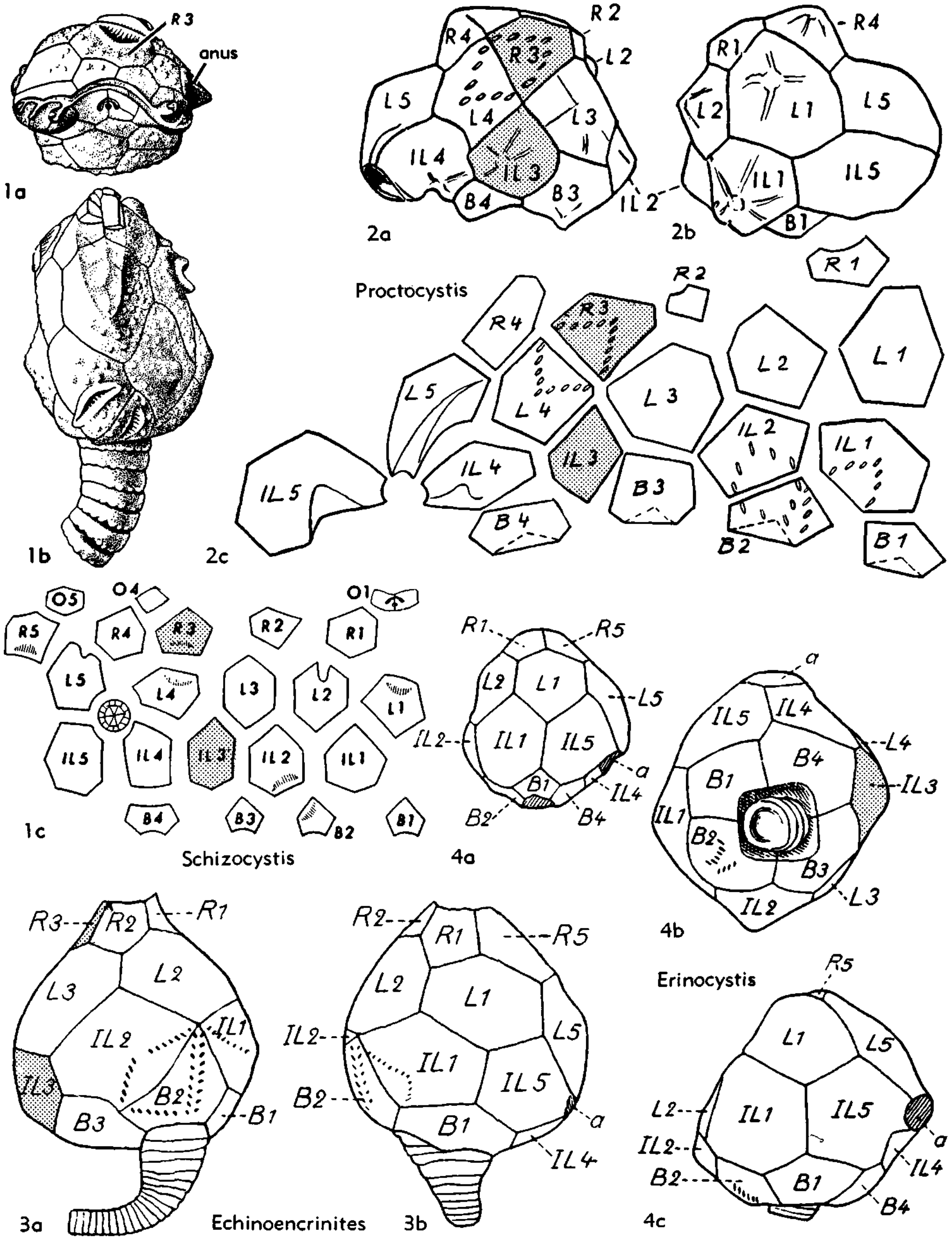


Fig. 90. Echinoencrinitidae, plates of *A*-ray shaded, plate designations as in Figure 38 (p. *S*187-*S*189, *S*191).

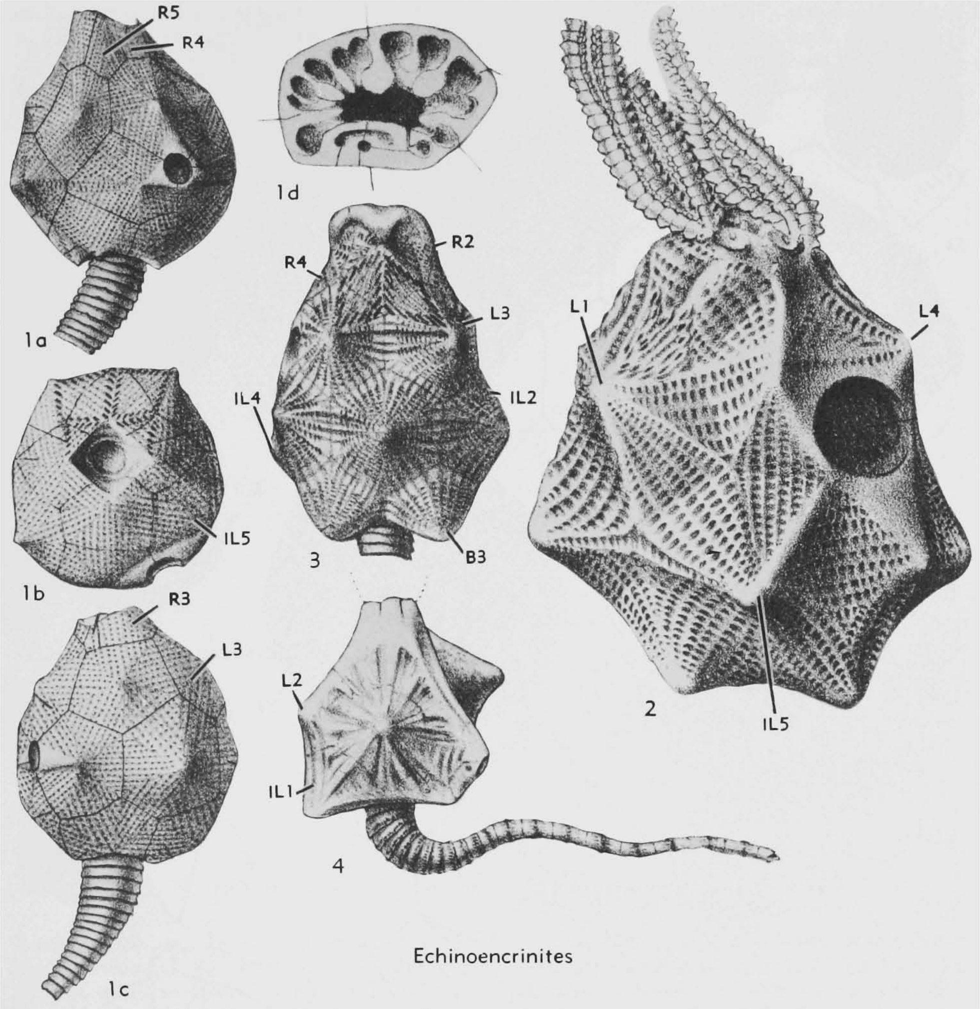


FIG. 91. Echinoencrinitidae, all L.Ord., USSR(Leningrad region), plate designations as in Figure 38 (p. *S*187-*S*189).

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

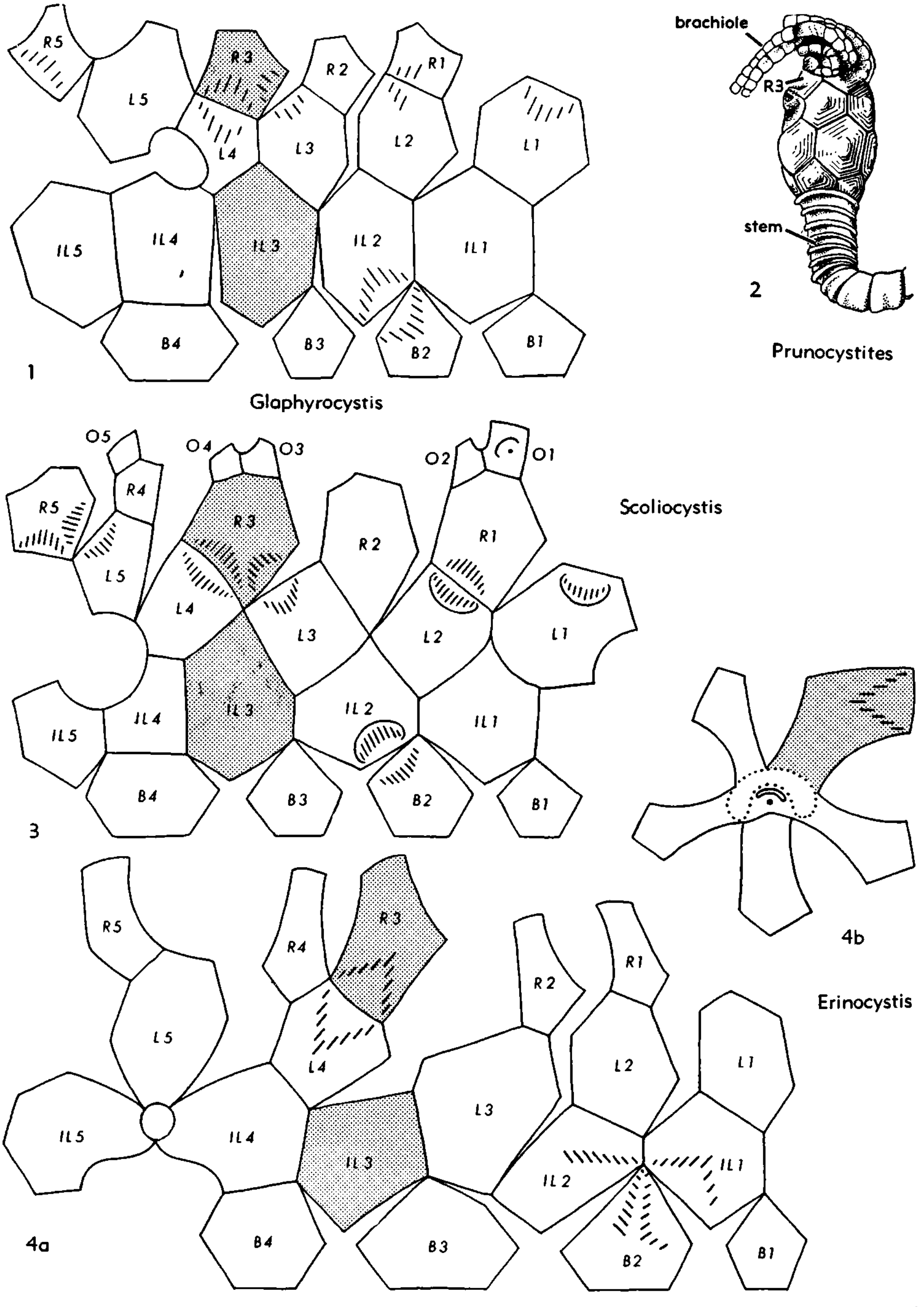


FIG. 92. Echinoencrinitidae. Plate diagrams, plates of *A*-ray shaded, plate designations as in Figure 38 (p. *S*189-*S*192).

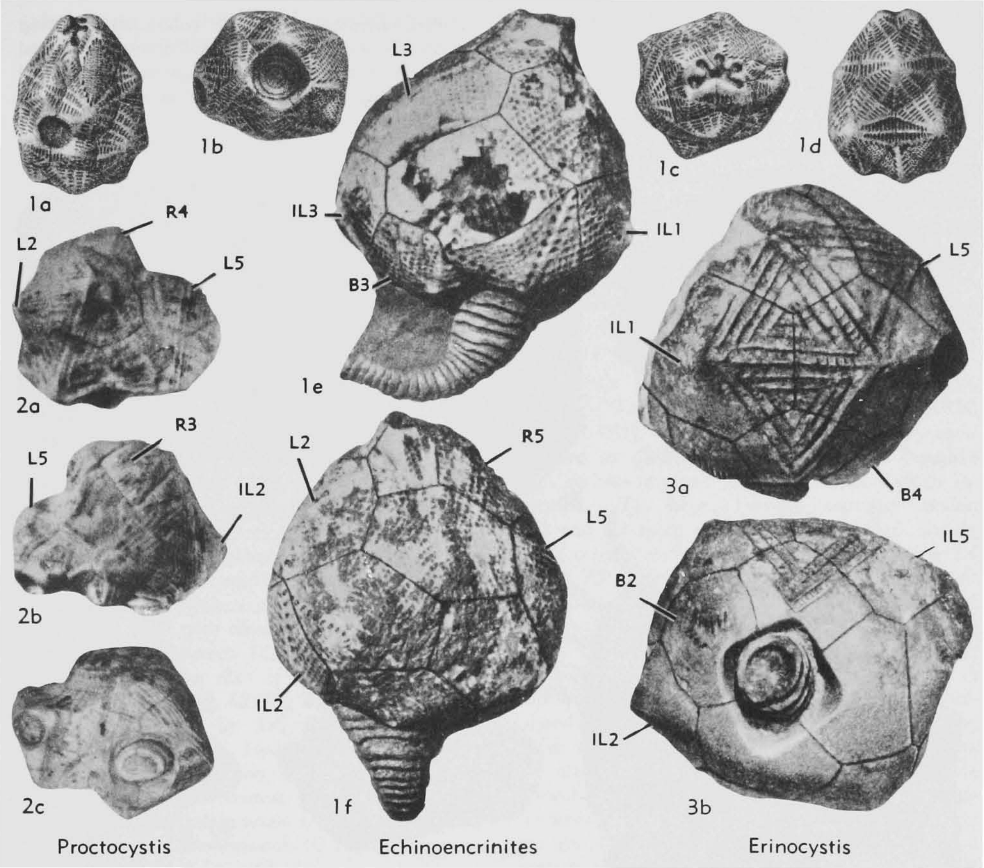


FIG. 93. Echinoencrinitidae (p. *S*187-*S*191). [Plate designations as in Figure 38.]

3 adjoining plates; all rows of thecal plates in complete circlets; *BB* well developed, indented to form quadrate depression for ample column. Brachioles 2 to 5 or more, set on short ambulacra on narrow crown. Three pore rhombs, *B2/IL1*, *B2/IL2*, and *L4/R3*. [*Eutretocystis*, created by PHLEGER for a specimen with an extra rhomb on *L3/R3*, may be an anomalous *Echinoencrinites*. Because many specimens are found with the proximal part of the column bent or curved, JAEKEL (71) suggested that the column was prostrate and the theca erect in *Echinoencrinites*. Because specimens were not rare, and because VON MEYER's publication was overlooked by subsequent workers, this cystoid was described under several names.] *L.Ord.*, Eu.(USSR-Norway-Sweden)-?Asia(Burma).——FIG. 89,*2a*; 91,*1a-d*; 93,*1a-d*. **E. senckenbergii*, Kunda(B_3), USSR(Leningrad region); 89,*2a*, plate diagram (Kesling, n, after 69); 91,*1a-c*, lat., aboral, and lat., ×1; 91,*1d*, oral region showing brachiole facets, ×3 (69); 93,*1a-d*, lat., aboral, oral, lat., ×1 (31).——FIG. 89,*2b,c*; 91,*3*. *E. lahuseni* JAEKEL, Kunda (B_3), USSR(Leningrad region); 89,*2b,c*, plate diagram and oral region (Kesling, n, after 69); 91,*3*, lat., ×4 (69).——FIG. 90,*3*; 93,*1e,f*. *E. senckenbergi acutangulatus* REGNÉLL, *Expansus* (3cβ), Norway; 90, *3a,b*, lat., diagram., ×1.5 (100); 93,*1e,f*, lat., 2 thecae, ×2 (100).——FIG. 91,*4*. *E. angulosus* (PANDER), B_2, USSR(Leningrad region); lat., ×3 (69).——FIG. 91,*2*. *E. reticulatus* JAEKEL, Kunda (B_3), USSR(Leningrad region); lat., ×3 (69).

Erinocystis JAEKEL, 1899, p. 252 [**E. sculpta*; OD]. Theca fig-shaped, orally strongly attenuated, base indented. *ILL* and *LL* with adjacent parts intercalated, *LL* forming complete circlet, but *ILL* interrupted by insertion of *L3* between *IL2* and *IL3*; *RR* elongate, sharply tapering to narrow crown. Periproct produced by prolongation of *IL4*, *IL5*, and *L5*, its opening rather small and directed aborally as well as outward. *OO* restricted to apex of theca, their number and arrangement obscured. Two brachioles, rather large for size of oral field, one facet atop *R1* and *R2* and other atop *R3* and *R4*. Three pore rhombs, *B2/IL1*, *B2/IL2*, and *L4/R3*, each rather high and sharply angled. Column with proximal thin-walled, circular, collar-like columnals, tapering to distal massive, compressed columnals. Thecal plates, particularly *ILL*, strongly sculptured and ornamented in some species, so much so that

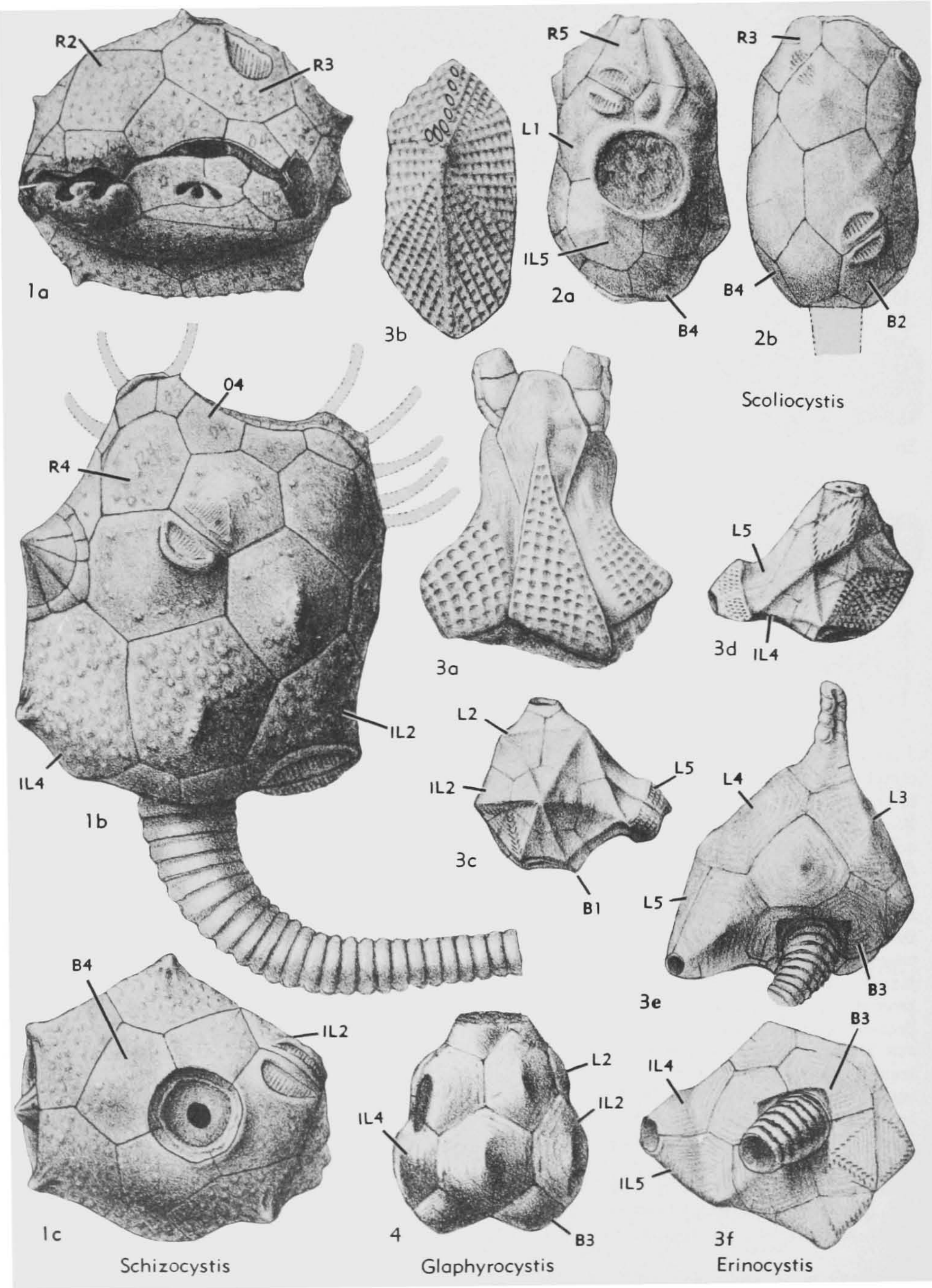


Fig. 94. Echinoencrinitidae (p. *S*189-*S*192). [Plate designations as in Figure 38.]

plate shapes and arrangements are difficult to define. _L.Ord._, USSR-Est.-Norway.——Fig. 90,_4_; 93,_3_. _E. broeggeri_ Regnéll, _Expansus_ Ls. (3cβ), Norway; 90,_4a_, lat., small theca, ×2; 90,_4b,c_, aboral and lat., ×2 (100); 93,_3a,b_, lat. and aboral, ×3 (100).——Fig. 92,_4_; 94,_3e,f_. _E. volborthi_ Jaekel, Kunda (B_3), Leningrad; 92,_4a,b_, plate diagram and oral region (Kesling, n); 94, _3e,f_, lat. and aboral, ×1 (69).——Fig. 94,_3a,b_. *_E. sculpta, Vaginatum_ Ls., Leningrad region; _3a_, lat., ×3.5; _3b_, rhomb-bearing plate, ×5 (69).——Fig. 94,_3c,d_. _E. angulata_ Jaekel, Kunda (B_3), Est. or Leningrad; _3c,d_, opposite lat., ×2 (69).

?**Eutretocystis** Phleger, 1935, p. 200 [*_E. similis_; OD]. Like _Echinoencrinites_ in all respects except for pectinirhomb _L3/R3_; this may well be an abnormal _Echinoencrinites_ with a supernumerary rhomb. _L.Ord._, Eu.(USSR).

Glaphyrocystis Jaekel, 1899, p. 196 [*_G. woehrmanni_; OD]. Theca irregularly ovate, narrow end oral, base indented. _IL_ circlet complete in most, but some have _L3_ reaching _B3_; _LL_ forming complete circlet; _L5_ prolonged orally between _R3_ and _R5_, with _R4_ rudimentary, absent, or fused with _L5_. Single basal pore rhomb, _B2/IL2_, and several upper rhombs between _LL_ and _RR_; type species strongly resembling that of U.Ord. _Lepadocystis_, with rhombs _L1/R5_, _L2/R1_, _L3/R3_, and _L4/R3_. Periproct bordered by _L4_, _IL4_, and _L5_, not strongly protuberant. Hydropore and gonopore reported, but oral region mostly unknown, including brachioles. Proximal part of column with swollen, projecting columnals. _U.Ord._, Est.——Fig. 92,_1_; 94,_4_. *_G. woehrmanni_; 92,_1_, plate diagram (Kesling, n); 94,_4_, lat., ×2 (69).

Proctocystis Regnéll, 1945, p. 85 [*_P. monstruosa_; OD]. Shape of theca very strongly influenced by large, protruding, aborally directed periproct, formed by _IL4_, _IL5_, and _L5_; only 4 _RR_ present, _R5_ absent; _L3_ in contact with _B3_, interrupting circlet of _ILL_; _OO_ apparently rudimentary; _BB_ invaginated to form quadrangular depression. Three rhombs in known species: _B2/IL1_, _B2/IL2_, and _L4/R3_; few slits in each rhomb. Proximal columnals oval, with large lumen. _L.Ord._, Sweden-USSR.——Fig. 90,_2_; 93,_2_. *_P. monstruosa, Expansus_ Ls., Sweden; 90,_2a,b_, lat., diagrammatic, ×2; 90,_2c_, plate diagram (99); 93,_2a-c_, 2 lat. and aboral, ×1.5 (100).

Prunocystites Forbes, 1848, p. 503 [*_P. fletcheri_; OD] [=_Prunocystis_ Carpenter, 1891, p. 135 _(nom. van.)_]. Theca small, ovate, its base not indented, set atop exceptionally large column more than half as wide as theca); theca said to resemble "fruit of the dog-rose." _BB_, _ILL_, and _LL_ circlets complete; _RR_ circlet broken by _L5_, which, as in many genera, extends from periproct to _OO_ circlet. _OO_ little known, set atop somewhat truncated theca and partly obscured by clustered brachioles; Forbes' (51) description and Jaekel's (69) comments indicate that some plates of the short ambulacra may be incorporated into the cover of the theca. Hydropore and gonopore present. Periproct bordered by 4 plates, _IL4_, _IL5_, _L4_, and _L5_, containing an anal pyramid and ring of plates, set at mid-height. Ambulacra long, their number unknown, but according to thickness of known fragments and size of oral region, each theca had only 5 to 10 at most; segments of brachioles ("digitalia") longer than broad, with nodose enlargements. Three pore rhombs, at common locations. Proximal columnals flanged. _U.Sil._, Eu.(Eng.).——Fig. 92,_2_. *_P. fletcheri_; lat., ×4 (10).

Schizocystis Jaekel, 1895, p. 193 (_non_ Léger, 1900) [*_Echinoencrinus armatus_ Forbes, 1848, p. 507; OD]. Theca ovate aborally, adorally compressed in direction of _B1-B3_, so that periproct lies on one of small sides; base only slightly indented. _ILL_ large, forming complete circlet; _L2_ and _L3_ more or less diamond-shaped, having little contact with adjacent _LL_; _L5_ separating _R4_ from _R5_; _OO_ relatively large, distorted to fit elongate, narrow oral field. Long ambulacral grooves across narrow oral field, one extending from each side of mouth slot in gentle curve, irregularly branched and leading to 4 or 5 brachiole facets of various sizes. Periproct bordered by _IL4_, _IL5_, _L4_, and _L5_, rather large, with high valvular pyramid and surrounding ring of plates, not strongly protuberant. Only 2 pore rhombs, _B2/IL2_ and _L4/R3_, each with moderate number of slits, basal rhomb diagonally opposite periproct on narrow side of theca. Hydropore a curved slit and gonopore a closely adjacent hole in large, elongate, tripartite _O1_, which fills most of one side of oral region. Column tapering distally, rather thick. _U.Sil._, Eng.——Fig. 89,_1_; 90,_1_; 94,_1_. *_S. armata_ (Forbes); 89,_1a,b_, plate diagram and oral region (Kesling, n, after 69); 90,_1a,b_, oral and lat., ×2; 90,_1c_, plate diagram (10); 94,_1a-c_, oral, lat., and aboral, ×5 (69).

Scoliocystis Jaekel, 1899, p. 196 [*_Caryocystites pumilus_ Eichwald, 1860, p. 629; OD]. Theca irregularly elongate ovate, tapering at both ends, base not indented; all circlets of plates nearly or quite complete, definitely so in type species, but in _S. thersites_ first 4 _LL_ nearly separated by aboral corners of _RR_ which extend to or almost to corresponding _ILL_ below, so that junctions of _IL1-L1-L2-R1_, _IL2-L2-L3-R2_, and _IL3-L3-L4-R3_ tend to be expressed as X's. In type species, _ILL_ vertically elongate and very narrow, inducing Jaekel (69) to describe the theca as "stunted." Periproct bounded by 5 plates, _IL4_, _IL5_, _L1_, _L4_, and _L5_, set at mid-height in _S. thersites_ and rather high in _S. pumilus_, not protuberant. One basal pore rhomb, _B2/IL2_, and several between _LL_ and _RR_; _S. pumilus_ with _L1/R5_, _L4/R3_, and _IL2/L3_, _S. thersites_ with _L1/R5_, _L2/R1_, _L3/R3_, and

L4/R3, same disposition as in *Glaphyrocystis*, its U.Ord. successor, or in *Lepadocystis*, U.Ord. callocystitid from N.Am. Ambulacra with few brachioles, concentrated near mouth. Hydropore and gonopore exactly as in *Echinoencrinites*. *L.Ord.*, USSR.——Fig. 92,*3*; 94,*2*. *S. thersites* Jaekel, Kunda (B_3), Leningrad; 92,*3*, plate diagram (Kesling, n); 94,*2a,b*, opposite lat., ×5 (69).

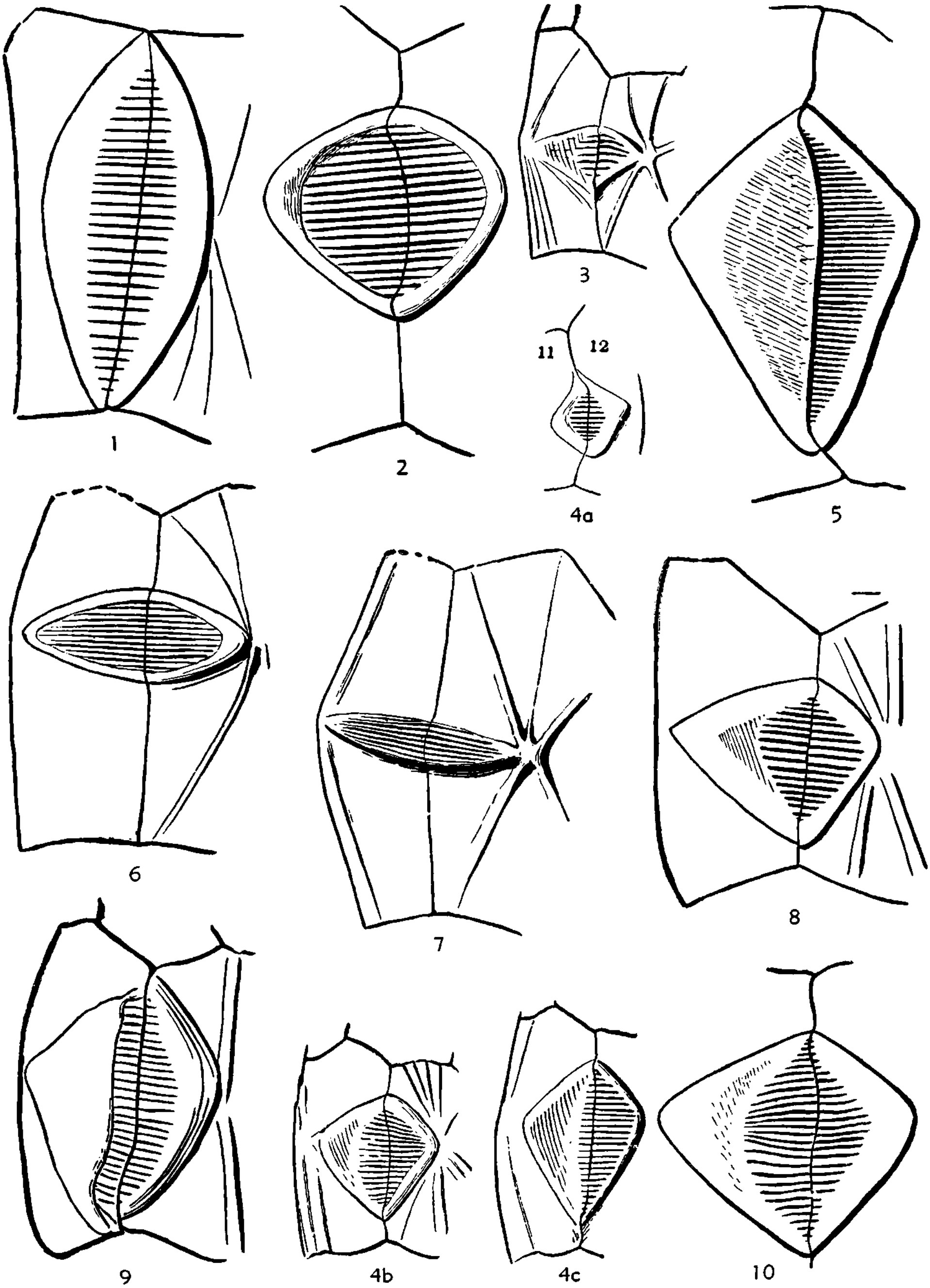


Fig. 95. Pleurocystitidae (p. *S*194-*S*199).——*1-10. Pleurocystites*, M.Ord.-U.Ord.; pectinirhomb *L1/L2* in various species, all ×5 *(12)*.

Family PLEUROCYSTITIDAE Neumayr, 1889

[*nom. correct.* Bassler, 1938, p. 11 (*pro* Pleurocystiden Neumayr, 1889, p. 413)]

Theca strongly compressed, with extremely large periproct comprising most of one side. Only two brachioles, long, extending forward from sides of narrow peristome. Hydropore and gonopore on anal side. Three rhombs or less. *M.Ord.-L.Dev.*

This rather well-known family has inspired considerable speculation as to its significance in evolution of the Crinozoa, the taxonomic position of the enigmatic *Amecystis,* and precise chronological succession of species in North America, Britain, Belgium, Germany, and China. In addition, authorities have differed in their interpretation of the living position of these cystoids, their motility, and their mode of respiration.

The Pleurocystitidae appear from known records to have originated in Ontario, wherefrom they spread during the Ordovician into other parts of eastern North America—New York, Michigan, Wisconsin, Minnesota, Iowa—and eastward across the Atlantic to the British Isles and Belgium. The doubtful species *Pleurocystites bassleri* Sun is said to come from strata of Llanvirn age in China, and may represent the ancestral stock of the family. Strangely, Silurian pleurocystitids are unknown. Undoubtedly the Lower Devonian *Regulaecystis* from Germany is a member of this family.

A chronological series of *Pleurocystites* species can be selected to show any one of several trends. First, enlargement of the periproct, which attained its maximum size in British Caradocian forms and which is correlated with the spreading of adoral plates, so that *L1* and *L4* became more widely separated. Whether plate *L5* is distinct, fused to *L4,* or absent is still open to question.

A second trend concerns the number of small plates in the periproct, the so-called "periproctals." These vary from about 50 to perhaps as many as 1,500. The diminution in size of the periproctals does not appear to have been a trend throughout the history of the genus, but possibly it occurred in separate lineages at different times.

Third, the reduction in number and size of pectinirhombs. This trend, if such it be, can be strongly presented in a carefully selected series. But if all species are considered, it is somewhat less spectacular. The *L3/L4* rhomb shows progressive restriction on the suture, as well as fewer slits in the series *Pleurocystites filitextus* (Fig. 95,*1*), *P. robustus* (Fig. 95,*2*), *P. squamosus* (Fig. 95,*8*), *P. anglicus* (Fig. 95,*6*), *P. rugeri* (Fig. 95,*7*), and *P. procerus* (Fig. 95,*3*). Another series can be chosen to demonstrate the loss of slits on one-half of this rhomb, *P. filitextus, P. foriolus* (Fig. 95,*4*), and *P. gibbus* (Fig. 95,*5*); in the last-named species, Bather (12) said that the "folds" on *L4* were "almost entirely closed by stereom." Other examples are seen in *P. elegans* (Fig. 95,*9*) and *P. quadratus* (Fig. 95,*10*). Rhomb *B2/IL2* is very small in *P. anglicus* and absent in *P. rugeri* and *P. procerus.* A drastic change also occurs in some Caradocian forms whereby the pore rhombs become elongate normal to the suture, rather than along it, attaining the ultimate expression in *P. rugeri.* It is true that Late Ordovician species all have restricted pectinirhombs, as compared with Middle Ordovician species, but the changes were evidently not attained in strict chronological sequence.

Other differences characterize species of *Pleurocystites.* The "shoulder-angle," defined by Bather (12) as the angle formed by projection of the edges of plates *L1* and *L4*, varies from 40 to 115 degrees (at least). Ratios of height and width also exhibit an appreciable range. These are useful in description of species, but can scarcely be established as trends.

The modification, diminution, and elimination of pectinirhombs in *Pleurocystites* raise the problem of the two other genera. *Regulaecystis* seems to be a Devonian descendant in which both *B2/IL2* and *L1/L2* pectinirhombs were eliminated. But *Amecystis,* with a plate pattern almost identical with that of *Pleurocystites* but lacking any discernible rhombs or pores, originated in the Middle Ordovician and was a contemporary of *Pleurocystites elegans* and *P. filitextus.* No progression of forms is known that could have led to *Amecystis.*

Question may be raised as to whether *Amecystis* should be classed as a cystoid at all, inasmuch as it lacks thecal pores.

DEHM (36) concluded that *Amecystis* provided evidence of close affinity of cystoids with "carpoids," and proposed a Soluta-Pleurocystitidae group as an intermediary or passage from the Hydrophoridea group (true cystoids) to the Cincta-Mitrata-Cornuta group (true "carpoids"), with closer affinity to the "carpoids" than to the cystoids. This relationship, as such, has been denied by GEKKER [HECKER] (54) and REGNÉLL (99). On the other hand, *Amecystis* is clearly not a member of any known "carpoid" lineage.

