# PARACRINOIDS

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## INTRODUCTION

Paracrinoids are extinct pelmatozoan echinoderms. Insofar as the paleontological record is known, they developed suddenly, flourished briefly, and became extinct, all in the span of Middle Ordovician time. Because the record is fragmentary, it seems quite reasonable to suspect that the paracrinoids made their appearance before this epoch, and that some lingered after it; at any rate, paleontologists should not confine their search to Middle Ordovician rocks in looking for Paracrinoidea.

Although they are locally abundant, the paracrinoids never achieved world-wide distribution, nor did they evolve enough diversity of form to require complicated taxonomy. As compared with other groups of echinoderms, the paracrinoids are a small, fairly homogeneous taxon. Needless to say, they are not considered as guide fossils.

Paracrinoids bear morphological similarities to other pelmatozoans (Fig. 158). They have a theca like that of the cystoids, pinnuliferous arms like those of the crinoids, and a column like that of the blastoids. At least some forms have a hydropore and gonopore like those of the cystoids. The thecal pores extend from the interior into the plates but terminate beneath the epitheca; thus, they have the same general plan as that present in the superfamily Caryocystitida of the cystoids.

Yet distinct differences set the Paracrinoidea apart as a class. They can be distinguished from cystoids and eocrinoids by the uniserial nature of their ambulacral structures, as well as by the presence of pinnules. They differ from crinoids in having the body covering arranged as a continuous theca, not divided into a calyx and a tegmen. They are separated from the blastoids by irregularity of plate arrangement and by form of the pore system. Therefore, a well-preserved specimen of the paracrinoids can be identified as such without difficulty.

Diagnostic features of many paracrinoids, however, are seriously affected by fossilization. In particular, the pinnules and arms are lost from many specimens. Details of hydropore, gonopore, anal pyramid, column, and surface ornamentation may not be preserved. Some of the genera are incompletely known.

Paracrinoids seem to have lived in much the same manner as many of their contemporary cystoid relatives. The animals were anchored to holdfasts by a flexible column. There is no conclusive evidence on whether adults were immovably fixed at one site, or whether they could release their hold and perhaps drift to a more desirable location. The paracrinoids possessed what appears to have been an effective strainer mechanism for gathering nutrition, consisting of pinnuliferous arms. Presumably the supply of microscopic food was an important, even limiting, ecological factor.

As with other classes of pelmatozoan echinoderms, the paleoecology of the Paracrinoidea needs more data, the morphology needs better-preserved specimens, and the classification needs discoveries to fill the gaps which we can reasonably infer between known taxa. Knowledge of these fossils has progressed slowly and sporadically. Although species have been known for more than a century, it was not until 1945 that the class was formally distinguished by Regnéll (99). Much of the classification is the work of Billings (18, 20). Articles by Foerste (47, 49, 148) added to understanding of morphology. From time to time, other writers described a new form or two, grouped genera into families, or noted additional occurrences, but their contributions were minor.

From this log of accomplishment, it is obvious that new advances will be made at such time, and only at such time, as new finds of paracrinoids come to light.

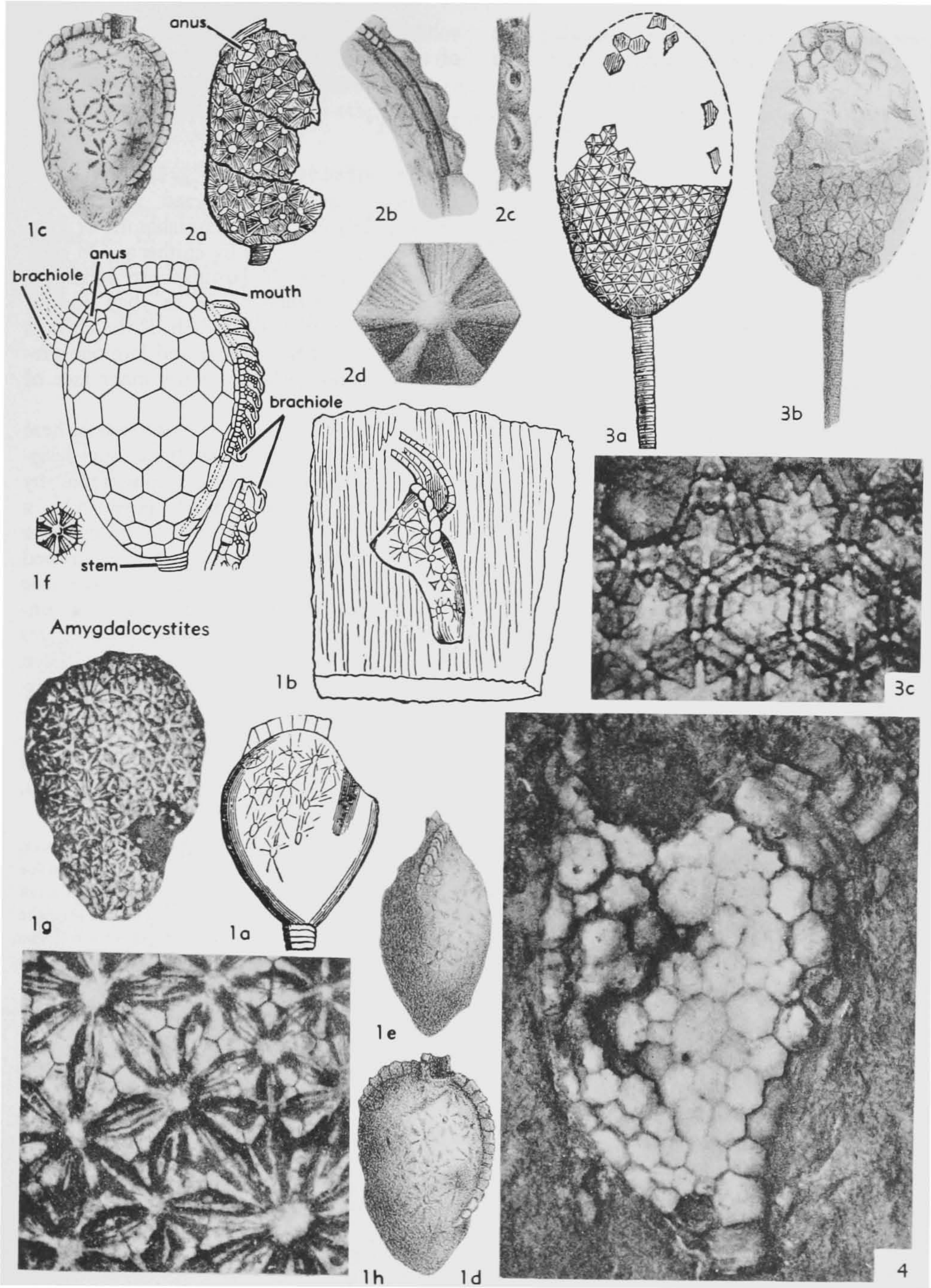


FIG. 158. Morphological features of Paracrinoidea illustrated by *Amygdalocystites*, all Middle Ordovician from Ontario; *1*, **A. florealis* BILLINGS; *2*, *A. tenuistriatus* BILLINGS; *3*, *A. radiatus* BILLINGS; *4*, *A. laevis* W. R. BILLINGS.

The treatment here must be considered as a summary of current concepts, not as a substantial addition to our understanding of the class.

# MORPHOLOGY

## PORE STRUCTURES

No pore structure is visible externally on any unweathered paracrinoid that has been investigated. The epitheca is unperforated, so that whatever pore structures are present lie in the stereotheca.

Only in certain species of *Comarocystites, Amygdalocystites* (Fig. 158), and *Canadocystis* has a concerted study of pore structures been made. This is unfortunate. In the closely related Cystoidea, the nature of pore structures is the basis for separation of the two orders. Possibly, it may prove to have greater taxonomic significance in the Paracrinoidea when more observations have been made.

### COMAROCYSTITES

The thecal plates of this genus are so unusual that Billings (18-20) mentioned the external features in early descriptions. Each plate has a deep central concavity and a raised border or margin. Billings (20) said:

> In certain states of preservation the sutures are marked by minute thickly set square or oblong rough punctuations, which do not however appear to penetrate through to the interior. . . . The greater portion of the area of the plate is marked with deep fissure-like striae at right angles to the suture, and with thin erect lamellae or partitions between them. These are sometimes crossed by other lamellae parallel with the edges of the plates the effect of which is to produce a pecularly rough surface. Sometimes none of these are visible, and the surfaces of the plates are then uniformly smooth and solid. These variations are the results both of weathering and of structure.

The inner surface of thecal plates was studied in greater detail by Foerste (47). The junction where three plates meet is marked on the interior by a deep triangular pit, so that the plates are very thin at the corners. The **stereotheca** of each plate contains vertical laminae distributed in triangular areas, one area along each side; the laminae are perpendicular to the side (suture) and continuous with the laminae of the adjacent plate (Fig. 159,*1i*). The laminae thus are restricted to rhombic areas, much like the pectinirhombs of cystoids, but covered over by **epitheca**. On each plate, the areas of laminae are separated by grooves, which taper as they radiate from the center toward each of the corners of the plate. The grooves and laminae produce a stellate pattern on the inner face of the theca.

Near the interface of the two layers, here called epitheca and stereotheca, but designated as epistereom and mesostereom by Foerste (47), are paired pores. On a weathered surface from which the epitheca has been removed, each pore is expressed as a lunate groove, with its concave side facing the other pore of the pair. On unweathered surfaces, the position of pores may be marked by short lunate ridges. Each pore extends down into the plate as a circular to oblong tube leading to an interlamellar space; the two pores of a pair invariably connect with different interlamellar spaces, being separated by one lamella. According to Foerste (47),

> The right hand pore of one pair, however, usually is connected with the same inter-lamellar space as the left hand pore of the nearest adjacent pair, proximally or distally, i.e., either nearer the center of the thecal plate or nearer the suture line. In this manner, three or four pores belonging to different pairs may be connected to the same inter-lamellar space. . . . The pores penetrating the outer continuous sheet of the mesostereom are directed perpendicularly toward the suture lines between the plates, but incline more or less obliquely downward. They apparently widen in a direction parallel to the inter-lamellar spaces in passing through the outer sheet of the mesostereom, since, in strongly weathered specimens showing the inter-lamellar spaces, the latter frequently appear interrupted by transverse partitions a short distance below the outer continuous sheet of the mesostereom.

In comparison with the pore system of cystoids, therefore, *Comarocystites* may be said to have an inner set of laminae like the pectinirhombs of the Glyptocystitida, an outer epitheca concealing the pore structure like that of the Caryocystitida, paired pores like the Diploporita, an external expression of subepithecal pores like the Hemicosmitida. Such a combination of characters is unknown in any other echinoderm.

## AMYGDALOCYSTITES

The inner structure of plates in this genus, as well as *Comarocystites,* was described by Foerste (47). The inner surface of each thecal plate is marked by radial ridges, in some specimens sufficiently developed to be called short plates (Fig. 158,*1h*). One ridge extends to each corner, and some paracrinoids have additional ridges to the mid-point of each side. Certain specimens have pores along the sutures, with half of each pore on one of the adjacent plates. Possibly these pores are covered over by epitheca in unweathered specimens. Either one pore occurs at the middle of each side, or two pores are on each side close to the radial ridges leading to the corners.

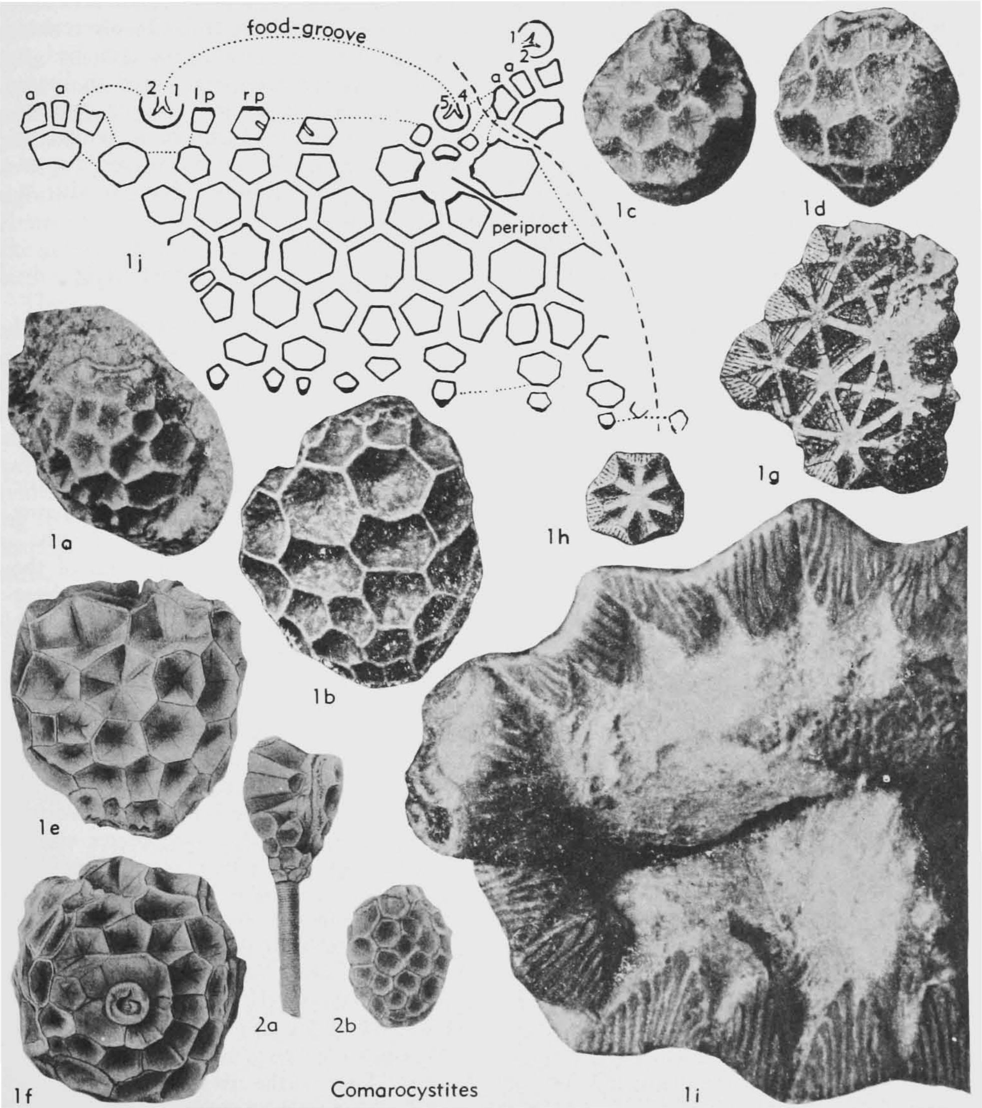


Fig. 159. Morphological features of Paracrinoidea illustrated by *Comarocystites,* all Middle Ordovician of Missouri; *1, C. shumardi* Meek & Worthen; *2, C. obconicus* Meek & Worthen.

## CANADOCYSTIS

Despite the close resemblance of the theca and arms of *Canadocystis* to those of *Amygdalocystites,* the former has no radiate ridges or sutural pores on its thecal plates. Further, *Canadocystis* lacks internal lamellae, such as occur in *Comarocystites.* It apparently had no pore structure in the thecal plates, at least not in the preserved stereotheca.

The absence of any kind of pore structure in a genus that otherwise seems related to genera in which they are well developed raises a serious question as to the function and significance of such structures. We have no answer at this time.

## THECA

The thecae of paracrinoids do not vary drastically. None are strongly compressed and most are somewhat globular. The periproct is not far removed from the peristome in any species. None are known to have pores visible on the exterior. Hence, a certain degree of homogeneity is present.

Thecae do exhibit variations in number of plates, ornamentation, and relationship to the arms. *Malocystites* may have as few as 30 thecal plates, and *Billingsocystis* as many as 175. *Comarocystites,* unquestionably a paracrinoid, has about 150 plates.

The ornamentation of plates can be classed in three major types: 1) plates concave, 2) plates radially ridged, and 3) plates with minor features of ornamentation. Concave plates occur in *Comarocystites* and *Sinclairocystis,* the former with free arms and the latter with attached arms. Radially ridged plates, in which ribs or ridges extend from the center to the corners of each plate, are found in *Amygdalocystites* and *Billingsocystis;* the former has attached arms and the latter, insofar as indicated in the account of Bassler (6), seems to have had free arms. Plates with smooth or slightly tuberculate surfaces occur in *Canadocystis* and probably in *Malocystites* and *Schuchertocystis.*

It appears from these data that arms (brachioles) and ornamentation have little correlation. If both kinds of arms occur with each of the three kinds of ornamentation of plates, then classification must be determined by only one character—in the *Treatise* and in previously adopted systems, the nature of the arms was the selected character.

In one group of paracrinoids, the arms rise free from the region of the mouth, being attached only by their proximal ends at facets; in the other group, the arms are attached along one edge, in somewhat the same manner as long ambulacra in certain glyptocystitidan cystoids. The attachment of plates of the ambulacral system to the thecal plates involves both kinds of plates. The integument which secreted one must have joined and fused with the integument which secreted the other. The arms that are recumbent on the theca are firmly attached to thecal plates. Insofar as reported in literature, the character of the arms is constant within a species and within a genus; no species has been discovered with some specimens having free arms and some with attached arms.

## AMBULACRAL SYSTEM

No paracrinoid has more than four arms **(brachioles)** and none has pentameral symmetry of any kind. The mouth is a relatively small circular or slightly elliptical hole; it lies in the bottom of a trough which could be regarded as a peristomial groove, roofed over by biserial plates. The basic structure common to all arms is this narrow extension on opposite sides of the mouth.

The free arms rise near the end of the peristomial groove. In all forms that have been described, the groove divides at each end into short, equal, diverging ambulacral grooves leading to the arms facets. In specimens which do not have the arms preserved, the facets are seen to lie as two pairs, one pair at each end of the elongate narrow peristome. The symmetry in this group of paracrinoids is more or less bilateral, with a plane of symmetry along the center of the peristome and also with a plane across the middle of the peristome.

Paracrinoids with attached arms also possess a long narrow **peristome,** and assume their characteristic shape according to the manner in which the arms grow onto the theca from the ends of the peristome. In *Malocystites* the arms branch several times. In *Canadocystis* the two arms are about equal in size and curvature. In *Sinclairo-*

*cystis* the two are curved in the same direction but with sharp differences in length and degree of curvature. In *Wellerocystis* one arm divides and the other curves sharply around the periproct. In *Amygdalocystites* the arms are long and unbranched, slightly curved, with the anus (periproct) on the convex side of the nearer arm (Fig. 158,*1f*).

Except in *Malocystites,* which has nearly straight branches of the arms, the attached arms of paracrinoids are curved clockwise as viewed orally. Thus, in *Canadocystis* the whole of the attached part has the form of a large letter S. In the almond-shaped *Amygdalocystites,* the curvature is less pronounced and follows the slightly skewed edges of the biconvex theca. In *Sinclairocystis* and *Wellerocystis,* one arm is short and curved tightly in the oral region, whereas the other (branched in *Wellerocystis*) is curved more like an arm of *Amygdalocystites* and extends farther aborally.

There is a tendency among paracrinoids, much stronger than among cystoids, for the periproct to lie opposite to the attachment of the column and for the peristome to be offset onto the side of the theca. This is particularly well exemplified by numerous specimens of *Canadocystis* and *Malocystites.* No evidence is seen that such asymmetry resulting from the offset peristome-columnar axis bears any relation to differences in the two arms.

All arms are uniserial, whether attached or free. Insofar as known, each brachial gives rise to a uniserial pinnule. Foerste (47) reported that some pinnules did not bear extensions of the ambulacral system; that is, some lacked a groove covered by tiny plates. Pinnules are rarely found, especially in a good state of preservation, so that no general conclusion about the ambulacral extent can be drawn.

In attached arms, the pinnules issue from the convex side of the curve; thus, they join onto the left side of the arm, as viewed orally. Concerning paracrinoids with free arms Foerste (47) stated, "Analogy with *Amygdalocystites* and *Canadocystites* [*sic*] suggests that the pinnules of all four arms of *Comarocystites* were attached to the right side of the arms, the aboral side of each arm facing the observer, and the distal end being directed upward."

The length of free arms was estimated to be about half again the greatest diameter of the theca in *Comarocystites.* The greatest length of attached arms is about equal to the height of the theca; the arms are curved, but do not extend to the columnar facet.

## HYDROPORE AND GONOPORE

The hydropore appears as a narrow, sinuous ridge with a slitlike opening along its crest. It is located near the mouth, as in Cystoidea. Nearby minute pits have been reported in some specimens but not found in others; the presence of a gonopore is not established. Nor has a hydropore been observed in *Amygdalocystites.* Additional specimens are needed to study these structures.

## COLUMN

The column observed by Foerste (47) in *Comarocystites shumardi* seems to be complete, extending from the theca to a structure interpreted as a holdfast. Unlike the column in cystoids, this structure is of nearly constant diameter throughout its length. The columnals are very thin, alternating in thickness.

### GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO PARACRINOIDEA

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

*abactinal. See* aboral.

**aboral.** Located away from mouth; used in a general way to indicate position of column, although mouth and column are not directly opposite in most paracrinoids.

*actinal. See* oral.

**adoral.** Located toward mouth.

**ambulacral.** Referring to food-gathering system.

**ambulacral covering plates.** Small plates arranged biserially and covering over ambulacral grooves in arms and pinnules.

**ambulacral groove.** Groove through which food was conveyed from pinnules through arms to mouth, a trough covered by movable ambulacral covering plates.

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

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

**anus.** Exit of alimentary canal or gut.

**ARM.** Main branch of ambulacral system, composed of uniserial brachials and bearing pinnules; in some paracrinoids arms are free, attached to theca only at their proximal ends; but in others, arms are attached, one edge being fastened to thecal plates.

**attached arm.** Arm fastened to thecal plates by one edge, with pinnules extending from opposite edge; such arm lies on thecal surface much as ambulacrum of a cystoid.

**basal.** Part of theca near base.

**base.** Aboral part of theca, that to which column is attached.

**BRACHIAL.** One of uniserial plates in arm.

**COLUMN.** Stemlike structure attached to aboral end of theca, used for anchorage of paracrinoid; distal end in some modified into disc-shaped holdfast.

**columnal.** Unit composing column.

**columnar facet.** Indentation in basal plates to accommodate proximal end of column.

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

*epistereom. See* epitheca.

**EPITHECA.** Thin, nonporous layer on outside of thecal plates.

**exothecal.** Outside of theca; secreted by integument not secreting thecal plates, especially applied to arms and pinnules.

*food groove. See* ambulacral groove.

**free arm.** Arm attached to theca only by its proximal end.

*genital pore. See* gonopore.

**GONOPORE.** Small opening or aperture in posterior region, close to mouth, penetrating thecal plates; presence of a gonopore has not been established in all paracrinoids.

**holdfast.** Disclike structure at distal end of column in some paracrinoids, presumably for attachment; no evidence on permanence of such attachment has been offered.

**HYDROPORE.** Opening or openings through thecal plates in posterior part of theca near mouth; presence of a hydropore not established for all paracrinoids.

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

**lamina.** Vertical plate of stereotheca, developed in some paracrinoids.

**lateral.** Located on side of theca.

*madrepore. See* hydropore.

*mesostereom. See* stereotheca.

**MOUTH.** Aperture at oral pole through which food entered body from ambulacral system; small circular opening in peristomial structure, lying in bottom of trough-shaped ambulacral groove, roofed over by covering plates.

**oral.** Associated with mouth.

**oral pole.** End of theca containing mouth.

**ornamentation.** Surficial features of thecal plates.

**PERIPROCT.** Major thecal opening containing anal pyramid.

**PERISTOME.** Major structures associated with mouth; used by FOERSTE (1916) to include the "transverse apical food-groove," troughlike part of ambulacral system extending on either side of mouth and continuous with arms; peristome is covered by peristomial covering plates.

**peristomial covering plate.** Any of small plates covering mouth and continuous with ambulacral covering plates of arms; peristomial covering plates may have been immovable.

**pinnular.** Any uniserial plate composing pinnule.

**PINNULE.** Terminal structure of ambulacral system, attached to arm, composed of uniserial pinnulars and biserial covering plates.

**plate.** Any calcareous secretion forming structural unit in paracrinoid.

**pore.** Perforation in thecal plate but not reaching exterior; pores present in some paracrinoids, not in others.

**posterior.** Part of theca containing hydropore; sector of paracrinoid in which hydropore is located.

*recumbent. See* attached arm.

**skeleton.** All carcareous parts of paracrinoid.

*stem. See* column.

**STEREOTHECA.** Inner layer of thecal plate, in some composed of vertical laminae; stereotheca houses all of pore structure present in paracrinoids.

*subvective appendage. See* arm.

*subvective groove. See* ambulacral groove.

**suture.** Contact between two plates; boundary line marking junction of two plates.

**THECA.** Plated structure housing body of paracrinoid.

**THECAL PLATE.** One of skeletal units comprising theca.

*water pore. See* hydropore.

## CLASSIFICATION

Taxonomy of the Paracrinoidea is not yet satisfactory. The treatment of the class here merely summarizes the classification that has been developed to date.

The paracrinoids that were described by Billings(18) in 1854 later were simply assigned by him to the "Cystideae" along with such cystoids as *Glyptocystites* and *Pleurocystites*. For nearly half a century, the paracrinoids were not differentiated from other pelmatozoans. Then Bather (9) created the families Comarocystitidae and Malocystitidae, which he placed in the order Rhombifera of the class "Cystidea." He defined the two families as follows:

> Fam. Comarocystidae. Thecal plates numerous, indefinite, with strong radial structure of stereom, but no pore-rhombs. Brachioles branched; columnals uniserial.
>
> Fam. Malocystidae. Thecal plates numerous, indefinite, radiately folded, no rhombs. Food grooves on exothecal processes pass over theca and bear brachioles.

It will be noted that the arms are called by Bather the "brachioles" in the Comarocystitidae and the "exothecal processes" in the Malocystitidae. According to this classification, the two families have in common numerous thecal plates of irregular arrangement and both lack pore rhombs; they differ in ambulacral arrangement.

In defining the Carpoidea, Jaekel (70) separated out one order, named Eustelea, to contain the paracrinoids. He distinguished those with attached arms as the suborder Varicata and those with free arms as the suborder Brachiata. This system is retained here as the best that has been proposed to date. In addition, Jaekel (70) distinguished the family Amygdalocystitidae, which he differentiated from the Malocystitidae by the presence of unbranched arms.

Foerste (47) was the first to study intensively the morphology of paracrinoids. He examined *Comarocystites* in particular, and compared its pore structure with that of *Amygdalocystites* and *Canadocystis*. Despite his contributions to morphology, Foerste offered little on taxonomy except to state that *Comarocystites* and its allies, because of their arm structure, were not normal cystoids.

In 1918, in his revision of the classification of pelmatozoan echinoderms, Jaekel (71) assigned *Malocystites* to the questioned order Deviata of the subclass Eocrinoidea of the class Crinoidea. As related forms, he mentioned *Amygdalocystites* and *Comarocystites*. Under the latter, he expressed doubt about position, and suggested that the uniserial condition of the ambulacral system, if established, might open possibilities of relationship to the "higher" Crinoidea, rather than Eocrinoidea. Evidently Jaekel was unaware of Foerste's work published two years previously; this would not be surprising, for the time was during World War I.

Bassler (5) and Bassler & Moodey (7) reverted to certain of Bather's (9-12) concepts of pelmatozoan classification. The class Cystoidea was maintained as a greatly expanded taxon. In the order Amphoridea were placed the families Malocystitidae and Comarocystitidae. *Amygdalocystites* was relegated to the Malocystitidae. Hence, no notice was taken of either Jaekel's (70) separation of these forms from the cystoids or his creation of the family Amygdalocystitidae. The taxonomy was not discussed in the two publications.

Regnéll (99) introduced the class Paracrinoidea, to which he assigned with certainty only *Comarocystites, Amygdalocystites,* and *Canadocystis,* defining the new class as follows:

> A class of Pelmatozoa, the plate-system of which is not affected by polymeric symmetry and shows no differentiation into a calycinal and a tegminal portion; the exothecal subvective skeletal appendages are developed as uniserial brachia (free or recumbent) bearing uniserial pinnulae; a sub-epithekal pore-system is present in typical forms.

Bassler (6) described numerous pelmatozoans, including paracrinoids. Unfortunately, his diagnoses tend to be cryptic and his illustrations leave details to be desired. Many of the characteristics described in the fossils are insignificant and many diagnostic features are omitted. Restudy is needed.

Characteristics of paracrinoid genera are listed in Table 1, in which genera are listed in order of geologic appearance. As shown in figures in the Systematic Descriptions, remarkable resemblances exist between the thecal plates of *Comarocystites* and Bassler's *Sinclairocystis*. They suggest that ornamentation (or external form) of thecal plates may have suprageneric value. In Table 2, therefore, genera are grouped according to plate ornamentation.

The classification adopted in the *Treatise* is based on Jaekel's (71) concept of the importance of the manner in which arms are attached. In Table 3, the grouping of genera follows the taxonomy and offers a simple key for practical identification. It will doubtless be modified when paracrinoids are better understood.

TABLE 1. *Characters of Paracrinoid Genera.*

| Genera | Shape of Theca | *No. Plates | Arms | Branching | Pore System | Plate Surface | Age |
|---|---|---|---|---|---|---|---|
| *Malocystites* | globular | 30 | attached | both | ? | smooth | Chazy. |
| *Canadocystis* | globular | 30 | attached | none | none | smooth | Chazy. |
| *Wellerocystis* | ovate | 40 | attached | one | ? | smooth | Blackriv. |
| *Schuchertocystis* | ovate | 35 | free | ? | lamellae? | smooth | Blackriv. |
| *Sinclairocystis* | globular | 30 | attached | none | ? | concave | Blackriv. |
| *Comarocystites* | ovate | 150 | free | ? | lamellae in rhombs | concave | Blackriv. |
| *Amygdalocystites* | biconvex | 90 | attached | none | rad. ridges, marg. pores | ridged | Trenton. |
| *Billingsocystis* | globular? | 175 | free | ? | ? | ridged | Trenton. |

* Typical or average number of plates.

TABLE 2. *Grouping of Paracrinoids According to Plate Ornamentation.*

| | | | |
|---|---|---|---|
| Concave; centers smooth, the margins elevated as flat rims bearing quadrate pits or punctae | Arms attached | | *Sinclairocystis* |
| | Arms free | | *Comarocystites* |
| Convex; central boss or umbo from which ridges radiate to the corners | Arms attached | | *Amygdalocystites* |
| | Arms free | | *Billingsocystis* |
| Convex; smooth, papillose, or tuberculate, no radial elements | Arms free | | *Schuchertocystis** |
| | Arms attached | Both arms branched | *Malocystites* |
| | | One arm branched | *Wellerocystis* |
| | | Neither arm branched | *Canadocystis* |

* Some doubt persists as to the original surface of thecal plates; holotype (only specimen known) may be weathered, to judge from BASSLER'S (6) description and figures.

TABLE 3. *Grouping of Paracrinoids According to Character of Arms.*

| | | | | |
|---|---|---|---|---|
| Order VARICATA: arms attached | Family Malocystitidae: arms branched | Both branched | | *Malocystites* |
| | | One branched | | *Wellerocystis* |
| | Family Amygdalocystitidae: arms unbranched | Theca compressed | | *Amygdalocystites* |
| | | Theca globular | Plates convex | *Canadocystis* |
| | | | Plates concave | *Sinclairocystis* |
| Order BRACHIATA, Family Comarocystitidae: arms free | Thecal plates few | | | *Schuchertocystis* |
| | Thecal plates numerous | Plates concave | | *Comarocystites* |
| | | Plates radiate | | *Billingsocystis* |

# SYSTEMATIC DESCRIPTIONS

## Class PARACRINOIDEA Regnéll, 1945

[Paracrinoidea Regnéll, 1945, p. 37] [=Eustelea Jaekel, 1900, p. 673; Deviata Jaekel, 1918, p. 27]

Calcareous plates encasing body constituting a theca, not differentiated into dorsal calyx and ventral tegmen; thecal plates variable in number, irregularly arranged, those of some species provided with pore structures in inner layer; theca invariably anchored by column of thin uniserial disc-shaped columnals. Ambulacral system made up of uniserial arms bearing uniserial pinnules. Arms may be free or attached on thecal surface, not more than four arms known in any species, although one or more arms may branch; ambulacral grooves covered by tiny plates, may not extend to ends of all pinnules. Hydropore present in some forms, not found in others; gonopore reported in some, not definitely established. Many forms with periproct opposite columnar facet and peristome offset to one side; periproct provided with anal pyramid. *M. Ord.*

Regnéll (99) first set these echinoderms apart as a distinct class, although the taxon was essentially constructed by Jaekel (70) when he placed the genera in his order Eustelea of the class Carpoidea. It seems preferable to use the name proposed by Regnéll.

The late erection of the class may be attributed to the poor state of knowledge concerning these pelmatozoans. Contrasts with other groups were not sufficiently clear to suggest that paracrinoids would be better fitted into the taxonomic pattern as a new class. Even now, essential information on many genera is not available.

The paracrinoids differ from crinoids in having a theca of irregular plates, from cystoids in having uniserial appendages, from blastoids in lacking symmetry and hydrospires, and from "carpoids" in having a uniserial column and less strongly compressed theca. The taxon is not very well known or understood. It suffers the disadvantage of inheriting all the problem genera of pelmatozoans after the cystoids, blastoids, crinoids, "carpoids," edrioasteroids, and eocrinoids were removed. The array of known forms emphasizes the paucity of the record. The ancestors of the paracrinoids are unknown, the diversity and evolutionary trends are incompletely founded, and morphology has not been studied at all in most species. The taxonomic divisions presented here are subject to revision whenever and as soon as new, reliable information is set forth.

### *Key to Orders and Families of Paracrinoidea*

1. Arms attached to thecal surface (Order Varicata) .................................................. 2
   Arms free (Order Brachiata) .................... .................................... Family Comarocystitidae
2. Arms branched, spread out over theca ......................................... Family Malocystitidae
   Arms unbranched, two simple curved rays, together forming a sort of S ...................... .............................. Family Amygdalocystitidae

The key stresses the fact that taxonomic divisions adopted here are based on the nature of the arms. Of greater significance, one would expect, is nature of the pore system. Unfortunately, this has not been studied in the majority of paracrinoids. When it is established, however, there can be little doubt that it will provide a substantially different taxonomic grouping of the genera. Still other divisions could be made by considering first the number of thecal plates; in *Amygdalocystites,* some species have few and other species have many plates, so that the number does not seem to have much taxonomic value, at least in this genus.

## Order VARICATA Jaekel, 1900

[Varicata Jaekel, 1900, p. 674]

Arms recumbent, attached to theca. *M. Ord.*

### Family MALOCYSTITIDAE Bather, 1899

[*nom. correct.* Bassler, 1938, p. 9 (*pro* Malocystidae Bather, 1899, p. 920)]

Arms branched, spread out over theca. *M.Ord.*

#### *Key to Genera of Malocystitidae*

Both arms branched, branches spreading over theca without regular curvature .. *Malocystites*

Only one arm branched, with all branches curved toward right; unbranched arm coiled about periproct ................ *Wellerocystis*

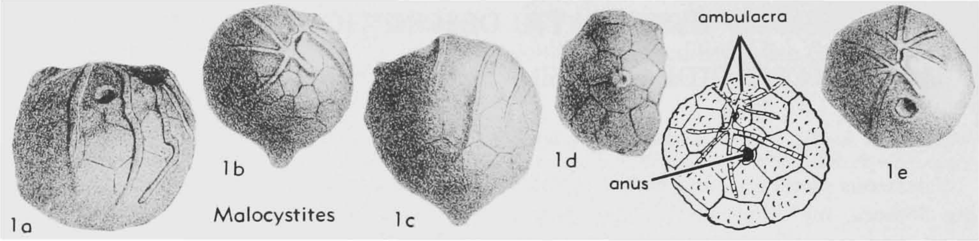


FIG. 160. Varicata (Malocystitidae) (p. S278).

**Malocystites** BILLINGS, 1857, p. 302 [**M. murchisoni;* OD] [=*Malocystis* CARPENTER, 1891, p. 27 *(nom. van.)*]. Theca globular, composed of about 30 irregularly distributed polygonal plates. Peristome consisting of transverse trough roofed by small plates, from each end of which 2 recumbent arms branch quickly, several long branches of each extending over theca without discernible pattern of curvature, arms uniserial, but distribution and nature of pinnules unknown; peristome not directly opposite columnar attachment or facet in known specimens; instead, peristome offset and periproct more nearly diametrically opposite column; thecal plates more or less smooth. [HUDSON (1916) stated, "Most specimens of *Malocystites* when rolled on a table come to rest with the food-collecting field uppermost."] *M.Ord.*, N.Am. (Que.-N.Y.).——FIG. 160,*1*. **M. murchisoni*, Aylmer F., Que.; *1a-e*, 3 lat., aboral, and oral, ×1 (Billings, 1858); *1f*, incl. oral, ×1 (70).

**Wellerocystis** FOERSTE, 1920, p. 36 [**W. kimmswickensis;* OD]. Theca ovoid, not compressed in any way, composed of about 40 polygonal plates of various sizes and shapes. Basals 3; other plates tending to be disposed in oblique rows parallel to direction of distal ends of arms; surface of plates relatively smooth, without radiate folds. Arms 2, one which remains undivided encircling periproct, other bifurcating almost immediately beyond peristome, so that the genus may be conveniently said to have 3 arms. In comparison with *Canadocystis,* this genus has added arm on left side of that opposite periproct and it has periproct on concave side of nearby arm instead of its convex side. As in *Amygdalocystites* and *Canadocystis,* curvature of arms is clockwise in oral view, and facets for pinnules are invariably on convex side of curved ambulacral grooves. Arm encircling periproct has about 5 facets; on opposite arm, left branch has about 10 and right branch about 8. Pinnules not known. Mouth elongate in direction of peristome connecting opposite arms, about 0.25 mm. wide and 1 mm. long in theca 20 mm. high. Periproct diametrically opposed to columnar facet. Hydropore and gonopore not known. *M.Ord.*, USA(Mo.).——FIG. 161,*1*. **W. kimmswickensis*; *1a,b,* lat. and oral, ×1; *1c,* plate diagram (148).

## Family AMYGDALOCYSTITIDAE Jaekel, 1900

[*nom. correct.* KESLING, herein (*pro* Amygdalocystidae JAEKEL, 1900, p. 675)]

Recumbent arms on theca unbranched. *M.Ord.*

### *Key to Genera of Amygdalocystitidae*

1. Theca almond-shaped, compressed; numerous (more than 80) plates in some species; thecal plates ornamented by central boss or umbo from which ridges radiate to corners ............................ *Amygdalocystites*
   Theca globular or slightly compressed, never almond-shaped with angular edge; plates few (seldom exceeding 50); plates not radially ridged .................................... 2
2. Plates convex; the surface smooth, slightly papillose, or tuberculate .............. *Canadocystis*
   Plates concave; centers smooth, margins adjacent to sutures elevated as flat rim bearing quadrate pits or deep punctae (not perforating full thickness of plate) ........................................................ *Sinclairocystis*

**Amygdalocystites** E. BILLINGS, 1854, p. 270 [**A. florealis;* OD] [=*Amygdalocystis* CARPENTER, 1891, p. 27 *(nom. van.); Ottawacystites* WILSON, 1946, p. 14 (type, *Amygdalocystites florealis laevis* W. R. BILLINGS, 1883)]. Theca almond-shaped (hence generic name), compressed, with sharp boundary or edge where 2 sides join. About 90-180 thecal plates, each ornamented by radial ridges extending from center to each corner; on inner surface also, plates bear radial ridges, one to each corner and, in some specimens, another to middle of each side. [FOERSTE (1916) reported that "in some specimens pores exist along the sutures between the plates, either a single pore at the middle of each side, or two pores along each side, close to the radial ridges extending to the angles of the plate. Half of each pore occurs on half of each of the adjoining plates." These pores were probably originally concealed by epitheca. The two arms extend more or less along the sharp edges of the theca and are slightly curved clockwise in oral view; therefore, the theca is not

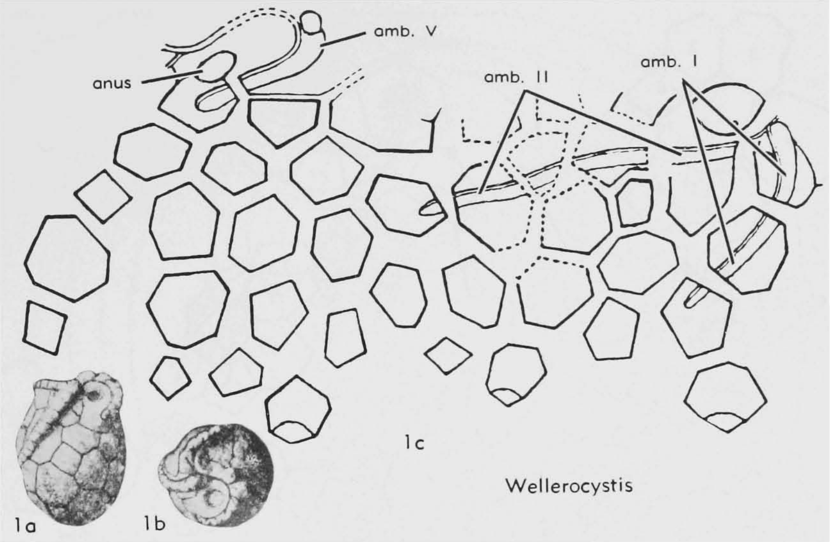


Fig. 161. Varicata (Malocystitidae) (p. *S*278).

simply biconvex but is twisted or skewed by several degrees. From each of the uniserial arms, uniserial pinnules are attached to facets on the convex side. The ambulacral extension lies facing the mouth on one of the narrower sides of the compressed pinnule. The facets supporting the pinnules are indented on the side where the branch from the main ambulacral groove passed on the base of the attached pinnule.] Periproct on convex side of nearest arm. Hydropore and gonopore not known. *M.Ord.*, N.Am.(Ont.-Que.-Ky.).——Fig. 158,*1a-h*. **A. florealis*, Hull Ls., Ont.; *1a,b*, lat., theca and fragment with pinnules, ×1 (18); *1c-e*, 3 lat., × (20); *1f*, theca with detail of plate (left) and arm (right), sl. enl. (10); *1g,h*, theca, ×1, and detail of plates, ×4 (141).——Fig. 158,*2*. *A. tenuistriatus* Billings, Hull Ls., Can.(Ont.); *2a*, lat., ×1 (18); *2b,c*, 2 views of arm, enl.; *2d*, thecal plate, enl. (20).——Fig. 158, *3*. *A. radiatus* Billings, Hull Ls., Can.(Ont.); *3a*, lat., ×1 (18); *3b*, lat., ×1 (20); *3c*, detail of plates, ×4 (141).——Fig. 158,*4*. *A. laevis* W. R. Billings, Hull Ls., Can.(Que); lat., ×4 (141).

**Canadocystis** Jaekel, 1900, p. 675 [**Malocystites barrandi* Billings, 1858, p. 67 (=*M. barrandei*, *nom. correct.* Kesling, herein); OD] [=*Sigmacystis* Hudson, 1911, p. 254 (type, *Malocystites emmonsi* Hudson, 1905)]. Theca globose or ovoid to subpyriform, basal part somewhat produced. Theca composed of about 30 to 40 polygonal plates of variable sizes, shapes, and arrangement, many thecae containing a few small diamond or triangular plates, most other plates irregularly pentagonal, hexagonal, or septagonal; basal plates 3, of which 1 is conspicuously smaller than other 2; theca variously ornamented by few scattered umbos on larger plates with connecting ridges and by granulations on all plates; large umbo between periproct and base in *C. emmonsi*. Finer radiating ridges may branch and cross sutures to form very fine reticulations. Inner surface of thecal plates relatively smooth, lacking pores or lamellae of any kind. Mouth not directly opposite columnar attachment; in *C. emmonsi*, periproct, opposite column and mouth strongly offset to one side; in *C. barrandei*, eccentric position of mouth not as strongly emphasized. Peristome slightly elevated in *C. barrandei*, set upon neck in *C. emmonsi*. The 2 arms and peristome combined forming an S, called by Hudson (149) the "sigma." Oral region of theca made up of 4 main plates or orals: 2 small plates in posterior and anterior positions (normally slightly offset clockwise around mouth), and 2 large semicircular plates filling each side of peristomial region, each bearing one arm. Arms uniserial, plates decreasing in size distally; each plate with its outer border convex, so that arm has scalloped edge. From each C-shaped ambulacral groove, short extensions on outer side of curve lead to facets for attachment of pinnules, which are unknown. Periproct rather small, set high on theca, bordered by 4 or 5 plates. Hydropore probably small roughened mound at junction of 3 plates: small posterior oral, large arm-supporting oral to right, and plate of circlet of 6 supporting the orals (one which curves aborally to the periproct). Gonopore reported to be small perforation through posterior oral, not said or shown to lie along a suture, as does the gonopore of cystoids. Column very small; column of *C. emmonsi*, at least, bent rather abruptly backward next to theca. [According to

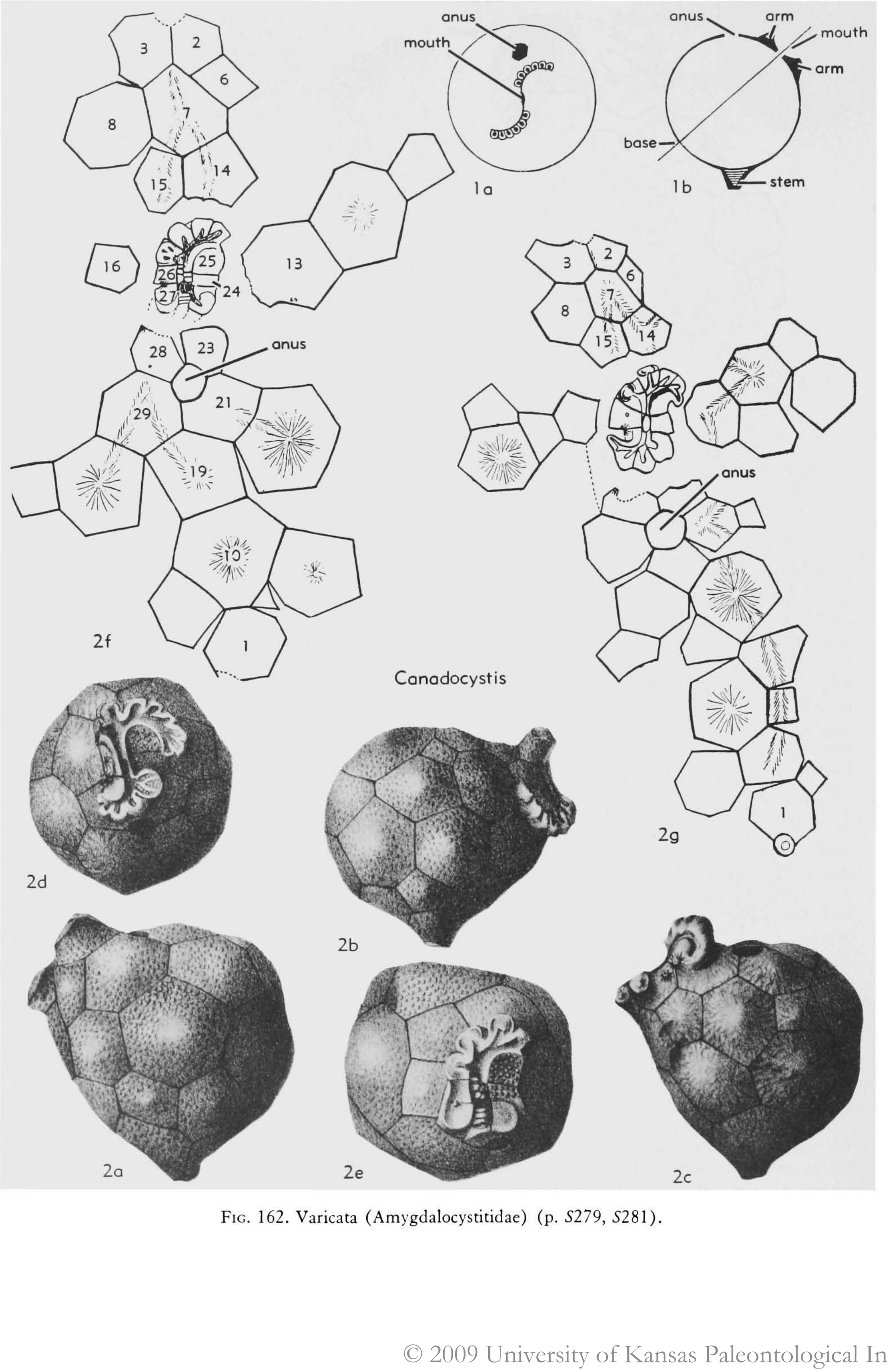


FIG. 162. Varicata (Amygdalocystitidae) (p. *S*279, *S*281).

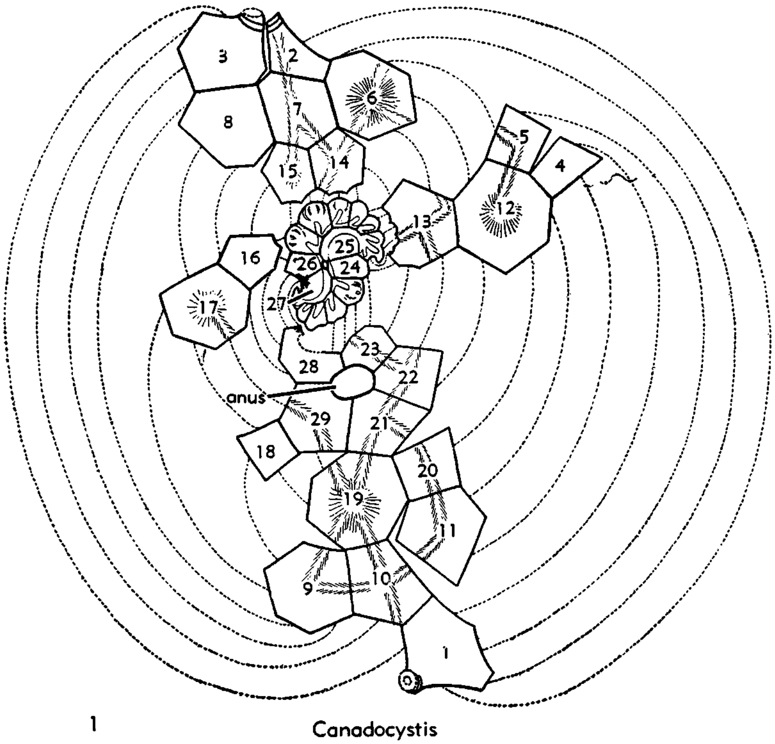


FIG. 163. Varicata (Amygdalocystitidae) (p. *S*279, *S*281).

HUDSON (149), "The stem appears to have been short and used perhaps as an anchor but not for complete support"; he also suggested that the ancestors of these paracrinoids "were once supported by the stem alone and had their arms in a normal position, but that descendants with weak stems often found themselves let down to the ocean floor and had to make shift to live under adverse conditions. Increased growth of the posterior plates or decreased growth of the anterior plates would have brought the arms again uppermost and given rise to a form like that shown here."] In proximal section of column, lumen is round and about half diameter of columnals. Species of this genus are marked by strong individual variations in plate arrangement, number of plates, plate shapes, ornamentation, and other features. *M.Ord.*, N.Am.(Que.-N.Y.).——FIG. 162,*1*. **C. barrandei* (BILLINGS), Aylmer F., Que.; *1a,b,* oral diagram and vert. sec. (20).——FIG. 162,*2*; 163,*1*. *C. emmonsi* (HUDSON), Chazyan, N.Y.; 162,*2a-e,* 3 lat. and 2 oral, X4 (149); 162,*2f,g,* 2 plate diagrams (149); 163,*1*, plate diagram with dotted lines connecting adjacent edges (149).

**Sinclairocystis** BASSLER, 1950, p. 276 [**S. praedicta*; OD]. Theca irregularly ovoid, composed of about 30 to 60 plates according to species, 3 basals and 4 plates bordering periproct in all specimens described; plates concave, with edges raised in rim or margin which contains very numerous rectangular deep pits (*S. praedicta, S. angulata*) or fewer circular pits (*S. sulphurensis*), which may not penetrate into "body cavity," as suggested by STRIMPLE (1952), but instead may constitute well-developed ornamentation (evidently true for *Comarocystites*); interior of thecal plates unknown. Two arms, both attached to theca, differently developed, one arm passing close along left side of periproct, looping clockwise (as seen orally), and in some species terminating high on theca; other arm longer, nearly vertical, extending in opposite direction from first, and nearly or quite reaching column in some species; each arm composed of relatively thick brachials, with pinnule attached to each brachial. Peristome not as strongly protuberant as arms, more or less expressed as saddle. Hydropore apparently a small pustule set very close to peristome. Gonopore unknown. Periproct filled by anal pyramid, set nearly diametrically opposite column. [In *S. sulphurensis,* the anterior side has fewer and much larger thecal plates than the posterior, with only 2 or 3 plates between the basals and

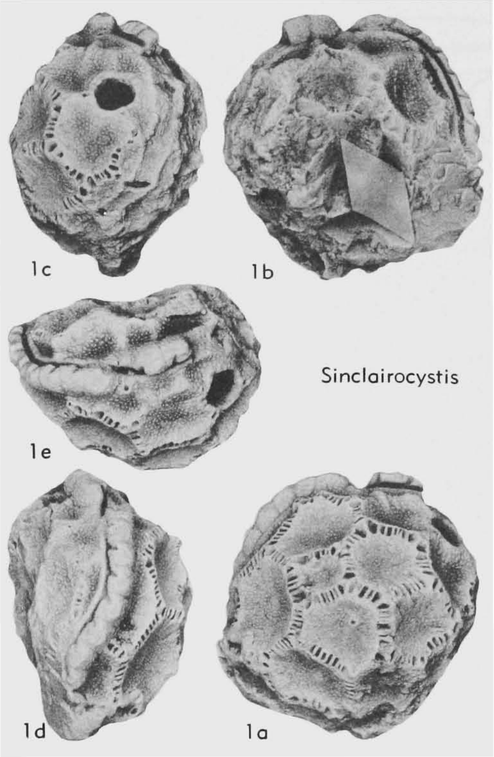


FIG. 164. Varicata (Amygdalocystitidae) (p. *S*281-*S*282).

circumperiproctal plates]. *M.Ord.*, USA(Okla.).——FIG. 164,*1*. **S. praedicta*, Bromide F.; *1a,b*, side with hydropore and opposite side; *1c*, side with anus showing partly exfoliated arm at right; *1d*, side showing longer arm; *1e*, oral view showing arms and small hydropore; all ×2 (Kesling, n).——FIG. 165,*1*. *S. sulphurensis* STRIMPLE, Bromide F.; *1a-d*, lat. views, ×4 (152).——FIG. 165,*2*. *S. angulatus* STRIMPLE, Bromide F.; *2a-d*, lat. views, ×2.5; *2e*, oral view, ×2.5 (152).

## Order BRACHIATA Jaekel, 1900

[Brachiata JAEKEL, 1900, p. 276]

Arms free above their proximal attachment to theca. *M.Ord.*

### Family COMAROCYSTITIDAE Bather, 1899

[*nom. correct.* BASSLER, 1938, p. 9 (*pro* Comarocystidae BATHER, 1899, p. 920)]

Characters of order. *M.Ord.*

At present the order Brachiata is undivided. Until the basis for paracrinoid classification is more firmly decided, it is not advisable to introduce more families.