Inclusion of *Amecystis* in the cystoids produces a difficult problem in defining the taxon. Although strongly reduced, at least some thecal pores occur in *Regulaecystis,* and although roofed over by epistereom, there are pores within the thecal walls of *Hemicosmites, Polycosmites,* and *Caryocystites.* Insofar as I am aware, no attempts have been made to section plates of *Amecystis* to look for pores *within* the thecal plates. In regard to reduction of rhombs in *Pleurocystites,* BATHER (12) suggested that in adapting to near-shore environment, the cystoids of this genus were confronted with a problem in respiration, and that when pectinirhombs became clogged with sand, they utilized rectal respiration, as do certain living echinoderms. Thus, he seems to have correlated increase in the periproct, at least in part, with the decrease in rhombs. If respiration was a function of the pectinirhombs, as generally conceded, and if respiration in some forms was accomplished otherwise so that the rhombs were no longer necessary or functional, and if with disuse the pectinirhombs finally disappeared—then, the position of *Amecystis* is decided, but the Cystoidea must be defined on other grounds than possession of thecal pores.

As to the position assumed by *Pleurocystites* in life, BATHER (12) assumed that the column coiled loosely around some upright object and the animal stretched out parallel to the sea-floor, with the periproct or anal face uppermost. This suggestion introduces another problem: if the pectinirhombs were on the lower face of the theca, where sediment was liable to clog them, then why was the basal *(B2/IL2)* rhomb first to disappear in the evolutionary sequence? One might expect all rhombs to be affected equally. Thus, although the Pleurocystitidae has been studied from more and better specimens than most families, its ecology and evolution are poorly known.

Key to Genera of Pleurocystitidae

1. No trace of pore rhombs, at least externally .... *Amecystis*
   One to three pore rhombs, distinct, slits well defined 2
2. Two or three rhombs *(L1/L2* and *L3/L4* invariably present, *B2/IL2* in most); anal pyramid at corner of periproct, in so-called "rectal lobe" .... *Pleurocystites*
   Only one rhomb *(L3/L4)*; anal pyramid subcentral in periproct .... *Regulaecystis*

Pleurocystites BILLINGS, 1854, p. 250 [**P. squamosus*; SD S. A. MILLER, 1899, p. 272] [=*Pleurocystis* CARPENTER, 1891, p. 12 *(nom. van.)* *(non Pleurocystis* HESSE, 1909); *Dipleurocystis* JAEKEL, 1918, p. 95 (type, *Pleurocystites anglicus* JAEKEL, 1899, p. 235)]. Pectinirhombs developed in various forms on the antanal face; *B2/IL2* smallest of rhombs, absent in some species; *L1/L2* never larger than *L3/L4,* may be conspicuously smaller; rhombs varying in degree of elongation normal to suture, number and length of slits, length of suture involved, development of bordering rim, and asymmetry of halves; *P. gibba* with slits in *L4* nearly obliterated by covering of stereom. *B1* and *B4* on anal side, forming aboral border of very large periproct, *B2* and *B3* on antanal side. *ILL* large, circlet interrupted by periproct between *IL4* and *IL5*; *LL* also well developed, particularly *L1* and *L4* which extend around edge of theca from antanal to anal sides and abut on short suture at adoral side of periproct; *L5* either absent, indistinct, or fused with *L4*. *RR* small, circlet interrupted between *R1* and *R5* by insertion of *O1*; *OO* forming complete circlet, with tripartite *O1* rather large and centered on adoral margin of anal side, *O2* giving rise to one brachiole and *O4* and *O5* to other, *O3* on antanal side directly opposite *O1*. Hydropore a curved slit and gonopore a small opening, both bisected by suture within *O1*. Periproct large, covered by 50 to about 1,500 small plates ("periproctals") with anal pyramid at aboral corner between *B4* and *IL4* in so-called "rectal lobe." Two brachioles, long, biserial as in other cystoids. Column long and tapering to very small diameter, end not known with certainty; proximal part composed of alternating inner and outer rings, probably interlocking, and distal part of longer columnals having much smaller lumen. The creation of *Dipleurocystis* by JAEKEL in 1918 (71) was due to a misunderstanding of the type species of *Pleurocystites.* The type was designated by S. A. MILLER (85) in 1889, as *P. squamosus.* Unaware of this action, HAECKEL (58) in 1896 also selected a type, *P. filitextus*. *P. squamosus* has very numerous small plates in the periproct, whereas *P. filitextus* has fewer, larger, more nearly polygonal plates. BATHER (12) called attention to the correct type species; but JAEKEL (71) evidently did not understand it, for he defined *Pleurocystites* as having large periproctals and sought to create a new genus with type species *P. anglicus* JAEKEL for the species with large periproct, minute periproctals, and narrow pore rhombs. As recognized by FOERSTE (in SLOCUM & FOERSTE, 1924), and emphasized by REGNÉLL (personal communication), *Dipleurocystis* cannot be maintained because by definition it would include the type species of *Pleurocystites*.

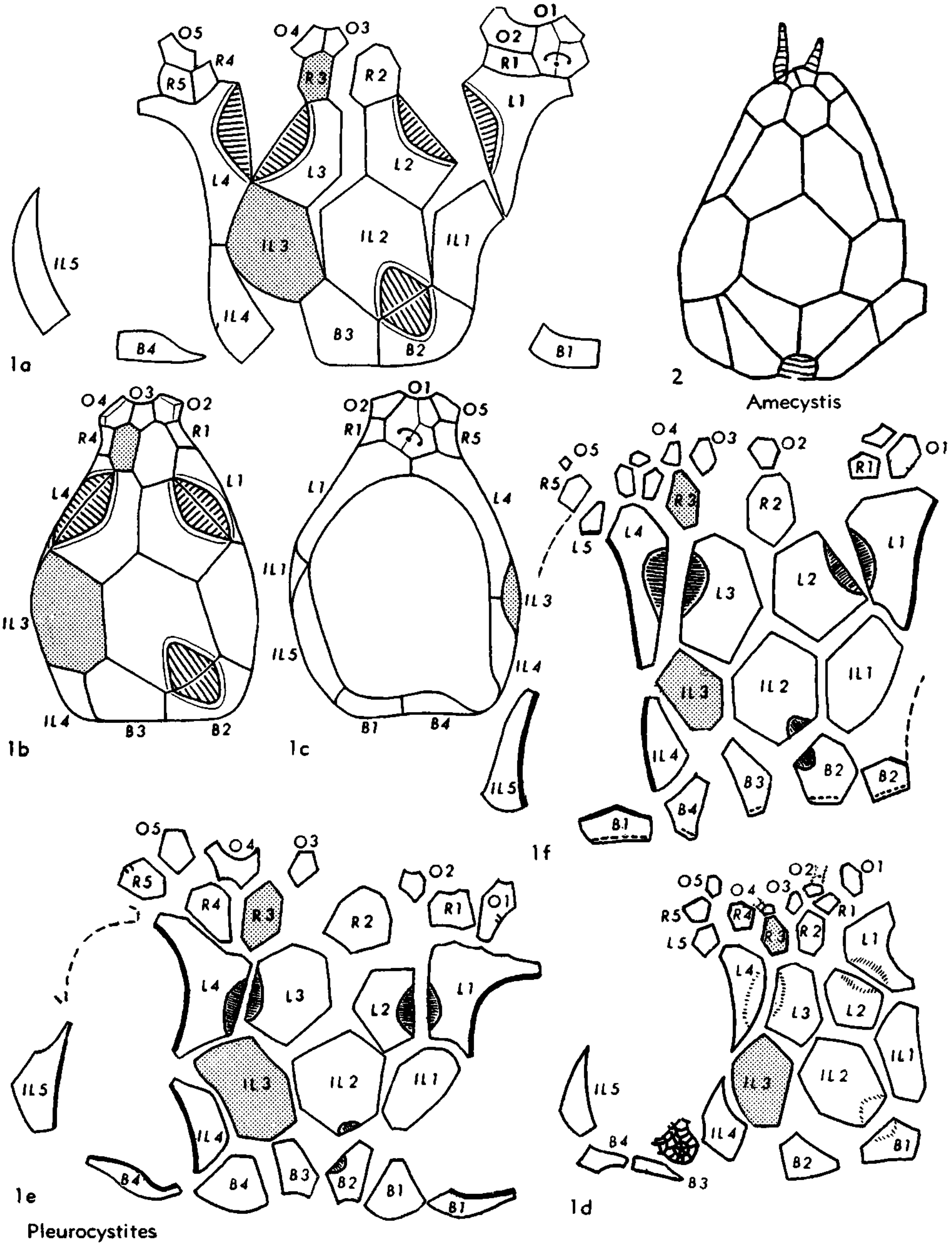


FIG. 96. Pleurocystitidae, plates of *A*-ray shaded (p. S194-S199). [Plate designations as in Figure 38.]

Further, REGNÉLL has informed me that the number of periproctals in known species falls into a nearly continuous series, with no appreciable hiatus between "few" and "numerous."] *M.Ord.-U.Ord.*, Eu.(Brit.-Belg.)-N.Am.-?China.——FIG. 95,*1-10.* Pectinirhomb *L1/L2* in various species, all ×5

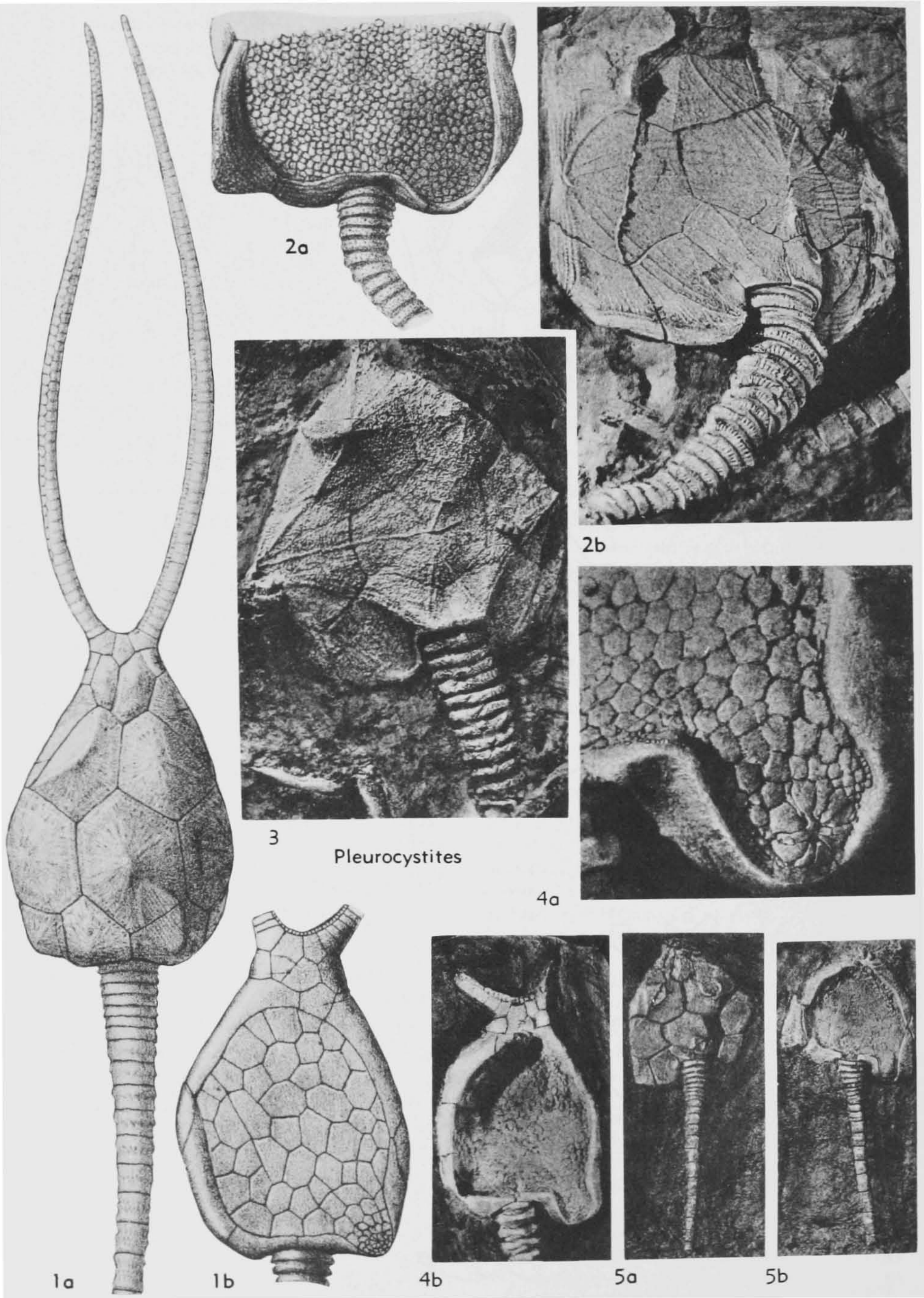


FIG. 97. Pleurocystitidae (p. *S*194-*S*199).

(12).——Fig. 96,*1;* 97,*1;* 98,*2a;* 99,*3.* *P. filitextus* Billings, M.Ord.(Trenton.), Ont.; 96,*1a-c,* plate diagram, antanal, and anal (Kesling, n); 96,*1d-f,* 3 plate diagrams showing various interpretations of plate number and arrangement (10, 12); 97,*1a,b,* antanal, anal views, ×2(69); 98,*2a,* antanal,

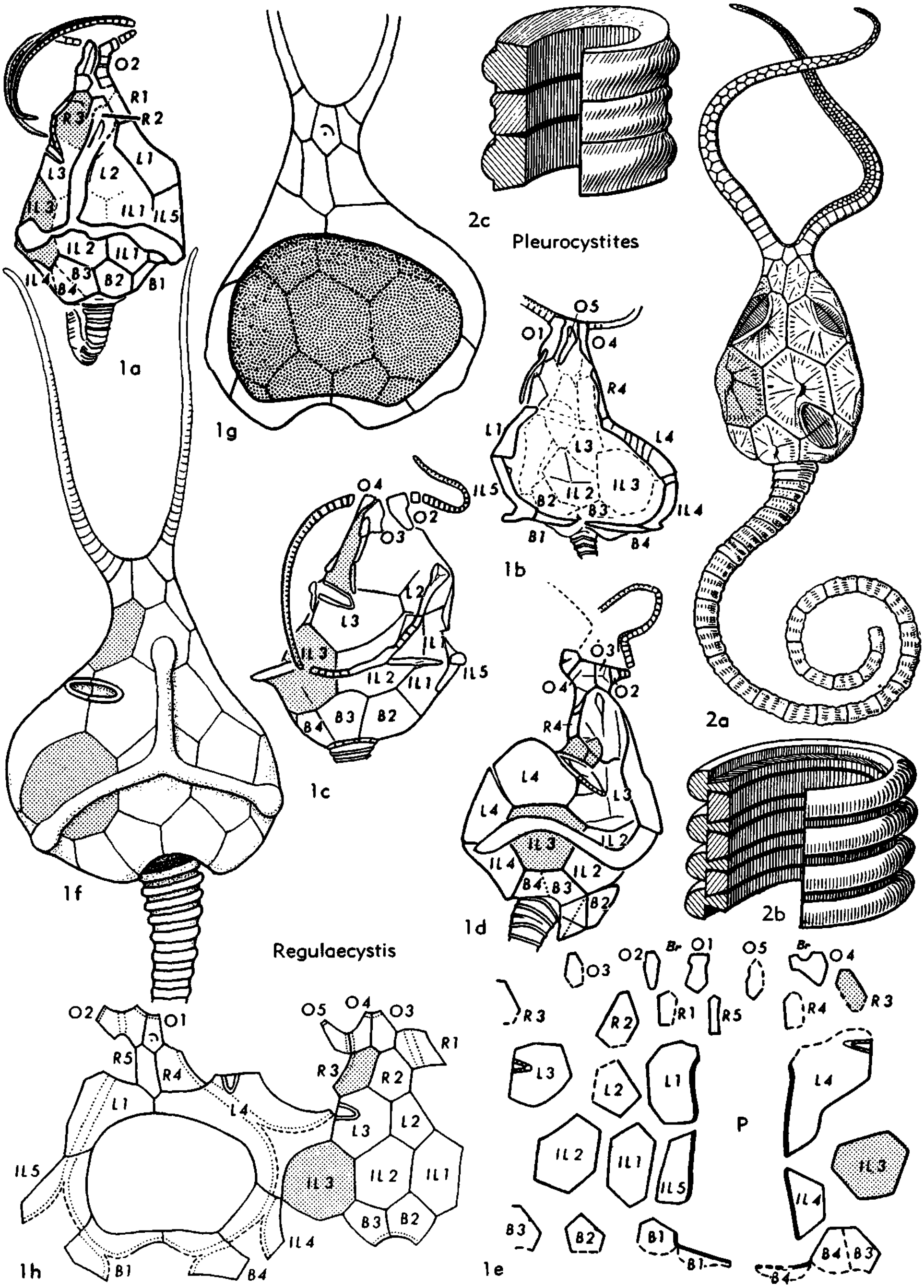


Fig. 98. Pleurocystitidae, plates of *A*-ray shaded (p. *S*194-*S*199). [Plate designations as in Figure 38.]

reconstr. (10); 99,*3a,b,* anal, antanal views, ×1 (20).——Fig. 97,*2. P. anglicus* Jaekel, U.Ord.(L. Ashgill.), Ire.; *2a,* anal, incomplete theca, ×2 (69); *2b,* antanal, ×2 (12).——Fig. 99,*2. P. elegans* Billings, M.Ord.(Trenton.), Ont.; *2a,b,* antanal, 2 thecas, ×1 (20).——Fig. 97,*5. P. foriolus* Bather, U.Ord.(Drummuck), Scot.; *5a,b,* antanal, anal views, ×1 (12).——Fig. 97,*3. P.*

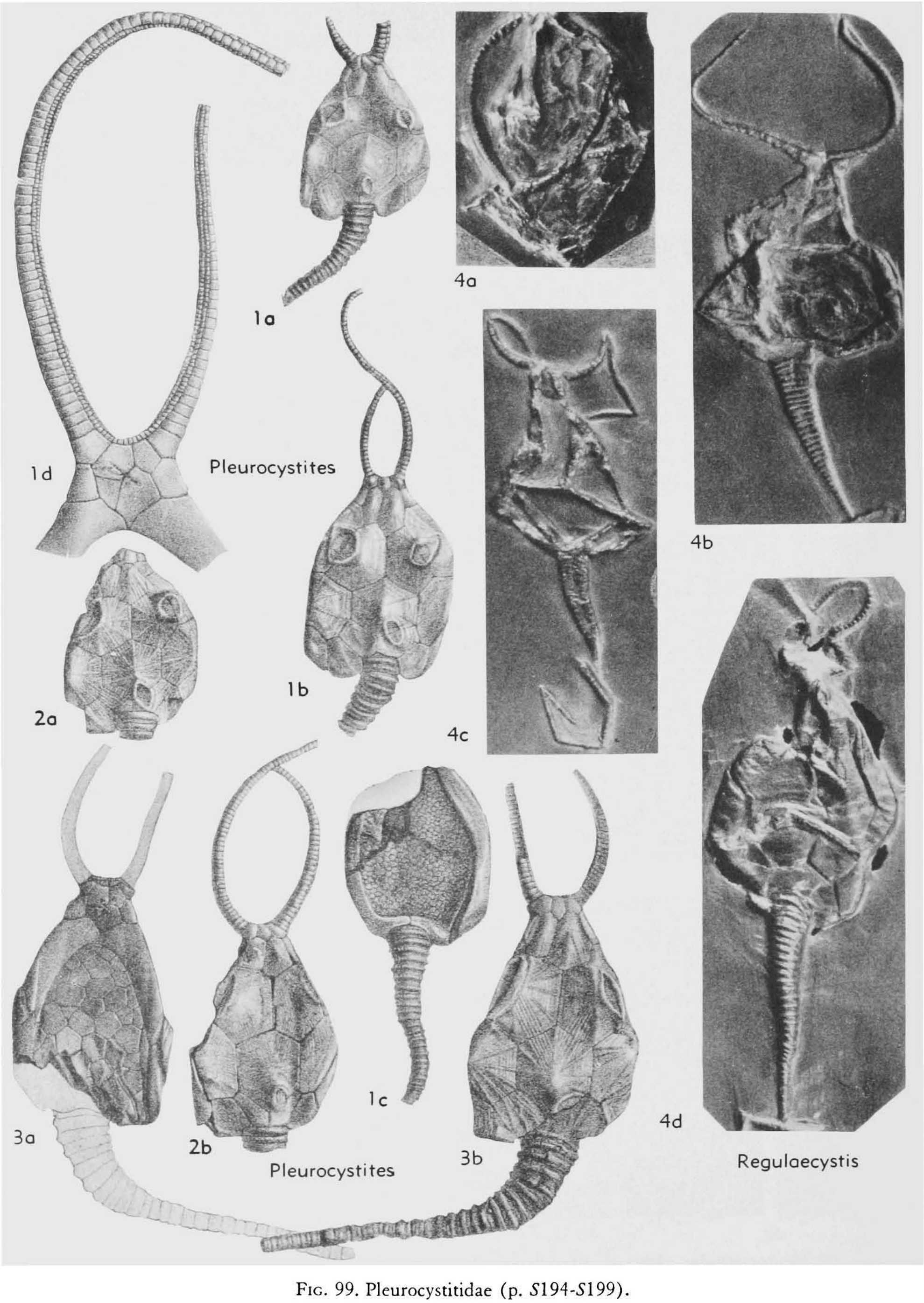


Fig. 99. Pleurocystitidae (p. S194-S199).

rugeri Bather, M.Ord(Caradoc.), Wales; antanal, ×2 (12).——Fig. 97,*4*. *P. quadratus* Bather, U.Ord.(Drummuck), Scot.; *4a*, "rectal" lobe of periproct with anal pyramid, ×4.5; *4b*, anal view, ×1 (12).——Fig. 98,*2b,c*; 99,*1a-d*. **P. squamosus*, M.Ord., Can.(Ont.); 98,*2b,c*, proximal and distal secs. of column (12); 99,*1a,b*, antanal, 2 specimens, ×1; 99,*1c*, anal, incomplete theca, ×1; 99,*1d*, oral regions and brachioles, enl. (20).

Amecystis Ulrich & Kirk, 1921, p. 147 [**Pleurocystites laevis* Raymond, 1921, p. 2; OD]. Theca with plate arrangement like that of *Pleurocystites*. No trace of pore rhombs, at least externally. [This genus is included here as a pleurocystitid despite its anomalous structure.] *M.Ord.*, N.Am.(Ont.-Minn.-Mich.-Pa.-Ky.).——Fig. 96,*2*. **A. laevis* (Raymond), Ont.; antanal (36).

Regulaecystis Dehm, 1932, p. 74 [**R. pleurocystoides*; OD]. Theca flattened, as in *Pleurocystites*, composed of thin, fragile plates. Four *BB* visible on antanal side, *B1* and *B4* with extensions on anal side to form lower border of periproct; *IL4, IL5, L1* and *L4* folded in thick rim, their antanal sides bordering periproct; *L4* especially large; *RR* and *OO* small. Only one rhomb, *L3/L4*, occupying short section of suture and elongate normal to suture; slits not reported. Three curious ridges radiating from center of *IL2*, to *R2*, to *IL5*, and to *IL3*, perhaps serve to give rigidity to antanal side of thin-plated theca. Periproct oval, transversely elongate. Oral end of theca very narrow, bearing 2 long, thin brachioles. Column long, tapering, with 20 to 30 columnals in proximal part and 60 to 80 in distal, structurally like column of *Pleurocystites*. Hydropore and gonopore not reported. *L.Dev.*, Ger.——Fig. 98,*1*; 99,*4*. **R. pleurocystoides*; 98,*1a-d*, sketches of 4 specimens (36); 98,*1e*, plate diagram (36); 98,*1f,g*, antanal, anal views (reconstr.) (Kesling, n); 98,*1h*, plate diagram, some sharply folded peripheral plates split (dashed lines) to show antanal and anal sides and marginal rim (dotted lines) (Kesling, n); 99,*4a-d*, 4 specimens, all distorted, ×? (36).

Family CALLOCYSTITIDAE Bernard, 1895

[*nom. correct.* Bassler, 1938, p. 10 (*pro* Callocystidés Bernard, 1895, p. 206)] [=Callocystidae Jaekel, 1899, p. 266]

Rhombiferan cystoids provided with distinct pectinirhombs; periproct relatively small, not produced; theca ovate, globular, biconvex, or ellipsoidal, not spindle-shaped or resembling a pentremite; rhombs relatively few, rarely developed as demirhombs; ambulacra long, extending down over theca; column present. *U.Ord.-U.Dev.*

This family includes many of the well-known genera of rhombiferans. It was long-lived and diverse, both in Europe and in North America.

The distinctive long ambulacra, "recumbent" on the theca, tend to obscure certain of the sutures and smaller plates. For this reason, details of many cystoids can only be established from specimens in which ambulacra have been exfoliated.

Subfamily CALLOCYSTITINAE Bernard, 1895

[*nom. transl.* Kesling, herein (*ex* Callocystidés Bernard, 1895, p. 206)] [=Callocystinae Jaekel, 1899, p. 287 (*partim*)]

Theca ovate, ellipsoidal, or globular; four or five ambulacra, branching; brachioles small, widely spaced; *LL* intercalated deeply into *ILL* circlet, as many as three *LL* in contact with *BB*. *M.Sil.-L.Dev.*

Key to Genera of Callocystitinae

1. *R1* and *R4* very small or absent; *L2* nearly or quite reaching *B2; L4* not forming a suture with *B4*, subtrapezoidal, four-sided .... *Sphaerocystites*
   All *RR* present; *L2* distinctly separated from *B2*; *L4* in contact with *B4*, five-sided 2
2. Theca ovate to ellipsoidal; pectinirhombs rather long, provided with numerous slits .... *Callocystites*
   Theca depressed globular; pectinirhombs small, with few slits .... *Coelocystis*

Callocystites Hall, 1852, p. 238 [**C. jewetti;* OD] [=*Anthocystis* Haeckel, 1896, p. 132 (type, *A. halliana*); *Callocystis* Carpenter, 1891, p. 135 (*nom. van.*)]. Theca ovate to ellipsoidal, base flat or truncated but not invaginated. *L1, L3*, and *L4* atop corresponding *BB*, with *ILL* forming tier of 8 plates; *BB* large, especially *B4*, which is in contact with *IL3, L4, IL4*, and *IL5*, as well as the adjacent *BB*; *L5* above periproct, inserted between *R4* and *R5*. Five long ambulacra, broad, normally one or more subdivided at about mid-length; brachiole facets rather numerous, alternating. Periproct bordered by elongate *IL4* and *IL5* and by subtrapezoidal smaller *L5*; anal pyramid surrounded by numerous small subquadrate platelets. Pectinirhombs rather well developed, intermediate between those of *Sphaerocystites* and *Coelocystis*, with numerous slits, halves on *IL2, L1*, and *L4* surrounded by prominent walls, those on *B2, R3*, and *R5* by high outer rim and lower inner ridge. Hydropore more or less 8-shaped with expanded distal parts; gonopore adjacent and small, said to be closed by pyramid of 4 pieces. Column stout, proximal part composed of rings wide in diameter; tapering rapidly in proximal half, more slowly in distal; total length unknown but exceeding 6 cm.; proximal columnals more highly ornamented and shorter than distal. *M.Sil.*, N.Am.(Ont.-N.Y.-Ohio).——Fig. 100,*3;* 101,*2a-g.* **C. jewetti*; Niagaran, USA(N.Y.) (101,*2a-g*); Can.(Ont.) (100, *3*); 100,*3a,b,* plate diagram and oral region (Kesling, n); 101,*2a-d,* 4 lat., ×1; 101,*2e,* enlarged pectinirhomb; 101,*2f,* diagram of ambulacra, hydropore, gonopore, periproct, and pectinirhombs (60); 101,*2g,* enlarged end of ambulacrum with

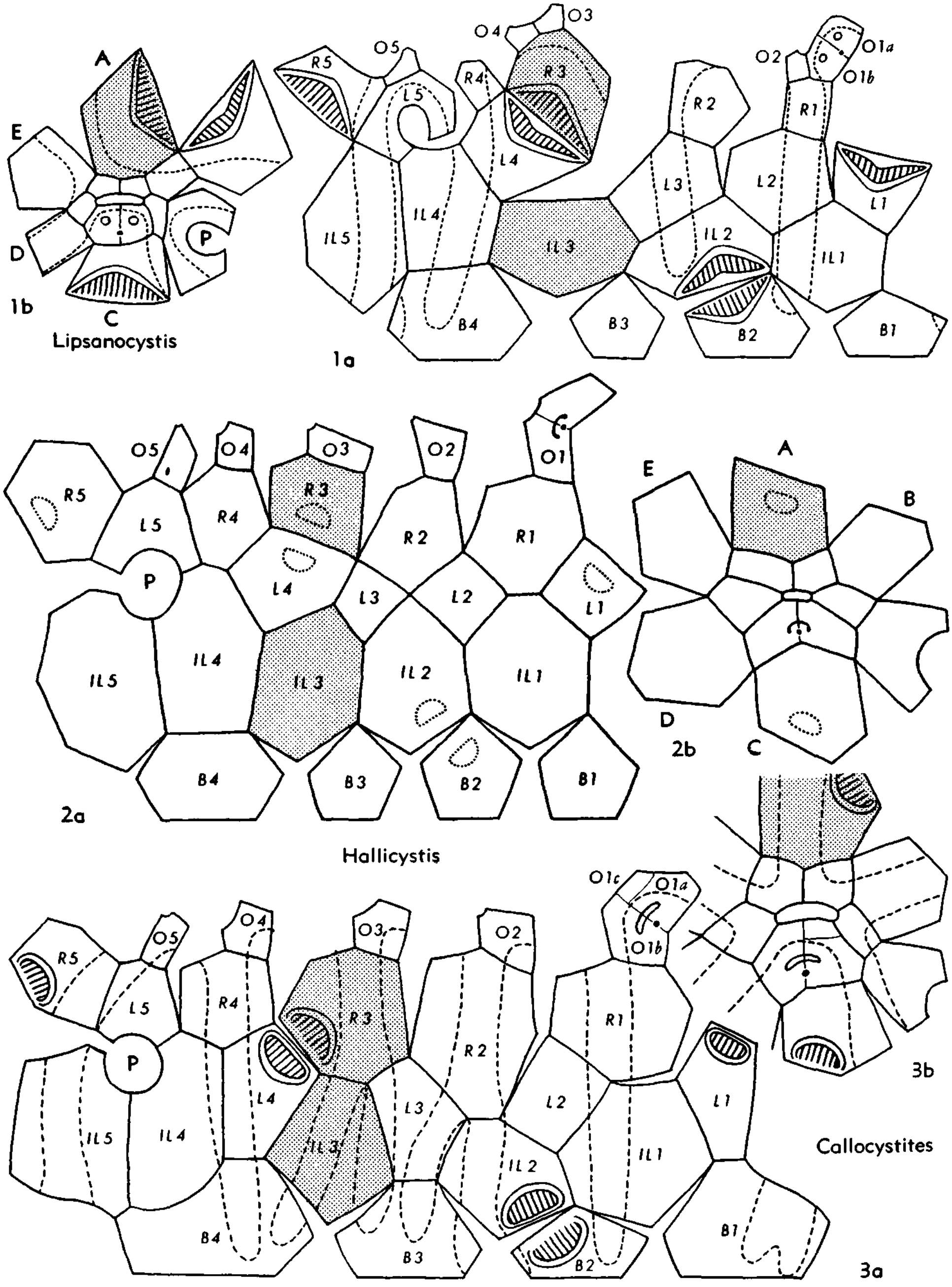


Fig. 100. Callocystitidae, Callocystitinae *(3)*, Apiocystitinae, *(1,2)*, plates of *A*-ray shaded (p. *S*199-*S*201, *S*209, *S*212-*S*213). [Plate designations as in Figure 38.]

1 brachiole (69).——FIG. 102,*1;* 101,*2h,i.* *C. jewetti elongatus* FOERSTE, Cedarville Dol., USA (Ohio); 102,*1,* plate diagram (49); 101,*2h,i,* 2 lat., steinkern, ×1 (47). [See also Fig. 44,*2;* 75,*1.*]

Coelocystis SCHUCHERT, 1903, p. 234 [**Hemicosmites subglobosus* HALL, 1867, p. 316; OD (=*Sphaerocystis dolomiticus* JAEKEL, 1899, p. 289; *Callocystites sphaeroidalis* FOERSTE, 1917, p. 239)]. Theca depressed globular. [Reports that the *BB* are deeply invaginated are based on stein-

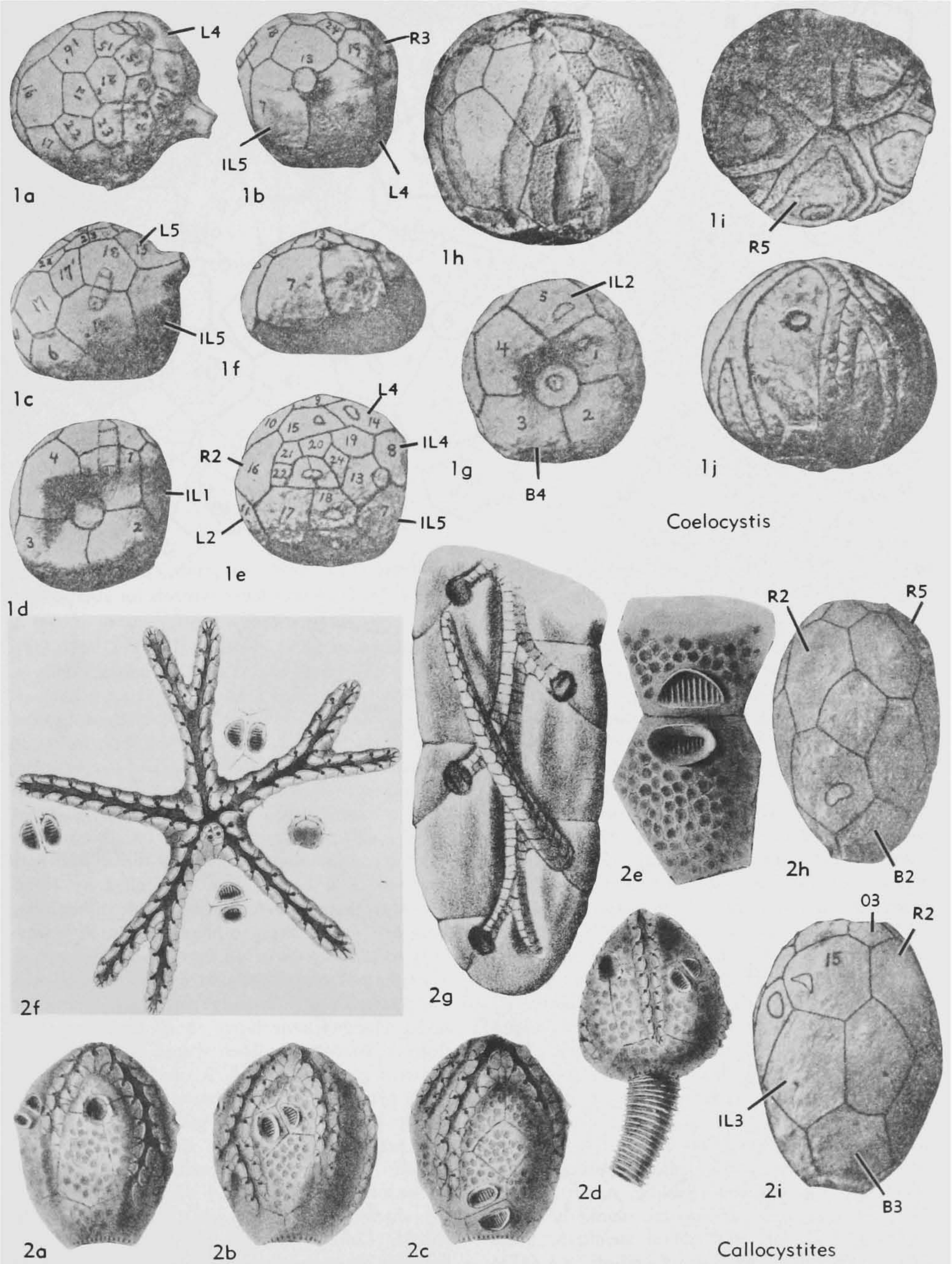


FIG. 101. Callocystitidae, Callocystitinae (p. *S*199-*S*202). [Plate designations as in Figure 38.]