### *Key to Genera of Comarocystitidae*

1. Thecal plates few (about 30 to 40) ............ ........................................................ *Schuchertocystis*
   Thecal plates numerous (more than 70) .... 2
2. Thecal plates deeply concave, their margins punctate (at least in worn specimens) .. ........................................................ *Comarocystites*
   Thecal plates highly irregular polygons, with radiating ridges to corners ............ ........................................................ *Billingsocystis*

**Comarocystites** BILLINGS, 1854, p. 268 [**C. punctatus*; OD] [=*Comarocystis* CARPENTER, 1891, p. 27 (*nom. van.*)]. Theca obovate, some attaining length of 75 mm., composed of about 150 plates (in type species) to about 65 (in *C. shumardi*); as many as 15 plates in the basal circlet, number and shape of plates variable, only those around peristome and periproct exhibiting considerable degree of fixity in number, position, and general outline. [According to FOERSTE (47), in the type species "certain tendencies may be observed even among these other thecal plates. For instance, the plate directly below the middle of the anal pyramid, but not in contact with the latter, is pentagonal in form, and has its upper angle inserted between the two plates forming the lower border of the pyramid. Directly beneath this pentagonal plate is a series of hexagonal plates which, instead of forming a strictly vertical row, are arranged along a line which curves moderately toward the front on approaching the base of the theca. Parallel to this series of plates, on its anterior side, are similar series of hexagonal plates, causing the anterior side of the theca to present the appearance of diagonally intersecting rows, with the angles of the thecal plates directed toward the top of the specimen. On the posterior side of the theca, a similar tendency toward the arrangement of plates in rows causes one of the sides of the hexagonal plates, rather than one of its angles, to face the top of the specimen."] Plates bordering peristome (in *C. punctatus*) include 2 on anterior side, about equal in size, their common suture located about midway on side of peristome and perpendicular to it, right anterior plate more or less obliquely hexagonal, and left posterior plate pentagonal; posterior edge of peristome also bordered by 2 plates, that at right hexagonal, occupying about 0.7 of border, much larger than small, quadrangular plate at left, right plate containing part of the hydropore. Periproct bordered by 5 thecal plates, 2 on aboral side, 2 lateral, and 1 inserted between periproct and nodular facets for right pair of arms; plate on right side invariably largest. Exterior surface of plates deeply concave, inner surface more or less stellately convex, cross sections perpendicular to mid-points of sutures showing that inner surface presents almost straight line from center of one plate to center of next, but toward angles where 3 plates meet, inner surface curves outward so strongly that deep triangular pits mark these junctions on interior; epithecal layer of plates thin and nonporous; greater part of stereotheca forming vertical lamellae which are not radial but perpendicular to sutures, lamellae in each sector of given plate being thus parallel and filling triangular space; they are continuous with lamellae of adjacent plates, forming rhombs on interior of theca; where epitheca is weathered away, short lunate pores are revealed in outermost part of stereotheca, extending parallel to epitheca and just beneath it, expressed on weathered stereotheca as short lunate grooves, of which concave sides of each pair face each other; presence of these pores may be indicated on exterior of epitheca by short lunate ridges; 3 or 4 series of pores may occur between center and sides of plate, the pairs of different series alternating in position, each lunate pore connected near its distal end with circular pore or tube leading to an interlamellar space; pores of pair invariably connecting with different spaces, being separated by one lamella. Peristome con-

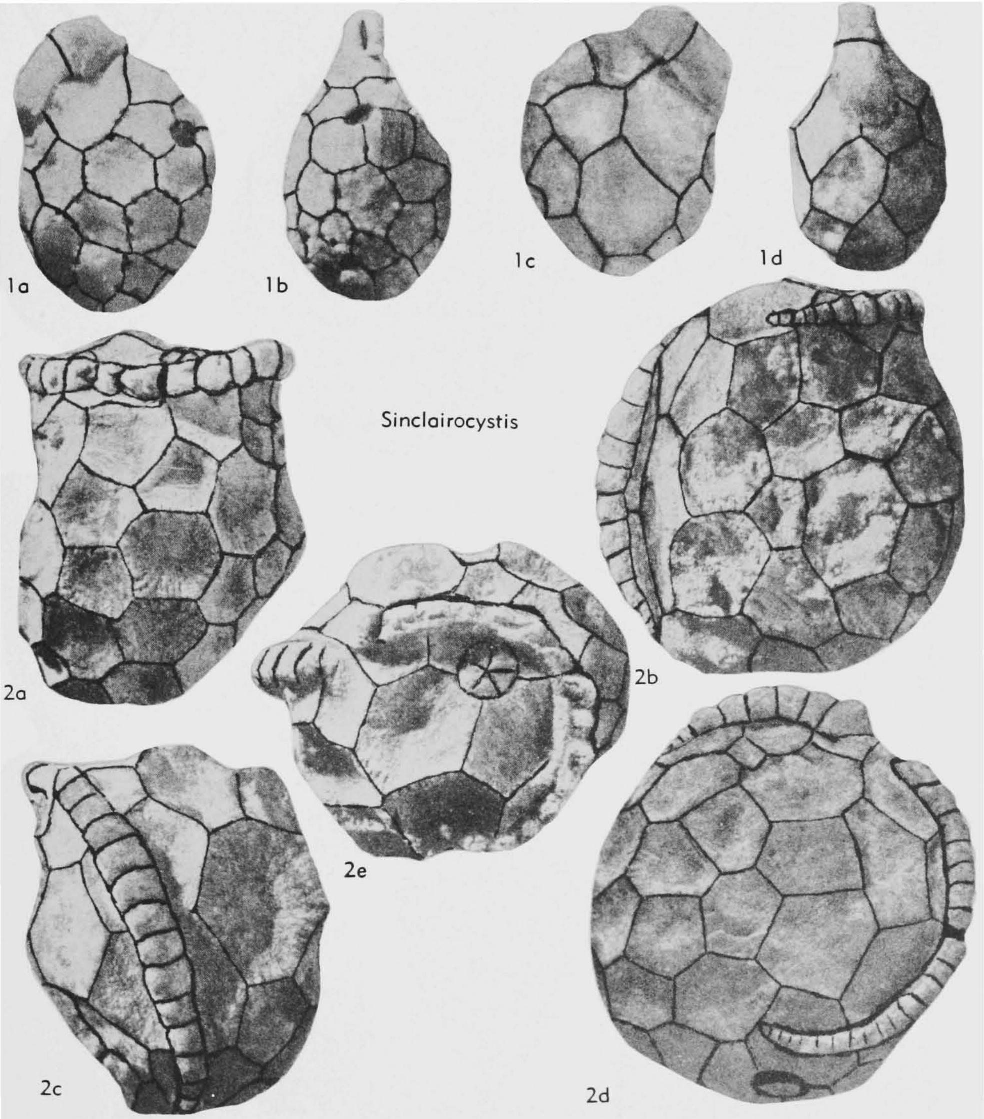


FIG. 165. Varicata (Amygdalocystitidae) (p. S281-S282).

stituting a "transverse apical food-groove" (FOERSTE, 1916), covered by biserial covering plates meeting along center line to form acute ridge. Mouth a small circular or oval opening

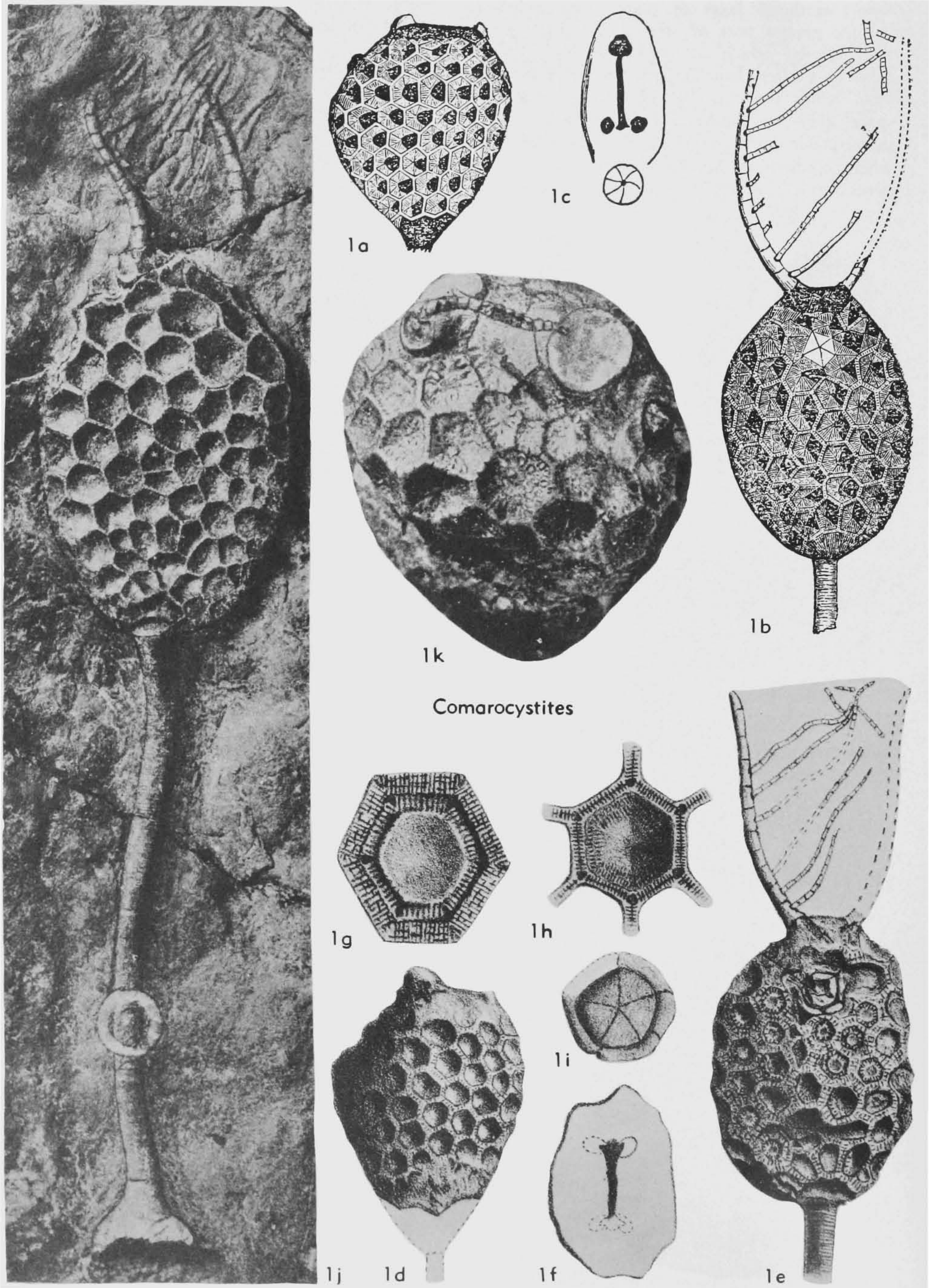


FIG. 166. Brachiata (Comarocystitidae) (p. S282-S287).

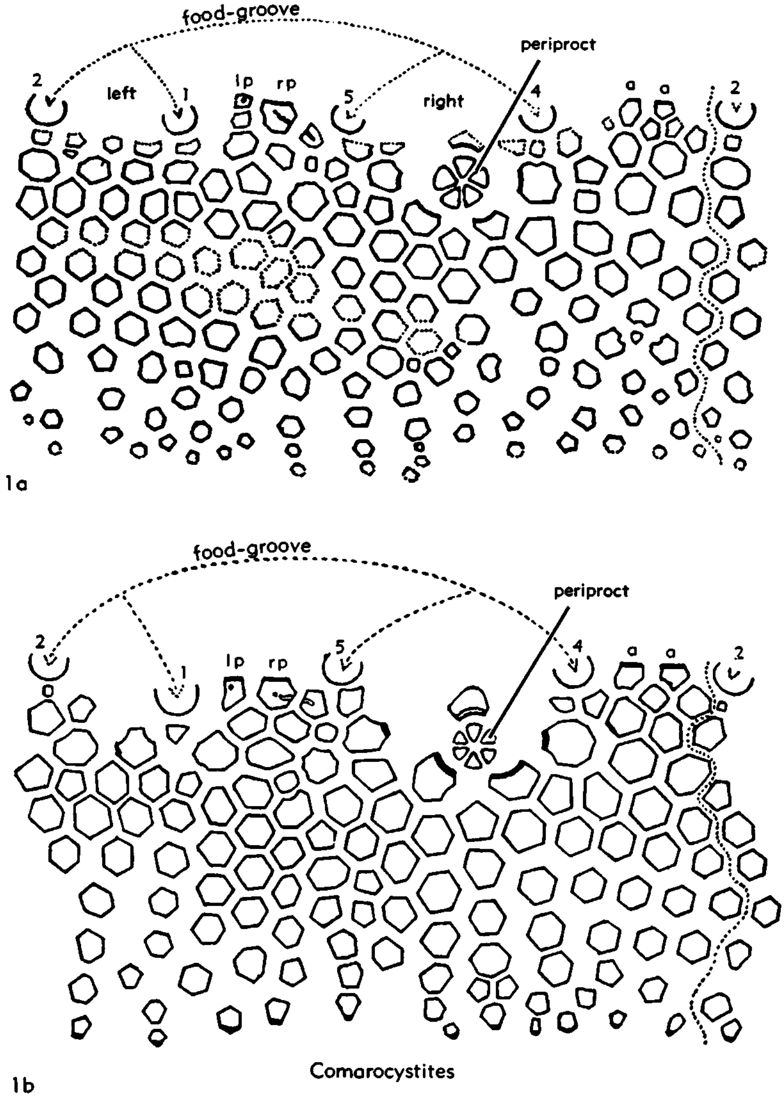


Fig. 167. Brachiata (Comarocystitidae; two plate diagrams) (p. S282-S287).

in bottom of groove at middle of peristome, ambulacral grooves at either side bifurcating in short branches that extend to 2 pairs of arm facets, each pair of facets constituting a single protuberance at one end of peristome, bilobed, with ambulacral groove rising from point of bifurcation onto the facet. Arms 4, uniserial, tapering gradually, estimated to have been 1.5 times height of theca, arm composed of at least 12 brachials, each of which bears single pinnule on its left side (as viewed orally); all brachials above first slightly compressed from front to back, length of each brachial about 1.5 times its lateral diameter. Facets for pinnules concave, margins distinctly raised, set slightly above middle of brachial. Pinnules uniserial, some attaining length nearly equal to half of theca height; pinnulars nearly equal in size, all except initial 2 or 3 in each pinnule strongly flattened transversely; covering plates on pinnules small, quadrangular. [The right posterior arm of one specimen exhibits an ambulacral groove only on the proximal part of the first brachial; not enough arms are preserved to venture an opinion on whether this is normal or abnormal.] No trace of ambulacral grooves observed on pinnules, and no indentation in pinnular facet to indicate its extension onto basal pinnular. [This is not decisive on specimens studied; a well-developed ambulacral system may have extended onto the pinnules without conspicuous grooves.] Periproct filled by anal pyramid of 5 or 6 triangular plates, which have general subglobose form with flattened apex. Hydropore expressed as faint narrow groove apparently representing aperture of thin slitlike stone canal, located on crest of narrow, sinuous ridge extending from center of larger posterior oral plate to center of adjacent plate on its aboral right border, some specimens with minute but distinct pit just beyond left end of hydropore-bearing ridge, but since most

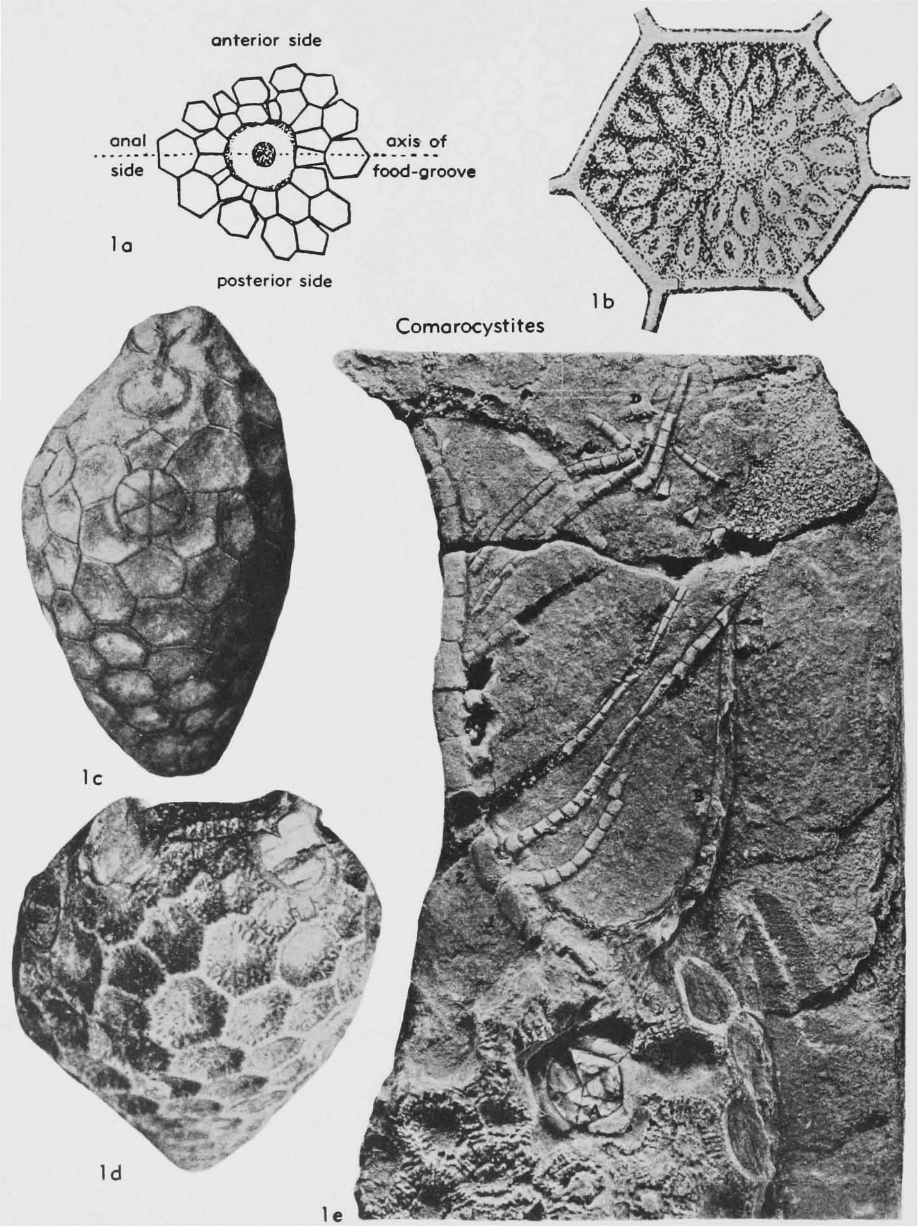


Fig. 168. Brachiata (Comarocystitidae) (p. S282-S287).

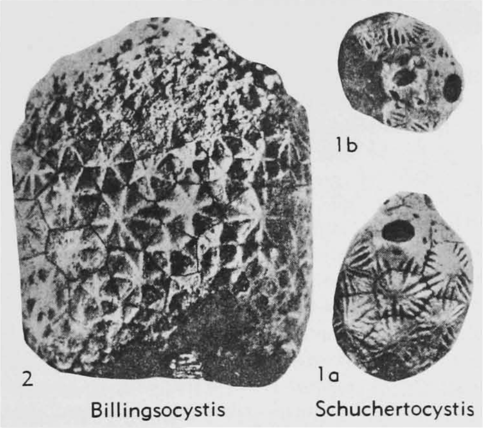


Fig. 169. Brachiata (Comarocystitidae) (p. S287-S288).

specimens lack this structure, interpretation of it as a gonopore is doubtful. The column shown by complete specimen of type species 108 mm. long (attached theca 65 mm. high) and about 5 mm. in diameter near middle, base expanded to form circular attachment disc or holdfast about 17 mm. in diameter; columnals very thin, circular, with lumen about 0.25 of diameter and with flat surface radially striate; exterior of column ornamented by minute granules arranged quincuncially in diagonally intersecting rows. *M.Ord.*, N.Am. (Ont.-Mo.).——Fig. 159,*1*. *C. shumardi* Meek & Worthen, Kimmswick Ls., USA(Mo.); *1a-d*, 4 lat. sl. incl., ×1 (47); *1e,f*, lat. and aboral, ×1 (151); *1g,h*, weathered specimen and isolated plate, ×1 (148); *1i*, weathered surface showing internal structures, enl. (47); *1j*, plate diagram (47).——Fig. 159,*2*. *C. obconicus* Meek & Worthen, Kimmswick Ls., USA(Mo.); *2a,b*, lat. views, ×1 (151).——Fig. 166,*1*; 167,*1*; 168,*1*. *_C. punctatus_, Hull Ls., Can.(Ont.); 166,*1a-c*, 2 lat. and oral, ×1 (18); 166,*1d-f*, 2 lat. and oral, ×1 (20); 166,*1g-i*, 2 plates and anal pyramid, enl. (20); 166,*1j*, nearly complete specimen, ×0.8 (47); 166,*1k*, incl. lat., ×3 (47); 167,*1a,b*, 2 plate diagrams (47); 168,*1a*, diagram of plates in aboral region; 168,*1b*, thecal plate, ×8; 168, *1c,d*, 2 lat., ×2.4 and ×3; 168,*1e*, part of theca with attached arms, ×2 (47).

**Billingsocystis** Bassler, 1950, p. 274 [*_B. invaginata_; OD]. Theca ovoid to oblong, base invaginated, sides somewhat compressed in only specimen described, composed of about 175 small polygonal plates disposed in 8 or 9 irregular circlets. Ambulacral system very imperfectly known, described by Bassler (1950) as: "Food-groove system confined to a single short, transverse, relatively deep, semilunate groove. No branches of this groove and no facets for the attachment of arms are present." [Inasmuch as attached arms of paracrinoids are either preserved or leave distinct marks on the thecal plates, it is presumed here that the arms of this genus are free.] Strong ridges radiating from center of each thecal plate to its corners, number of rays in each star thus formed equal to number of sides of plate on which it occurs; inner surface of thecal plates unknown. Periproct small, situated near peristome. Column composed of thin columnals. *M.Ord.*, USA(Ky.).——Fig. 169,*2*. *_B. invaginata_; lat., ×2 (6).

**Schuchertocystis** Bassler, 1950, p. 274 [*_S. radiata_; OD]. Original description stated: "Theca resembling a small *Amygdalocystites* but lacking recumbent arms. The base consists of three plates, two on the antanal and one on the anal side. Plate sutures crossed at right angles by long slits in the mesostereom that shorten at their passage through the hypostereom into elliptically elongate pores." [The similarity to the theca of *Amygdalocystites* is difficult to envisage. *Schuchertocystis* has only slight lateral compression of the theca with exposure of a few coarse parallel grooves perpendicular to each suture extending from one plate to another, the arms appearing to have been free. In contrast, *Amygdalocystites* has strong lateral compression with a sharp edge between the 2 halves; plates marked by radial ridges; and arms attached. Each genus has about 30 thecal plates. *Schuchertocystis* resembles *Canadocystis* and some other paracrinoids in location of the periproct, rather than peristome, nearly opposite the columnal attachment. The main problem of interpretation is the nature of the thecal plates. If the deep sets of grooves are indeed in the stereotheca, then all epitheca is destroyed and the nature of the ornamentation cannot be determined.

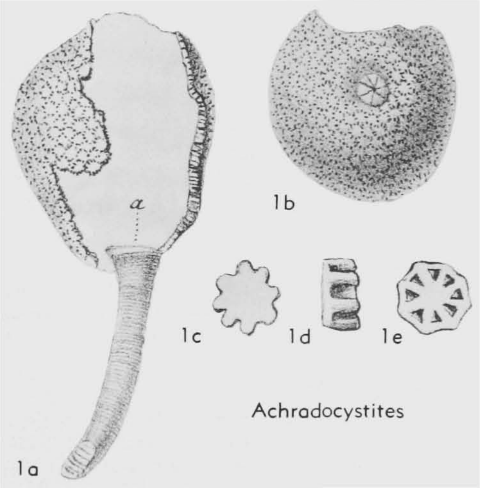
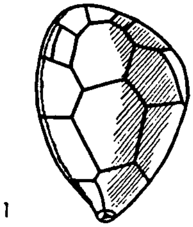


Fig. 170. Class, Order, and Family Uncertain (p. S288).



**Platycystites**

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

The illustrations show nothing of the "elliptically elongate pores" mentioned by BASSLER.] *M.Ord.*, USA(Tenn.).——FIG. 169,*1*. **S. radiata*; *1a,b*, lat. and oral, ×2 (6).

## Order and Family UNCERTAIN

**Achradocystites** VON VOLBORTH, 1870, p. 9 [**A. grewingkii*; OD] [=*Achradocystis* HAECKEL, 1896, p. 56 *(nom. van.)*]. Theca composed of very numerous small plates of various sizes, each strongly marked by radial ridges to its corners and (if one may credit certain figures) by a marginal rim; edges of plates scalloped, perhaps by pores inward reaching along sutures, scalloped edges more apparent on inner surface than exterior. [VON VOLBORTH (1870) reported that on the inner surface the plates lay with "tooth against tooth," and "canal against canal," which is interpreted to mean that there were pores along the sutures.] Theca (as preserved) incomplete, but apparently pear-shaped, with smaller end attached to column; periproct filled by anal pyramid, composed of 7 triangular plates; peristome unknown. Column round, consisting of numerous thin columnals, not much flared at junction with theca. No traces of arms discerned in preserved portion, indicating that perhaps arms were free (inasmuch as some traces of attached arms could be expected). *U.Ord.*, Eu.(Est.).——FIG. 170,*1*. **A. grewingkii*; *1a,b,* lat. and anal, ×1; *1c-e,* int., side, and ext., thecal plate, ×4 (137).

**Platycystites** MILLER, 1889, p. 272 [**P. faberi*; OD] [=*Platycystis* BATHER, 1900, p. 51 *(nom. van.)*]. Theca, if such it be, subpyriform, tapering to scar of attachment as for a column; form somewhat compressed, compared originally to a peach seed with "a narrow rim on the border," specimen reported to be worn, with no traces of openings; 3 plates adjoining attachment scar, others large and irregularly polygonal, each said to be filled with minute pores. [The age of this fossil is doubtful, since MILLER (1885) reported that "it was received by Charles Faber among a lot of fossils from the Kaskaskia Group in the southern part of West Virginia, but as no cystideans have ever been found above the Lower Devonian, and as the specimen is worn as if it had been drifted, the probability is that it belongs to the Silurian rocks." BATHER (1900) tentatively classified the specimen as "a worn Anomalocystid of indeterminable affinities," but later (1913) suggested that it could be columnar appendage of *Rhipidocystis* (L.Ord.-M.Ord.). BASSLER & MOODEY (1943), without question, recorded *P. faberi* as occurring in the Heiskell Shale, of Chazyan(M.Ord.) age. The curious lack of thecal openings in a completely plated form suggests that BATHER's interpretation of it as a columnar appendage of some pelmatozoan may be correct.] *?M.Ord.*, USA(Va.).——FIG. 171,*1*. **P. faberi*; lat., ×1 (12).

## REFERENCES

Most references cited in this chapter relate to the list given under Cystoidea, with index numbers used in that list. Additional references for paracrinoids are numbered 148 to 152.

**Foerste, A. F.**

(148) 1920, *The Kimmswick and Plattin Limestones of northeastern Missouri:* Denison Univ. Bull., Jour. Sci. Lab., v. 19, p. 175-224, pl. 21-23.

**Hudson, G. H.**

(149) 1905, *Contributions to the fauna of Chazy Limestone on Valcour Island, Lake Champlain:* N.Y. State Museum, Bull. 80, Paleont. 10, Rept. State Paleontologist 1903, Appendix 3, p. 270-95, pl. 1-5, 7 text fig.

(150) 1916, *Some notes on fossil collecting, and on the Edriosateroidea* [*sic*]*:* Ottawa Naturalist, v. 30 (Trans. Ottawa Field-Naturalists' Club, v. 32), p. 21-25, 40-46.

**Meek, F. B., & Worthen, A. H.**

(151) 1868, *Fossils of the Trenton Group:* in Meek & Worthen, Palaeontology of Illinois, Illinois Geol. Survey, v. 3, p. 291-300.

**Strimple, H. L.**

(152) 1952, *Two new species of Sinclairocystis:* Washington Acad. Sci., Jour., v. 42, no. 5, p. 158-60, fig. 1-4.

# EDRIOBLASTOIDS

By Robert O. Fay
[Oklahoma Geological Survey]

## INTRODUCTION

Primitive attached echinoderms which different authors have variously associated with blastoids, cystoids, and edrioasteroids now are considered to belong in a class of their own, named Edrioblastoidea (Fay, 1962). The fossils occur in the Middle Ordovician of Canada, and except for the importance of their known morphological features might be relegated to an *incertae sedis* pigeonhole on the ground of extreme rarity. Only two specimens have been collected and one of them subsequently has been lost. The type specimen, which belongs to the Geological Survey of Canada, is well preserved and reasonably complete, satisfactorily showing all essential external features at least. The theca is modest in size, measuring 21 mm. in height and 19 mm. in width. It displays regular pentameral symmetry and a blastoid-like form, with evenly conical aboral side and strongly rounded oral side.

## MORPHOLOGY

The theca is composed of 20 main plates arranged in four circlets, from the stem attachment upward consisting of five basals, five radials, five deltoids, and five orals (Fig. 172). Elements of each circlet alternate in position with those of adjoining ones. In addition, numerous small plates occur. These include variously shaped and somewhat unevenly disposed infradeltoid plates located interradially and a host of regular, nearly even-sized ambulacral plates in double rows within each ambulacrum. The infradeltoids are interposed between the radial limbs and deltoids, supplemented on the anal side by many small plates (up to 30) surrounding the anal orifice (Fig. 173,*2*). The ambulacral cover plates are parallel-sided elongate ossicles which extend obliquely in adoral inward direction from outer margins of the subpetaloid ambulacral tracts, those of opposed rows meeting in a zigzag line along the longitudinal axis of the ambulacrum.

All of the main plates, and to some extent the infradeltoids also, are characterized by relatively broad and deep infolds which tend to cross plate sutures at right angles (Fig. 172, 174). They are somewhat irregular and a majority have short branched extensions laterally and terminally. Some of the infolds coincide with sutures, running along them in part of their course. These inflections of thecal stereom are not associated with slits or pores leading to the interior of the theca and seem

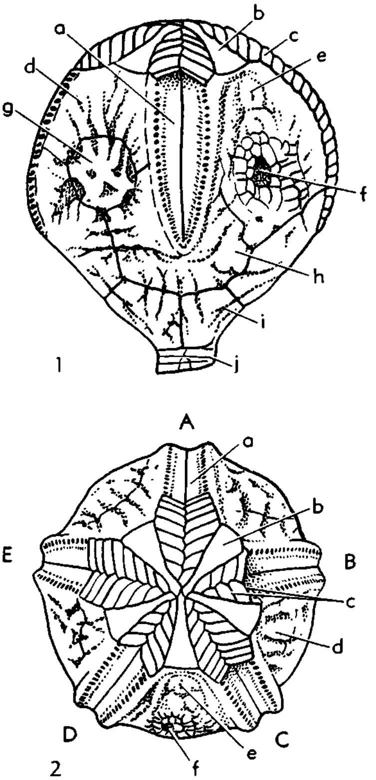


Fig. 172. Morphological features of edrioblastoids—oral *(1)* and *D*-ray *(2)* views of theca of **Astrocystites ottawaensis,* ×2 (reconstr.) (1). [Explanation: *a,* part of ambulacrum with cover plates removed, showing marginal rows of pores in floor plates; *b,* oral plate; *c,* cover plates; *d,*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

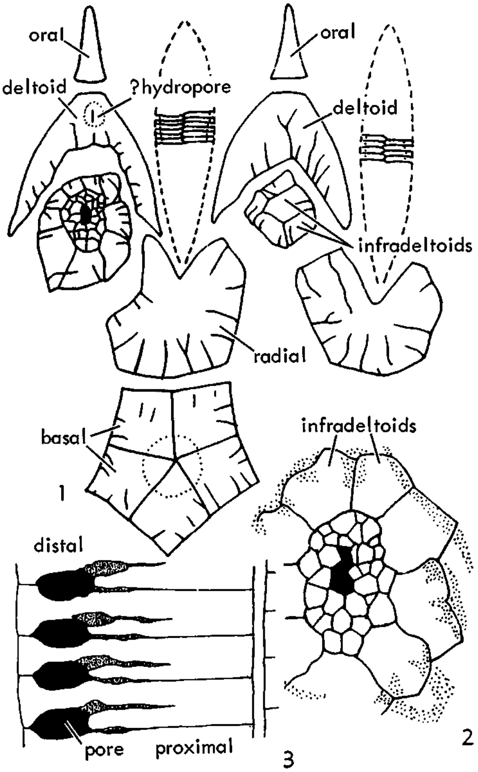


FIG. 173. Morphological features of edrioblastoids—**Astrocystites ottawaensis*.——*1*. Partial plate layout, ×2.5 (based on HUDSON, 4).——*2*. Plates surrounding anal orifice, ×5 (based on HUDSON, 4).——*3*. Part of ambulacral floor showing marginal pores with depressions on plates extending toward perradial groove, ×20 (2).

to be entirely unrelated to the pore rhombs of cystoids or hydrospires of blastoids. The grooves provide a distinctive pattern of surface ornament and may have served as skin gills, but possible functions otherwise are unknown.

The margins of each ambulacrum are marked by evenly distributed, closely spaced pores, a single row occurring along any one margin (Fig. 173,*3*). They are placed next to outer edges of the ambulacral plates and are not associated with any sign of brachiolar facets. Accordingly, as stated confidently by BATHER (1900, p. 209; 1914, p. 202), these echinoderms differed from blastoids and cystoids in lacking brachioles, and BATHER was first to point out morphological resemblance to edrioasteroids.

A hydropore appears to have been located either within the anal deltoid or in a separate plate aborally placed next to its adoral extremity (Fig. 172,*2*).

The surface of most thecal plates bears closely spaced minute pore or pits that seem not to penetrate far into the plates. The pits may constitute features of ornament.

A stem is represented by columnals, each of which is composed of five or more curved polygonal small plates, together forming a circular disc. Although only the topmost part of this attachment stalk is known, it tapers somewhat distally.

## Class EDRIOBLASTOIDEA Fay, 1962

[Edrioblastoidea FAY, 1962, p. 201]

Theca blastoid-like in shape and symmetry, composed of five mutually similar basals, five radials, five deltoids, and five orals, supplemented by a moderately large number of small interradially disposed plates called infradeltoids and around the anal orifice numerous still smaller plates; ambulacra subpetaloid, long, in that they reach below mid-height of the theca, their margins converging aborally and each bearing single row of close-spaced pores, elongate cover plates extending from margins to mid-line of ambulacra, double rows of these plates in each ambulacrum meeting in zigzag line; inferred hydropore between anal orifice and summit of theca. Main thecal plates marked by pattern of relatively broad and deep grooves representing inflections of stereom, not associated with openings to interior of theca. Stem composed of small polygonal plates grouped to form circular columnals. *M.Ord.*

The single known species placed in this class is *Astrocystites ottawaensis* WHITEAVES (1897), from the Cobourg Limestone (Trentonian) in Ottawa, Ontario, Canada. Although it was originally interpreted as a cystoid, virtually none of the attributes of this class, such as possession of brachioles, perforation of thecal plates by paired pores (as in the Diploporita) or pore rhombs (as in the Rhombifera), and prevailing lack of clearly marked pentameral symmetry, is found in *Astrocystites*.

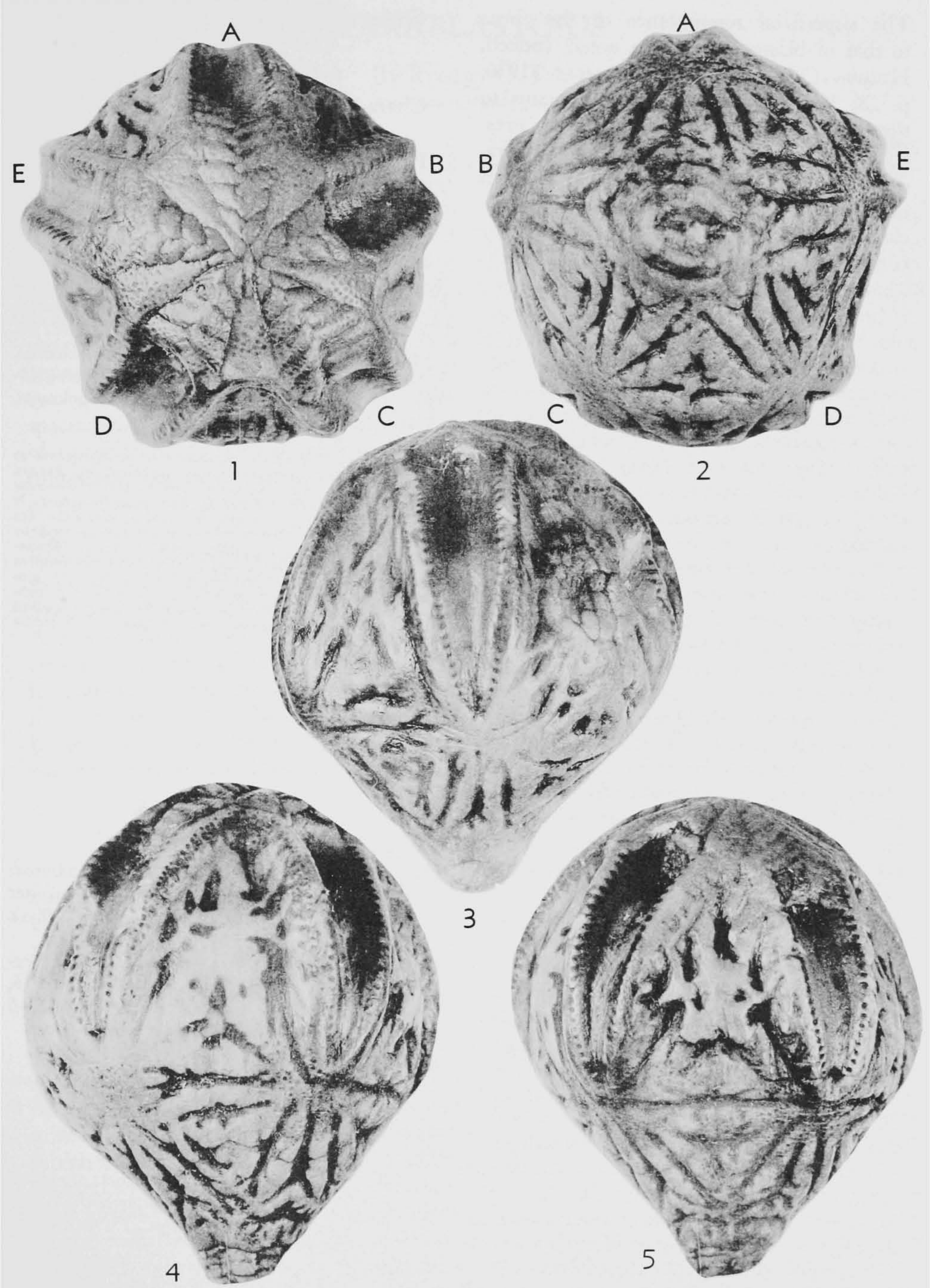


FIG. 174. Astrocystitidae (*Astrocystites ottawaensis*) (p. S292).

The superficial resemblance of the theca to that of blastoids has been noted. Indeed, HUDSON (1927, p. 97) and BASSLER (1936, p. 23; 1938, p. 13) assigned the genus to the Blastoidea. Taking account of the presence of the numerous small plates (infradeltoids) irregularly intercalated between the radials and deltoids of *Astrocystites,* closer similarity of the type form of the edrioblastoids to that of the parablastoids represented by *Blastoidocrinus* than to true blastoids is seen. Both blastoids and parablastoids have numerous brachioles arising from margins of the ambulacra, however. It is mainly on account of the lack of brachioles in *Astrocystites* that this genus was transferred by BATHER (1900) and others (SPRINGER in ZITTEL, 1913, p. 160; BASSLER & MOODEY, 1943, p. 8; CUÉNOT, 1948, p. 29; PIVETEAU, 1953, p. 655) to the Edrioasteroidea.

It is possible that the Blastoidea descended from the Edrioblastoidea, with the Fissiculata and Spiraculata perhaps arising independently as derivatives of the class, or the Fissiculata alone, with the Spiraculata developed later from fissiculate progenitors. These suggested phylogenetic relationships are speculative, but it is reasonable to presume that the ambulacral pores of the edrioblastoids differed in function from those of the blastoids, in the former serving as passageways for tube feet instead of inlets for movement of water to the hydrospires, as in the latter. With atrophy of the postulated edrioblastoid tube feet, gaps would be left between outer extremities of the ambulacral cover plates (corresponding to blastoid side plates). If thecal infolds along ambulacral margins of the radial and deltoid plates of edrioblastoids became aligned with these margins, they may readily have evolved to become hydrospires. The gaps along the ambulacral margins would become hydrospire pores. The secretion of stereom around the median ambulacral canal to protect it could explain the origin of lancet plates, which are a unique skeletal element of the Blastoidea. The brachioles of blastoids probably developed by the formation of tiny biserially arranged rows of plates around fleshy food-gathering outgrowths produced from edges of the ambulacra.

## Order PENTACYSTIDA Jaekel, 1918

[Pentacystida JAEKEL, 1918, p. 99]

Characters of class. *M.Ord.*

### Family ASTROCYSTITIDAE Bassler, 1938

[Astrocystitidae BASSLER, 1938, p. 13] [=Steganoblastidae BATHER, 1900, p. 209]

Characters of order. *M.Ord.*

**Astrocystites** WHITEAVES, 1897, p. 287 [**A. ottawaensis*; OD, M] [=*Steganoblastus* WHITEAVES, 1898, p. 395]. Characters of family. *M.Ord.,* N. Am.(Can.).——FIG. 174,*1-5*. **A. ottawaensis,* Cobourg Ls., Ottawa, Ont.; *1-5,* oral, aboral, *D*-ray, *BC*-interray, *AB*-interray views of holotype, ×3.3 (3).

[Publication of the name *Steganoblastus* by WHITEAVES as replacement for *Astrocystites* was suggested by BATHER (1914, p. 193), who erroneously thought that *Asterocystis* HAECKEL, 1896, is a senior homonym of *Astrocystites.* It is not. Although the family name Steganoblastidae has long priority over Astrocystitidae and has been used by several authors, including CUÉNOT (1948, p. 11, as Stéganoblastinés) and PIVETEAU (1953, p. 655), it must yield to the junior name, since the Code (1961, Art. 11,c) provides that "A family-group name must, when first published, be based on the name then valid for a contained genus. . . ." *Steganoblastus* does not qualify as a family name-giver.]

## REFERENCES

**Bather, F. A.**

(1) 1900, *The Echinoderma. The Pelmatozoa:* in A Treatise on Zoology. E. R. Lankester (ed.), pt. 3, 216 p., text fig., A. & C. Black (London).

(2) 1914, *I. Studies in Edrioasteroidea, V. Steganoblastus:* Geol. Mag., new ser., dec. 6, v. 1, no. 5, p. 193-203, pl. 15, text fig. 1-6 (May).

**Fay, R. O.**

(3) 1962, *Edrioblastoidea, a new class of Echinodermata:* Jour. Paleontology, v. 36, no. 2, p. 201-205, pl. 34, text fig. 1-3 (March).

**Hudson, G. H.**

(4) 1927, *The surface characteristics of Astrocystites (Steganoblastus) ottawaensis:* Vermont, State Geologist, Rept. 15, p. 97-110, pl. 6-10.

**Whiteaves, J. F.**

(5) 1897, *Description of a new genus and species of cystideans from the Trenton limestone at Ottawa:* Canadian Rec. Sci., v. 7, p. 287-292, fig. 1-3 (July); also Postscript, p. 395-396.

# PARABLASTOIDS

By ROBERT O. FAY
[Oklahoma Geological Survey]

## INTRODUCTION

Parablastoids are pelmatozoan echinoderms that were attached to the sea bottom by a cylindrical stalk composed of thin discoid columnals resembling those of many blastoids and crinoids. The theca has a general blastoid-like form, with strongly developed pentameral symmetry and stellate appearance in oral or aboral views. Only two genera, each represented by a single species, have been described. They consist of a poorly known form which has not been illustrated, reported from the upper part of the Lower Ordovician of the Leningrad region, USSR, and a comparatively well-known form from the lower part (Chazyan) of the Middle Ordovician of New York and Quebec. Many specimens of the American parablastoid, known as *Blastoidocrinus,* have been collected and they serve to demonstrate the morphological distinctness of the group. The parablastoids are judged to be not closely related to either edrioblastoids or true blastoids.

## MORPHOLOGY

The theca is composed of rather numerous plates, so arranged that the oral and aboral portions are well differentiated. The aboral (or dorsal) region is formed by three or more circlets of plates, the lowermost of which consists of small basals placed deeply within the basal concavity and largely or entirely concealed by the proximal stem segment. Seemingly, they are five in number. Next above the basals and alternating with them are five moderately large radials, which are narrow below and widen upward to slightly beyond their mid-length and then narrow to a point (Fig. 175,*2*). Plates of the radial circlet are widely in contact with each other all around. In line with the radials are five pairs of elongate plates named bibrachials with long perradial sutures between them (Fig. 175,*2,4,5*). A group of approximately 13 interbrachials, arranged in one or more transverse rows, occurs between each two pairs of bibrachials.

The oral (or ventral) side of the theca is formed by numerous plates belonging to the five radially placed subpetaloid ambulacra and five large interradial plates identified as deltoids (Fig. 175,*1,4,5*). No lancet plate is present in an ambulacrum but biserially alternating sets of adambulacrals support the food groove. Relatively large cover plates alternate with the adambulacrals, occurring above them with 3 wing plates above the cover plates. Each adambulacral plate bears a long brachiole with biserially arranged tiny ossicles attached to its admedial side (Fig. 175,*3*). The brachioles rise parallel to one another packed closely together along sides of wing plates in the middle of each ambulacrum. They extend to the upper edge of the wing plates. The oral opening is tightly covered by a thick pentalobate apical plate, which has a large crescentic orifice on the inner surface of its anal side, perhaps opening outward laterally but not upward at the summit. The apical plate fits closely against the distal wing plates of the five ambulacra (Fig. 175,*1,4,5*).

Five large triangular deltoids are present between the ambulacra. They are shallowly concave transversely and moderately convex longitudinally along their mid-lines, which slope upward rather steeply in convergent manner to their tips. Each deltoid has many sets of parallel infolds, termed cataspires. They extend to pores along the ambulacral margins and reach aborally to pores along the aboral margin of the deltoid. The cataspires are not interconnected laterally, but those joined to pores along the ambulacral margins are seemingly connected to the aborally directed set of cataspires, so that water entering the ambulacral pores could pass along cataspires to outlets along the aboral margin of the deltoids. Evidently, the cataspires were not outwardly open slits, for they are covered by stereom which produces small parallel ridges on the surface of the deltoids.

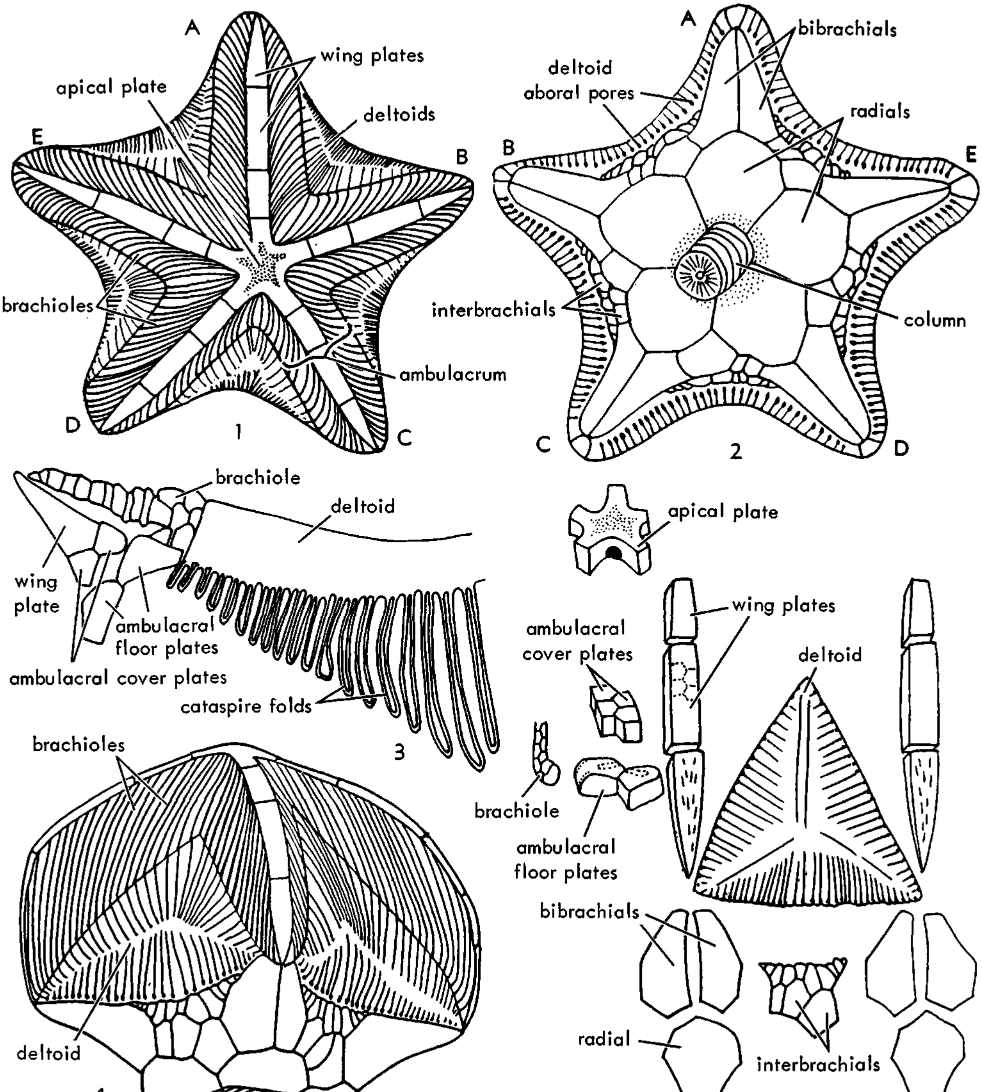


FIG. 175. Morphological features of parablastoids.——**Blastoidocrinus carchariaedens* (all Fay, n).——*1,2*. Oral and aboral view of theca, ×2.4.——*3*. Cross section of part of deltoid and ambulacrum showing cataspires, ×8.——*4*. *D*-ray view of theca, ×2.4.——*5*. Partial layout of plates, ×2.4.

## Class PARABLASTOIDEA Hudson, 1907

[Parablastoidea HUDSON, 1907, p. 97]

Stem-bearing pelmatozoan echinoderms with blastoid-like theca formed by three or more circlets of plates on aboral side, and by ambulacral wing plates and biserial cover plates covering numerous adambulacrals along five radii, apical plate at summit, and five large triangular deltoids; radial plates surmounted by pairs of bibrachials; rows of small interradials between bibrachial pairs; adambulacrals bearing parallel rows of moderately elongate biserial brachioles;

pores along ambulacral margins connected with cataspire infolds of deltoids, which include aborally directed sets joined to pores on aboral margins of each deltoid. Stem composed of discoid columnals. _L.Ord.-M.Ord._

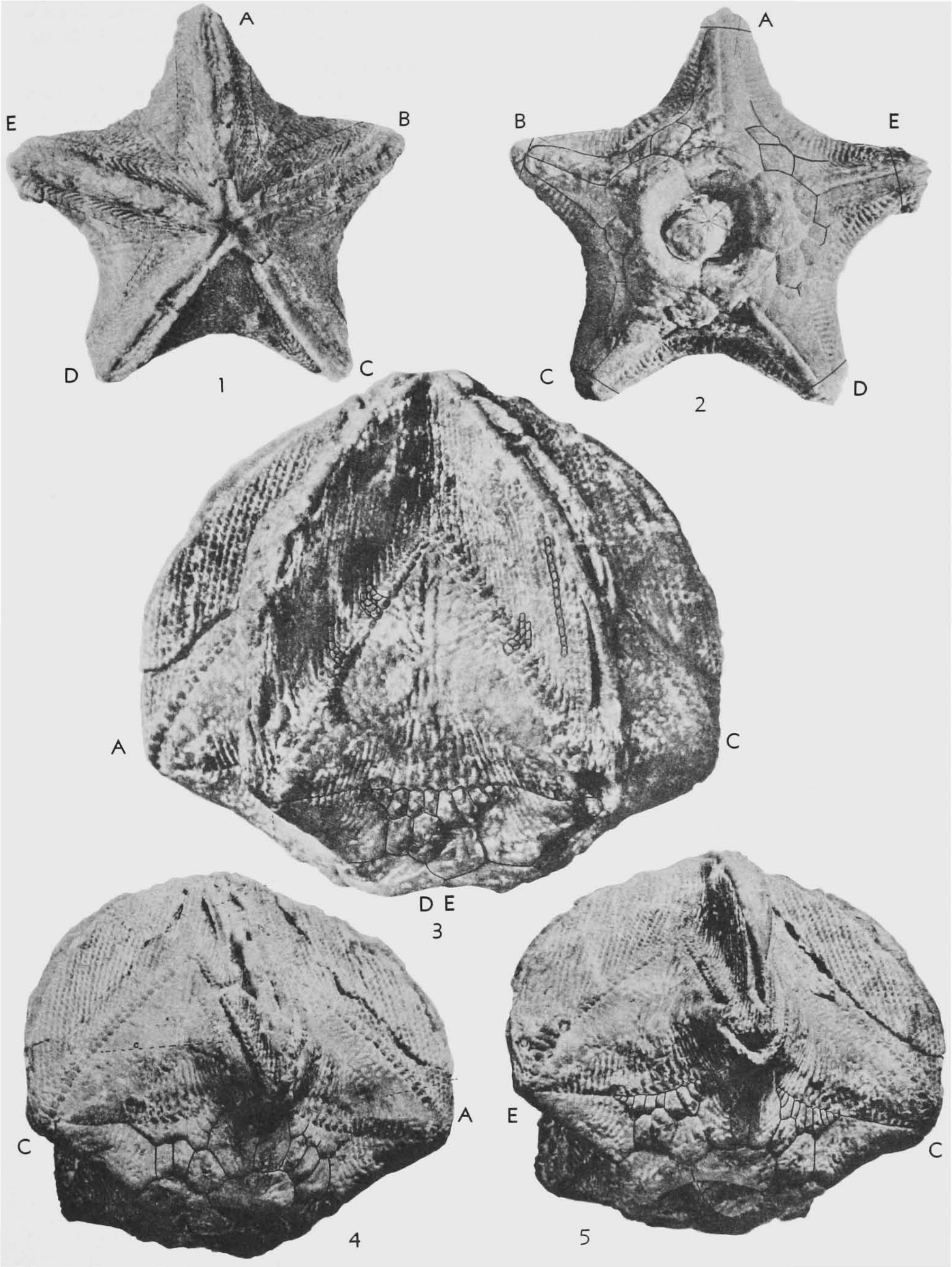


FIG. 176. Blastocystidae (_*Blastoidocrinus carchariaedens_) (p. S296).

## Family BLASTOCYSTIDAE Jaekel, 1918

[Blastocystidae JAEKEL, 1918, p. 107]

Characters of class. *L.Ord.-M.Ord.*

**Blastocystis** JAEKEL, 1918, p. 107 [**B. rossica*; OD, M]. Large interradials below triangular deltoids. [Not figured or well understood. Type specimen probably lost. Even so, valid name-giver for family.] *Up.L.Ord.* (Kunda Formation, $B_3$), near Leningrad, USSR.

**Blastoidocrinus** BILLINGS, 1859, p. 18 [**B. carchariaedens*; OD, M]. Characters of class; pentamerous symmetry strongly defined; theca composed of approximately 90 somewhat regularly arranged plates. [Seemingly unlike *Blastocystis* in having rows of small interradials. The best available description of the genus is that published by HUDSON (1907).] *Low.M.Ord.(Chazy.),* N. Am. (Que.-N.Y.).——FIG. 176,*1-5*. **B. carchariaedens,* USA(N.Y.); *1,2,4,5,* oral, aboral, *B*-ray, *D*-ray views of typical specimen, ×2.2 (2); *3, DE*-interray view of same specimen, ×3 (2).

## REFERENCES

### Billings, Elkanah

(1) 1859, *On the Crinoidea of the Lower Silurian rocks of Canada:* Geol. Survey Canada, Figures and Descriptions of Canadian Organic Remains, dec. 4, vi+72 p., 10 pl., 9 text fig.

### Hudson, G. H.

(2) 1907, *On some Pelmatozoa from the Chazy Limestone of New York:* N.Y. State Museum, Bull. 107, p. 97-152, pl. 1-10.

### Jaekel, O. M. J.

(3) 1918, *Phylogenie und System der Pelmatozöen:* Paläont. Zeitschr., v. 3, no. 1, 128 p., 114 text fig. [Republished in 1921.]

### Schmidt, Friederich

(4) 1874, *Ueber einige neue und wenig bekannte baltisch-silurische Petrefacten:* Acad. Impér. Sci. St. Pétersbourg, Mém. (Akademiya Nauk SSSR, Leningrad), ser. 7, v. 21, no. 11, p. 1-48, pl. 1-4.

# PART S

# ECHINODERMATA 1

## GENERAL CHARACTERS

## HOMALOZOA—CRINOZOA (EXCEPT CRINOIDEA)

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

## VOLUME 2

## BLASTOIDS

By Harold H. Beaver,[1] Robert O. Fay,[2] Donald B. Macurda, Jr.,[3] Raymond C. Moore,[4] and Johannes Wanner[5]

## CONTENTS

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# INTRODUCTION

By Robert O. Fay

Blastoids are moderately small stemmed echinoderms having a calyx that mostly measures less than 25 mm. in diameter or height. They are restricted to marine Paleozoic rocks ranging from Silurian to Permian, attaining greatest abundance and variety in Lower Carboniferous (Mississippian) deposits.

The **stem** which attached blastoids to the sea bottom is rarely preserved in position joined to the theca, but a sufficient number of specimens makes clear that it was very slender and comparatively short, with probable maximum length amounting to little more than 25 cm. It was composed of thin discoid ossicles (Fig. 177).

The main part of the animal, at the top of the stem, consisted of a globular to pyriform body armored by regularly arranged calcareous plates (**calyx** or **theca**). This relatively thin-plated theca enclosed the viscera, of unknown nature, and along the borders of five linear or petaloid tracts termed **ambulacra,** disposed in regular radial positions extending downward from the summit of the theca, very numerous thread-like armlets **(brachioles)** projected upward as food-gathering appendages. The whole structure borne by the stem was a fringed budlike form termed **anthus** (Greek, blossom) or crown (Fig. 177).

The **mouth** of blastoids is centrally located at the summit of the theca and median grooves in each ambulacrum connect with it, for they were the main passageways on the surface of the theca for transportation of food particles brought to them by the brachioles by way of lateral grooves on the ambulacra (Fig. 178). The outlet of the digestive system is an orifice on the posterior side of the theca known as the **anus,** or it may be located in the summit area as part of the vent termed **anispiracle** (Fig. 178,*1*). It is invariably interambulacral in position and located not far below the mouth. Other openings in the theca are rounded or slitlike vents which functioned as outlets (**spiracles, hydrospire slits**) of the respiratory system and with these belong numerous diminutive openings (**hydrospire pores**) which served as water inlets. The hydrospires are internal thin-walled folds of calcareous tissue which are characteristic of the blastoids and which are described in some detail in the section on Morphology. Possibly the hydrospire structures served reproductive functions, as well as respiration.

As a rule, the theca of blastoids is composed of 18 to 21 main plates and myriad diminutive ones. The main plates are regularly arranged in definite cycles or circlets, in upward succession from the stem consisting of (1) **basals,** (2) **radials,** (3) **lancets**

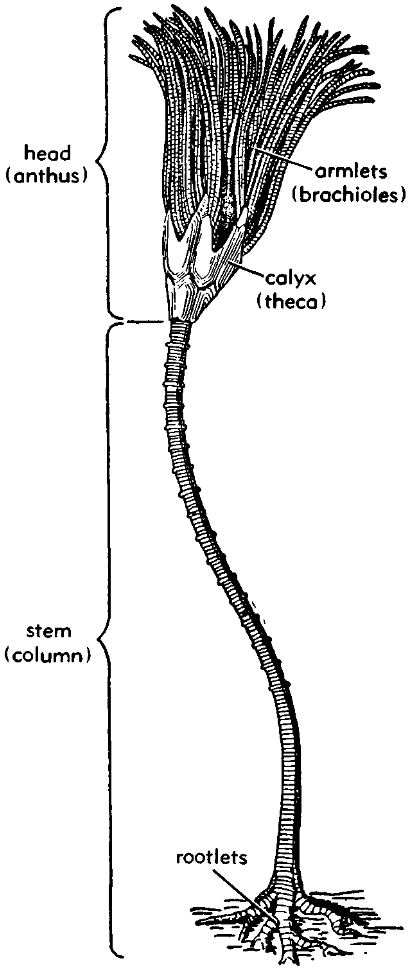

Fig. 177. Reconstruction of entire blastoid (*Orophocrinus,* Miss., N.Am.), showing principal parts (Bather).

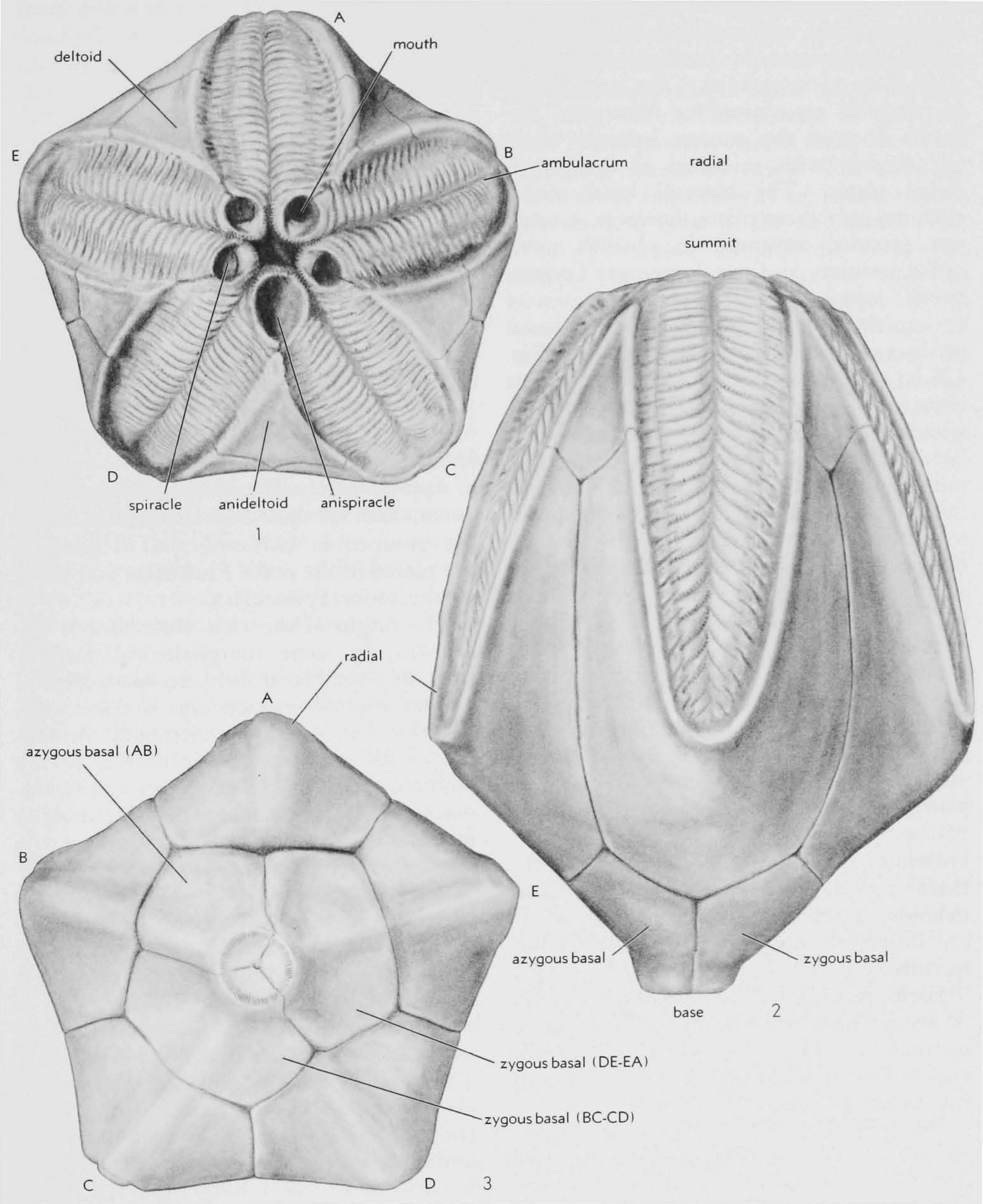

FIG. 178. Calyx of typical blastoid, *Pentremites symmetricus* HALL, U.Miss.(Chesteran), USA(Ill.), showing externally visible parts of theca, ×4.5 (drawings by Roger B. Williams; Beaver, n).——*1.* Summit (oral) view, mouth opening at center surrounded by 4 spiracles (relatively small rounded orifices in interambulacral position) and large anispiracle in posterior interambulacrum (below mouth), also showing petaloid ambulacra (*A* at top, followed in clockwise direction by *B, C, D,* and *E* ambulacra) deltoid plates next to summit between ambulacra.——*2.* Lateral view of calyx from the anterior (*A*-ray) side, especially showing deeply sulcate form of radial plates embracing aboral parts of ambulacra.——*3.* Basal (aboral) view showing the stem impression borne by the basal circlet consisting of 2 large (zygous) plates and 1 small (azygous) plate.

and (4) **deltoids.** Plates in position of the five ambulacra and radials are defined as radial and plates in position alternating with them as interradial. The basal plates of blastoids are classed as interradial elements because the sutures between them all coincide with mid-lines of contiguous radial plates. The blastoid basal circlet contains only three plates, however, a small one (termed **azygous**) in obvious interradial position, and two large ones (**zygous** basals) which occur directly below two of the radials because each represents the fused product of two interradial elements (Fig. 178,*2*,*3*). The radial plates are more or less elongate U- or V-shaped skeletal elements which enclose the ambulacra between their lateral extension, known as **limbs.** Interradially disposed plates at or near the summit of the theca are rhomboid to subtriangular (delta-shaped) elements termed **deltoids.** The **lancets** are elongate spear-shaped plates inserted between the deltoids and hence radial in position; actually they extend aborally well beyond the aboral limits of the deltoids, occupying most of the spaces (sinuses) between the radial limbs and underlying very numerous small plates of the ambulacra. These latter consist of so-called **side plates** and **outer side plates.** The **brachioles** are attached to these plates.