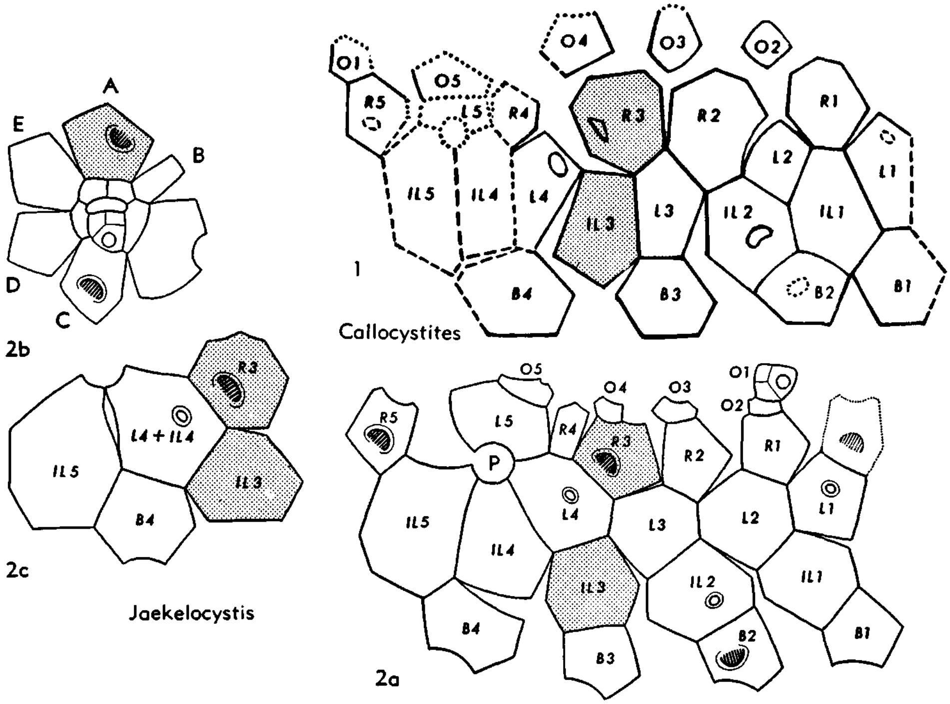


FIG. 102. Callocystitidae, Callocystitinae *(1)*, Apiocystitinae *(2)*, plate diagrams, plates of *A*-ray shaded (p. *S*199-*S*201, S209). [Plate designations as in Figure 38, Carpenter letter symbols for rays in *2b*.]

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

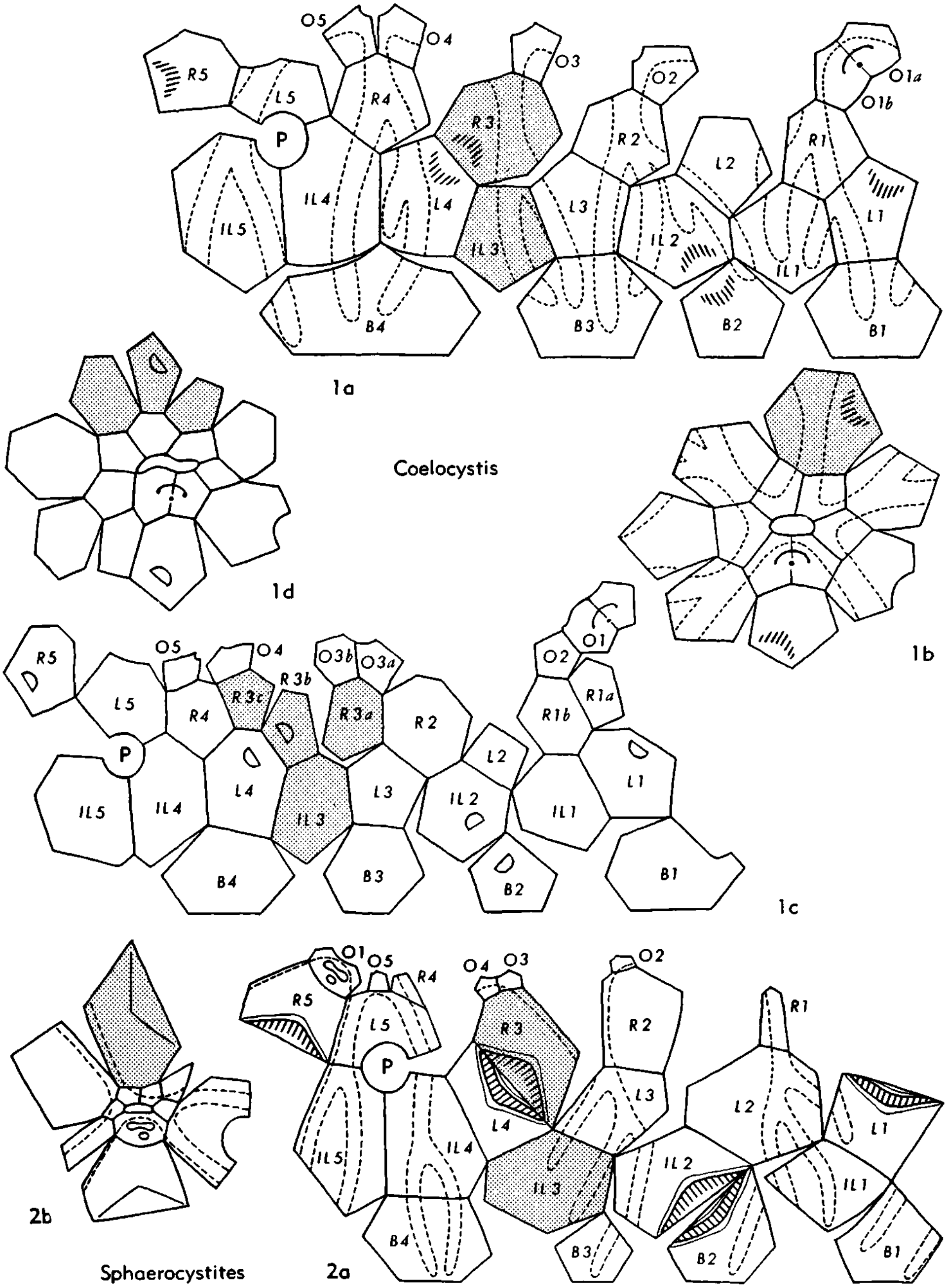


FIG. 103. Callocystitidae, Callocystitinae. Plate diagrams, plates of *A*-ray shaded (p. *S*201-*S*203). [Plate designations as in Figure 38.]

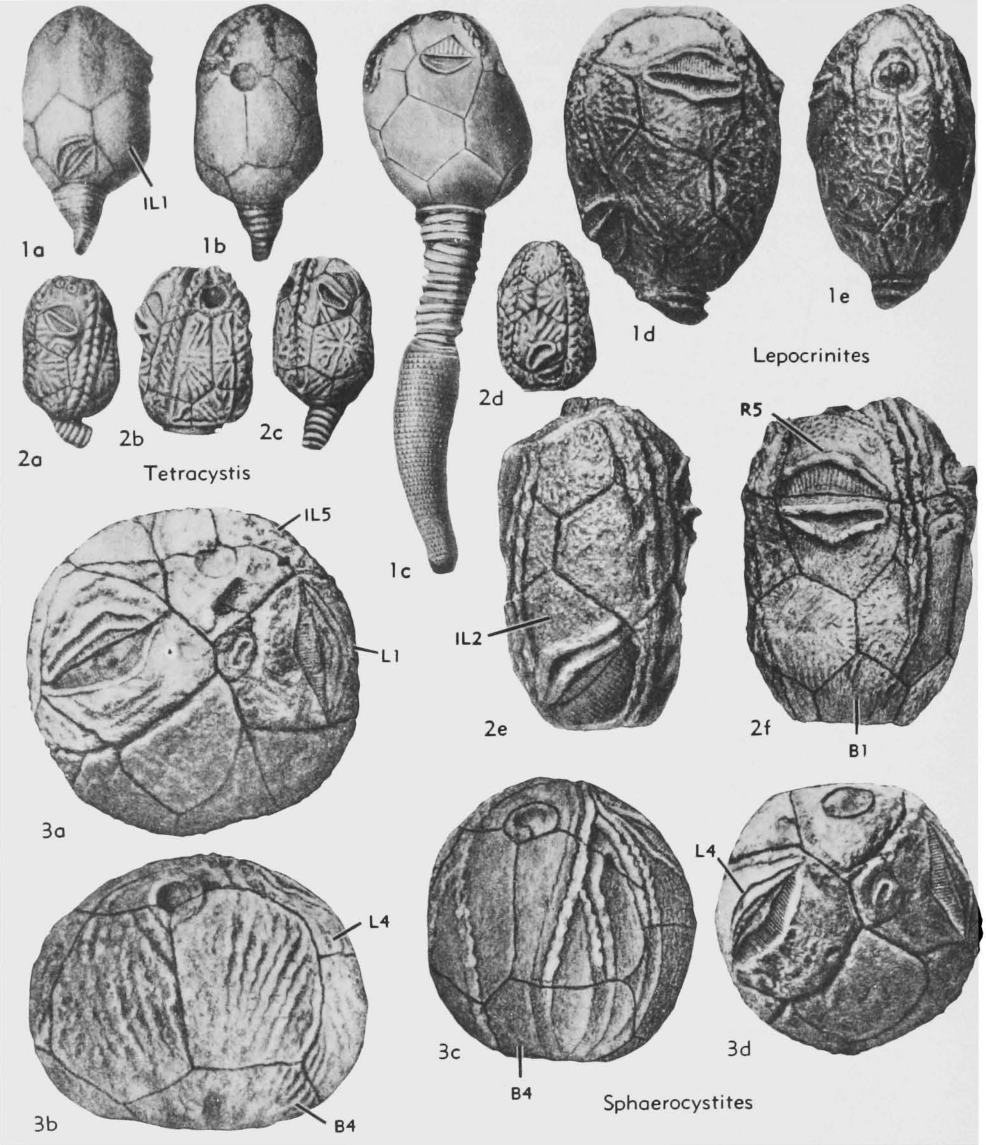


FIG. 104. Callocystitidae, Callocystitinae *(3)*, Apiocystitinae *(1,2)* (p.*S*202-*S*203, *S*211, *S*214). [Plate designations as in Figure 38.]

(Md.); *3a,b,* oral and lat., ×2 (116A).——FIG. 103,*2*; 104,*3c,d*. *S. globularis* SCHUCHERT, Keyser F., USA (Md.); 103,*2a,b,* plate diagrams, lat. and oral (Kesling, n); 104,*3c,d,* lat. and oral, ×2 (116A).

Subfamily APIOCYSTITINAE Jaekel, 1899

[*nom. correct.* KESLING, herein (*pro* Apiocystinae JAEKEL, 1899, p. 277)]

Theca ovate or ellipsoidal; four or five ambulacra, unbranched (except in *Strobilocystites*) and not protuberant; brachioles rather widely spaced; *ILL* forming a closed circlet. *U.Ord.-U.Dev.*

The position of *Strobilocystites,* the last surviving cystoid, is not clearly manifest. In branching of the ambulacra, it is allied with the Callocystitinae, but in the complete circlet of *ILL,* it shows definite affinities with the Apiocystitinae. Furthermore, the branches are only short lateral processes from the main ambulacra, not major divisions like those of *Sphaerocystites,* youngest of the Callocystitinae. In shape of thecal plates, structure of the hydropore, and general organization, *Strobilocystites* has closest resemblance to the slightly older *Lipsanocystis.* It also has ambulacra somewhat entrenched, although not to the degree present in *Jaekelocystis.* Therefore, I place it in the Apiocystitinae, contrary to previous assignments.

With inclusion of *Strobilocystites,* the Apiocystitinae portrays some interesting evolutionary trends. As recognized by JAEKEL (69), BATHER (10), REGNÉLL (99), and others, the Upper Ordovician *Lepadocystis* of southern Indiana and Ohio is the oldest known genus of the subfamily. From this ancestor, with five ambulacra and five pectinirhombs, the Lower Silurian *Brockocystis* developed in eastern North America by loss of the *L2/R1* pectinirhomb and addition of globular projections on the major thecal plates. All subsequent genera had only four ambulacra; apparently, ambulacrum *III,* already short in *Lepadocystis* and *Brockocystis* (in which it was obstructed by the two half-rhombs on *R3*), failed to form in Middle Silurian and later genera. Also in the Middle Silurian, the number of pectinirhombs stabilized at three—*B2/IL2, L1/R5,* and *L4/R3.*

Another trend involved the hydropore. In *Lepadocystis,* this structure is a long U-shaped slit, with a few crossbars to form a grating. In the Devonian *Lipsanocystis* and *Strobilocystites,* the central part of the hydropore is absent, and the ends are greatly enlarged and elevated as two separate sieve-plates. In *Tetracystis* and *Jaekelocystis,* a single large complex sieve-plate occurs, evidently representing one end of the ancestral structure. *Lovenicystis* is intermediate between *Lepadocystis* and *Lipsanocystis;* it has two openings, one piercing each of the two parts of *O1* bearing the hydropore, with a shallow groove leading from one to the other.

Certain Middle Silurian and later genera exhibit a reduction in the number of thecal plates bordering the periproct. *Tetracystis* has four, *Apiocystites* has three, and *Lipsanocystis* has the periproct nearly surrounded by *L5.* Although this may have been a trend in one lineage, the Upper Devonian *Strobilocystites* has four plates involved.

Key to Genera of Apiocystitinae

[After REGNÉLL, 1945 (99)]

1. Ambulacra five more than three pectinirhombs, with two half-rhombs on *R3* .. 2
Ambulacra four; only three pectinirhombs, with single half-rhomb on *R3* 3

2. Pectinirhombs five; *IL4* and *IL5* elongate vertically; *R* circlet interrupted by *L5;* no globular projections on thecal plates .... *Lepadocystis*
Pectinirhombs four; *IL4* and *IL5* not elongate; *R* circlet complete; major thecal plates with globular projections .. *Brockocystis*

3. *L* and *R* circlets complete 4
LL and *RR* intercalated, one or both interrupted 6

4. Periproct bordered by four plates, including *L4* .... *Lovenicystis*
Periproct bordered by three plates, not *L4* 5

5. Pectinirhombs short, with few slits; ambulacra long, nearly reaching the column .... *Apiocystites*
Pectinirhombs long, with numerous slits; ambulacra rarely extending below *LL* .... *Lepocrinites*

6. Periproct enclosed mainly by *L5* .. *Lipsanocystis*
Periproct bordered by three plates, not *L4* 7
Periproct bordered by four plates, including *L4* 8

7. Pectinirhombs small, with few slits; *L1, L2,* and *L3* diamond-shaped, scarcely in contact, if at all; *ILL* much larger than *LL* .... *Hallicystis*
Pectinirhombs large, long, with numerous slits; *L1, L2,* and *L3* large, with sutures between; *ILL* not much larger than *LL* .... *Lepocrinites*

8. Hydropore represented by two separate openings; anal pyramid very small, with aboral bordering plates very large and elongate; ambulacra divided in most mature specimens .... *Strobilocystites*
Hydropore represented by only one opening; anal pyramid relatively large, with bordering plates (if present) subequal; ambulacra undivided in normal specimens 9

9. Pectinirhombs long, with nearly equal halves; anal pyramid with marginal ring of plates; hydropore elongate .... *Tetracystis*
Pectinirhombs short, with half-rhombs on *IL2, L1,* and *L4* reduced to small circular

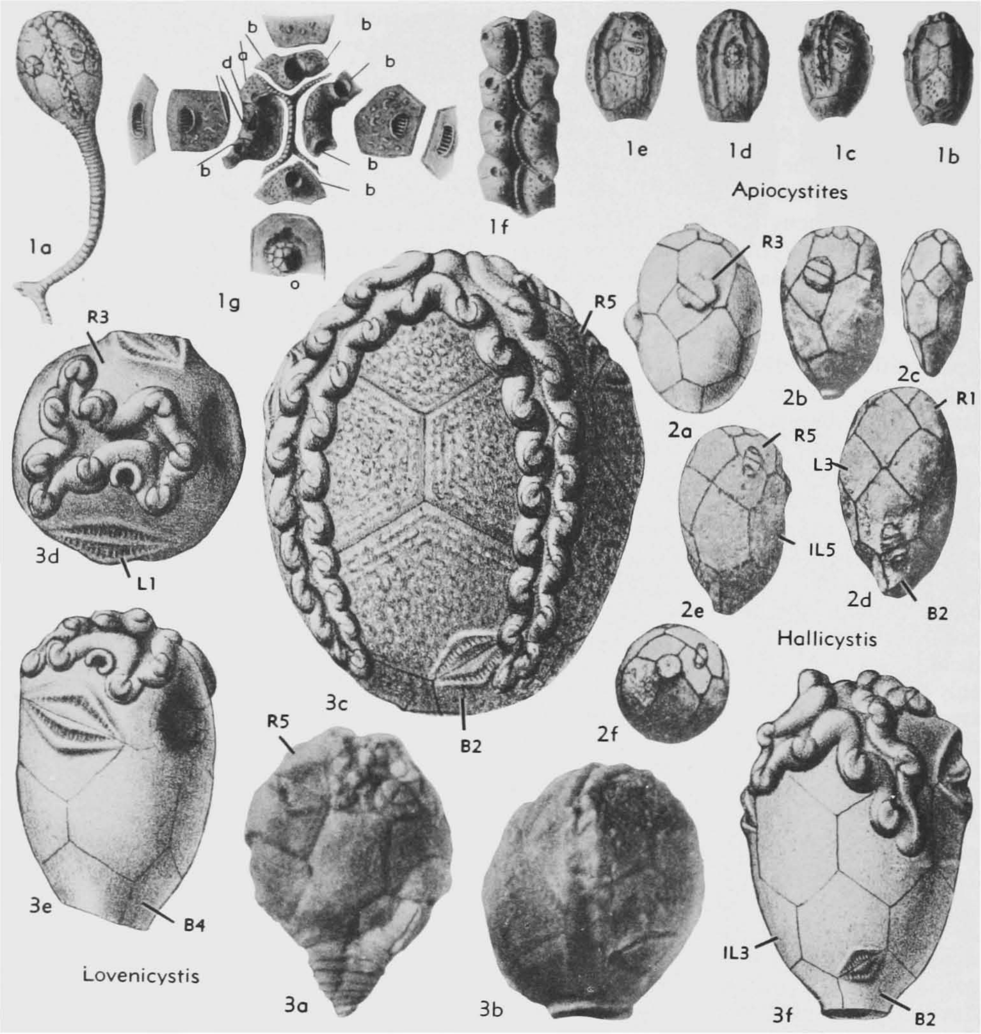


FIG. 105. Callocystitidae, Apiocystitinae (p. S206, S209, S212-S214). [Plate designations as in Figure 38.]

> openings with tubular rims; anal pyramid lacking marginal ring; hydropore large, subcircular .... *Jaekelocystis*

Apiocystites FORBES, 1848, p. 501 [**A. pentrematoides;* OD] [=*Apiocystis* BATHER, 1889, p. 268 *(nom. van.)*]. Theca regularly ovate, elongate or slightly compressed, plum-shaped, with long axis not exactly vertical. *L* and *R* circlets complete. Ambulacra 4, long, attenuated, nearly reaching column, never branched or entrenched in thecal plates; brachioles spaced farther apart than in other genera of subfamily, so that each ambulacrum has only 20 to 36 facets. Pectinirhombs 3, small, short, and discrete, with few slits; no notable difference between the 2 halves of each rhomb; rhombs *L1/R5* and *L4/R3* inclined. Periproct small, bordered only by *IL4, IL5,* and *L5;* anal pyramid of 6 plates, outer ring of 9 plates. Hydropore and gonopore present on *O1;* other *OO* very small. *M.Sil.-L.Dev.,* Eu.(Eng.)-N.Am. (N.Y.-Tenn.-Ont.).——FIG. 105,*1a.* **A. pentrematoides,* M.Sil.(Wenlock), Eng.; lat., reconstr., ×1 (69).——FIG. 105,*1b-g. A. elegans* HALL, M.Sil.(Niagaran), USA(N.Y.); *1b-e,* 4 lat., ×1; *1f,* detail of ambulacrum, enl.; *1g,* plate diagram of oral region (*a,* hydropore; *b,* oral plates; *d,* gonopore; *o,* periproct) (60).

Brockocystis FOERSTE, 1914, p. 469 [**Apiocystites? tecumsethi* BILLINGS, 1866, p. 91; OD]. Theca ovate, many thecal plates strongly modified by large hemispherical protuberance occupying most of plate. *R* circlet complete; *IL4* and *IL5* not elongate; *R3* distinctive, nearly square, and like corresponding plate in *Lepadocystis* bearing 2 half-rhombs on its aboral sides, separated only by

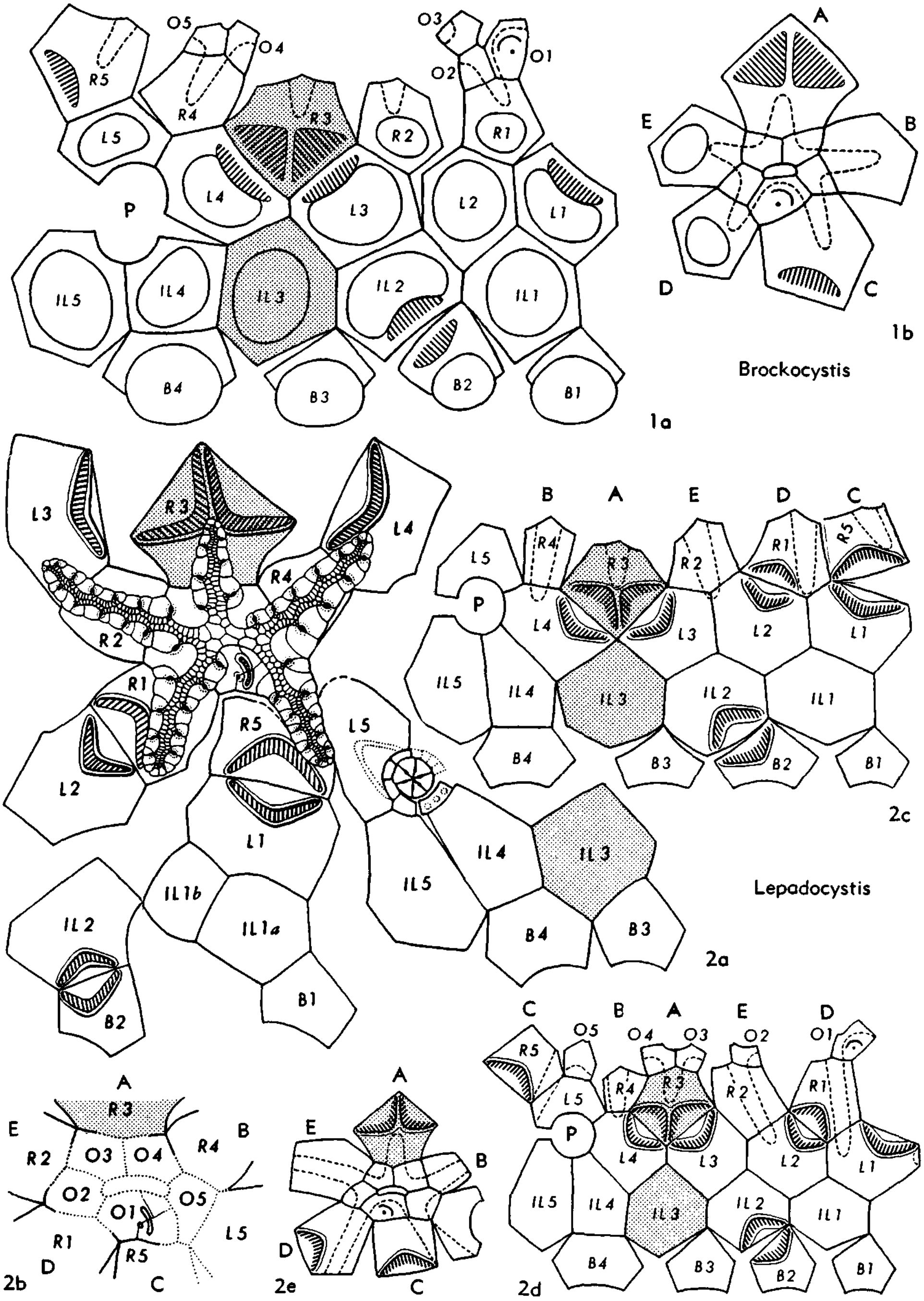


Fig. 106. Callocystitidae, Apiocystitinae, plates of *A*-ray shaded (p. *S*206-*S*211). [Plate designations as in Figure 38.]

narrow ridge; *OO* little known. Periproct large, nearly circular, its plates unknown, bordered by *IL4, IL5, L4,* and *L5.* Ambulacra 5, relatively short, few extending below *RR,* ambulacrum III short and obstructed by the close-set half-rhombs on *R3;* ambulacral grooves in trimerous arrangement in oral region; brachioles few. Pectinirhombs 4, B2/*IL2*, *L1*/*R5*, *L3*/*R3*, and *L4*/*R3*, each with long slits. In known examples, column tapering distally for about 12 columnals, lower end of this section set deeply in curious kind of cup formed by about 4 greatly expanded columnals, beyond which column tapers rapidly to very narrow diameter; distal end unknown. *L.Sil.,* N.Am.(Ont.-Ohio).——FIG. 106,*1;* 107,*1a-d.* **B. tecumsethi* (BILLINGS), Cataract Ls., Ont.(Manitoulin Is.);

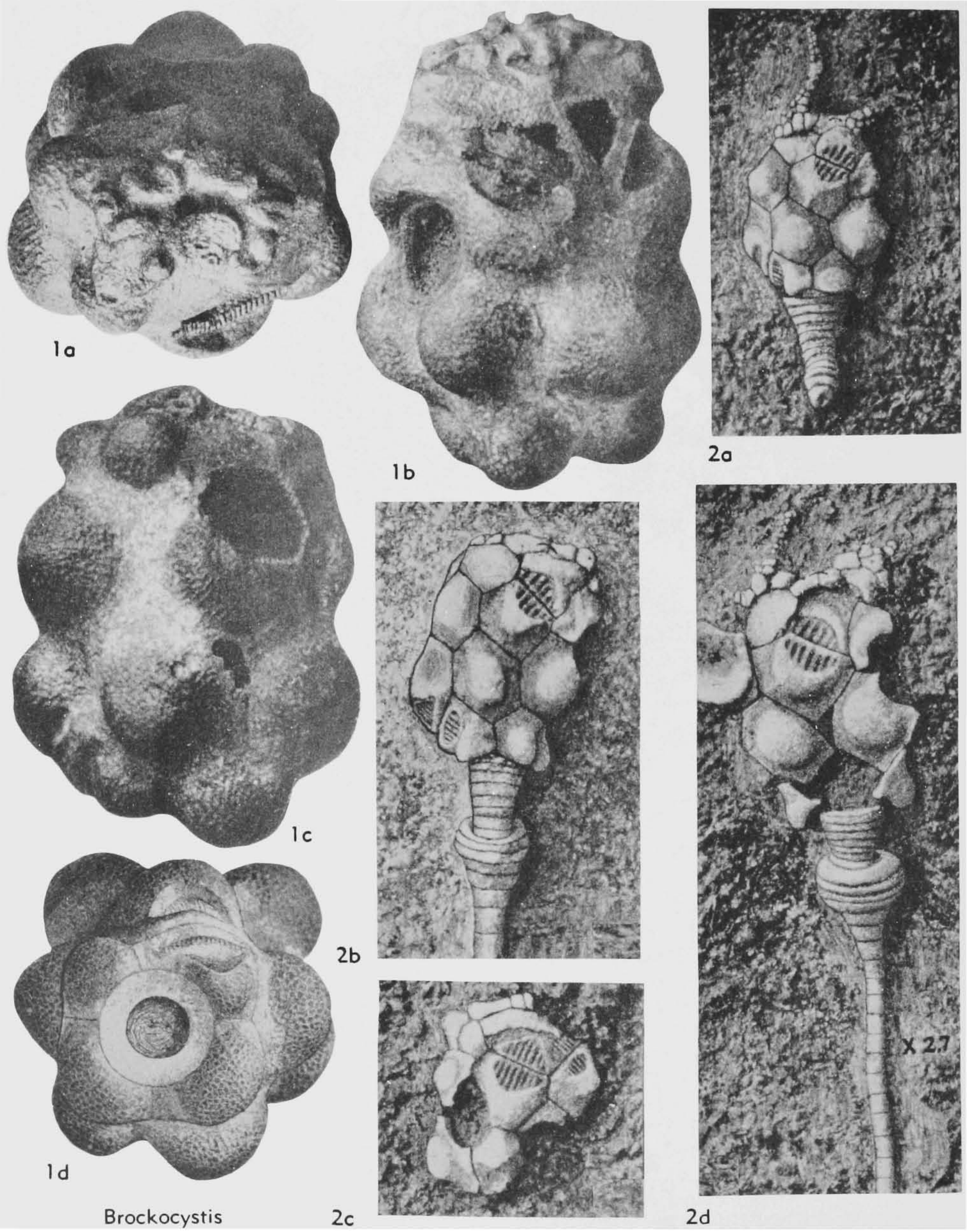


FIG. 107. Callocystitidae, Apiocystitinae (p. *S*206-*S*209).

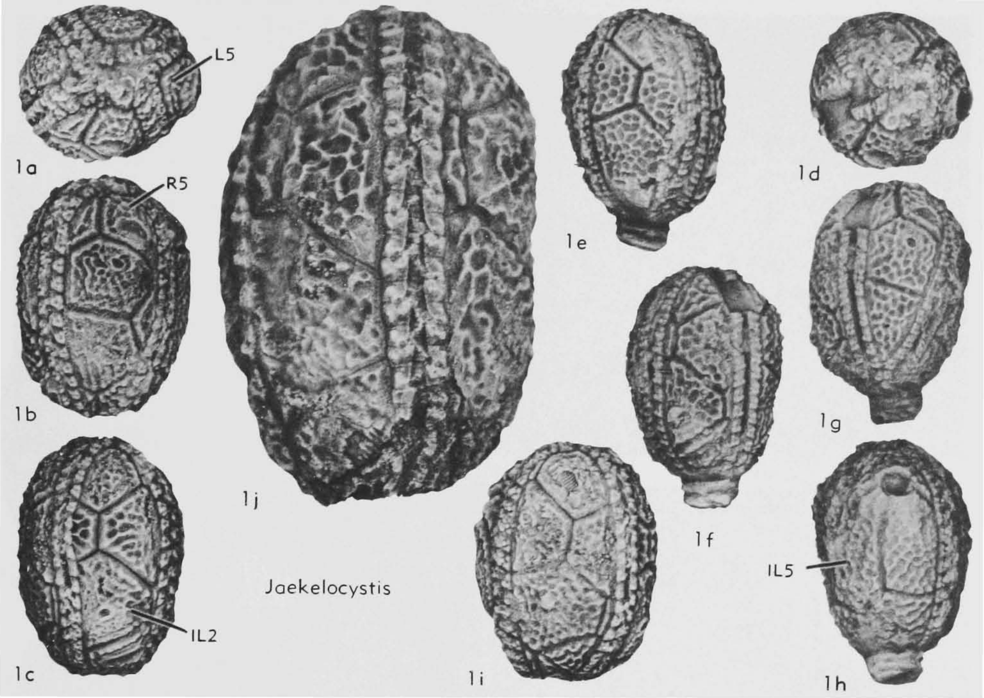


FIG. 108. Callocystitidae, Apiocystitinae (p. *S*209). [Plate designations as in Figure 38.]

106,*1a,b,* plate diagram and oral region (Kesling, n); 107,*1a-c,* oral and 2 lat., holotype, ×3 (46); 107,*1d,* aboral, holotype, ×3 (48).——FIG. 107, 2. *B. nodosaria* FOERSTE, Brassfield Ls., USA (Ohio); *2a-d,* lat., 4 thecas, ×2.7 (48).

Hallicystis JAEKEL, 1899, p. 286 [**Apiocystites imago* HALL, 1864, p. 10; OD]. Theca acorn-shaped, base not indented. *LL* and *RR* intercalated, not forming complete circlets; *L5* between *R4* and *R5; L1, L2,* and *L3* diamond-shaped, scarcely in contact, if at all; *ILL* much larger than *LL. OO* relatively large. Pectinirhombs 3, *B2/IL2, L1/R5,* and *L4/R3,* each half in form of a semicircle, with few slits. Periproct bordered by 3 plates, *IL4, IL5,* and *L5;* anal pyramid enclosed by circle of minute plates. Ambulacra 4. [Genus only known from steinkerns, but plates apparently bearing radial ridges, according to FOERSTE (1917).] *M.Sil.,* N.Am.(Wis.-Ill.-Ohio).——FIG. 100,*2;* 105,*2.* **H. imago* (HALL); 100,*2a,b,* plate diagram and oral region (Kesling, n); 105,*2a,* lat., steinkern, ×1 (69); 105,*2b,c,* 2 lat., steinkerns, ×1; 105,*2d-f,* 2 lat. and aboral, steinkerns, ×0.9 (49).

Jaekelocystis SCHUCHERT, 1903, p. 230 [**J. hartleyi;* OD]. Theca ovate to ellipsiform, some forms tending to be subquadrate in cross section. *ILL* forming complete circlet, *IL4* and *IL5* large and elongate; *R* circlet interrupted by large *L5, R4* very small, mostly concealed by ambulacrum *IV.* Periproct conspicuous, somewhat protruding in some specimens, bordered by *IL4, IL5, L4,* and *L5;* anal pyramid without surrounding accessory plates. Ambulacra long, 4 in normal specimens, flooring plates deeply embedded in thecal plates; brachiole facets discrete but numerous. Hydropore (possibly combined with gonopore) consisting of very large circular opening filled by sieve plate with vermicular, somewhat radiating slits, whole being set within *O1,* which appears to be substantially fused into single plate. Pore rhombs 3, highly specialized; halves on *B2, R3,* and *R5* nearly semicircular, provided with few, distinct slits and bordered by outer rim, but halves on *IL2, L1,* and *L4* reduced to small circular openings (at surface) with high rim, more or less tubular. [Certain significant variations can be determined from study of numerous exceptionally well-preserved specimens available. Despite deep entrenching of the ambulacra, their course across the thecal plates varies greatly. One specimen exhibits a branched ambulacrum; others have one short or completely aborted ambulacrum. Certain plate anomalies also occur.] *L.Dev.,* N.Am.(W.Va.).——FIG. 108,*1;* 102,*2.* **J. hartleyi;* 108,*1a-c,* oral and 2 lat., paratype, ×2; 108,*1d-h,* oral and 4 lat., another paratype, ×2; 108,*1i,* lat., third paratype, ×2; 108,*1j,* lat. showing details of ambulacrum *I,* ×4; 102,*2a,b,* plate

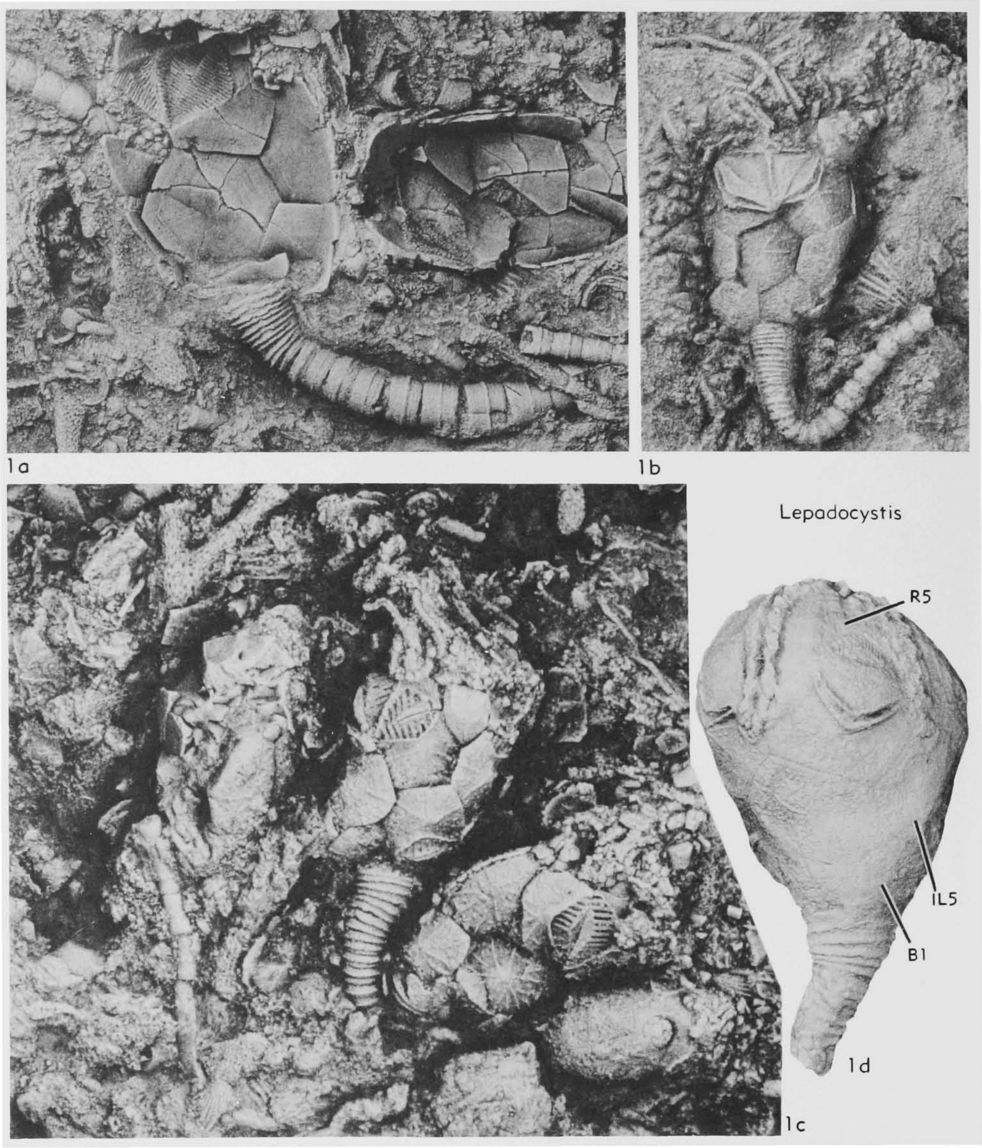


FIG. 109. Callocystitidae, Apiocystitinae (p. *S*210-*S*211).

diagram and oral region, normal specimen; 102, *2c,* anomalous plate development (73). [See also Fig. 43.]