Deltoid plates on the posterior side of the theca are collectively designated as **anal deltoids.** They include special types which are differently named, as described subsequently.

Each plate of the blastoid theca consists of crystalline calcite having its own optical orientation. The plates expand laterally and in thickness during growth from juvenile to adult stages.

Blastoids commonly occur in limestones, calcareous shales, and in some light-colored clayey shales; they are rarely found in black shales and are virtually unknown in sandstones. Some Mississippian (especially Chesteran) shaly limestones are locally so crowded with specimens of *Pentremites* that these strata became known to early geologists as the Pentremital Beds. Blastoids are also very abundant in parts of the Permian in Timor (East Indies). The known stratigraphic range of the class is Silurian to Permian, with maximum dispersion in Devonian, Lower Carboniferous (Mississippian), and locally in Permian deposits. They have been reported from all continents except Antarctica, but largest collections have been made in North America, Europe, and the island of Timor.

Approximately 78 presently distinguished genera and 350 described species of blastoids are grouped in 12 families, of which five are placed in the order Fissiculata and seven in the order Spiraculata.

The origin of the class Blastoidea is unknown. In some morphological features striking resemblance between blastoids and various rhombiferan cystoids is discernible, but this has not been acceptably demonstrated to have genetic significance. In my opinion, the Middle Ordovician Edrioblastoidea possess characters which are judged most likely to belong to ancestors of the blastoids, even though only a single edrioblastoid genus now is known.

A blastoid consists primarily of two connected parts, a **stem (column)** which was anchored to the sea bottom by branching rootlets, and a "head" **(anthus)** composed of a central budlike body and numerous attached armlets termed **brachioles** (Fig. 177). The budlike body is covered by skeletal plates, collectively forming the **theca (calyx)**, and internally there are thin-walled folded structures, named **hydrospires.**

# MORPHOLOGY

By Harold H. Beaver

[Esso Production Research Company]

## COLUMN

Although the stem attachment of a blastoid, known as the **column,** was first described approximately 140 years ago (Say, 1820), little has been added subsequently to our knowledge of this structure. Virtually all skeletal parts of blastoids are more commonly preserved than the stem, at least in its attached position to the theca. Most unattached segments of blastoid stems have not yet been discriminated definitely from columnal fragments of crinoids and cystoids. According to ETHERIDGE & CARPENTER (1886, p. 9), the column of a specimen of *Pentremites* in the collections of WACHSMUTH ends below in a branching root. The column measures 5 to 8 inches in length. GALLOWAY & KASKA (1957, p. 8) have reported a length of 1 to 3 inches for length of the column in *Pentremites*. All available information indicates that the stems of blastoids generally were quite short, much shorter than most crinoid columns, although seemingly similar in structure and appearance. At present no trustworthy criteria for distinction of discrete segments of blastoid and crinoid columns other than absence of nodal and internodal columnals and absence of cirri in blastoids have been reported. Further, no blastoid stems with pentagonal, elliptical, or crescentic transverse section are known, whereas these are found in some crinoid genera.

The stems of blastoids consist of many small circular segments called **columnals,** each with a tiny round central opening **(lumen)** which is inferred to have functioned as a neurovascular canal. This axial canal opened into the central cavity of the theca. The margins of top and bottom surfaces of each columnal have alternating fine ridges **(culmina)** and grooves **(crenellae)** which interlock with similar markings on adjoining columnals, so that a moderately firm articulation results. With exception of a specimen of *Pentremites conoideus* in the collection of GALLOWAY & KASKA (1957, pl. 13, fig. 8) which has small spines on the exterior of the column, nothing is known of columnal ornamentation. Some blastoid genera (e.g., *Astrocrinus, Eleutherocrinus, Notoblastus*) seem to have lacked a column, at least in the adult stage (ETHERIDGE & CARPENTER, 1886, p. 9; FAY, 1961, p. 9). A distinct stem facet is seen in adult specimens of *Timoroblastus*.

## CALYX

The term **calyx** (Greek, bud of flower) is an appropriate designation for the bud-shaped skeletal structure borne at top of the stem (column) of the echinoderms known as blastoids (Greek, *blastos*, bud). It comprises the complete head **(anthus)** of these echinoderms, minus the threadlike brachiolar appendages borne by the ambulacra (Fig. 177). This portion of the hard parts is also properly named **theca** (in Greek signifying sheath or case). The principal plates of the calyx (theca) are basals, radials, deltoids, and those of the ambulacra (Fig. 178). The **basals** compose the lower portion of the calyx and articulate with the stem. Overlying and alternating or in series with the basals are **radials,** each of which is partially divided by a **sinus** for reception of the aboral portion of an ambulacrum. Above the radials and alternating with them are interambulacral plates designated as **deltoids.**

### SHAPE AND SIZE

Blastoids exhibit many variations in shape of the calyx. These differences are seen in genera from all geologic systems in which blastoids occur, but are most pronounced in forms of Permian age. Representatives of the various genera can be separated into four broad groups (Fig. 179).

Group 1, characterized by a pyriform outline, includes both spiraculate and fissiculate blastoids (defined later). The typical form (e.g., *Pleuroschisma*, Fig. 179,*4*) has ambulacra that nearly equal half the height of the theca. At one extreme are steeply conical types with short ambulacra largely confined to the summit (e.g., *Ceratoblastus*, Fig. 179,*8*), whereas the other extreme is marked by genera with expanded summits and relatively long ambulacra (e.g., *Orophocrinus*, Fig. 179,*1*).

Group 2 is distinguished by blastoids having a globose shape. Two subgroups are readily recognized, the first having short ambulacra confined to the summit (*Paracodaster, Agmoblastus*, Fig. 179,*9,10*), and the second with ambulacra nearly equal in length to height of the theca (*Poroblastus, Nymphaeoblastus, Granatocrinus, Auloblastus*, Fig. 179,*11-14*). Studies of many specimens of *Globoblastus*, a globose type belonging to the second subgroup, show that individuals commonly change shape with age. Young specimens are generally elongate globose, whereas old ones are depressed globose.

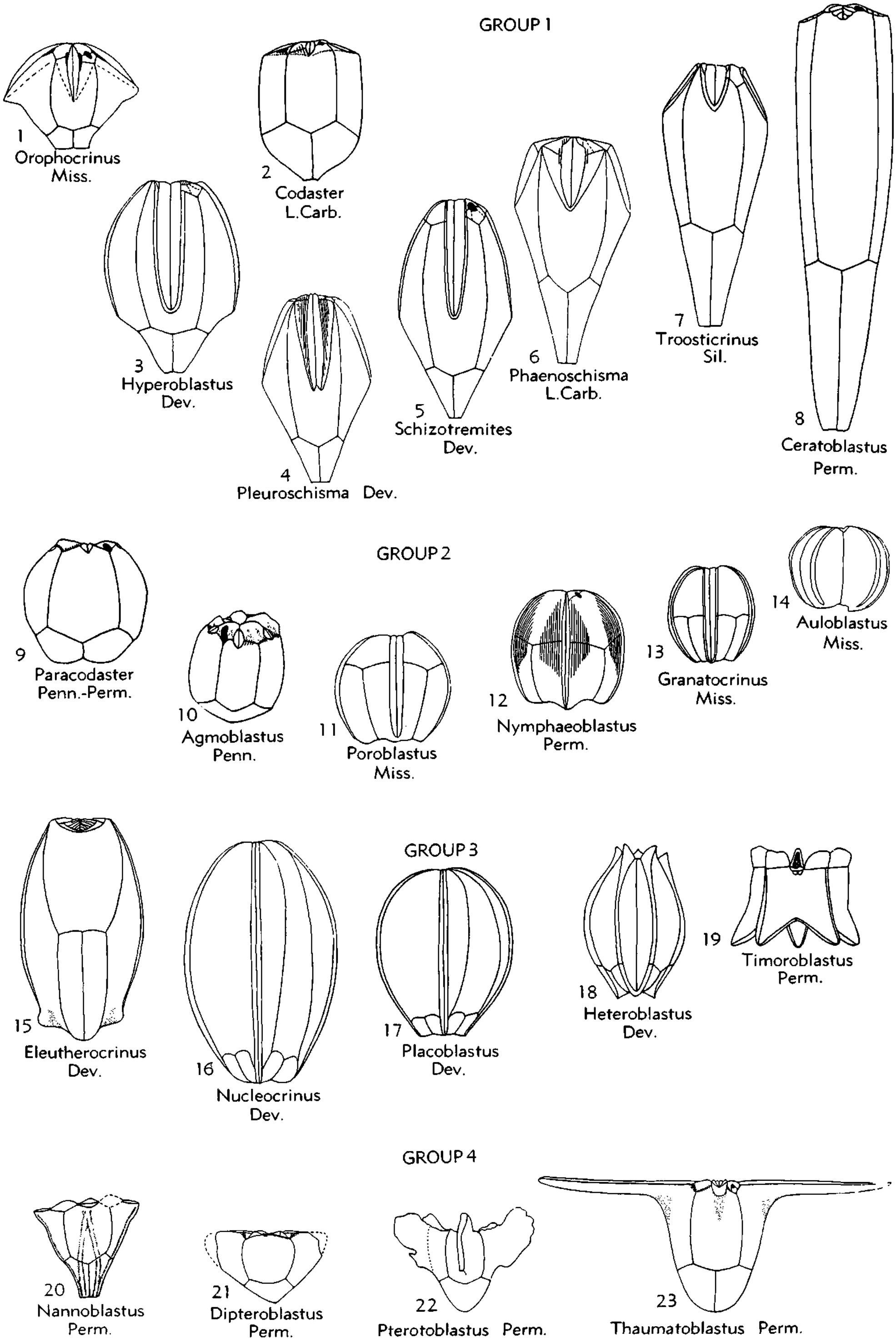

FIG. 179. Shapes of blastoid calyces, shown in lateral views. Groupings are not inferred to delineate phylogenetic assemblages (drawings from Fay, n).

Group 3 includes types which in adult growth stages are elongate globose (e.g., *Eleutherocrinus, Nucleocrinus, Placoblastus, Heteroblastus,* Fig. 179,*15-18*) or are highly irregular in shape but have height and width of the calyx nearly equal (e.g., *Timoroblastus,* Fig. 179,*19*). Some genera have pointed protruding deltoid tips (e.g., *Heteroblastus*), whereas others may have projecting radials and deltoids (e.g., *Timoroblastus*).

Group 4 is composed of vase-shaped blastoids (e.g., *Nannoblastus, Dipteroblastus,* Fig. 179,*20,21*) and similar genera with extended radials and accompanying long ambulacra (e.g., *Pterotoblastus, Thaumatoblastus,* Fig. 179,*22,23*).

Variations in shape commonly are significant at specific levels and, in conjunction with other morphological features such as patterns of the hydrospires, may aid in determining phylogenetic trends. Detailed examinations of species belonging to *Pentremites* have established phylogenetic lineages within this genus (Fig. 180). The oldest known representative, *P. elongatus* (Fig. 180,*A*) of Osagian age, is elongate globose, with an essentially flat base and ambulacra nearly equal to height of the theca. It is succeeded in the Meramecian by *P. conoideus* (Fig. 180,*B*) with similar characteristics. In the later Meramecian, however, two types diverged from *P. conoideus,* one characterized by a nearly flat base (Fig. 180, *D,F,H,I,K,L*) and the other by a pyriform or inverted-pear shape (Fig. 180, *C,E,G,J*). Offshoots of the flat-based group, mainly species closely related to *P. sulcatus* (Fig. 180,*I*), developed in the middle and late Chesteran. Thecal variations include a marked increase in size (up to twice or more common pentremite size), the development of protruding deltoids, nodose thecal exteriors, or serrated ambulacral rims.

Blastoid calyces differ greatly in thecal length from one genus to another and also may show considerable variation within a given genus. In addition, no consistent change in size of calyx is apparent in blastoids as a class from their earliest occurrence in the Silurian to their last-known appearance in the Permian.

Specimens of *Placoblastus obovatus,* some species of *Pentremites* (e.g., *P. sulcatus, P. obesus, P. maccalliei*), and *Tricoelocrinus woodmani* are representative of very large blastoid species, commonly having a height of 2 inches or more. Seemingly adult specimens of *Diploblastus glaber, Mesoblastus crenulatus, Monadoblastus granulosus,* and a few species of *Pentremites* (e.g., *P. princetonensis, P. pulchellus*) are typically small blastoids, generally having a height of about 0.25 inch.

Silurian genera (e.g., *Troosticrinus, Polydeltoideus, Decaschisma*) commonly are represented by specimens having a height slightly less than one inch. Devonian genera exhibit greater range in height, some forms being very large (e.g., *Placoblastus*), whereas representatives of other genera are relatively small (e.g., *Heteroschisma*). Mississippian blastoids vary greatly in size, some being very small (e.g., *Diploblastus, Mesoblastus*), others intermediate (e.g., *Globoblastus, Schizoblastus, Orbitremites, Codaster*), and a few very large (e.g., *Tricoelocrinus,* some species of *Pentremites*). Penn-

[*See* pages S304-S305]

FIG. 180. Calyx shape correlated with accompanying structural modifications, including character of internal features, in succession of Mississippian blastoids belonging to the genus *Pentremites,* interpreted to show phylogenetic trends. Letters refer to photographs (X1) and drawings based on thin sections on opposite page (position of section indicated by pairs of arrows).——*A. P. elongatus* SHUMARD, L.Miss. (Burlington Ls.), near Springfield, USA (Mo.).——*B. P. conoideus* HALL, U.Miss.(Salem Ls.), Spergen Hill, USA (Ind.).——*C. P. princetonensis* ULRICH, U.Miss.(Ste. Genevieve Ls.), Cedar Bluff, USA (Ky.).——*D. P. pulchellus* ULRICH, U.Miss. (Ste. Genevieve Ls.), Cedar Bluff, USA (Ky.).——*E. P. symmetricus* HALL, U.Miss.(Paint Creek F.), near Floraville, USA(Ill.).——*F. P. godoni* (DEFRANCE), U.Miss.(Paint Creek F.), near Floraville, USA (Ill.).——*G. P. pyriformis* SAY, U.Miss.(Golconda F.), near Vienna, USA (Ill.).——*H. P. tulipaformis* HAMBACH, U.Miss.(Bangor Ls.), near Rockwood, USA (Ala.).——*I. P. sulcatus* (ROEMER), U.Miss.(Glen Dean Ls.), near Vienna, USA (Ill.).——*J. P. girtyi* ULRICH, U.Miss.(Menard Ls.), near Chester, USA (Ill).——*K. P. halli* GALLOWAY & KASKA, U.Miss.(Kinkaid Ls.), SE of Chester, USA(Ill.).——*L. P. rusticus* HAMBACH, L.Penn.(Bloyd Sh.), near Fort Gibson. USA (Okla.).

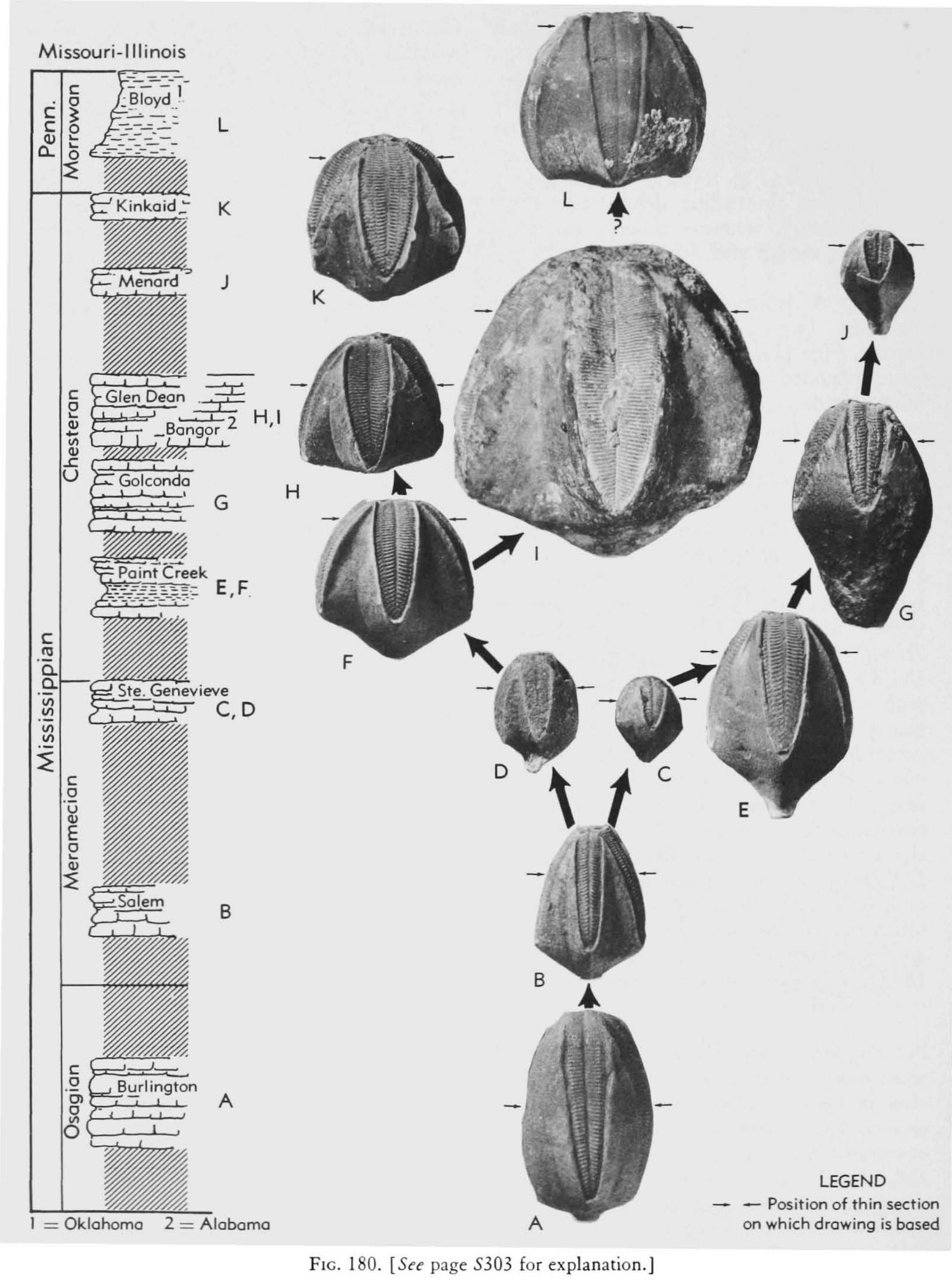

FIG. 180. [*See* page S303 for explanation.]

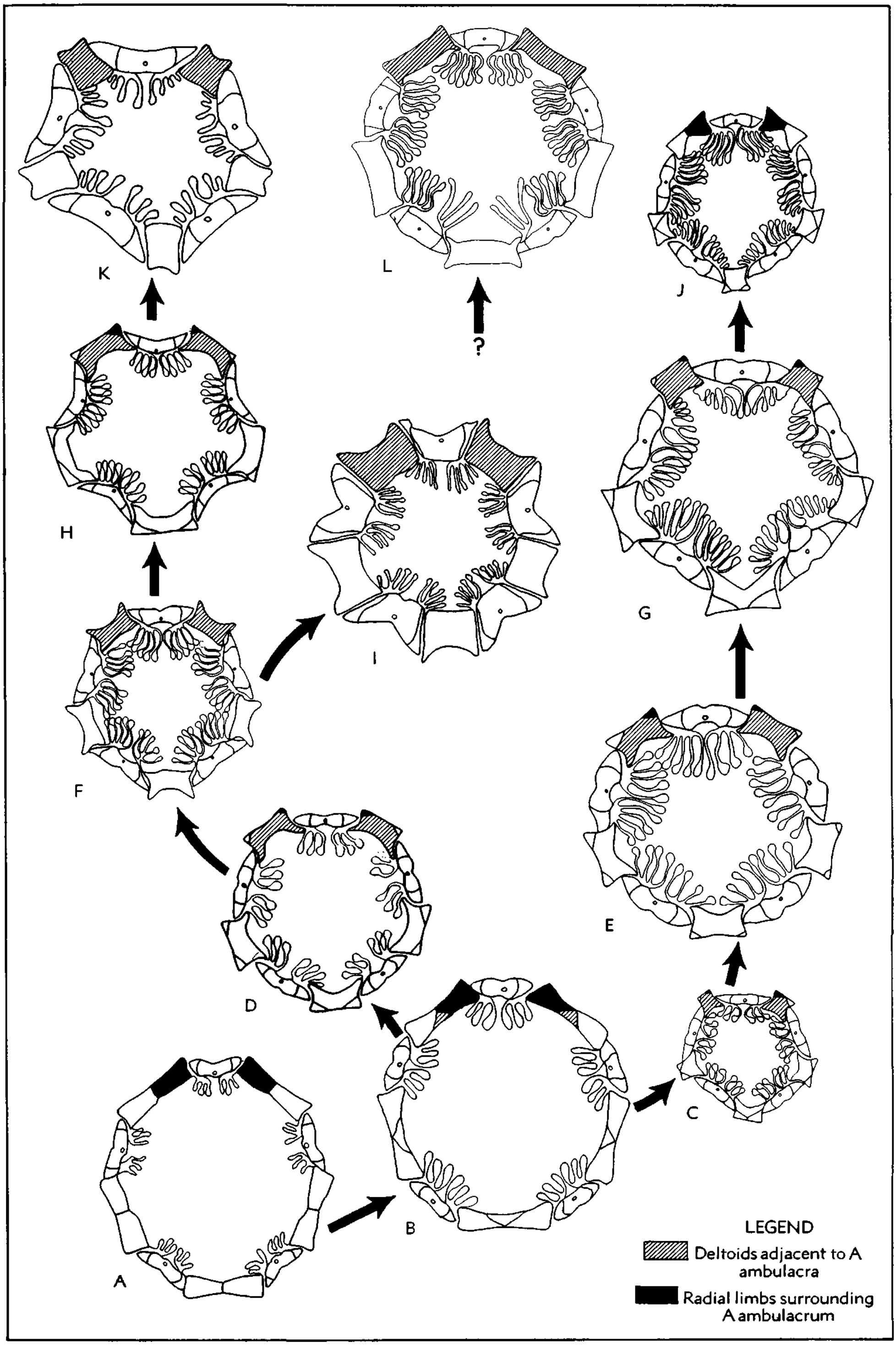

Fig. 180. *(Continued)*.

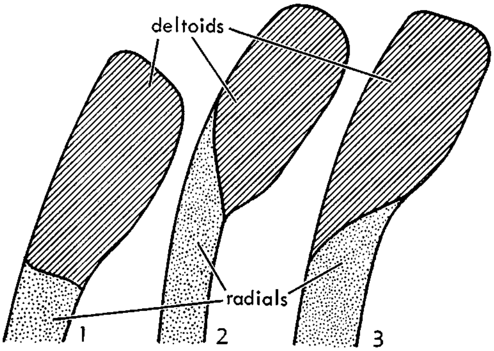

FIG. 181. Radial-deltoid relationships illustrated by diagrammatic sections; *1,* normal abutment; *2,* radial overlap; *3,* deltoid overlap (radials stippled, deltoids oblique ruled, exterior of calyx toward left).

sylvanian blastoids, represented by few species, and Permian forms, consisting of many species and genera, show about the same range in the size of specimens as do Mississippian and older blastoids.

## STRUCTURAL FEATURES

Although the blastoid calyx normally consists of a constant number of plates, their range in shape and structure is great enough to aid in generic distinctions. Features commonly used in classification include shape, respective size of the plates, and position of other structures in relation to the thecal plates (e.g., relationships of spiracles to deltoids). One useful observation, mostly unmentioned in the literature, is the nature of sutural contacts between radials and deltoids.

In various genera three different conditions are found, even though gradation of one to another introduces some intermediate types which reduce sharpness of distinction. The contacts may be illustrated by sections cut approximately at right angles to the radial-deltoid suture (Fig. 181). A simplest condition (type 1) is marked by the sutural (contact) surface disposed perpendicularly to the outer and inner surfaces of the plates; then abutment of radial against deltoid is **normal** (e.g., *Codaster*). In other conditions the abutment may be more or less strongly oblique. If the sutural surface is inclined outward adorally or adlaterally (type 2), the radial margin overlies an edge portion of the deltoid and this is designated as **radial overlap** (e.g., *Globoblastus*). If the sutural surface is inclined inward, adorally or adlaterally (type 3), the deltoid margin overlies an edge portion of the radial and this is designated as **deltoid overlap** (e.g., *Schizoblastus*).

The calyx is pierced by numerous openings, some of which are illustrated here (Fig. 178,*1*) and some later. A central opening at the summit **(mouth)** served as an inlet to the digestive tract of the living animal. The **anus** is a relatively large orifice (anal opening) located in the posterior *(CD)* interray. It functioned as the excurrent opening of the digestive tract. Small, generally rounded apertures **(spiracles)** penetrate the deltoids or occur adjacent to them in some (spiraculate) blastoids. Typically in such blastoids tiny openings parallel the sides of ambulacra and connect internally with the hydrospires. These openings, called **hydrospire pores,** are located between the margin of the ambulacrum and the adjacent radial and deltoid plates, or they may be excavated in the radial and deltoid plates. In other (fissiculate) blastoids, the hydrospire pores may be replaced by long, very narrow **hydrospire clefts,** which open directly into the hydrospires. Generally, these clefts are excavated in the radial and deltoid plates and transect the radial-deltoid suture. In a few blastoids the spiracles are lengthened into long slits **(spiracular slits)** along the sides of an ambulacrum.

In well-preserved specimens, thecal openings in the vicinity of the summit (mouth, anus, spiracles) are covered by tiny skeletal plates, collectively termed **summit plates.** These plates, however, are commonly highly specialized and differ in number, shape, and size from one genus to another.

## ORNAMENT

The exterior surface of blastoid calyces may be quite smooth, or it may bear various sorts of sculpture. Ornamentation of the theca, where present, commonly consists of growth lines and ridges or rows of nodes distributed over the surface. Generally, growth lines of the basals are parallel to the plate margins, such lines being crowded together next to the column, less closely

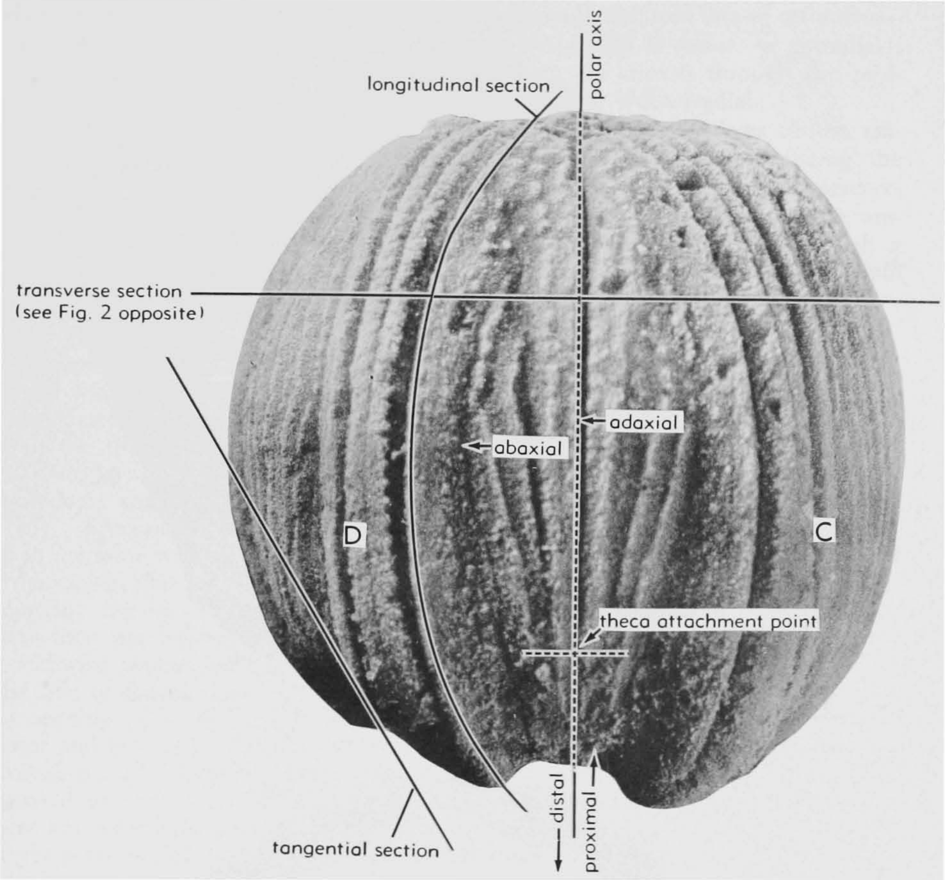

FIG. 182. Terminology related to orientation of blastoid theca illustrated on side view of *Globoblastus norwoodi* (OWEN & SHUMARD), L.Miss.(Burlington Ls.), Burlington, USA (Iowa) (Beaver, n).

spaced adjacent to the interbasal sutures, and farthest apart near the radial-basal sutures (FAY, 1961, p. 10). This arrangement reflects differential expansion of the plates during ontogeny, growth distally and laterally being greater than proximally. The growth lines of the radials are parallel to the margins of the plates, indicating that accretion occurred along edges next to basals, deltoids, and contiguous radials. On deltoids the growth lines usually are most widely spaced parallel to the radial-deltoid sutures, for the adoral tips of the deltoids were secreted first and growth occurred around sides of the plates, particularly in an aboral direction.

## ORIENTATION

For purposes of description and comparison of blastoid calyces, standards of orientation and designations of corresponding parts must be agreed on. Mostly, these matters offer little difficulty, since the mouth, at the summit of the calyx, furnishes reference for defining adoral and aboral directions and differentiation of the rays may be decided according to a simple, practicable system. The treatment of blastoids from these viewpoints and nomenclature for descriptive purposes are explained in this section.

An imaginary line extending from the mouth of a blastoid to the center of its column is called the **polar axis** (Fig. 182). Any section in a plane coinciding with this axis or parallel and close to it is termed a **longitudinal section** and any section perpendicular to it is a **transverse section.** A section tangent to the outer surface of the theca and relatively near it is called a **tangential section.** Any direction toward the polar

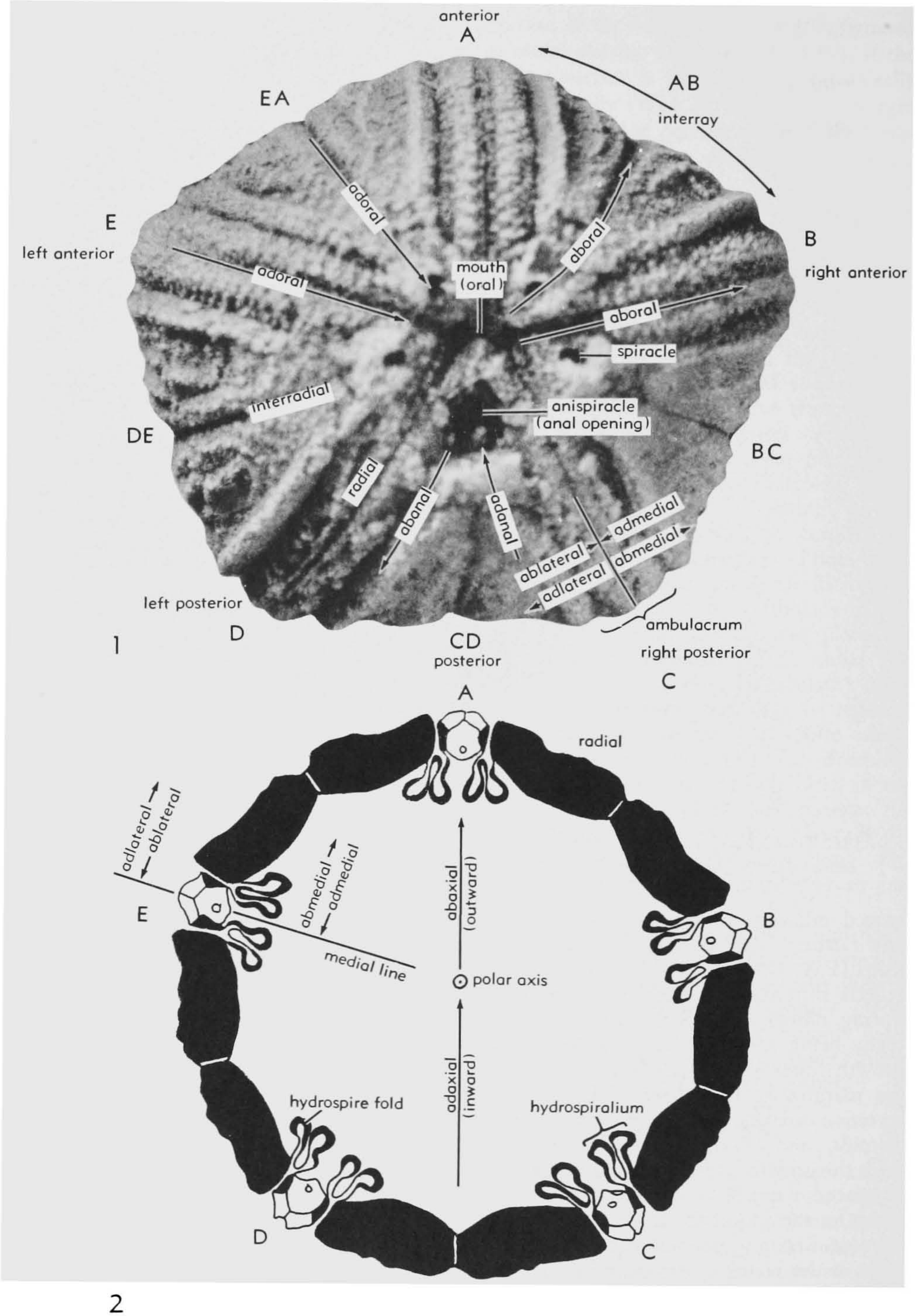

FIG. 183. Terminology related to orientation of blastoid theca illustrated by oral view *(1)* and transverse section *(2)* of *Globoblastus norwoodi* (scale same as in Fig. 193) (Beaver, n).

axis and approximately perpendicular to it is **adaxial** and any away from it is **abaxial.** Directions toward the geometric center of the theca are **inward** and those away from it are **outward.** The area surrounding the mouth is termed **oral.** Any direction toward the mouth is **adoral** and any away from it is **aboral.** A direction toward the point of attachment of column and theca is defined as **proximal**; a direction away from this point is **distal.**

According to nomenclature introduced by Carpenter (1878) and adopted herein, when a blastoid specimen is viewed from the oral side with the anal opening directed toward the viewer, the ambulacrum on the far side of the theca is designated by the letter *A*; then, in a clockwise direction the other ambulacra are lettered *B* through *E* (Fig. 183). Specimens viewed aborally, oriented in the same way with the anal side toward the viewer, also have the *A* ambulacrum opposite the viewer, but the other ambulacra then are lettered *B* to *E* in a counterclockwise manner. A direction toward the side of the theca which contains the anal opening (*CD* interray) is classed as posterior and that away from it (toward the *A* ambulacrum) is anterior. Areas may be designated similarly. The *B,C,D,* and *E* ambulacra are sometimes termed right anterior, right posterior, left posterior, and left anterior, respectively. A line from the mouth through the mid-line of an ambulacrum is designated as **radial** (or **perradial**); a line from the mouth through the mid-line of a deltoid is **interradial.**

Directions relative to plates of the ambulacrum may be made by utilizing the mid-line of an ambulacrum as a reference. A direction toward the mid-line of an ambulacrum thus is **admedial** or **ablateral**; a direction away from the mid-line is **abmedial** or **adlateral** (Fig. 183,*1*).

## BASALS

The basal circlet of blastoid calyces consists of three plates, two major ones of approximately equal size and shape, termed **zygous basals,** and a minor one that is smallest and quite different in shape from the others; this last-mentioned plate is termed **azygous basal** (Fig. 178,*3*), a name signifying unyoked (unfused) in contrast to the major zygous basals, each of which evidently is the product of fusion together of two pre-existing plates comparable in size and shape to the azygous basal. Aborally, the basals are attached to the column; adorally, they are overlain by the radials. Normally, the azygous basal lies in the position of the *AB* interray. Rarely, the basals seem to be fused into a single plate (e.g., *Acentrotremites*).

[*See* pages *S*310-*S*311]

Fig. 184. Morphological features shown by disarticulated parts of blastoid theca, illustrated by fragments of *Pentremites godoni* (Defrance), U.Miss.(Chester), near Floraville, Ill., all ×7 except *1* (×3.5), *7* (×8) and *8b* (×8) (Beaver, n).——*1.* Basal circlets; *1a-e,* interior views showing median excavation in C-ray zygous basal; *1f,* exterior view showing thickened area around stem impression.——*2.* Deltoids; *2a,* exterior of deltoid body with beveled aboral tips which project beneath adoral extremities of radial limbs (illustrating radial overlap) ( cf. *4a,b*); *2b,* exterior surface of deltoid body with lateral lips covered by attached side plates of ambulacra; *2c,* side view showing hydrospire canal and admedial surface of side plates.——*3.* Lancets; *3a,* exterior surface with well-preserved median and lateral food grooves; *3b,* interior surface showing 2 longitudinal ridges which carry attachments of admedial ends of hydrospire folds.——*4.* Radials; *4a,* exterior surface showing sloping sides of radial sinus and admedial abaxial surfaces of adjacent hydrospiralia (not underlancet plate); *4b,* interior surface showing beveled adoral extremities of limbs which overlap borders of deltoids (radial overlap) and partly preserved hydrospires in radial sinus.——*5.* Basals; *5a,* interior surface showing elongate depression (aligned with *C* ambulacrum) on *C* zygous basal; *5b,* exterior surface of circlet showing central moundlike elevation (consisting of secondary calcite) which bears stem attachment.——*6.* Lancet plate; *6a,* exterior surface showing side plates attached along margins; *6b,* interior surface showing hydrospire pores and their relation to side plates and outer side plates.——*7.* Deltoid; interior surface of specimen shown in Fig. *2b,* showing position of hydrospire canals and their relation to deltoid septum.——*8.* Summit part of theca composed of deltoid and adjoining ambulacra; *8a,* oblique view of outer surface showing spiracle at tip of deltoid; *8b,* interior surface showing deltoid septum which connects deltoid body and lip, lancet plates at left and right.

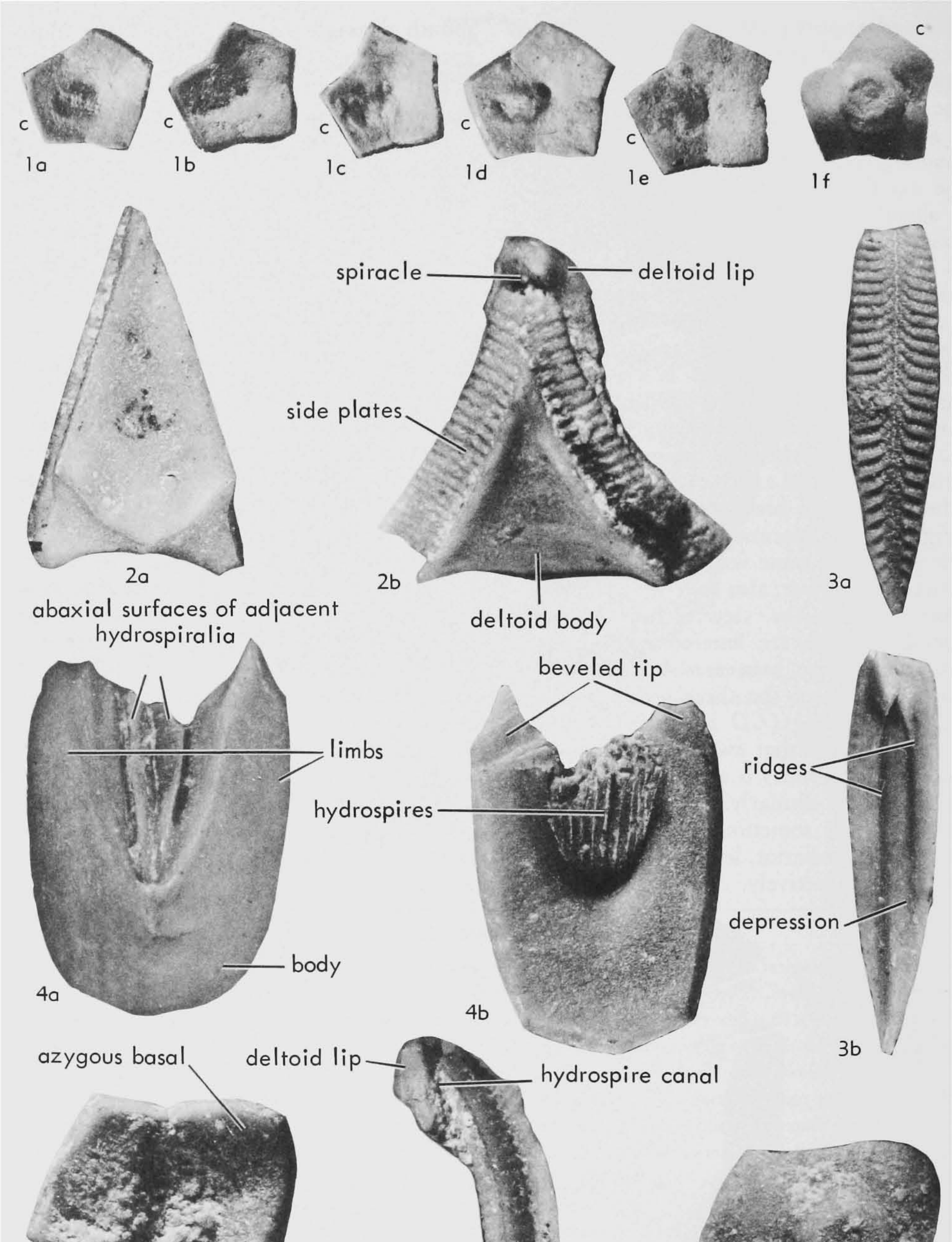

FIG. 184. [*See* page S309 for explanation.]

Lyons (1857, p. 469) described what he presumed to be a circlet of plates in some blastoids below the basals. Although this interpretation was supported by Billings (1869, p. 83), subsequent evidence has shown that these presumed extra plates consist merely of thickened calcite adjacent to the stem impression (Fig. 184,*1f,5b*) (Etheridge & Carpenter, 1886, p. 21).

## DIMENSIONS

The basals may be relatively large, forming most of the proximal part of the theca, or they may be very small and difficult to

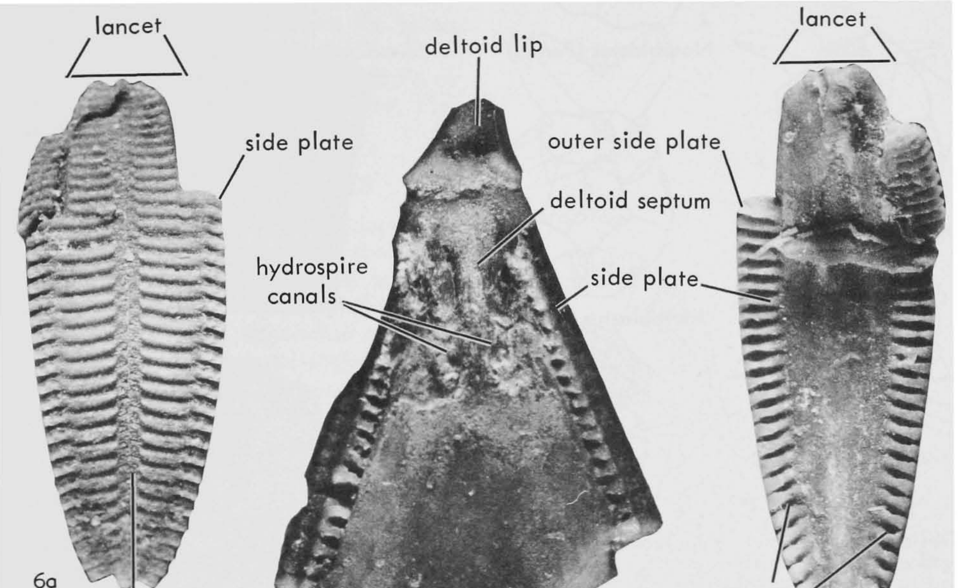

Fig. 184. *(Continued.)*

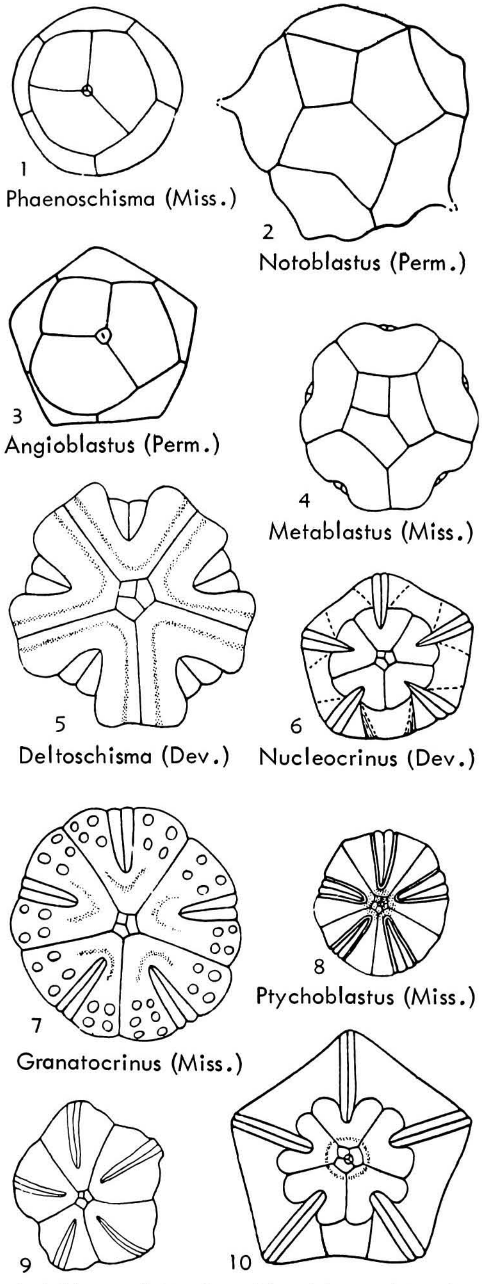

FIG. 185. Aboral views of blastoid calyces showing variation in relationships of basal circlet to adjacent plates of theca; *1-4,* basal circlet relatively large; *5-10,* basal circlet diminutive (not to scale) (Fay, n).

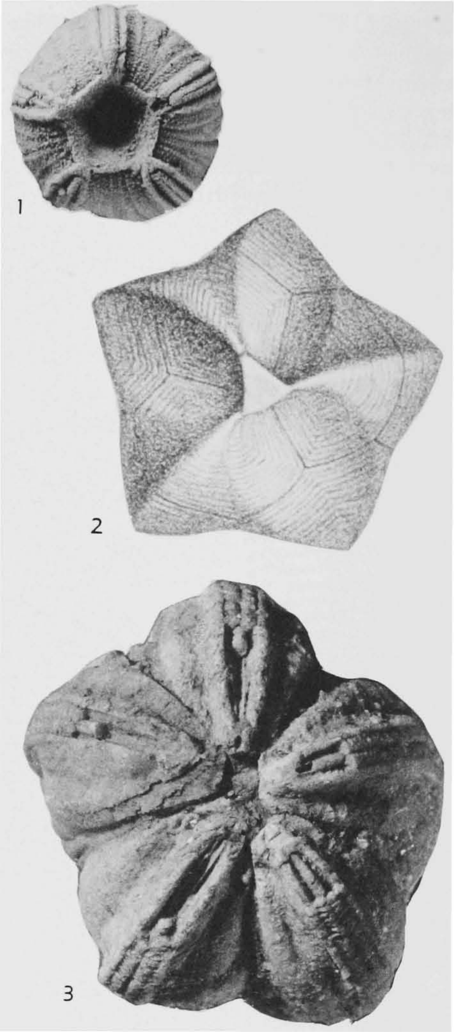

FIG. 186. Aboral views of blastoid calyces showing different types of basal relationships, all ×2.——*1. Globoblastus norwoodi* (OWEN & SHUMARD), L.Miss.(Osagian), Burlington, USA(Iowa) (Beaver, n).——*2. Tricoelocrinus woodmani* (MEEK & WORTHEN), Miss., loc. unknown (Etheridge & Carpenter, 1886).——*3. Auloblastus clinei* BEAVER, L. Miss.(Osagian), near Springfield, USA (Mo.) (Beaver, n).

observe (Fig. 185). They make up much of the basal view in most genera with moderate to short ambulacra (e.g., *Tricoelocrinus,* Fig. 186,*3*). In examples with ambulacra that nearly equal height of the theca, the basals are generally small and occupy very little of the basal view (e.g., *Globoblastus,*

Fig. 186,*1*). Some blastoids exhibit unusual basals because of asymmetrical thecas or poorly known basal relationships (Fig. 187). For example, *Astrocrinus* has a small quadrangular plate in the position of the azygous basal (*AB* interray), suggesting that the two other basals were resorbed (Fig. 187,*3*) (Fay, 1961, p. 10). In many genera with extended ambulacra the basals may be partially hidden in a shallow-basal depression (e.g., *Auloblastus,* Fig. 186,*3*), or in a deep cavity (e.g., *Globoblastus,* Fig. 186,*1*).

## EXTERNAL FEATURES

Swellings and ridges are developed on the basals of some genera. Many specimens of *Pentremites* exhibit a swollen area on each basal, the largest one located on the azygous basal in an interradial position. The swellings on the large zygous basals are developed beneath ambulacra *C* and *E,* appearing as enlargements of ridges that extend from the aboral tip of each ambulacrum to the point of column attachment.

Prominent ridges are developed on the basals of *Tricoelocrinus* (Fig. 186,*2*). The azygous basal is trisected by two ridges which extend from the point of column attachment to the lower tip of ambulacra *A* and *B*. Each of the zygous basals is transected by a strong ridge projecting from the point of attachment to the lower tip of ambulacra *C* and *E,* respectively. More weakly developed ridges follow a curved path from the point of column attachment to the ambulacra located at right and left of the ambulacrum to which the strong ridge leads.

## INTERNAL FEATURES

Little attention has been devoted to the internal nature of blastoid basals. Carpenter (1884, p. 413) speculated that the median canals of the lancets connected with the axial canal of the column by way of passageways within the basals and radials. Sections of the lancets near their aboral extremities indicate that the median canals of the lancet progressively decrease in size and seem to disappear. Careful examination of sections through the basals has failed to establish the presence of canals in the basals. A passageway connects the axial canal of the column with the central cavity of the theca.

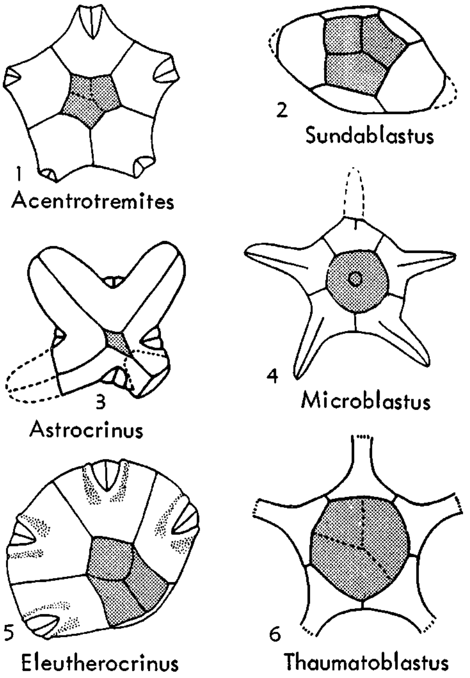

Fig. 187. Aboral views of blastoid calyces showing unusual features or relationships of basal circlets (shaded) (Fay, n).

Disarticulated basal plates permit study of internal surfaces and possible structures. An interesting feature of uncertain significance is an elongate depression on the inner surface of the *BD* zygous basal of *Pentremites* (Fig. 184,*1a-e*). This shallow trough is in the position of the *C* ambulacrum and aligned with it.

## RADIALS

Radial plates of the blastoid calyx overlie and alternate with the basals. The upper portion of each radial is divided by a deep sinus which is occupied by an ambulacrum (Fig. 178,*2*). The lower, undivided part of the plate is the **radial body**; the portions of the radial separated by the ambulacrum are the **radial limbs.** Each of the five radials is the same except in asymmetrical blastoids (e.g., *Eleutherocrinus,* Fig. 179,*15*).

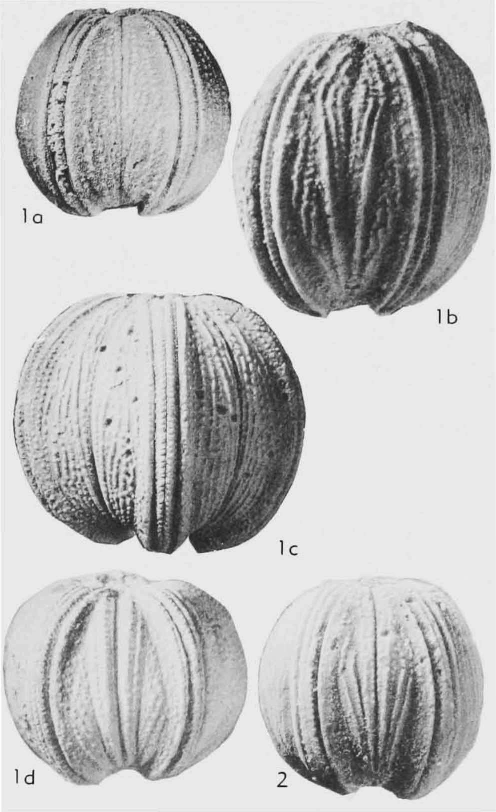

FIG. 188. Variation in ornament of radial plates of *Globoblastus norwoodi* (OWEN & SHUMARD), L. Miss.(Osagian), all ×2; *1a,c,d, 2,* specimens from Burlington Ls., at Burlington, Iowa; *1b,* specimen from Burlington Ls., near Springfield, Mo. (Beaver, n).

### SIZE AND SHAPE

The size and shape of radials vary greatly. Generally they equal half to two-thirds of the height of the theca (e.g., *Troosticrinus,* Fig. 179,*7*). In some elongate-globose forms the radials are very small and make up little of the theca (e.g., *Nucleocrinus,* Fig. 179,*16*). The shape of the radials may be governed largely by length of the ambulacra in blastoids where the ambulacra are confined to the summit. The radials may be only slightly notched if the ambulacra are short (e.g., *Agmoblastus,* Fig. 179,*10*) or wing-shaped if the ambulacra are long (e.g., *Thaumatoblastus,* Fig. 179,*23*).

### PORES OR SLITS

The radials are perforated by pores or slits only where these lead adaxially to the hydrospires. In some genera a row of tiny pores **(hydrospire pores)** connect the hydrospires with the exterior. In such genera the pores occur in a row parallel to an ambulacrum (Fig. 184,*6b*). The portion of each radial between the row of hydrospire pores and this ambulacrum is sometimes called the **hydrospire plate.** In other blastoids the radials (and deltoids) may be pierced by extended slits **(hydrospire clefts** or **spiracular slits)** that parallel the ambulacra and lead to the hydrospires. Generally two or more such clefts occur on either side of an ambulacrum.

### ORNAMENT

Surface sculpture of radials commonly ranges widely between genera. Many genera have radials which are nearly smooth except for the slight ridges indicating growth stages. Others, however, are strongly ornamented with nodes arranged in a random pattern or with rows of nodes in a symmetrical arrangement. Variations of ornament exist, not only between genera but between individuals of the same genus and species. For example, individuals of *Globoblastus norwoodi* show considerable difference in arrangement of nodes on the radials (Fig. 188).

## DELTOIDS

The deltoids are a circlet of interradially placed subtriangular plates which abut adoral edges of the radials (Fig. 178,*1,2*). Their sides normally are bounded by the ambulacra. The adoral portion of each deltoid bordering the mouth is called the **deltoid lip** (Fig. 184,*2b,7,8b*). Aborally, the deltoid lip is connected with the main portion of the deltoid, termed **deltoid body** (Fig. 184,*2a,b, 8b*), by a narrow internal connecting septum, termed **deltoid septum** (Fig. 184,*7, 8b*). In some genera, an external ridge called the **deltoid crest** longitudinally divides the deltoid (e.g., *Codaster*).

### VARIATIONS

The length of the deltoids is variable in different genera and, to a limited degree, within a given genus. The deltoids may be very large, exceptionally nearly equal to the total height of the theca (e.g., *Nucleo-*

*crinus,* Fig. 179,*16*), or oppositely, they may be so small as to be barely visible (e.g., *Troosticrinus,* Fig. 179,*7*). In *Pentremites,* slight differences of deltoid length are observed, but no definite trend during some portion of geologic time is recognized (Fig. 180). In the past, species having widely different deltoid lengths but apparently similar morphology otherwise have been grouped together in a single genus. Additional research on such species has shown that commonly they are characterized by important structural differences in addition to dissimilarity of the deltoids.

## ANAL DELTOIDS

[Section on anal deltoids by H. H. Beaver, R. O. Fay, and R. C. Moore]

Posterior interradial elements (in *CD* interray) of the blastoid theca are collectively termed **anal deltoids,** because they are associated in various ways with the anal opening. This orifice may or may not be confluent with spiracles of the posterior interray. Clearly, the anal deltoids are important morphological features.

### NOMENCLATURE

During the past 50 years various names have been introduced for different anal deltoids. The more important of these are **hypodeltoid** and **epideltoid** (Wanner, 1924), **subdeltoid** and **superdeltoid** (Cline & Heuer, 1950), **cryptodeltoids** (Beaver, 1961), and **paradeltoids** (Reimann & Fay, 1961). Usage of these and other terms has varied a good deal when applied to genera of differing age and morphology. It seems evident that precision in morphological descriptions and systematic diagnoses will be enhanced by agreement on terminology, accompanied by consistent use of appropriate names for the different kinds of anal deltoids.

Generally, plates classed as anal deltoids are clearly visible on the exterior surface of the blastoid calyx, or at least a major part of each such plate can be seen. Marginal features, however, are likely to be concealed and some anal-deltoid elements are largely or entirely hidden beneath the surface. Removal of skeletal material to expose the concealed plate or plates may be effected by weathering, by etching with an acid, and by grinding. Correct understanding of morphological relationships and nomenclature of features dependent on this call for thorough investigation of concealed characters, along with observation of surface features.

**Anideltoid.**—The name anideltoid is employed for an externally visible anal deltoid which is proved or not known to be accompanied by any others and which lies almost wholly on the aboral side of the anal opening *(Acentrotremites)* or anispiracle *(Pentremites, Ambolostoma)* (Fig. 189, *1a,b*). In genera with an anispiracle, this orifice seems to be located beyond the adoral extremity of the anideltoid, separating this plate from the mouth. Actually, a very small part of this undivided anal deltoid is visible externally between the anispiracle and the mouth. It is connected internally with the main part of the anideltoid by a slender, extremely fragile bar (deltoid septum) which extends beneath the anal opening and in nearly all specimens is concealed by matrix (Fig. 189,*1a*). Anideltoids and other deltoids of this type are termed **disjunct.**

**Hypodeltoid.**—Many blastoids have a single unpaired anal deltoid bordering the anal orifice on its aboral side. This plate is named hypodeltoid (Greek, *hypo-,* below, beneath) (Fig. 189,*2a-c, 3-5*). Hypodeltoids range in size from diminutive to very large, in some genera (e.g., *Granatocrinus,* Fig. 189,*4c*) comprising most of the posterior interray. Typically, the hypodeltoid overlaps adjacent anal deltoid plates and may form a hood over the anal opening. Oppositely, it may be concealed by bordering parts of the *C* and *D* radial limbs and in various genera judged to have possessed a small hypodeltoid, specimens fail to reveal its presence, owing to concealment and lack of detection by grinding, or possibly by separation and loss of the plate, or perhaps because of atrophy during ontogeny.

**Epideltoid.** An unpaired anal deltoid bordering the anal orifice on its adoral side is named epideltoid (Greek, *epi-*, above, upon) (Fig. 189,*1c, 2a-c*). An epideltoid may extend along the left and right sides of the anal opening but not the aboral side. Normally, epideltoids are associated with hypodeltoids, but in at least six genera *(Agmoblastus, Codaster, Microblastus, Para-*

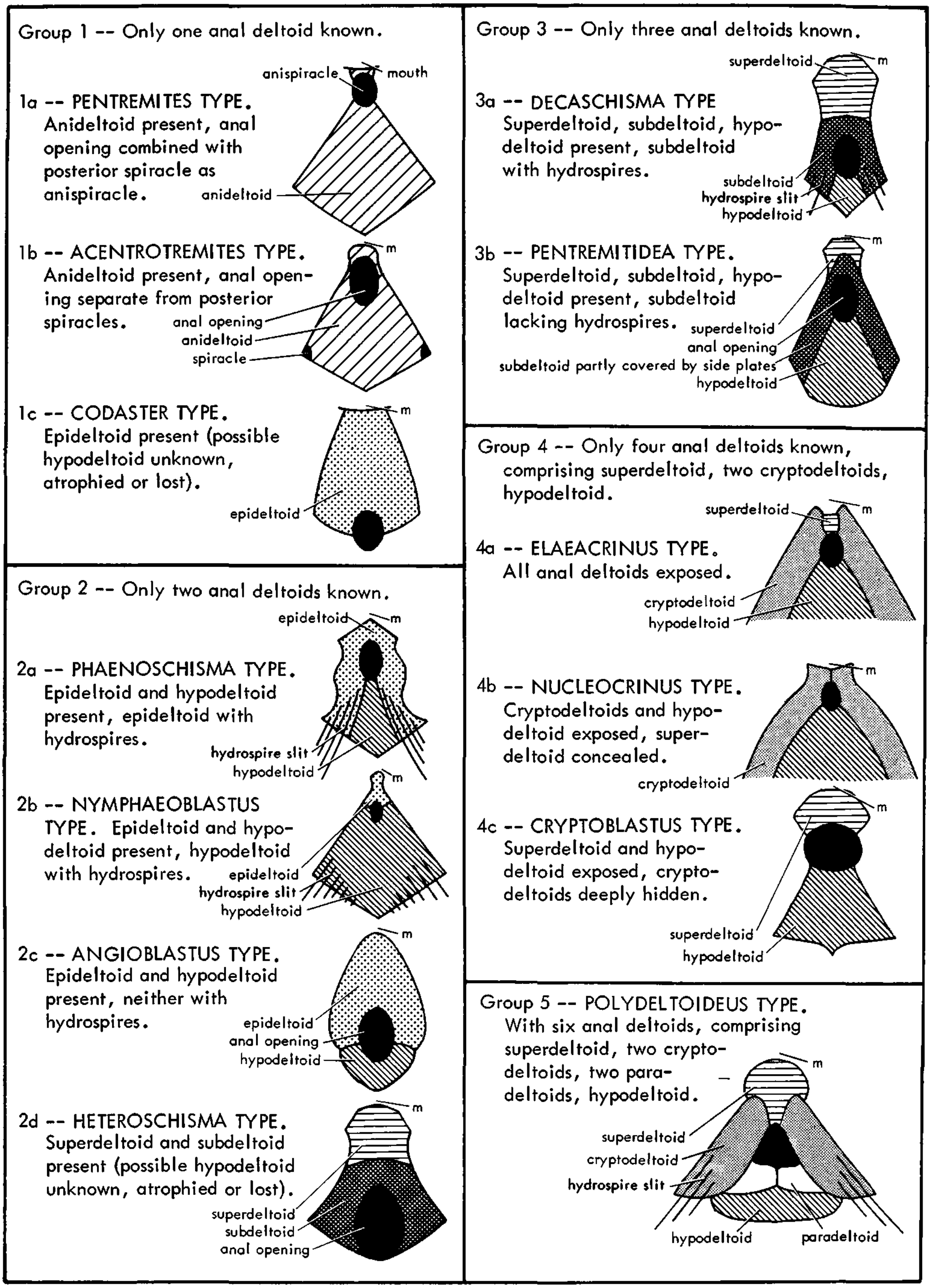

FIG. 189. Types of anal-deltoid relationships in blastoids (see Table 1 for distribution among genera) (Beaver, Fay, & Moore, n).

*codaster, Pterotoblastus, Sagittoblastus)* a hypodeltoid is missing or its presence is unproved (Fig. 189, *1c*). The unpaired well-exposed anal deltoid in these genera is identified as an epideltoid (rather than anideltoid) because it lies above the anal opening in manner exactly corresponding to undoubted epideltoids. Normally, epideltoid plates border the mouth, as well as the anal opening. Internally, the lateral portions of epideltoids may be infolded into hydrospires or conversely, epideltoid plates are not known to bear hydrospires. Table 1 records 32 genera having epideltoids with hydrospires and 12 genera having epideltoids without associated hydrospires.

**Subdeltoid.** A subdeltoid is defined as a small to moderately large, inverted U-shaped plate of the posterior interray in a few blastoids, located on the adoral and lateral margins of the anal orifice and abutting the aboral edge of a plate called superdeltoid (Fig. 189,*2d, 3*). As previously noted, subdeltoid and superdeltoid are terms introduced by CLINE & HEUER (1950) and, although considered to be undesirable on etymological grounds, they are adopted because of their morphological significance. Subdeltoids now are recognized in five genera *(Decaschisma, Brachyschisma, Pentremoblastus, Heteroschisma, Pentremitidea)* among which this plate in the first three listed contains hydrospires, whereas no hydrospires have been observed in anal deltoids of the others. In MOORE's opinion, comparison of subdeltoids with the paired plates called cryptodeltoids in several genera (e.g., *Polydeltoideus,* Fig. 189,*5*) strongly suggest homology because fusion of the adoral extremities of the cryptodeltoids would produce a plate exactly like the narrow-limbed inverted U-shaped subdeltoid seen in *Decaschisma,* for example. Conversely, a separation of the subdeltoid limbs would yield a pair of cryptodeltoids.

**Superdeltoid.**—A fourth kind of unpaired anal deltoid (counting anideltoid, hypodeltoid, and epideltoid as others) has been termed superdeltoid. Such a plate invariably is located at the summit of the posterior interray, adjoining the mouth, and is distinguished from epideltoid, which also may border the mouth, by lack of any contact with the anal opening in genera which possess a subdeltoid (Fig. 189, *2d,3*) and in other genera by association with cryptodeltoids (Fig. 189,*4-5*). If the cryptodeltoids do not meet each other on the adoral side of the anus the superdeltoid may border both oral and anal orifices (as shown in numerous diagrams illustrating adoral parts of subdeltoid- and cryptodeltoid-bearing blastoids which accompany systematic descriptions in the *Treatise*). As a "rule of thumb" we may say that all blastoids with a subdeltoid or pair of cryptodeltoids have a superdeltoid and no epideltoid. All blastoids lacking a subdeltoid or cryptodeltoids have an epideltoid, or the single anal deltoid is an anideltoid.

**Cryptodeltoids.**—Anal deltoids located on opposite lateral margins of the anal opening and invariably paired are termed cryptodeltoids (Greek, *crypto-,* hidden) because generally they are only partly visible externally and in some genera they are entirely concealed by other plates of the theca. They may be short and small (e.g., *Troosticrinus*) or relatively long and large (e.g., *Elaeacrinus, Nucleocrinus,* Fig. 189,*4a,b*); they may be entirely separated from one another (e.g., *Elaeacrinus,* Fig. 189,*4a,c,5*) or may meet adorally (e.g., *Nucleocrinus,* Fig. 189,*4b*) in manner cutting off contact of a superdeltoid from the anal opening. Substance of the cryptodeltoids may be infolded in the form of hydrospires. In at least a dozen genera, all with two externally visible anal deltoids, the presence of cryptodeltoids can be demonstrated by grinding or by cutting properly oriented thin sections (Table 1). Such preparations show that the cryptodeltoids mostly are slender elongate plates which are overlapped on their aboral parts by the hypodeltoid, invariably present in blastoids provided with cryptodeltoids. The cryptodeltoids may form internal walls between spiracular and anal passageways of an anispiracle and adorally they may be confluent with superdeltoid extensions (septa). Exceptionally, cryptodeltoids are very large, almost completely exposed plates which are prominent components of the theca (e.g., *Nucleocrinus, Elaeacrinus, Placoblastus,* Fig. 189,*4a,b*).

**Paradeltoids.**—Small paired plates termed paradeltoids (Greek, *para-,* associated) are distinguished in a single genus (*Polydeltoid-*

TABLE 1.--Distribution of Anal-deltoid Types among Blastoid Genera

[Explanation.--Numbered anal-deltoid types correspond to those described in accompanying text. Each kind of anal-deltoid plate is indicated by letter designation, as follows: A = anideltoid, C = cryptodeltoids, E = epideltoid, H = hypodeltoid, S = subdeltoid, SS = superdeltoid. Symbols for hydrospire slits or infolds: + indicates present, o indicates absent.]

| Anal-deltoid Types | | | | | Suprageneric and Generic Taxa | Anal-deltoid Plates | | | | | | Age |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 2 | 3 | 4 | 5 | | A | C | H | E | S | SS | |
| | | | | | FISSICULATA | | | | | | | |
| | | | | | PHAENOSCHISMATIDAE | | | | | | | |
| ?1d | - | - | - | - | Microblastus | - | - | ?H | E + | - | - | Perm. |
| - | 2a | - | - | - | Phaenoschisma | - | - | H o | E + | - | - | Miss. |
| - | 2a | - | - | - | Hadroblastus | - | - | H o | E + | - | - | Miss. |
| - | 2a | - | - | - | Phaenoblastus | - | - | H o | E + | - | - | L.Carb. |
| - | 2a | - | - | - | Dipteroblastus | - | - | H o | E + | - | - | Perm. |
| - | 2a | - | - | - | Neoschisma | - | - | H o | E + | - | - | Perm. |
| - | 2a | - | - | - | Notoblastus | - | - | H o | E + | - | - | Perm. |
| - | 2a | - | - | - | Sphaeroschisma | - | - | H o | E + | - | - | Perm. |
| - | 2a | - | - | - | Sundablastus | - | - | H o | E + | - | - | Perm. |
| - | 2a | - | - | - | Thaumatoblastus | - | - | H o | E + | - | - | Perm. |
| - | 2a | - | - | - | Timoroblastus | - | - | H o | E + | - | - | Perm. |
| - | 2b | - | - | - | Nymphaeoblastus | - | - | H + | E o | - | - | Miss. |
| - | - | 3a | - | - | Decaschisma | - | - | H o | - | S + | SS | Sil. |
| - | - | - | 4a | - | Deltoschisma | - | C + | H o | - | - | SS | Dev. |
| - | - | - | 4a | - | Pleuroschisma | - | C + | H o | - | - | SS | Dev. |
| - | - | - | 4c | - | Hyperoblastus | - | C + | H o | - | - | SS | Dev. |
| - | - | - | - | 5 | Polydeltoideus | - | C + | H o | - | - | SS | Sil. |
| | | | | | BRACHYSCHISMATIDAE | | | | | | | |
| - | - | 3a | - | - | Brachyschisma | - | - | H o | - | S + | SS | Dev. |
| | | | | | CODASTERIDAE | | | | | | | |
| 1c | - | - | - | - | Codaster | - | - | ?H | E o | - | - | Miss. |
| 1c | - | - | - | - | Agmoblastus | - | - | ?H | E o | - | - | Penn. |
| 1c | - | - | - | - | Paracodaster | - | - | ?H | E o | - | - | Perm. |
| 1c | - | - | - | - | Pterotoblastus | - | - | ?H | E o | - | - | Perm. |
| 1c | - | - | - | - | Sagittoblastus | - | - | ?H | E o | - | - | Perm. |
| - | 2c | - | - | - | Angioblastus | - | - | H o | E o | - | - | Perm. |
| - | 2c | - | - | - | Indoblastus | - | - | H o | E o | - | - | Perm. |
| - | 2c | - | - | - | Nannoblastus | - | - | H o | E o | - | - | Perm. |
| - | 2d | - | - | - | Heteroschisma | - | - | ?H | - | S o | SS | Dev. |
| | | | | | OROPHOCRINIDAE | | | | | | | |
| - | 2a | - | - | - | Orophocrinus | - | - | H o | E + | - | - | Miss. |
| - | 2a | - | - | - | Pentablastus | - | - | H o | E + | - | - | Penn. |
| - | 2a | - | - | - | Anthoblastus | - | - | H o | E + | - | - | Perm. |
| | | | | | ASTROCRINIDAE | | | | | | | |
| ?1a | - | - | - | - | ?Pentephyllum | ?A | - | - | - | - | - | L.Carb. |
| - | 2c | - | - | - | Cryptoschisma | - | - | H o | E o | - | - | Dev. |
| - | 2c | - | - | - | Astrocrinus | - | - | H o | E o | - | - | L.Carb. |
| - | 2c | - | - | - | Ceratoblastus | - | - | H o | E o | - | - | Perm. |
| - | - | ?3b | - | - | Pentremitidea | - | - | H o | - | S o | SS | Dev. |

TABLE 1 (continued)

| Anal-deltoid Types | | | | | Supragenetic and Generic Taxa | Anal-deltoid Plates | | | | | | Age |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 2 | 3 | 4 | 5 | | A | C | H | E | S | SS | |
| | | | | | SPIRACULATA | | | | | | | |
| | | | | | TROOSTICRINIDAE | | | | | | | |
| - | - | - | 4a | - | Troosticrinus | - | C + | H o | - | - | SS | Sil. |
| - | - | - | 4a | - | Schizotremites | - | C + | H o | - | - | SS | Dev. |
| - | - | - | 4a | - | Metablastus | - | C + | H o | - | - | SS | Miss. |
| - | - | - | 4a | - | Tricoelocrinus | - | C + | H o | - | - | SS | Miss. |
| | | | | | DIPLOBLASTIDAE | | | | | | | |
| - | 2a | - | - | - | Nodoblastus | - | - | H o | E + | - | - | Miss. |
| - | - | - | 4c | - | Diploblastus | - | C + | H o | - | - | SS | Miss. |
| | | | | | GRANATOCRINIDAE | | | | | | | |
| - | 2a | - | - | - | Granatocrinus | - | - | H o | E + | - | - | Miss. |
| - | 2a | - | - | - | Carpenteroblastus | - | - | H o | E + | - | - | Miss. |
| - | 2a | - | - | - | Cribroblastus | - | - | H o | E + | - | - | Miss. |
| - | 2a | - | - | - | Dentiblastus | - | - | H o | E + | - | - | Miss. |
| - | 2a | - | - | - | Heteroblastus | - | - | H o | E + | - | - | Miss. |
| - | 2a | - | - | - | Monadoblastus | - | - | H o | E + | - | - | Miss. |
| - | 2a | - | - | - | Monoschizoblastus | - | - | H o | E + | - | - | Miss. |
| - | 2a | - | - | - | Poroblastus | - | - | H o | E + | - | - | Miss. |
| - | 2a | - | - | - | Ptychoblastus | - | - | H o | E + | - | - | Miss. |
| - | - | - | 4a | - | Pyramiblastus | - | C + | H o | - | - | SS | Miss. |
| - | - | - | 4c | - | Cryptoblastus | - | C + | H o | - | - | SS | Miss. |
| - | - | - | 4c | - | Mesoblastus | - | C + | H o | - | - | SS | Miss. |
| - | - | - | 4c | - | Tanaoblastus | - | C + | H o | - | - | SS | Miss. |
| | | | | | SCHIZOBLASTIDAE | | | | | | | |
| 1b | - | - | - | - | Acentrotremites | ?A+ | - | - | - | - | - | L.Carb. |
| - | 2a | - | - | - | Strongyloblastus | - | - | H o | E + | - | - | Dev. |
| - | 2a | - | - | - | Deltoblastus | - | - | H o | E + | - | - | Miss. |
| - | 2a | - | - | - | Lophoblastus | - | - | H o | E + | - | - | Miss. |
| - | 2a | - | - | - | Orbiblastus | - | - | H o | E + | - | - | Miss. |
| - | 2a | - | - | - | Schizoblastus | - | - | H o | E + | - | - | Miss. |
| - | - | - | 4c | - | Auloblastus | - | C + | H o | - | - | SS | Miss. |
| | | | | | NUCLEOCRINIDAE | | | | | | | |
| - | - | - | 4a | - | Elaeacrinus | - | C + | H o | - | - | SS | Dev. |
| - | - | - | 4a | - | Placoblastus | - | C + | H o | - | - | SS | Dev. |
| - | - | - | 4b | - | Nucleocrinus | - | C + | H o | - | - | SS | Dev. |
| | | | | | PENTREMITIDAE | | | | | | | |
| 1a | - | - | - | - | Pentremites | A + | - | - | - | - | - | Miss.-Penn. |
| 1a | - | - | - | - | Ambolostoma | A + | - | - | - | - | - | Miss. |
| - | ?2a | - | - | - | Belocrinus | - | - | H o | ?E + | - | - | Dev. |
| - | 2a | - | - | - | Petaloblastus | - | - | H o | E + | - | - | Miss. |
| - | 2a | - | - | - | Calycoblastus | - | - | H o | E + | - | - | Perm. |
| - | - | 3a | - | - | Pentremoblastus | - | - | H o | - | S + | SS | Miss. |
| - | - | - | 4a | - | Eleutherocrinus | - | C + | H o | - | - | SS | Dev. |
| - | - | - | 4a | - | Rhopaloblastus | - | C + | H o | - | - | SS | Perm. |
| - | - | - | 4c | - | Cordyloblastus | - | C + | H o | - | - | SS | Dev. |
| - | - | - | 4c | - | Devonoblastus | - | C + | H o | - | - | SS | Dev. |
| | | | | | ORBITREMITIDAE | | | | | | | |
| - | - | - | 4c | - | Orbitremites | - | C + | H o | - | - | SS | Miss. |
| - | - | - | ?4c | - | Doryblastus | - | ?C + | H o | - | - | SS | Miss. |
| - | - | - | 4c | - | Ellipticoblastus | - | C + | H o | - | - | SS | Miss. |
| - | - | - | 4c | - | Globoblastus | - | C + | H o | - | - | SS | Miss. |

*eus,* Fig. 189,*5*), which has externally visible cryptodeltoids, a hypodeltoid, and a superdeltoid. The paradeltoids adjoin aboral parts of the cryptodeltoids and rest on the adoral margin of the hypodeltoid.

### RELATION OF HYDROSPIRES TO ANAL DELTOIDS

Information is yet far from sufficient for full appraisal of the infolding of anal deltoid plate substance into hydrospires or of septal extensions of such plates adjoining hydrospires. Also, the extent to which hydrospire relationships may bear on discrimination of different kinds of anal deltoids is now incompletely determined. An objective in preparing Table 1, given on later pages, has been to record what may be considered as reasonably known, bearing in mind that present lack of observations on hydrospire characters by no means established their nonexistence.

### TYPES OF BLASTOIDS BASED ON ANAL-DELTOID CHARACTERS

Blastoids are classifiable in groups defined by the kinds, numbers, and arrangements of anal deltoids. These are described briefly in following paragraphs with designations of included types and the distribution of genera among the types as indicated in Table 1. Inasmuch as assemblages differentiated on the basis of anal-deltoid characters may include representatives of two or more families belonging either to the Fissiculata, or Spiraculata, or both, it is evident that the placement of blastoid genera in one anal-deltoid type or another is unrelated to systematic classification.

#### Group 1

Genera in which only one anal deltoid is known are placed in Group 1, and these are divisible into three types, as follows.

**Type 1a—Pentremites Type.**—In this type the single anal deltoid recognized consists of an anideltoid, in which the anal opening is combined with the posterior spiracle to form an anispiracle located near the adoral extremity of the plate (Fig. 189,*1a*). The anideltoid is disjunct. Only the comparatively uncommon *Ambolostoma* is joined with myriads of *Pentremites* individuals assigned to numerous species in Type 1a.

**Type 1b—Acentrotremites Type.**—An anideltoid is present in Type 1b, as in 1a, but distinguished by separateness of the anal opening from a pair of posterior spiracles and by the location of all of these near the aboral margin of the anideltoid, which is described as conjunct (Fig. 189,*1b*). *Acentrotremites* is the sole known representative of the type. The possible occurrence of an additional anal deltoid or deltoids, as reported by Joysey & Breimer (1963, p. 483), is very uncertain.

**Type 1c—Codaster Type.**—In this type the single observed anal deltoid is identified as an epideltoid, with the anal opening medially placed on its aboral margin (Fig. 189,*1c*). A hypodeltoid, which is unknown, may be atrophied or lost in all specimens studied. Type 1c includes *Agmoblastus, Codaster, Microblastus, Paracodaster, Pterotoblastus,* and *Sagittoblastus,* all of which belong to Fissiculata.

#### Group 2

Group 2 is characterized by the presence of only two known anal deltoids. It is by far the largest of the differentiated anal-deltoid groups, for its 39 contained genera are approximately one-half of all known blastoid forms. Among four types that are discriminated, two are represented only by their single name-giving genus, whereas the others contain 31 and six genera, respectively.

**Type 2a—Phaenoschisma Type.**—The two anal-deltoid plates of Type 2a are an epideltoid and hypodeltoid, the epideltoid bearing hydrospires (Fig. 189,*2a*). Counting one questionably assigned spiraculate genus, the Spiraculata outnumber the Fissiculata in the ratio of 19 to 12. The spiraculates are distributed among four families and the fissiculates among three families (Table 1). Listed alphabetically (with spiraculates distinguished by an asterisk), the genera of Type 2a are as follows: *Anthoblastus, ?*Belocrinus, *Calycoblastus, *Carpenteroblastus, *Cribroblastus, *Deltoblastus, *Dentiblastus, Dipteroblastus, *Granatocrinus, Hadroblastus, *Heteroblastus, *Lophoblastus, *Monadoblastus, *Monoschizoblastus, Neoschisma, *Nodoblastus, Notoblastus, *Orbiblastus, Orophocrinus, *Pentablastus, *Petaloblastus, Phaenoblastus, Phaenoschisma, *Poroblastus, *Ptychoblastus, *Schizoblastus, Sphaeroschisma, *Strongyloblastus,* *Sundablastus, Thaumatoblastus, Timoroblastus.*

**Type 2b—Nymphaeoblastus Type.**—As in Type 2a, the two anal deltoids are epideltoid and hypodeltoid, distinction of Type 2b resting on the occurrence of hydrospires in the hypodeltoid of *Nymphaeoblastus* (Fig. 189,*2b*).

**Type 2c—Angioblastus Type.**—The two anal deltoids are an epideltoid and a hypodeltoid, neither of which bears hydrospires, on this basis being assigned to a separate type (Fig. 189,*2c*). Six fissiculate genera are included in Type 2c, three belonging to the Codasteridae and three to the Astrocrinidae (Table 1). They are as follows: *Angioblastus, Astrocrinus, Ceratoblastus, Cryptoschisma, Indoblastus,* and *Nannoblastus.*

**Type 2d—Heteroschisma Type.**—This type differs from the others of Group 2 in that the two anal deltoids are distinguished as a superdeltoid and a subdeltoid. A postulated possible hypodeltoid is unknown, perhaps atrophied or lost (Fig. 189,*2d*). Only *Heteroschisma,* among blastoids now known, belongs to Type 2d.

### Group 3

Blastoids having three, but only three, known anal deltoids comprise Group 3, within which two types are distinguished.

**Type 3a—Decaschisma Type.**—The three anal deltoids consist of a superdeltoid, a subdeltoid, and a hypodeltoid, the subdeltoid bearing hydrospires (Fig. 189,*3a*). The type includes two fissiculate genera *(Brachyschisma, Decaschisma)* and a single spiraculate genus *(Pentremoblastus).*

**Type 3b—Pentremitidea Type.**—This type corresponds to Type 3a in having superdeltoid, subdeltoid, and hypodeltoid plates but is distinguished by lack of hydrospires in the subdeltoid (Fig. 189,*3b*). Only *Pentremitidea* appears to belong here.

### Group 4

Blastoids characterized by the possession of four anal deltoids, but no more than four, are placed together in Group 4. The four anal-deltoid plates comprise a superdeltoid, two cryptodeltoids, and a hypodeltoid, all of which may be at least partly visible externally or some concealed.

**Type 4a—Elaeacrinus Type.**—In blastoids of Type 4a all anal deltoids are entirely or at least partially exposed (Fig. 189,*4a*). The type includes two fissiculate genera—*Pleuroschisma, Deltoschisma*—and nine spiraculate genera—*Elaeacrinus, Eleutherocrinus, Metablastus, Placoblastus, Pyramiblastus, Rhopaloblastus, Schizotremites, Tricoelocrinus,* and *Troosticrinus* (Table 1).

**Type 4b—Nucleocrinus Type.**—In the *Nucleocrinus* Type, which includes only this genus, the cryptodeltoids and hypodeltoid are large, fully exposed anal deltoids but the superdeltoid is a small concealed plate (Fig. 189,*4b*).

**Type 4c — Cryptoblastus Type.** — Anal-deltoid Type 4c is characterized by external visibility of the superdeltoid and hypodeltoid, combined with complete concealment of the cryptodeltoids, which in some genera are deeply hidden (Fig. 189,*4c*). The type includes one fissiculate genus, *Hyperoblastus,* and 11 spiraculates: *Auloblastus, Cordyloblastus, Cryptoblastus, Devonoblastus, Diploblastus, ?Doryblastus, Ellipticoblastus, Globoblastus, Mesoblastus, Orbitremites, Tanaoblastus.*

### Group 5

No blastoid has only five anal-deltoids but one form with six such plates is known. It is assigned to Group 5 and Type 5.

**Type 5—Polydeltoideus Type.**—The anal deltoids of *Polydeltoideus,* which is the only presently known representative of Type 5, consist of a superdeltoid, two cryptodeltoids, two paradeltoids, and a hypodeltoid, all more or less exposed (Fig. 189,5).

Not definitely placed in any anal-deltoid type is the problematical genus *Pentephyllum,* described from a fossil that evidently is a steinkern (internal mold) and presently available for study only from artificial replicas. Efforts by Macurda (personal communication) and others to locate the type specimen have been fruitless. On this account and because of anomalous features shown by the replicas, in the view of Macurda, Beaver, and Moore, this nominal genus should be disposed of as "Unrecognizable"' or at least "Classification Uncertain." Fay, however, considers it assignable to the Astrocrinidae, and thinks that its anal deltoid, without known anal orifice, is a doubtful sort of anideltoid. To place *Pentephyllum* as questionable representative

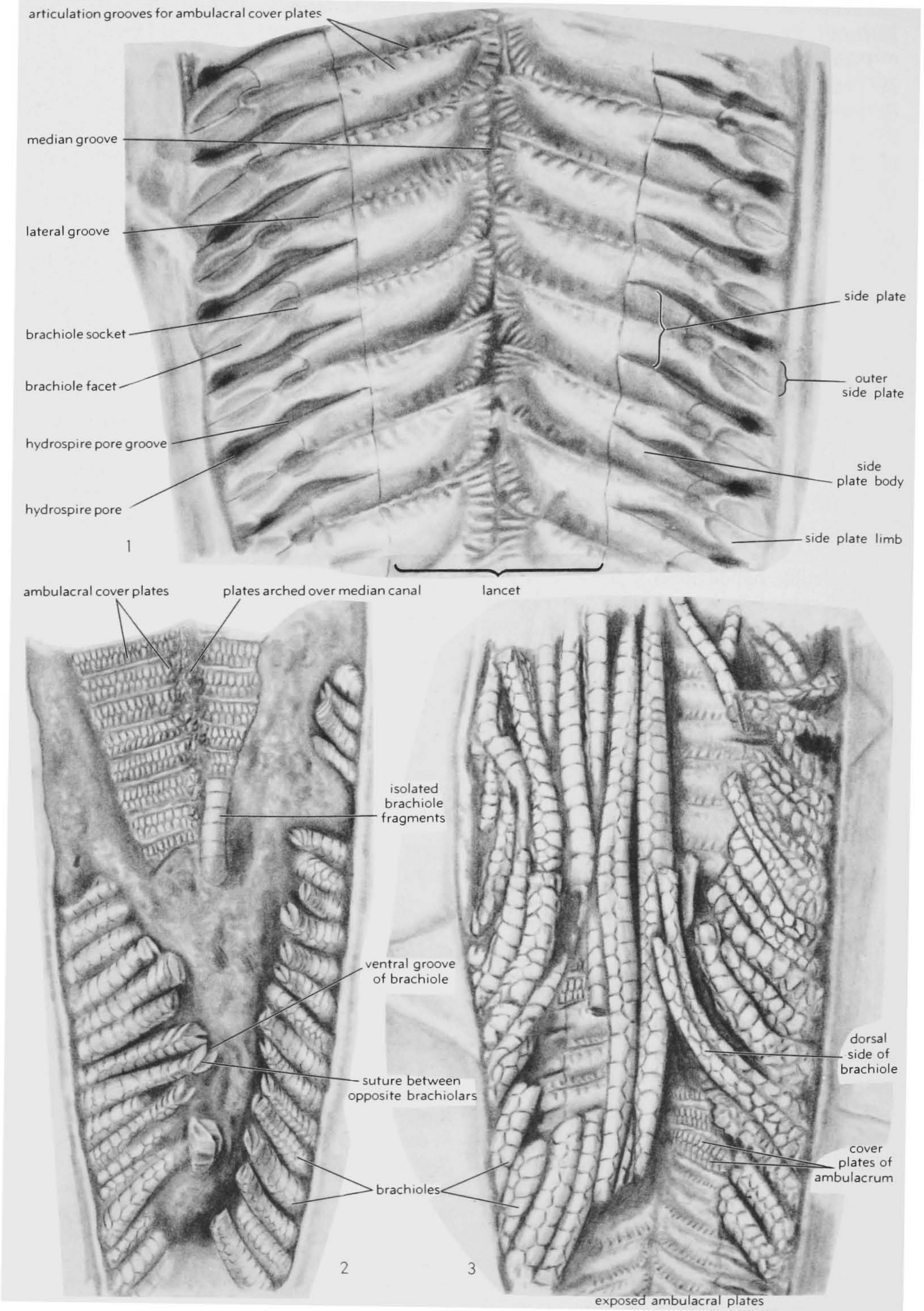

FIG. 190. [*Explanation on facing page.*]

of anal-deltoid Type 1b, associated with *Acentrotremites,* as proposed by FAY, or alternatively, to introduce a separate type for it (say Type 1d) are equally undesirable.

## AMBULACRA AND AMBULACRAL PLATES

The ambulacra normally consist of five petaloid to narrowly linear areas which radiate from the vicinity of the mouth (Fig. 178,*1*). The length of the ambulacra may be short, as in *Codaster,* or very long, with ambulacra equal to length of the theca, as in *Globoblastus* (Fig. 188). In profile, the exposed abaxial surfaces of the ambulacra may be convex, flat, or concave. For example, in *Orbitremites* and *Cryptoblastus,* genera with side plates lying on the lancet, the ambulacra are convex, but in *Pentremites* with side plates abutting against the lancet, the ambulacra may be convex, flat, or concave (Fig. 180). The principal structures of the ambulacra concerned with food gathering are the median groove, lateral grooves, brachiole sockets, and ambulacral cover plates; the hydrospire pores, commonly considered structures of the ambulacra, are part of the water-vascular system (Fig. 190).

### MEDIAN AND LATERAL GROOVES

The **median groove** is a shallow V-shaped groove that notches the mid-line of an ambulacrum longitudinally (Fig. 191). The groove passes under the summit into the mouth adorally; termination of the groove occurs at the aboral end of the lancet. The sides of the groove are marked by tiny indentations (crenulations); the covering plates of the ambulacrum are seated in these indentations.

**Lateral grooves,** located at intervals equal to the width of the side plates, lead from the brachiole sockets to the median groove (Fig. 191,*1*). Small indentations similar in design and function to those of the median groove occur on either side of each lateral groove. Transverse ridges lie parallel to and alternate with the lateral grooves, sides of the ridges sloping into the grooves.

The median groove is entirely located on the side plates in many pre-Mississippian genera. Among Mississippian blastoids (e.g., *Cryptoblastus, Orbitremites, Globoblastus*), in which the side plates rest on the lancet, the adoral portion of the median groove is located on the lancet, whereas the aboral part of the groove rests on the side plates. In *Pentremites,* the median groove and the admedial part of the lateral grooves are excavated in the lancet.

### LANCET

A relatively narrow linear thecal element in the longitudinal middle part of each ambulacrum is known as the **lancet plate** (Fig. 184,*3a,b, 6a,b,*). In many genera (e.g., *Orbitremites*) the lancet nearly fills the radial sinus, and the side and outer side plates rest upon it. In *Pentremites,* however, the side plates abut against the lancet, rather than lie on it, and the lancet fills only about half the width of an ambulacral area (Fig. 184,*2b,c, 6a,b*).

The internal (adaxial) surface of the lancet is smooth except for two longitudinal adaxial ridges which nearly equal the length of the lancet (Fig. 184,*3b*). A shallow medial depression occurs between these ridges.

#### TRANSVERSE SHAPE

The transverse shape of the lancet may be nearly flat, concave, or convex. Within the limits of a species, however, and at a given transverse level, the shape and struc-

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[*See facing page*]

FIG. 190. Morphological features of blastoid ambulacra illustrated by *Pentremites symmetricus* HALL, U. Miss.(Chester), USA(Ill.).——*1*. Part of ambulacrum lacking brachioles, ×9.——*2*. Part of ambulacrum with proximal portions of numerous brachioles in position of attachment, biserial arrangement of brachiolars clearly shown on their dorsal (external) side and broken terminations demonstrating presence of deep V-shaped ventral food groove; biserially arranged small cover plates over lateral grooves of ambulacrum shown in upper part of figure, but along median groove they fail to show any systematic arrangement, ×4.2.——*3*. Brachioles resting on ambulacrum in position of their articulation, exposing dorsal or side portions, with biserial arrangement of brachiolars clearly evident, ×4.2 (Beaver, n).

ture of this plate are fairly constant. For example, thin sections of typical specimens of *Globoblastus* cut at the radial-deltoid suture show the adaxial surface of the lancet to be nearly flat (Fig. 191,6); in sections made distally from the mid-length of

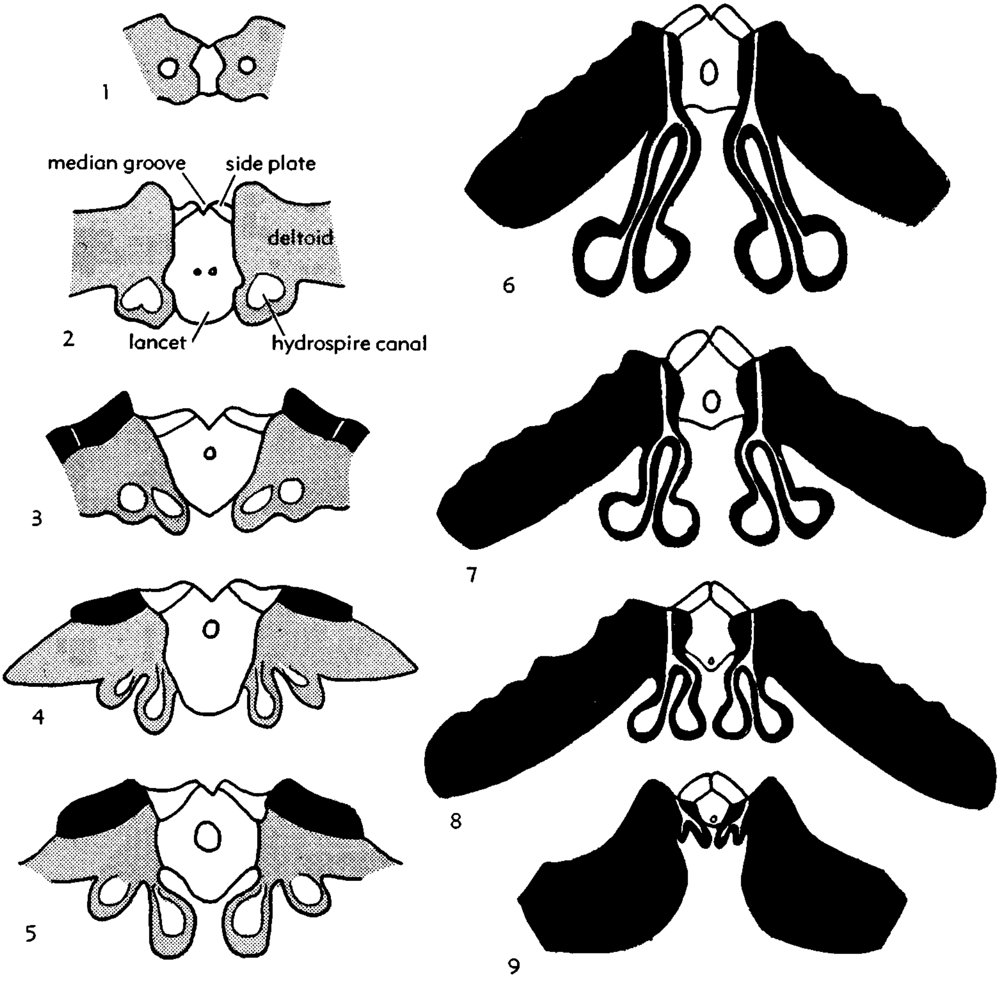

Fig. 191. Lancet and hydrospire structures of *Globoblastus,* L.Miss.(Osag.), USA(Mo.); drawings of thin sections of *G. norwoodi* cut perpendicular to an ambulacrum showing development of hydrospires; (lancet and side plates unshaded, deltoids shaded, radials black), ×8 (Beaver, 1961).——*1*. Section at adoral end of ambulacrum showing one of divided hydrospire canals on each side of lancet.——*2*. Section slightly below *1,* division of hydrospire canals produced by infolding of deltoidal material; longitudinal canal of lancet divided here into two canals which separate farther and farther and leave lancet on their respective sides to form oral ring canal.——*3*. Section just below radio-deltoid suture, radials resting on deltoids. The division of the hydrospire canals within the deltoids has been completed.——*4*. Section below *3,* showing hydrospire folds beginning to form.——*5*. Section below *4,* hydrospire development still in deltoid material.——*6*. Section short distance below radio-deltoid suture showing fully developed hydrospires composed entirely of radial material.——*7*. Section about 0.3 length of ambulacrum below summit of calyx.——*8*. Section just below half length of ambulacrum showing hydrospires noticeably shortened and longitudinal canal of lancet adaxially migrated.——*9*. Section near lower end of ambulacrum showing adaxial parts of radials about to envelop tiny hydrospires.

the ambulacrum, the lancet protrudes adaxially toward the interior of the calyx (Fig. 191,*8,9*). Specimens that deviate widely from the lancet structure observable in typical specimens of a species should be examined for other morphological differences, indicating that they may belong to other species or genera.

### CANALS

Three longitudinal passageways (median canal and two lateral canals) are excavated partially or entirely in the lancet. The **median canal** is a small longitudinal internal canal that extends from the distal end of the lancet to the vicinity of the summit, where it divides to form part of the oral ring canal. For example, in *Globoblastus* (Fig. 191), from the vicinity of the summit aborally, this canal decreases in size and changes position from the center of the lancet to its median adaxial margin. The **lateral canals** are two small passageways lying on either side and obliquely adaxial to the median groove; they are excavated in lancet and side plate material along the suture between the lancet and side plates. The lateral canals parallel the median groove from its aboral extremity to beyond the radial-deltoid suture. The course of the lateral canals in the vicinity of the summit is unknown. They have been recognized in *Auloblastus* and WANNER indicated their presence in *Thaumatoblastus*.

### "UNDERLANCET"

The so-called "underlancet" or "sublancet" plate was first illustrated (WACHSMUTH & SPRINGER, 1879, p. 387, pl. 17) in a cross-sectional drawing of *Pentremites* which showed a triangular-shaped plate lying beneath the lancet. The "underlancet" was shown to be perforated by a longitudinal canal, whereas the lancet was indicated to be imperforate. An examination of several hundred thin sections of *Pentremites* under binocular and petrographic microscopes has failed to show this "underlancet." The observed structure apparently is either a deposit of secondary calcite beneath the lancet, a thickening of the inner walls of the hydrospires, or a filling of fine clay in the area bounded by the inner surface of the lancet and upper walls of the hydrospires. Similar "underlancet" structures have been reported in *Orophocrinus, Pentablastus,* and *Calycoblastus,* in which this element is recognized to consist of two adjacent hydrospire plates joined beneath the lancet, or formed by thickening of the inner walls of hydrospires beneath the lancet (FAY, 1961, p. 15). JOYSEY & BREIMER (1963, p. 479-481) have recently described in considerable detail the so-called "underlancet" plate of *Pentablastus.* Their description agrees essentially with that of FAY, for they state that the "two halves of the underlancet are continuous with a pair of hydrospire plates" (Fig. 192). The name "fused hydrospire plate" is undoubtedly a more suitable term than "underlancet," but even the name hydrospire plate is not desirable, because it refers only to the portion of the radial and deltoid occurring between the hydrospire pores or slits, and the ambulacral margin (lancet and side plates). In reality, therefore, when the terms "fused hydrospire plate" or "underlancet" are used, they refer to the juncture of radial or deltoid material beneath a lancet.

## SIDE PLATES AND OUTER SIDE PLATES

The **side plates** of ambulacra consist of numerous small skeletal elements which either rest on the lancet (Fig. 193,*2*), or lie between the walls of the radial sinus and the lancet (Fig. 190,*1*). The abmedial, adoral portion of each side plate is excavated for the reception of an outer side plate. The wider, admedial portion of the side plate is called the **side-plate body**; the narrower, abmedial area is the **side-plate limb.**

### SIDE PLATES RESTING ON LANCET

*Globoblastus* is representative of blastoids in which the side plates rest on the lancet. Approximately 50 to 60 side plates are arranged along either side of each ambulacrum. At the aboral end and along the mid-line of an ambulacrum, the admedial ends of the side plates are in contact with each other and the median groove is developed on these side plates. The abmedial ends of the side plates rest with a slanted surface against the portion of the radials which is sometimes called the hydrospire plate.

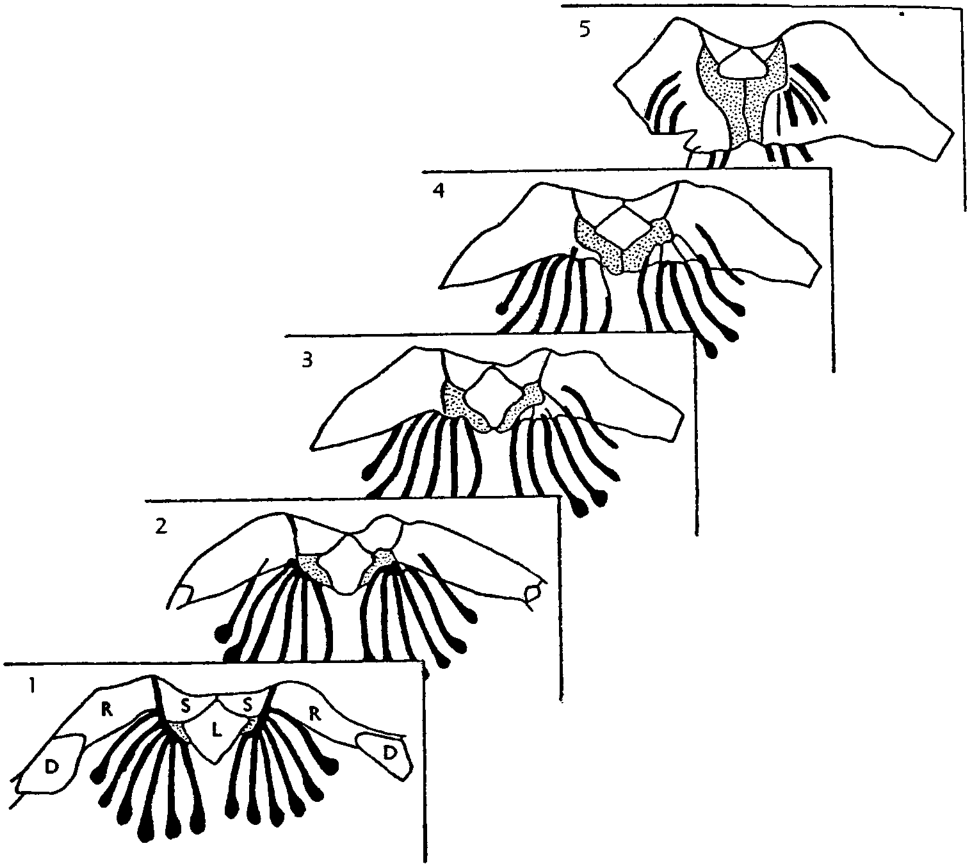

Fig. 192. Serial sections of *Pentablastus supracarbonicus* Sieverts-Doreck, U.Carb., Spain, showing hydrospire plates (stippled) coming together admedially beneath lancet to develop so-called "underlancet" in aboral to spiracular slits; section *1* is at level of spiracular slits, whereas section *5* is at aboral extremity of ambulacrum, ×5. [Deltoid (D), lancet (L), radial (R), side plates (S).] (Joysey & Breimer, 1963.)

### SIDE PLATES ABUTTING LANCET

In *Pentremites* the side plates are located between the walls of the radial sinus and the lancet. The surface of contact between the lancet and the side plates commonly is curved, the abmedial convex surface of the

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[*See facing page*]

Fig. 193. Ambulacral structures especially in relation to hydrospires (lancet and side plates shaded, deltoids oblique-ruled, radials black) (Beaver, n).——*1. Orbitremites derbiensis* (Sowerby), L.Carb. (Middle Ls.), Eng.(Yorks.); ×10.——*2. Globoblastus norwoodi* (Owen & Shumard), L.Miss.(Burlington Ls.), near Springfield, Mo.; ×4.5.——*3. Placoblastus obovatus* (Barris), M.Dev.(Thunder Bay Ls.), near Alpena, Mich.; ×4.4 (from Fay, 1961, fig. 194).——*4. Mesoblastus crenulatus* (Roemer), L.Carb. (Tournais.), Belg.; ×5.8 (from Fay, 1961, fig. 153).——*5. Troosticrinus reinwardti* (Troost), Sil. (Niagara Gr.), Decatur Co., Tenn.; ×9.1 (from Fay, 1961, fig. 220).——*6. Auloblastus clinei* Beaver, L.Miss.(Burlington Ls.), near Springfield, Mo.; ×5.8.——*7. Pentremites godoni* (Defrance), U.Miss. (Paint Creek F.), near Floraville, Ill.; ×7.——*8. Orophocrinus stelliformis* (Owen & Shumard), L.Miss. (Burlington Ls.), near Hannibal, Mo.; ×9.5.——*9. Eleutherocrinus cassedayi* Shumard & Yandell, M. Dev.(Hungry Hollow F.), Thedford, Ont.; ×7.5 (from Fay, 1961, fig. 134).——*10. Pentremites rusticus* Hambach, L. Penn.(Bloyd Sh.), near Fort Gibson, Okla.; ×5.2.——*11. Hyperoblastus filosus* (Whiteaves), M.Dev.(Hungry Hollow F.), near Thedford and Arkona, Ont.; ×15.4 (from Fay, 1961, fig. 31).

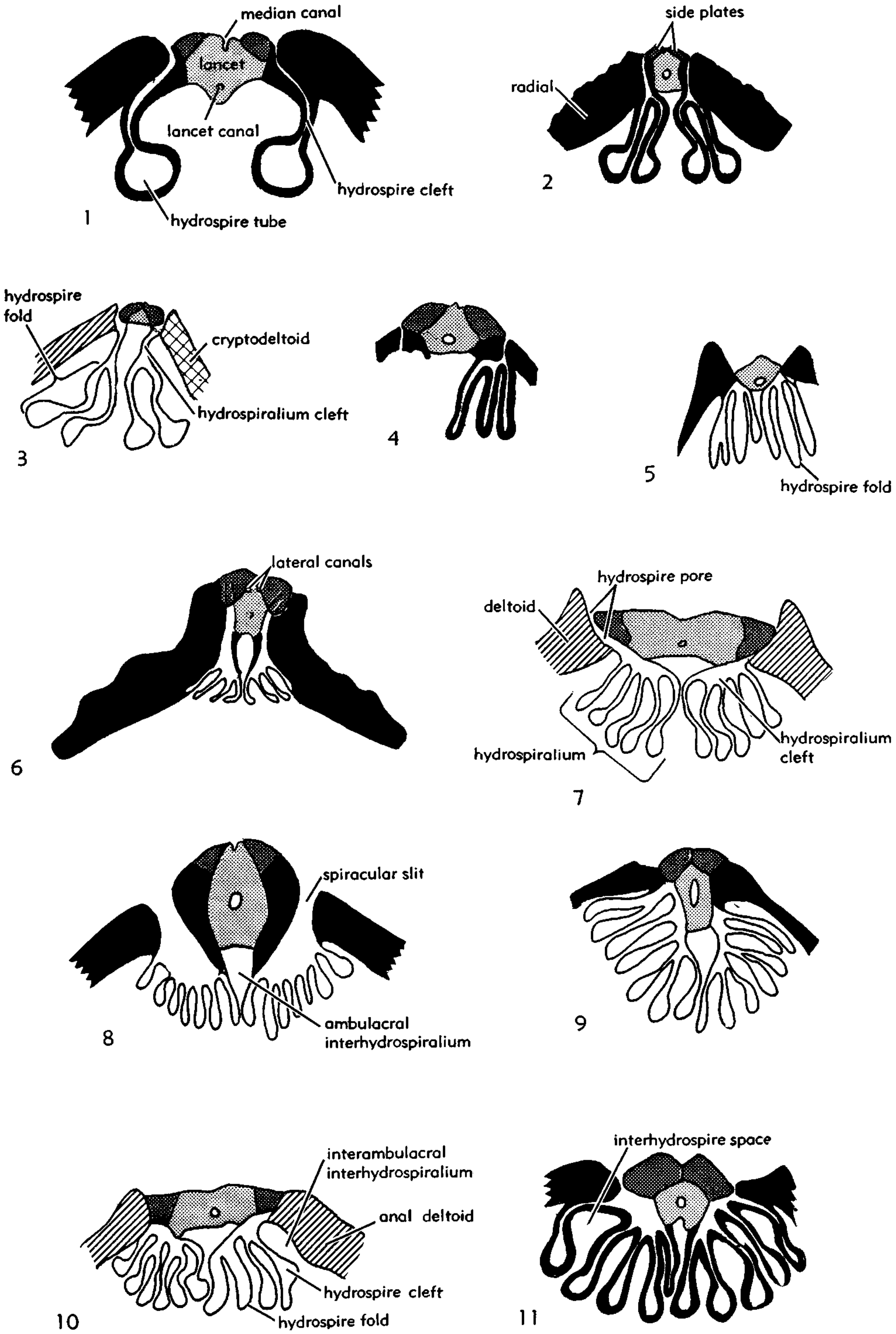

Fig. 193. [*Explanation on facing page.*]

lancet fitting snugly into the abmedial concave surface of the side plates (Fig. 184, *2b,c*; 193,*7*). The adoral and aboral sutures between side plates of *Pentremites* do not coincide with the lateral grooves as in some genera, but alternate with them. The lateral groove of the lancet extends onto the side-plate body and leads to the **brachiolar socket** (place of attachment of a brachiole), located on the admedial portion of the side-plate limb. A deep pore groove or pore furrow located on the suture between the side and outer plate leads to the hydrospire pore.

### OUTER SIDE PLATES

The outer side plates, for example in *Pentremites,* are located adorally from the side-plate limb and aborally from a hydrospire pore groove. The aboral portion of the outer side plate forms half of the brachiolar socket and includes one of the brachiolar facets or articulation depressions (Fig. 190,*1*; 194,*1*).

In *Globoblastus* the outer side plates are relatively large, their length being approximately two-thirds the length of the side plates. The width of the outer side plate increases abmedially from the admedial contact of each outer plate with the side plate to the margin of the radial sinus, the width of the outer side plate equaling that of the side plate. One outer side plate adjoins each side plate.

## BRACHIOLAR SOCKETS

A brachiolar socket is a pit centrally placed on a prominent round mound or knob located at the adlateral end of a lateral groove, generally near the margin of an ambulacrum (Fig. 190,*1*). In genera with side plates lying on the lancet (e.g., *Globoblastus*), the socket is located on the admedial, adoral portion of each side plate; each socket has tiny ridges and grooves extending down and away from the summit of its mound or knob. The ridges and grooves aid in articulation of the brachioles and ambulacral covering plates. In *Pentremites,* each brachiolar socket is located on the admedial portion of a side-plate limb, similar to its position in *Globoblastus.* Between the brachiolar socket and margin of the radial sinus, two gently depressed surfaces, the brachiolar facets, occur. The aboral facet is located on the side-plate limb; the adoral facet is developed on the outer side plate. The presence of a suture between the facets may have provided flexibility to the biserially arranged brachiole.

## AMBULACRAL COVER PLATES

The **ambulacral cover plates** are tiny polygonal plates which roof over the lateral and median grooves to provide a series of passageways from the brachiolar sockets to the vicinity of the mouth (Fig. 194,*1*). The plates covering the lateral grooves are seated in tiny depressions, termed **cover plate sockets,** which alternate on either side of the lateral grooves (Fig. 190,*1*). In general, the tips of the plates are arranged in a biserial pattern; this system is not always perfect, however, and commonly the upper ends of the plates merely abut. The plates

[*See facing page*]

FIG. 194. Ambulacral and summit structures of calyx illustrated by *Pentremites godoni* (DEFRANCE), U.Miss. (Chester.), U.S.A.(Ill.), ×12 (drawings by Roger B. Williams; Beaver, n).——*1*. Ambulacrum showing well-preserved cover plates in position over lateral and median grooves, part of single small brachiole preserved on right side of ambulacrum; cover plates biserially arranged over lateral grooves but lacking orderly pattern over median groove. The cover plates are inferred to have roofed over the grooves in manner forming conduits for passage of fluids from brachioles to the mouth.——*2*. Oral pyramid viewed from anal *(CD)* interray, mouth concealed by solid triangular slightly curved elongate plates which appear to be seated in regularly spaced sockets around mouth, anal opening covered by smaller spinose plates arranged in alternating rows, and spiracles also concealed by relatively broad plates disposed in imbricating manner. Movements of the plates which would facilitate flow of fluids through these orifices are inferred to have been possible.——*3*. Specimen shown in Fig. *2* rotated slightly toward right, providing nearly direct view of plates covering *DE* spiracle, ×12. Although relationships of the median groove (with its cover plates) to the oral pyramid is not clear, owing to imperfect preservation, the passageway along the median groove is interpreted to enter the mouth beneath the oral pyramid, but no evidence of an external opening appears at the point of entry.

which roof over the median groove are arranged in a much less symmetrical manner than those of the lateral grooves and the "roof" is higher.

In well-preserved specimens of *Pentremites godoni,* 11 or 12 cover plates occur along each side of a lateral groove. Allowing about 22 plates for each lateral groove

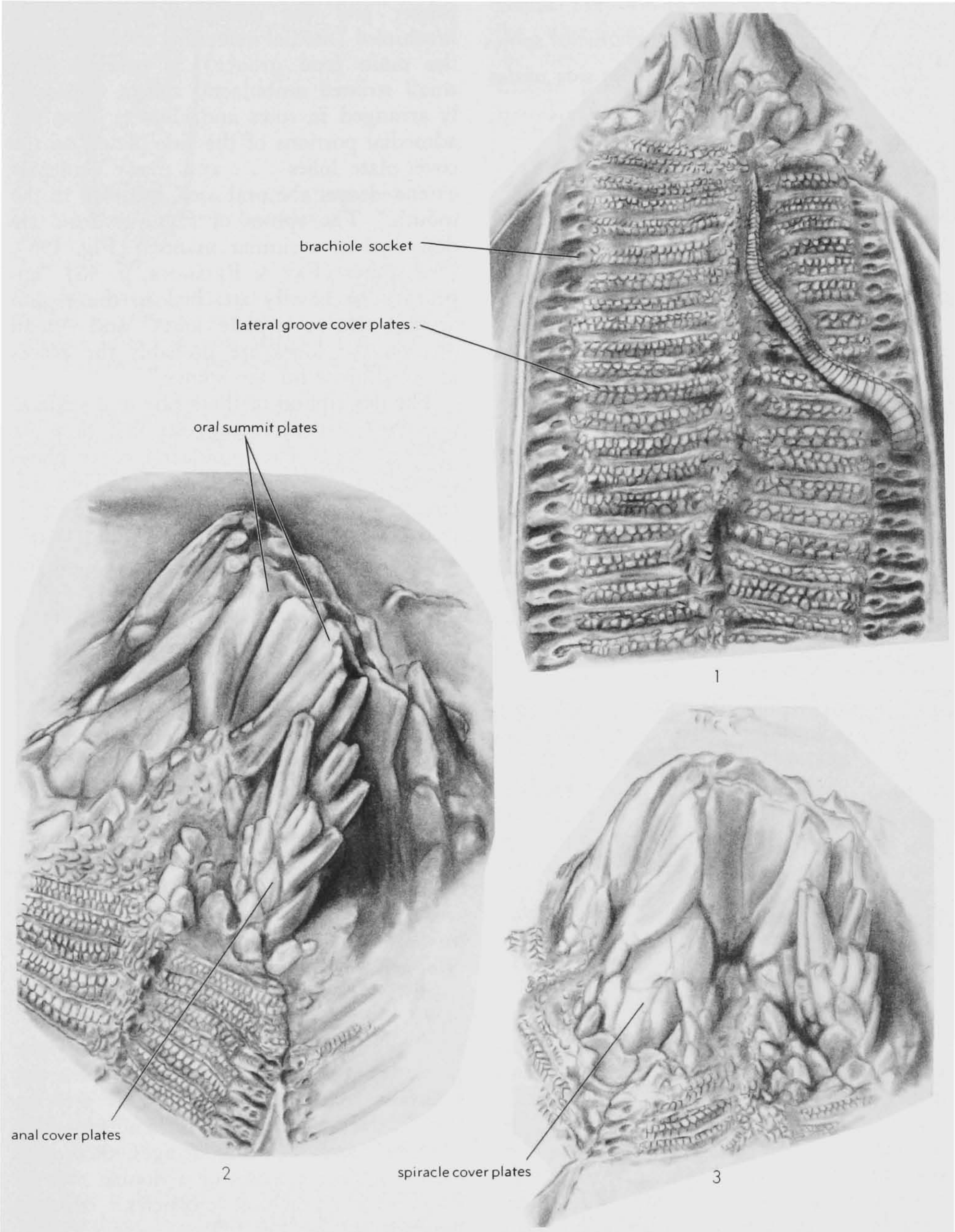

FIG. 194. [*Explanation on facing page.*]

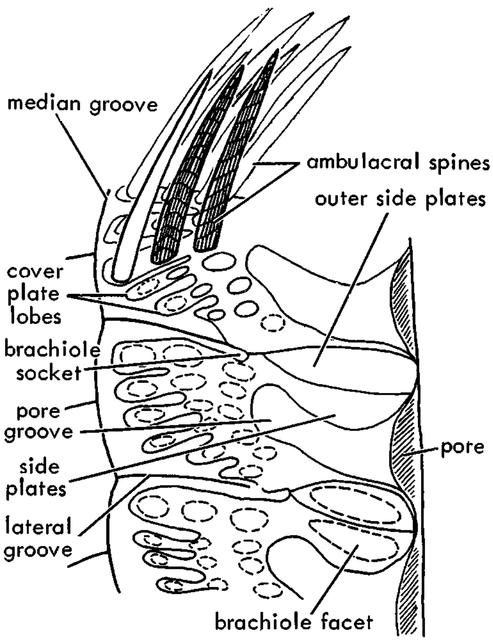

FIG. 195. Composite diagrammatic drawing of side plates in *Hyperoblastus nuciformis* (REIMANN), M. Dev.(Hungry Hollow F., Widder beds), near Thedford, Ontario; showing probable position of ambulacral spines, ×75 (Fay & Reimann, 1962).

and approximately 100 grooves for each of the five ambulacra, an adult individual of *P. godoni* must have had some 10,000 or more cover plates for the lateral grooves, not including the hundreds that covered the median grooves of the five ambulacra. In the area of the summit the covered median groove seems to pass between the plates of the anal pyramid so as to lead to the mouth (Fig. 194,*2,3*).