Lepadocystis CARPENTER, 1891, p. 10 [*_Lepocrinites moorei_ MEEK, 1871, p. 296; OD (=*Lepadocrinites moorei* MEEK, 1871, *nom. null.*)] [=*Meekocystis* JAEKEL, 1899, p. 278 (obj.)]. Theca subovate to ellipsoidal, gerontic forms becoming pyriform and tapering to column. *R* circlet interrupted by *L5;* periproct bordered by *IL4, IL5, L4,* and *L5; IL4* and *IL5* vertically elongate; *R3* very distinctive, nearly square, with 2 half-rhombs on aboral sides of plate separated only by narrow ridge; *OO* rather large, *O1* tripartite. Ambulacra 5, relatively short, few extending below *RR,* ambulacrum III *(A)* short and obstructed by 2 half-rhombs on *R3.* Pectinirhombs 5, *B2/IL2, L1/R5, L2/R1, L3/R3,* and *L4/R3.* Gonopore and hydropore bisected by suture through *O1;* hydropore shaped like broad U, slot provided with grating or crossbars. Column with large narrow rings near theca, distally decreasing in diameter, its end variously modified for attachment to objects. Ornamentation increasing in complexity to

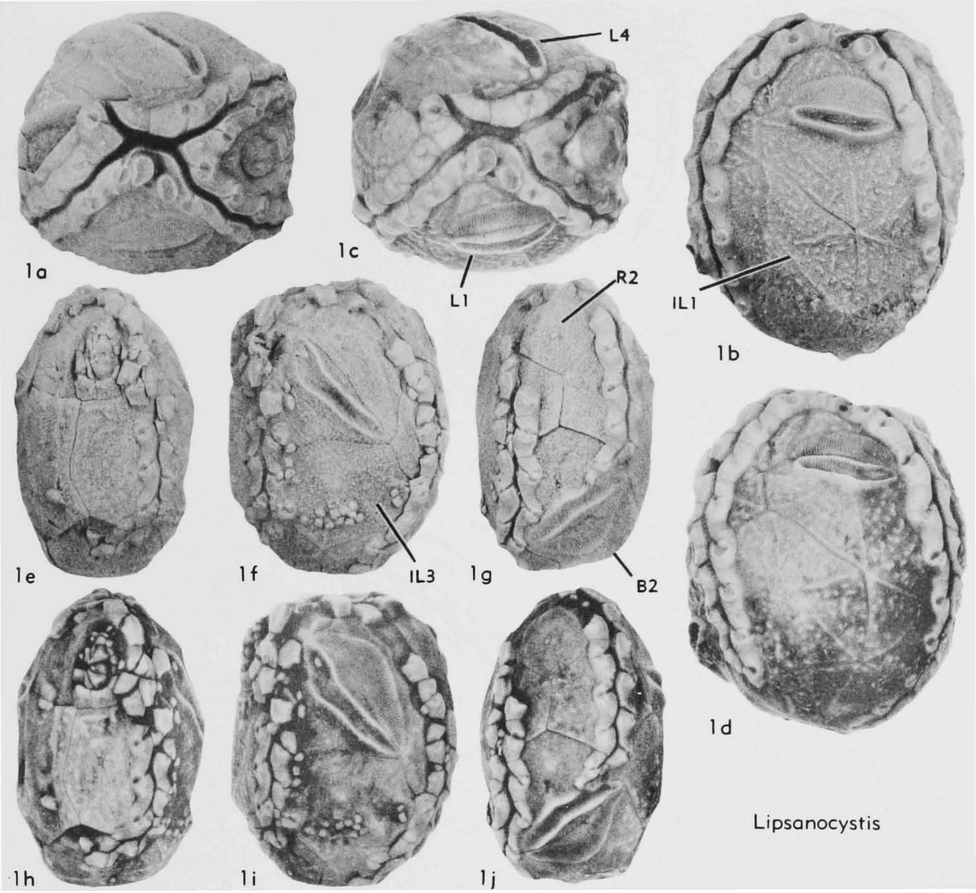


FIG. 110. Callocystitidae, Apiocystitinae (p. *S212-S213*). [Plate designations as in Figure 38.]

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,

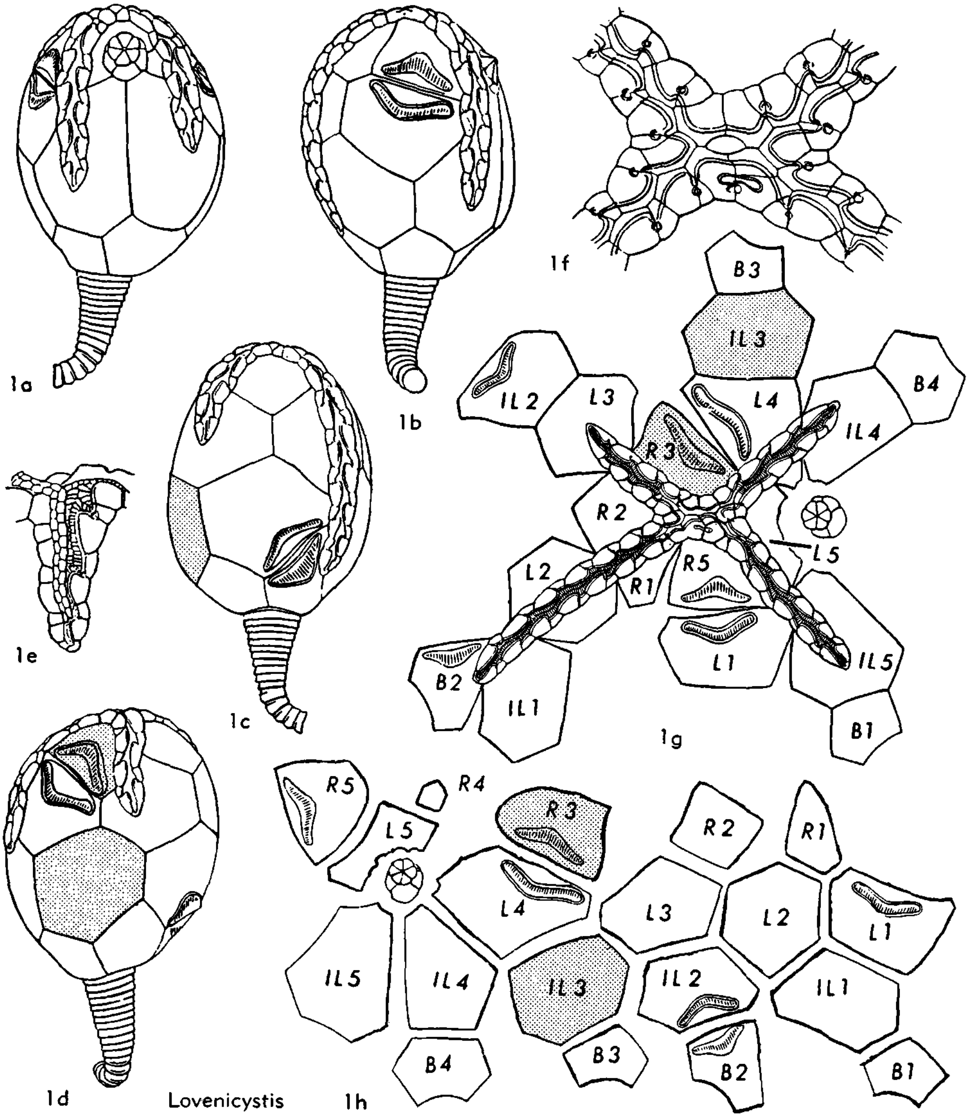


FIG. 111. Callocystitidae, Apiocystitinae. Lateral views (reconstr.) and plate diagrams; plates of *A*-ray shaded (p. *S*213-*S*214). [Plate designations as in Figure 38.]

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;*

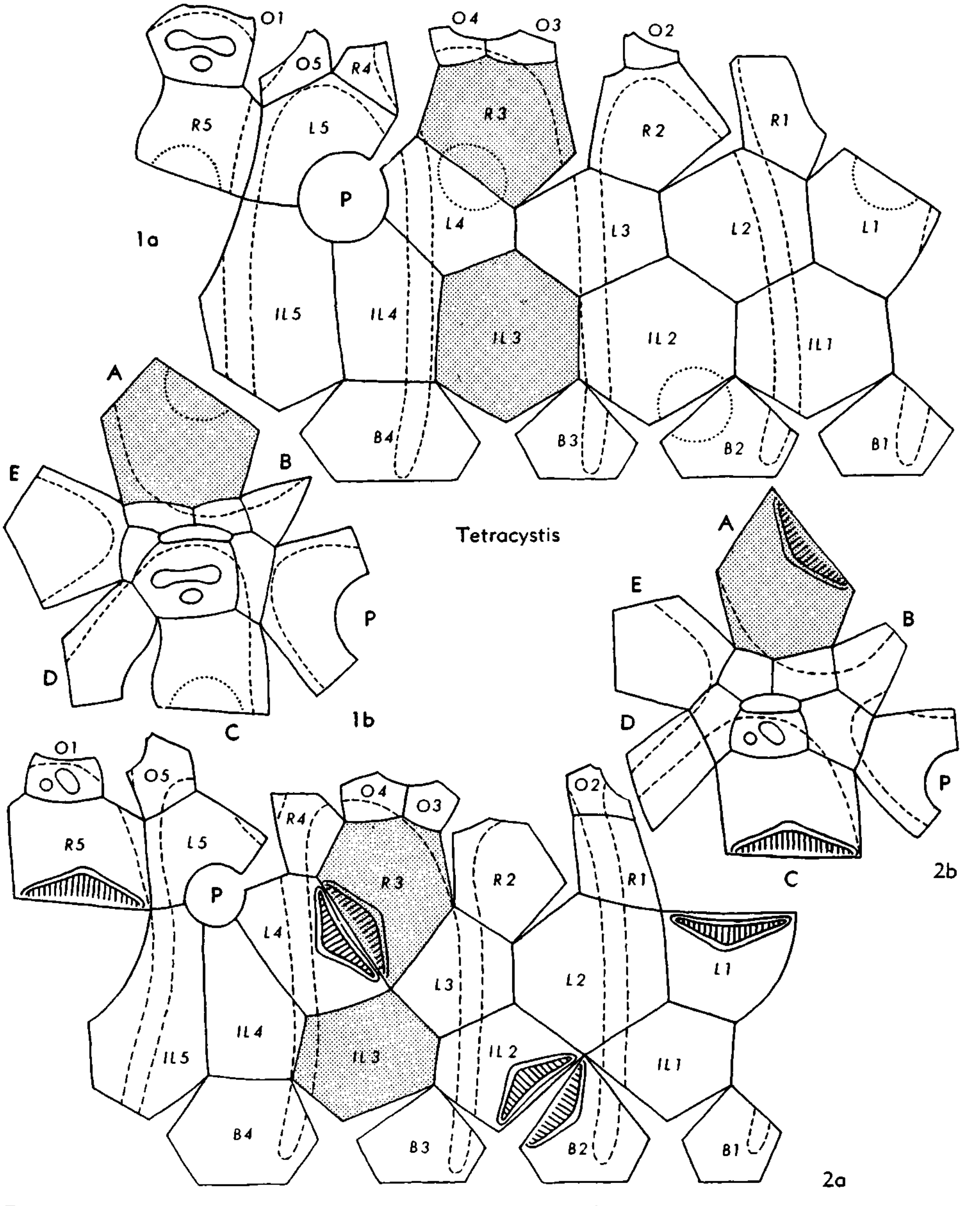


FIG. 112. Callocystitidae, Apiocystitinae. Plate diagrams, plates of *A*-ray shaded (p. S214). [Plate designations as in Figure 38, Carpenter letter symbols for rays in *1b,d.*]

100,*1a,b,* plate diagram and oral region (Kesling, n); 110,*1a,b,* oral and lat., ×2, coated with ammonium chloride; 110,*1c,d,* same, submersed in xylol; 110,*1e-g,* 3 lat., ×2, coated; 110,*1h-j,* same, submersed (Kesling, n).

Lovenicystis REGNÉLL, 1945, p. 90 [**Apiocystites angelini* JAEKEL, 1899, p. 282; OD (=*Lepadocrinus angelini* HAECKEL, 1896, p. 135, *nom. nud.*)]. Theca ovate to globular, nearly circular in cross section. *LL* and *RR* forming closed circlets; *IL4* and *IL5* vertically elongate; *O1* tripartite, with *O1a*/*O1b* suture bisecting hydropore and gonopore, each of which has 2 openings. Periproct bordered by *IL4, IL5, L4,* and *L5,* filled by anal pyramid of 6 pieces and 5 or 6 aboral bordering plates. Ambulacra 4, long, one or more extending nearly to base; brachioles numerous but not closely spaced. Pectinirhombs 3, *B2/IL2, L1/R5,* and *L4/R3. U. Sil.,* Eu.(Sweden).——Fig. 105,*3;* 111,*1.* **L. angelini* (Jaekel), L. Ludlow, Gotl.; 105,*3a,b,* lat., 2 thecae, ×2.25 (99); 105,*3c,* lat., adult, ×6; 105,*3d,e,* oral and lat., juvenile, ×6; 105,*3f,* lat., juvenile, ×6 (69); 111,*1a-d,* lat., reconstr.; 111, *1e,* short ambulacrum with flooring and covering plates; 111, *1f,* peristomial region, covering plates removed from peristome and ambulacra; 111,*1g,* plates projected radially from peristome along ambulacra; 111,*1h,* plate diagram (99). [See also Fig. 36,*1*; 45,*1*.]

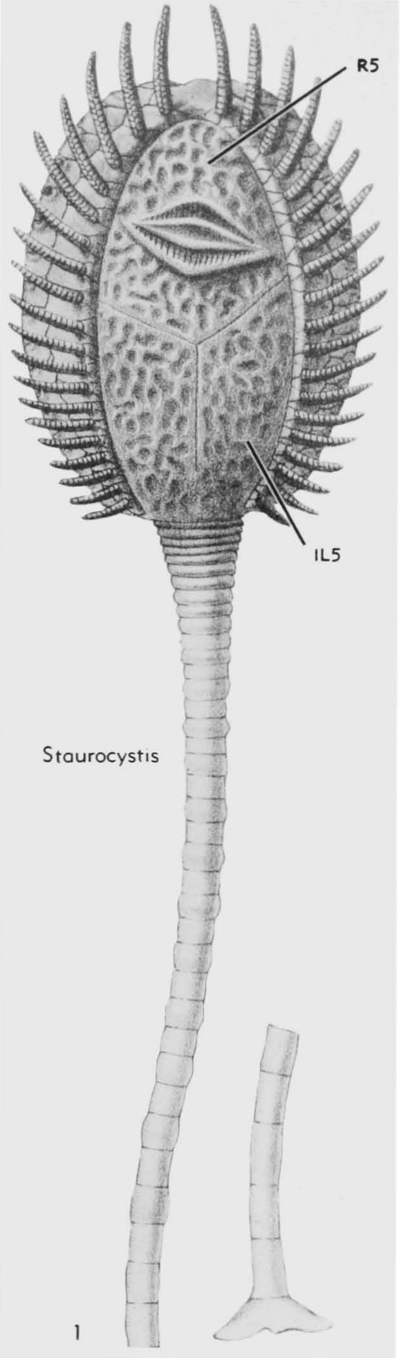


Fig. 113. Callocystitidae, Staurocystinae (p. *S*217-*S*218). [Plate designations as in Figure 38.]

Strobilocystites White, 1876, p. 28 [**S. calvini;* OD] [=*Strobilocystis* Carpenter, 1891, p. 5 *(nom. van.)*]. Theca subovate. *L* and *R* circlets complete. Periproct bordered by 4 plates, *IL4, IL5, L4,* and *L5;* anal pyramid small, subcircular, acuminate, surrounded by ring of accessory plates, of which aboral plates are exceptionally large and elongate radially to pyramid. Ambulacra 4, long, branched in adults of most known species, rather broad, slightly entrenched in thecal plates. Pectinirhombs long, provided with numerous slits, angulated, with halves on *IL2, L1,* and *L4* surrounded by prominent rim; rhomb *L1/R5* nearly horizontal, *L4/R3* exceptionally long, nearly vertical. Hydropore divided into 2 discrete parts, each nearly circular, on opposite sides of suture through *O1;* gonopore a small opening bisected by this suture. *OO* very thick, to attain level of thick ambulacral flooring plates. Branching of ambulacra and elongation of *L4/R3* rhomb emphasized in large (mature and gerontic) specimens. *M.Dev.-U.Dev.,* USA(Iowa).——Fig. 49,*1-14.* **S. calvini,* M.Dev.; 49,*1,* reconstr., ×2; 49,*2-4,* plate diagrams of normal and 2 anomalous specimens; 49,*5-9,* ontogenetic series of ambulacra; 49,*10-14,* variations in periproct (120). [See also Figs. 36,*2,* 45,*2,* 48,*2*.]

Tetracystis Schuchert, 1904, p. 217 [**T. fenestratus;* OD (=*Echinoencrinites fenestratus* Troost, 1849, p. 419, *nom. nud.*)]. Theca elongate, subquadrate in cross section, its ends subovate. *L5* interrupting *R* circlet; *ILL* and *LL* forming definite circlets in some, tenuous circlets in others in which *IL1/IL2, L3/L4,* and/or *L1/L5* contacts are reduced to points. Periproct bordered by 4 plates, rather prominent, filled by acutely pointed pyramid and numerous surrounding platelets. Pectinirhombs 3, long, bearing numerous slits. Ambulacra 4, long, narrow, one along each edge of subquadrate theca; brachioles relatively few, slender, widely separated. *M.Sil.-L.Dev.,* N.Am. (Tenn.-W.Va.)——Fig. 104,*2a-d;* 112,*1.* **T. fenestrata,* M.Sil.(Niagaran), USA(Tenn.); 104, *2a-d,* 4 lat., ×1 (Springer, 1926); 112,*1a,b,* plate diagrams, lat. and oral (*A*-ray shaded) (Kesling, n).——Fig. 104,*2e,f;* 112,*2.* *T. chrysalis* Schuchert, L.Dev.(Keyser F.), USA(W.Va.); 104,*2e,f,* 2 lat., ×2 (116A); 112,*2a,b,* plate diagrams, lat. and oral (*A*-ray shaded) (Kesling, n).

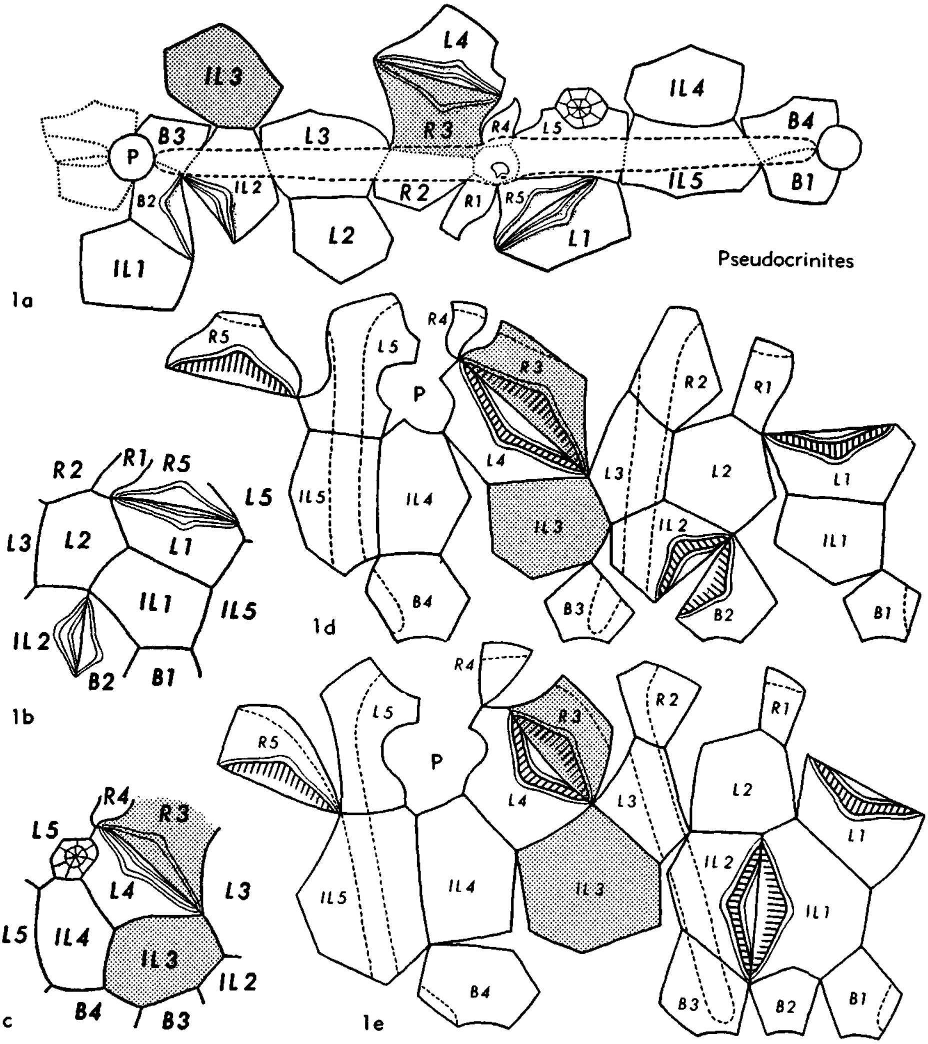


FIG. 114. Callocystitidae, Staurocystinae. Plate diagrams, plates of *A*-ray shaded (p. *S*218). [Plate designations as in Figure 38.]

Subfamily STAUROCYSTINAE Jaekel, 1899

[Staurocystinae JAEKEL, 1899, p. 282]

Theca ovate or biconvex. Shape and arrangement of plates strongly modified by shape of theca. Ambulacra two to four, undivided, strongly protuberant, provided with very numerous, closely spaced brachioles. *U.Sil.-L.Dev.*

Within the well-known *Pseudocrinites,* several anomalies occur. As KESLING (73) has pointed out, in four sets of four plates each, the plates practically meet at a point: *B2-IL2-L2-IL1, IL3-L4-R3-L3, L1-L2-R1-R5,* and *L4-L5-R4-R3.* This reduction in sutures seems to have induced instability in the theca, which fulfills its normal function by rigidity. Plate arrangements vary, at least in minor details. A specimen called *P. abnormalis* by SCHUCHERT (116) has the basal rhomb between *IL1/IL2* instead of the regular location between *B2/IL2,* with corresponding alterations in the *BB* and *ILL* to accommodate this large structure. The cystoid called *Trimerocystis* by SCHUCHERT (116) appears to have the same plate arrangement as species of *Pseudocrinites* with

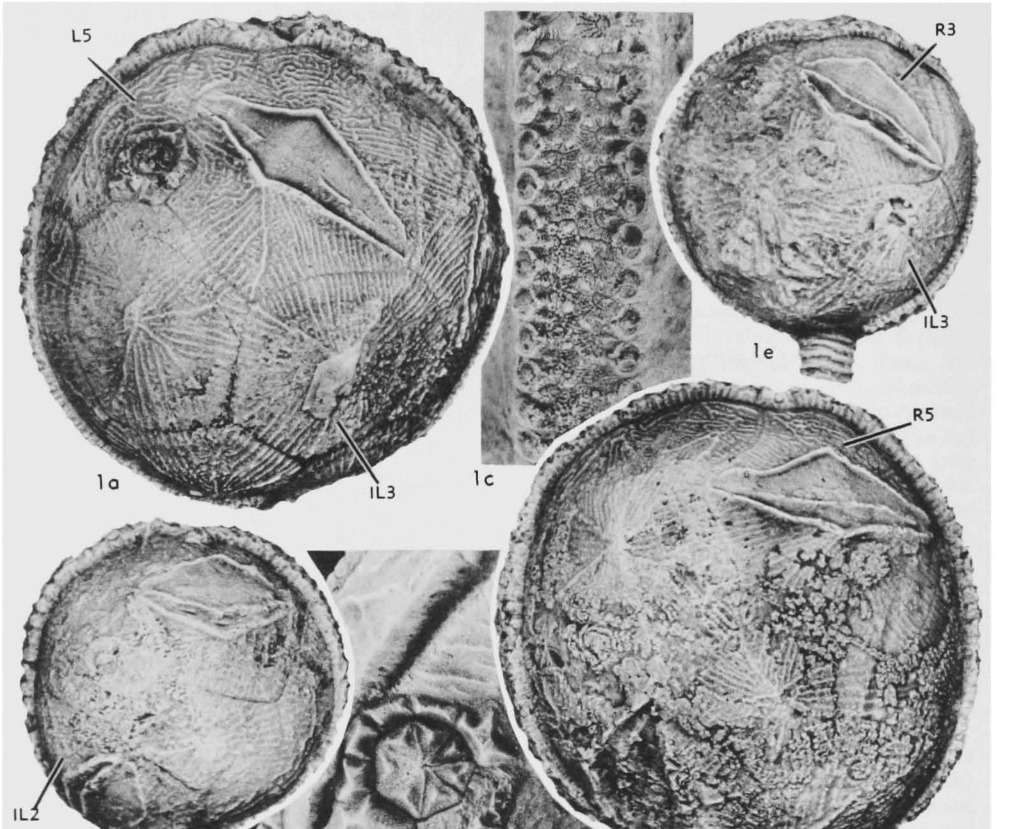


FIG. 115. Callocystitidae, Staurocystinae (p. S218). [Plate designations as in Figure 38.]

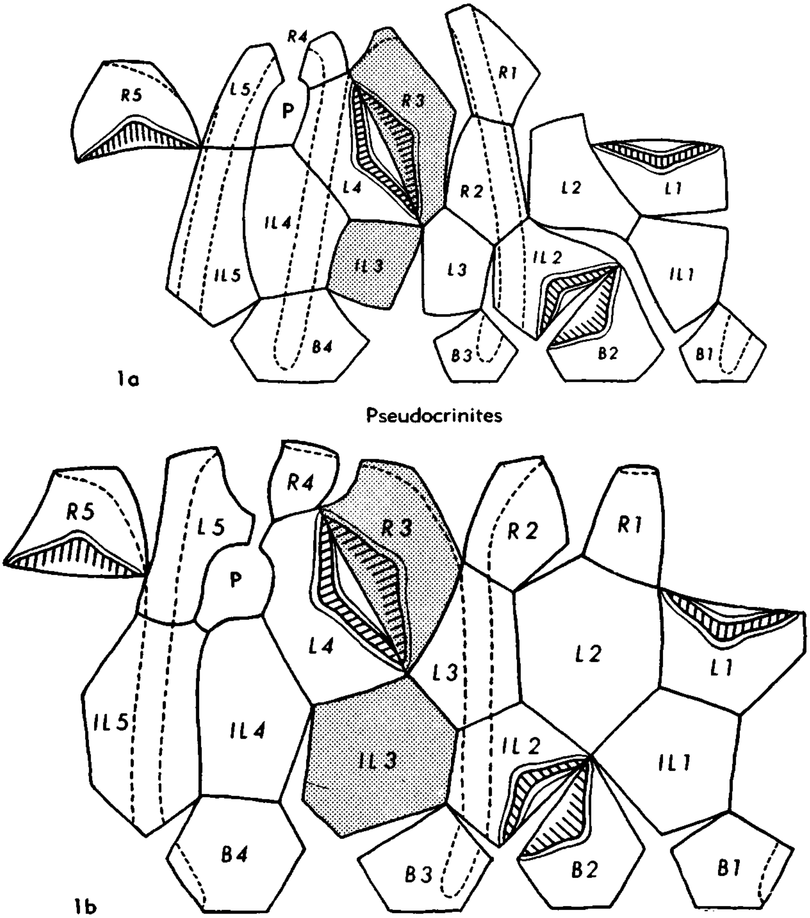


FIG. 116. Callocystitidae, Staurocystinae. Plate diagrams, plates of *A*-ray shaded (p. *S*217-*S*218). [Plate designations as in Figure 38.]

which it occurs, differing only in having a supernumerary third ambulacrum.

In the Staurocystinae, the ambulacral flooring plates are remarkably thick, so that the ambulacral groove is perched well above the level of the thecal plates. The spacing of these flooring plates, insofar as known, remains constant throughout ontogeny, indicating that the contact between these plates and the expanding thecal plates required continuous readjustment and repositioning during growth of the cystoid. The specialization of the ambulacra has obscured details of the oral region, although the *OO* were presumably also highly protuberant to receive the ambulacral groove from the ambulacra.

Key to Genera of Staurocystinae

Theca subovate; ambulacra four .... *Staurocystis*

Theca biconvex, lenslike; ambulacra two, forming thick peripheral rim .... *Pseudocrinites*

Staurocystis HAEKEL, 1896, p. 134 [**Pseudocrinites quadrifasciatus* PEARCE, 1843, p. 160; OD]. Theca subovate, suboctagonal in cross section because of strongly protuberant ambulacra; exposed part of theca in middle about twice as wide as ambulacra, gently convex. *IL1, IL2,* and *IL3* hexagonal, with distinct sutures between them; *IL4* and *IL5* vertically elongate; *IL3-L3-R3-L4* tending to meet at a point, other plates with definite sutures. All ambulacra extending to column, each with about 40 brachiole facets in adult specimens. Periproct small, subcircular, bordered by *IL4, IL5, L5,* and narrow corner of *L4*. Pectinirhombs large, long, angulated, provided with numerous slits, with

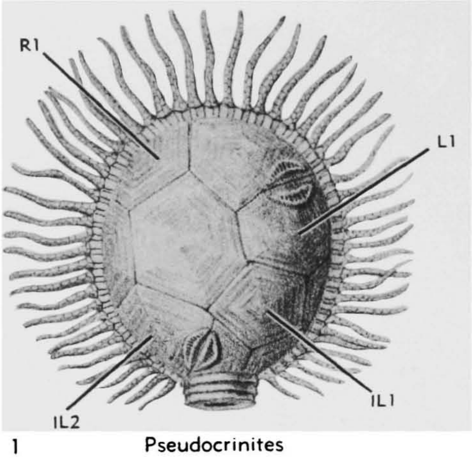


FIG. 117. Callocystitidae, Staurocystinae (p. S217-S218). [Plate designations as in Figure 38.]

halves on *IL2, L1,* and *L4* enclosed by sharply raised rim, their opposite halves with outer rim only; rhomb *B2/IL2* between ambulacra I and II, *L4/R3* between II and IV, and *L1/R5* between I and V; periproct between IV and V. Column long, as usual in family tapering rapidly distally from short wide columnals to long narrow columnals. *U.Sil.*(Wenlock), Eu.(Eng.).——FIG. 113,*1*. **S. quadrifasciata* (PEARCE); reconstr., ×5 (69).

Pseudocrinites PEARCE, 1842, p. 472 [**P. bifasciatus* PEARCE, 1843, p. 160; SD HAECKEL, 1896, p. 135 (=*P. bicopuladigiti* GARNER, 1844, p. 160)] [=*Phacocystis* HAECKEL, 1896, p. 135 *(obj.); Pseudocrinus* HAECKEL, 1896, p. 135 *(nom. van.); Trimerocystis* SCHUCHERT, 1904, p. 237 (type *T. peculiaris*)]. Theca biconvex, shaped like round or oval inflated disc, with ambulacra forming thick, heavy rim around periphery. Ambulacra 2, accounted as II and V, each composed of exceptionally thick flooring plates that raise narrow ambulacral groove well away from thecal plates, long, in many specimens attaining column, in some even longer and deflected to side of column; brachioles numerous, alternating in separate rows, those in each row close-set in circular facets; sides of ambulacral covering plates forming high palisade, obscuring details of *OO;* oral region apparently boxlike, with hydropore on top and gonopore (closed by pyramid of tiny plates) on side; other thecal plates distinct; 4 points tending to serve as junction of sets of 4 plates each, *B2-IL2-L2-IL1, IL3-L4-R3-L3, L1-L2-R1-R5,* and *L4-L5-R4-R3,* thus reducing number of sutures greatly and creating relatively unstable arrangement; *R1* and *R4* small, curved; *R* circlet interrupted by *L5* between *R4* and *R5.* Pectinirhombs large and long, with numerous slits, rimmed like those in *Staurocystis; L4/R3* exceptionally long, about 0.6 diameter of theca; rhombs *B2/IL2* and *L1/R5* on one face of theca, rhomb *L4/R3* and periproct on other. Periproct bounded by *IL4, L4,* and *L5,* not by *IL5* as in other genera of family; anal pyramid with wide border of accessory plates. *U.Sil.-L. Dev.,* Eu.(Eng.)-N.Am.(W.Va.-Md.-Pa.).——FIG. 114,*1;* 115,*1*. *P. gordoni* SCHUCHERT, L.Dev., USA (Md.); 114,*1a,* plate diagram expanded along ambulacra; 114,*1b,c,* plates on opposite sides, ambulacra not shown, about ×1 (73); 114,*1d,* plate diagram of holotype (Kesling, n); 114,*1e,* plate diagram of abnormal specimen, the "holotype" of *P. "abnormalis"* SCHUCHERT, in which rhomb *B2/IL2* is in the *IL1/IL2* position (Kesling, n, after 116); 115,*1a,b,* opposite lat., holotype (large specimen), ×2; 115,*1c,* ambulacrum, enl.; 115,*1d,* oral end of holotype, enl. to show rhomb *L1/R5* and gonopore (closed by tripartite pyramid); 115,*1e,f,* opposite lat., smaller specimen, ×2; 115,*1g,* periproct of another specimen, ×5 (73).——FIG. 116,*1b*. *P. perdewi* SCHUCHERT, U.Sil.(Manlius Ls.), USA(W.Va.); plate diagram (Kesling, n).——FIG. 116,*1a*. *P.* sp. cf. *P. perdewi,* U.Sil.(Manlius Ls.), USA(W.Va.); plate diagram of type and only specimen of *"Trimerocystis peculiaris"* SCHUCHERT (Kesling, n).——FIG. 117,*1*. *P. magnificus* FORBES, U.Sil.(Wenlock), Eng.; lat., ×1 (69).

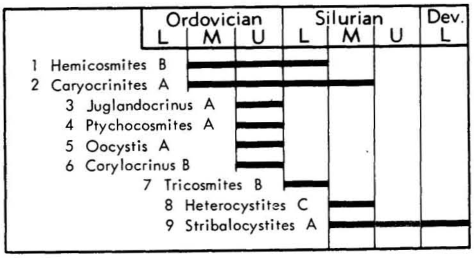


FIG. 118. Stratigraphic distribution of genera belonging to the superfamily Hemicosmitida. Classification of the genera in families is indicated by letter symbols: A—Caryocrinitidae, B—Hemicosmitidae, C—Heterocystitidae. The following alphabetical list of genera furnishes cross reference to the serially arranged numbers on the diagram (Kesling and Moore, n).

Generic Names of Hemicosmitida and Index Numbers

Caryocrinites—2
Corylocrinus—6
Hemicosmites—1
Heterocystites—8
Juglandocrinus—3
Oocystis—5
Ptychocosmites—4
Stribalocystites—9
Tricosmites—7

Superfamily HEMICOSMITIDA Jaekel, 1918

[*nom. transl.* REGNÉLL, 1945, p. 97 (*ex* Hemicosmitidae JAEKEL, 1918, p. 97)] [=suborder Hemicosmites JAEKEL, 1918, p. 97)]

Theca composed of four *BB*, six to ten *ILL*, eight or more *LL*, and several *RR*. Rhombs with inner side of strong folds or laminae perpendicular to sutures; distal end of each pore terminating in tubercle covered by epitheca (opening exposed only in weathered specimens), some ends branching into short cavities within tubercle. *M. Ord.-L.Dev.*

The designation of plates offers a problem, inasmuch as organization of the theca is different from that of the Glyptocystitida. JAEKEL (69) preferred to use the same terminology for successive circlets as he had for Glyptocystitida: basalia [*BB*], infralateralia [*ILL*], mediolateralia [*LL*], and radiolateralia [*RR*]. CARPENTER (32) and BATHER (10) used terminology comparable to that for dicyclic crinoids: infrabasalia, basalia, radialia+interradialia, and deltoidia. BATHER subsequently (1910) denoted the circlets by numerals I to IV "to avoid confusion." Whether all plates in the respective circlets in Glyptocystitida and Hemicosmitida are homologous or not, the designations of *BB, ILL, LL,* and *RR* are useful notations and can be understood to apply to thecal location only.

The stratigraphic distribution of genera belonging to the Hemicosmitida is shown in Figure 118.

Family HEMICOSMITIDAE Jaekel, 1918

[Hemicosmitidae JAEKEL, 1918, p. 97]

Theca ovate, acorn-shaped, or elongate, composed of four *BB*, six *ILL*, eight or nine *LL*, and circlet of *RR*. Brachioles few, clustered at apex of theca and connected with mouth by short ambulacral grooves. Periproct lateral, never above *LL*. *M. Ord.-L. Sil.*

The separation of the Hemicosmitidae and Caryocrinitidae is based primarily on the presence of a "tegmen" of plates roofing over the ambulacral grooves in the latter and its absence in the former. The distinction is obvious in the type genera, but not so clear in certain other genera of the two families, which to date have not been as well understood or completely known. The development of the structure known as the "tegmen" has not been satisfactorily traced, although its plates are probably homologous to the ambulacral covering plates of other rhombiferans, as suggested by JAEKEL (69).

Key to Genera of Hemicosmitidae

1. *LL* eight; periproct between two *LL*, not in contact with any *IL;* theca spindle-shaped, tapering at both ends .... *Corylocrinus*

   LL nine; periproct normally bordered by two *ILL* and one *L* plates; theca subovate 2

2. Pores in fairly regular, radiating rows; three large brachioles set close to top of theca; in many species, *ILL* and *LL* with central nodes; in some, nodes accentuated on three *LL* aligned with brachioles .... *Hemicosmites*

   Pores rather irregular; three brachioles set on three large processes on *LL*, near border of theca; plates strongly tumid or "swollen," no nodes or ridges .... *Tricosmites*

Hemicosmites VON BUCH, 1840, p. 149 [**H. pyriformis*; OD] [=*Hexalacystis* HAECKEL, 1896, p. 142 (type, *Hemicosmites verrucosus* EICHWALD, 1856)]. *BB* 4, of which 2 adjacent are pentagonal and other 2 large and hexagonal; *ILL* 6, large, 2 above hexagonal *BB* being pentagonal, 1 between hexagonal *BB* narrower than others and indented at adoral left corner for periproct, and other 3 heptagonal, with adoral indentation for juncture with 3 narrow "interradial" *LL; LL* 9, hexagonal except for 3 narrow "interradial" plates and for indentation in *L* above periproct; *RR* 9, more or less equal and pentagonal, attenuated toward mouth. Periproct small, circular, bordered by 2 *ILL* and 1 *L*, hence lateral on theca. Brachiole facets 3, large, each shared by pair of *RR;* 1 *R* without facet between each pair of facet-bearing *RR*, so that brachioles were equally spaced around mouth to form triangle; pavement of small covering plates over 3 short ambulacral grooves, converging to cover mouth. Rhombs numerous between plates of *B, IL,* and *L* circlets; pores covered, expressed as small tubercles (except in weathered specimens, in which they appear as pustules) in rows more or less radiating from umbos of plates. Rugosity near mouth in posterior position may be trace of hydropore (10), but its presence not established with certainty (69). Shape of theca varying from ovate to cuplike, depending upon development of nodes on *LL*. *M.Ord.-L.Sil.*, Asia(China-Burma)-Eu. (USSR-Est.-Sweden-Norway-Brit.).——FIG. 119, *1a*. Plates diagrammed in comparison with crinoid (*IB*, infrabasal; *B*, basal; *R*, radial; *iR*, interradial; *h*, hydropore; *ant.*, anterior; *l*, left; *r*,

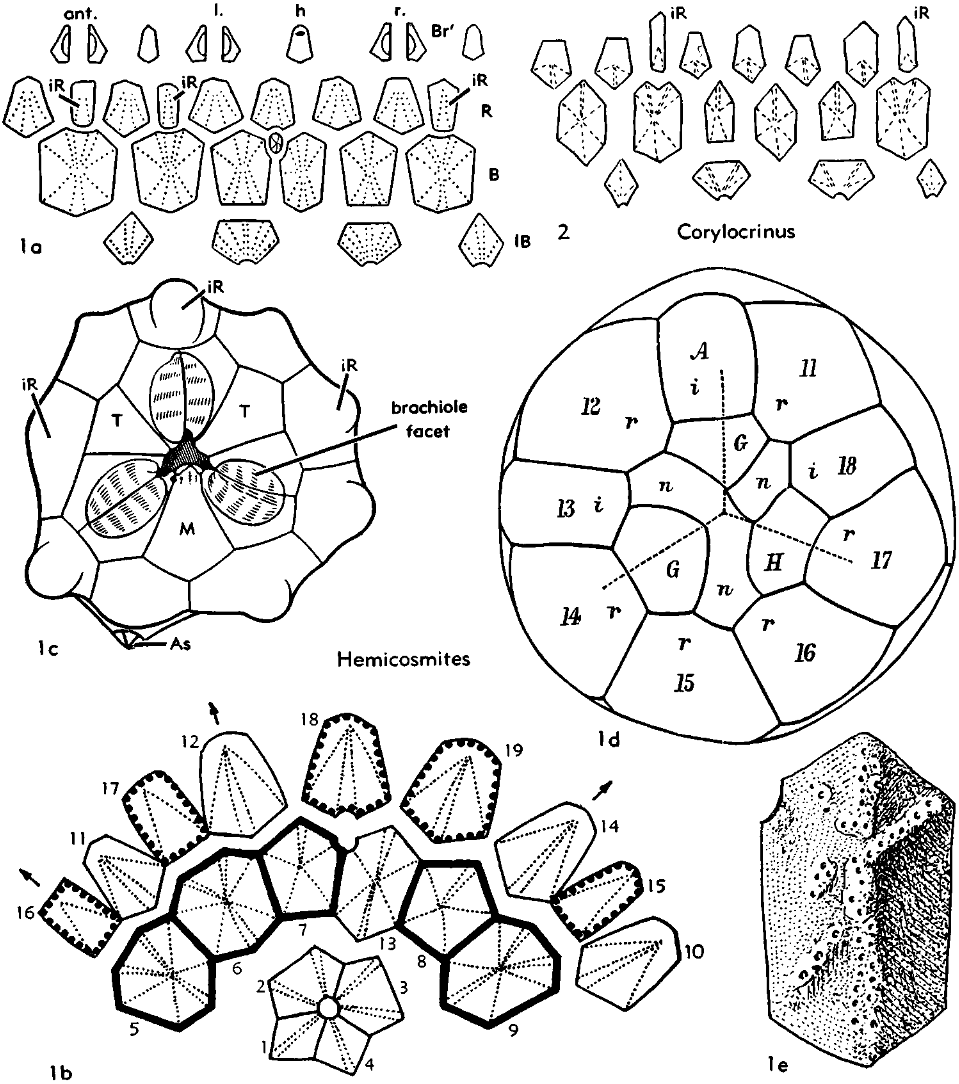


Fig. 119. Hemicosmitidae. Plate diagrams and oral views of theca (p. S219-S221). [Plate designations as in Figure 38.]

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

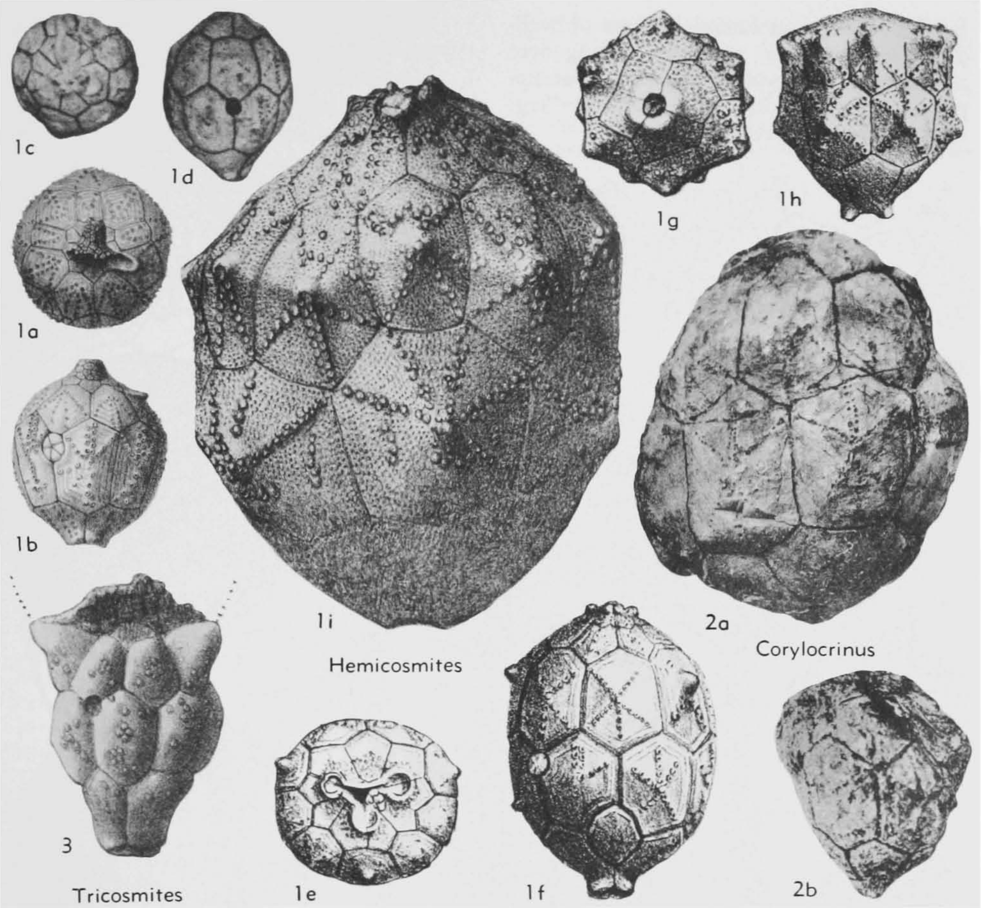


FIG. 120. Hemicosmitidae (p. S219-S221).

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

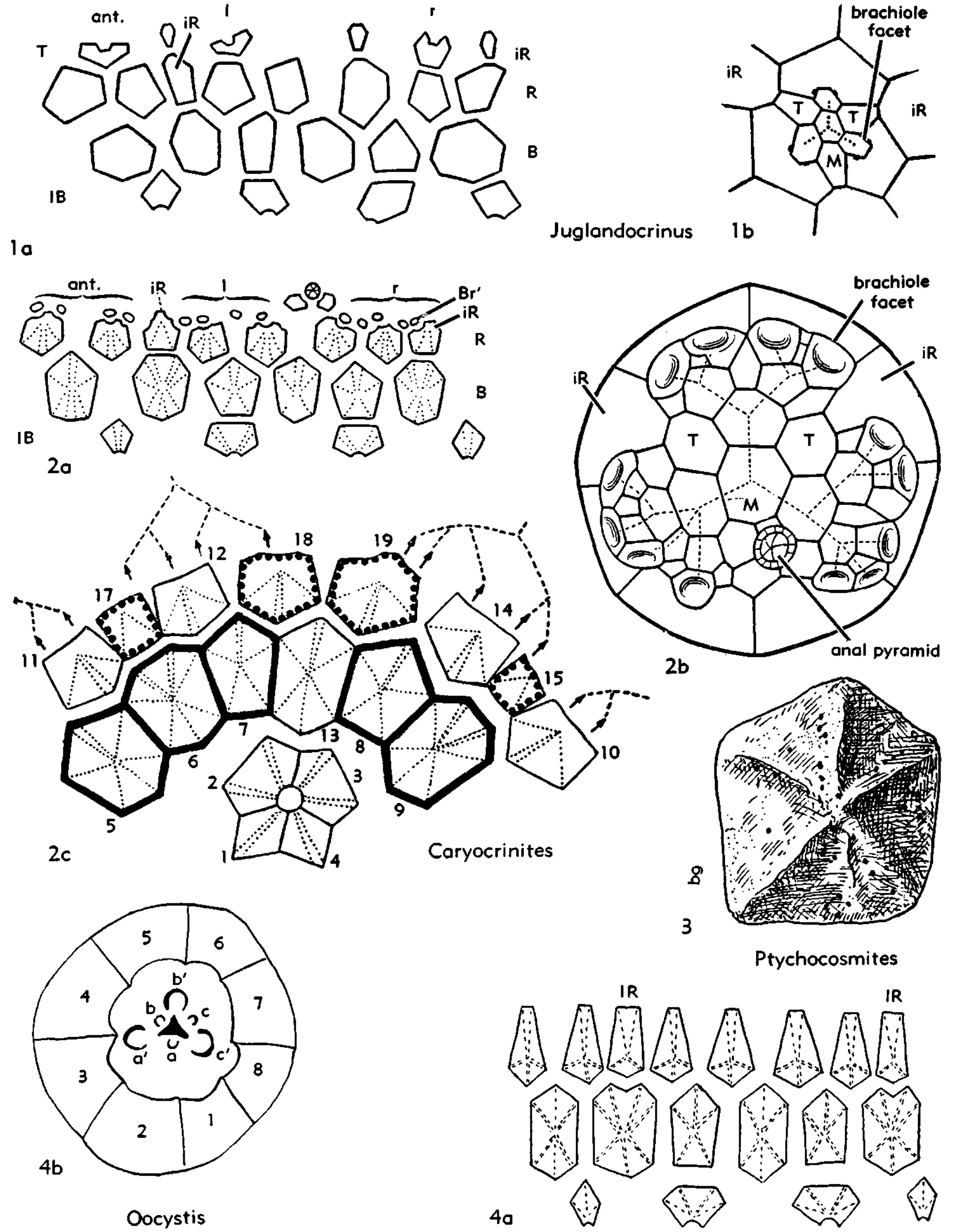


FIG. 121. Caryocrinitidae. Plate diagrams and oral views of theca (p. S223-S225).

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

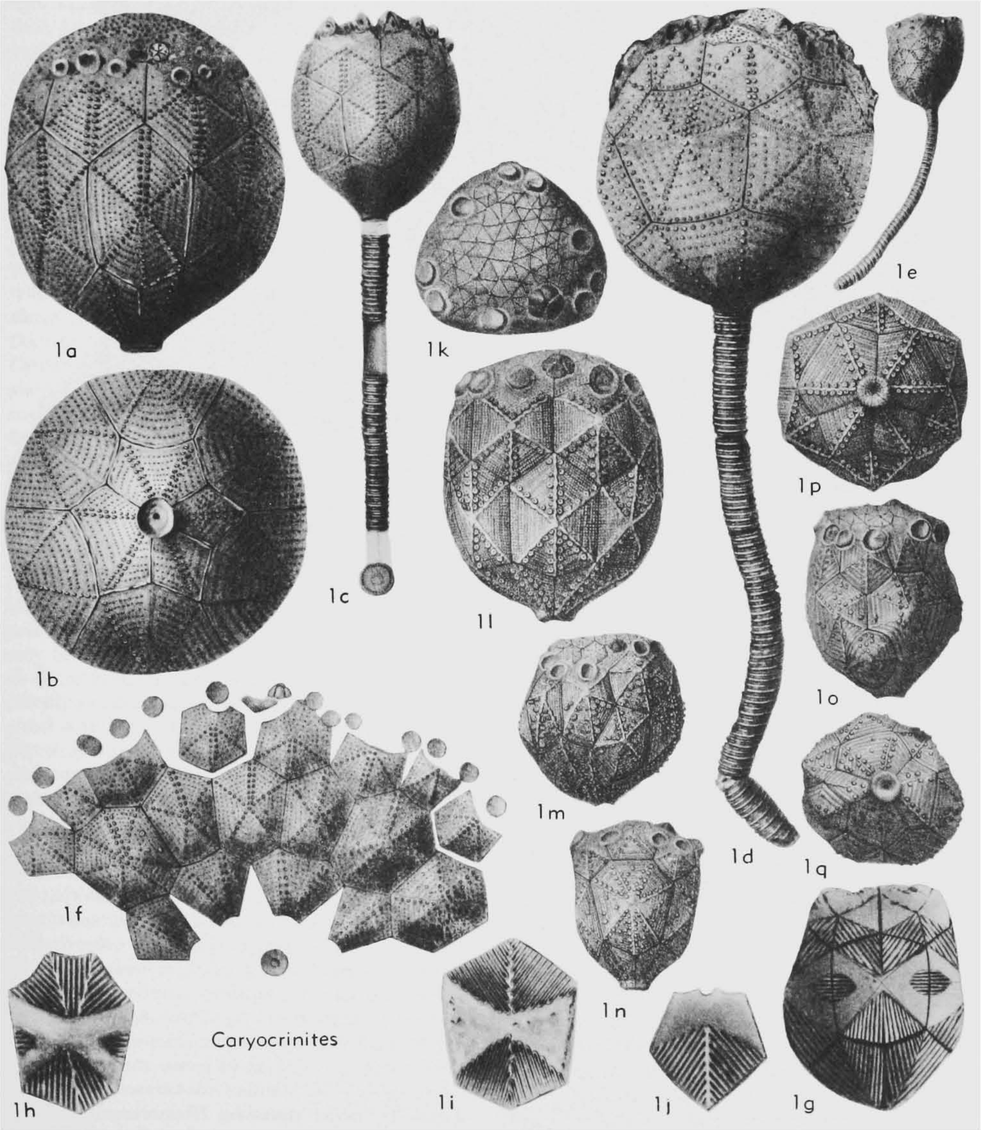


Fig. 122. Caryocrinitidae (p. S223-S225).

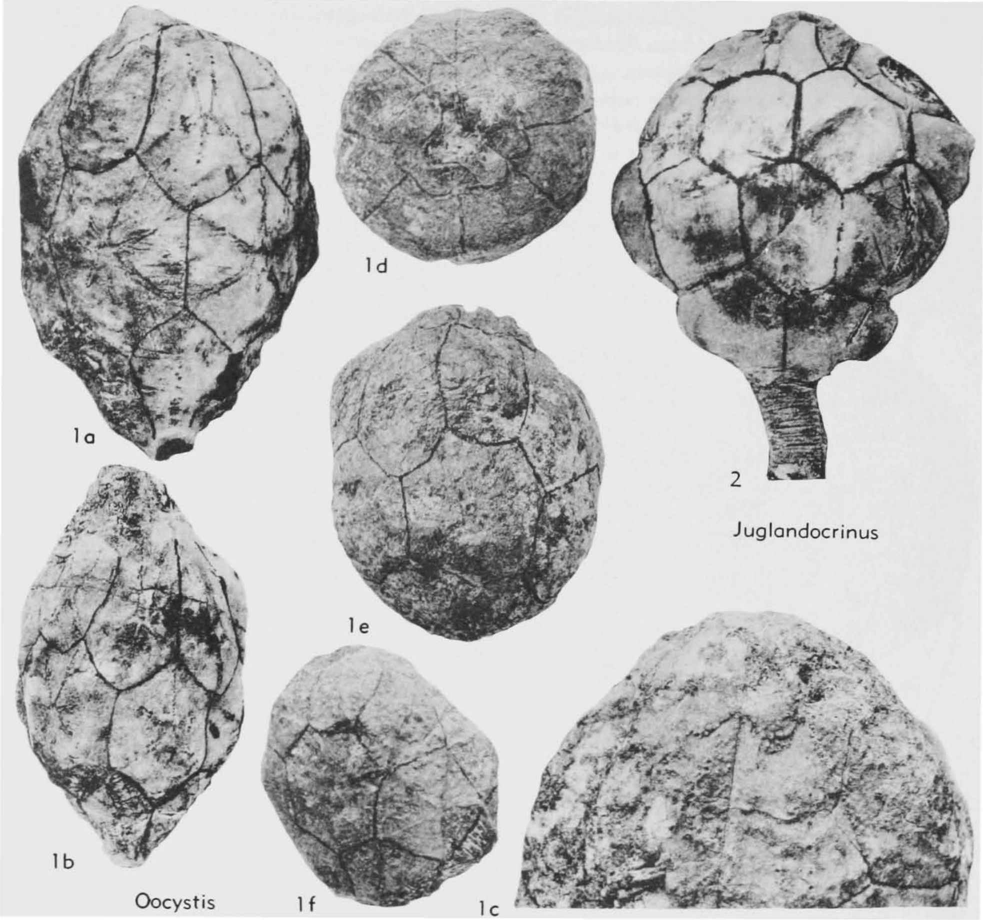


FIG. 123. Caryocrinitidae (p. S225).

base slightly tapered and oral surface rather gently convex. *BB* 4, 2 large and hexagonal and 2 small and pentagonal. *ILL* 6, large and polygonal, *IL* plate above junction of 2 hexagonal *BB* being hexagonal, whereas *2ILL* immediately above hexagonal *BB* are pentagonal; on each side, over junction of hexagonal and pentagonal *B, IL* plate is 7-sided, occupying so-called "interradial" position and directly supporting plate of *LL* series; above junction of 2 pentagonal *BB, IL* plate is subhexagonal. *LL* 8, presumably polygonal but with their adoral borders obscured in part by "tegmen" comprising plate cluster that covers ambulacral grooves and forms a vault over peristome, variously indented to accommodate small irregular plates in next circlet. Periproct relatively small, set high on theca within tegminal region, above *LL*, subcircular and containing anal pyramid. Brachiole facets at borders of "tegmen" and set upon adoral margins of *LL*, arranged in 3 general groups as result of subtegminal branching of 3 ambulacral grooves; number of brachiole facets related directly to ontogeny, small specimens having been observed with only 3 and very large specimens with 14 facets, most adults provided with 12 or 13. [As made known by FOERSTE (47), the type species is provided with pinnulate free arms, composed of biserial brachials and pinnulars; in the biserial nature of its pinnules, *Caryocrinites* differs from crinoids, in which pinnules have only a single row of pinnulars. JAEKEL (69) described internal structures of *Caryocrinites ornatus* in which traces of the alimentary canal can be seen within the theca, preserved by fortunate calcification of the gut-wall. Species vary in degree of radial ornamentation on the plates, number and distribution of pores, and proportions of the theca. The Middle Ordovician *Caryocrinites aurora* (BATHER) resembles *Hemicosmites* in having excavated brachiole facets and in exhibiting

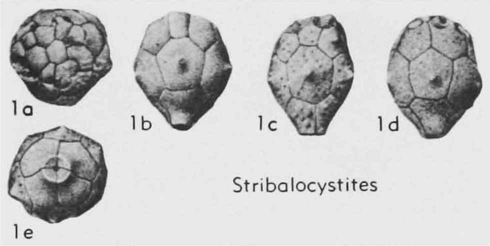


FIG. 124. Caryocrinitidae (p. *S225-S226*).

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).

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

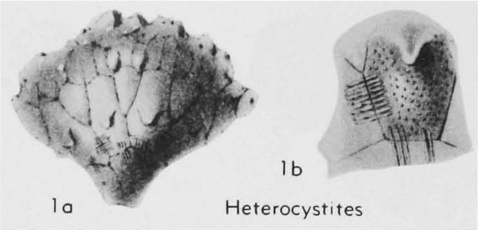


FIG. 125. Heterocystitidae (p. S226-S227).

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

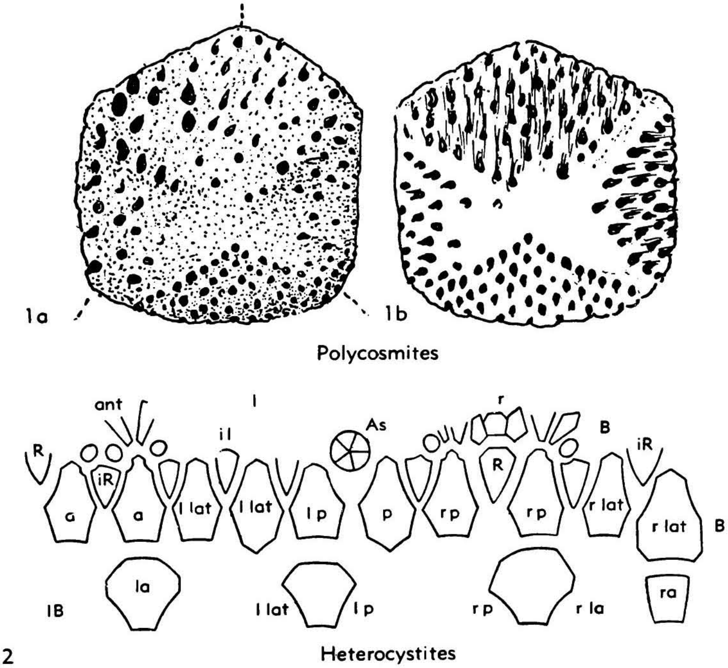


FIG. 126. Polycosmitidae *(1)*; Heterocystitidae *(2)*. Plates and plate diagram (p. S226-S227).

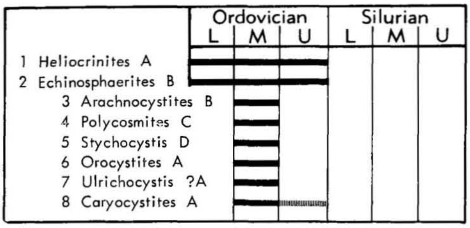


FIG. 127. Stratigraphic distribution of genera belonging to the superfamilies Polycosmitida and Caryocystitida. Classification of the genera in families is indicated by letter symbols: A—Caryocystitidae, B—Echinosphaeritidae, C—Polycosmitidae, D—Stichocystidae. The following alphabetical list of genera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

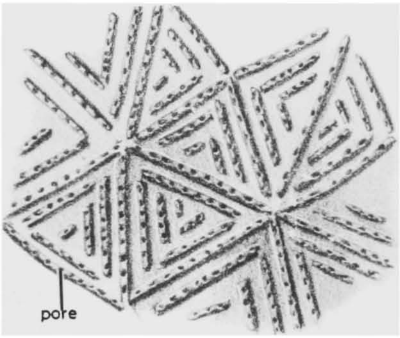
Polycosmites JAEKEL, 1918, p. 98 [**P. bohemicus;* OD]. Theca including at least some polygonal plates penetrated by simple pores distributed in rhombic sectors but not arranged in long rows. *M.Ord.*, Eu.(Boh.).——FIG. 126,*1.* **P. bohemicus; 1a,b,* thecal plate ext. and int. (71).

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.

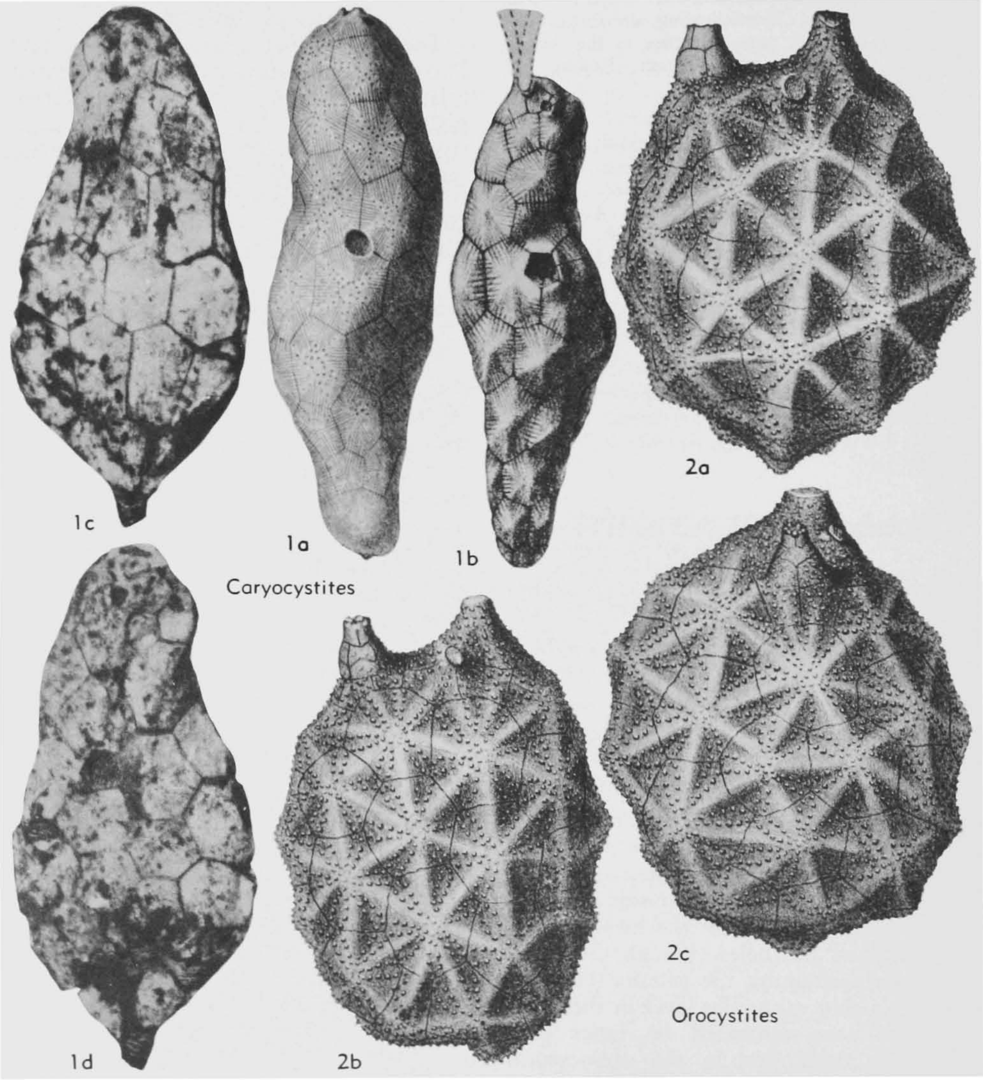


FIG. 129. Caryocystitidae (p. S229, S231).

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

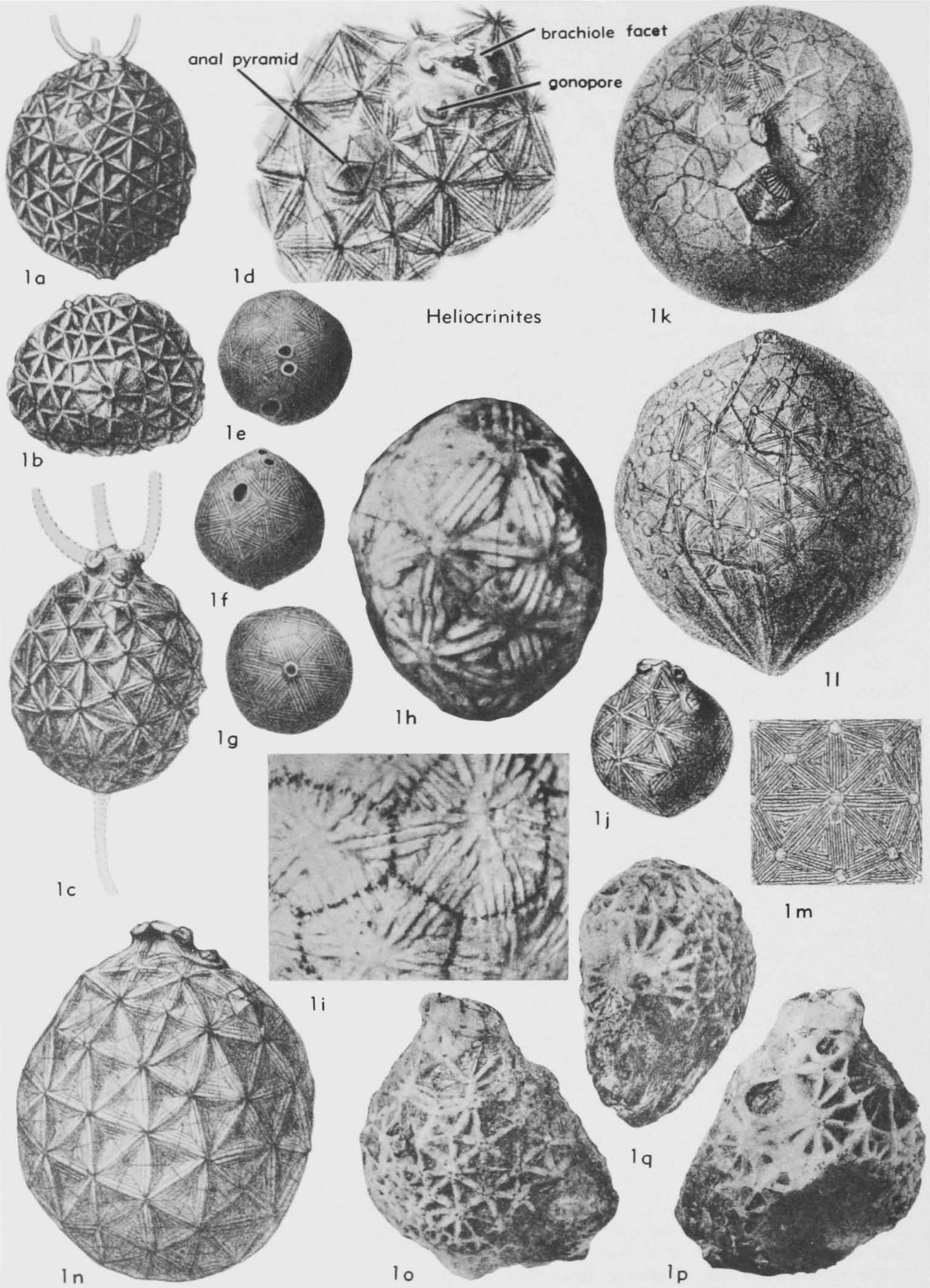
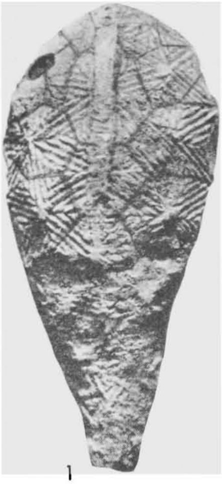


FIG. 130. Caryocystitidae (p. S229-S230).

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.(Dd4), 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*, Dd4, 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).