## AMBULACRAL SPINES

Small needle-like curved plates (**ambulacral spines**) attached to the side plates and arranged in rows along sides of the ambulacral median groove have recently been described by FAY & REIMANN (1962). Each of the spines is about 1 mm. long and 0.1 mm. wide and has spiral striations. The spines have been recognized in *Placoblastus, Devonoblastus,* and *Hyperoblastus.* In *Placoblastus* they are attached to the side plates and seem to be restricted to the area adjacent to the median groove. Concerning *Devonoblastus* FAY & REIMANN (p. 35, 36) stated, "The region adjacent to the thecal main food groove, between the food grooves proper and the admedial walls of the brachioles (medial referring to the line of the main food groove), is covered with small striated ambulacral spines, apparently arranged in rows and clusters upon the admedial portions of the side plates, on the cover-plate lobes . . . and many evidently extended over the oral area, adjacent to the mouth." The spines of *Hyperoblastus* are described in a similar manner (Fig. 195). The spines (FAY & REIMANN, p. 48) "appear to be basally attached to the region around the cover-plate lobes" and "small pits on the lobes are probably the places of attachment for the spines."

The description of these rare and seldom-preserved structures suggests that they are different from the ambulacral cover plates so well preserved in *Pentremites.* They differ in being more spinelike and in their location away from the median and lateral grooves proper. The occurrence of ambulacral spines in the summit area indicates that some Devonian genera (e.g., *Hyperoblastus*) probably had an oral pyramid similar to that of *Pentremites.*

## BRACHIOLES

Brachioles are armlet appendages which articulate with the brachiolar facets of the side plates and outer side plates, and rise from the margin of each ambulacrum, adoral ones extending well above the summit of the theca. They have been described from a number of genera, including *Devonoblastus, Diploblastus, Eleutherocrinus, Globoblastus, Hyperoblastus, Pentremites, Pleuroschisma, Pyramiblastus, Troosticrinus, Orophocrinus,* and *Placoblastus.* Examination of many almost complete specimens of *Pentremites* from Chesteran rocks of southwestern Illinois, as well as excellently preserved individuals belonging to other genera of different ages, show that each brachiole consists of a double row of alternating brachiole ossicles, termed **brachiolars** (Fig. 190,*2,3*).

In *Pentremites* each brachiolar is slightly longer than wide and is longitudinally grooved by approximately 12 striations.

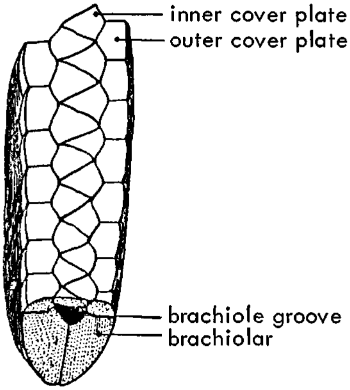

FIG. 196. Diagram of brachiolar fragment *Hyperoblastus nuciformis* (REIMANN), M.Dev., Ontario, showing inner and outer series of brachiole cover plates, ×35 (Fay & Reimann, 1962).

The upper surface of each joint is heavily crenulated and serves as an articulating surface in the same manner that columnals of the stem articulate with each other. The brachiolars are smallest where they articulate with the brachiolar facets; they become progressively longer for a short distance, and then attain a uniform length. The average length of each brachiolar is approximately 0.5 mm. The ventral or admedial side of each brachiole bears a V-shaped groove **(brachiolar groove),** formed by two rows of adjacent and alternating joints (Fig. 190,2); the groove extends over the brachiolar socket (Fig. 194,*1*). Although cover plates have not been observed to enclose ventral grooves of brachioles, such plates probably existed. The length of the brachioles ranges from 1 to 2 times the height of the theca. Seldom, even in excellently preserved specimens, are all brachioles preserved and consequently, the very large number of brachioles borne by a complete individual is not commonly realized. A count of the brachiolar sockets shows that average-sized specimens of *Pentremites godoni* had approximately 500 brachioles; larger specimens possessed nearly 600, but young individuals only about 200.

FAY & REIMANN (1962, p. 48) have described the brachiole cover plates of *Hyperoblastus nuciformis.* The brachiole groove is covered by an inner and outer series of alternating cover plates (Fig. 196). The outer series (called outer cover plates) occurs along either side of the ventral brachiole surface as alternating plates; each brachiolar carries about four outer cover plates. The brachiole groove is bounded by the outer cover plates and is roofed over by the biserially arranged small triangular-shaped inner cover plates, which correspond in number to the outer cover plates.

## SUMMIT PLATES

For a century or more, controversy has existed over the presence or absence of summit plates in blastoids. If their presence was admitted, details of their appearance, arrangement, and function have been disputed (OWEN & SHUMARD, 1850, p. 65; SHUMARD, 1858, p. 244; WHITE, 1863, p. 482; HAMBACH, 1884, p. 541; ETHERIDGE & CARPENTER, 1886, p. 70; WACHSMUTH & SPRINGER, 1887; FAY & REIMANN, 1962). The principal reason for disagreements and differing descriptions is that various blastoid genera apparently have different types of summit structures and that in the overwhelming number of blastoids collected, summit plates are lacking, or poorly preserved.

At least three different types of summit structures are known to occur. A first type characterized by many small polygonal plates which cover the general vicinity of the mouth is designated as the *Globoblastus* type. A second type distinguished by the presence of approximately six relatively large many-sided oral plates is designated as the *Placoblastus* type. A third type having a pyramid-like structure of numerous plates over the mouth is defined as the *Pentremites* type.

### GLOBOBLASTUS TYPE

The summit of *Globoblastus norwoodi* is covered by numerous very tiny plates which completely cover the peristome (Fig. 197,*3b*) and seem to extend down each ambulacrum where they become the ambulacral cover plates (WHITE, 1863, p. 483). Nothing is known of plates that may cover the spiracles and anus, but by analogy with other genera, it is assumed they also were present.

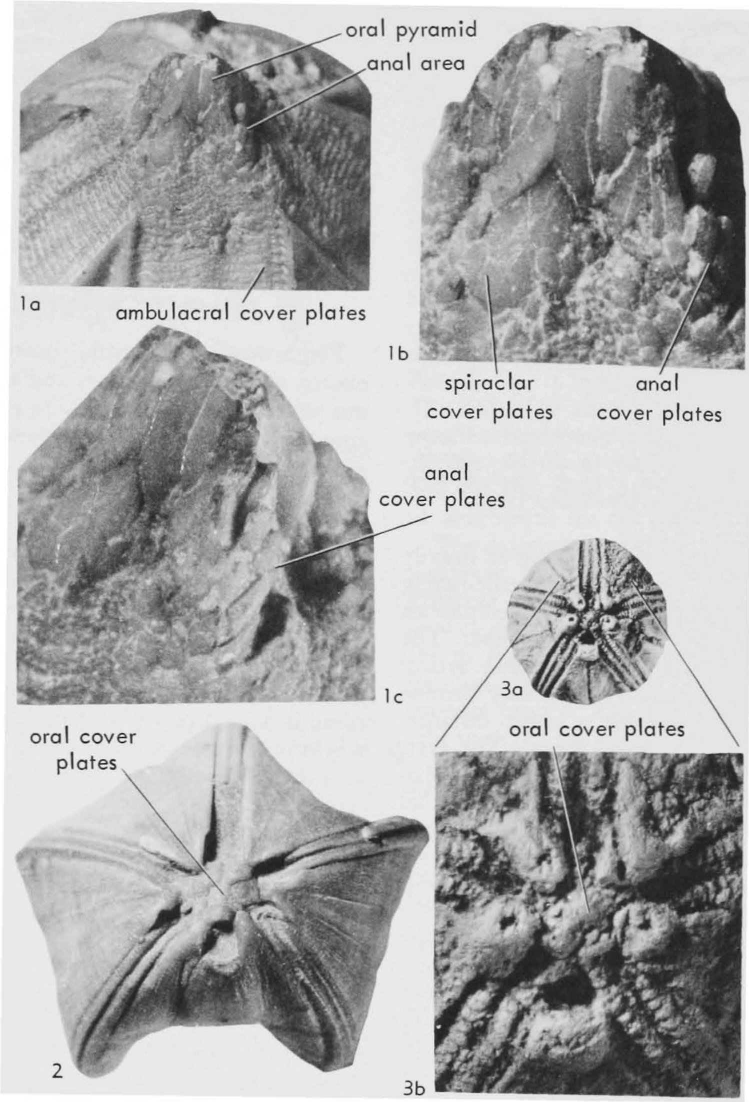

FIG. 197. Types of blastoid summit plates (Beaver, n).——*1. Pentremites godoni* (DEFRANCE), U.Miss. (Chester.), USA(Ill.); *1a,* summit view showing pyramid-like structure over mouth area and ambulacral cover plates, ×6; *1b,* oral pyramid and plates covering spiracle and anal opening, ×15; *1c,* anal cover plates, ×15.——*2. Placoblastus obovatus* (BARRIS), M.Dev., USA(Mich.); oral cover plates, ×3.——*3. Globoblastus norwoodi* (OWEN & SHUMARD), L.Miss.(Osag.), USA(Iowa); *3a,* summit view showing tiny oral plates, ×2; *3b,* oral cover plates, ×7.

## PLACOBLASTUS TYPE

*Placoblastus* is representative of blastoids having approximately six oral plates which completely roof over the summit area between the deltoid tips (Fig. 197,*2*). The plates are irregular in outline, with five or six ill-defined sides. Several of them seem to be located at adoral tips of the deltoids, but two of the plates are adoral of ambulacra *D* and *E*.

### PENTREMITES TYPE

*Pentremites* represents a blastoid group distinguished by having a pyramid-like structure, termed **oral pyramid,** developed over the mouth area (Fig. 194,*2,3*; 197,*1*). The pyramid is composed of numerous solid, slightly curved, toothlike plates which arch over the summit so that the mouth, spiracles, and anal openings are completely covered by them.

The lower ends of the plates covering the mouth articulate with the theca along adoral extremities of the deltoids. The deltoid lips, adjacent to the mouth, have alternating ridges and grooves, the toothlike plates being seated in the latter.

The plates covering the spiracles, which are broader and shorter than those above the mouth and seemingly immovable, pass adorally between and beneath the plates over the mouth (Fig. 194,*3*; 197,*1b*).

Plates covering the anus are short toothlike spines which become gradually larger near the plates covering the mouth. They are arranged biserially along both sides of the opening (Fig. 194,*2*; 197,*1c*).

The lower ends of the plates covering the spiracles and anus are attached to the theca along inner margins of the spiracles and anal opening. The toothlike plates above the anus and plates concealing the mouth appear to be more flexible than those covering the spiracles and probably were able to open and close.

## HYDROSPIRES

Distinctive internal structures of blastoids are known as **hydrospires.** Each such structure is a calcareous thin-walled linear infold extending adaxially beneath either side of an ambulacrum. Hydrospires may occur singly (e.g., *Orbitremites,* Fig. 193,*1*), or as a group of associated hydrospires (**hydrospiralium,** Fig. 193,*7*). The hydrospiralium (or alternatively, a single hydrospire) connects abaxially with hydrospire pores or slits which penetrate various thecal plates (radials, deltoids, and anal deltoids), or occur beneath them and an ambulacrum. It leads adorally to a simple hydrospire canal which opens into a spiracle or has its external outlet in a single spiracular slit or in a number of subparallel hydrospire slits. The thin calcareous wall surrounding a hydrospire is termed a **hydrospire fold** (Fig. 193,*3*), and the space enclosed by the fold is a **hydrospire cleft** (Fig. 193,*1*). Commonly, the adaxial portion of a hydrospire is expanded to develop a **hydrospire tube** (Fig. 193,*1*). Space within a hydrospiralium exclusive of the hydrospire clefts is the **hydrospiralium cleft** (Fig. 193,*3*). The area between adjacent hydrospires of the same hydrospiralium is an **interhydrospire space** (Fig. 193,*11*). Space between adjacent hydrospiralia is termed an **interhydrospiralium.** It may refer to an area adaxial to the lancet, and thus be ambulacral (Fig. 193,*8*), or may concern a space adaxial to the deltoids or adjacent radial limbs, and be interambulacral (Fig. 193,*10*).

### DEVELOPMENT OF HYDROSPIRES

Hydrospires develop through infolding of deltoid and radial material adaxially adjacent to the lancet. The most admedial hydrospire of blastoids develops first and then other folds are formed successively in an abmedial direction. From maximum size near the radial-deltoid suture, the hydrospires diminish in size and finally disappear at the aboral end of an ambulacrum.

Hydrospire development in *Globoblastus* is representative of that observed in many other blastoid genera. Development, as shown by serial sections cut normal to an ambulacrum, begins when the single external spiracle opening divides initially into two hydrospire canals. Each of the canals leads into a hydrospiralium developed beneath the nearest sides of adjacent ambulacra. Formation of two canals, one on either side of a lancet, into the hydrospires within adjacent deltoids is illustrated in Figure 191,*1-5*. Each of the canals subdivides into two hydrospires by infolding of the deltoid material (Fig. 191,*2-5*). At this position, with the hydrospires completely formed, transition from deltoid to radial material occurs.

The hydrospires attain greatest size just below the deltoids, and from this area they progressively decrease in size aborally (Fig. 191,*6-9*). Hydrospire size and greatest thecal diameter do not correspond longitudinally; maximum hydrospire size occurs substantially adoral to the greatest thecal diameter.

## STRUCTURE OF HYDROSPIRES

Some workers (e.g., WACHSMUTH & SPRINGER, 1879) have supposed that the hydrospire folds of blastoids expanded and contracted during life. Serial sections of numerous specimens representing several genera, however, indicate a remarkable constancy of hydrospire shape at various levels of the theca and in different hydrospiralia. Minor differences may occur in parts of any given hydrospiralium (Fig. 191,*4-9*), but these are introduced gradually between its adoral and aboral extremities. Also the hydrospiralia of any given specimen or species may display minor differences when one is compared to another. In a few species (e.g., *Pentremites rusticus,* Fig. 180,*L*; 194,*10*) the hydrospire folds of the anal hydrospiralia differ markedly in configuration from others. All of these features suggest that the hydrospire folds were relatively inflexible.

Petrographic examination shows that the walls of hydrospires are composed of very small calcite crystals. Whether the folds were permeable in life is not determinable, but it seems reasonable to suppose that they were.

## NUMBER OF HYDROSPIRE FOLDS

The number of hydrospire folds in blastoids of any given species and constancy of this number in different individuals of the species differ from species to species and from genus to genus. For example, *Orbitremites* (Fig. 193,*1*) and *Monoschizoblastus* have a single hydrospire fold on each side of an ambulacrum, whereas *Schizoblastus* and *Globoblastus* (Fig. 193,*2*) have two folds in each hydrospiralium, and various species of *Pentremites* (Fig. 180) have three to seven or more folds in each hydrospiralium. *Orophocrinus* may have as many as 11 folds in each hydrospiralium. Constancy in the number of hydrospire folds belonging to individual hydrospiralia in Silurian and Devonian genera is poorly known but examination of many thin sections of Mississippian blastoids (e.g., *Orbitremites, Cryptoblastus, Globoblastus, Schizoblastus*) show that the number of folds in each of the hydrospire groups is very constant.

Species of *Pentremites,* particularly geologically younger ones, show less consistency in the number of hydrospire folds belonging to a hydrospiralium. For example, *P. princetonensis* (Fig. 180,*C*) and *P. pulchellus* (Fig. 180,*D*), both from the Ste. Genevieve Limestone of Meramecian age, typically have three folds in each of the ten hydrospiralia, although one specimen of the latter species has been found to possess a fourth fold in one hydrospiralium. *P. godoni* (Fig. 180,*F*) and *P. symmetricus* (Fig. 180,*E*), from the Paint Creek Formation of early Chesteran age, normally have four or five folds in each hydrospiralium, but a specimen of *P. symmetricus* has been observed which shows four folds in some hydrospiralia and five folds in others. *P. halli* (Fig. 180,*K*), from the Kinkaid Limestone of late Chesteran age, has three or four folds in each hydrospiralium, some showing three folds in each hydrospiralium, others four folds in each, and a few four folds in certain hydrospiralia and three folds in remaining ones.

Early Pennsylvanian *Pentremites,* from the Morrowan of Oklahoma, exhibit greater variability in the number and shape of the hydrospires, particularly in the hydrospiralia adjacent to the anal interradius, than any older species of the genus among those studied. *P. rusticus* (Fig. 180,*L*), which belongs to this group, commonly has five to seven folds in hydrospiralia not adjacent to the anal *(CD)* interradius, whereas hydrospiralia next to the anal interradius contain only three or four folds and these are markedly different from the others in shape (the entire fold being expanded, rather than just the adaxial portion). Although the number of folds is constant in each of the two types of hydrospiralia, serial sections near the summit show differences in shape of the hydrospire folds, both in the hydrospiralia adjacent to the anal interradius and in the remaining eight hydrospiralia adjoining other interradii. Hydrospire folds in *P. rusticus* are generally much thicker than those of pre-Pennsylvanian *Pentremites.*

## THECAL OPENINGS

Openings in the blastoid theca are related primarily to the digestive system (mouth, anus) and respiratory system (spiracles, spiracular slits, hydrospire pores, hydrospire slits). The mouth is centrally placed at the summit of the theca and the anus is generally located between posterior deltoid elements (anal deltoids) or excavated in deltoid material slightly below and behind the mouth. The spiracles and spiracular slits, inferred to have served as excurrent openings of the respiratory system, generally are observed in the vicinity of the summit. The hydrospire pores and slits, which open into the hydrospires, occur along margins of the ambulacra.

### MOUTH

The mouth is the inlet to the digestive tract of the living animal. In blastoids the oral orifice is a small opening, commonly pentagonal in outline, at the apex of the summit (Fig. 178,*1*). The shape and size of the mouth opening in the theca are determined by the gap between the adoral tips of the five deltoids. In general, the mouth is smaller than the anus but approximately equal in size to one of the spiracles. Weathering of the summit may make the mouth aperture appear to be abnormally large. The connection of the mouth and digestive tract and the path of this tract aborally have not been recognized positively, although questionable traces of the digestive tract immediately below the mouth have been observed. As already described, the mouth in well-preserved fossils is covered by a complex arrangement of summit plates.

### ANUS

The anus, which is the exit of the digestive system, may be excavated in a single posterior deltoid plate (e.g., *Pentremites*), surrounded by various posterior deltoid plates (e.g., *Globoblastus*), or located along the sutures between posterior deltoids and adjacent limbs of the radials (e.g., *Heteroschisma*). The anus may be confluent with the posterior spiracles, so as to form a single opening termed **anispiracle** (e.g., *Pentremites, Cryptoblastus*), or it may be separate from them (e.g., *Schizoblastus*). In size, the anus is invariably larger than the spiracles and generally bigger than the mouth. The rim of the plates surrounding the anus generally conforms to the surface of the surrounding thecal plates, but in some genera (e.g., *Lophoblastus*), the opening is partially sheltered aborally by a hoodlike projection of the hypodeltoid. The passageway connecting the anus with the digestive tract is not well known, but traces of it have been seen in *Globoblastus* and its influence in modifying adjacent structures is apparent in Early Pennsylvanian specimens of *Pentremites,* for example in pushing the posterior hydrospiralia apart and in affecting the shape and number of posterior hydrospire folds. Analogous effects of the anus on the respiratory system are the absence (e.g., *Heteroschisma*) or reduction in number (e.g., *Thaumatoblastus*) of hydrospire slits on the posterior side. The plates that cover the anus are poorly known in many blastoid genera, but are observed to differ from those over the spiracles and mouth in some genera (e.g., *Pentremites*).

### SPIRACLES

Five to ten generally rounded openings adjacent to the mouth are called **spiracles** (Fig. 178,*1*). Blastoids with spiracles and hydrospire pores are said to be spiraculate. Spiraculate genera can be divided into three main types based on the number of spiracular openings and their relationship with the anus. They are named from selected representative genera as (1) *Elaeacrinus* type, (2) *Tanaoblastus* type, and (3) *Pentremites* type.

#### ELAEACRINUS TYPE

Blastoids of *Elaeacrinus* type are characterized by having ten spiracles located round the mouth (Fig. 198). The anus is separate from spiracles in the posterior interray. Generally each spiracle lies in an excavation along either side of a deltoid; a lancet and side plates bound the opening laterally. In most genera, the spiracles occur near the adoral tips of the deltoids, but in some (e.g., *Acentrotremites,* Fig. 198,*4*) they are located near the aboral margin of the deltoids.

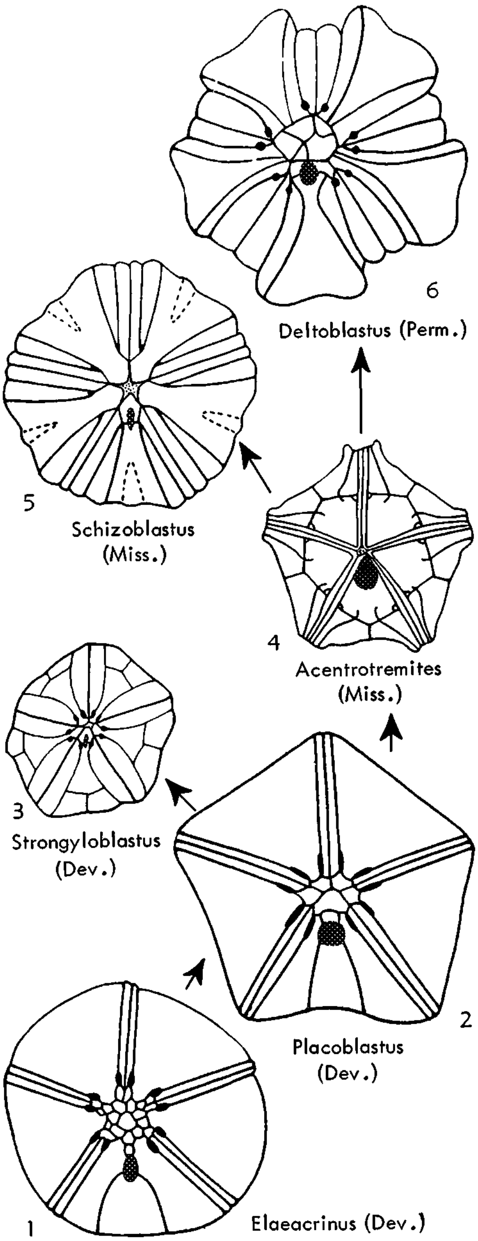

FIG. 198. Variations in spiracles of *Elaeacrinus* type, characterized by 10 spiracles surrounding mouth and separate anus, genetic lineages not implied (drawings from Fay).

### TANAOBLASTUS TYPE

The *Tanaoblastus* type is distinguished from the *Elaeacrinus* type in that the posterior spiracles are confluent with the anus forming an **anispiracle.** Thus, eight spiracles and an anispiracle are present (Fig. 199). The spiracles are very small and are located along the adoral margins of the deltoids.

### PENTREMITES TYPE

Blastoids like *Pentremites* with four single external spiracles and an anispiracle and genera such as *Doryblastus* and *Nodo-*

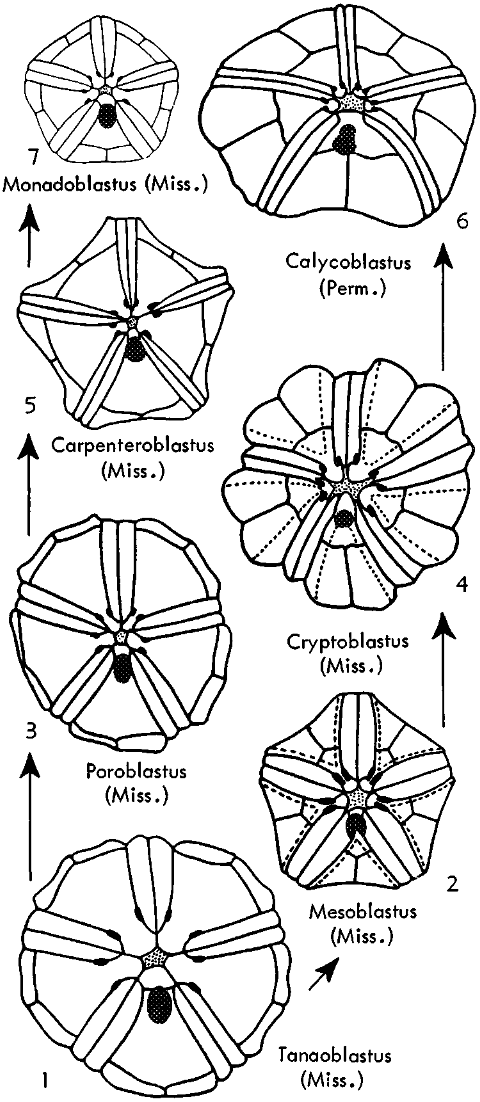

FIG. 199. Variations in spiracles of *Tanaoblastus* type, distinguished by 8 spiracles around mouth and posterior spiracles confluent with anus forming anispiracle, genetic lineages not implied (drawings from Fay).

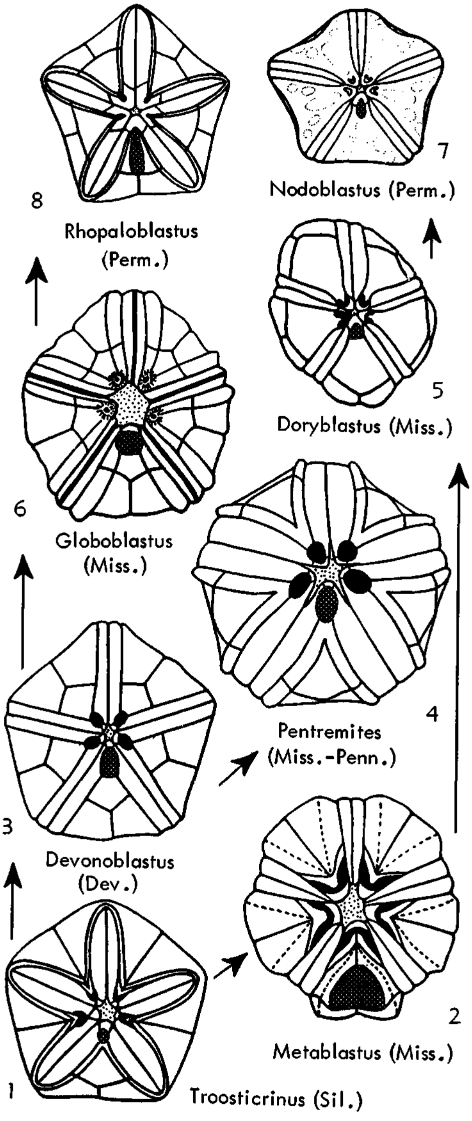

FIG. 200. Variations in spiracles of *Pentremites* type, having four spiracles or four paired spiracles and anispiracle surrounding mouth area, genetic lineages not implied (drawings from Fay).

*blastus* in which an anispiracle is accompanied by four external spiracles nearly divided by a strongly developed deltoid septum (called **paired spiracles**) are designated as spiraculate forms of *Pentremites* type (Fig. 200). The size of the spiracle openings in forms with four external spiracles is generally greater than in genera having eight or ten spiracles.

## SPIRACULAR SLITS

In many genera an elongated spiracle, termed **spiracular slit,** may be seen on each side of an ambulacrum (Fig. 201,*1*). Typically, the spiracular slits are excavated in marginal parts of deltoids and radials and they run parallel to the ambulacra. The thin body of skeletal substance between slit and ambulacrum commonly is referred to as the **hydrospire plate** (Fig. 193,*8*). Blastoids with exposed spiracular slits and hydrospire slits are termed fissiculate. Those with spiracular slits may be grouped on the basis of relationship of the slits to the anus.

### OROPHOCRINUS TYPE

In the *Orophocrinus* type, distinguished by the presence of two distinct slits in each interray, ten in all, the slits may be very short or relatively long and generally they transect the deltoid-radial suture (Fig. 201, *1-3*). Also, the slits may be located adjacent to the mouth area or at a considerable distance from it.

### SAGITTOBLASTUS TYPE

In the *Sagittoblastus* type only eight distinct slits occur, for those belonging in the posterior *(CD)* interray are coalesced with the anus to form an anispiracle (Fig. 201, *4-7*).

## HYDROSPIRE SLITS

Longitudinal openings excavated in plate substance of the deltoids and radials and disposed parallel to adjacent ambulacral margins are defined as **hydrospire slits.** They lead inward to **hydrospire clefts** (Fig. 193,*11*; 202).

As many as 18 of these slits may be found on either side of an ambulacrum. Three groups of blastoids bearing hydrospire slits, respectively designated by the names of representative genera, can be discriminated on the basis of relationship of the slits in the posterior interray to the anus.

### POLYDELTOIDEUS TYPE

The *Polydeltoideus* type, illustrated by *Polydeltoideus, Pleuroschisma, Hadroblastus,* and *Neoschisma,* is characterized by the presence of slits in all interrays, those

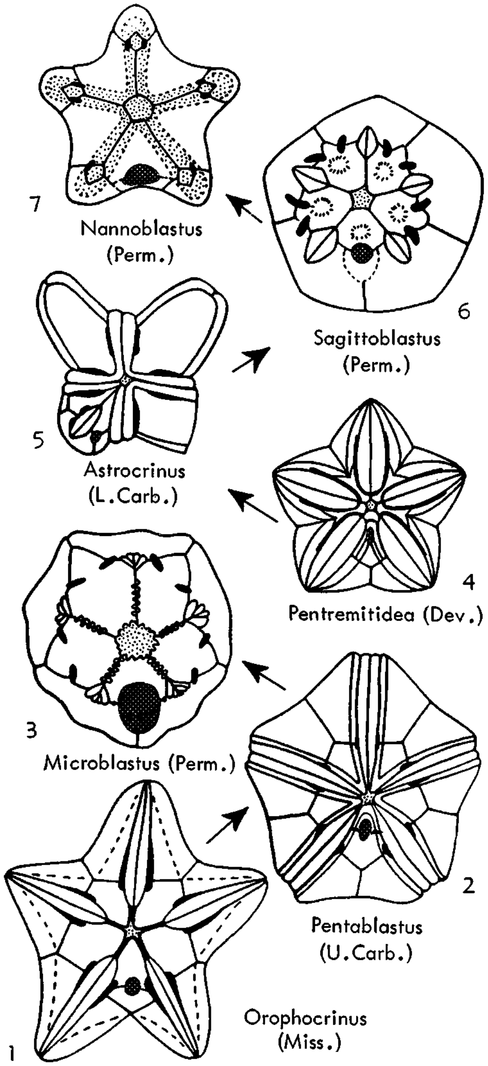

FIG. 201. Variations in spiracular slits. The *Orophocrinus* type is characterized by having 10 slits around mouth and separate anus. The *Sagittoblastus* type differs in that posterior slits are confluent with the anus, resulting in 8 slits and an anispiracle, genetic lineages not implied (drawings from Fay).

of the posterior interray being entirely separate from the anus (Fig. 202,*1-4*). The fully or partly exposed slits of the calyx are arranged in ten fields. Commonly, however, the number of slits in the posterior interray is markedly reduced (e.g., five slits in each posterior field of *Neoschisma,* in contrast to 18 slits in normal fields as observed in this genus).

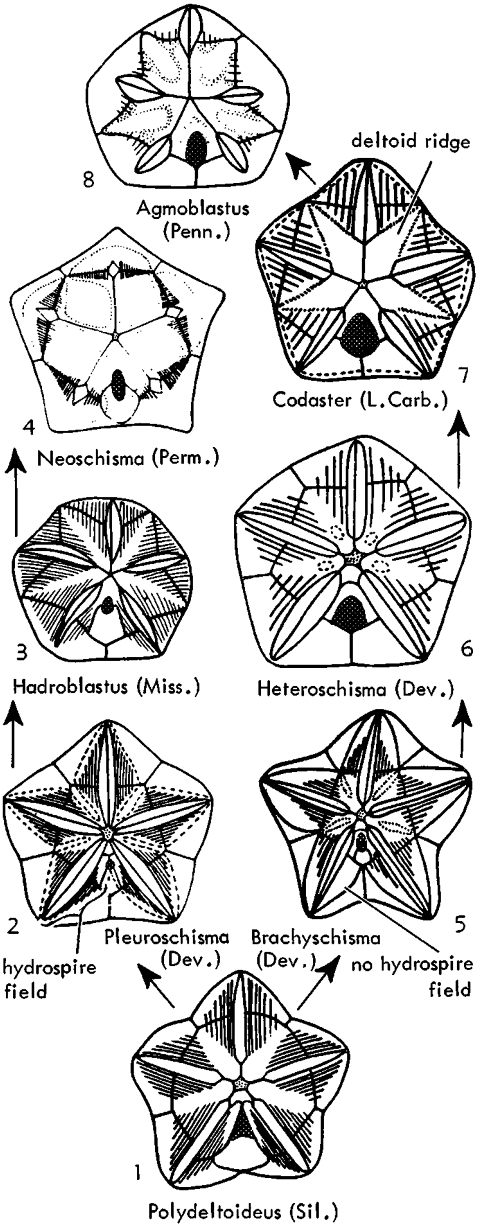

FIG. 202. Variations in hydrospire slits. *1-4,* genera of *Polydeltoideus* type, with slits exposed or partially exposed in 10 fields and separate anus. *5. Brachyschisma,* sole representative of *Brachyschisma* type, with nine exposed hydrospire fields and separate anus, slits lacking on left side of anus. *6-8.* Genera of *Codaster* type, differing from others in entire lack of slits in posterior interray (drawings from Fay).

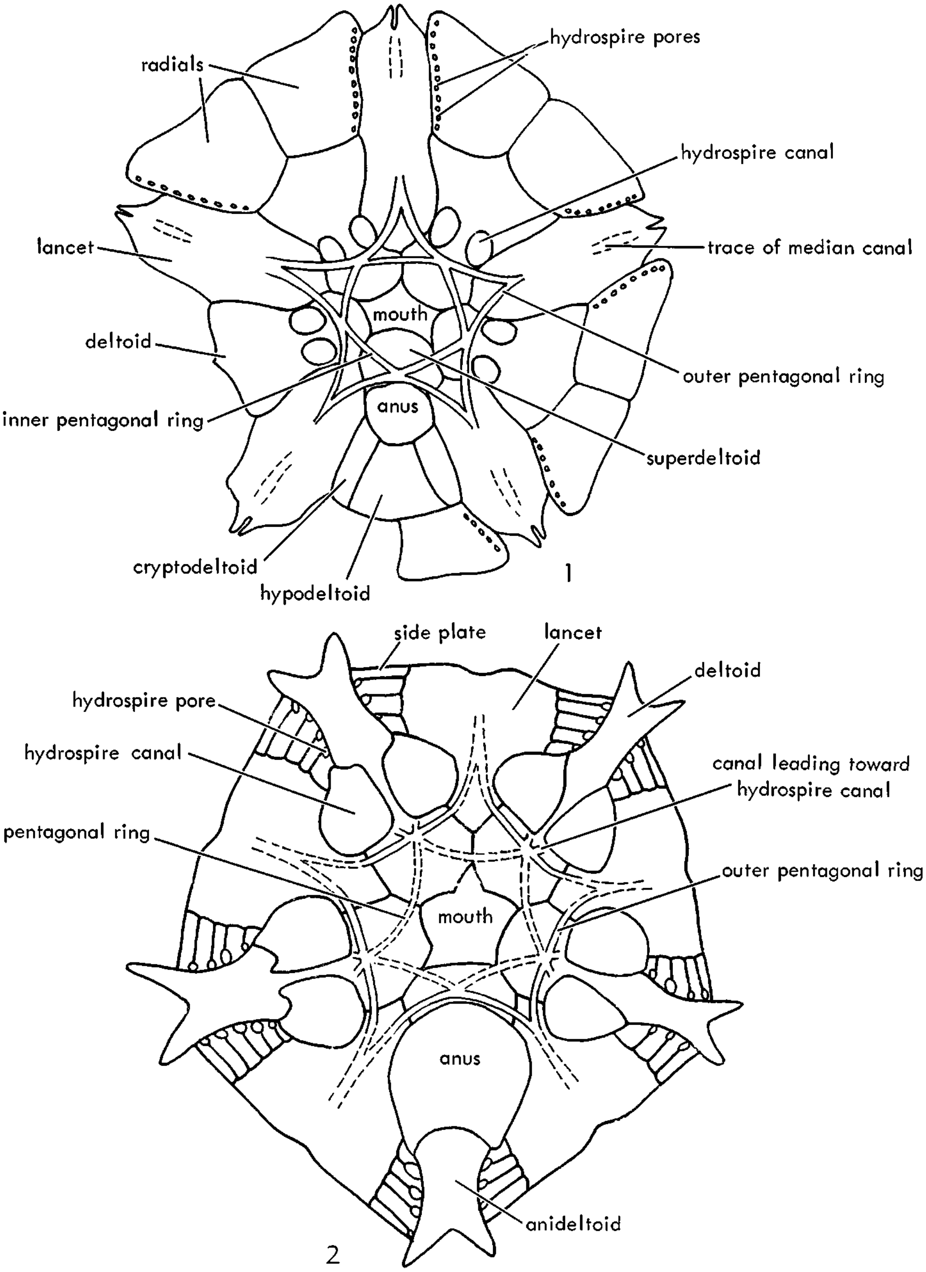

FIG. 203. Drawings based on thin sections of oral ring canal.——*1. Globoblastus norwoodi* (OWEN & SHUMARD), L.Miss.(Burlington Ls.), near Springfield, Missouri; inner and outer pentagonal ring canals, each branch of outer ring connecting aborally with median canal of lancet.——*2. Pentremites godoni* (DEFRANCE), U.Miss.(Paint Creek F.), near Floraville, Ill.; oral ring canal with short canals that lead from interradial mid-point of outer pentagonal ring toward each hydrospire canal, connection of small canals with outer ring canal clearly shown but opposite connection of short canals with hydrospire canals indistinct.

#### BRACHYSCHISMA TYPE

The *Brachyschisma* type differs from the first in having a single hydrospire field in the posterior interray, located on the right side of the anal opening. Thus, the calyx has a total of nine fields. *Brachyschisma* (Fig. 202,*5*) is the sole known representative.

#### CODASTER TYPE

In the *Codaster* type no hydrospire slits are found in the posterior interray, and accordingly the calyx shows eight fields distributed around the summit, two in each interray other than the posterior. Representative genera are *Heteroschisma, Codaster,* and *Agmoblastus* (Fig. 202,*6-8*).

### HYDROSPIRE PORES

**Hydrospire pores** are minute openings arranged in a row next to each ambulacral margin. They lead to the hydrospires and occur mainly in spiraculate blastoids. Two groups are readily differentiated, designated as *Globoblastus* and *Pentremites* types, respectively.

#### GLOBOBLASTUS TYPE

The *Globoblastus* type includes genera in which the pores are larger and less closely spaced near the summit than in aboral parts of the ambulacra where many more pores in a unit distance are observed (Fig. 194,*1,2*). The number and distribution of pores in each row are independent of such ambulacral elements as side plates and outer side plates, which are constant in width throughout the ambulacra. In one subtype the pores are restricted to borders of the radials (e.g., *Globoblastus*) and in another some of the pores pierce both radial and deltoid plate margins (e.g., *Orbitremites*).

#### PENTREMITES TYPE

The *Pentremites* type is characterized by hydrospire pores distributed along the entire length of ambulacra on each of their sides, each pore being bounded by a side plate and outer side plate (Fig. 193,*6,7*). Thus, the number of pores is directly proportional to that of the side plates and outer side plates. Representative examples are *Pentremites, Auloblastus,* and *Schizoblastus.*

### THECAL CANALS

The existence in blastoids of ring canals surrounding the mouth and uniting with the longitudinal canals of the lancet plates has been known for nearly 80 years. The ring canals are termed **circumesophageal rings.** Etheridge & Carpenter (1882, p. 217-219) observed their presence in *Pentremites, Globoblastus, Schizoblastus, Phaenoschisma, Orophocrinus,* and *Codaster.* The structure probably is best known in *G. norwoodi.*

The longitudinal canal of each lancet plate in *Globoblastus* divides near the summit of the theca, giving rise to branches which pass through the deltoid under the paired spiracles and adoral to them. The branches then join with others given off from the longitudinal canals of adjacent lancets so as to form a pentagonal ring (Fig. 203,*1*). A smaller pentagonal ring inclosed by this one joins with it at lengthwise mid-points of inner parts of the deltoids in positions just adoral to the divided spiracles. On the anal side, the circumesophageal rings pass through the superdeltoid. Angles of the outer pentagonal ring are interradial, whereas those of the inner ring are radial in position.

The circumesophageal rings of *Pentremites* are similar to those of *Globoblastus* except that traces of a canal can be seen leading from the interradial mid-points of the outer ring toward each hydrospire canal (Fig. 203,*2*). Canals of this type have been observed to penetrate each of the deltoids other than the anideltoid. The open connections of the small canals with circumesophageal rings are quite distinct but exact relationships of opposite extremities of the diverging canals to the hydrospires are obscure. They appear to open into the spiracles.

## PHYSIOLOGICAL FEATURES

### FOOD-CARRYING SYSTEM

The food-carrying system of blastoids is complex, being supported externally by the brachioles and structures of the ambulacra and internally by unknown structures of the alimentary tract which doubtless existed. The number of plates directly related to the extrathecal food-carrying sys-

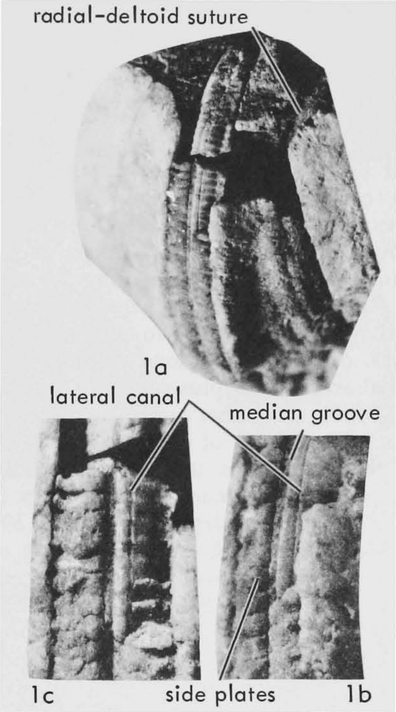

FIG. 204. Lateral canals in *Auloblastus clinei* BEAVER, Miss.(Osag.), near Springfield, Mo.; *A*, ×4; *B,C*, ×10 (*A*, Beaver, n; *B,C*, Beaver, 1961).

tem is tremendously greater than the number involved in the water-vascular or other systems. The total number of plates in a representative genus (e.g., *Pentremites*), including brachiole and ambulacra cover plates, certainly amounts to tens of thousands and possibly to hundreds of thousands.

By analogy with modern crinoids and other echinoderms, food is inferred to have entered the food-carrying system along the brachiole median grooves and to have moved along these grooves to the brachiole sockets, located on the ambulacral margins. From these points of brachiole attachment the food moved admedially along the lateral grooves to the ambulacral median groove and then was transported adorally to the mouth at the summit of the calyx. It seems reasonable to suppose that the brachiole cover plates were movable and that cover plates of the lateral grooves also may have been able to move. The general lack of symmetry in the arrangement of cover plates of the ambulacral median groove suggests that these plates may not have been movable. The small elongate plates covering the anus (e.g., *Pentremites*) were probably capable of movement, and thus could have disposed of waste products.

Virtually nothing is known of the digestive tract within the central cavity of the animal.

## WATER-VASCULAR SYSTEM

The water-vascular system of blastoids includes the hydrospires and associated thecal openings and canals. In spiraculate blastoids sea water is inferred to have entered the hydrospires through the hydrospire pores and to have moved adorally through the hydrospire canals to the spiracles. Fluids from the spiracles are interpreted to have entered the area beneath the summit plates of the mouth, and to have emerged from the theca through them, or possibly between the plates covering the spiracles, if these were movable. In fissiculate genera without hydrospire pores, but with spiracles, sea water apparently entered the hydrospires through hydrospire slits and emerged from the theca through the summit plates or possibly through the spiracles. Where neither pores nor spiracles are present, hydrospire slits must have served both as an entrance and exit to water entering the hydrospires.

The large surface area represented by the hydrospire folds, inferred to have been semipermeable, permitted sea water within the hydrospires to aerate the fluids of the body cavity. Little is known about trends involving an increase or decrease in hydrospire surface area through geologic time in selected blastoid lineages. Factors affecting hydrospire surface area include length of ambulacra, number and shape of hydrospire folds in each hydrospiralium, and adaxial extension of the hydrospire folds. Variation in hydrospire wall thickness is an undetermined feature in evaluating the effectiveness of the water-vascular system.

## NERVOUS SYSTEM

The circumesophageal rings and their lateral branches in the lancets (median canals) are inferred to represent the nervous system in blastoids. This system of canals encircles the mouth area and seemingly ends at the aboral extremities of the lancets. An apparent connection between the circumesophageal rings and the spiracles has been recognized in *Pentremites* (Fig. 203, *2*). The median canals are entirely embedded in the lancets and do not open into other systems (i.e., hydrospiralia). The lateral canals which lie on either side and obliquely adaxial to the median canal in *Auloblastus* possibly may be a part of the nervous system (Fig. 204). Lack of knowledge of their adoral and aboral extent and relationships to other structures limits an interpretation of their function.

## ABNORMALITIES

Blastoids with malformed structural elements are fairly common in various species represented by abundant specimens.

Wanner (1932) distinguished 133 abnormal specimens of *Deltoblastus* from the Permian of Timor in a large collection of more than 24,000 specimens, or a proportion of one abnormal specimen to every 182 examples. While a thorough examination has not been conducted on the proportion of malformed *Pentremites* from the Upper Mississippian of the Ohio River area, the above ratio probably is not far out of line. Deformed specimens of numerous other genera have been reported in the literature, but generally the number of abnormal individuals is small and prevents generalization.

Abnormalities may occur in any of the blastoid structural elements, including the column and brachioles. Doubtless owing to the rarity of preserved intact columns and brachioles, however, known examples are confined to structures of the theca. Wanner (1932) recognized three principal groups of malformed specimens of *Deltoblastus*. One group, composing 3.6 percent of total abnormal specimens, is characterized by thecae with 2 to 4 normal radial areas, combined with one or more stunted radial areas, or surplus plates, or both (Fig. 205,*1,2,4*). Another group, representing about 13 percent of all malformed *Deltoblastus* individuals, includes normal thecae except for the presence of extra plates (Fig. 205,*3*), or with enlarged plates (Fig. 205,*5*). A third group, making up 83 percent of all deformed specimens, is distinguished by some combination of too few structural elements. These include near-obliteration of interradial elements which gives rise to seemingly double ambulacra (Fig. 205,*6*), lack of ambulacra (Fig. 205,*7,9,11*), and abnormally shortened ambulacra (Fig. 205, *8,10*). Defects observed in *Pentremites* (Fig. 206,*8*) are similar in many respects to those of *Deltoblastus*. The deformities described by Wanner and some of those recognized in *Pentremites* and *Globoblastus*

[*See opposite page*]

Fig. 205. Abnormal specimens of *Deltoblastus* from the Permian of Timor, all *D. permicus* (Wanner), except *7*, which is *D. batheri* (Wanner).——1. Lateral and basal views of theca with three normal radials and ambulacra; *1a*, radial *(A)* shortened, with no evidence of sinus; *1b*, one ambulacrum *(E)* with surplus plates; ×2.5.——*2*. Basal and lateral views of calyx with 3 normal radials and ambulacra; one abnormal radial and deltoid indented with trace of a radial sinus *(A)*; double ambulacra in position of *E* ambulacrum; ×2.5.——*3*. Normal specimen except for protruding lower half of a deltoid (*CD* interray); ×2.——*4*. Calyx with 4 normal radials and ambulacra, sinus for abnormal ambulacrum *(B)* reduced to notch; 2 extra plates present, ×2.——*5*. Normal theca except for extra plate between 2 radials and slightly shortened and modified overlying deltoid (*AB* interray); ×2.——*6*. Calyx with radial limbs and deltoid lying between 2 ambulacra nearly obliterated so as to give appearance of double ambulacra (*AB* interray); ×3.——*7*. Theca with 3 normal radials and ambulacra, positions of missing ambulacra *(C,D)* indicated by poorly developed radial sinuses and abnormal rays slightly shorter than normal rays, ×2.5.——*8*. Calyx with one ambulacrum greatly shortened and apparently without facets for covering plates and brachioles, associated radial much smaller than normal; basals in contact with only 4 radials, laterally adjacent ambulacra somewhat shortened, ×2.5.——*9*. Calyx with 3 normal radials and ambulacra, 2 rays entirely missing, 3-sided in basal view, ×2.5.——*10*. Normal theca except for shortened ambulacrum *(A)* and adjacent deltoid (*AB* interray) which is stunted at its upper end, ×2.5.——*11*. Theca with one abnormal ray *(E)*, ambulacrum entirely missing but radial sinus partially preserved, abnormal radial greatly shortened and malformed, ×2.5 (Wanner, 1932).

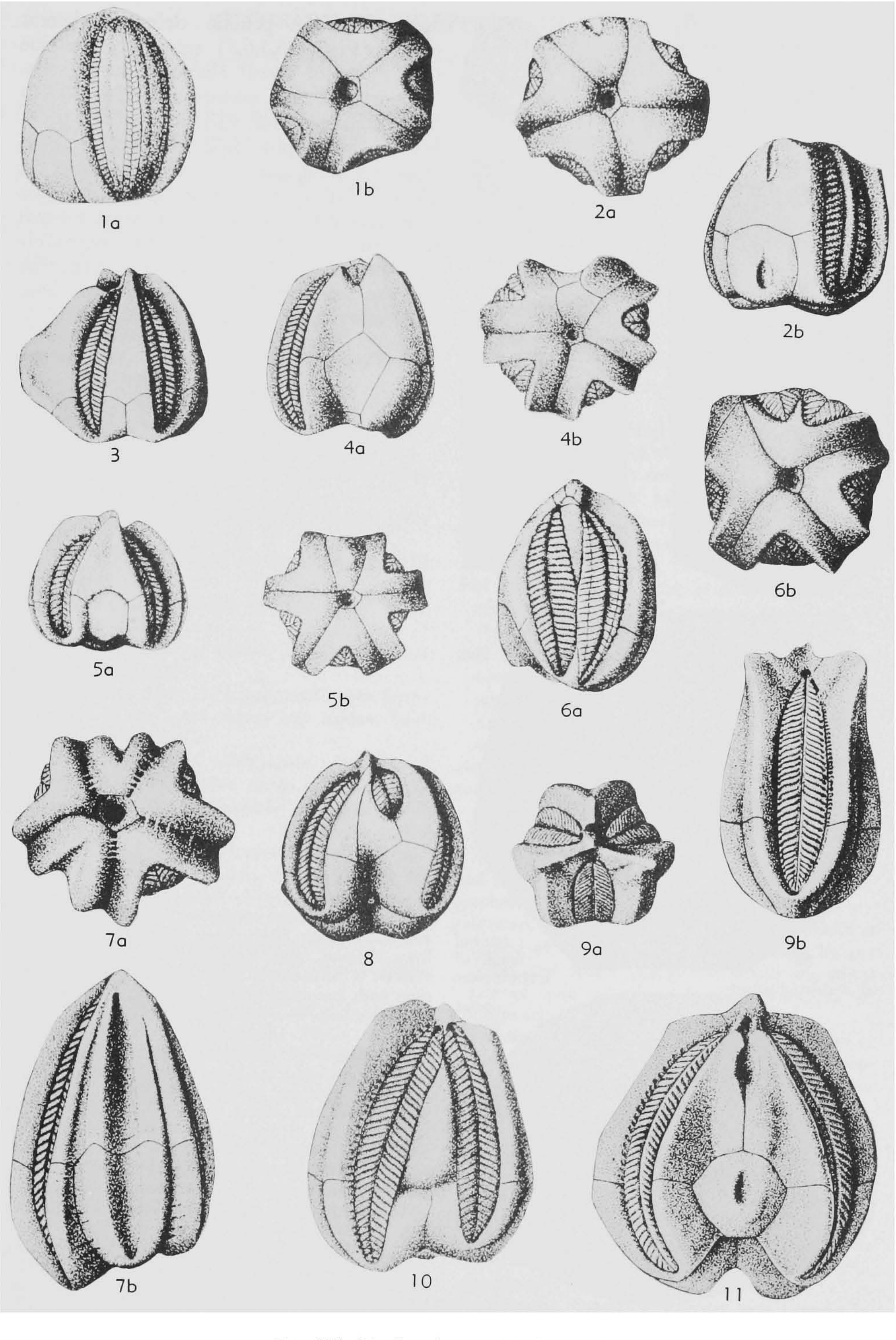

FIG. 205. [*Explanation on opposite page.*]

apparently are genetic defects, whereas others (Fig. 206,*5,6,8*) seemingly are due to damage of thecal elements during life.

ETHERIDGE & CARPENTER (1886, p. 41) have suggested that variations in the number of hydrospire folds in hydrospiralia represent irregularities and inequalities of growth. Although this may be true, it seems more likely that such variations are normal in some species. Hydrospires commonly may be broken or lacking, but generally one can ascertain that they have been damaged after death of the individual.

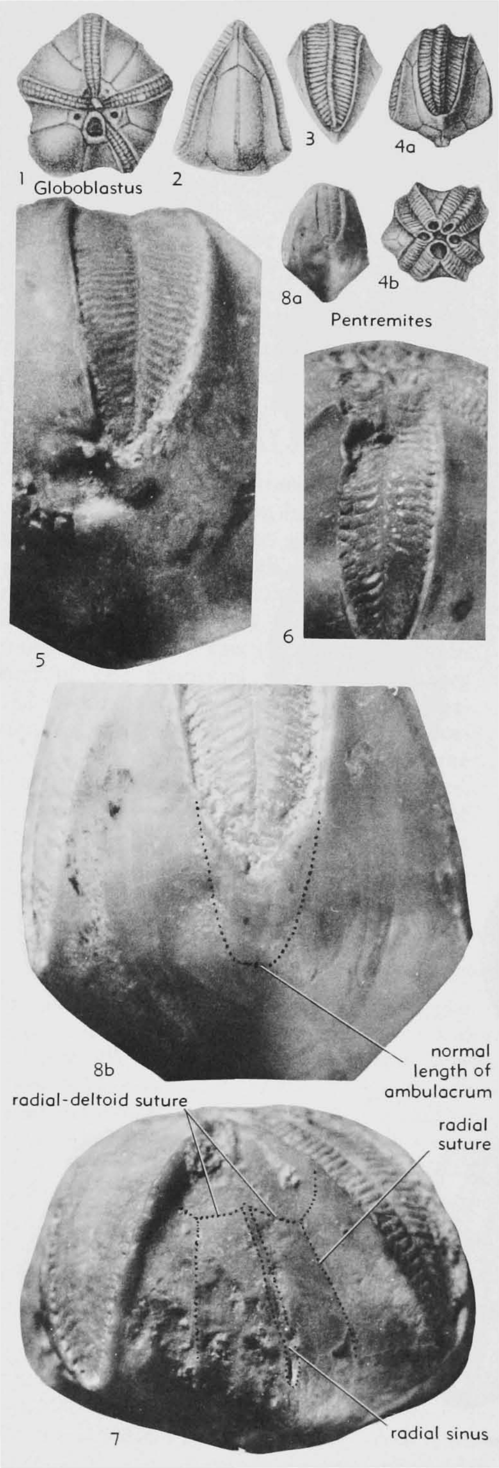

FIG. 206. Abnormal specimens of *Globoblastus (1)* and *Pentremites (2-8)* from Mississippian rocks of Iowa, Illinois, and Alabama.——*1. G. norwoodi* (OWEN & SHUMARD), Iowa; adoral view of specimen with abnormal radials, ambulacrum lacking in *D* ray, ×1.3.——*2-7. P. godoni* (DEFRANCE) from Alabama *(2-4)* and Illinois *(5-7)*; *2,* specimen with radial sinus reduced to narrow slit without ambulacrum, ×1.3; *3,* specimen showing ridge instead of median groove in ambulacrum, ×2.2; *4a,b,* lateral and adoral views of specimen having only 4 radials, *A* and *B* rays with abnormal combined ambulacrum, ×1.3; *5,* specimen with damaged radial body and aboral part of ambulacrum, ×4.5; *6,* specimen with deformed *A* ambulacrum, ×4.5; *7,* specimen with extra radial in *AE* interray, its sinus reduced to narrow slit (sutures and sinus marked by dotted lines), ×4.5.——*8. P. symmetricus* HALL; *8a,b,* lateral views of specimen with one considerably shortened ambulacrum, normal outline indicated by dotted line in *8b,* ×1, ×4.5 (*1-4,* Etheridge & Carpenter, 1886; *5-8,* Beaver, n).

## GLOSSARY OF MORPHOLOGICAL TERMS

By Harold H. Beaver, Robert O. Fay, and Raymond C. Moore

**A ray, radial and ambulacrum.** Distinguished by location opposite interradially placed anal opening or anispiracle; also termed anterior.

**abanal.** Direction away from anus (in plane of theca near anus).

**abaxial.** Direction perpendicularly away from polar axis.

**ablateral.** Direction away from margin of ambulacrum toward its mid-line.

**abmedial.** Direction away from mid-line of ambulacrum toward either margin.

**aboral.** Direction away from mouth (in plane of theca or along polar axis).

**accessory oral plate.** One of many small plates of peristome surrounding 5 main oral plates, adoral to side plates and meeting cover plates.

**adanal.** Direction toward anus (in plane of theca near it).

**adaxial.** Direction perpendicularly toward polar axis.

**adlateral.** Direction toward one or other margin of ambulacrum.

**admedial.** Direction toward mid-line (main food-groove) of ambulacrum.

**adoral.** Direction toward mouth (in plane of theca or along polar axis).

**ambulacral cover plate.** Tiny polygonal ossicle forming part of roof over lateral and median food grooves of ambulacrum.

**ambulacral field.** Entire ambulacrum exclusive of brachioles, including side plates and associated structures, in addition to exposed portion of lancet plate.

**ambulacral flange.** Clifflike enclosure of ambulacrum produced by abruptly elevated edges of deltoids and radial sinus above general level of ambulacrum.

**ambulacral groove.** *See* main food-groove.

**ambulacral half-field.** One-half of ambulacral field, on either side of main food-groove.

**ambulacral ratio.** Maximum length of ambulacrum divided by its maximum width.

**ambulacral rim.** Entire margin of ambulacrum from deltoid tips to bottom of radial sinus; may be flush with surface of theca or accented by ambulacral flange.

**ambulacral spine.** Small needle-like curved spine attached to the side plate body, arranged in rows along sides of main food-groove; each is approximately 1 mm. long by 0.1 mm. wide, with spirally arranged striations.

**ambulacrum.** Radially disposed area extending aborally from mouth, with narrow depression (main food-groove) running longitudinally along its center, with side food-grooves joined to this groove, and with side plates and associated structures, including brachioles; exposed portion of lancet plate may be included as part of ambulacrum. Viewing specimen from oral side, with anal opening toward observer, ambulacrum opposite anal opening is lettered *A* and considered to be anterior. Proceeding clockwise, other ambulacra are designated *B* (right anterior), *C* (right posterior), *D* (left posterior), and *E* (left anterior).

**anal area.** Region near anal opening.

**anal cover plate.** One of many small polygonal plates which may extend over and conceal anal opening in theca, bordered marginally by anal deltoid or deltoids.

**anal deltoid.** Undivided interradial plate on posterior *(CD)* part of theca below circlet of orals or mouth opening; collectively, anal deltoids include all differently named kinds of such plates of the posterior interray (anideltoid, cryptodeltoid, epideltoid, hypodeltoid, paradeltoid, subdeltoid, superdeltoid).

**anal opening.** Large orifice in theca marking position of anus in living animal, located in *CD* (posterior) interradius.

**anal plate.** One of many small polygonal plates covering immediate anal opening, bordered marginally by anal deltoid, epideltoid, hypodeltoid, superdeltoid, subdeltoid, cryptodeltoids, or paradeltoids.

**anal pore.** *See* anispiracle.

**anal pyramid.** Cone-shaped anal structure composed of elongate, imbricate anal plates, above smaller polygonal plates, arranged in several rows; may include anal oral plates also.

**anal sac.** *See* anal pyramid.

**anephebic.** Mature but smaller than normal.

**anideltoid.** Externally visible anal deltoid which is proved or not known to be accompanied by any others and which lies almost wholly on aboral side of anal opening *(Acentrotremites)* or of anispiracle *(Pentremites, Ambolostoma).*

**anispiracle.** Enlarged opening in summit portion of posterior interray, formed by union of anal opening and posterior spiracle (or spiracles), also termed anal pore (see paired anispiracle).

**anterior ambulacrum.** *See A* ambulacrum.

**anthus.** Complete blastoid calyx and brachioles borne by it; entire skeleton of blastoid exclusive of stem (Greek, *anthus*, flower or blossom).

**anus.** Excurrent opening of digestive tract in living animal, located in summit part of *CD* interray, generally indenting anal deltoids and possibly may border posterior radial or oral plates.

**anus separate.** Condition whereby anal opening is separate from adjacent spiracles.

**apex.** Highest distal point on theca.

**axis.** *See* polar axis.

**azygous basal plate.** Smallest of 3 plates of basalia (name signifying unyoked or unfused), normally located in anteroright *(AB)* interray but may be posteroleft *(DE)*.

**B ray, radial and B ambulacrum.** *See* ambulacrum.

**basal angle.** *See* pelvic angle.

**basal circlet.** *See* basalia.

**basal periphery.** Outline of calyx seen from base.

**basal plate.** Component of proximal circlet of theca adjoining stem, or rarely adjoining subbasal plates, almost invariably consisting of 2 subequal large zygous plates (*BD*, right posterior and *DA*, left anterior) and a small azygous basal plate (*AB*, anteroright); in a few forms the small (azygous) basal plate may be in *DE* (posteroleft) in position. The basals may be reduced to a single plate by atrophy, resorption, or coalescence, and in some forms the basals may be irregular in position.

**basalia.** Basal circlet of plates in blastoid theca, normally consisting of 2 large (zygous) and 1 small (azygous) plates but may include 1 large basal plate formed from coalesced basals or 1 small basal where others have atrophied or have been resorbed.

**base.** *See* pelvis.

**brachiolar facet.** Large elliptical scarlike area on side plate limb and outer side plate, adlateral to brachiolar pit or side food-groove, being bifascicular, with aboral portion on side plate limb and adoral portion on outer side plate; also termed brachiolar socket or brachiole facet.

**brachiolar groove.** Depression running along ventral surface of brachiole, vaulted over by series of cover plates, serving for transport of food particles to lateral and median grooves of ambulacrum.

**brachiolar pit.** Small round depression at adlateral termination of side food-groove.

**brachiolar plate.** One of biserially arranged plates of brachiole, semielliptical in cross section and subquadrangular in side view, with basal pair attached at brachiolar facet.

**brachiolar socket.** Centrally placed pit on rounded knob located at adlateral extremity of lateral groove on ambulacrum, providing for articulation of brachiole; also termed brachiole socket.

**brachiole.** Slender food-gathering appendage attached to border of ambulacrum, composed of numerous, short, biserially arranged ossicles (brachiolars), with subvective system and covering plates on ventral surface; brachioles on one side of ambulacrum alternate in position with those on opposite side, and where reclined, they form an imbricate pattern (also termed pinnule).

**C ray, radial and ambulacrum.** Elements next clockwise from *B* ray in oral view of theca, also, termed right posterior (*see* ambulacrum).

**calyx.** Skeletal cover (theca) of blastoid including internal structures (hydrospires, etc.) but excluding appendages (brachioles) and stem (calyx literally signifies cup; *see* anthus).

**central canal.** *See* median canal.

**circumesophageal ring.** Double pentagonal ring of canals around esophagus, with corners of outer ring meeting meeting median canals of lancet plates, and corners of inner ring joining sides of outer ring beneath spiracles at adoral ends of deltoids. Although previously thought to be part of water-vascular system, recent opinions indicate that this structure is part of the nervous system.

**column.** *See* stem.

**columnal.** Individual segment of blastoid stem.

**conjunct deltoid process.** Ventrally raised portion of adoral tips of deltoids and adjacent radial limbs.

**cover plate.** One of tiny polygonal plates arranged in double alternating series over side and main grooves; quadruple alternating series placed on brachioles, inner double set termed inner cover plates and outer set termed outer cover plates; also, *see* anal cover plate.

**cover plate lobe or ridge.** Small rounded elongate raised area along edges of side and main food-grooves extending to lancet stipes and deltoid lips; presumably sutures between adjacent cover plates are along median lines of each lobe.

**cover plate socket.** Depression between adjacent cover plate lobes, presumably place of attachment for cover plate.

**crenella** (pl., **crenellae**). Small radially disposed groove on stem impression at base of theca and on distal and proximal surfaces of columnals, commonly extending less than one-third of distance from perimeter toward center; *see* culmen.

**cross section.** Section normal to polar axis, also termed transverse section.

**crown.** *See* anthus.

**cryptodeltoid plate.** One of 2 plates on either side of anal opening, generally overlapped aborally by hypodeltoid and adjacent radial limbs, abutting against superdeltoid plate adorally, bordering lancet plate laterally, and infolded into hydrospire folds on inner side. By adoral extension and fusion together above anal opening, cryptodeltoids may form horseshoe-shaped subdeltoid developed in some genera, such plate being adjoined on adoral side by superdeltoid.

**culmen** (pl., **culmina**). Ridge between crenellae on articular surface of columnal.

**D ray, radial and ambulacrum.** Elements next clockwise from *C* ray in oral view of theca, also termed left posterior ambulacrum (*see* ambulacrum).

**deltoid body.** Main portion of deltoid plate, seen externally, comprising median and aboral regions, term applicable also to anideltoid but not to other anal deltoids.

**deltoid crest.** Raised ridge, seen externally, connecting deltoid body with deltoid lip, with depressions on either side (termed oral crest by some authors); same as raised deltoid septum.

**deltoid head.** Adoral part of externally visible deltoid plate (including anideltoid) set off from deltoid body by lateral indentations produced by paired spiracles or entirely separated surficially by interruption due to spiracle (or anispiracle).

**deltoid lip.** Adoral margin of deltoid contiguous to mouth opening.

**deltoid plate.** Interradial subtriangular plate near summit of theca but aboral to oral plates, between adjacent ambulacra and above radial plates, internally infolded into hydrospire folds, with spiracles excavated at adoral end; on anal side 1 to 6 deltoid plates may be present, each specially named, but only single deltoid is present in each of other 4 interradial positions.

**deltoid septum.** Thin internal portion of deltoid plate between adjacent hydrospire canals, connecting deltoid lip to deltoid body; on anal side are 2 septa formed by variously named plates.

**deltolancet suture.** Common line or division between deltoid and lancet plates.

**disjunct deltoid.** Deltoid with lip externally separated from body by spiracle or anispiracle.

**distal.** Direction away from point of stem attachment with theca (compare ventral). [BATHER, CLINE, and WANNER ill-advisedly used this term in describing hydrospires and ambulacra to mean away from the mouth, but otherwise they followed definition here given.]

**dorsal.** Direction toward point of attachment of stem with theca (compare proximal).

**dorsal pole.** Center of dorsal surface of theca.

**dorsal region.** *See* pelvis.

**double spiracle.** *See* paired spiracle.

**E ray, radial and ambulacrum.** Elements next clockwise from *D* ray in oral view of theca, also termed left anterior ambulacrum; (*see* ambulacrum).

**ephebic stage.** Mature or adult growth stage.

**epideltoid.** Anal deltoid bordering adoral side of anal opening and adjoining mouth opening, with or without hydrospires; differs from superdeltoid in lacking association with cryptodeltoids.

**equator.** Circumference about theca at one-half height of theca.

**esophogeal ring.** *See* circumesophageal ring.

**fissiculate.** Having exposed or partly exposed hydrospire slits or spiracular slits.

**food-groove.** *See* main food-groove.

**fused basal plate.** Large single basal plate seen in some blastoids, formed by fusion of entire basal circlet.

**fused hydrospire plate.** Elongate thickened projection of radial and deltoid plates beneath lancet plate, generally accompanied by lateral displacement of pores and slits away from ambulacral margins (formerly termed sublancet or underlancet plate). If projection is thin, each side is termed a hydrospire plate.

**gerontic stage.** Old-age growth stage.

**granulostriations.** Ornamentation of some brachiolars with microstriations parallel to brachiolar food-groove and small ridges at right angles to groove.

**hydrospiralium.** Group of two or more (to 18) conjoined hydrospires located along border of ambulacrum.

**hydrospiralium cleft.** Space within hydrospiralium exclusive of hydrospire clefts.

**hydrospire.** Infolded thin-walled calcareous linear structure on either side of ambulacrum, excavated in radial and deltoid plates, approximately parallel to ambulacral margin; on anal side, this may be excavated in cryptodeltoids, epideltoid, subdeltoid, and (in *Nymphaeoblastus*) in hypodeltoid.

**hydrospire canal.** Adorally directed tubular passageway in adambulacral part of deltoid leading from hydrospire, hydrospiralium, or confluent hydrospiralia to spiracle (or anispiracle).

**hydrospire cleft.** Space inclosed by hydrospire fold.

**hydrospire field.** Area of theca underlain by single group of hydrospires (hydrospiralium).

**hydrospire fold.** Thin calcareous wall surrounding hydrospire.

**hydrospire pore.** Minute rounded opening between side plates or outer side plates near margin of ambulacrum, leading into hydrospire.

**hydrospire slit.** Longitudinal opening of hydrospire fold excavated in substance of deltoids and radials parallel to ambulacral margins on either side.

**hydrospire tube.** Expanded adaxial portion of hydrospire fold.

**hypodeltoid.** Interradial plate on anal side adjacent to posterior radial limbs, forming aboral part of anal opening; internal portions may rest upon cryptodeltoids, subdeltoid, and septal projections of epideltoid, in addition to parts of hydrospire plate and fused hydrospire plate.

**inner cover plate.** One of series of biserial kite-shaped small plates over brachiolar food-groove, alternating with set of pentagonal outer cover plates on margins.

**inner side plate.** Small triangular plate between side plates at admedial corners near main food-groove, present in some genera (*see* side plate, outer side plate).

**interambulacral.** *See* interradial.

**interdeltoid suture.** Common line or suture between adjacent deltoid plates.

**interhydrospiralium.** Space between adjacent hydrospiralia.

**internal.** Toward inside of theca, same as inward.

**interradial.** Position of line extending from mouth halfway between adjoining radii or ambulacra, through mid-line of any deltoid plate. Orals, deltoids, and azygous basal are interradial in position. If 5 deltoids are present, they are termed *AB* (anteroright), and *BC* (posteroright), *CD* (posterior), *DE* (posteroleft), *AE* (anteroleft); same as interambulacral.

**interradial suture.** Common line or division between adjacent radial plates.

**inward.** Direction toward geometric center of calyx or polar axis of theca or stem, or toward inside of brachiole; same as internal.

**lancet plate.** Elongate spear-shaped plate extending from aboral tip of ambulacrum to oral opening, located along mid-line of ambulacrum, with elongate central canal (median canal) that connects with circumesophageal ring adorally. Adoral end, termed lancet stipe, adjoins adjacent spiracles laterally and internally rests on adjacent deltoid plates. In primitive blastoids, lancet is covered by side plates, but in advanced forms it supports main and side food-grooves also. In some forms, lateral canals are excavated in its outer surface beneath side plates, parallel to main food-groove.

**lancet-side plate suture.** Common line or division between lancet plate and side plate.

**lancet stipe.** Restricted adoral extension of lancet plate, resting internally on truncated ventral surface of adjacent deltoid lips, but adjoining oral orifice externally and generally bordering adjacent spiracles laterally; small cover plate lobes and sockets may be present.

**lateral.** Direction toward margin of ambulacrum or brachiole.

**lateral canal.** One of 2 small longitudinal canals on outer surface of lancet plate, beneath side plates, parallel to and on either side of main food-groove.

**lateral food-groove.** *See* side food-groove.

**left anterior ambulacrum (E).** *See* ambulacrum.

**left posterior ambulacrum (D).** *See* ambulacrum.

**length.** Vertical distance between apex and base of theca.

**length-width ratio.** Length of theca divided by width of theca.

**limb.** Adoral portion of radial plate along side of ambulacrum; *see* radial limb.

**longitudinal section.** Section parallel to polar axis.

**lumen.** Small round opening in center of stem columnals, which may or may not be continuous with body cavity above basal plates of theca; also termed stem cavity.

**main food-groove.** Longitudinal depression extending length of middle line of ambulacrum, excavated in side plates or lancet plate, bordered by cover plate lobes and sockets; also termed median groove, food-groove, and ambulacral groove.

**medial.** Line or direction of main food-groove.

**median canal.** Internal central opening of lancet plate, extending longitudinally to circumesophageal ring; also termed radial canal and central canal.

**median groove.** *See* main food-groove.

**median pit.** External depression in middle of side plate body.

**median ridge.** Small, regularly curved ridge around median pit on side plate body, curving adlaterally around brachiolar pit, joining ridge on adjacent side plate, parallel to adoral, admedial, and aboral edges of side plate body.

**metaphebic.** Mature and normal in size.

**mouth.** Central opening at summit of theca leading to digestive tract.

**neanic stage.** Youthful or immature growth stage.

**nepionic stage.** Growth stage between embryonic and neanic stages.

**oral.** Region about mouth; of or pertaining to mouth; *see* peristome and summit.

**oral crest.** *See* deltoid crest.

**oral groove.** Medial groove of lancet stipe and adjacent deltoid lips, adjacent to oral opening.

**oral hood.** *See* oral pyramid.

**oral opening.** Pentagonal opening at summit of theca, marking position of mouth in living animal.

**oral plate.** One of 5 main interambulacrally located polygonal plates covering mouth, but may include other summit plates where 5 main plates are lacking; *see* accessory oral plate, posterior oral plate, peristome, oral pyramid, oral spine, cover plate, and summit plate.

**oral pyramid.** Conical structure about oral opening, which comprises specialized elongate oral and accessory oral plates (termed oral spines) or oral cover plates, basally adjacent to many small polygonal accessory orals that cover spiracles (spiracular plates); also termed oral hood.

**oral ring canal.** *See* circumesophageal ring.

**oral spine.** Elongate conical oral or accessory oral or specialized anal plate around oral opening, forming part of anal and oral pyramids.

**outer cover plate.** One of polygonal cover plates along ventral margins of brachiole, single set on one side alternating in position with that on opposite side, brachiolar food-groove between these plates, roofed over by biserial set of inner cover plates that fit tightly against outer cover plates in zigzag pattern and alternate with them.

**outer side plate.** Small semielliptical to subtriangular plate that generally rests upon adlateral margin of side plate, bearing part of brachiole; in some specimens position may be more admedial; same as secondary side plate (*see* side plate, inner side plate).

**outward.** Direction away from geometric center of theca or polar axis of stem, or away from inside of brachiole.

**paired spiracle.** Spiracle with deltoid septum almost at surface externally so that V-shaped spiracle is formed, giving appearance of 2 connected spiracles with actually single opening; also termed double spiracle.

**paradeltoid plate.** One of 2 small subtriangular plates resting upon beveled adoral margin of hypodeltoid, on aboral side of anal opening, resting upon cryptodeltoids and not infolded into hydrospire folds.

**parephebic.** Mature but larger than normal in size.

**pelvic angle.** In side view, angle measured from dorsal pole (as center) to aboral tips of ambulacra farthest apart, with one radial position toward observer; same as basal angle.

**pelvis.** Portion of theca from aboral tips of ambulacra to dorsal pole; also termed base and dorsal region.

**periphery.** Circumference of theca at its widest part.

**peristome.** Area of oral and accessory oral plates around oral opening, located at summit of theca.

**pinnules.** *See* brachioles (not same as crinoid pinnules).

**polar axis.** Line extending from oral center to center of stem.

**pore.** *See* hydrospire pore.

**pore furrow.** Elongate depression on side plate handle extending abmedially from side plate body to hydrospire pore, between adjacent brachioles.

**posterior oral plate.** One of 5 main oral plates, larger than others and located in anal *(CD)* interradius.

**primary side plate.** *See* side plate.

**primary side plate suture.** *See* side plate suture.

**profile.** Outline of theca in side view.

**proximal.** Direction toward point of attachment of stem and calyx (compare dorsal). [According to Bather, Cline, and Wanner with respect to ambulacra, direction toward center of the mouth is proximal, but they used the definition first given for thecal orientation.]

**pyriform.** Pear-shaped.

**radalia.** Radial plates of theca.

**radial.** Position of line extending from centrally placed mouth to aboral end of any ambulacrum; lancets, radials, and ambulacra are radial in position.

**radial body.** Portion of radial plate below or aborally away from aboral tip of ambulacrum; same as trunk.

**radial canal.** *See* median canal.

**radial circlet.** *See* radalia.

**radial limb.** Adoral portion of radial plate along side of ambulacrum; sometimes termed limb.

**radial lip.** Thickened portion of radial plate at aboral tip of radial sinus.

**radial plate.** One of 5 cleft plates above basalia, radial in position, that receives aboral extremity of ambulacrum.

**radial sinus.** V-shaped indentation in adoral part of radial plate which receives ambulacrum.

**radiodeltoid suture.** Line or division between deltoid plate and adjacent radial limbs.

**right anterior ambulacrum (B).** *See* ambulacrum.

**right posterior ambulacrum (C).** *See* ambulacrum.

**root.** Presumably expanded, branching, treelike extension at distal end of stem.

**secondary side plate.** *See* outer side plate.

**side food-groove.** One of many short transverse depressions on ambulacrum, subparallel to each other, adorally directed at oblique angle to and emptying into main food-groove from base of brachiole, alternating in position on either side of main food-groove, and commonly bordered by cover plate lobes and sockets.

**side plate.** One of many small subquadrangular plates of ambulacrum, partly superposed on lancet plate or on its adlateral margin, arranged alternately on either side of main food-groove and between side food-grooves, bearing outer side plate and brachiole; also termed primary side plate (*see* inner side plate, outer side plate).

**side plate body.** Admedial portion of side plate, admedial to outer side plate.

**side plate limb.** Abmedial portion of side plate, normally aboral to outer side plate; sometimes termed side plate handle.

**side plate suture.** Line or division between adjacent side plates along line of lateral food-groove.

**sinus.** V-shaped indentation of ambulacrum along deltoid and radial margins.

**sinus edge.** Margins of radial and deltoids bounding ambulacrum; also termed ambulacral rim.

**sinus flange.** Clifflike enclosure of ambulacrum produced by abruptly elevated margins of radial and deltoids above general level of ambulacrum; same as ambulacral flange.

**spiracle.** Opening, generally rounded, near adoral tip of deltoid and excavated within it, bounded adorally by deltoid lip and aborally by deltoid body, and generally adjoined laterally by lancet stipe and side plates; *see* paired spiracle. Where deltoid septum is exposed externally, 2 spiracles are formed in deltoid.

**spiracular cover plate.** One of series of small polygonal plates that cover spiracles, extending adorally into oral spines; these may be part of series of accessory oral plates that are highly specialized; *see* oral pyramid.

**spiracular slit.** Elongate spiracle at side of ambulacrum, excavated in adjoining radial and deltoid plates, with fused hydrospire plate forming admedial wall and one or more hydrospire folds opening into hydrospire canal.

**spiraculate.** Having spiracles, in some genera including anispiracle.

**stem.** Cylindrical column beneath theca that may have served as means of support, composed of numerous discoid, button-shaped columnals, with central lumen, supposedly attached to root distally. The axial canal represented by the lumens of columnals connects with the body cavity. The stem also is termed column. Some forms probably lacked a stem.

**stem cavity.** *See* lumen.

**stereome.** Calcareous tissue in the mesodermal endoskeleton of the living echinoderm. This, together with the stroma, where both are replaced by calcium carbonate, forms the material of blastoid plates.

**stroma.** Organic tissue in mesodermal endoskeleton of living echinoderm.

**subbasal plate.** Small plate, or one of 3 plates, secreted between basal plates and top of the stem; also termed supplementary basal plate.

**subdeltoid.** Small to moderately large anal deltoid, typically inverted U-shaped, located on adoral and lateral margins of anal opening and on aboral border of superdeltoid; *see* epideltoid.

**sublancet plate.** *See* fused hydrospire plate (=underlancet).

**subradial plate.** *See* fused hydrospire plate.

**summit.** Distal extremity of theca.

**summit plates.** Oral and accessory oral plates.

**superdeltoid.** Anal deltoid on border of mouth opening, associated either with subdeltoid or pair of cryptodeltoids abutting its aboral margin and in some genera bordering anal opening.

**supplementary basal plate.** *See* subbasal plate.

**suture.** Plane of junction between adjacent plates.

**tangential section.** Section tangent to outer surface of theca.

**theca.** Main skeleton enclosing body of blastoid, including ambulacra but excluding stem and brachioles (equivalent to "calyx").

**transverse section.** Section perpendicular to longitudinal section.

**trunk.** *See* radial body.

**underlancet.** *See* sublancet plate.

**vault.** Portion of theca above pelvis; also termed ventral region.

**vault-pelvis ratio.** Height of vault divided by height of pelvis, measured parallel to polar axis.

**ventral.** Side of theca containing mouth or direction toward it (compare distal).

**ventral pole.** Geometric center of oral opening.

**ventral region.** *See* vault.

**width.** Maximum width of theca, measured at right angles to polar axis.

**zygous basal.** Large plate of basal circlet in *BD* (right posterior) or *DA* (left anterior) position, formed by fusion (*zygos*, yoked) of pair of antecedent small basals comparable to azygous basal in *AB* (anteroright) interray.

# TECHNIQUES

By Harold H. Beaver

Many techniques have been used over the years in studying blastoids. Those particularly well suited to solving problems of blastoid morphology are discussed briefly here.

## WEATHERED, REPLACED, AND DISARTICULATED SPECIMENS

Morphological features probably can be studied best on deeply weathered specimens and those consisting of disarticulated remains. Surfaces of internal structural elements, many complexly sculptured, may be well preserved and easily photographed in this condition. Exquisitely preserved specimens may be collected in large numbers along weathered joint surfaces (e.g., Burlington Ls., Mississippian). Disarticulated plates may be abundant in washed samples from shales rich in blastoids (e.g., Paint Creek F., Chesteran). Silicified thecas commonly are excellent for external study but provide little information on internal structures because obliteration of sutures prevents examination of plate relationships. Replacement of thecal elements by iron oxides, however, may be advantageous for morphological study. Hydrospires, for example, may be especially accentuated.

## GROUND SURFACES

Ground surfaces may be prepared readily to show internal relationships of blastoid skeletal parts. The various plates reflect light differently so that plate boundaries may be seen easily. Joysey & Breimer (1963, p. 472) accentuated the effect by increasing contrast during photography. A camera lucida is commonly used to produce drawings.

## ACETATE PEELS

Acetate peels can be made rapidly, cheaply, and they can be enlarged photographically. If serial sections are desired, the fossil surface may be ground to any number of desired levels and peels prepared. Peel quality is dependent on the nature of the calcite of the theca and the enclosed matrix material. Peels are well suited for many purposes, but are generally less desirable

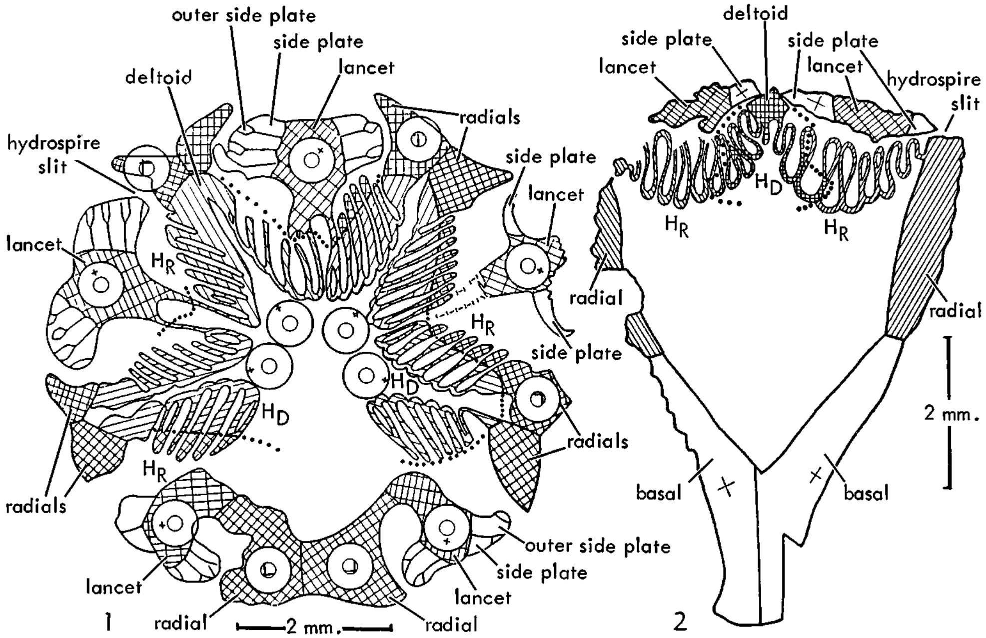

FIG. 207. Optical properties of *Cryptoschisma schultzii* (D'ARCHIAC & DE VERNEUIL).——*1.* Drawing of transverse section in summit area (Lucas, 1953).——*2.* Drawing of slightly inclined longitudinal section through an interray. [$H_R$, part of hydrospires interpreted to have formed from the radials; $H_D$, part of hydrospires interpreted to have formed from the deltoids. Circles indicate position of crystallographic axes of calcite for each thecal plate; in inner circles the interference figure in convergent polarized light is shown where the calcite optic axis is nearly vertical; in outer circles the positions of the crystallographic axes are shown as they would appear plotted in stereographic projection. The ruled lines are parallel to the vibration directions of the ordinary and extraordinary ways in the calcite crystals, rectangles (square, if the section were perpendicular to the crystallographic axis) being more elongate as the crystallographic axis is increasingly inclined with respect to the polar axis of the blastoid.]

than thin sections for detailed morphological investigations.

## THIN SECTIONS

Thin sections are advantageous for studying internal structural elements of blastoids such as hydrospires, concealed anal deltoids, and canals such as the oral ring canal and its aboral extensions. Very thin sections are best for studies involving polarized light, whereas thicker sections are superior for distinguishing plate relationships and sutures. Furthermore, relatively thick sections provide better photographs than excessively thin sections.

Serial thin sections are particularly useful for determining progressive changes in structural elements (e.g., development of hydrospires). The main problems in preparing serial thin sections are the impossibility of obtaining closely spaced sections and the tendency of specimens to shatter during sawing. Recently, JOYSEY & BREIMER (1963, p. 473) have described a new saw which apparently is capable of ameliorating these problems.

## STAINS

Stains may be useful in emphasizing certain plates and thus in making plate relationships more apparent. The stains commonly are used on ground surfaces and for working with acetate peels and thin sections.

## OPTICAL CHARACTERISTICS OF PLATES

For many years optical properties have been utilized to determine plate relationships in echinoderm skeletons. As reviewed by RAUP (1959, p. 661), each of the structural elements of echinoderms behaves as a single calcite crystal. Thus, the various plates of a blastoid theca become extinguished in different positions when viewed in thin section with a polarizing microscope. The technique is most often used to observe the boundaries and relationships of thecal plates and to differentiate between plate sutures and adventitious cracks in the theca. LUCAS (1953, p. 635-637) used this method in attempting to determine which thecal plates of *Cryptoschisma schultzii* contributed to the development of the hydrospires. He concluded that the lancets, radials, and deltoids all shared in their formation (Fig. 207). More recently JOYSEY & BREIMER (1963, p. 472-473), in studying *Pentablastus,* used the technique in distinguishing plate relationships but found that "both optical continuities and discontinuities can be the product of secondary recrystallization."

Examination of thin sections of *Pentremites* and *Globoblastus* under polarized light aids in distinguishing plate relationships, sutures, and cracks in the theca, but is not useful in determining the identity of thecal plates which contribute to the hydrospires. The hydrospire folds are composed of very small calcite crystals, so tiny that at magnifications up to ×450 it is not possible to recognize when the crystals are extinguished. Mostly, the thecal interior is filled with large calcite crystals which generally are in optical continuity with the nearest thecal plates.

# ONTOGENY

By HAROLD H. BEAVER

Numerous publications, particularly in recent years, have been concerned with blastoid ontogeny. Principal in importance are papers by ETHERIDGE & CARPENTER (1886), HAMBACH (1903), SMITH (1906), ULRICH (1918), WELLER (1920), BATHER (1922), CRONEIS & GEIS (1940), MOORE (1940), BURMA (1948), WANNER (1951), JOYSEY (1953, 1959), GALLOWAY & KASKA (1957), and REGNÉLL (1960). Growth series have been described for a number of genera, including *Codaster, ?Diploblastus, Globoblastus, Orbitremites, Orophocrinus,* and *Pentremites.* Published growth series of various species of *Pentremites* are particularly numerous because of the relative abundance of collected specimens. Nearly complete series have been illustrated for *P. conoideus* (SMITH, 1906, pl. 46), *P. girtyi,* and *P. okawensis* (GALLOWAY & KASKA, 1957, pl. 11).

## LARVAL AND JUVENILE STAGES

Almost nothing is known about the earliest growth stages of blastoids. CRONEIS & GEIS (1940) described some extremely tiny forms (length or diameter as small as 0.1 mm.) which they identified as *Mesoblastus* [*Diploblastus*] *glaber* and *Pentremites princetonensis.* Very much doubt remains, however, as to whether the specimens studied by them actually are blastoids. They have not been reported on further or made available for examination by other workers. Also, efforts to duplicate collections used by CRONEIS & GEIS have been unsuccessful.

The smallest specimens of *Pentremites* yet found in the Salem and Harrodsburg Limestones (Meramecian) of Indiana are reported by SMITH (1906) to be approximately 0.8 mm. in length. These specimens had three basals and five radials, but the plates in the oral region were not preserved.

In general, young blastoid individuals tend to be elongate. This appears to be true not only in genera with species which may be flat-based or pyriform as adults (e.g., *Pentremites*), but also in typically globular types. As previously mentioned, the young of *Globoblastus* are typically elongate globular, whereas adult specimens are nearly globular. It is presumed that the same is true of many other blastoids.

## ADULT AND GERONTIC STAGES

Large collections of blastoids, such as are obtainable at many places, especially in outcrop areas of fossiliferous Upper Mississippian (Chesteran) strata, consist predominantly of specimens having approximately the same size and all relatively large. They obviously represent a mature growth stage and may be classed as adults, though no sharp boundary separates them from slightly undersized and distinctly smaller-than-average specimens. The small individuals, comprising a minority, grade downward to the smallest, interpreted as juveniles.

Old-age blastoids generally have a tendency to become obese. Globular types in old age are commonly depressed globular (e.g., *Globoblastus*). Flat-based *Pentremites* tend to increase width of the theca relative to thecal length, with a resultant increase in the ambulacral length.

## GROWTH SERIES OF PENTREMITES

Examination of fine fractions of shale, rich in *Pentremites* from the Paint Creek (Chesteran) Formation, near Floraville, Illinois, shows that the smallest specimens are about 2 mm. in height. They are clearly recognizable as belonging to *Pentremites*. Because blastoids change shape and because some structures are modified during growth, it is commonly difficult to distinguish youthful individuals on the specific level if two or more specimens occur together. For example, abundant specimens generally identified as *P. godoni, P. gemmiformis, P. pyramidatus,* and *P. symmetricus,* may be collected from this same formation and locality. Many thousands—in all probability many tens of thousands—of *Pentremites* have been taken from two adjacent exposures at the Floraville locality. In adult or near-adult stages, *P. symmetricus* may be identified by shape of the calyx and length of the ambulacra. Progressively smaller specimens of this and other species are increasingly difficult to distinguish because all representatives of *Pentremites* are steeply conical when young, with ambulacral aras largely confined to the summit of the theca. Close examination of ambulacral features indicates that minor differences in characters of the side plates, transverse ridges, and hydrospire pore grooves may aid in recognizing species of different types. Two major types are distinguished, the first (Type 1) consisting of calyces with a nearly flat base in the adult stage *(P. godoni)* (Fig. 208), and the second (Type 2) characterized by calyces with a pyriform outline in the adult stage (Fig. 209). This type includes *P. gemmiformis, P. pyramidatus,* and *P. symmetricus*.

The relatively flat-based Type 1, represented solely by *Pentremites godoni,* includes specimens ranging from about 2 mm. to more than 20 mm. in height. The very small specimens (Fig. 208,*1-3*) are steeply conical, the ambulacra are short and the basals make up a considerable part of the theca. The ambulacra are extremely short and nearly confined to the summit in the tiniest specimens (Fig. 208,*1*). Only seven or eight side plates occur along either margin of an ambulacrum. Much of the summit is occupied by the spiracles, anal opening, and mouth. With increase in size, the ambulacra lengthen progressively. In larger specimens, three trends in shape are distinguishable, the first (Subtype 1a) including individuals with nearly equidimensional calyces, with height of theca approximately the same as width (Fig. 208,*4-9*), another (Subtype 1b) represented by specimens having calyces which become increasingly slender, with height greater than width (Fig. 208,*10-14*), and a third (Subtype 1c) characterized by calyces which are wider than high (Fig. 208,*15-19*). All three subtypes may be presumed to develop from juveniles which in most diminutive examples show steep-sided conical form (Fig. 208,*1-3*).

Species of *Pentremites* with pyriform adult calyces, grouped in Type 2, include *P. symmetricus, P. pyramidatus,* and *P. gemmiformis.* Very small individuals presumed to represent the same species are essentially similar in shape and size to representatives of Type 1. The pyriform thecal shape of the diminutive calyces persists, however, in larger specimens, among which three different trends are discernible. In one group (Subtype 2a) the theca becomes more slender and the ambulacra ex-

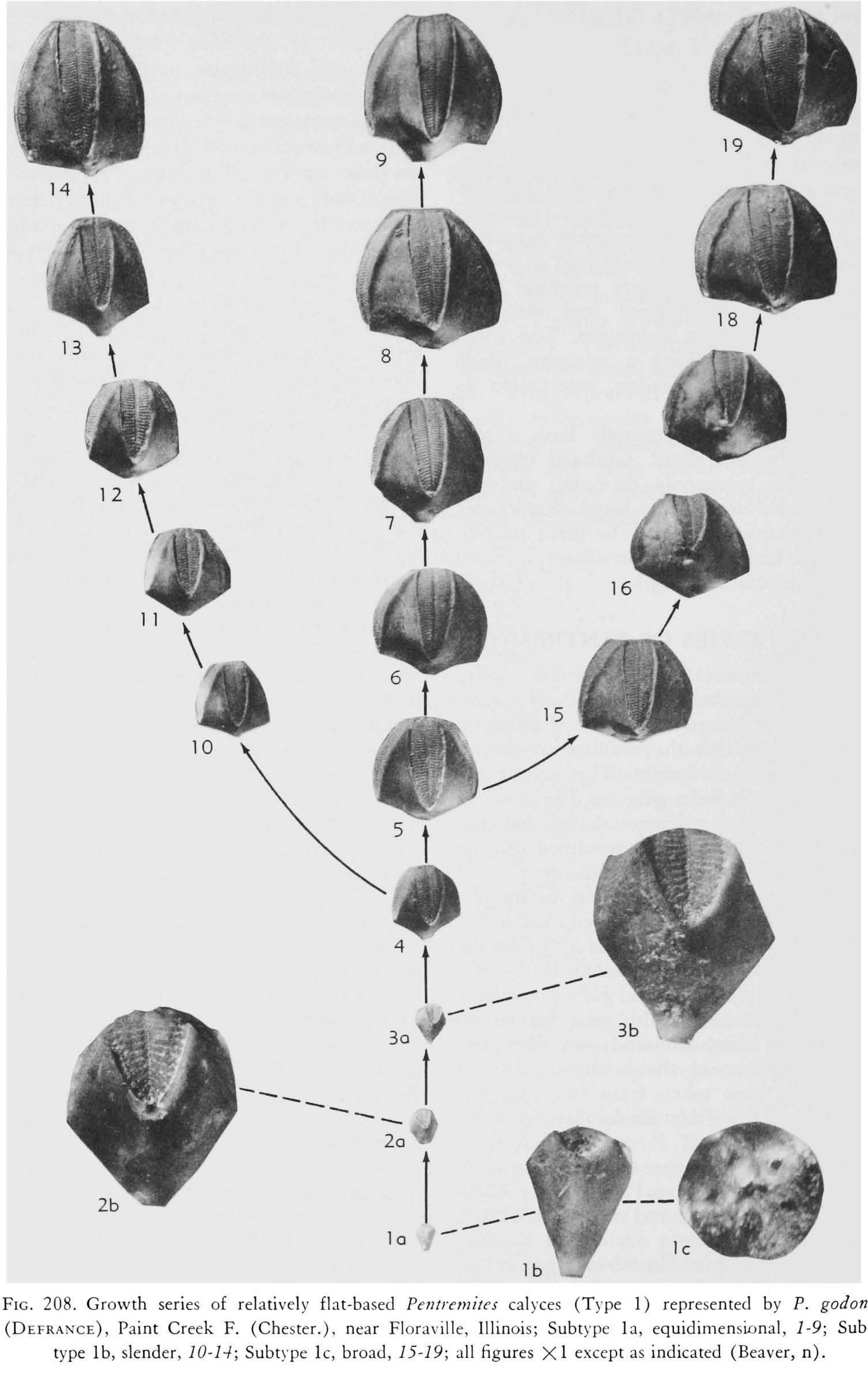

FIG. 208. Growth series of relatively flat-based *Pentremites* calyces (Type 1) represented by *P. godoni* (DEFRANCE), Paint Creek F. (Chester.), near Floraville, Illinois; Subtype 1a, equidimensional, *1-9*; Subtype 1b, slender, *10-14*; Subtype 1c, broad, *15-19*; all figures ×1 except as indicated (Beaver, n).

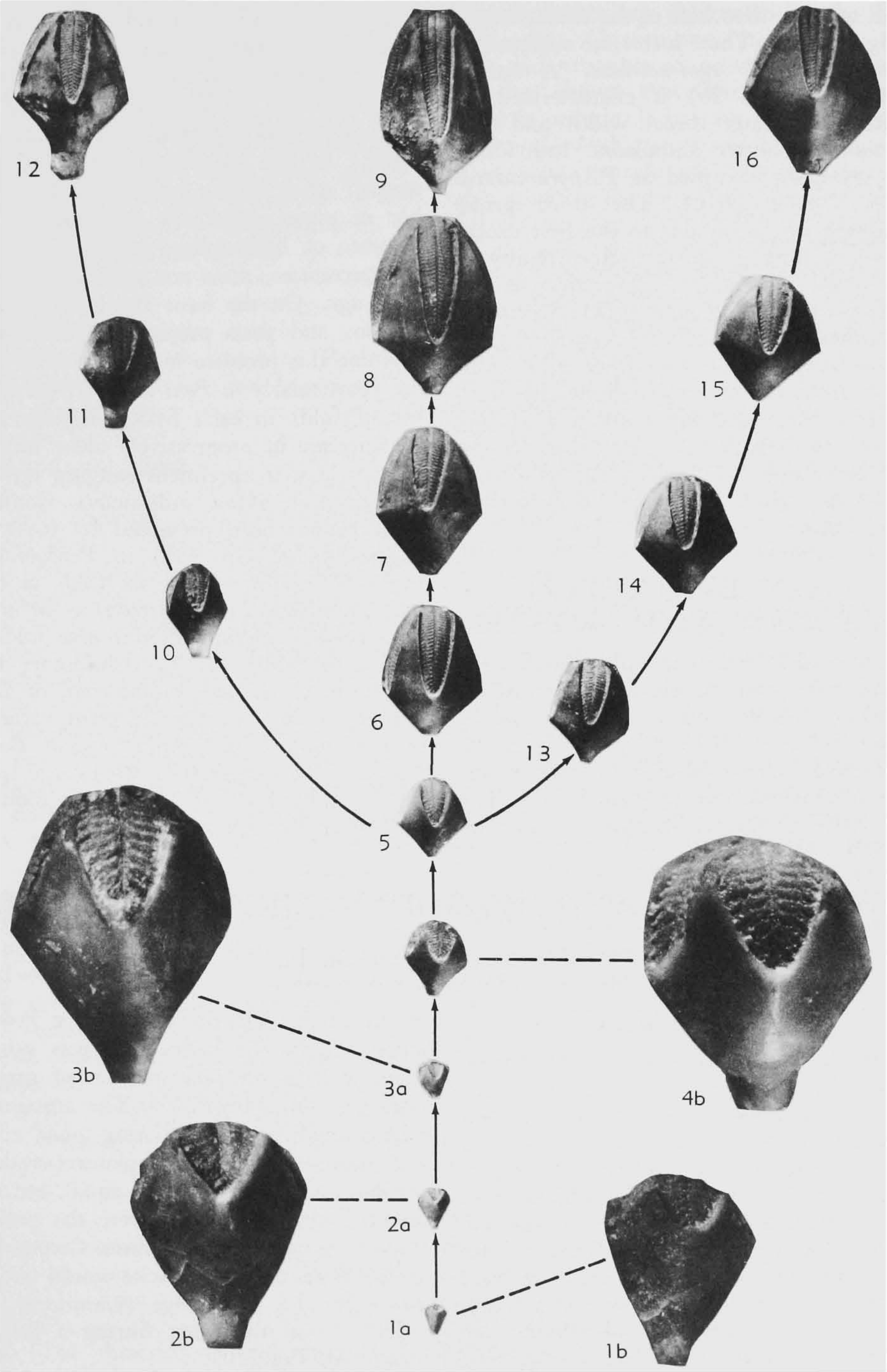

FIG. 209. Growth series of pyriform *Pentremites* calyces (Type 2), all from Paint Creek F. (Chester), near Floraville, Illinois; Subtype 2a, *P. symmetricus* HALL, *6-9*; Subtype 2b, *P. gemmiformis* HAMBACH, *10-12*; Subtype 2c, *P. pyramidatus* ULRICH, *?13,14-16*; all figures ×1 except as indicated (Beaver, n).

tend to more than half of the thecal height (Fig. 209,*6-9*). These forms are customarily identified as *P. symmetricus.* A second group (Subtype 2b) is characterized by somewhat greater thecal width and proportionally shorter ambulacra. Individuals are generally identified as *P. pyramidatus* (Fig. 209,*?13, 14-16*). The third group (Subtype 2c) is similar to the first except for thickening of the aboral extremity of the theca, seemingly by accretion of secondary calcite (Fig. 209,*10-12*). Specimens with these characteristics are assigned to *P. gemmiformis.* The possibility that adult pyriform calyces of Type 2, generally interpreted to represent these different species, actually belong to a single species having variable shape and ambulacral length or thickened aboral extremity needs further investigation.

## CHANGES IN THECAL ELEMENTS WITH GROWTH

It is well known that with growth some thecal and brachiole elements increase in number, whereas other elements simply become larger. Major plates, such as the basals, radials, and deltoids, increase in size with age, as indicated by growth lines. The ambulacra, however, increase in size by adding side and outer side plates at the aboral tips of the ambulacra. These plates are accompanied, of course, by additional brachioles and auxiliary elements such as ambulacral and brachiole cover plates. Additions to the ambulacral system during growth result in the extremely large number of plates previously mentioned. The number of hydrospires, contrary to some interpretations, does not seem to increase with age. On the basis of numerous thin sections and peels prepared specifically to examine this problem in a number of genera (particularly in *Pentremites*), the number of folds in each hydrospiralium does not increase in progressively older individuals, at least in specimens ranging upward in size from a few millimeters. Contrary evidence has been presented by Joysey & Breimer (1963, p. 481) in *Pentablastus,* where a specimen with six folds in each hydrospiralium is interpreted to be older than another individual with five folds in each hydrospiralium. This difference may be due to unlike age, as inferred, or alternatively, it may merely represent variation in the number of hydrospires in *Pentablastus.* The examination of a large number of individuals of all ages is required to answer this question.

# DEVELOPMENT AND HYDRODYNAMICS OF BLASTOIDS

By Donald B. Macurda, Jr.
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## DEVELOPMENT

The skeleton of living echinoderms is an endoskeleton, secreted by mesodermal tissue. The microstructure of this skeleton was likened to the open girderwork of a modern skyscraper by Nichols (1962, p. 93). By analogy with Recent echinoderms, the calcite of the blastoid skeleton was also formed by the mesoderm. Growth lines are commonly preserved on outer surfaces of the principal calyx plates (Fig. 210). Growth was accretionary and episodic, occurring in a lateral direction, although occasional secondary deposits are found covering the origins of the plates.

The tissue which secreted the calcite lay between opposing plate edges. The width of the calcite laid down during a growth increment on the plate edge was usually small, with a multiple number of growth lines per mm. (Fig. 210). The amount of calcite deposited on opposing plate edges within the same series of plates (as along the interradial suture) was equal, but differential rates of growth were the general rule along radiodeltoid sutures. Commonly, several times as much calcite would be laid down on one plate edge (commonly the radial) as on the other during a growth increment (Fig. 210).

The microstructure of the calcite in blastoid plates is usually destroyed by recrystallization, but plates belonging to *Rhopaloblastus* from the Permian of Western

Australia have a reticulate pattern (Fig. 210) suggestive of the calcite latticework of modern echinoderms. The calcite of the external surface has a fenestrate appearance, with the long axes or ribs very closely spaced and arrayed perpendicular to edges of the plates along which growth occurred. A very sharp divergence of the long axes is observed at the intersection of adjacent growth fronts. The cross bars connecting long axes are as wide as the axes; the fenestrules or openings are approximately rectangular and are not as wide as the ribs of the crossbars. They are evenly spaced. Internal and lateral edges have a very fenestrate appearance. Secondary calcite has filled in the open spaces in the lattice and appears as clear blebs of calcite.

Growth lines are preserved only on the external surface. NISSEN (1963) has presented data suggesting that the calcite of an echinoid plate is a composite of tiny crystal units, with the c-axes oriented in the same direction. Each individual plate of a blastoid behaves optically as one crystallographic unit. The maximum size for one plate may be several tens of millimeters, a large size for an individual crystal. The latticework of the blastoid skeleton may have consisted of many individual fibers similar to those found in echinoids, which were added onto the lattice during each growth increment, and then subsequently recrystallized to form an individual crystal. It is unclear why growth lines are only reflected externally.

The growth lines preserved on the external surfaces of the plates record the complete postmetamorphic development of the blastoid. The principal plate of the calyx is the radial, which usually has six edges. The growth lines converge toward the origin of the radial which is at the aboral end of the ambulacrum. The radial has grown outward in three primary directions perpendicular to the sutures along which calcite was added (growth fronts) (Fig. 211). Each axis and front has a complement on the opposite side of the radial. The direction of growth toward the radiodeltoid suture is designated the *RD* axis, that toward the interradial suture the *RR* axis, and that toward the radial basal suture, the *RB* axis (Fig. 211). Growth fronts are designated as the *RD* front, etc. Quantitative analysis of the rates and amounts of growth along these axes has shown that development of the radial is orderly, indicating a close genetic control. Growth curves can be constructed by plotting growth axes against one another to show the ontogenetic development of the plate (Fig. 212,*2*). Most growth curves are isometric, there being little change in rates relative to one another. When the amount of growth along an axis is plotted against the width of the growth front for an ontogenetic series, a well-ordered pattern is found (Fig. 212,*1*). An ontogenetic study of *Orophocrinus* (MACURDA, 1965, 107; 1966, 109) showed that quantitative measurements of growth axes and fronts were useful and discriminatory taxonomic characters and permitted greater insight into blastoid development, morphology, and physiology.

Quantitative analysis of the development of the radial in genera other than *Orophocrinus* has shown that the development is almost always isometric as well. The amount of calcite added along a growth front during one increment is almost constant throughout the entire ontogenetic history of the individual from a neanic to a gerontic stage. The development was thus under close genetic control. The length of a growth axis provides a time character by which the relative level of development of different individuals can be compared. The *RR* axis was used in the study of *Orophocrinus* previously cited (MACURDA, 1965, 107; 1966, 109); study of other genera suggests that the sum of the *RD, RR,* and *RB* axes for an individual is a better time character.

Analysis to date has treated the growth axes as two-dimensional parameters, i.e., as though they were all arrayed in one plane. The radial plates of blastoids have many different shapes as a result of growth along the sutures (Fig. 213,*1-3,7*). It will be necessary to array the axes in a three-dimensional matrix to realize the full potential of ontogenetic analysis and specific differentiation. The lengths of the axes of two plates may be very similar, but the directions of growth of these in a third dimension may result in a globular form such as *Orbitremites* or *Globoblastus,* or

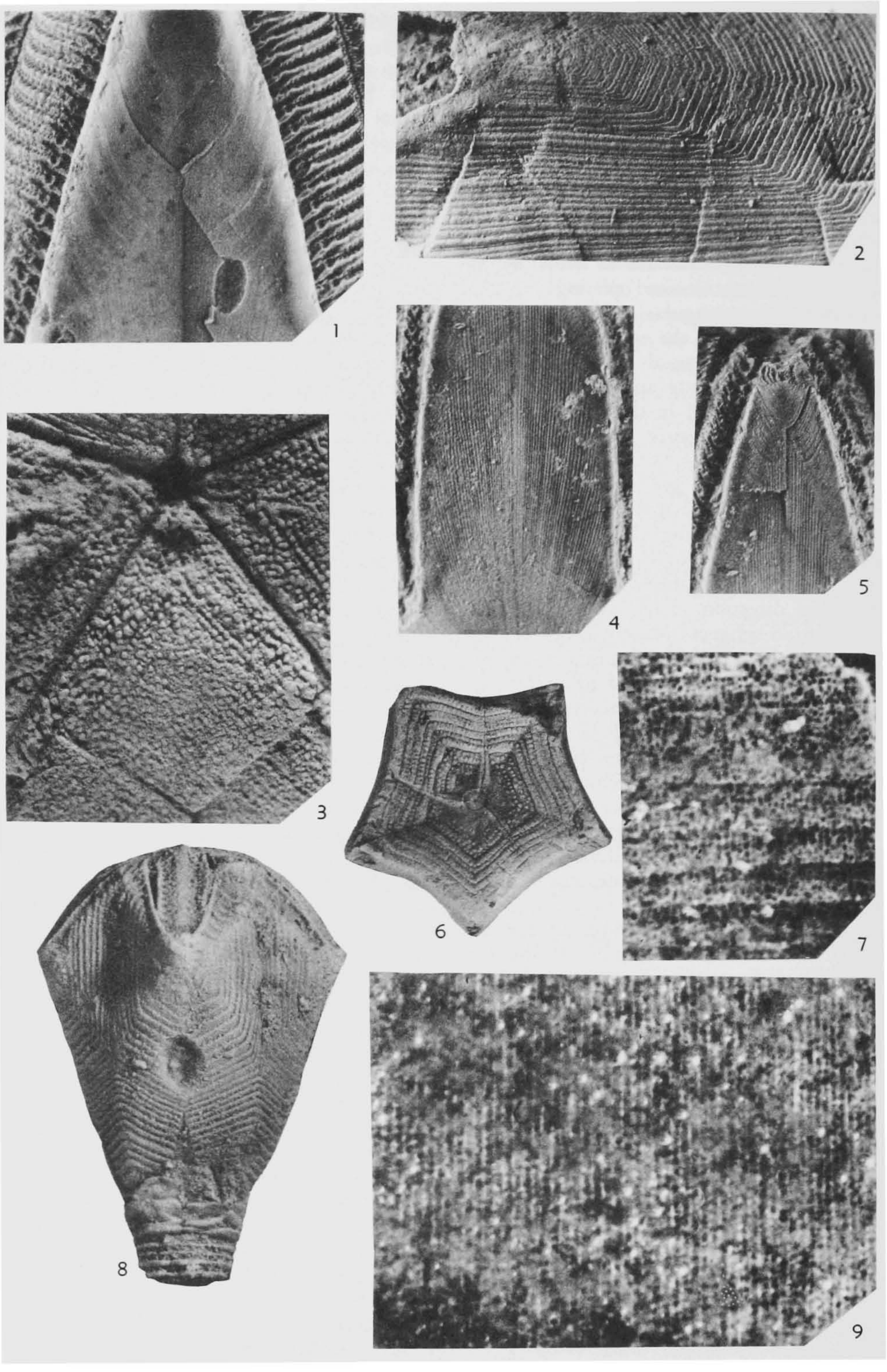

FIG. 210. [*Explanation on facing page.*]

produce a very angular form, as *Hadroblastus* or *Codaster.*

The origin of the radial is commonly obscured by secondary deposits of calcite (Fig. 213,*5-6*). These secondary deposits may result from the more intensive physiological activity which took place at the aboral end of the ambulacrum where new side plates were formed. Some blastoids utilized the ability to secrete this extra calcite to form a prong on the radial (Fig. 213,*4*), by which the length of the ambulacrum could be extended and the food-gathering capacity multiplied without effecting a change in the shape of the calyx. This evolutionary experiment occurred several times, as in the Mississippian genus *Dentiblastus* and the Permian *Thaumatoblastus.*

The basals of a blastoid are usually small in relation to the radials. Most show two primary directions of growth, toward the radial-basal (*BR* axis) and interbasal sutures (*BB* axis) (Fig. 214,*11*). The rate of growth along the *BR* axis is usually several times that of the *BB* axis; the origin of the basal is located near the distal end .of the plate.

The rate of growth of the *BR* axis of the basal is usually about equal to the *RB* axis of the radial, one half of the pelvis being formed by the basals, one half by the radials (Fig. 214,*1*). In a few genera with a narrow, conical pelvis, the area available for basal growth is unconfined, not being restricted by the radials in globose genera such as *Mesoblastus* or *Cryptoblastus,* and the rate of growth on *BR* may be several times that of *RB* as in *Belocrinus* (Fig. 214, *11*).

The stem was attached to the distal ends of the three basals. The mass and volume of the calyx increased throughout the ontogenetic development of the organism. If the original growth pattern of the basals was maintained without any modification, the attachment of the calyx to the stem would be highly unstable. It would consist of three points resting on a cylinder (Fig. 212,*3*). Therefore, the configuration of the plate had to be modified. In most genera this was accomplished by the secretion of a secondary deposit over the origin of the basal, thus modifying the three points to a cylinder (Fig. 212,*4*; 214,*3-4,7,9*). The secondary deposits increased during development. An alternative mechanism was adopted by some genera, as *Phaenoschisma* and *Rhopaloblastus,* with long, narrow basals. There is a third growth axis (the *BA* axis), directed toward the stem attachment area, which maintained the flat circular attachment area at the base of the calyx (Fig. 214,*10*).

The entire calyx and thus the weight of the blastoid were supported by a cylindrical, jointed stem in its aqueous environment. As the surface area of the plates increased, the weight of the organism would multiply at an increasingly accelerating rate, since it is a function of the volume ($V^3$). The cross-sectional area of the stem attachment in ephebic individuals was apparently insufficient for support of neanic or gerontic individuals, for the diameter of the crenellar ring (Fig. 214,7) and thus the effective cross-sectional area of the stem-calyx joint increased throughout ontogenetic development of the individual. In

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[*See facing page*]

FIG. 210. Plate growth in blastoids.

*1*. Growth lines of radials and deltoid in interambulacral area of *Pentremites godoni* DEFRANCE, U.Miss., USA(Ill.), ×7.5 (Macurda, n).

*2*. Growth lines in interradial and radial-basal sectors of radial of *Rhopaloblastus belfordi* (CROCKFORD & BROWN), Perm., Australia, ×7.5 (Macurda, n).

*3*. Growth lines of deltoid, paralleling radial-deltoid and interdeltoid sutures in *Indoblastus granulatus* WANNER, Perm., Timor, ×6 (Macurda, n).

*4*. Growth lines in interambulacral area of *Hyperoblastus filosus* (WHITEAVES), reflecting accelerated growth along radial-deltoid axis, Dev., Can.(Ont.), ×7.5 (Macurda, n).

*5*. Opposing growth lines of radial and deltoid reflecting faster growth on radial, in *Hyperoblastus filosus* (WHITEAVES), Dev., Can.(Ont.), ×7.5 (Macurda, n).

*6*. Growth lines of basals in *Timoroblastus coronatus* WANNER, Perm., Timor, ×2 (Macurda, n).

*7*. Fenestrate structure of calcite in interradial sector (7) and radial-basal sector (9) of radial of *Rhopaloblastus belfordi* (CROCKFORD & BROWN), plate edge toward bottom of figure, Perm., Australia, ×38 (Macurda, n).

*8*. Opposing growth lines of radials and basals in *Orophocrinus conicus* (WACHSMUTH & SPRINGER), L.Miss., USA(Iowa), ×6 (107).

FIG. 211. Growth axes and fronts of radial plate in *Belocrinus cottaldi* (MUNIER-CHALMAS), Dev., Fr., ×8 (Macurda, n).

*Orophocrinus,* new stem plates apparently were added at the junction of the calyx and stem, starting to form initially in a small depression of the basals, then being moved into position and completed. Once formed, the size of the plate was apparently fixed, for the height of stem plates is constant throughout the stem and if the diameter was to be increased, it would involve resorption of the crenellar ring which is part of an interlocking projection and depression between plates in *Orophocrinus* (Fig. 214,*5-6*). The diameter of stem plates decreases gradually down the column. By increasing the cross-sectional area of the stem-attachment area, greater stability would be provided against fluctuations in wave or current energy in the environment. A similar pattern can be found in other stemmed echinoderms, as the crinoid *Neoplatycrinus* and the cystoid *Strobilocystites,* as the area to which the stem was attached increased during ontogeny. Some genera (e.g., *Globoblastus, Orbiblastus, Deltoblastus*) developed a concave base (Fig. 214,*8*), which would shield the stem-attachment area and buffer it against energy fluctuations. Other genera (e.g., *Eleutherocrinus, Dipteroblastus*) completely lost their stem and adopted a free-living life mode (Fig. 214,*2*). The growth pattern of the basals and radials has been altered by adoption of a bilateral symmetry characteristic of organisms with a nonattached mode of life.

The deltoids which surrounded the mouth had complex growth patterns because of the bordering peristome, entrances to hydrospires, presence of food grooves, and the hydrospires themselves (Fig. 215, *2-3*). The adoralmost edge of the deltoid borders the peristome. The adoral lateral edges bear the adoral ends of the main food grooves. The aboral lateral edges are usually bordered by ambulacra; an entrance to the hydrospires is usually present on the median lateral edge of most spiraculate genera. The aboral edge of the plate abuts against the adoral edges of two adjacent radial limbs. When first formed, the adoral portion of the plate is quite large in relation to the aboral part (Fig. 212,*5*). After metamorphosis, the space around the peristome had to be filled by five plates. This meant rapid development of the adoral portion of the plate. After an individual has reached 3 to 4 mm. in length and width, most development is directed in an aboral direction (the *DR* axis). Calcite is secreted along the radiodeltoid suture; the rate of growth of the *DR* axis is usually several times less than that of the opposing *RD* axis. Each deltoid normally bears the adoral ends of two groups of hydrospires, which hang as pendant-like folds into the visceral cavity. The two groups of hydrospires are normally separated at their adoral ends (Fig. 215,*1*). This separation may reflect the initial size of the plate or reflect the formation of hydrospires when the deltoid reached a particular size. When calcite was added to the radials and deltoids along the radiodeltoid suture, it was also added to the hydrospires; their length increased throughout the ontogenetic development of the individual. Their greatest height is at the radiodeltoid suture (Fig. 215,*5*); this increases with age. The radiodeltoid suture can be traced across the hydrospires. Once formed, the number of hydrospires per group was usually constant throughout the ontogenetic development of the individual. However, in some fissiculate genera, the hydrospires occupy the entire width of the *RD* and *DR* growth fronts, each hydrospire exiting individually to the exterior (Fig. 215). As the blastoid grew, the number of hydrospires in these genera (e.g., *Codaster, Hadroblastus, Notoblastus*) increased, to a maximum number of 60 on one edge of a radial of *Hadroblastus.*

In spiraculate genera there are pores along the margins of the ambulacra. In some genera (e.g., *Cryptoblastus, Globoblastus, Mesoblastus*) the pores pierce the solid calcite of the radials (Fig. 216,*3-4*). New pores were formed when new calcite was added along the radiodeltoid suture. In other genera (e.g., *Cordyloblastus, Lophoblastus, Pentremites, Rhopaloblastus, Schizoblastus*), the pores are formed as a gap between the edges of the side plates and adjacent radials and deltoids (Fig. 217,*4-5*). These pores were formed at the same time that new ambulacral plates were added at the aboral end of the ambulacrum. In *Cordyloblastus* and *Rhopaloblastus,* new calcite was eventually added which filled in the adoral or earliest-formed pores; they are thus absent along part or all of the

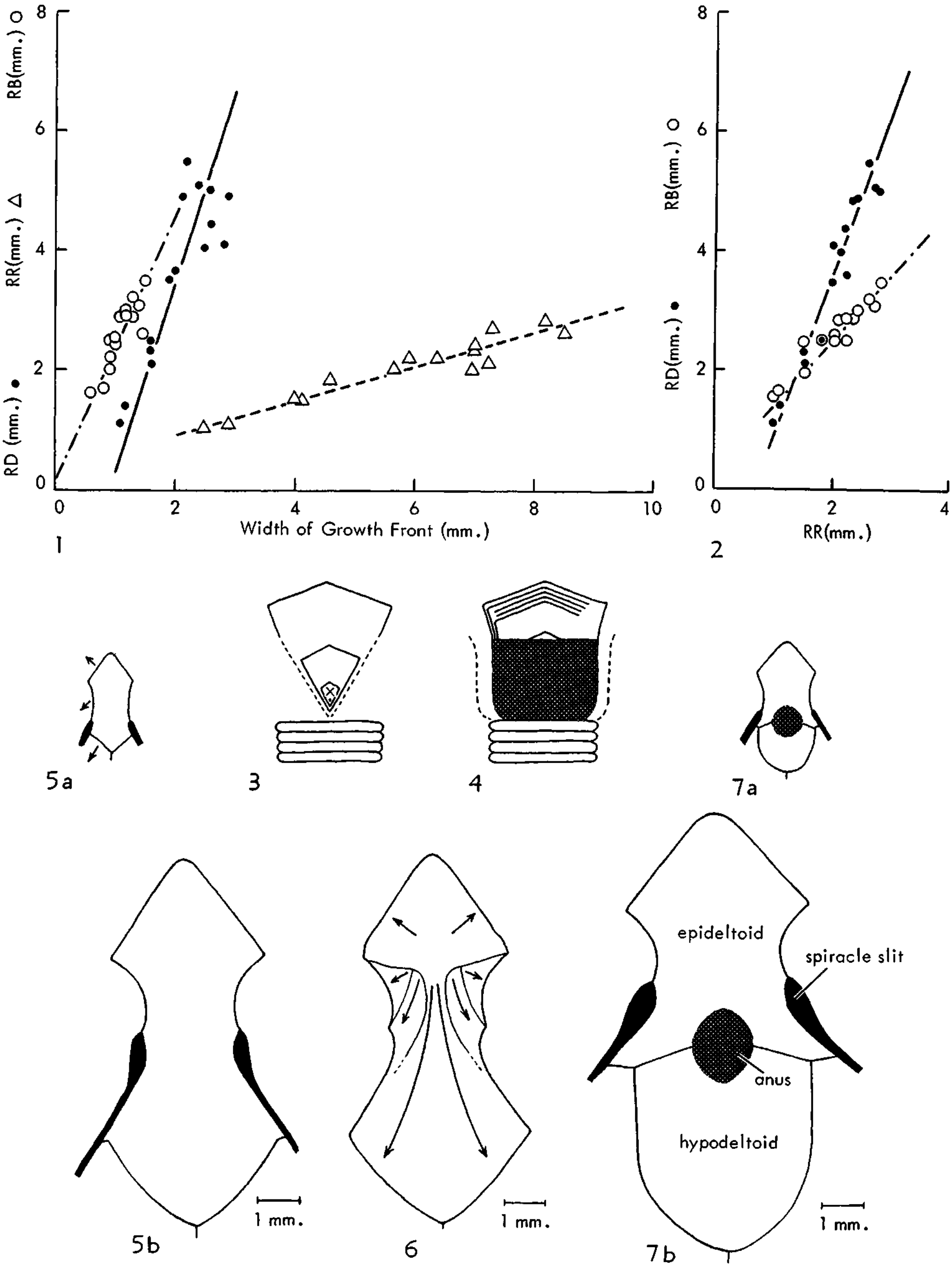

FIG. 212. Growth of radials, basals, and deltoids.