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

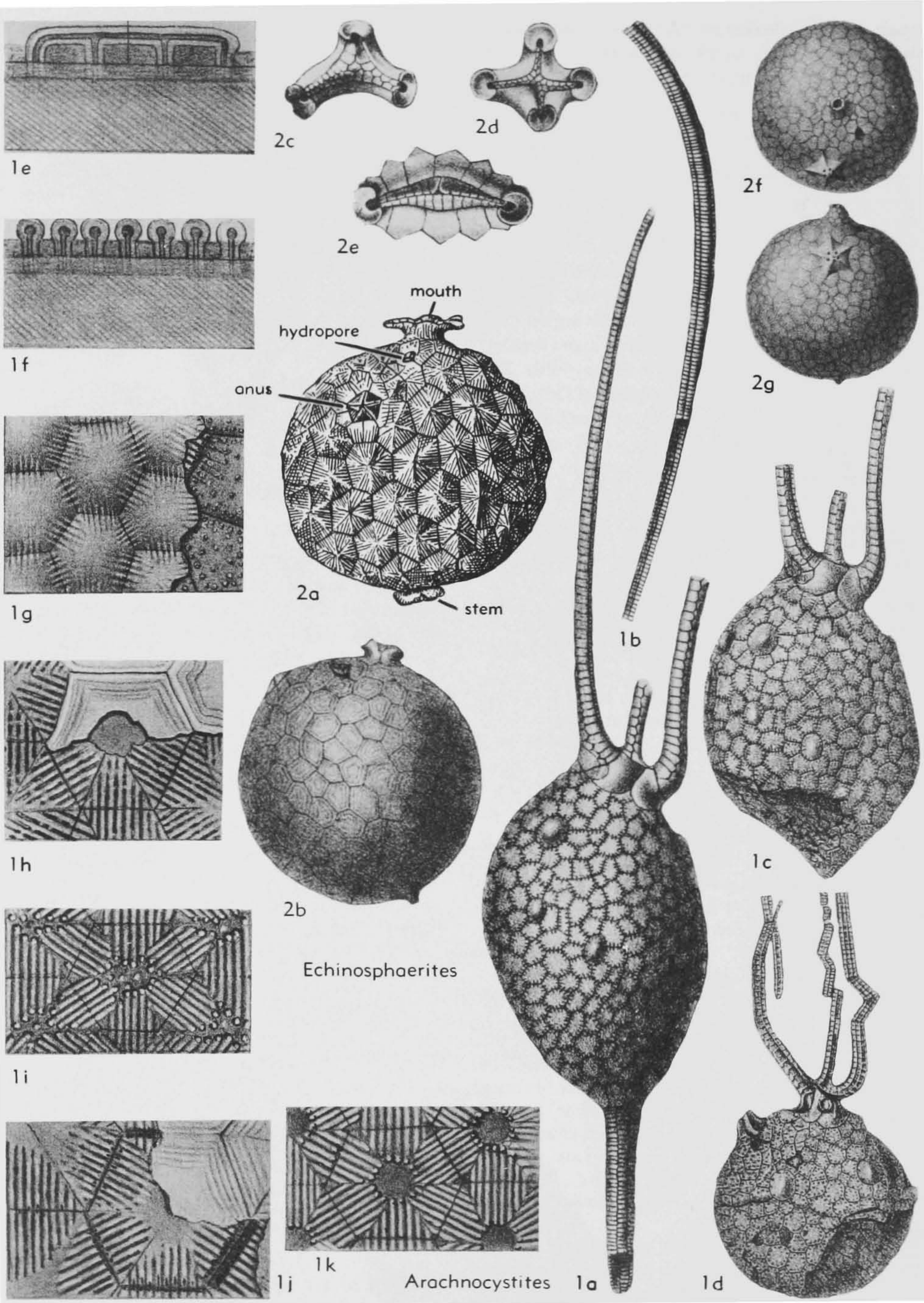


FIG. 132. Echinosphaeritidae (p. *S*233).

form with polymorphous plates; two to five ambulacra short but distinct, set upon oral projection .... *Echinosphaerites*

Theca pear-shaped, tapering to remarkably prolonged, thin, stemlike section of alternating rows of tiny hexagonal plates; most other plates small (200 to 800) but few larger plates interspersed, very few plates hexagonal; two or three brachioles springing more or less directly from oral projection with little or no development of intervening ambulacra ...... *Arachnocystites*

Echinosphaerites Wahlenberg, 1818, p. 44 [**Echinus aurantium* Gyllenhaal, 1772, p. 245 (=*Sphaeronites citrus* Hisinger, 1837, p. 91; *S. pomum* Hisinger, 1828, p. 196, *partim; Leucophthalmus strangwaysi* Koenig, 1825, pl. 1, fig. 1)] [=*Echinosphaera* Angelin, 1878, p. 28 *(nom. van.) non* Hertwig, 1879; *Echinosphora* Scudder, 1882, p. 118 *(nom. null.); Deutocystites* Barrande, 1887, p. 145 (type, *D. modestus*); *Deutocystis* Bather, 1889, p. 269 *(nom. van); Leucophthalmus* Koenig, 1825, pl. 1, fig. 1 (type, *L. strangwaysi=Echinus aurantium* Gyllenhaal); *Citrocystis* Haeckel, 1896, p. 68 (type, *Sphaeronites citrus* Hisinger=*Echinus aurantium* Gyllenhaal); *Crystallocystis* Haeckel, 1896, p. 66 (type, *Echinus aurantium* Gyllenhaal); *Trinemacystis* Haeckel, 1896, p. 65 (type, *Echinosphaera aurantium triactis=Echinosphaerites aurantium* var. Müller, 1854)]. Theca in type and many other species subsphaeroidal, for which reason these abundant cystoids have long been called "crystal apples"; in some (e.g., *E. pirum*) theca aborally produced to attain pear shape. Adults composed of 200 to several hundred polygonal plates; one form with many plates hexagonal and nearly all subequal, and another form with considerable variation in size, with plates having 3 to as many as 10 sides, both forms occurring within same species. Tangential pore canals exposed on weathered specimens as very regular, straight grooves distributed in rhombic areas, each rhomb formed by 2 triangular sectors of adjacent plates and nearly filled by several equally spaced, subparallel grooves. Each end of tangential pore canal joined to vertical pore canal, commonly called pore, leading to interior of theca, fillings or casts of vertical canals commonly appearing as granules or short pegs on steinkerns of thecae. Tangential canals compound as a rule, 2 to 4 of them extending between paired pores. Tangential pore canals covered in well-preserved specimens by generally smooth epitheca of several thin laminae, each somewhat distinctively ornamented with concentric lines, probably growth lines. Brachiole facets upon peristomial or oral projection, which in many forms is emphasized by slight constriction giving oral field appearance of small platform resting upon neck. Ambulacra commonly arranged in triradiate or tetraradiate pattern, although specimens have been figured and reported with only 2 brachioles attached to facets at each end of narrow peristomial-ambulacral series of plates; ambulacra short, facets distinct, rimmed concavities; number of brachioles not constant within a species. Anal pyramid in upper part of theca, closed by variable number of triangular plates. Gonopore rounded to triangular, about half diameter of anal pyramid, closed by few valvular plates in form of flat pyramid; gonopore offset to right from line connecting mouth and anal pyramid; relative spacing of mouth, anal pyramid, and gonopore fairly constant within a species. Remnants of feeble column known, most thecae without any column; few circlets of plates adjacent to base more regularly disposed than other plates. [The subequal- and unequal-plated forms within a species have been interpreted (99) as individuals that "have attained a certain degree of stability as to the increase of the skeleton" and others that are expanding by "abundant growth of new plates." The type species, *E. aurantium*, and closely allied forms have been recorded from many areas in Sweden, where they are exceedingly abundant in many strata, and from Yunnan, USSR, Estonia, Norway, Poland, northern Germany, Great Britain, and the United States (Pa., Va., Tenn.). *L.Ord.-U.Ord.*, Asia (Burma-China) - Eu.(USSR-Est.-Sweden-Norway-Pol.-Ger.-Belg.-Brit.-Boh.)-N.Am. (USA).——Fig. 132,*2*. **E. aurantium* (Gyllenhaal); *2a*, reconstr., ×1 (10); *2b*, reconstr., ×1 (69); *2c-e*, oral regions, 3 specimens, showing different numbers of brachiole facets, enl. (69); *2f,g*, oral and lat., ×1 (31). [See also Fig. 33,*1*; 37,*3*.]

Arachnocystites Neumayr, 1889, p. 403 [**Echinosphaerites infaustus* Barrande, 1887, p. 155] [=*Arachnocystis* Bather, 1889, p. 268 *(nom. van.)*]. Theca subpyriform, strongly inflated adorally and tapering to unique prolonged, thin, stemlike section of alternating rows of tiny hexagonal plates; most other plates small, so that theca contains 200 to 800, but few larger plates interspersed; very few plates in main part of theca hexagonal. Pore canals like those of *Echinosphaerites*, of which this genus was considered synonym by Jaekel (69) and Gekker (53). Periproct in upper half of theca, filled by anal pyramid. Gonopore somewhat offset from line connecting anal pyramid and mouth. Mouth in peristomal projection, with 2 or 3 brachioles springing more or less directly from it, with little or no development of ambulacra. *M.Ord.*, Eu.(Boh.).——Fig. 132,*1*. **A. infaustus* (Barrande); *1a*, lat., reconstr., ×1; *1b*, long section of column, ×1 (69); *1c,d*, lat., 2 specimens, ×1; *1e,f*, enlarged sections along and through pore canals; *1g-k*, enlarged parts of thecal plates in various stages of exfoliation (3).

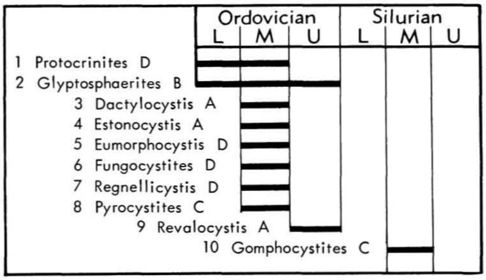


FIG. 133. Stratigraphic distribution of genera belonging to the superfamily Glyptosphaeritida. Classification of the genera in families is indicated by letter symbols: A—Dactylocystidae, B—Glyptosphaeritidae, C—Gomphocystitidae, D—Protocrinitidae. The following alphabetical list of genera furnishes cross reference to the serially arranged numbers on the diagram (Kesling and Moore, n).

Order DIPLOPORITA Müller, 1854

[*nom. correct.* BATHER, 1899, p. 920 (*pro* Diploporiten MÜLLER, 1854, p. 249)] [=Diploporitidées EICHWALD, 1860, p. 616; Gemellipora ANGELIN, 1878, p. 30]

Thecal pores developed as units mostly confined to single plates, typically in form of diplopores but in some present as haplopores. *L.Ord.-L.Dev.*

Thecal plates in the majority of these cystoids are irregularly arranged, but the Asteroblastida contain some genera with regularity approaching that of the Glyptocystitida in the Rhombifera.

The thecal pores tend to be confined to ambulacral plates in the Glyptosphaeritida and to special interambulacral plates in the Asteroblastida. Pores are small and very numerous in the Glyptosphaeritida and Sphaeronitida but relatively large and few in most of the Asteroblastida.

A column is never strongly developed. It is absent in adults of nearly all Sphaeronitida and some Glyptosphaeritida. It is small in the Asteroblastida.

Superfamily GLYPTOSPHAERITIDA Bernard, 1895

[*nom. transl. et correct.* KESLING, herein (*ex* Glyptosphaeridés BERNARD, 1895, p. 204)] [=order Seriolata JAEKEL, 1918, p. 101 (*nom. neg.*)]

Diplopore-bearing cystoids with globular, ovate, pear-shaped, or saclike thecae. Ambulacra radial, extending over theca, with alternating lateral branches (single or in groups) leading to brachiole facets; in many genera, ambulacra bordered by alternating "adambulacrals" on which facets are located. Diplopores invariably present on ambulacra-bearing plates, in some forms also in the interambulacral areas. Most with column, a few molting column as adults. *L.Ord.-M.Sil.*

The stratigraphic distribution of genera belonging to the Glyptosphaeritida is shown in Figure 133.

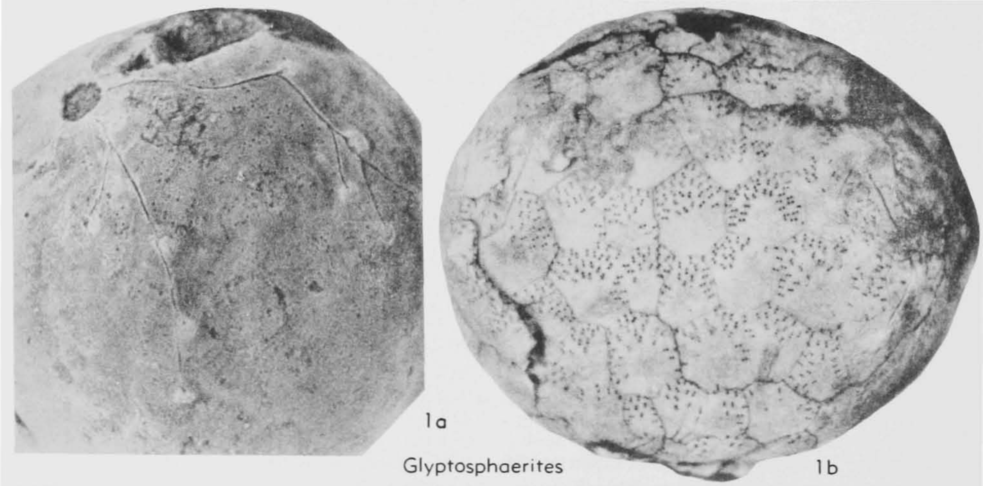


FIG. 134. Glyptosphaeritidae (p. S235).

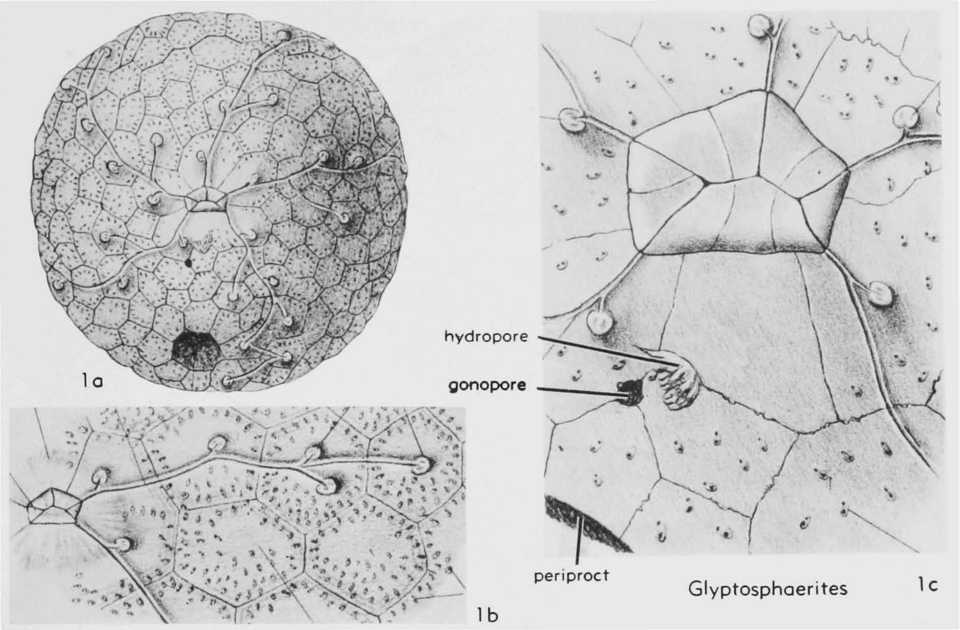


FIG. 135. Glyptosphaeritidae (p. *S*235).

Family GLYPTOSPHAERITIDAE Bernard, 1895

[*nom. correct.* BASSLER, 1938, p. 12 (*pro* Glyptosphaeridés BERNARD, 1895, p. 204)] [=Glyptosphaeridae BATHER, 1899, p. 920]

Theca apple-shaped, thin-walled. Short column present. Oral region pentagonal, with peristomial covering plates displaying nearly perfect trimerous fivefold suture pattern, one suture aligned with each ambulacrum; other thecal plates irregularly polygonal, numerous. Diplopores distributed over theca except in oral region, some more or less radially oriented. Ambulacral grooves narrow, each branching to few irregularly alternating small brachiole facets. *L.Ord.-U.Ord.*

Glyptosphaerites MÜLLER, 1854, p. 186 [**Sphaeronites leuchtenbergi* VOLBORTH, 1846, p. 187] [=*Glyptosphaera* ANGELIN, 1878, p. 31 (*nom. van.*); *Glyptosphora* SCUDDER, 1882, p. 145 (*nom. null. pro Glyptosphaera*)]. Theca large in some species, attaining size as well as shape of apple, with oral half hemispherical and aboral half indented at junction with column. Ambulacra normally slightly arcuate, groove very narrow and radiating over thecal plates without reference to plate boundaries; most ambulacra curved slightly clockwise, with first branch on left and other branches alternating, but pattern of branching somewhat irregular, particularly in distal part. Brachiole facets small, not strongly developed, only about 6 or 7 in each ambulacrum, rarely found on aboral half of theca. Periproct rather large, situated in posterior interambulacrum, provided with valvular pyramid. Diplopores in some forms concentrated in adoral parts of thecal plates, absent in oral region; each diplopore in simple elliptical depression. Hydropore 3-cornered, spongy and not solidly skeletonized, located between periproct and peristome; gonopore a small circular perforation to left and aboral to hydropore. *L.Ord.-U.Ord.*, Eu.(USSR-Sweden-N.Ger.-Boh.).——FIG. 134,*1*; 135,*1*. **G. leuchtenbergi* (VOLBORTH), L.Ord.(*Platyurus* Ls.), Sweden (134,*1*); L.Ord., USSR (135,*1*); 134,*1a*, inclined oral, ×2.5; 134,*1b*, lat. showing distribution of diplopores, ×2.5 (99); 135,*1a*, oral, adult, ×1; 135,*1b*, peristome and ambulacrum, ×3; 135,*1c*, oral region of juvenile, ×6 (69). [See also Fig. 44,*1*.]

Family DACTYLOCYSTIDAE Jaekel, 1899

[Dactylocystidae JAEKEL, 1899, p. 425] [=Estonocystidae JAEKEL, 1918, p. 101]

Theca oviform to pear-shaped, thick-plated, with or without column. Ambulacra five, long, straight, pentamerally arranged, vertical; numerous brachioles, at ends of short, very regularly alternating branches, so that those on each side of an

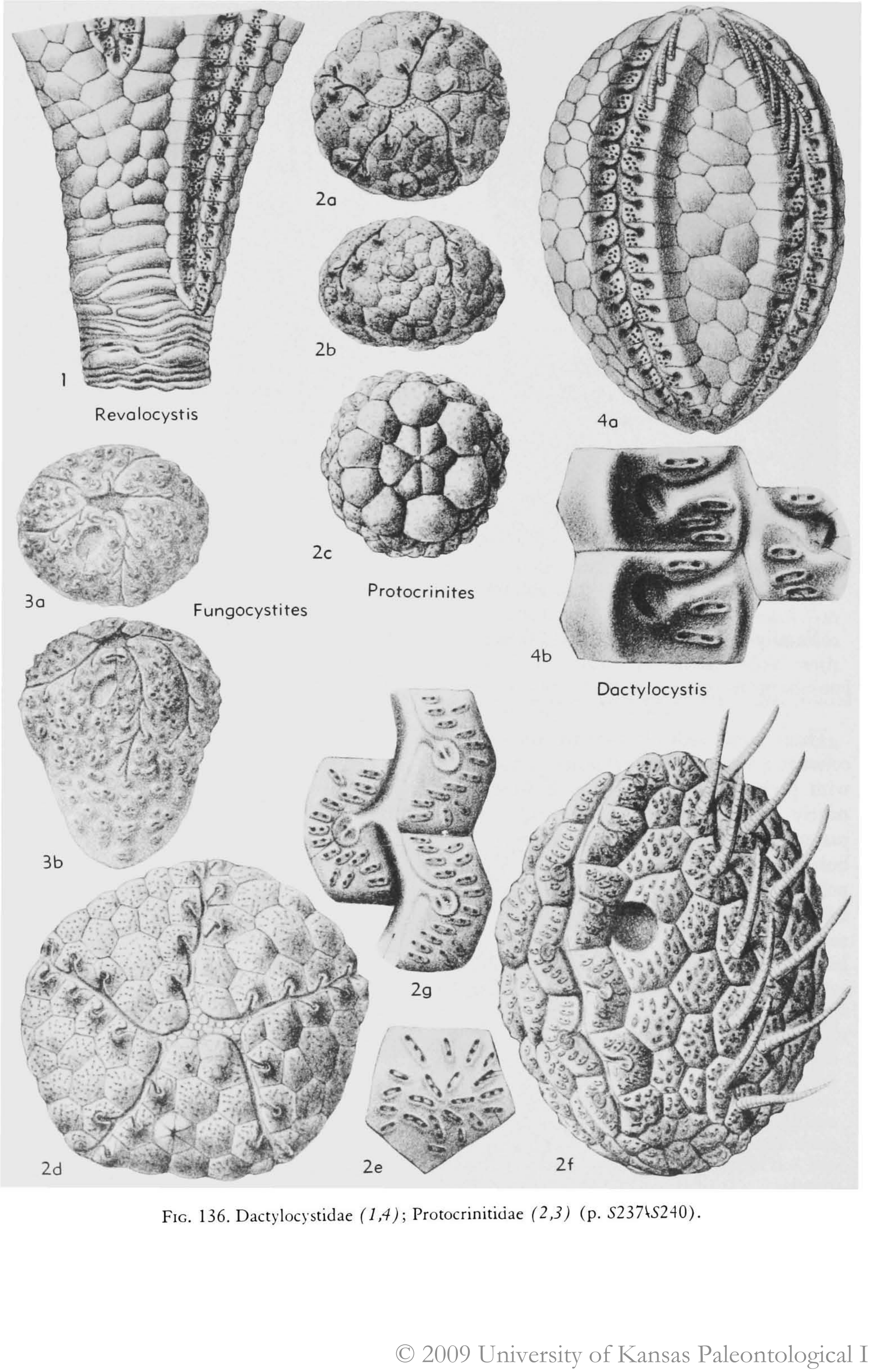


Fig. 136. Dactylocystidae *(1,4)*; Protocrinitidae *(2,3)* (p. S237–S240).

ambulacrum are aligned. Diplopores restricted to brachiole-bearing plates or "adambulacrals," which regularly alternate in paired vertical rows. Interambulacral plates irregularly arranged, without diplopores. Periproct large, circular, at mid-height. *M. Ord.-U.Ord.*

This family displays much higher regularity and symmetry than other families assigned to the superfamily Glyptosphaeritida. Its strong pentamerism might be compared with that in the Asteroblastida, but the ambulacra do not terminate on plates that can be classed as *RR,* the brachiole-bearing "adambulacrals" are not as highly developed, and the diplopores occur in the ambulacral areas rather than interambulacral. The restriction of diplopores to different areas of the theca may be regarded as evidence of extensive divergence.

Key to Genera of Dactylocystidae

1. Theca pear-shaped, gradually tapering to broad column; ambulacra of unequal length .... *Revalocystis*
   Theca ovate or ellipsoidal, distinctly set off from column; ambulacra of equal length 2
2. Each ambulacral area of two long, vertical rows of alternating large irregular-shaped plates, each of which has one large and several small brachiole facets with diplopores between ambulacral extensions; each interambulacral area with one vertical row of plates of irregular shape .... *Estonocystis*
   Each ambulacral area of two long, vertical rows of alternating small, transversely elongate plates, each of which has only one brachiole facet and bears diplopores; each interambulacral area filled with irregular plates, not arranged in vertical row and some larger than ambulacral plates, entire area depressed ....*Dactylocystis*

Dactylocystis JAEKEL, 1899, p. 434 [**D. schmidti;* OD] [=*Proteroblastus* JAEKEL, 1895, p. 116 *(nom. nud.)*]. Theca ovate to ellipsoidal, with strong pentameral symmetry, distinctly set off from thin column. Ambulacra of equal length, branching with precise regularity to alternating brachiole facets, one on each "adambulacral." Brachiole-bearing "adambulacrals" small, hexagonal, transversely elongate plates, elevated and distinct from interambulacral plates, set in 2 vertical rows, one on each side of straight ambulacrum; diplopores restricted to these plates. Each diplopore with 2 openings at opposite ends of narrow groove surrounded by thin rim, diplopores tending to be aligned horizontally and confined to area between brachiole facets. Interambulacral plates irregular, polygonal, some larger than "adambulacrals," set in elongate, lanceolate, depressed area. Brachioles small and short, their length not exceeding one-fourth diameter of theca. *M.Ord.,* Eu.(Est.).——FIG. 136,*4.* **D. schmidti; 4a,* lat., ×3; *4b,* part of ambulacrum enl. to show diplopore arrangement (69). [See also Fig. 33,*6*.]

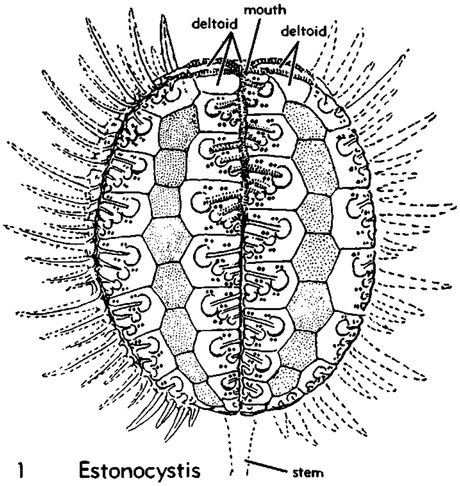


FIG. 137. Dactylocystidae (p. S237).

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-

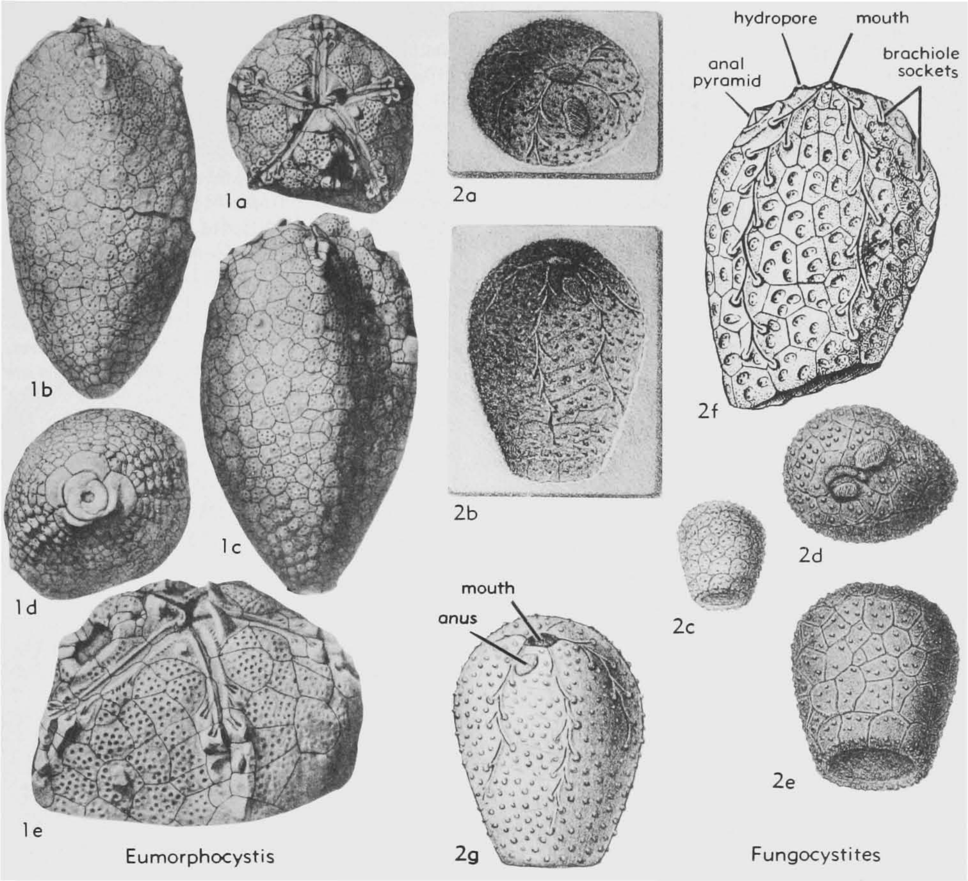


FIG. 138. Protocrinitidae (p. *S*239-*S*240).

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

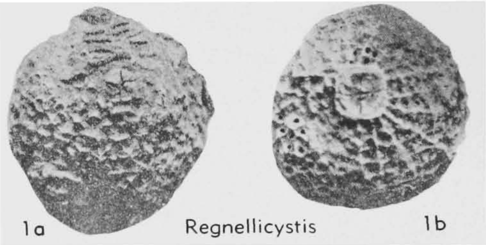


Fig. 139. Protocrinitidae (p. S240).

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

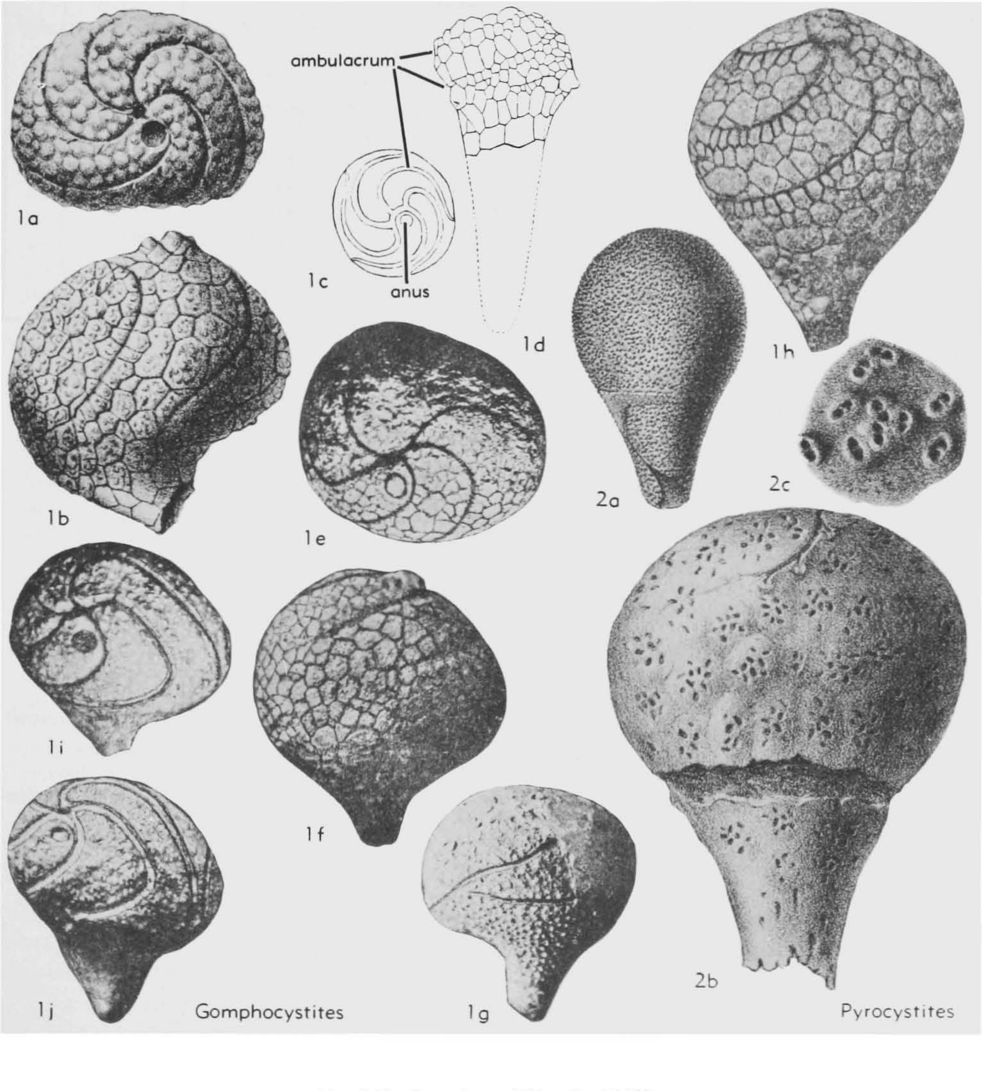


FIG. 140. Gomphocystitidae (p. S240).

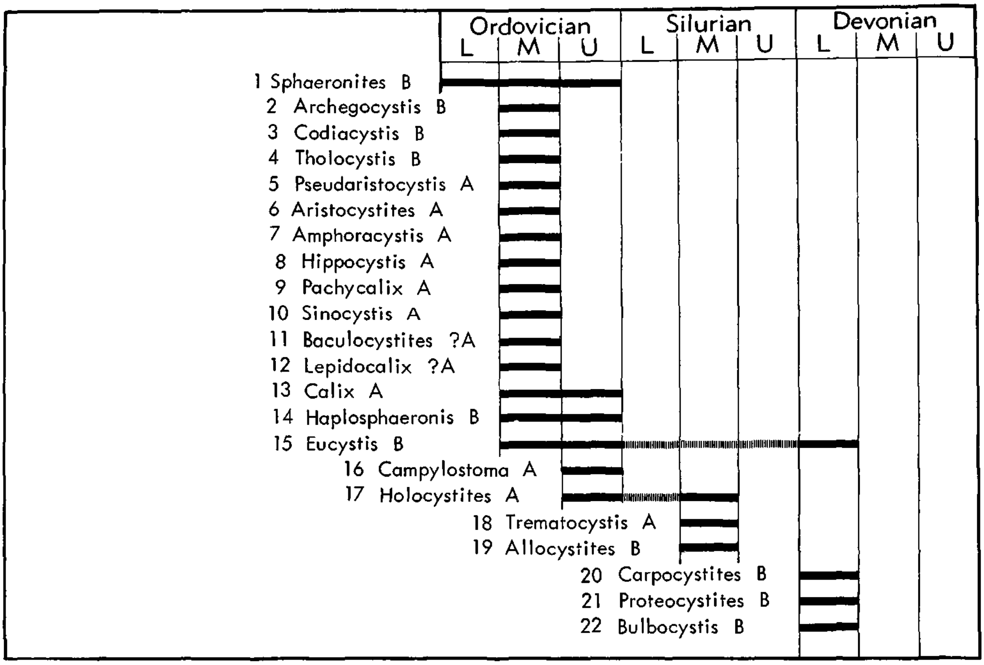


FIG. 141. Stratigraphic distribution of genera belonging to the superfamily Sphaeronitida. Classification of the genera in families is indicated by letter symbols: A—Aristocystitidae, B—Sphaeronitidae. The following alphabetical list of genera furnishes cross reference to the serially arranged numbers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

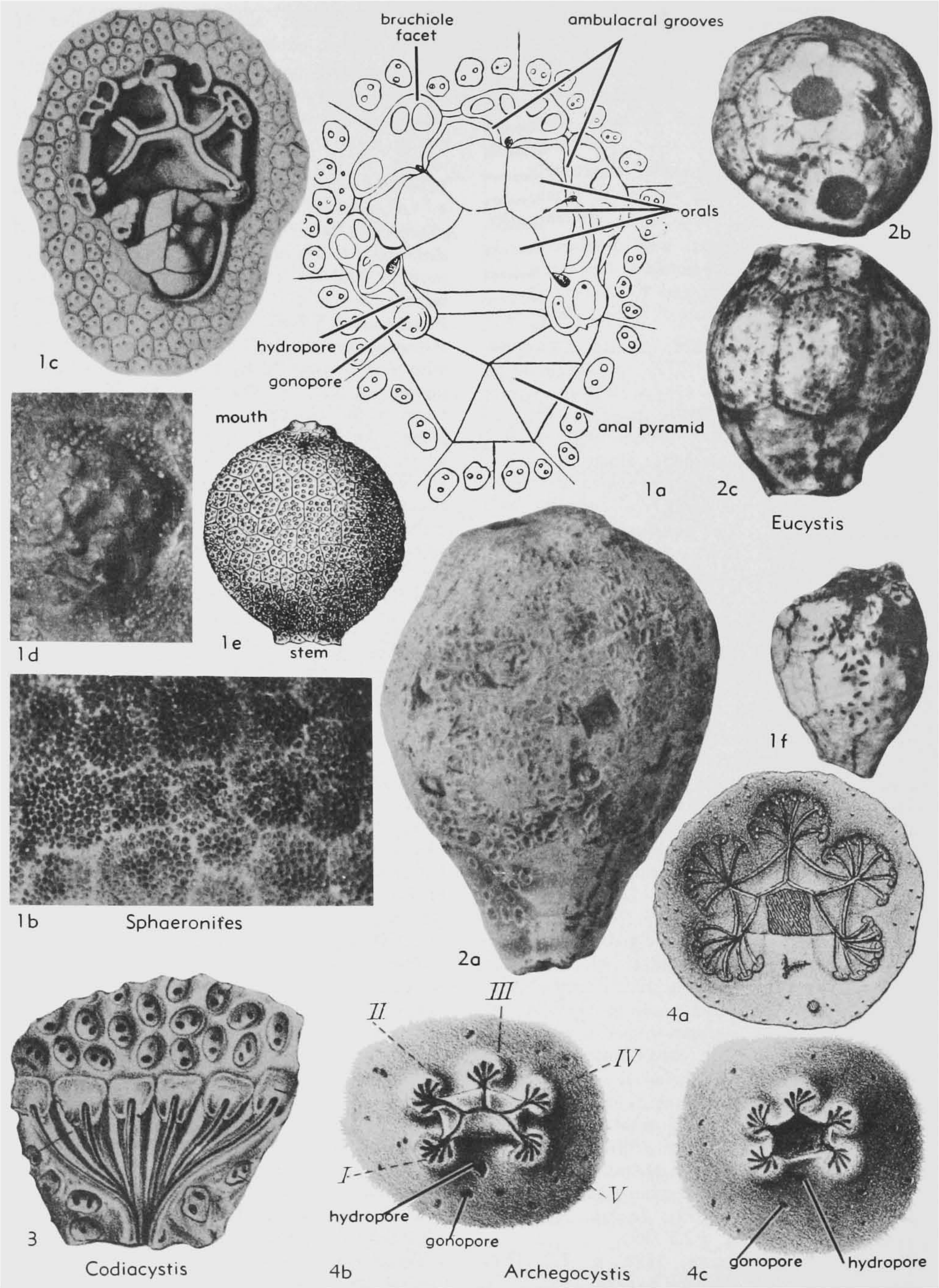


FIG. 142. Sphaeronitidae (p. S243, S245, S247).