*1.* Growth of radial growth axes (*RD*=radial-deltoid, *RR*=interradial, *RB*=radial basal) against width of growth fronts in *Phaenoblastus caryophyllatus* (DE KONINCK & LEHON), L.Carb., Tournais., Belg. (Macurda, n).

*2.* Growth of *RD* and *RB* axes against *RR* axis in *Phaenoblastus caryophyllatus* (DE KONINCK & LEHON), L.Carb., Tournais., Belg. (Macurda, n).

deltoid. In large specimens of *Schizoblastus,* the pores in the middle of the ambulacra were eventually sealed off.

New calcite was also added along the adoral edges of the deltoid in some genera (*DD* axis) (Fig. 212,*6*). As a consequence,

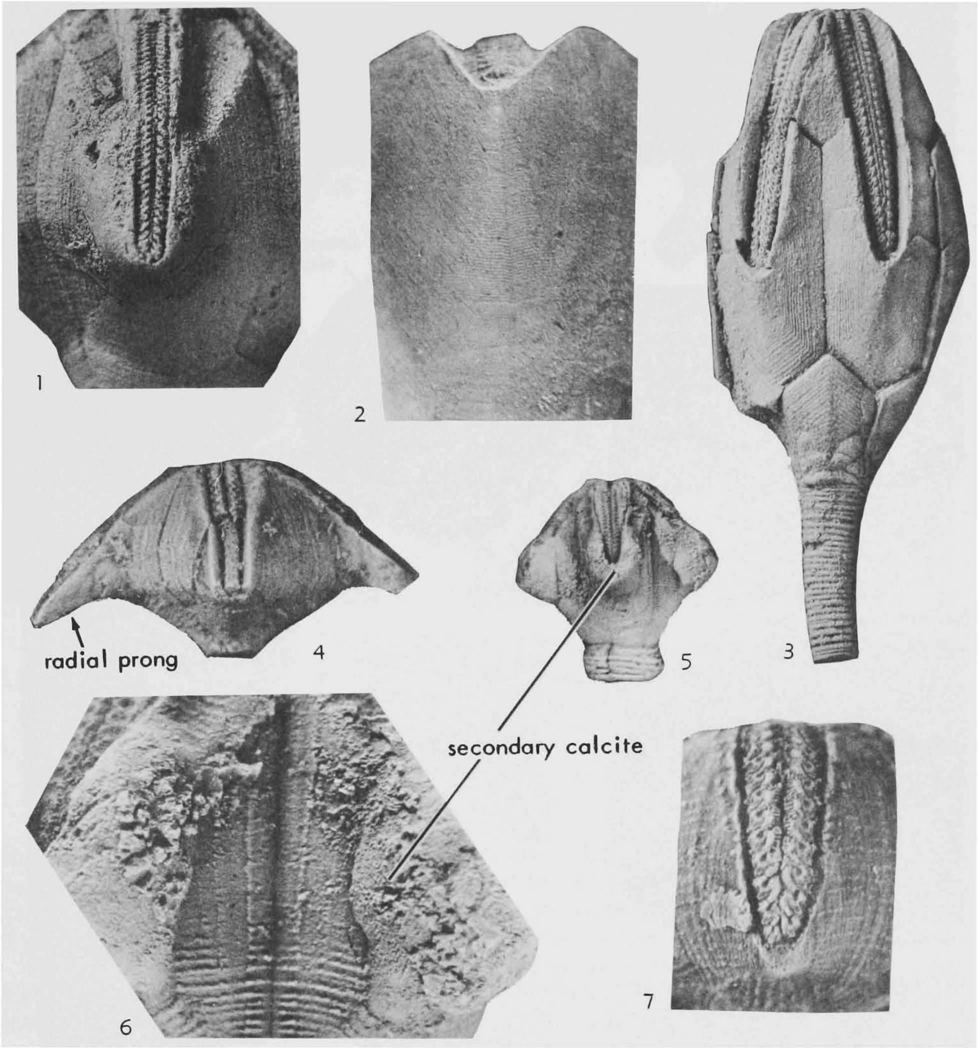

FIG. 213. Growth patterns of radials and secondary calcite deposits.

*1. Orophocrinus stelliformis* (OWEN & SHUMARD), L.Miss., USA(Iowa), ×3 (108).

*2. Heteroschisma canadense* (BILLINGS), Dev., Can. (Ont.), ×7.5 (Macurda, n).

*3. Pyramiblastus fusiformis* (WACHSMUTH & SPRINGER), L.Miss., USA(Iowa), ×3 (104).

*4. Dentiblastus sirius* (WHITE), L.Miss., USA(Mo.), ×6 (102).

*5-6. Orophocrinus stelliformis* (OWEN & SHUMARD), L.Miss., USA(Mo.), *5,* ×2 (109), *6,* ×7.5 (Macurda, n).

*7. Monadoblastus crenulatus* (ROEMER), L.Carb., Tournais., Belg., ×7.5 (Macurda, n).

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FIG. 212. *(Continued.)*

*3-4.* Growth of basals of *Orophocrinus stelliformis* (OWEN & SHUMARD) and secondary overgrowth (x marks origin) (109).

*5-7.* Growth of deltoids of *Orophocrinus stelliformis* (OWEN & SHUMARD) showing growth of small plate to maturity and growth axes of plate (109) (*5a, 7a,* youthful phases).

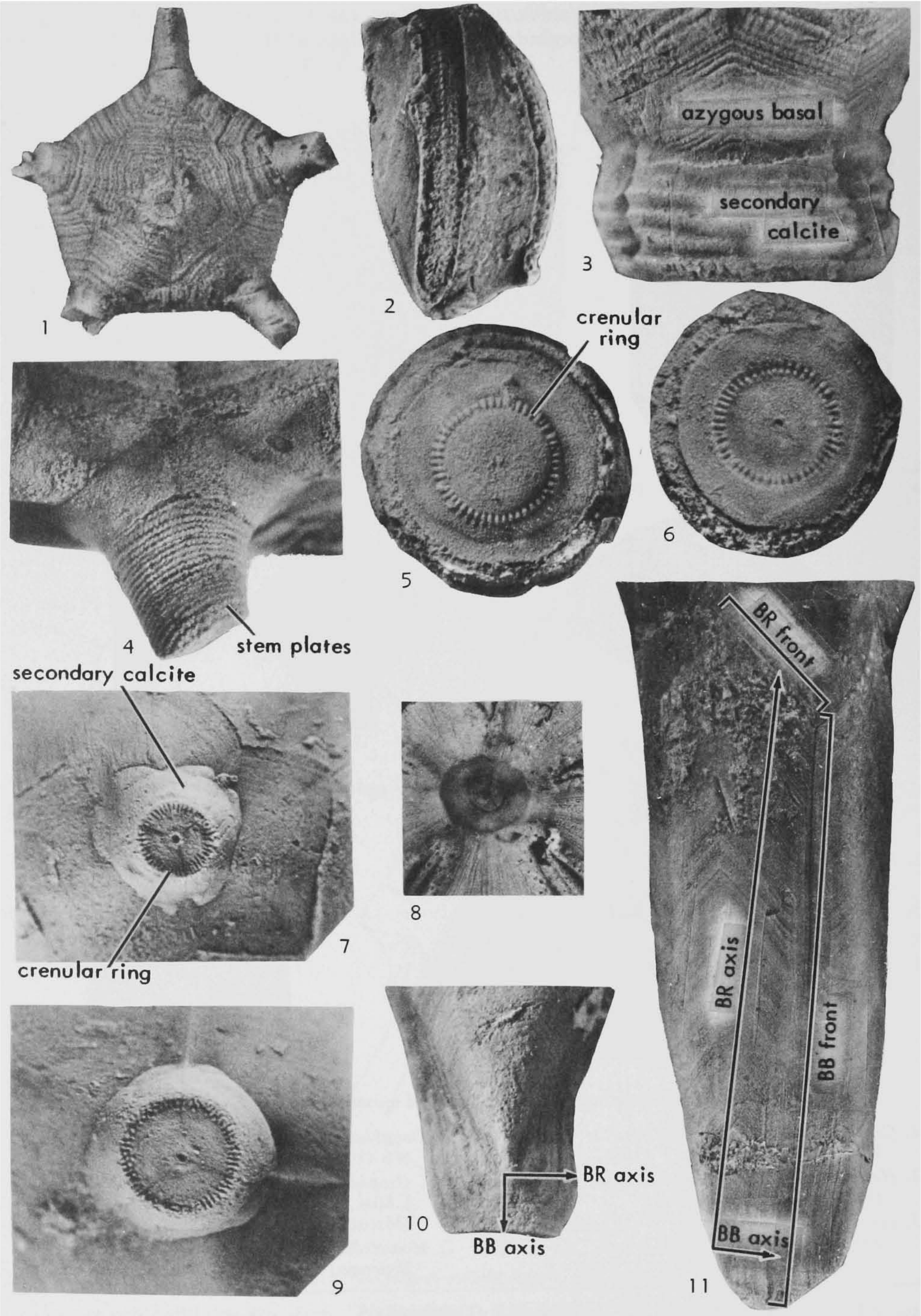

Fig. 214. Growth of basal and stem plates. *(Continued on facing page.)*

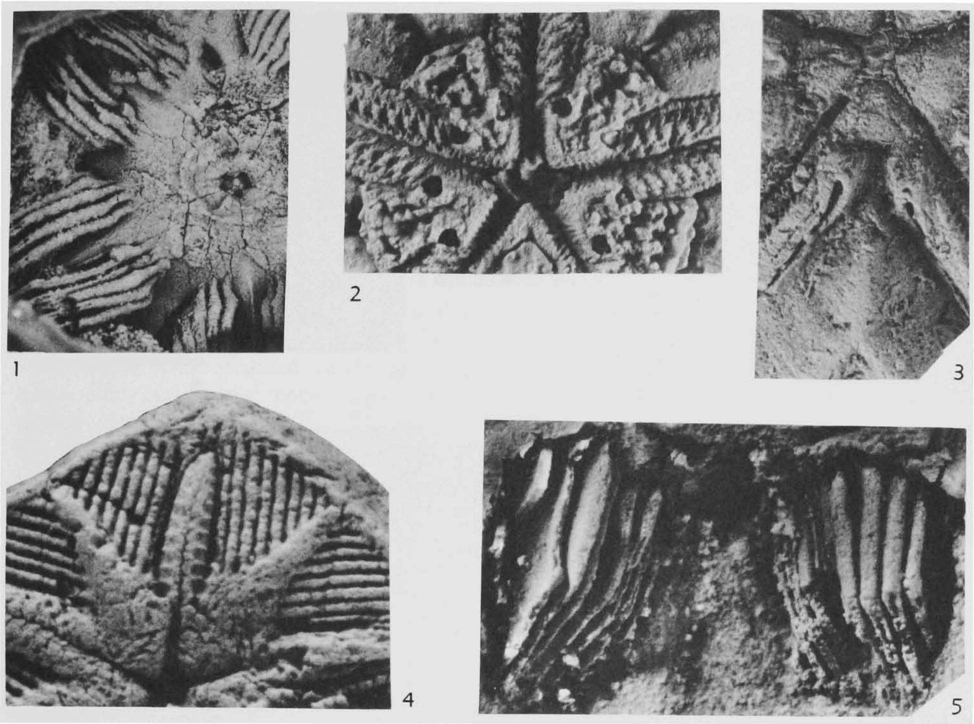

FIG. 215. Deltoids and hydrospires.

1. Internal view of hydrospires of *Orophocrinus stelliformis* (OWEN & SHUMARD), L.Miss., USA (Iowa), ×2 (109).
2. Deltoids of *Cryptoblastus melo* (OWEN & SHUMARD), L.Miss., USA (Ill.), ×7.5 (Macurda, n).
3. Deltoid of *Orophocrinus stelliformis* (OWEN & SHUMARD), L.Miss., USA (Iowa), ×4 (109).
4. Hydrospire slits of *Codaster acutus* M'COY, L. Carb., Eng., ×6.5 (Macurda, n).
5. Hydrospires of *Orophocrinus stelliformis* (OWEN & SHUMARD), L.Miss., USA (Iowa), ×7.5 (109).

the food groove was constantly being reformed. If no calcite was added on the free edge bordering the peristome, then the latter's area increased with age.

The adoral openings to the hydrospires, either as spiracles, or spiracle slits, may undergo little ontogenetic modification or may migrate, as in *Orophocrinus* (Fig. 212,6; 217,6). Spiracles of *Globoblastus* are single openings which pierce the calcite of the deltoid (see Fig. 219). They increased in diameter with age, which implies resorption.

The development of the anal deltoids

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[*Continued from facing page*]

1. *Dentiblastus sirius* (WHITE), L.Miss., USA (Mo.), ×6 (102).
2. *Eleutherocrinus cassedayi* SHUMARD & YANDELL, Dev., Can. (Ont.), ×3 (Macurda, n).
3. *Orophocrinus stelliformis* (OWEN & SHUMARD), L.Miss., USA (Mo.), ×7.5 (Macurda, n).
4. *Pentremites* sp., U.Miss., USA (Tenn.), ×7.5 (Macurda, n).
5-6. Stem plates of *Orophocrinus stelliformis* (OWEN & SHUMARD), L.Miss., USA (Ill.), ×7.5 (109).
7-9. *Pentremites godoni* DEFRANCE, U.Miss., USA (Ill.), ×7.5 (Macurda, n).
8. *Orbiblastus hoskynae* MACURDA, L.Miss., USA (Ark.), ×2 (106).
10. *Rhopaloblastus belfordi* (CROCKFORD & BROWN), Perm., Australia, ×7.5( Macurda, n). [For BR read BB, and for BB read BA.]
11. *Belocrinus cottaldi* (MUNIER-CHALMAS), Dev., Fr., ×4 (Macurda, n).

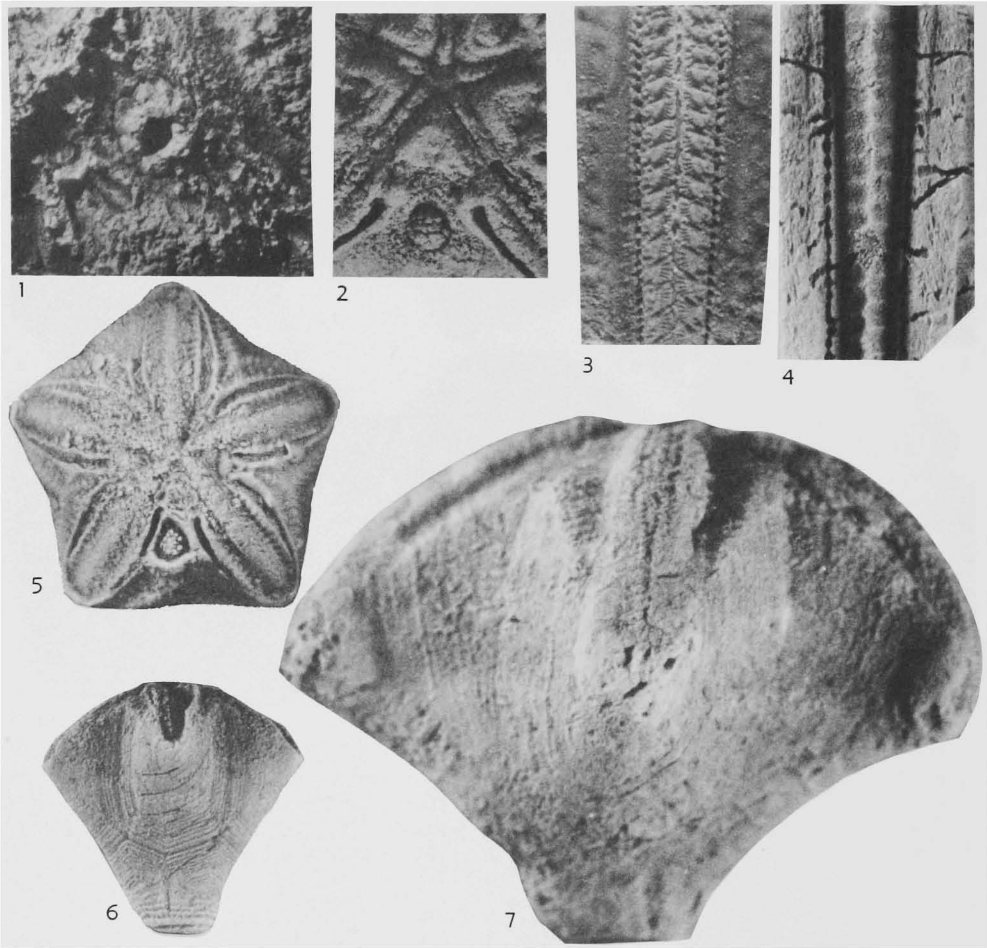

FIG. 216. Cover plates, hydrospire pores, and ontogenetic change in calyx shape.

*1.* Anal pyramid of *Orophocrinus stelliformis* (OWEN & SHUMARD), L.Miss., USA(Mo.), ×7.5 (109).

*2.* Oral and anal cover plates of *O. stelliformis* (OWEN & SHUMARD), L.Miss., USA(Iowa), ×6 (109).

*3.* Hydrospire pores of *Cryptoblastus melo* (OWEN & SHUMARD), L.Miss., USA(Ill.), ×7.5 (Macurda, n).

*4.* Hydrospire pores of *Globoblastus norwoodi* (OWEN & SHUMARD), L.Miss., USA(Mo.), ×7.5 (Macurda, n).

*5.* Oral, ambulacral, and anal cover plates of *Orophocrinus conicus* WACHSMUTH & SPRINGER, L.Miss., USA(Iowa), ×6 (107).

*6-7.* Ontogenetic change in calyx shape of *Orophocrinus stelliformis* (OWEN & SHUMARD), L. Miss., USA(Mo.), ×3 (Macurda, n).

parallels that of the regular deltoids. The presence of multiple anal deltoids allowed the size of the anal opening to increase with growth. The development of the adoral part of an epideltoid is identical to a regular deltoid; if hydrospires were present, their length increased by the addition of calcite along the epiradial suture. The anus embays the aboral edge of the epideltoid in *Orophocrinus*; it migrated aborally as the epideltoid increased in size (Fig. 212,*7*). The hypodeltoid also migrated aborally from the mouth, increasing in size by the addition of calcite along the edges, the rate being faster along the hyporadial suture. Secondary calcite was deposited on the hypodeltoid of *Orophocrinus* to form a ramp to guide the anus when it was extended (Fig. 217,*10*). Little is known about the ontogenetic development of other types of anal deltoids. Cryptodeltoids apparently increased in length by the addition of calcite along the cryptoradial suture.

The ambulacra are composed of a central lancet plate which extends the full length of the ambulacrum, side and outer side plates which rest upon the lancet and in many genera completely conceal it, brachioles which were attached to the side and outer side plates, and cover plates which roofed the food grooves (Fig. 216,*2,5*; 217,*8*). Commonly an ambulacrum is partially or completely surrounded by a radial and two deltoids. The only way it could increase in length was by growth along the margins of the principal calyx plates; this created free space into which the ambulacrum could then grow. New additions of side plates and outer side plates occurred at the aboral end of the ambulacrum. Shortly after its formation, the size of a side plate and the outer side plate were stabilized. The brachiolar facet thus had a constant dimension. No new calcite was added between side plates insofar as is known, but calcite may have been added on the admedial edges of side plates, as in *Orophocrinus* (Fig. 217,*3*). Side plates shifted adorally with respect to topographic points on the radial during development.

The growth of the lancet is not fully understood, apparently varying somewhat between genera. New calcite was added at the aboral end in all genera, increasing the length. In some genera (e.g., *Orophocrinus*), the main food groove is initially borne by the admedial edges of the side plates but as development proceeded, the main food groove migrated to the lancet (Fig. 217,*9*). The lancet thus also grew upward and side plates were shifted laterally. The main food groove on the side plates was apparently filled in but the admedial edge of these plates did not expand. In *Orophocrinus* the lancet also increased in width. The cross section is rhombic and new calcite was apparently added to the rhombic faces. In other genera (e.g., *Pentremites*) the main food groove is borne by the lancet from the offset. The plate is more rectangular in cross-section. No new calcite was added to the upper surface but lateral growth did occur, resulting in the side plates being laterally displaced; the side food grooves thus increased in length (Fig. 217,*5*). In still other genera where the lancet is completely concealed by the side plates, as in *Pentremitidea,* the lancet must increase in length but further detail is unknown. Further investigation of the patterns of development of this plate are needed.

The side and main food grooves are roofed by a series of ambulacral cover plates (Fig. 216,*5*; 217,*2*). These are seldom preserved. In *Orophocrinus,* polygonal plates covering the peristome are the largest cover plates (Fig. 217,*7*). When a peristome increased in size, the cover plates would also have to increase. The length of the main food groove borne by the deltoids increased in length during the ontogenetic development of *Orophocrinus.* In small specimens, there are usually four cover plates which roof over the width of the food groove. As the groove increased in length, the plates were reorganized; this proceeded aborally. They increased in size and only a pair ultimately covered the food groove. Thus, by increasing the cover plates in size and shifting them aborally, the increasing length of the groove was accommodated without forming new plates. New cover plates on the ambulacrum proper were formed at the same time as new side plates and brachioles were added at the aboral end of the ambulacrum. There was no shifting of these relative to the side plates in *Orophocrinus.* Since the length of the side food grooves increased in *Pentremites,* the cover plates of these grooves would either have to undergo reorganization or growth (or both) or new ones would have been added.

The growth of brachioles is poorly understood. The largest plates are located at or near the bottom and they decrease in size upward, as in *Pyramiblastus* (Fig. 217,*8*). The size of the lower plates was stabilized very shortly after the addition of the brachiole to the ambulacra. This may imply very rapid initial growth with a constant length thereafter. Since the brachioles are biserial and the centers are offset, one edge

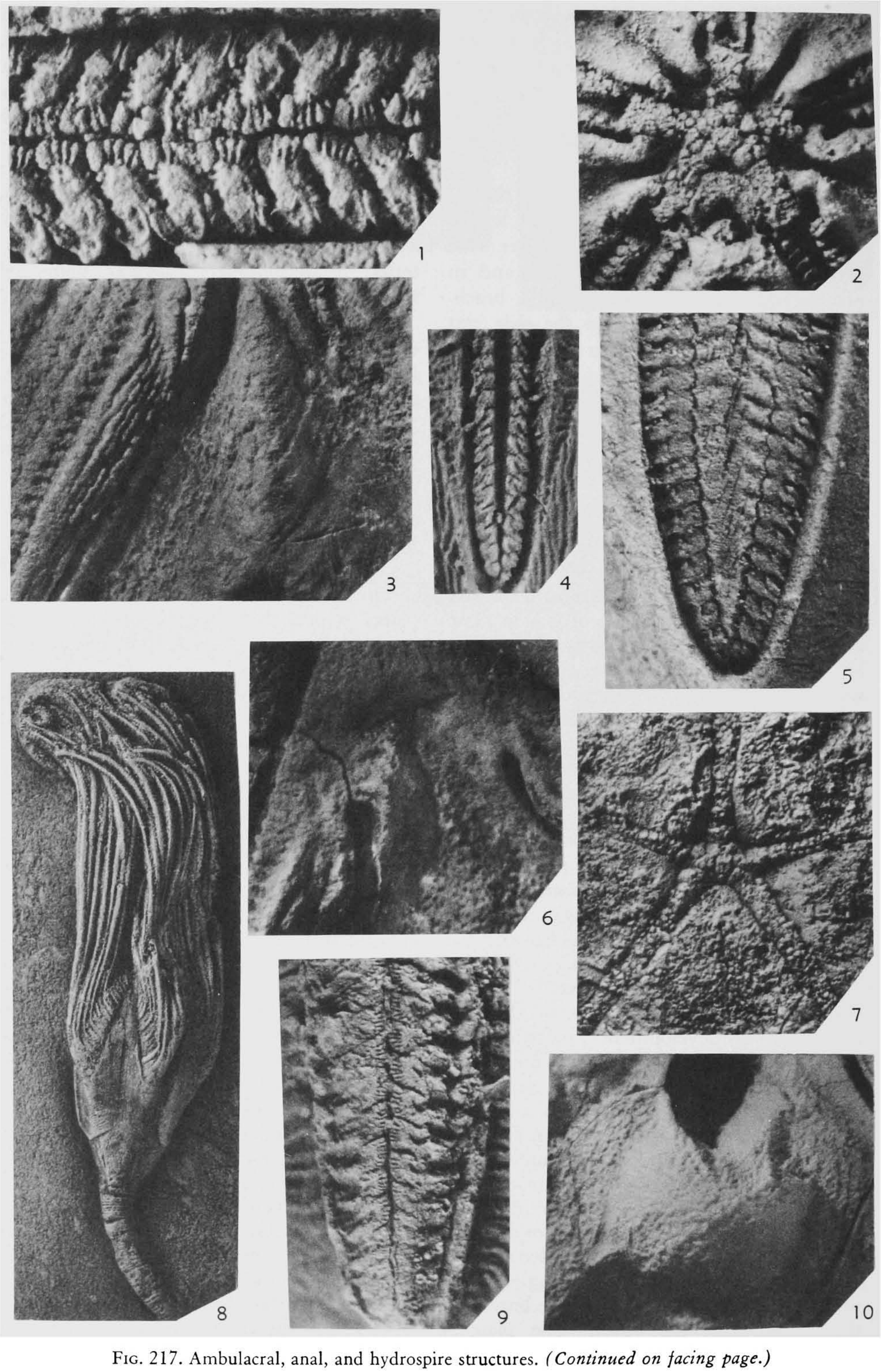

FIG. 217. Ambulacral, anal, and hydrospire structures. *(Continued on facing page.)*

of the brachiolar facet was set lower than the other to permit their attachment to the side and outer side plates (Fig. 217,*1*).

The curves of most growth axes are linear. Only a few instances of nonlinear development are known, as in *Orophocrinus stelliformis* (Fig. 218). In this species, the *RB* axis slowed down with growth and the *RD* accelerated. As a result, the space available for ambulacral development increased (and thus the food-gathering capacity) at an increasingly faster rate. This change is reflected in the change of shape of the calyx with development (Fig. 216, *6-7*).

## HYDRODYNAMICS

The visceral mass of a blastoid was completely isolated and protected from the outside environment by the calcareous endoskeleton. Blastoids were passive feeders and some kind of propulsive mechanism was necessary to convey food particles captured by the brachioles through the tunnels of the ambulacral system to the peristome. In Recent echinoderms this is accomplished by ciliary action. The hydrospires of blastoids are apparently rigid structures, as their shape is constant from specimen to specimen in the same species. Their only means of communication with the exterior is through a series of pores, slits, or spiracles. The function of hydrospires is not clear, but a respiratory or reproductive function, or both, are those commonly suggested. If they served a respiratory or reproductive function, it would be necessary to move a water mass through the hydrospires. Ciliary action might provide a mechanism for doing so. Since both the hydrospires and food-gathering-ambulacral-alimentary canal-anal system involve water transport through enclosed passages, the laws of hydrodynamics are involved. Functionally, a blastoid would probably be better adapted to its environment if various structures evolved to an optimum hydrodynamic configuration.

In spiraculate blastoids, the circulation system in the hydrospires was a two-way affair. Spiracles provided one entrance or exit, ambulacral pores the other. The flow pattern was apparently in through the pores and out through the spiracles (Fig. 219,*7*). Evidence for this is twofold: pore furrows and spiracle and anispiracle cover plates. In most spiraculate blastoids, a pore furrow (Fig. 219,*2*) leads to the entrance of each pore. The function of this structure is not clear but its troughlike nature, even though usually vertical in a living animal, is suggestive of a guide for currents. In some spiraculate blastoids the anal spiracles are combined with the anus to form an anispiracle. If water currents entered the hydrospires through an anispiracle, there would have been a danger of fecal material fouling the hydrospires. With water entering the hydrospires through the pores and exiting from the anispiracle, fecal matter would be carried away from the calyx. In *Pentremites,* the spiracles were closed by a series of toothlike plates (Fig. 219,*3*). This is the only genus known with spiracle cover plates. They may have been present in other genera but not preserved. In some specimens of *Globoblastus,* the adoral edge of the spiracle was formed by oral cover plates, whereas usually it is formed completely by deltoid material

[*Explanation of Fig. 217, continued*]

*1*. Brachiolar facets and food grooves, *Rhopaloblastus belfordi* (Crockford & Brown), Perm., Australia, ×5 (Macurda, n).

*2*. Oral cover plates of *Schizoblastus sayi* (Shumard), L.Miss., USA(Ill.), ×7.5 (Macurda, n).

*3*. Growth lines, admedial edge of side plates and deltoid in *Orophocrinus stelliformis* (Owen & Shumard), L.Miss., USA(Mo.), ×7.5 (109).

*4*. Pore furrows and hydrospire pores in *Lophoblastus neglectus* (Meek & Worthen), L.Miss., USA(Mo.), ×7.5 (Macurda, n).

*5*. Lancet and hydrospire pores of *Pentremites* sp., U.Miss., USA(Ill.), ×7.5 (Macurda, n).

*6*. Growth lines bordering spiracle slits in *Orophocrinus stelliformis* (Owen & Shumard), L. Miss., USA(Ill.), ×7.5 (Macurda, n).

*7*. Oral cover plates in *O. stelliformis* (Owen & Shumard), L.Miss., USA(Mo.), ×7.5 (109).

*8*. Brachioles in *Pyramiblastus fusiformis* (Wachsmuth & Springer), L.Miss., USA(Iowa), ×3 (105).

*9*. Lancet and side plates in *Orophocrinus catactus* (Rowley), L.Miss., USA(N.Mex.), ×7.5 (Macurda, n).

*10*. Secondary secretion and trough for extension of anus, *Orophocrinus stelliformis* (Owen & Shumard), L.Miss., USA(Iowa), ×7.5 (109).

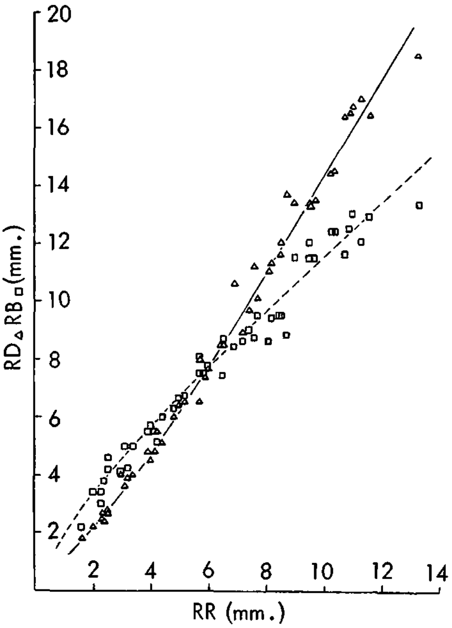

FIG. 218. Growth of *RD* (radial-deltoid) and *RB* (radial-basal) axes of *Orophocrinus stelliformis* (OWEN & SHUMARD) plotted against growth of *RR* (interradial) axis, L.Miss., USA(Iowa-Mo.) (109).

(Fig. 219,*6-7*). Cover plates of the anispiracle are different from spiracle cover plates in *Pentremites,* consisting of rod-shaped elements (Fig. 219,*10*). This probably provided greater ease for anal opening and closing to get rid of fecal wastes.

The circulation in the ambulacral system was fairly complex. Some genera preserve brachiolar cover plates. If these plates were movable, then the brachiolar food groove could be exposed to capture food particles. If they were immobile, an additional brachiolar protoplasmic extension would be required. Once entrapped, food particles would be carried downward to the ambulacrum. The entrance to the side food groove is very small, thus limiting the maximum size of food particles. These particles would then be conducted laterally to the main food groove. The side food grooves are offset from one another and inclined at approximately 45 degrees to the main food groove (Fig. 219,*1*). With this offset, there is a gradual buildup in the volume of water entering the main food groove tunnel, rather than a sudden jump. By having the side food grooves inclined to the main food groove, rather than at right angles, the passage of water from the side to the main food groove was facilitated. If it was at a right angle, there would have been a sharp drop in water velocity where it had to enter the main food groove. Less energy was expended in an inclined configuration. Similar orientations are found in some cystoids, as *Lipsanocystis* and *Strobilocystites.* Once the food entered the main food groove, convection was against the force of gravity in most genera, the ambulacra lying topographically below the peristome which is at the top of the calyx (Fig. 219,*7*). In *Pterotoblastus,* however, the ambulacra are elevated above the mouth (Fig. 219,*5*). In *Orophocrinus,* there are apparently points of attachment for the alimentary canal located on the underside of the deltoids (Fig. 219,*8*). The flow of water through the alimentary canal could have been facilitated by muscular expansions and contractions of the canal. The exit for water in the canal was the anus, which was closed by a series of small polygonal plates and roofed by a small dome (Fig. 216,*1-2*), of rodlike plates (Fig. 219,*10*), or elongated in the form of an anal tube as in *Schizoblastus* (Fig. 219,*4*). Indentations of plates appar-

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[*Explanation of Fig. 219, facing page*]

*1.* Ambulacrum of *Timoroblastus granulatus* WANNER, Perm., Timor, ×7.5 (Macurda, n).

*2.* Brachiolar facets, *Pentremites* sp., U.Miss., USA (Ill.), ×7.5 (Macurda, n).

*3.* Spiracle cover plates of *Pentremites* sp., U.Miss., USA(Tenn.), ×7.5 (Macurda, n).

*4.* Anal tube of *Schizoblastus sayi* (SHUMARD), Miss., USA(Mo.), ×7.5 (Macurda, n).

*5.* *Pterotoblastus gracilis* WANNER, Perm., Timor, ×3 (Macurda, n).

*6.* Oral cover plates and spiracles of *Globoblastus norwoodi* (OWEN & SHUMARD), Miss., USA (Iowa), ×5.9 (108).

*7.* Spiracles, *G. norwoodi* (OWEN & SHUMARD), Miss., USA(Iowa), ×6.2.

*8.* Depressions on undersurface of deltoids around peristome (attachment for alimentary canal?), *Orophocrinus stelliformis* (OWEN & SHUMARD), L.Miss., USA(Iowa), ×6 (107).

*9.* Facets of anal tube of *Deltoblastus* sp., Perm., Timor, ×7.5 (Macurda, n).

*10.* Anal and spiracle cover plates of *Pentremites* sp., U.Miss., USA(Tenn.), ×7.5 (Macurda, n).

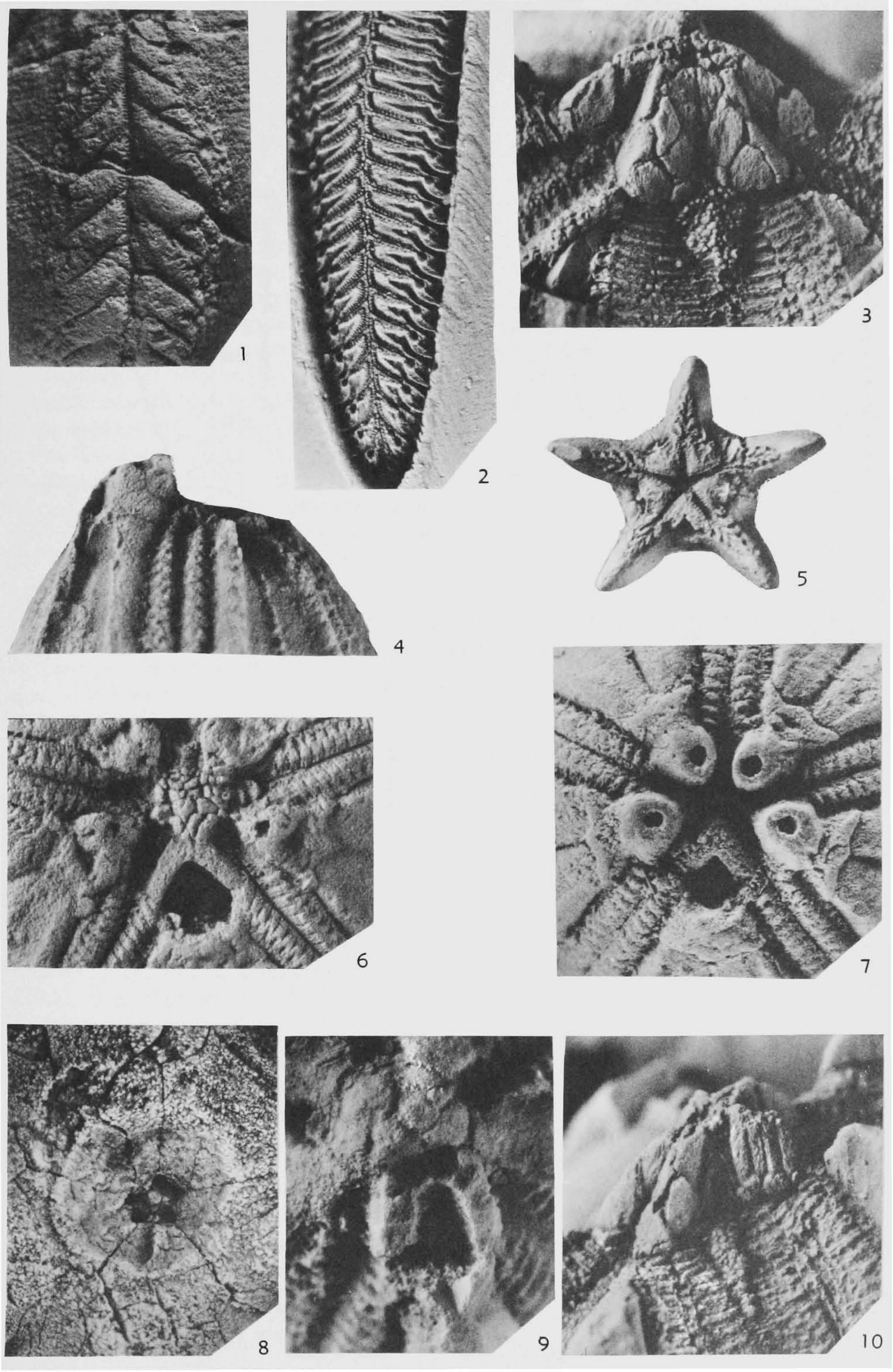

FIG. 219. Ambulacral, oral cover plates, anal, and alimentary canal structures.

ently forming an anal tube are preserved in *Deltoblastus* (Fig 219,9). The presence of an anal tube would further reduce fouling of the brachioles and indicates that the anus was a muscular organ capable of extension and retraction. The cover plates

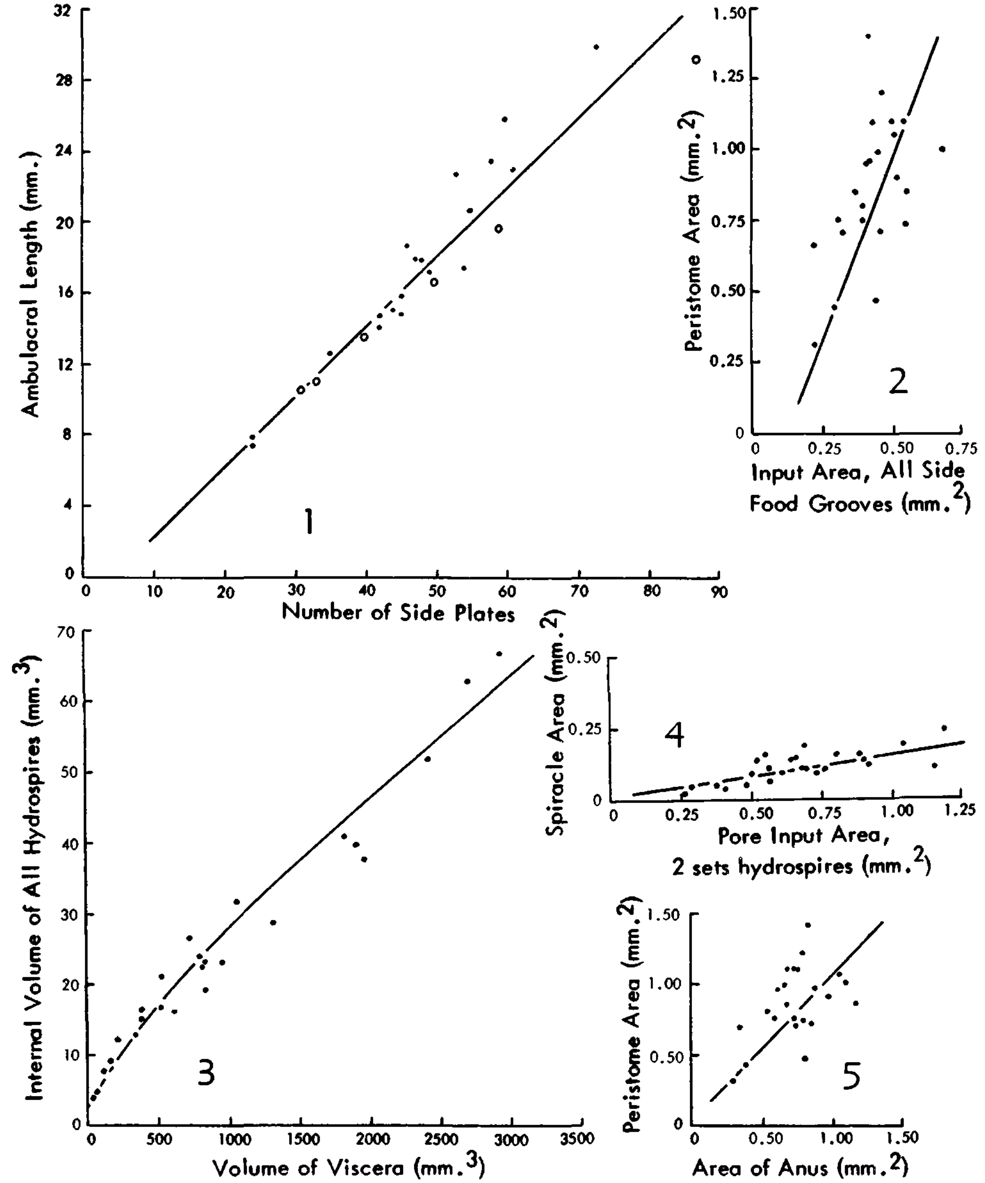

FIG. 220. Hydrodynamics of *Globoblastus norwoodi* (OWEN & SHUMARD), L.Miss., USA(Iowa), throughout an ontogenetic series (108).

*1.* Ambulacral length plotted against number of side plates on side of ambulacrum.

*2.* Area of peristome plotted against cross-sectional input area of side food grooves on all ambulacra.

*3.* Total internal volume of all hydrospires plotted against volume of viscera.

*4.* Area of one spiracle plotted against input area of pores associated with two sets of hydrospires with which former connects.

*5.* Area of peristome plotted against cross-sectional area of anus.

in *Orophocrinus* would apparently be carried outward when the anus was extended.

Various quantitative parameters reflect the conditions of flow in the hydrospire and ambulacral sytems, and indirectly the physiology of the animal. These characters are best studied throughout an ontogenetic series, as their configuration at any one time is determined by ontogenetic development and probably reflects the needs of the animal. The number of pores, volume of the hydrospires, area of the peristome, number of arms (and thus food-gathering capacity), etc., all changed during development. The only genus on which a complete hydrodynamic analysis has been made is *Globoblastus* (Macurda, 1965, 108).

The input area of the hydrospire system in *Globoblastus* is reflected by the cross-sectional area of the pores, while the output area is that of the spiracle openings throughout an ontogenetic series (Fig. 220,*4*). Since input area is six times output area, the outgoing current could have had a maximum velocity of six times the input current. In *Rhopaloblastus belfordi,* however, the ratio is 1:1. The volume of the hydrospires in *Globoblastus* increased sharply (Fig. 221); the increase in entrance and exit dimensions apparently facilitated change of the water mass in the hydrospires. Assuming an arbitrary input velocity of 0.1 mm./sec., the entire water mass in the hydrospires could be changed in 40 seconds in a small specimen and 100 seconds in a large specimen. The internal volume of the hydrospires compared to the volume of the viscera is rather large (Fig. 220,*3*), varying from 1:20 in small specimens to 1:45 in large ones. The surface area of the hydrospires is also large in relation to the visceral volume (Fig. 221). These data reinforce the interpretation of the hydrospires having a respiratory function, since the capacity for water replacement and the surface area for $CO_2/O_2$ exchange are large in relation to the volume of tissue in the viscera. The gases would have had to diffuse through the hydrospire wall. The microstructure of this wall is poorly known but the calcite is thinner than that of the calyx wall and may have a filamentous appearance.

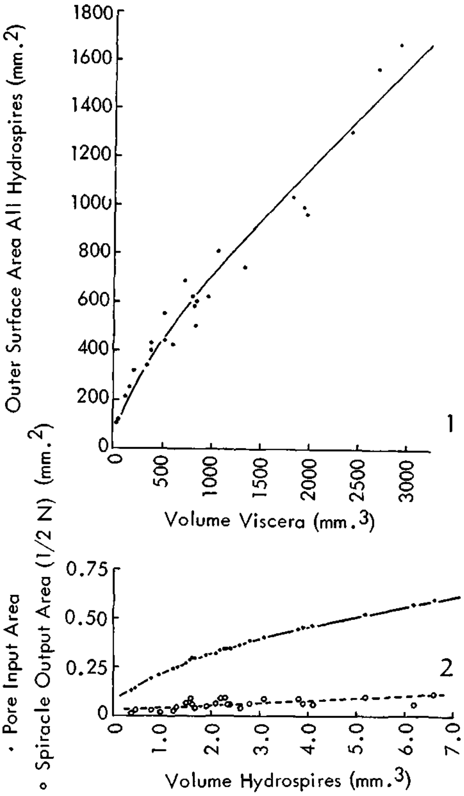

Fig. 221. Hydrodynamics of *Globoblastus norwoodi* (Owen & Shumard), L.Miss., USA(Iowa), throughout ontogenetic series (108).

*1.* Total outer surface area of all hydrospires plotted against volume of viscera.

*2.* Input area of pores along one side of ambulacrum and output area for one set of hydrospires (one-half spiracle area) plotted against internal volume of one group of hydrospires.

The hydrodynamics of circulation in fissiculate blastoids has not been determined. In forms with exposed hydrospire slits, each hydrospire would have been an individual circulation cell, with water entering one part and exiting from the other. This may have been less efficient than the two-way system of spiraculate genera. In the same ecological situation, the number of hydrospires in a fissiculate genus and thus the surface area available for respiration may be much greater than in a spiraculate, as in the occurrence of *Codaster* (fissiculate—number of hydrospires increases during ontogeny) and *Orbitremites* (spira-

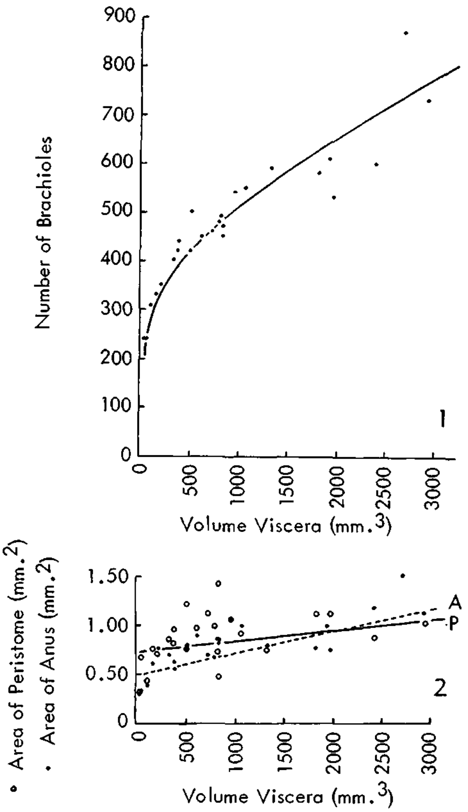

FIG. 222. Hydrodynamics of *Globoblastus norwoodi* (OWEN & SHUMARD), L.Miss., USA(Iowa), throughout ontogenetic series (108).

*1*. Number of brachioles plotted against volume of viscera.

*2*. Area of peristome and anus plotted against volume of viscera.

culate, number constant throughout growth, one hydrospire per group) in the Lower Carboniferous of England near Grassington, Yorkshire. If circulation of an individual exposed hydrospire slit was less efficient, a greater number would be needed to provide a respiratory capacity equal to that of the spiraculate form. This may explain the presence of almost 600 hydrospires in a large specimen of *Hadroblastus* (MACURDA, 1965, 106).

As a blastoid grew, the number of arms and thus the food-gathering capacity, constantly increased (Fig. 220,*1*). In *Globoblastus,* most of the growth of the radials was along the *RD* axis which facilitated a rapid increase in ambulacral length. An increasing food-gathering capacity was necessary to support the increasing volume of tissue in the viscera (Fig. 222). In some Permian genera (e.g., *Timoroblastus*) the ambulacral area and thus number of arms were extremely small in relation to volume of viscera (see Fig. 226). The volume of water entering the main food groove from the more numerous side food grooves in *Globoblastus* increased during development; the area of the peristome increased to accommodate the increased water flow (Fig. 220,*2*). Area of the anus increased at the same rate as the peristome to provide easier egress for greater volumes of water (Fig. 220,*5*). Areas of the peristome and anus increased linearly in relation to the expanding volume of the viscera (Fig. 222).

The use of hydrodynamic studies in blastoids provides a dynamic interpretation of the organism and should find increasing utilization in taxonomy, and interpretations of functional morphology, physiology, and ecology.

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[*Explanation of Figure 223*]

*1-2*. *Polydeltoideus enodatus* REIMANN & FAY, Sil., USA(Okla.), ×2 (Macurda, n).

*3*. *Cryptoschisma schultzii* (D'ARCHIAC & DE VERNEUIL), Dev., Spain, ×3 (Macurda, n).

*4*. *Hyperoblastus filosus* (WHITEAVES), Dev., Can. (Ont.), ×2.5 (Macurda, n).

*5*. *Brachyschisma subcrassum* REIMANN, Dev., USA (N.Y.), ×3 (Macurda, n).

*6-7*. *Heteroschisma canadense* (BILLINGS), Dev., Can.(Ont.), ×3 (Macurda, n).

*8*. *Belocrinus cottaldi* (MUNIER-CHALMAS), Dev., France, ×2 (110).

*9*. *Devonoblastus leda* (HALL), Dev., USA(N.Y.), ×3 (Macurda, n).

*10*. *Placoblastus ehlersi* FAY & REIMANN, Dev., USA(Mich.), ×2 (Macurda, n).

*11*. *Phaenoschisma laeviculum* (ROWLEY), Miss., USA(Mo.), ×4.5 (104).

*12*. *Cryptoblastus melo* (OWEN & SHUMARD), Miss., USA(Ill.), ×3 (Macurda, n).

*13*. Radial of *Pentablastus supracarbonicus* SIEVERTS-DORECK, L.Carb., Spain, ×3 (Macurda, n).

*14*. *Pentremites elongatus* SHUMARD, L.Miss., USA (Iowa), ×2 (Macurda, n).

*15*. *Codaster acutus* M'COY, L.Carb., Eng., ×3 (Macurda, n).

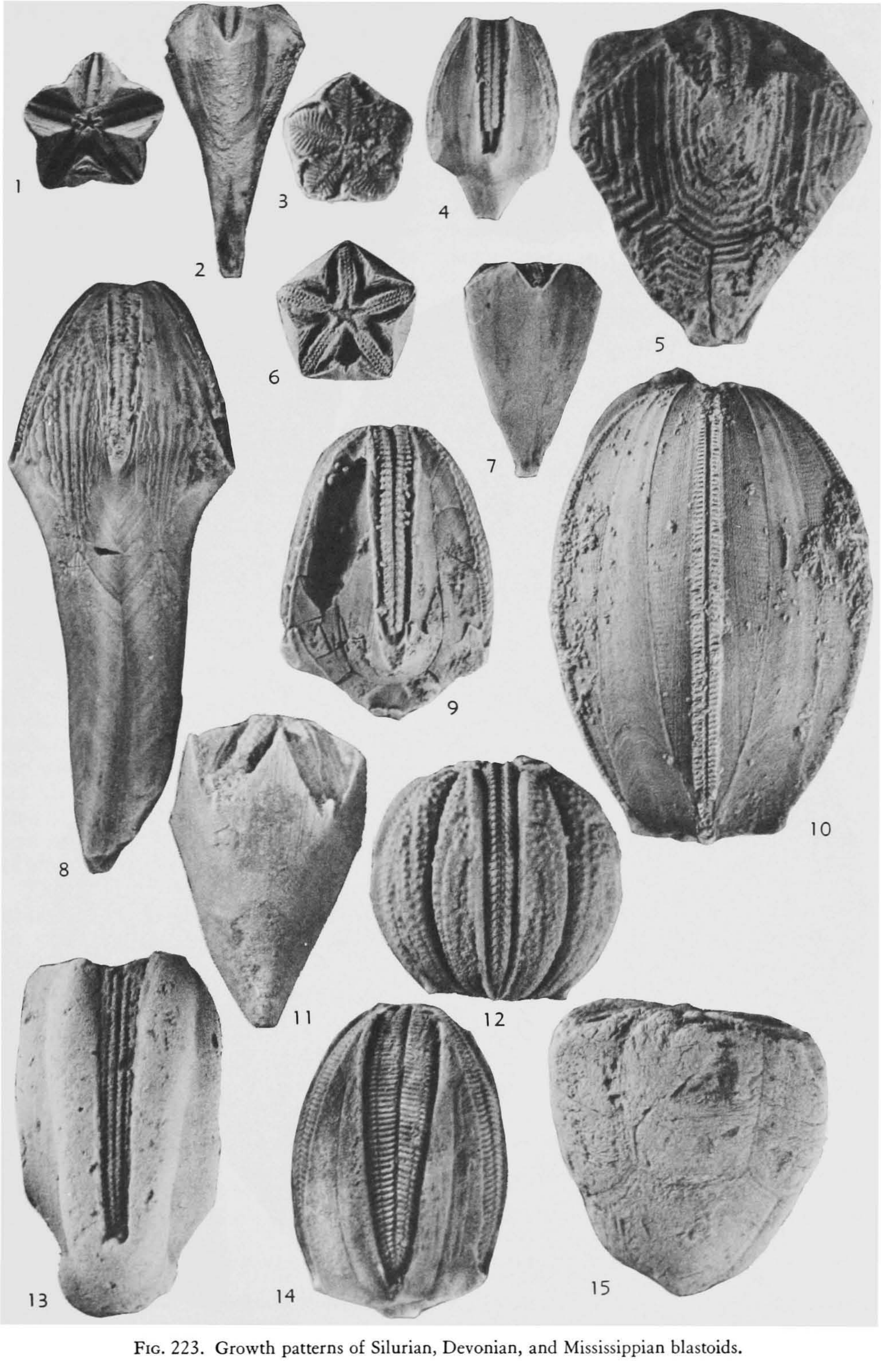

FIG. 223. Growth patterns of Silurian, Devonian, and Mississippian blastoids.

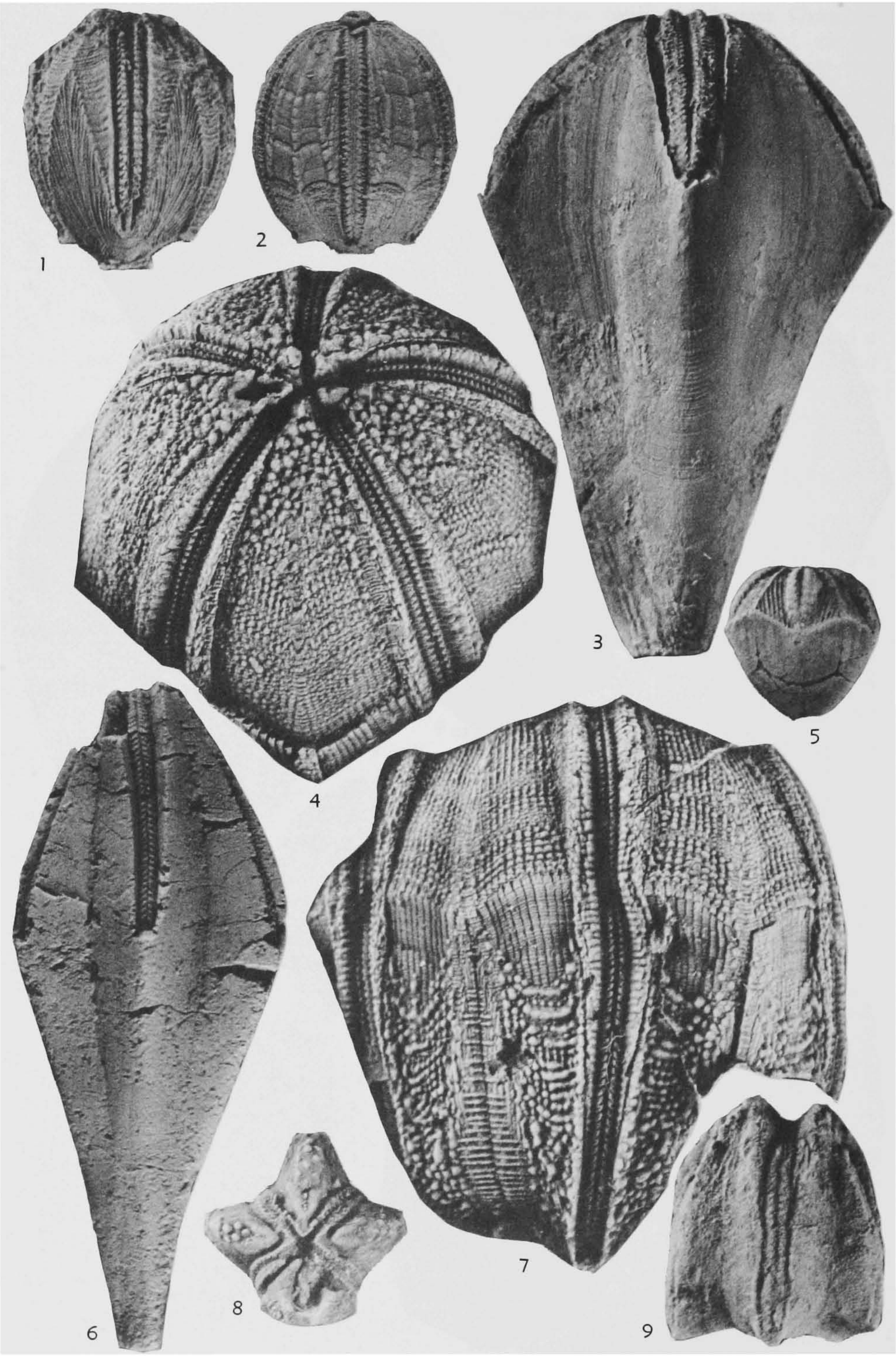

FIG. 224. Growth patterns of Mississippian blastoids. (Continued on facing page.)