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*

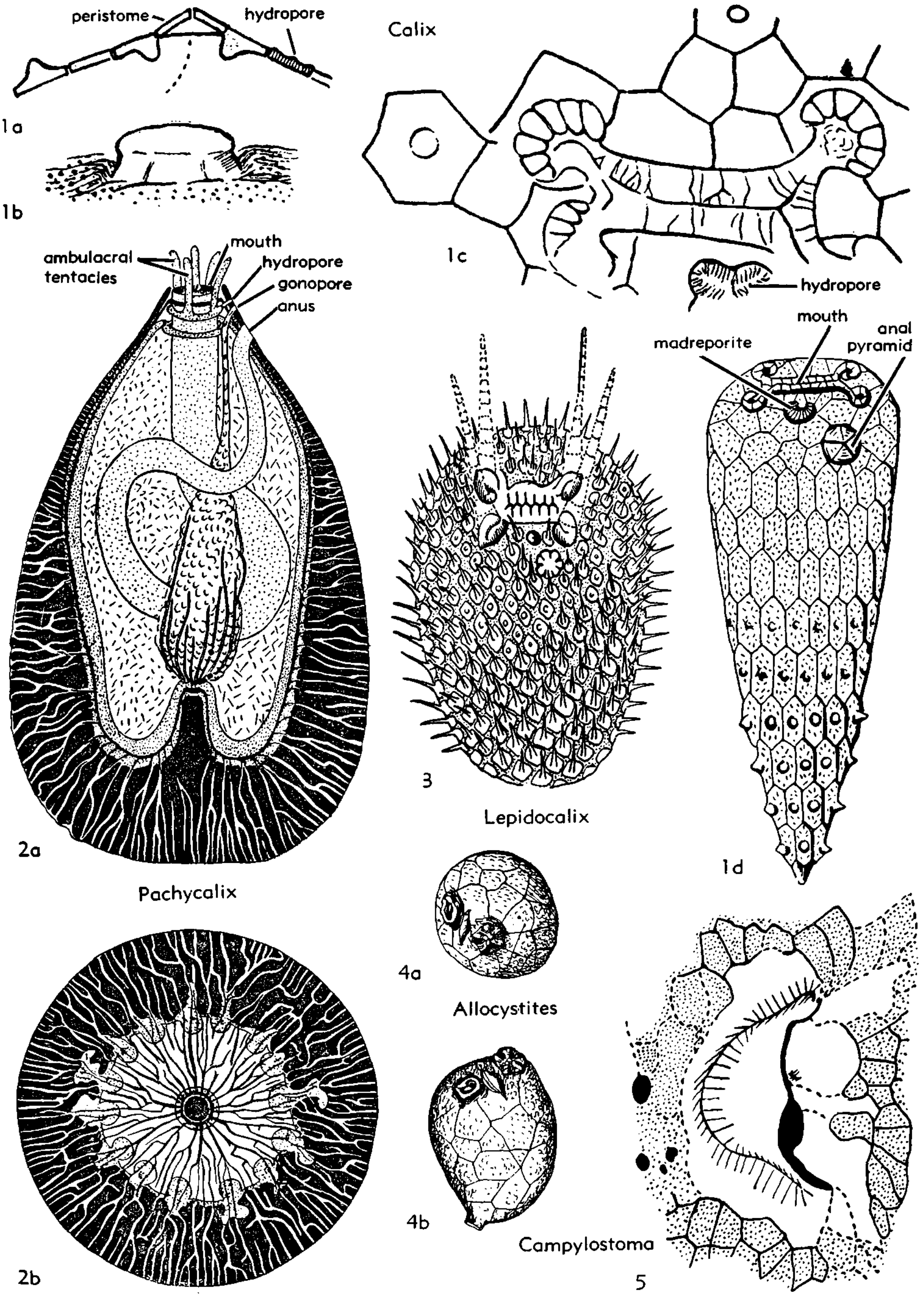


FIG. 143. Aristocystitidae *(1-3,5)*; Sphaeronitidae *(4)* (p. S243, S254-S256).

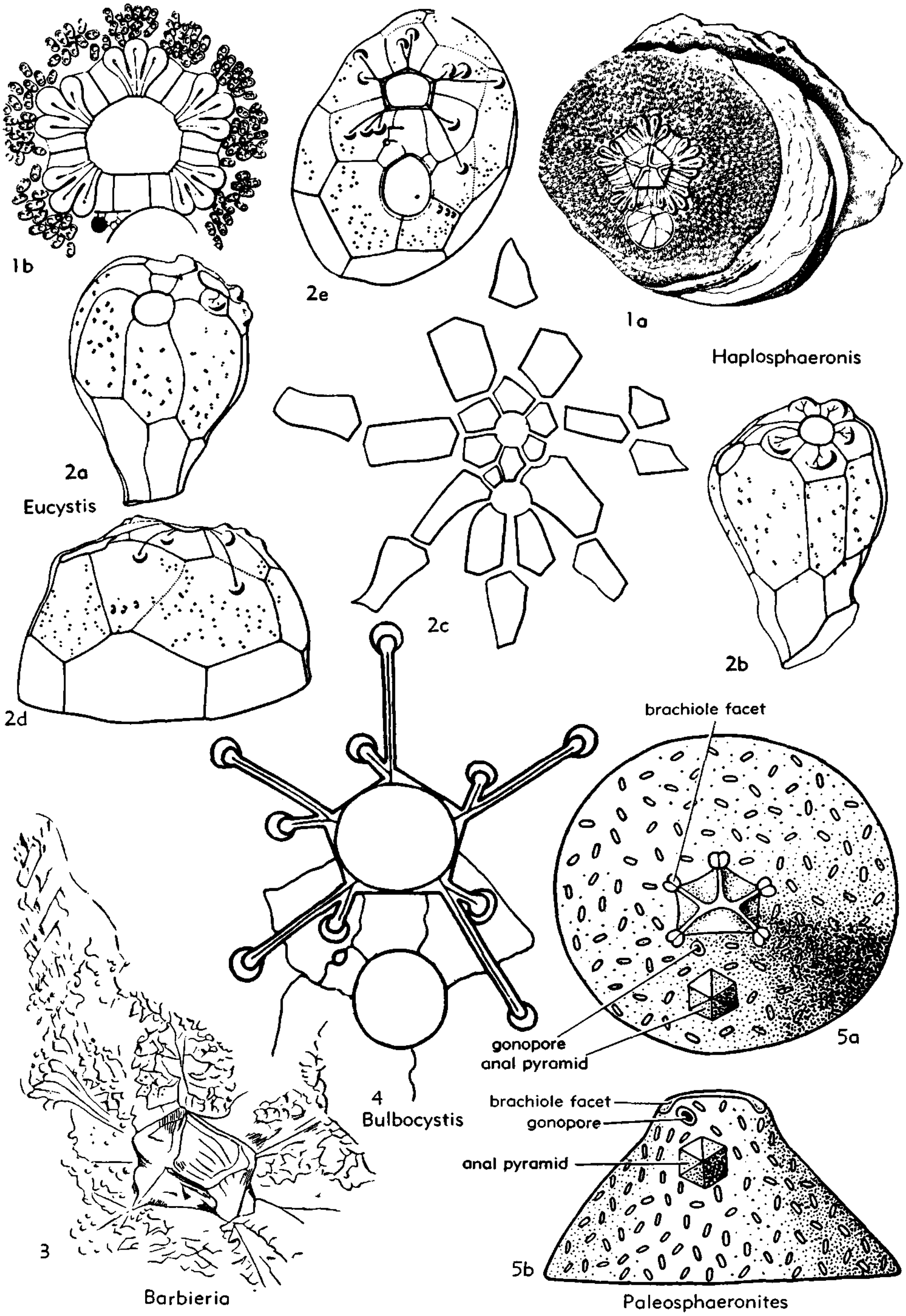


Fig. 144. Sphaeronitidae (p. S243, S247-S248).

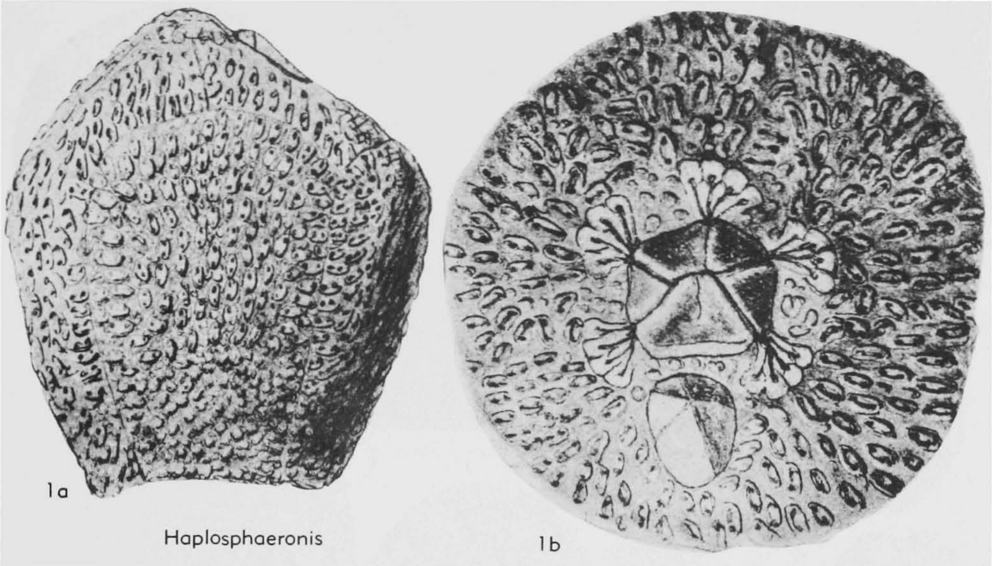


FIG. 145. Sphaeronitidae (p. *S*247-*S*248).

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. ḳiaeri;* OD] [=*Pomocystis* HAECKEL, 1895, p. 401 (type, *Sphaeronis uva* ANGELIN, 1878); *Pomosphaera* HAECKEL, 1896, p. 99 (type, *Sphaeronis oblonga* ANGELIN, 1878)]. Theca ovoid to spherical, composed of few thick plates, attached directly by basal surface. Thecal plates in 2 circlets, lower of 7 rectangular to trapezoidal plates (called *LL*) and upper of 5 hexagonal to pentagonal plates (called *RR*) around peristome, which forms nearly regular pentagon, only very slightly elongate, covered over by 5 plates (called *OO*), *O1* largest and bearing slit that may possibly be hydropore. Base generally broad and flat, in some attached to other organisms. Diplopores very numerous all over surface of plates, in part radially arranged. Pores within elongate peripores, many of which are dumbbell-shaped and have raised margins.

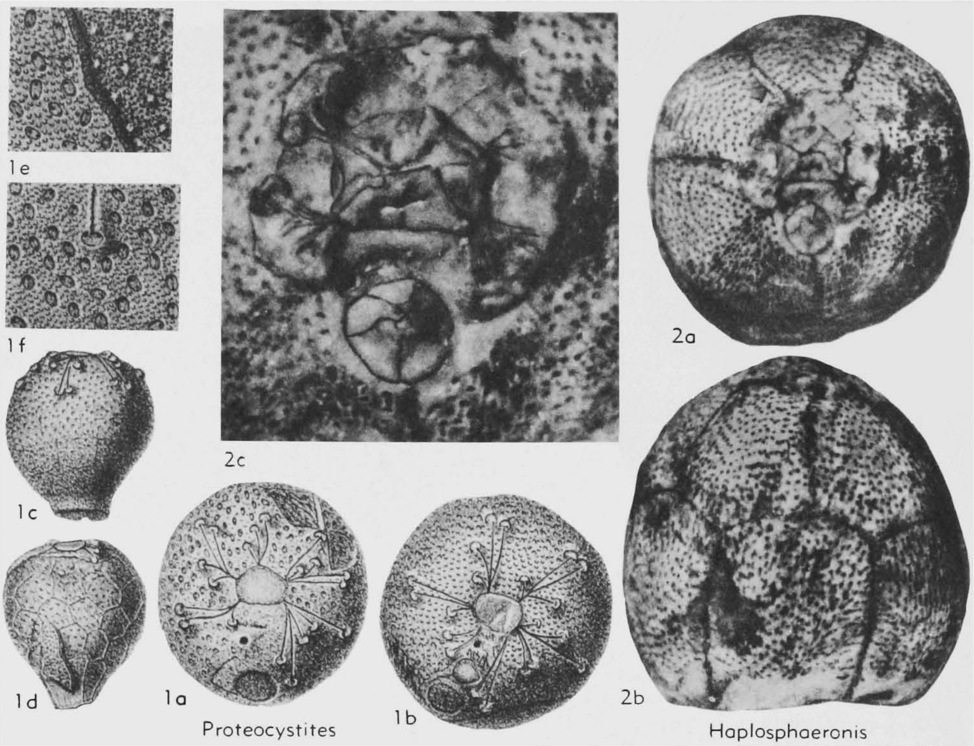


Fig. 146. Sphaeronitidae (p. S247-S249).

Ambulacral branches spread fan-wise from corners of pentagonal peristome, not curved, subequal; 3 or 4 branches of each ambulacrum crossing only 1 circumoral _(R)_ plate to brachioles along its outer edge. Periproct subcircular, set close to circumoral circlet _(RR)_, filled by anal pyramid of 6 or 7 irregular pieces. Gonopore small, circular, set at adoral left side of anal pyramid. _M.Ord.-U.Ord._, Eu.(Norway-Sweden-USSR-Belg.)——Fig. 144,_1;_ 146,_2_. _H. oblonga_ (Angelin), M.Ord(Kullsberg Ls.), Sweden; 144,_1a_, oral, ×3; 144,_1b_, oral region, ×9; 146,_2a,b_, oral and lat., ×2.5; 146._2c_, oral region, ×4.5 (99).——Fig. 145,_1_. *_H. ḳiaeri_, M.Ord., Norway; _1a_, lat., enl.; _1b_, oral, enl. (72).

Paleosphaeronites Prokop, 1964, p. 9 [*_Sphaeronites crateriformis_ Růžička, 1927, p. 12 (=_Sphaeronites batheri_ Růžička, 1927, p. 12, _partim_); OD]. Theca with flat base, typically conical, some dome-shaped to bell-shaped. Base containing 8 trapezoidal, radially arranged plates; large conical oral surface not divided into plates. Peristomial cover plates forming broad pentagon; 2 close-set oval brachiole facets very close to each corner of peristome. Anal pyramid hexagonal, containing 6 nearly equal plates, situated midway between peristome and border of oral surface; gonopore circular, in center of crater-like elevation, offset to left between largest peristomial plate and anal pyramid, closer to former. Diplopores large, scattered, each surrounded by large longitudinally elliptical depression. Surface of plates smooth to finely granulose. [Differs from _Sphaeronites_ in having conical shape, smaller anal pyramid, distinct separation of peristome and anal pyramid, and larger, more elliptical diplopores. This genus resembles members of the Aristocystitidae in having brachiole facets practically at corners of the peristome, but it seems closer to the Sphaeronitidae in all other respects.] _L.Ord._, Eu.(Boh.).——Fig. 144,_5_. *_P. crateriformis_ (Růžička); _5a,b_, lat. and oral, ×4 (95a).

Proteocystites Barrande, 1887, p. 78 [*_P. flavus;_ OD] [=_Proteocystis_ Bather, 1889, p. 269 _(nom. van.)_]. Theca with broad attachment surface or short, thick columnar process. Ambulacra rather long, unequal, irregularly branched, not strongly developed. Several brachiole facets, unevenly spaced and distributed, in each ambulacrum. Diplopores numerous, apparently in elliptical peripores. Hydropore and gonopore between mouth and anal pyramid. [Genus considered by Jaekel (69) and Regnéll (99) to be a junior synonym of _Eucystis_, but maintained by Bather (10).] _L. Dev._, Boh.——Fig. 146,_1_. *_P. flavus_, F_2; _1a,b_, 2 oral, ×2; _1c_, lat., ×1; _1d_, lat., exfoliated, ×1; _1e_, surface of thecal plate at left, steinkern at

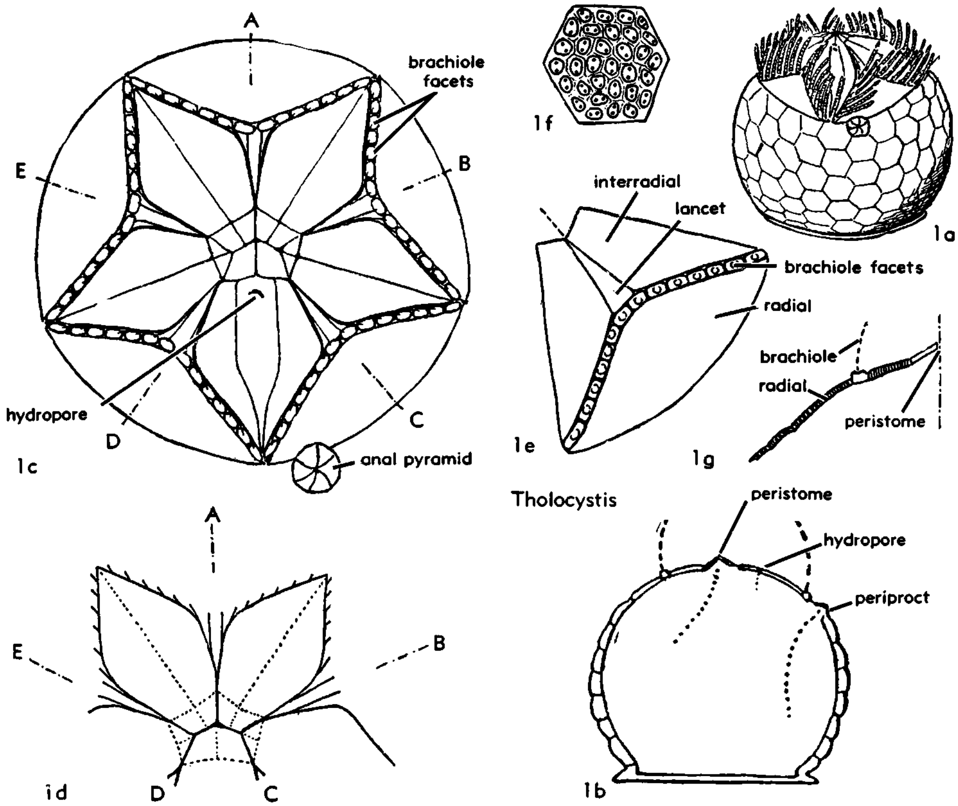


FIG. 147. Sphaeronitidae (p. S249-S250).——1. *Tholocystis kolihai* CHAUVEL, M.Ord., France; *1a,b,* posterior (*CD* interray) view of theca (reconstr.) and hypothetical cross section through peristome, ×2; *1c-e,* diagrammatic analyses of ambulacral field, ambulacral branching, and sector of ambulacral field, with ambulacral positions indicated as *A-E,* ×5; *1f,* plate from side of theca, showing diplopores, ×9; *1g,* section through peristome and attachment of brachiole, ×3 *(34).*

right, enl.; *1f,* surface of thecal plate showing diplopores and brachiole facet, enl. (3).

Tholocystis CHAUVEL, 1941, p. 88 [*T. kolihai; OD]. Theca globose, shaped like kettle resting on its broad base, with large adoral area, corresponding to lid of kettle, consisting of *RR, OO,* and peristomial covering plates in very regular arrangement; remainder of theca composed of flat base with surrounding rim and globose walls of numerous polygonal plates, mostly hexagonal, bearing abundant diplopores in subpolygonal peripores. Periproct small, circular, filled with anal pyramid, located in posterior interambulacrum at junction of *RR* circlet and many-plated sides of theca. Numerous brachiole facets along the adoral margins of *RR,* forming star. *RR* 5, each an obtuse subspherical triangle, bearing diplopores. Five large *OO* forming star within brachiole facets, bearing diplopores, each pentagonal and meridionally elongate, posterior one tripartite, others apparently bipartite, with meridional suture dividing each into symmetrical halves; adjacent *OO* said to be separated by narrow wedgelike plate comparable to lancet-plate of blastoids. Ten covering plates of peristome forming broad pentagon, arranged in trimerous pentamerism with 2 plates in each interambulacrum, smooth, devoid of diplopores. Ambulacra represented by 2 main branches radiating from each angle of peristome, slightly diverging for half their length, then strongly diverging so that each main branch terminates at tip of oral plate, there meeting end of main branch from adjacent ambulacrum; from each main branch, short secondary branches lead aborally to brachiole facets; about 7 facets on each main branch, making 70 in all; apices of star formed by brachiole facets thus interradial and attaining circle that marks distal limit of oral field. Crescentic slit in posterior oral interpreted as hydropore. Each of wedgelike "lancet" plates extending from reentrant angle of star of brachiole-facets adorally to corner of peristome, supporting flooring plates of adoral sections of branches of ambulacra. Brachiole facets borne on quadrangular plates, thicker than other plates and analogous to adambulacrals in *Mesocystis*. [The exceptional symmetry developed in the oral region might be considered sufficient ground to erect a separate family for this unusual cystoid.] *M.Ord.*, Fr.——FIG. 147,*1*. **T. kolihai; 1a,b,* reconstr. of theca and hypothetical cross section through peristome, ×2; *1c-e,* diagrams of ambulacral field, ambulacral branching, and sector of ambulacral field, with ambulacral positions indicated as *A-E,* ×5; *1f,* plate from side of theca, showing diplopores, ×9; *1g,* section through peristome and attachment of brachiole, ×3 (34).

Family ARISTOCYSTITIDAE Neumayr, 1889

[*nom. correct.* BASSLER, 1938, p. 8 (*pro* Aristocystiden NEUMAYR, 1889, p. 413)]

Theca ovate to elongate, typically tapered or constricted at aboral end, containing numerous, irregularly arranged plates. Column small and degenerate where present, absent in most forms. Most pores confined to one plate, canals simple, irregularly branched, or regularly divided to form typical diplopores. Brachioles arising from facets adjacent to mouth; ambulacra very short and unbranched, scarcely developed in some. *L.Ord.-M.Sil.*

Of all families of cystoids, the Aristocystitidae contain the most diverse and heterogeneous assemblage of forms. The difficulty in precise definition and taxonomy is compounded by the fragmentary nature of specimens representing many genera. The thecal pores are not developed as classic diplopores in some of the genera, and may not branch at all in a few. The character of the thecal pores does not appear to be correlated with other features of the theca, so that certain genera rest solely upon their kind of pores. Thus, in a manner of speaking, *Pseudaristocystis* is an *Aristocystites* in which the pores are not developed as diplopores, and *Pachycalix* is a *Calix* in which the pore canals do not divide regularly. The general strong resemblances of the genera concerned are interpreted here as expressions of relationship rather than convergence. It may be worth mentioning, perhaps, that in *Hippocystis,* remarkable for the classic form of its diplopores, a few pores are not diplopores. At any rate, the concept of taxonomy should not be dominated by the name "Diploporita," but instead should be guided by consideration of the significant contrast between perforations which almost invariably pass from one plate to another and those which are predominantly confined to one plate.

For many years, the Aristocystitidae were assigned to the order Amphoridea of HAECKEL (58), along with genera properly referable to the Paracrinoidea, Eocrinoidea, and Carpoidea. BATHER (10-13) was a longtime champion of the Amphoridea, strongly defending exclusion of the Aristocystitidae from the Diploporita, until finally (15) he capitulated and dropped Amphoridea in his last summary of cystoids. As late as 1943, however, BASSLER & MOODEY (7) maintained the order Amphoridea, in which they placed, in addition to the Aristocystitidae, the families Eocystitidae (with seven eocrinoids and two paracrinoids), Anomalocystidae (with 18 "carpoids" and one eocrinoid), Dendrocystitidae (with two "carpoids" and an eocrinoid), Cothurnocystidae (with two "carpoids"), Malocystitidae (with four paracrinoids and one eocrinoid), and Comarocystitidae (with two paracrinoids). Such radically different kinds of pelmatozoans can scarcely be maintained as an order, whether or not they are assigned to the cystoids.

JAEKEL (69, 71) referred the Aristocystitidae to the Diploporita, placing them close to the Sphaeronitidae. REGNÉLL (99) summed up his discussion with "From this review it should have appeared, though there remains some doubt as to the position of a few genera, that the fam. Aristocystitidae has to be removed from the fatal Amphoridea and to be placed mainly in the Diploporita. By this procedure there is nothing to be left of the order Amphoridea in the sense of BASSLER 1938."

Key to Genera of Aristocystitidae

[Including only genera that appear to be well founded; key highly artificial and not intended to indicate phylogenetic relationships]

1. Theca very elongate conical, commonly more than 30 cm. high and attaining height of 40 cm.; provided with aboral terminal tubercle and composed of about 2,000 small plates, some ornamented .. *Calix*

   Theca not in form of very elongate cone, seldom exceeding height of eight cm.

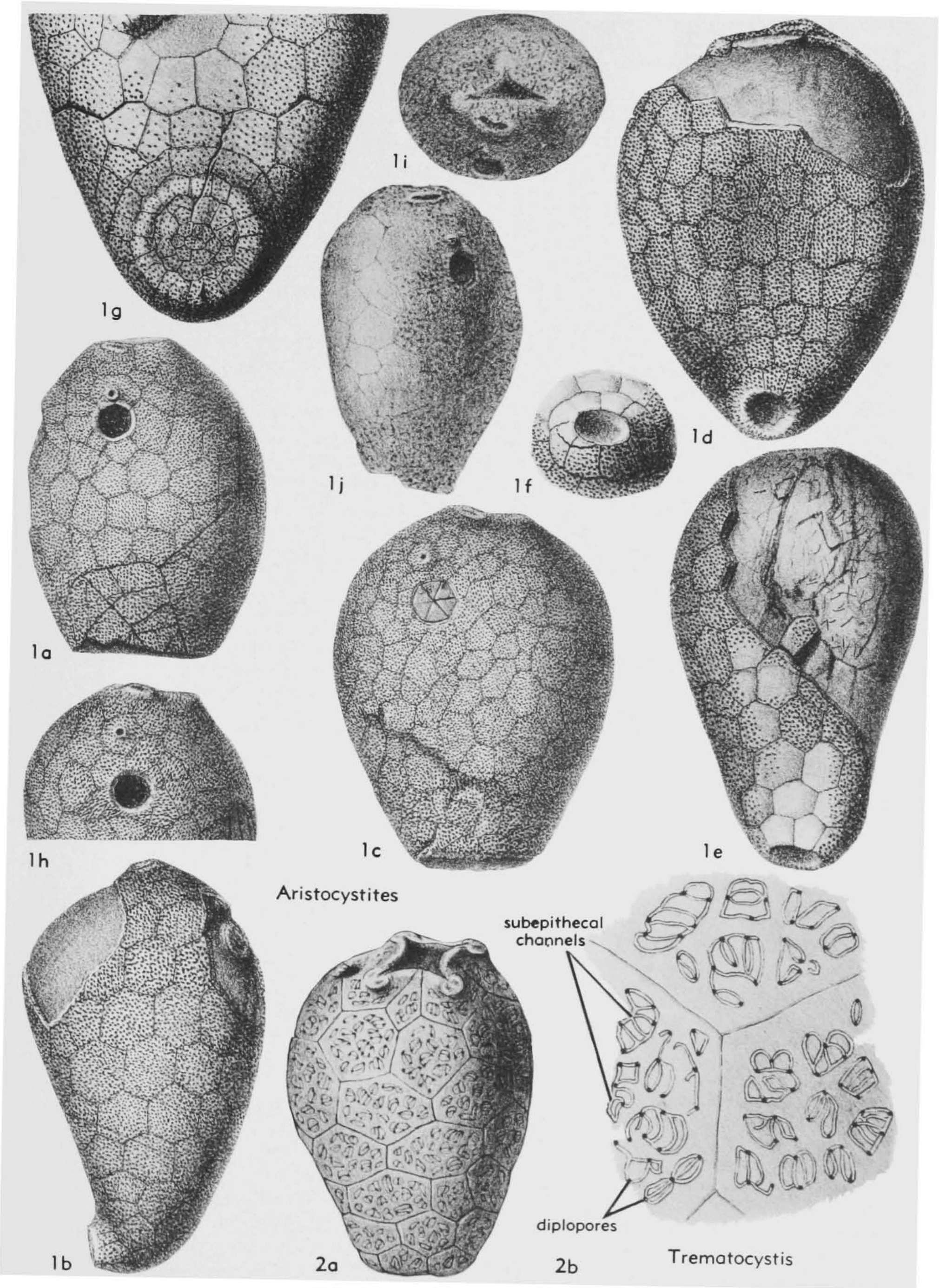


Fig. 148. Aristocystitidae (p. S252-S253, S258).

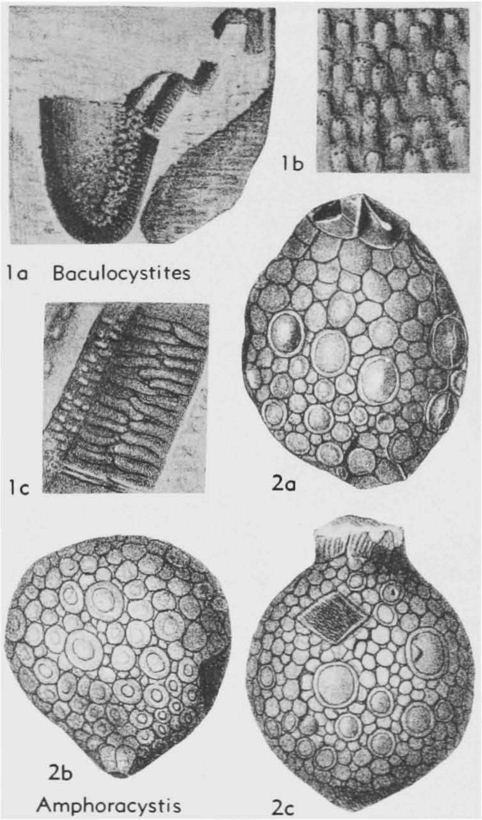


FIG. 149. Aristocystitidae (p. S253-S254).

and most forms smaller; no aboral tubercle, theca composed of only a few hundred plates, at most 2

2. Adult theca composed of plates of two drastically different sizes, large primary plates and small intercalated secondary or accessory plates 3

   Adult theca composed of subequal plates 4

3. Primary and secondary plates polygonal .... *Holocystites*

   Primary plates oval, secondary plates rounded or subpolygonal .... *Amphoracystis*

4. Mouth sinuous, bordered on one side by single large crescentic plate .... *Campylostoma*

   Mouth not sinuous, more than one plate on either side 5

5. Theca shaped like flared cone or bell, aboral part of theca exceptionally thick .... *Pachycalix*

   Theca more or less ovate, theca not exceptionally thick 6

6. Subepithecal channels connecting pores in shape of horseshoe .... *Hippocystis*

   Subepithecal channels, if present, not shaped like horseshoe 7

7. Normally two brachioles set at ends of elongate mouth, or oral slit, three known (?anomalous) .... *Aristocystites*

   Normally four brachioles 8

8. Thecal perforations large, not developed as diplopores, some continuing from one plate to another .... *Pseudaristocystis*

   Thecal perforations small, developed as diplopores, very few if any continuing from one plate to another 9

9. Mouth narrow and elongate, with short ambulacral grooves diverging from each end; brachiole facets set as at corners of oblong rectangle .... *Sinocystis*

   Mouth large and nearly square, with ambulacral grooves scarcely more than extensions of corners of mouth; brachiole facets set as at corners of square *Trematocystis*

Aristocystites BARRANDE, 1887, p. 95 [**A. bohemicus*; OD (=*A.? grandiscutum* BARRANDE, 1887, p. 109)] [=*Aristocystis* BATHER, 1889, p. 259 *(nom. van.)*]. Theca ovate to subpyriform or bulb-shaped, tapering aborally, base commonly truncate and shaped according to object to which attached. Young specimens may have possessed a column, but all traces of such attachment are absent in large forms. Thin epidermal layer, seldom preserved, smooth. Inner layer, composed of numerous polygonal plates, rather thin in oral region and becoming much thicker aborally, very thick at aboral pole; thickness also related to size (probably age) of individual. Pores numerous on most plates, shown on steinkerns as protuberances formed by casts (fillings) of inner portions of canals, on thick inner layer as openings connected by grooves or channels in groups of 2 to 6 (commonly 2). Mouth or peristomial opening elongate, more or less pointed at each end, set at right angles to plane through periproct and peristome; 2 brachiole facets normal, one specimen known with 3. Gonopore a small round opening between periproct and mouth, much closer to former. Hydropore an elongate slit near mouth and subparallel to it, in left posterior region. Periproct apparently filled by anal pyramid, hexagonal. [Some question remains of the nature of the pores. BATHER (12) stated, "The order Amphoridea, however much it be dismembered, still seems to find justification in the existence of genera, such as *Aristocystis,* which have neither diplopores (so far as I can observe) nor epithecal extensions of the subvective grooves. . . ." On the other hand, SUN (123) spoke of "double pores" in *Aristocystites* specimens from China. JAEKEL (69, 71) referred the family to the Diploporita, and other authors have followed his example.] *M. Ord.*, Eu.-Asia (China).——FIG. 148,*1*. **A.*

bohemicus, Dd_4, Boh.; *1a-d*, lat., 4 thecae, ×1; *1e,f*, lat. and part of aboral end of specimen, ×1; *1g*, aboral end, enl.; *1h*, oral end, ×1 (3); *1i,j*, oral and lat., specimen with 3 brachiole facets, ×1 (69). [See also Fig. 39.]

Amphoracystis HAECKEL, 1896, p. 52 [**Deutocyst-*

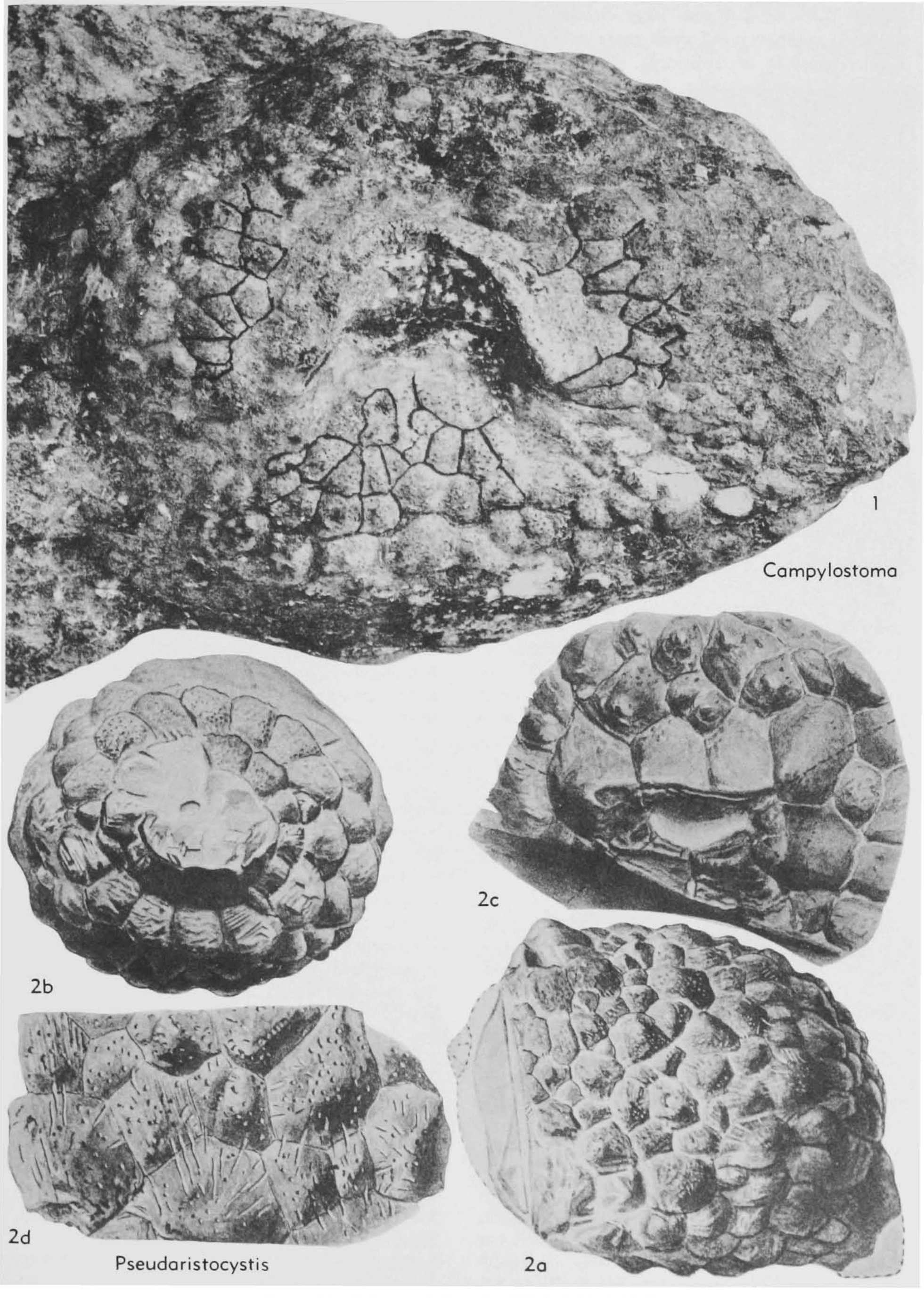


FIG. 150. Aristocystitidae (p. S254, S256-S257).

ites irregularis Barrande, 1887, p. 147; OD]. Theca small, ovoid, tapering slightly at base. Oral aperture elongate, probably produced (to judge from published figures). Periproct rhombic. Thecal plates of 2 types: large circular or oval (probably primary) and small more nearly polygonal (secondary or accessory). Pores unknown. *M.Ord.*(D_4), Boh.——Fig. 149,*2*. **A. irregularis* (Barrande); *2a-c*, 3 lat., ×2 (3).

?**Baculocystites** Barrande, 1887, p. 118 [**B. simplex;* OD]. Known only from fragment. Plates 3 to 4 mm. thick comprising conical base, externally smooth. Steinkern with fillings or casts of pores irregularly distributed and partly grouped, said to resemble features of *Codiacystis* more than *Aristocystites*. *M.Ord.*(D_4), Boh. —— Fig. 149,*1*. **B. simplex*; *1a*, fragment with thecal wall mostly dissolved, ×1; *1b,c*, int. mold and long. sec., enl. (3).

Calix Rouault, 1851, p. 358 [**C. sedgwicki;* OD] [=*Dorycystites* Kloucek, 1917, p. 3 (type, *D. purkynei*) (*fide* Chauvel, 1941, p. 82]. Theca cylindrical to conical or carrot-shaped, very elongate, bearing aboral terminal tubercle, very large, attaining height of 40 cm., making it largest known cystoid; theca composed of about 2,000 small plates in adult form, many with central tubercle or prominence. Mouth elongate, with brachiole facet at each end. Diplopores with simple oval or slightly curved pits covered over by epitheca, which seldom is preserved. Chauvel (33) differentiated 3 stages of development in type species: (1) aboral zone composed entirely of primary plates bearing tubercles, (2) appearance of secondary or supplementary plates between tuberculiferous plates (single circle of secondary between 2 circles of tuberculiferous primaries), and (3) appearance of secondary tubercles on primary plates, secondary plates, and possibly on plates of oral zone. Top of theca comprising corona of 8 to 12 plates without diplopores. Anal pyramid with 6 triangular plates. *M.Ord.-U.Ord.*, Eu.(Boh.-Fr.-Port.-Spain).——Fig. 143,*1*. **C. sedgwicki*, M. Ord., Fr.; *1a*, section through peristome and hydropore; *1b*, internal mold of peristome; *1c*, diagram of oral region (34); *1d*, reconstr., about ×0.2 (128). [See also Fig. 39,*2*.]

Campylostoma Dreyfuss, 1939, p. 118 [**C. grandis;* OD]. Theca apparently oviform, to judge from only specimen well preserved, with short height, composed of very numerous plates without orderly arrangement; plates thick, convex. Pores single or in groups of 2 or 3, irregularly distributed. Mouth or peristome sinuous, bordered on one side by large, unique, crescent-shaped plate and on other by 4 or 5 plates not convex and 2 or 3 times as large as other plates of theca; 4 depressions near crescentic plate, of which one may be gonopore and others probably are brachiole facets. *U.Ord.*, Fr.——Fig. 143,*5;* 150,*1*. **C. grandis;* 143,*5*, oral region; 150,*1*, oral, holotype, ×0.9 (39).

Hippocystis Bather, 1919, p. 72 [**Aristocystites bohemicus subcylindricus* Barrande, 1887, p. 114; OD]. Theca ovoid, composed of numerous polygonal plates, many of which are subhexagonal. General organization like that of *Aristocystites*, genus in which it was originally included. Diplopores distinctly defined as pairs of pores linked by horseshoe-shaped grooves, as exposed on weathered surfaces of plates. Diplopores obscured or covered in specimens in which smooth external layer is preserved. [This genus presents the classic example of diplopores.] *M.Ord.*, Boh.——Fig. 151,*2*. **H. subcylindrica* (Barrande), Dd$_4$; *2a-d*, 3 lat. and aboral, ×1; *2e*, aboral pole, enl.; *2f,g*, 2 plates, somewhat weathered, enl. (3).

Holocystites Hall, 1864, p. 7 [**Caryocystites cylindricum* Hall, 1861, p. 23; OD] [=*Holocystis* Carpenter, 1891, p. 47 *(nom. van.)* *(non* Lonsdale, 1849); *Megacystites* Hall, 1865, p. 380 *(nom. subst. in errore pro Holocystites* Hall, 1864, not preoccupied by *Holocystis* Lonsdale, 1849); *Megacystis* Angelin, 1878, p. 29 *(nom. van.)*]. Theca elongate subovate, aborally tapering; plates arranged in more or less alternating transverse or more or less alternating vertical rows, polygonal, in some predominantly hexagonal; large plates considered primary and small ones secondary or accessory, intercalation of smaller plates probably a feature of ontogeny, not a specific character. Mouth terminal, periproct nearby in oral part of theca, filled with anal pyramid of 5 or 6 triangular plates. [Difficulty in interpreting this genus arises from preservation of the type and related species as steinkerns, which reveal only traces of diplopores as internal casts or fillings and furnish no information on the brachioles, subepithecal connections of pores, ornamentation of plates, etc. Some, possibly most, of the cystoids ascribed to this genus by S. A. Miller (85) perhaps properly were separated as *Trematocystis* by Jaekel (69), although he mentioned only *T. subglobosus* (Miller), the type species, in particular. In cystoids which he assigned to *Holocystites*, Foerste (49) reported forms with 4 and with 5 grooves from the oral opening, presumably leading to brachiole facets.] *U.Ord.-M.Sil.*, Eu. (Sweden)-N. Am.(Wis.-Ill.-Ind.-Ohio-Tenn.)——Fig. 152,*1a-e*, *H. alternatus* (Hall), M.Sil.(Racine Dol.), Wis. *(1a-d)*, M.Sil.(Cedarville Dol.), Ohio *(1e)*; *1a*, lat., plates classed as primary indicated by letters A, B, C, D, in successive rings aborally, ×1 (Foerste, 1917); *1b-d*, lat., 3 thecae, ×0.8; *1e*, lat., ×0.8 (49).——Fig. 152,*1f-h*. *H. greenvillensis* Foerste, M.Sil.(Cedarville Dol.), Ohio; *1f-h*, lat., 3 thecae, ×1 (Foerste, 1917).——Fig. 152,*1i*. *H. gyrinus* Miller & Gurley, M.Sil. (Osgood Ls.), Ind.; oral region, ×1 (10).

?**Lepidocalix** Termier & Termier, 1950, p. 26 [**L. pulchrum;* OD). Theca known from plates, which show external perforation ending as pustule and 2 corresponding internal pores. Said by the authors to resemble *Calix* and *Pachycalix* but with spine-bearing and imbricating plates. As reconstructed its oral region resembles that of *Calix* or *Sinocystis,* with adjacent anal pyramid, and pore between them. [TERMIER & TERMIER (128) thought the pustule or perforated tubercle was articular, bearing a spine; if so, this would be drastically different from other cystoids, more nearly resembling a primitive echinoid.] *M.Ord.,* Algiers.——FIG. 143,*3*. **L. pulchrus*; reconstr. (128).

Pachycalix CHAUVEL, 1936, p. 3 [**Calix halli*

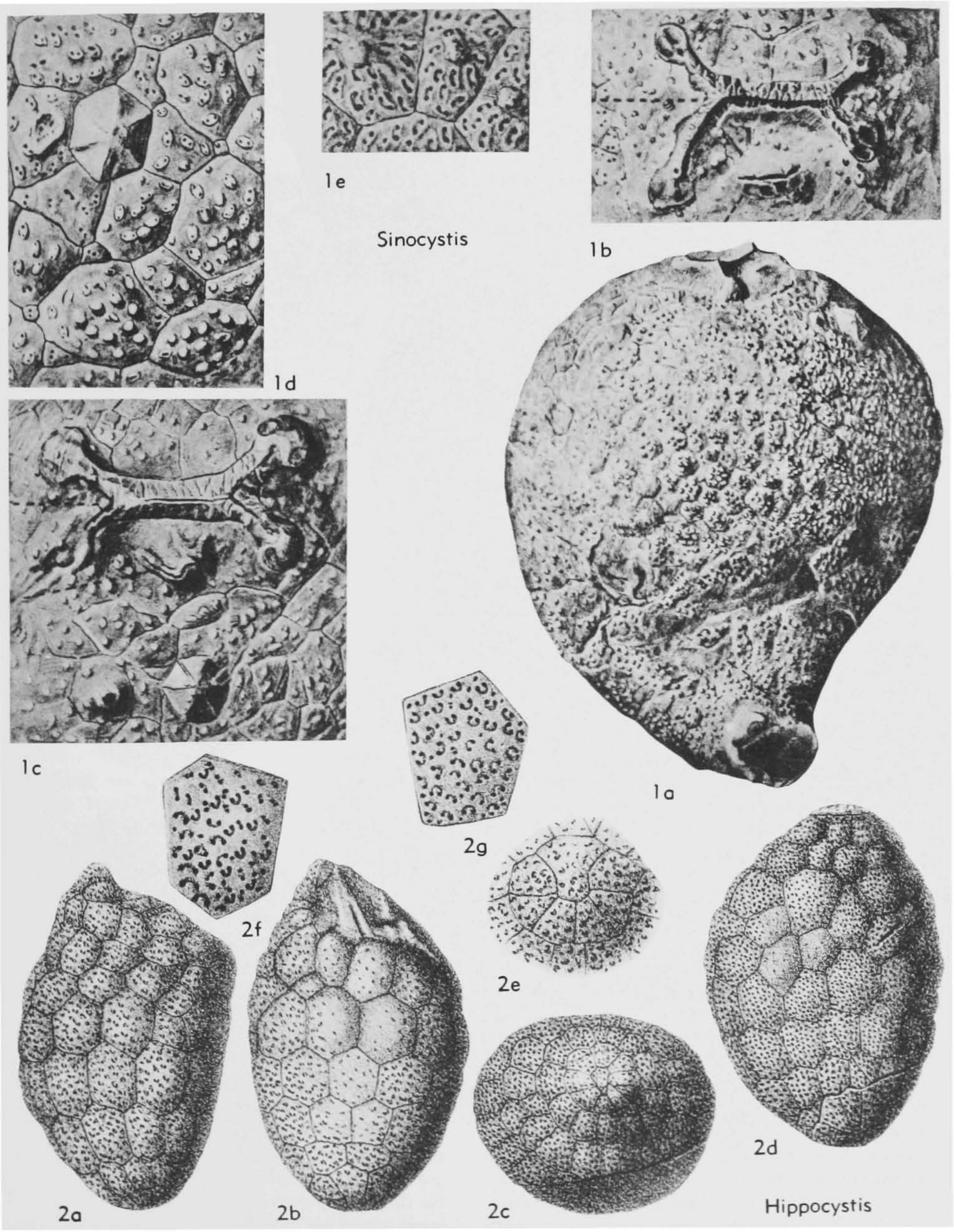


FIG. 151. Aristocystitidae (p. S254, S257-S258).

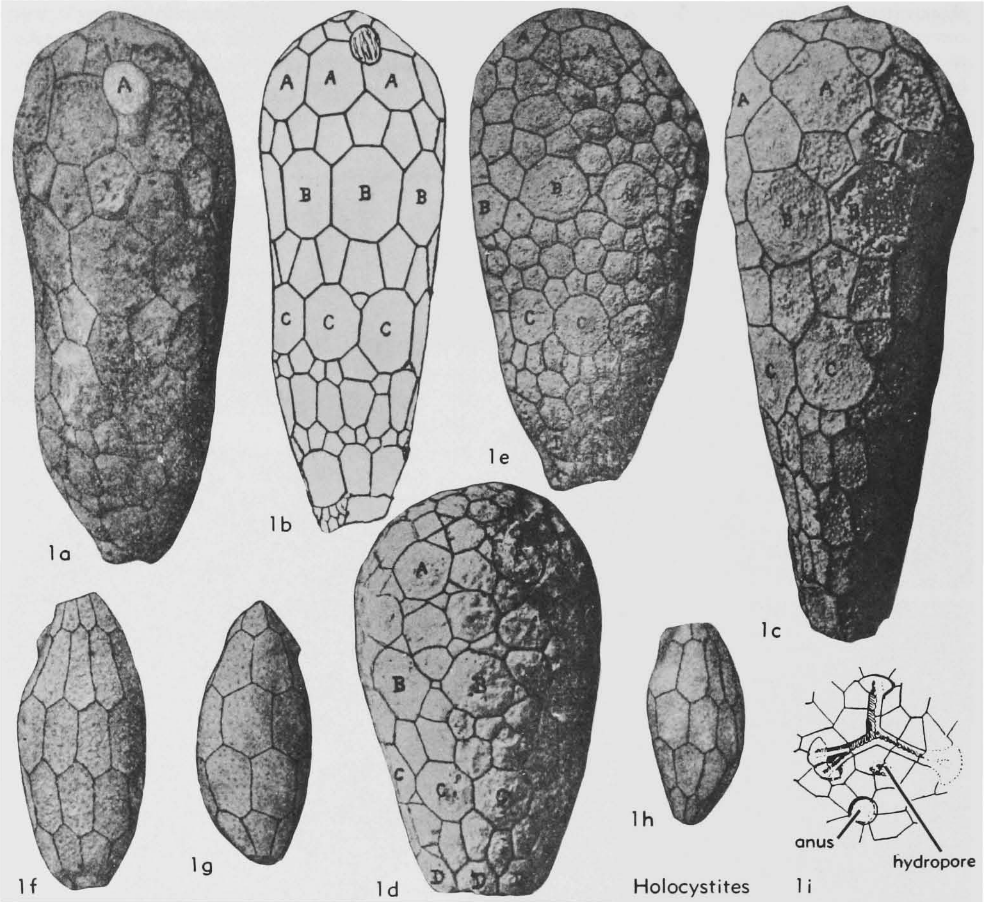


Fig. 152. Aristocystitidae (p. S254).

Rouault, 1851, p. 358; OD]. Theca with shape of flaring cone, devoid of tubercles, composed of very thick plates (8 to 12 mm.). Pores of large diameter (1 to 2 mm.), some ramified in form of Y, many sinuous, many in groups of 2 but not necessarily in typical diplopore form; by some authors referred to as haplopores. Between mouth and periproct is hydropore. *M.Ord.*, Eu.-N.Afr. ——Fig. 143,*2*. *P. pachythecus* Termier & Termier, Caradoc, Morocco; *2a,b,* long. and transv. secs. (reconstr.) (128). [See also Fig. 33,*3*.]

Pseudaristocystis Sun, 1936, p. 480 [**Aristocystis dagon* Bather, 1906, p. 8; OD] [=*Dagoncystis* Chauvel, 1941, p. 52 *(obj.)*]. Theca ovoid, judged from incomplete holotype of only known species to have been pear-shaped and to have lived in prostrate position with narrower end bent downward for attachment to sea floor. Mouth elongate, surrounded by 7 plates with longer axes radiating from center, edges of plates beveled (presumably to accommodate peristomial covering plates); at each end of oral opening circumoral plates indented, forming facets for 2 brachioles; 4 facets arranged at corners of long trapezoid, with those on anterior side farther apart than those on posterior. Obscure opening near mouth in posterior area thought to be hydropore. Periproct not preserved. Thecal plates 150 to 200, irregularly arranged but tending to be disposed in rows, plates at aboral constriction in 2 circlets; 2 or 3 rows of plates around circumorals conspicuously smaller and quite irregular, considered by Bather (12) to represent region of thecal growth; plates swollen, with rather rough irregular surface, stout. Large pore canals pierce plates of oral and aboral regions with irregular courses more or less at right angles to general surface, but in plates of side walls canals tend to be directed toward sutures between plates, and some pass across sutures although not disposed into rhombs; no differentiation of canals to form diplopores. [BATHER (12) regarded the pore canals as an incipient stage leading to pore rhombs.] *M.Ord.*, Burma.——FIG. 150,*2*. **P. dagon* (BATHER), Naungkangyi Beds; *2a,b*, lat. and aboral, ×1; *2c*, oral region, ×2; *2d*, weathered plates showing directions of pores, ×2 (12). [See also Fig. 33,*2*.]

Sinocystis REED, 1917, p. 3 [**S. loczyi;* SD BATHER, 1918, p. 51] [=*Ovocystis* REED, 1917, p. 7 (type, *O. mansuyi*)]. Theca variable in shape, roughly ovate pyriform, tapering to base which may be prolonged as short unspecialized stem, composed of 100 to 600 irregular polygonal plates bearing conspicuous diplopores, several to a plate. Peristome elongate, with 2 short ambulacra diverging from each end and terminating in large brachiole facets; 4 brachioles, therefore, set at corners of small oblong. Periproct in posterior region, about midway between peristome and periphery as viewed orally. Gonopore situated left of periproct; hydropore a curved slit between gonopore and peristome. Covering plates of ambulacra and peristome irregular, biserial. [In some species, the crowding of diplopores is made possible by elevations, called "turrets" by BATHER (12), each containing a few diplopores.] *M.Ord.*, China.——FIG. 151,*1a-d*. **S. loczyi*, Shih-tien, *1a*, lat., ×1; *1b,c*, 2 oral regions, ×2, ×2.5; *1d*, periproctal

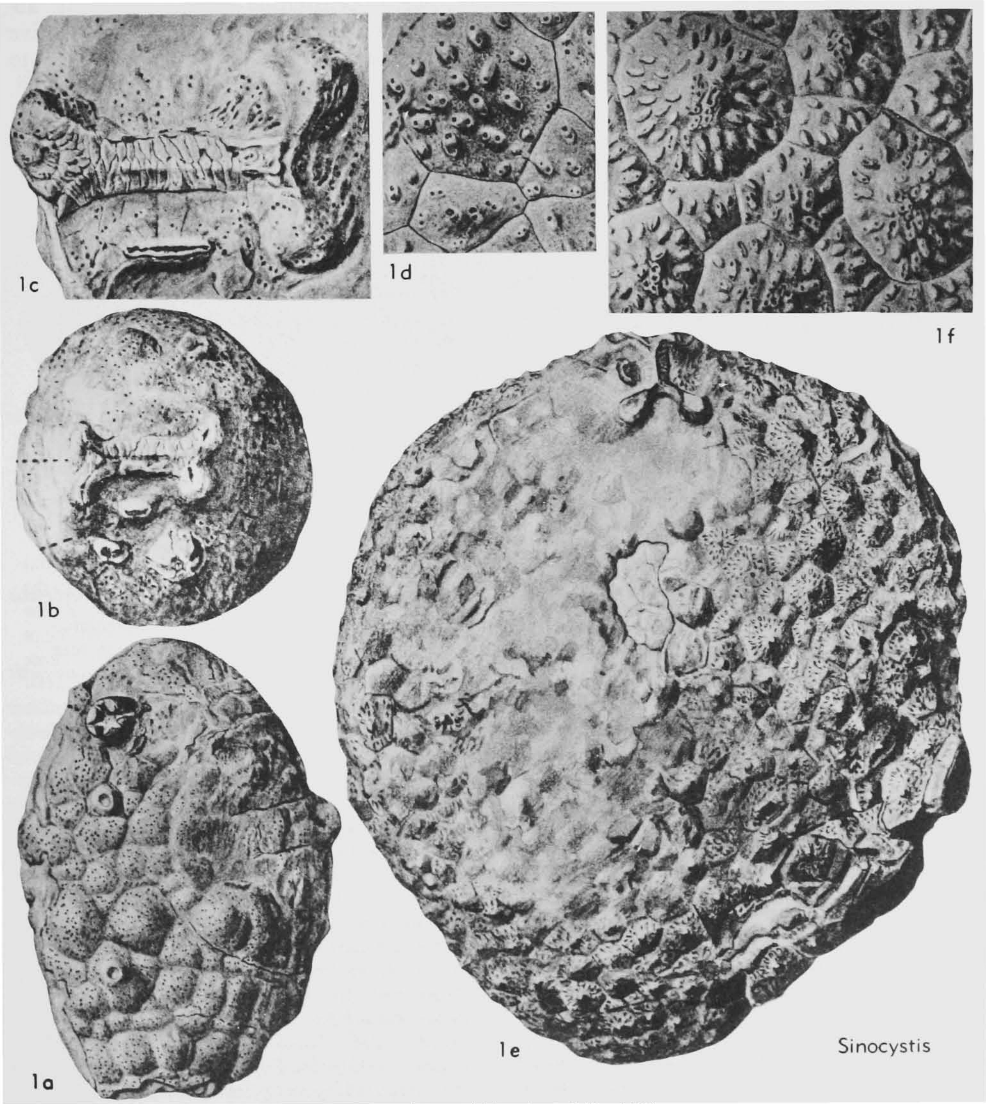


FIG. 153. Aristocystitidae (p. S257-S258).

region, ×3 (98).——Fig. 151,*1e;* 153,*1e,f.* *S. yunnanensis* Reed, Shih-tien; 151,*1e,* weathered plates, ×5; 153,*1e,* lat., crushed specimen, ×1; 153,*1f,* plates, ×4 (98).——Fig. 153,*1a-d.* *S. mansuyi* (Reed), Shih-tien; *1a,* lat., ×1; *1b,* oral, young specimen, ×2; *1c,* oral region, ×2.5; *1d,* thecal plates, ×4 (98).

Trematocystis Jaekel, 1899, p. 414 [**Holocystites subglobosus* S. A. Miller, 1889, p. 255; OD]. Theca subovate to subpyriform, tapering to rather blunt or truncated base. Mouth large, bordered by prominent rim, with corners leading to 4 brachiole facets, spaced at corners of square. Periproct in upper part of theca, near mouth. Subepithecal multiple, twisted or winding channels connecting diplopores. Pores small. Thecal plates apparently subequal, although this may only be a feature of youth in which accessory plates have not developed. [Foerste (49) predicted that *Trematocystis* would become eventually a junior synonym of *Holocystites.* Apparently, however, the mouth is much larger, the theca less elongate, and the plates more nearly equal in size.] *M.Sil.,* E.C. N.Am.——Fig. 148,*2.* **T. subglobosa* (Miller); *2a,* lat., reconstr., ×1; *2b,* weathered surface, enl. (69).

Superfamily ASTEROBLASTIDA Bather, 1900

[*nom. transl.* Kesling, herein (*ex* Asteroblastidae Bather, 1900, p. 80)] [=order Asterocystida Jaekel, 1918, p. 100]

Diplopore-bearing cystoids in which diplopores are restricted to interambulacral areas. Theca pentremite-, bud-, or bullet-shaped, with strong pentameral symmetry. Ambulacra five, straight, each bearing numerous brachioles, distally resting on *RR.* Specialized oral or deltoid plates, angular and close-fitting around small mouth opening, plate in posterior interradius divided. Column present. *L.Ord., ?M.Ord.*

Considerable interest has been stirred by the fossils assigned to this superfamily because of their resemblance in general form to the blastoids. As early as 1874, Schmidt (114) concluded that these Estonian cystoids were transitional forms leading to the blastoids. The lack of conclusive evidence, however, is exemplified in the 1953 volume of the *Traité de Zoologie,* in which Cuénot placed *Asteroblastus* in his chapter on cystoids and Bergounioux included it in his chapter on blastoids. Wanner (1951) became convinced that if the eublastoids were at all descended from cystoids, only the Asteroblastidae satisfied the prerequisites. It is worth consideration that the author of the family Asteroblastidae originally placed it in the Blastoidea; and Bassler (5) assigned these genera to the Protoblastoidea. Unfortunately, much of the morphology of these interesting pelmatozoans is known only in gross aspect, and especially the internal structures need additional study.

Family ASTEROBLASTIDAE Bather, 1900

[Asteroblastidae Bather, 1900, p. 80] [=Asterocystidae Jaekel, 1918, p. 101]

Theca pentremite or bud-shaped; aborally conically globose; orally with five broad, flat, distally tapering, linguloid to spatulate ambulacra sloping from small, truncate oral area to join aboral half of theca, interambulacral spaces being filled with various plates. Column present, rather thin. *L.Ord., ?M.Ord.*

Key to Genera of Asteroblastidae

1. In each interambulacrum diplopore-bearing area composed of one large, sub-rhombic suboral plate (so-called "subdeltoid"); four plates in vertical row in each interambulacrum except that with periproct, here called *O,* suboral, *L,* and *IL* .... *Asteroblastus*
   In each interambulacrum diplopore-bearing area composed of several small plates, not single large suboral plate 2
2. On aboral side of theca, each interambulacrum (except that having periproct) composed of *IL* and *L,* with few small accessory plates .... *Asterocystis*
   On aboral side of theca, each interambulacrum composed of small plates in four to six rows .... *Metasterocystis*

Asteroblastus Eichwald, 1862, p. 62 [**A. stellatus* Eichwald, 1862 (=**Protocrinites foveolatus* Eichwald, 1860, p. 623; OD]. Theca composed of relatively few definitely arranged plates comparable with those in Rhombifera. *BB* 4, small, 2 hexagonal, one on each side of posterior interambulacrum, other 2 pentagonal, occurring together on opposite side. Above circlet of *BB* is circlet of 6 plates, distributed 2 in posterior interambulacrum and 1 in each other interambulacrum, apparently representing 5 *ILL* and 1 anal, or *X;* from latter, a series of polygonal plates leads adorally to periproct. In addition, each interambulacrum contains vertically elongate hexagonal plate *(L),* subpentagonal plate bearing numerous diplopores (suboral or pore-plate), and crescentic elongate plate *(O)* bordering small pentagonal mouth opening; plates in these *LL,*

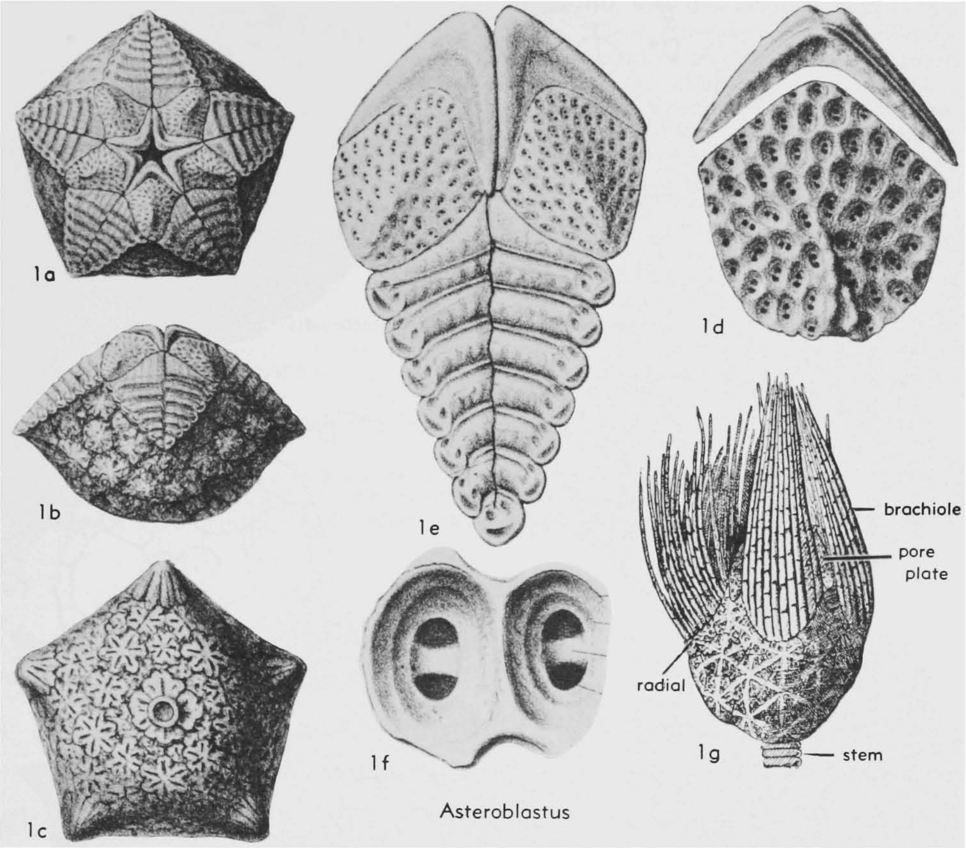


Fig. 154. Asteroblastidae (p. *S*258-*S*259).

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,

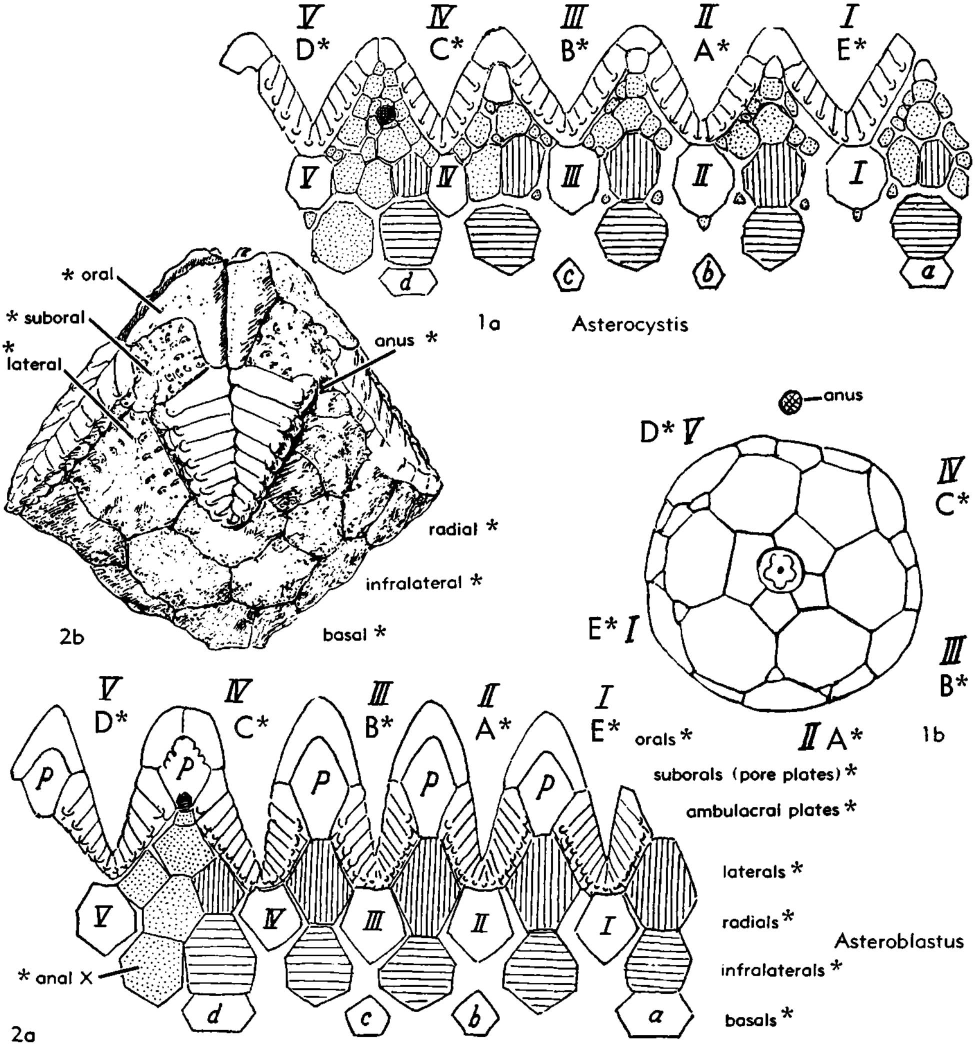


Fig. 155. Designations of plates and rays in Asteroblastidae, given by Jaekel and identifications of them (marked by asterisks) judged by Kesling to be appropriate (Kesling, n).

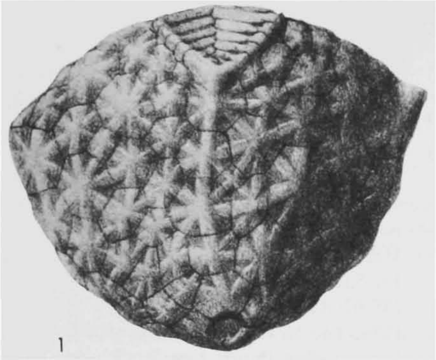
orally theca resembles that of *Asterocystis.* On aboral side, however, each interambulacrum composed of small plates in 4 to 6 rows or circlets. *L.Ord.,* Eu.(USSR).——Fig. 156,*1.* **M. micropelta,* L.Ord.(Kunda,B_3), Leningrad; incl. lat., ×2 (69).

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 pusirefsḳii* Hoffman, 1866, p. 4; OD (=*Agelacrinus pusyrewsḳii* Schmidt, 1874, p. 34; *Mesocystis pusirefsḳi* Bather, 1900, p. 76; *Mesocystis pusirewsḳii* Wanner, 1933, p. 491; *Mesocystis pusireffsḳyi*



Metasterocystis

Fig. 156. Asteroblastidae (p. *S*259-*S*260).

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).

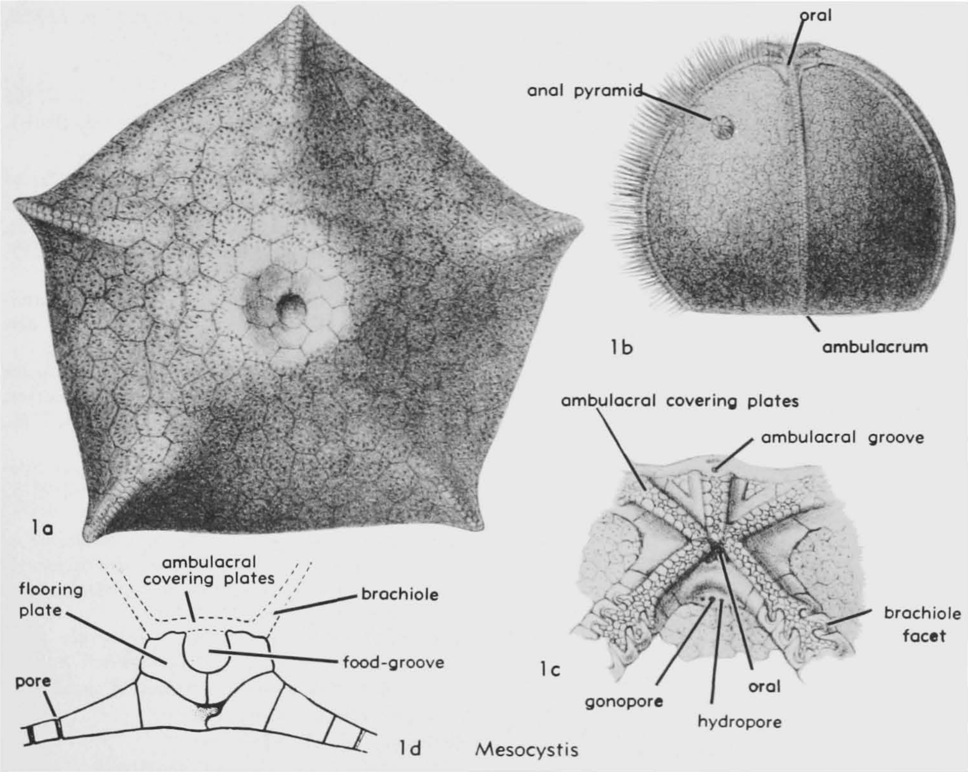


Fig. 157. Mesocystidae (p. *S*260-*S*261).

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