## TEMPORAL DISTRIBUTION OF GROWTH PATTERNS IN BLASTOIDS

The first blastoids, as the class is now understood, appeared in the Middle Silurian. The number of principal plates and their basic mode of growth (lateral accretionary addition) was stable until blastoids became extinct in the Permian. Growth patterns are important in any discussion of the derivation of evolutionary record of blastoids. If calyx shape changed from pyramidal to globose through time, then visceral shape, points of origin of the plates relative to the viscera, and rates of growth along plate-growth axes must be modified to produce this change.

The three or four known Silurian fissiculate and spiraculate blastoid genera have an obconical calyx, with a long pelvis and a short vault (e.g., *Polydeltoideus,* Fig. 223). Thus the basals had a high rate of growth, as did the *RB* axis of the radials. Growth rates of the *RR* and *RD* axes and the deltoid were small and the aboral growth of the deltoid was confined to the ambulacral sinus, since no radiodeltoid growth occurs outside the sinus (Fig. 223,*2*). Reflexed growth lines are lacking by the ambulacral sinus, and the aboral portion of the deltoid is a sharp crest. The ambulacra are short and confined to the uppermost part of the calyx. This basic growth pattern may have been present in the ancestor of Silurian blastoids.

The growth pattern of Silurian forms carries on into the Devonian, particularly in the fissiculate genera. It is found in *Deltoschisma, Heteroschisma* (Fig. 223), *Pentremitidea,* and *Pleuroschisma. Cryptoschisma* is similar but has expanded the ambulacral field; it is one of the few early blastoids in which the lancet is exposed (Fig. 223,*3*). *Hyperoblastus* has modified growth rates of the radial so that the *RD* axis is dominant and the ambulacra are much longer but still narrow, producing a club-shaped theca. The base is conical. The deltoid still does not grow outside the radial sinus (Fig. 223,*4*). The only Devonian fissiculate blastoid in which an external growth sector is found on the deltoid is *Brachyschisma.* The growth of the *RB* and *BR* axes is still about equal, producing a conical pelvis, but the rates and directions of *RD* and *RR* have been modified to produce a parachute-shaped calyx (Fig. 223,*5*).

Much more experimentation is found in the Devonian spiraculates. Most species of *Cordyloblastus* are suggestive of the basic Silurian growth pattern. *Belocrinus* is somewhat similar (Fig. 223). However, *Schizotremites* and *Devonoblastus* (Fig. 223) (particularly the latter) modified the growth of the radials and deltoids so that the *RD* axis became the dominant radial growth axis, permitting an increase in ambulacral length; the deltoid also grew outside the ambulacral sinus. The calyx shape became biconvex to subovoid; the pelvis of each, however, is still conical. *Strongyloblastus* is similar to these genera but has more petaloid ambulacra, exposing the lancet. The most radical change in growth patterns is found in the closely related genera *Elaeacrinus—Nucleocrinus—Placoblastus* and *Eleutherocrinus.* In the former group (Fig. 223,*10*), rate of growth of the basals has become quite reduced and they are confined to a basal concavity. The growth rates of the radials are also quite modified, being reduced; they are confined to the base of the calyx. The rate of growth of the deltoids has become extremely high, *DR* being several times *RD,* and the deltoids extend almost to the base of the globose calyx. The ambulacra are still narrow, however. *Eleutherocrinus* (Fig.

[*Explanation of Figure 224, continued*]

*1. Lophoblastus neglectus* (Meek & Worthen), L.Miss., USA(Mo.), ×3 (Macurda, n).

*2. Schizoblastus sayi* (Shumard), L.Miss., USA (Iowa), ×3 (Macurda, n).

*3. Orophocrinus praelongus* Bailey, L.Carb., Ire., ×2 (Macurda, n).

*4,7. Nymphaeoblastus bancroftensis* McKellar, L. Carb., Australia, ×3 (Macurda, n).

*5. Hadroblastus conicus* Fay, L.Miss., USA(N. Mex.), ×3 (Macurda, n).

*6. Metablastus lineatus* (Shumard), Miss., USA (Iowa), ×2 (Macurda, n).

*8. Astrocrinus benniei* (Etheridge), L.Carb., Scot., ×8.3 (Macurda, n).

*9. Nodoblastus librovitchi* (Yakovlev), L.Carb., USSR, ×3 (Macurda, n).

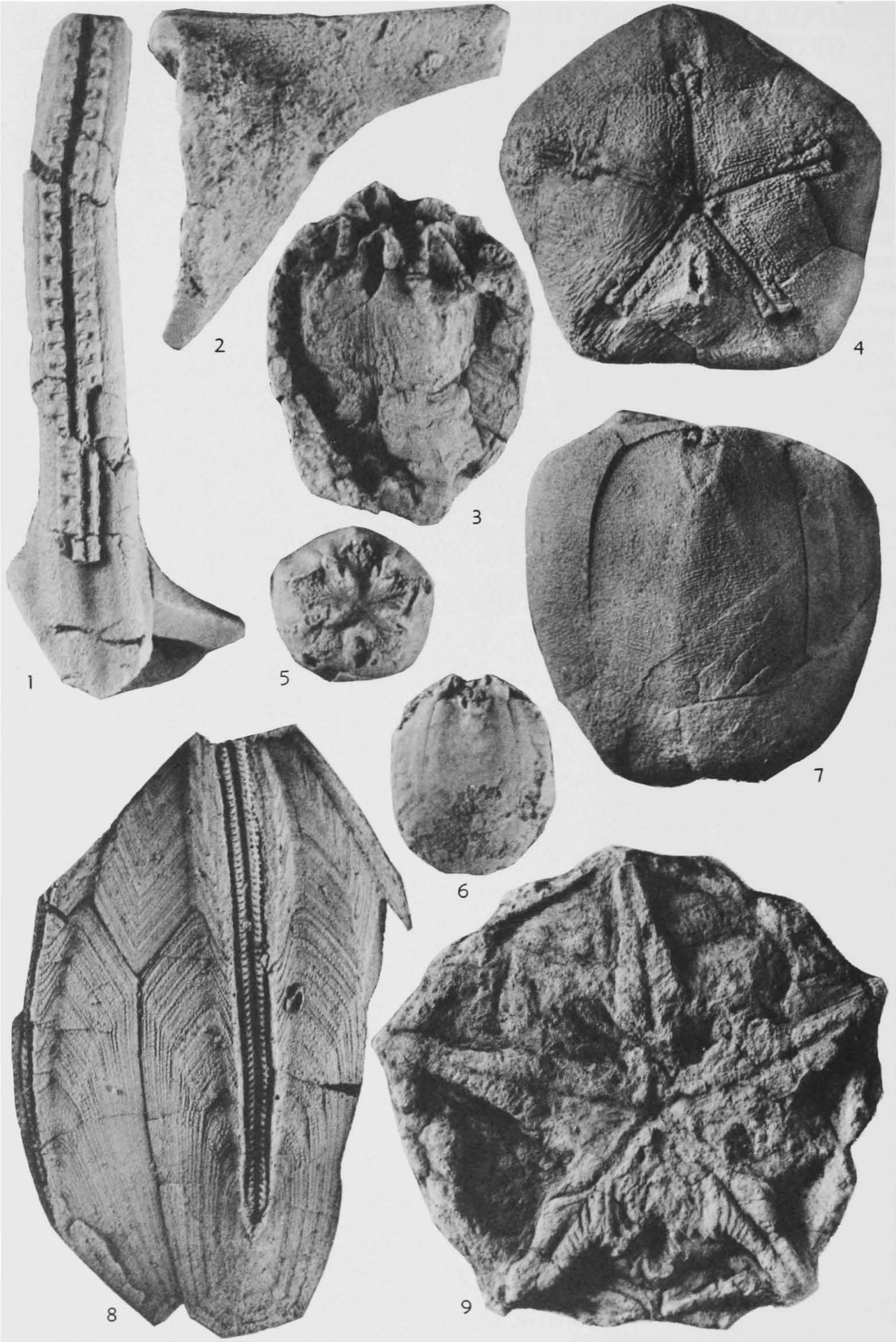

FIG. 225. Growth patterns of Pennsylvanian and Permian blastoids (*See* facing page.)

214) represents the most radical departure. The *RD* axis has become dominant, allowing the ambulacra to expand almost to the base of the calyx. The deltoids also grew outside the radial sinus. The most extreme feature is the adoption of an eleutherozoic habit. One ambulacrum *(D)* became quite shortened so as to allow the animal to lie free on the ocean floor. The basals lying in this radius grew halfway up the calyx.

The Lower and Middle Mississippian saw a great proliferation of globose genera in which the deltoids are relatively short, their growth being confined to the top portion of the calyx. The *RD* axis of the radial was dominant and the arcuate ambulacra extend almost to or to the base of the calyx, and the basals are small, being confined to the very base of the calyx (Fig. 223,*12*) (genera *Auloblastus, Carpenteroblastus, Cribroblastus, Cryptoblastus, Diploblastus, Doryblastus, Globoblastus, Mesoblastus, Monadoblastus,* and *Tanaoblastus*). In a few of these globose blastoids (*Ambolostoma, Ellipticoblastus, Granatocrinus, Lophoblastus, Orbiblastus, Poroblastus,* and *Ptychoblastus*), the deltoid grew at a faster rate, extending one-third the length of the calyx (Fig. 224,*1*) and in a few (*Heteroblastus, Monoschizoblastus, Orbitremites,* and *Schizoblastus*), it grew much faster, reaching almost to the base (Fig. 224,*2*). However, the basic form and extent of the ambulacra are the same. A few of these globose genera developed slight or deep basal concavities (Fig. 214,*8*) to which the basals were confined (*Cribroblastus, Doryblastus, Globoblastus, Granatocrinus, Monoschizoblastus, Orbiblastus, Poroblastus,* and *Ptychoblastus*). A few of the Mississippian spiraculate genera (*Metablastus, Pyramiblastus,* and *Tricoelocrinus*) have an obconical or biconical calyx with relatively short ambulacra (Fig. 224,6), reminiscent of growth patterns in *Troosticrinus* and *Schizotremites.* Other genera (*Pentremites, Pentremoblastus,* and *Petaloblastus*) developed an obconical or club-shaped theca with a large exposed lancet and relatively large ambulacral areas (Fig. 223,*14*). *Pentremites* underwent a great deal of evolutionary experimentation, persisting into the Lower Pennsylvanian. *Acentrotremites* and *Nodoblastus* (Fig. 224) developed dome-shaped calyces, pentagonal in outline with flat bases and relatively long ambulacra. One new evolutionary experiment was attempted in *Dentiblastus,* in which the ambulacra extended out beyond the discoidal theca on prongs (Fig. 213,*4*).

The growth patterns in some Mississippian fissiculate genera are little changed from those of the Devonian. *Phaenoblastus* and *Phaenoschisma* (Fig. 223) have club-shaped or obconical thecas with conical pelvises; growth of the deltoid was confined to the ambulacral sinus. In *Codaster* (Fig. 223), *Hadroblastus* (Fig. 224), and *Pentephyllum*(?) the theca is still conical, or biconical, but the deltoid grew outside of the ambulacral sinus and there was a proliferation of the number of hydrospire slits. *Orophocrinus* (Fig. 224) retained a conical pelvis but underwent a great deal of experimentation in growth rates in the radials, producing thecas ranging from narrow, conical to flaring, parachute-shaped (Fig. 216,*7*). *Nymphaeoblastus* (Fig. 224) is highly unusual, as it is a globose form with exposed hydrospire slits; the rate of growth of the deltoid was high. *Pentablastus* is unique among the blastoids. The shape of the calyx (ovoid) with relatively long ambulacra and a rather flat base is conventional, but the radial is split into a number of separate plates (Fig. 223). *Astrocrinus* is another peculiar eleutherozoic form, the basic growth patterns having been modified to produce a tetragonal outline with one shortened ambulacrum (Fig. 224). As in *Eleutherocrinus,* the *D* ambulacrum was the modified one.

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[*Explanation of Figure 225, continued*]

*1-2*. Ambulacral prong and radial of *Thaumatoblastus longiramus* WANNER, Perm., Timor, ×3 (Macurda, n).

*3*. *Agmoblastus dotti* (MOORE & STRIMPLE), Penn., Okla., ×3 (Macurda, n).

*4,7*. *Indoblastus granulatus* WANNER, Perm., Timor, ×2.5 (Macurda, n).

*5-6*. *Sagittoblastus wanneri* (YAKOVLEV), Perm., USSR, ×3 (Macurda, n).

*8*. Undescribed blastoid, U.Carb., Australia, ×2 (Macurda, n).

*9*. *Notoblastus brevispinus* BROWN, Perm., Australia, ×2.5 (Macurda, n).

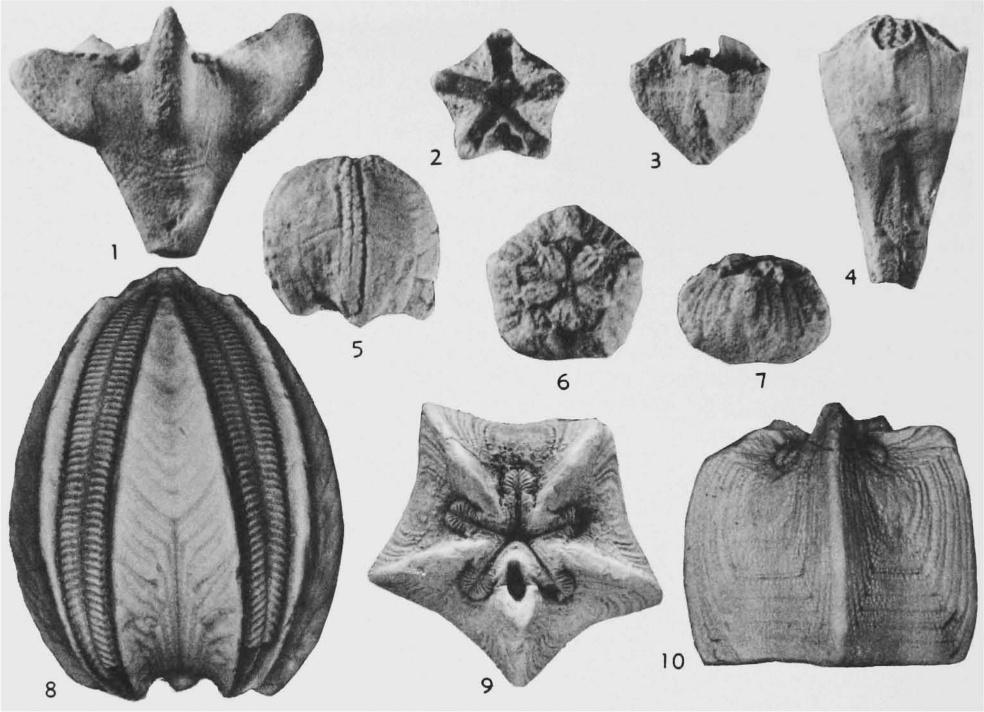

FIG. 226. Growth patterns of Permian blastoids.

1. *Pterotoblastus gracilis* WANNER, Perm., Timor, ×3 (Macurda, n).
2-3. *Nannoblastus pyramidatus* WANNER, Perm., Timor, ×3 (Macurda, n).
4. *Rhopaloblastus timoricus* WANNER, Perm., Timor, ×3 (Macurda, n).
5. *Orbitremites malaianus* WANNER, Perm, Timor, ×3 (Macurda, n).
6-7. *Angioblastus variabilis* WANNER, Perm., Timor, ×3 (Macurda, n).
8. *Deltoblastus* sp., Perm., Timor, ×2 (Macurda, n).
9-10. *Timoroblastus coronatus* WANNER, Perm., Timor, ×3 (Macurda, n).

The known record of Pennsylvanian blastoids is very sketchy. *Pentremites* extended into the lowermost Pennsylvanian. The growth pattern of a new Pennsylvanian spiraculate genus (Fig. 225,*8*) from Queensland does not depart extensively from those found in the Mississippian. The calyx is elongate ovoid, with large deltoids; the *RD* axis is dominant on the radial and probably slightly greater in rate of growth than *DR*, and the pelvis is conical. The only known Pennsylvanian fissiculate genus, *Agmoblastus* (Fig. 225), appears to be transitional in its form between *Codaster* and some of the Permian forms. The calyx is subcylindrical, the basals being relatively large in their development, producing a broad base. *RB* is the dominant growth axis of the radial. The ambulacra are short and confined to the summit. The deltoids and *RD* fronts have exposed hydrospire slits; the deltoids begin to develop elevated processes.

The pattern of development of some Permian fissiculate genera (*Angioblastus,* Fig. 226; *Microblastus, Paracodaster, Sagittoblastus,* Fig. 225; and *Sundablastus*) is similar to that of *Agmoblastus*; the calyx is subcylindrical to flattened discoidal. The ambulacra are quite small in relation to the calyx and lanceolate. The basals are relatively large, the deltoids small. One can expand the basals of *Timoroblastus* (Fig. 226) or draw out the peculiar winged radials of *Pterotoblastus* (Fig. 226) from this basic plan, but these two genera are peculiar in their development. The development of a few Permian genera (*Neo-*

*schisma, Notoblastus,* Fig. 225) resembles that of the discoidal, open fissiculate *Hadroblastus. Indoblastus* (Fig. 225) has the same general calyx shape as *Codaster* but lacks any exposed hydrospire slits. The ovoid, flattened form of *Dipteroblastus* with its two elongate and three shortened ambulacra represents another eleutherozoic experiment. *Thaumatoblastus* (Fig. 225), with its elongate, needle-like radial spines which bore the ambulacra attempted to extend the food-gathering area, in contrast to some of the other genera. The ovoid form of *Sphaeroschisma* is unusual among the usually conical fissiculates. Some forms (*Anthoblastus, Ceratoblastus,* and *Nannoblastus,* Fig. 226) are highly peculiar and specialized.

Developmental patterns among the few Permian spiraculate genera are much more conventional by comparison. The only globose form, *Deltoblastus* (Fig. 226), has long ambulacra with high rates of growth on the *DR* and *RD* axes. The basals are indented in the deepest basal concavity of any genus. The biconvex, ovoid form of *Calycoblastus* with its long ambulacra and greater rate of growth of *RD* resembles a Mississippian developmental plan. *Rhopaloblastus* (Fig. 226), a conical form with much more restricted ambulacra, resembles some of the early spiraculates in its general form. The species of *Orbitremites* (Fig. 226) are apparently congeneric with *Orbitremites* from the Mississippian.

The earliest and presumably primitive developmental pattern in blastoids resulted in an obconical calyx with a long pelvis. The *RB* axis of the radials had the greatest rate of growth in the radials, the deltoids grew only in the ambulacral sinus, the ambulacra were narrow, and the lancet was concealed. This pattern carried over into most of the Devonian fissiculate genera, was partially modified by some spiraculate forms, and extensively modified by others. The basic developmental pattern of Mississippian spiraculate genera produced globular calices with long ambulacra; the deltoid was usually short but in some forms extended well down on the calyx. A few genera had an obconical or biconical calyx. Some Mississippian fissiculate genera had developmental patterns similar to those of Silurian and Devonian blastoids; others modified this and faintly suggest things to come. Knowledge of Pennsylvanian developmental patterns is limited. Spiraculate forms in the Permian are not very far removed from their precursors but fissiculates have many new and different plans of development, with the addition of extensive basal, radial, or deltoid processes, restricted ambulacra, and new calyx shapes.

## PALEOECOLOGY

### By Harold H. Beaver

Available published information on the paleoecology of blastoids is largely limited to three recent articles (Allen & Lester, 1953; Joysey, 1955; Cline & Beaver, 1957).

Allen & Lester compared the occurrence of large species of *Pentremites* in argillaceous limestones of Mississippian (Chesteran) age in Georgia with *Pentremites* of smaller size in underlying and overlying relatively pure crystalline or oölitic limestones. They interpreted the difference in size as related to availability of food and inferred that *Pentremites* living under silty conditions of deposition found it necessary to sieve larger amounts of water for food than those living in clear water. Conceivably, forms living in turbid water needed enlargement of the food-gathering system and a resultant relatively large theca. Galloway & Kaska (1957, p. 70) doubted that the large size of the species was due to a change from clear water to a silty depositional environment. Collections of *Pentremites* from rocks of the same age in other areas (e.g., southern Illinois) show that large calyces similar in size and shape to the robust specimens found in Georgia occur in both pure and impure limestones in Illinois.

Joysey (1955, p. 209-220) described the distribution of Lower Carboniferous blastoids in the vicinity of Grassington, Yorkshire, England. In this area three depositional environments, classed as shelf, shelf margin, and basin, have been described. Shelf-limestone deposition occurred on a relatively stable platform located north of an area of fault movements in the Craven fault belt; south of this belt, sandstone and shale accumulated in a rapidly subsiding basin. In the latter part of Early Carboniferous time the shelf-basin boundary shifted northward, and transitional beds of the shelf margin (Middle Limestone) are found to be intermediate between the underlying shelf facies and the overlying basin facies.

Blastoids occur in two facies of the shelf margin designated as shell banks (called reef knolls by Bond, 1950) and crinoid banks. The "shell banks" are discrete unbedded limestone mounds which developed to heights of several feet above the sea floor; bryozoans and crinoid remains are an important part of the fauna contained in this unbedded limestone. The mounds were subsequently buried by the crinoidal debris of the "crinoid banks," which were located shoreward of the shell banks. The blastoid *Orbitremites* is associated with the crinoid remains, occurring sparsely in the upper part of the shell banks, but it is more abundant in the overlying crinoidal debris. In some parts of the area the blastoids of the crinoid banks (*Orbitremites, Codaster*) are confined to thin rock layers a few to several inches in thickness; in other places, they are distributed in random manner through strata ranging from 10 to 30 feet in thickness. Where the blastoids occur in thin layers, the boundary between barren and blastoid-bearing layers is sharp. The blastoid calyces are buried in unsorted crinoidal debris. Bryozoan remains may be common, but invariably are subordinate to the crinoidal detritus. Basinward the limestone beds containing blastoids grade into deposits characterized by an abundant fauna of small brachiopods and the coral *Lonsdaleia*.

After an attempt to compile an annotated bibliography of the paleoecology of blastoids, which was unsuccessful owing to the absence of significant published investigations, Cline & Beaver (1957) summarized their own observations and inferences pertinent to the subject. Since blastoids are associated typically with rugose corals, brachiopods, fenestellid bryozoans, and crinoids, they concluded that blastoids lived in a normal marine environment which was characterized by at least some agitated water. The nature of their food-gathering system requires some current action and possibly a sea bottom with a substratum of skeletal debris that was most satisfactory for attachment. Evidence supporting these inferences is found at outcrops of the Paint Creek Formation (Chesteran), northeast of Waterloo, Illinois, where strata above red clay at the base of the formation comprise a sequence of beds in which specimens of *Pentremites* are alternately abundant and entirely absent. The succession of deposits

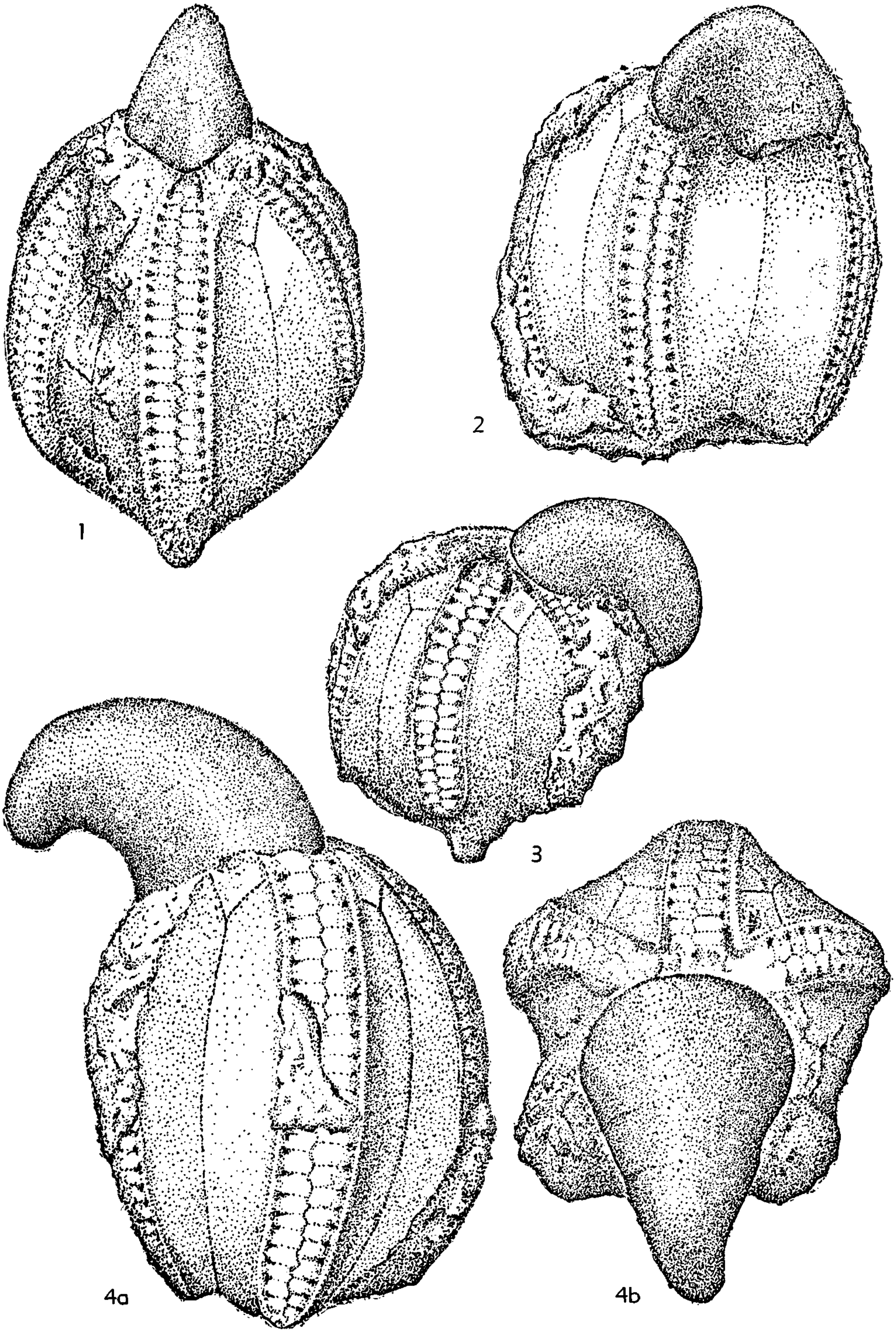

Fig. 227. Symbiotic association of blastoids, *Diploblastus kirkwoodensis* (Shumard), with coprophagous gastropods, *Platyceras (Platyceras)* sp., Miss. (Meramec., St. Louis Ls.), near St. Louis, Mo.; *1, A*-ray lateral view of specimen D; *2, D*-ray view of specimen C; *3, E*-ray view of specimen B; *4a,b, B*-ray and adoral views of specimen A; all ×9.5 (Levin & Fay, 1964).

is cyclic, a typical cycle consisting of a 0.5- to 1-inch layer of uncemented echinoderm remains overlain by nearly unfossiliferous, thinly bedded clay layers, 1 or 2 inches thick. *Pentremites,* brachiopods, and crinoid remains are common to abundant in the lower layer and are found in various states of preservation. Specimens of *Pentremites* with part of the column, brachioles, ambulacral covering plates, and summit plates are commonly preserved in the lower layer of echinoderm debris. Some specimens are abraded, however, and indicate agitated debris. The overlying clay layer has virtually no fossil remains, except for bryozoan fronds found locally. Apparently fine mud spread over the sea floor and smothered individual organisms living at the time. Cycles of this sort are repeated again and again.

The preservation of the upper Burlington (Osagian) blastoid fauna in the Ashgrove quarries several miles south of Springfield, Missouri, indicates that these specimens accumulated in shallow agitated water, probably near the zone of surf action. The blastoid calyces and the associated crinoid and brachiopod remains are broken, much abraded, and worn; preservation of internal features is poor. The interior of the calyces of *Pentremites elongatus* are filled with clear calcite crystals and practically none of the hydrospire folds are preserved.

The type of food on which blastoids lived can only be guessed at. Because food was taken from the water by ciliated furrows lining the brachioles and was transported along food grooves to the mouth, it is reasonable to assume that blastoids fed on planktonic organisms (CLINE & BEAVER, 1957, p. 959). Living comatulid crinoids, some of the nearest living relatives of the blastoids, live primarily on unicellular green algae (CLARK, 1915, p. 144).

The gregarious nature of many echinoderms frequently has been recorded. In rock strata their fossil remains may occur in a particular bed for long distances, or they may be abundant locally but laterally absent. As noted previously, sparse occurrences of blastoids have been recorded from the upper portion of some English "shell banks" termed reef knolls by some workers. Specimens are most common in the beds of crinoidal debris overlying the shell banks. Examination of a large blastoid collection made by LAUDON and BOWSHER from the Lake Valley Formation (Mississippian) of New Mexico showed that all the specimens had been collected from a nonreef facies (CLINE & BEAVER, 1957).

A previously unknown symbiotic relationship of blastoids and coprophagous gastropods has been discovered recently by LEVIN & FAY (1964), who report nearly a dozen individuals of *Diploblastus kirkwoodensis* (SHUMARD) with specimens of *Platyceras (Platyceras)* attached to the calyx (Fig. 227). The gastropods, which are small, with smooth apertural lip and constant angle of expansion, are found perched in various positions over the anal opening of the blastoids. Apparently they are mature individuals that fed on fecal pellets of their host and benefited by the association. The blastoids seem to have been neither harmed nor benefited by their molluscan "fellow travelers." Coprophagous gastropods attached to crinoid calyces are better known, several examples of them having been described by BOWSHER (1955). The *Platyceras*-bearing specimens of *Diploblastus* occur in shaly layers of the St. Louis Limestone (Meramecian) near St. Louis, Missouri; they are associated with many more blastoids which lack adherent gastropods, suggesting that the association is uncommon.

# STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION

By Donald B. Macurda, Jr.

The earliest known blastoids are found in the Silurian. From the United States, 3 or 4 genera are represented by species found in Illinois, Ohio, Indiana, Kentucky, Tennessee, and Oklahoma (Fig. 228). One occurrence has been reported from the Silurian of Bohemia. It is identified as being congeneric with the Oklahoma genus, but the anal structure is unknown and the generic identification must be considered provisional.

The blastoids had become world-wide in their distribution by the Devonian (Fig. 228). Most forms are known from the Middle Devonian of the United States and Lower and Middle Devonian of western Europe. Some 11 genera have been described from the United States and range geographically from the Appalachians westward to Iowa (West Virginia, New York, Ontario, Ohio, Michigan, Indiana, Illinois, Wisconsin, Iowa, Kentucky, Tennessee, Missouri). There are also records from the Devonian of Oklahoma and New Mexico. In Europe, five or six genera have been reported from Spain, France, Great Britain, Belgium, and Germany. They also have been reported from Manchuria in China, Victoria in Australia[1], northwestern Africa, and fragments are known from South Africa and Bolivia in South America. These last-mentioned occurrences are poorly known taxonomically and may represent new genera. Individual Devonian genera do not appear to have a intercontinental distribution. There may be one that occurs in both the United States and Spain, and *Devonoblastus,* a New York genus, has been reported from China. Some genera have a fairly wide geographic range, as *Cordyloblastus* is found in France, Spain, and Germany; and *Nucleocrinus* ranges

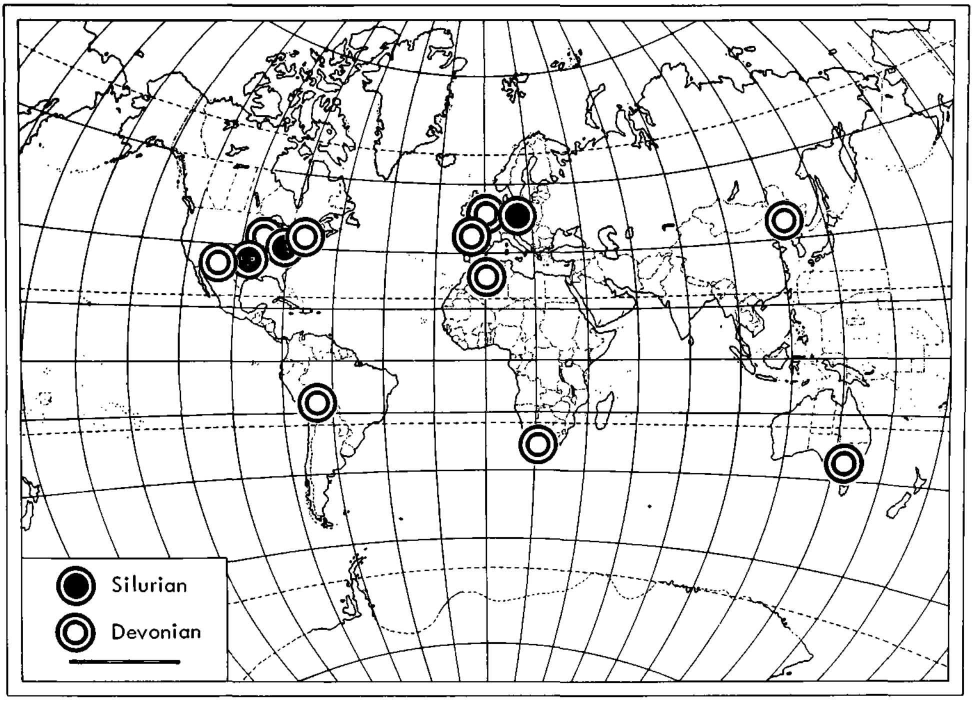

Fig. 228. Geographic distribution of Silurian and Devonian blastoids (Macurda, n).

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[1] Australian "blastoids" now are judged to be inadunate crinoids (J. Sprinkle, personal communication).

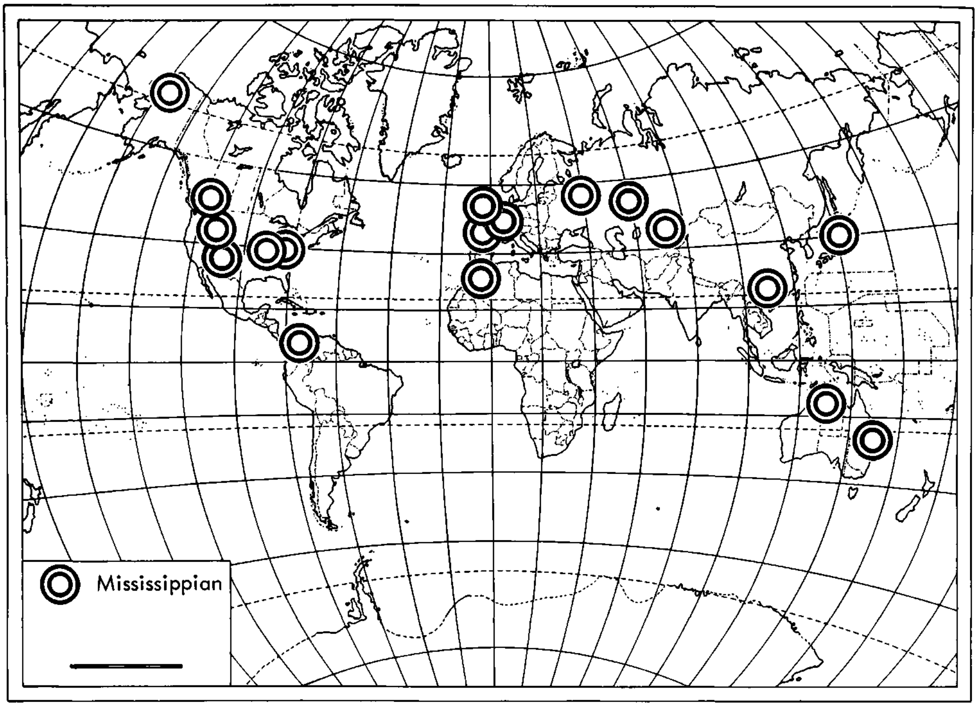


FIG. 229. Geographic distribution of Mississippian blastoids (Macurda, n).

from New York to Iowa and Missouri. A few of the known occurrences are Lower Devonian; most are Middle Devonian. Almost no Upper Devonian blastoids have been discovered.

The Mississippian represents the maximum known development of the blastoids (Fig. 229). About 45 genera (some undescribed) have been found in rocks of this period. About 25 of these have been collected from Mississippian deposits in states bordering the Mississippi River, all but a few from the Kinderhookian and Lower Valmeyeran. The Burlington Limestone has a greater diversity than any other formation. In the eastern and central United States, blastoids have been found in Alabama, Georgia, Mississippi, Kentucky, Tennessee, Virginia, West Virginia, Ohio, Indiana, Illinois, Iowa, Missouri, Arkansas, and Oklahoma. Most of the easternmost occurrences are Upper Mississippian; blastoids range throughout the Mississippian in the other states. Knowledge of blastoid distribution in the western United States is poorer because less attention has been given to search for them but they are known from New Mexico, Arizona, Nevada, Utah, Idaho, Wyoming, and Montana. Preliminary field work suggests that a large and varied blastoid fauna is present. Blastoids are also known from the Canadian Rockies and Brooks Range in Alaska; their description is in progress. The greatest diversity of blastoids occurs in the Lower Mississippian; the number of genera becomes sharply restricted after the Lower Valmeyeran.

Blastoids are also common in the Lower Carboniferous (Mississippian equivalents) of western Europe, some 14 genera being described from Eire, North Ireland, England, Scotland, Germany, Belgium, and Spain. Most of these occurrences are Tournaisian and Visean. They are also known from the Lower Carboniferous of the USSR, China, Japan, Australia, northwestern Africa, and South America (Colombia). Some Mississippian forms are cosmopolitan in distribution, *Pentremites*

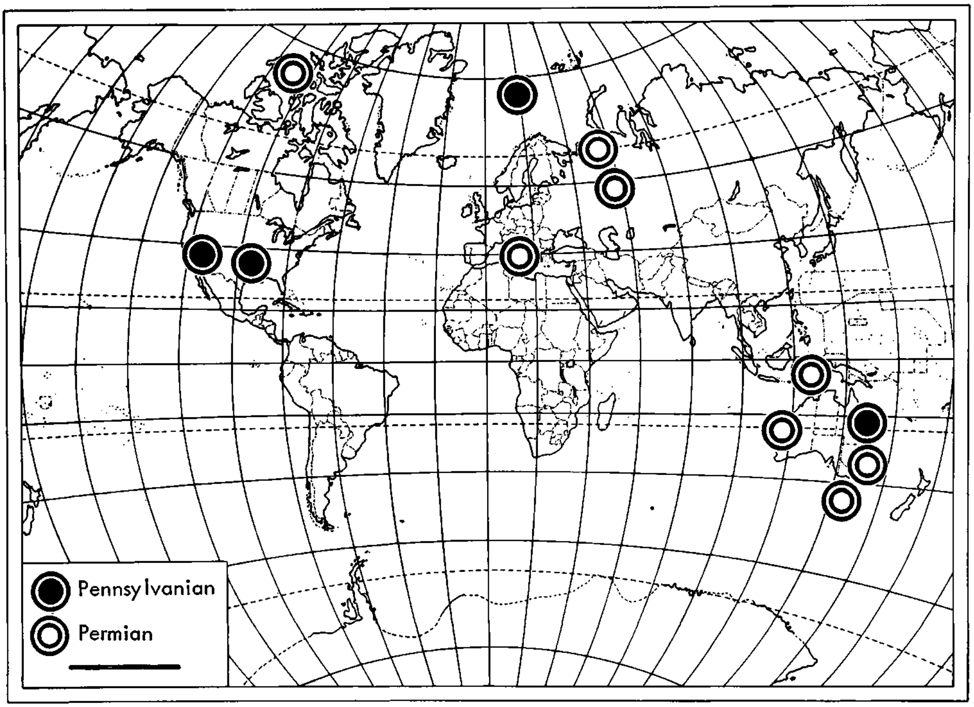


FIG. 230. Geographic distribution of Pennsylvanian and Permian blastoids (Macurda, n).

ranging from Alaska to Colombia, *Orophocrinus* from Arizona to Belgium, *Phaenoschisma* from New Mexico to England, *Cryptoblastus* from Missouri to Arizona, Alaska, and possibly to the central USSR, and *Nymphaeoblastus* from the USSR to Japan and Australia. All occurrences other than those in the eastern United States and western Europe are known only on a reconnaissance basis.

The record of the blastoids in the Pennsylvanian is very sparse (Fig. 230), only three or four genera being known from a period approximately in length to the Mississippian. Whether the paucity of Pennsylvanian blastoids represents an evolutionary crisis or nonpreservation in the geologic record is speculative. *Pentremites* lingered into the Pennsylvanian in Arkansas, Oklahoma, Utah, and Nevada. Other than this genus the only other known occurrences are in the mid-Pennsylvanian of Oklahoma, the Westphalian of Queensland, Australia, and the Upper Carboniferous of Spitzbergen.

During the Permian, most blastoids apparently were found in the eastern hemisphere (Fig. 230). The island of Timor in Indonesia is the most prolific locality, for 16 genera have been found there. Three or four genera are known from Australia (Western Australia, New South Wales, Tasmania). Some of these are congeneric with the Indonesian forms. Two or three genera are known from the USSR, one of which is congeneric with an Indonesian genus. A fragmentary blastoid has been reported from Sicily. Recently, the first Permian blastoid in the Western Hemisphere has been found on Melville Island in the Canadian Arctic.

Existing knowledge of the stratigraphic distribution and paleogeography of blastoids is incomplete. The occurrences described above show an obvious relationship to centers of research; with further exploration, it may change considerably. At least ten new genera from fairly well-known areas currently await description.

# CLASSIFICATION

By R. O. Fay

## PREVIOUS INVESTIGATIONS

The first descriptions and illustrations of a blastoid known to me were published by S. L. Mitchill (1808) and J. Parkinson (1808), who referred to an "Asterite" or "asterial fossil" from Kentucky and illustrated specimens of the species subsequently named *Pentremites godoni*. The specimens obtained by Dr. Samuel Brown in 1805 (Fay, 1961, 55) evidently were collected from beds now known as the Paint Creek Formation (U.Miss,. Chester.) of the Mammoth Cave or Bowling Green region of central Kentucky. In 1819, J. L. M. Defrance named this fossil *encrina Godonii*, thus applying the first binomial zoological designation for a blastoid species. In 1825, Thomas Say proposed the "family" Blastoidea as a separate group of the Echinodermata, the name referring to the predominant budlike form of the theca.

In 1851, the first morphologic study of blastoids was published by C. F. Roemer, who reported the discovery of ambulacral pores and internal folds that terminate near the mouth. These folds were termed hydrospires by Elkanah Billings in 1869. Roemer divided the blastoids into four groups, named Floreales (conical theca, petaloid ambulacra), Elliptici (globular theca), Truncati (flat summit), and Clavati (conical theca, linear ambulacra). Although these groupings were arbitrary, it is true that globular and conical blastoids may be separated into natural lineages.

In 1886, Robert Etheridge & P. H. Carpenter published a comprehensive study of the blastoids, based on seven years of intensive study by them on specimens in the British Museum (Natural History) and others obtained by loan. This work has served as basic reference material for all subsequent textbooks and treatises concerned with blastoids. Most pre-Permian genera were illustrated, and the first record was made of the double circumesophageal ring, hydrospire plates, and the occurrence of the abnormal specimens. Etheridge & Carpenter divided the Blastoidea into two orders called Regulares (five normal ambulacra) and Irregulares (four normal ambulacra and one short ambulacrum). The Regulares included five families termed Pentremitidae (pyriform, five spiracles); Troostoblastidae (conical, ten spiracles); Nucleoblastidae (globular, ten spiracles); Granatoblastidae (globular, five spiracles); and Codasteridae (without hydrospire pores). The Irregulares comprised one family, Astrocrinidae, with three genera *(Astrocrinus, Pentephyllum, Eleutherocrinus)*. The classification given by Etheridge & Carpenter is unnatural but nevertheless important, because emphasis was placed upon profiles and spiracles, in addition to the presence or absence of pores as fundamental taxonomic features. The illustrations are works of art which illustrate excellently the shapes, sizes, and general plate relationships of numerous blastoids, even though they are somewhat inaccurate in showing details of the anal deltoids and relative exposure of the lancet plates. Many internal features were not reported, and no mention was made of the relative overlap of deltoids on radials or of radials on deltoids. As a result, it will be necessary to restudy almost all of the blastoid specimens in the British Museum and those in other collections before attempting to make a trustworthy classification of the blastoids.

In 1896, Charles Wachsmuth, who wrote the blastoid chapter in the first English edition of Zittel's *Textbook of Palaeontology*, followed Etheridge & Carpenter in almost every detail. In 1899, F. A. Bather in a short paper gave a new classification which is as follows.

*Classification of Blastoidea by Bather (1899)*

Grade Protoblastoidea
  Family Asteroblastidae [now classed with diplopore cystoids]
  Family Blastoidocrinidae [now classed as parablastoids]
Grade Eublastoidea [same as Blastoidea]
 Series A. Codonoblastida
  Family Codasteridae (hydrospire slits exposed)
  Family Pentremitidae (hydrospire slits covered)
 Series B. Troostoblastida

Family Troostocrinidae (conical forms, with hydrospire pores)
Family Eleutherocrinidae (one ambulacrum shorter than others)
Series C. Granatoblastida
Family Nucleocrinidae (lacking hydrospire plate)
Family Orbitremitidae (hydrospire plate present)
Family Pentephyllidae (stemless, large subpentagonal theca)
Family Zygocrinidae (stemless, small depressed theca)

BATHER expressed the belief that blastoids were derived from diplopore cystoids through a form like *Asteroblastus*, but intermediate forms are lacking to prove this concept. His classification is a mixture of unnatural units and the "Series" designated by him were never defined. The most important item suggested by BATHER's classification is that the Codasteridae and Pentremitidae may be more closely interrelated than the Orbitremitidae and Pentremitidae. Evidently BATHER did not believe that the presence or absence of hydrospire pores was fundamental.

In 1908, BATHER reported the occurrence of Permian blastoids on Timor Island in the Dutch East Indies, and subsequently similar Permian fossils were found in Russia, Sicily, and Australia (New South Wales). Only two or three genera were named up to 1918 and these finds did not affect previous classifications.

In 1918, OTTO JAEKEL defined the Blastoidea as a subclass of the Cystoidea, linking the two by means of *Cystoblastus*, and he thus derived the blastoids from pore-rhomb cystoids. BILLINGS (1869) and MOORE (1954) have expressed similar views, but all attempts to find intermediate forms to trace lineages connecting cystoids with blastoids have failed. JAEKEL's classification is as follows.

### *Classification of Blastoidea by Jaekel (1918)*

Class Cystoidea
Subclass Blastoidea
  Order Parablastida (large number of thecal plates) (Blastocystidae)
  Order Radiolata [now termed Blastoidea proper]
    Suborder Spiraculata (hydrospire slits hidden, pores present)
      Families Troostoblastidae, Pentremitidae, Nucleoblastidae, Granatoblastidae (as defined by Etheridge & Carpenter, 1886)
    Suborder Fissiculata (hydrospire slits exposed)
      Family Orophocrinidae (spiracular slits present)
      Family Codasteridae (hydrospire slits exposed)
  Order Coronata [now transferred to the Crinoidea] (plates like those of blastoids, but lacking hydrospires, pores, slits, side plates, and brachioles)

The important contribution of JAEKEL is partition of the blastoids into groups designated as Fissiculata and Spiraculata, and the separation of fissiculate blastoids into those having spiracular slits from those with exposed hydrospire fields. The Parablastida are here set apart as the Class Parablastoidea, probably not related to the Blastoidea. The order Coronata is classed under the Crinoidea because the fossils in this group have crinoid-type arms, lack hydrospires and pores, and lack brachioles (FAY, 44, 57, 66). BATHER's and JAEKEL's studies indicate that the Blastoidea and Cystoidea are not closely related.

In 1924, J. WANNER described many new genera and species of Permian blastoids from Timor. Subsequently, H. MATSUMOTO (1929) modified BATHER's classification by dividing the class Blastoidea into three orders: Protoblastida, Mesoblastida (Fissiculata plus *Astrocrinus*), and Eublastida (Spiraculata minus *Astrocrinus*), thus arriving at a classification almost identical with that of JAEKEL. The Eublastida were divided into three "series," termed Troostoblastida, Pentremitida, and Granatoblastida.

In the 1930's, L. M. CLINE published on some Devonian and Mississippian blastoids of North America, and since 1935, I. G. REIMANN has described various Devonian blastoids. New morphological features, such as ambulacral spines and anal-deltoid plates, were investigated by these authors and questions began to be raised about generic relationships of known blastoid genera.

In 1940, WANNER described new Permian genera and species from Timor, in addition to those of his previous publications (1931, 1932). In all, he described 48 new species belonging to 16 new genera and provided morphological information which called for a revised classification of the blastoids. The most important part of WANNER's taxonomic changes was removal of the parablastoids, protoblastoids, and coronates from the Blastoidea, which thus were left with only two orders (Fissiculata, Spiraculata), and he concluded that the Fissiculata were in need of extensive subdivision. WANNER's classification is indicated in the following outline.

### *Classification of Blastoidea by Wanner (1940)*

Class Blastoidea SAY, 1825
Order Fissiculata JAEKEL, 1918
  Family Codasteridae ETHERIDGE & CARPENTER, 1886 (eight hydrospire groups, anal deltoid present)
  Family Dipteroblastidae WANNER, n. fam. (ten hydrospire groups, epideltoid and hypodeltoid present, plates irregular)
  Family Zygocrinidae BATHER, 1899 (eight hydrospire groups, plates irregular)
  Family Angioblastidae WANNER, n. fam. (eight hydrospire groups, one to three slits in each, epideltoid and hypodeltoid present)
  Family Phaenoschismidae ETHERIDGE & CARPENTER, 1886 (*recte* Phaenoschismatidae) (ten hydrospire groups, many slits, plates irregular, base pyriform)
  Family Nymphaeoblastidae WANNER, n. fam. (ten hydrospire groups, many slits, plates regular, base flat to concave)
  Family Anthoblastidae WANNER, n. fam. (ten hydrospire groups, one slit in each, plates regular)
  Family Neoschismidae WANNER, n. fam. (*recte* Neoschismatidae) (ten hydrospire groups, interradial areas prolonged)
  Incertae sedis, *Thaumatoblastus* WANNER, 1924
Order Spiraculata JAEKEL, 1918
Suborder Troostoblastida BATHER, 1899
  Family Troostocrinidae BATHER, 1899 (*recte* Troosticrinidae)
  Family Eleutherocrinidae BATHER, 1899
Suborder Granatoblastida BATHER, 1899
  Family Nucleocrinidae BATHER, 1899
  Family Orbitremitidae BATHER, 1899
  Family Pentephyllidae BATHER, 1899
Suborder Pentremitida MATSUMOTO, 1929
  Family Pentremitidae D'ORBIGNY, 1851

Several difficulties are inherent in the above classification. The Eleutherocrinidae should belong with the Pentremitidae, the Pentephyllidae probably belong under the Fissiculata, and the Orbitremitidae may include diverse groups of globular blastoids, of unrelated origin. Several genera (e.g., *Brachyschisma, Thaumatoblastus*) had no place in the classification, and questions on morphology of old genera arose, especially in connection with anal structures. WANNER's works were a great step forward because he began to realize the importance of anal, oral, and internal structures, and their bearing on classification. By 1951 it was apparent that we would have to restudy all previous blastoid species.

In 1943, R. S. BASSLER & M. W. MOODEY prepared a bibliographic index to genera and species, recognizing approximately 50 genera and 350 species. They recognized the Protoblastoidea and Eublastoidea as orders, the latter being the Blastoidea of most authors. The protoblastoids included the Asteroblastidae (now removed to the diplopore cystoids) and the Blastoidocrinidae (relegated to the Parablastoidea). The eublastoids were divided according to WANNER's classification, rather than as was done by BASSLER in the *Fossilium Catalogus* (1938). There is present need for a comprehensive bibliography, objective index, and stratigraphic and geographic cross-index to the Blastoidea. One important contribution of BASSLER & MOODEY was transfer of the Coronata to the crinoids.

In 1945, GERHARD REGNÉLL transferred the blastoids to the cystoids on the ground that pores pierce the theca and biserial brachioles are common to both groups. His classification is as follows.

### *Classification of Blastoidea by Regnéll (1945)*

Class Cystoidea VON BUCH, 1846
Subclass Hydrophoridea VON ZITTEL, 1903
Subclass Blastoidea SAY, 1825 [now a separate class]
  Order Coronata JAEKEL, 1918 [now transferred to Crinoidea]
  Order Parablastoidea HUDSON, 1907 [now segregated as separate class]
  Order Eublastoidea BATHER, 1899 [now same as Class Blastoidea]

The Parablastoidea have a type of hydrospires unknown in blastoids and contain many more thecal plates. It would be difficult to place this group with any known class of echinoderms and therefore it is best to raise them to the rank of a class. One important contribution of REGNÉLL's is that he removed the diplopore cystoids (e.g., *Asteroblastus*) from the Protoblastoidea, thus wiping out a separate group known as protoblastoids.

In 1953, F. M. BERGOUNIOUX followed the classification of BASSLER & MOODEY (1943) for the French *Traité de Paléontologie*. In this work, the genus *Asteroblastus* was

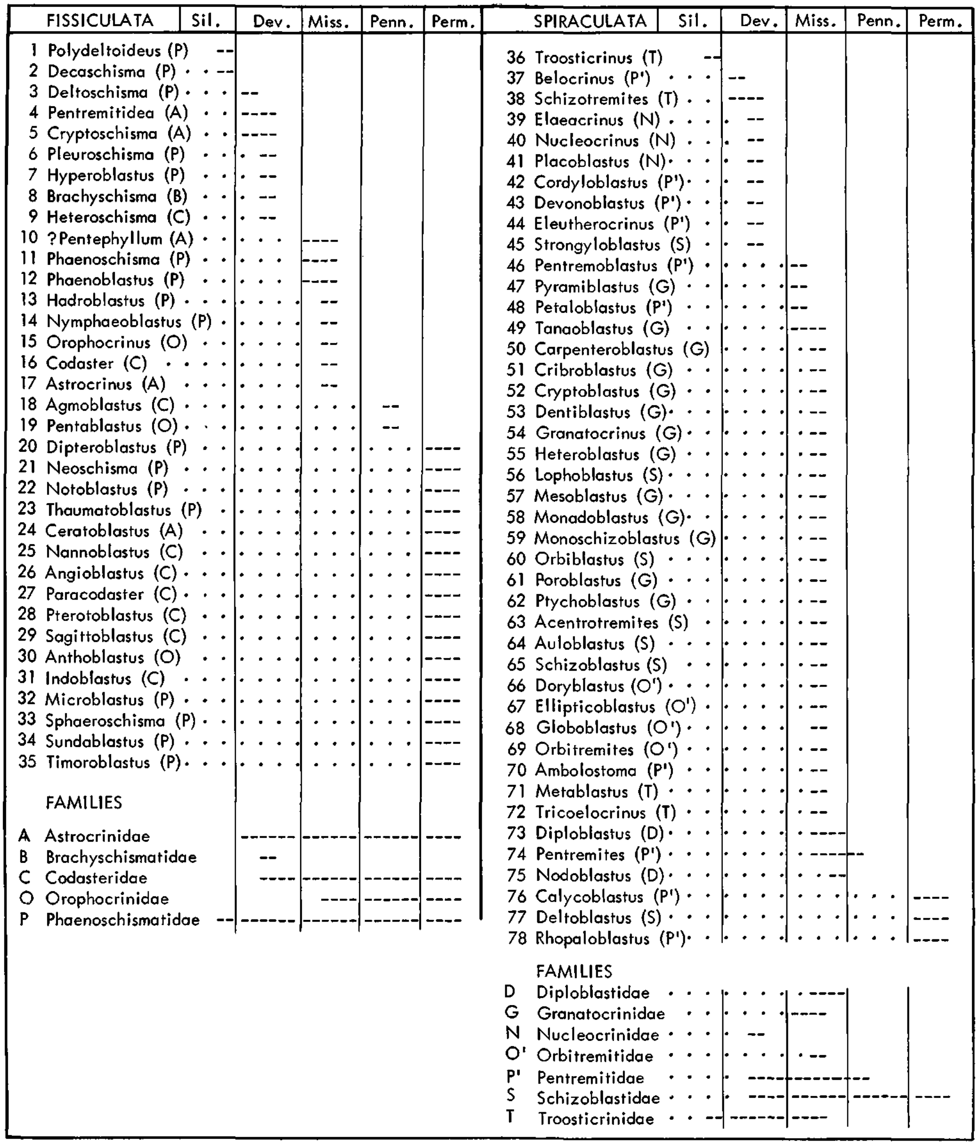


FIG. 231. Stratigraphic distribution of blastoid genera. The letter symbols after the generic names refer to the families in which they are classified, with familial names listed at bottom of chart (Moore & Fay, n).

treated as a protoblastoid and in another section as a diplopore cystoid.

In 1961, FAY published a comprehensive study on pre-Permian blastoids, with revision of many genera and species. The work was incomplete and approximately 30 short papers were written from 1960 to 1962 as supplements to it. A new classification of the Blastoidea was presented, and sections were written on morphology, taxonomy, phylogeny, and bibliography, with the conclusion that a great amount of work is needed before we may begin to understand the features of blastoids that now exist in various museums. After these specimens are studied, we may have a better system of classification. The classification followed in the *Treatise* is essentially that of FAY

(1961, 60), and should be considered as tentative.

Currently several persons working on blastoids include J. A. Arendt (Moscow, USSR), H. H. Beaver (Houston, Texas), Albert Breimer (Amsterdam, Netherlands), R. O. Fay (Norman, Oklahoma), Alan Horowitz (Bloomington, Indiana), K. A. Joysey (Cambridge, England), R. G. McKellar (Brisbane, Australia); D. B. Macurda, Jr. (Ann Arbor, Michigan), I. G. Reimann (Ann Arbor, Michigan), and J. S. Sprinkle (Cambridge, Massachusetts). Much of their work has been on statistics, morphology, and taxonomy, with little emphasis on bibliographic compilations.

## TREATISE CLASSIFICATION

In our present state of knowledge of the Blastoidea it is premature to present a definitive arrangement of these fossils. The primary basis for classification of Blastoidea, as now understood, is a combination of characters, especially of deltoid plates on the anal side. These features include (1) presence, absence, or reduction of hydrospires on the anal side, (2) number, type, and arrangement of the anal deltoids, (3) relative exposure of the deltoids, (4) relative closure of the radial sinuses, (5) number, type, and arrangement of the spiracles, (6) number, type, and arrangement of the hydrospires, (7) number, type, and arrangement of the hydrospire pores, (8) relative overlap of radials and deltoids along the radiodeltoid sutures, (9) number, type, and arrangement of the oral plates, (10) shape of the theca, and (11) relative exposure of the lancet plates to the exterior and position of the lancet stipe.

Separation of the orders Fissiculata and Spiraculata is based essentially on relative exposure of the hydrospire slits and the development of hydrospire pores and spiracles.

Families of the Fissiculata are separated by features that include formation of spiracular slits or reduction of hydrospire fields (hydrospiralia) on the anal side or both of these, combined with retention of exposed hydrospire slits, associated with atrophy of them on the anal side. The families of the Spiraculata are distinguished by type and arrangement of the spiracles and the conical to globular shape of the theca.

Genera of the Blastoidea are differentiated by the above-cited features in a variety of combinations. Ornamentation, shape, and statistical measurements are used to define species.

## DISTRIBUTION

Many geographic and stratigraphic gaps exist in our knowledge of the class. For instance, a few nominal genera of blastoids have been recorded from Africa, South America, China, Japan, and the North Polar regions, whereas only three genera are recorded from Pennsylvanian rocks of the world. Only three Silurian genera are recorded, all from the United States and one of them also in Czechoslovakia. Of 78 described genera, it is possible to group a few in natural families or related categories, but almost impossible to trace direct lineages. It is quite possible that the families here outlined are polyphyletic and that in the future these may be raised to suborders or otherwise changed. There must be two to three times as many undescribed genera as now known and until these are described, it seems best to retain a simple classification of the Blastoidea. The stratigraphic distribution of blastoid genera is given in Figure 231.

## PHYLOGENY AND EVOLUTION

### By Robert O. Fay

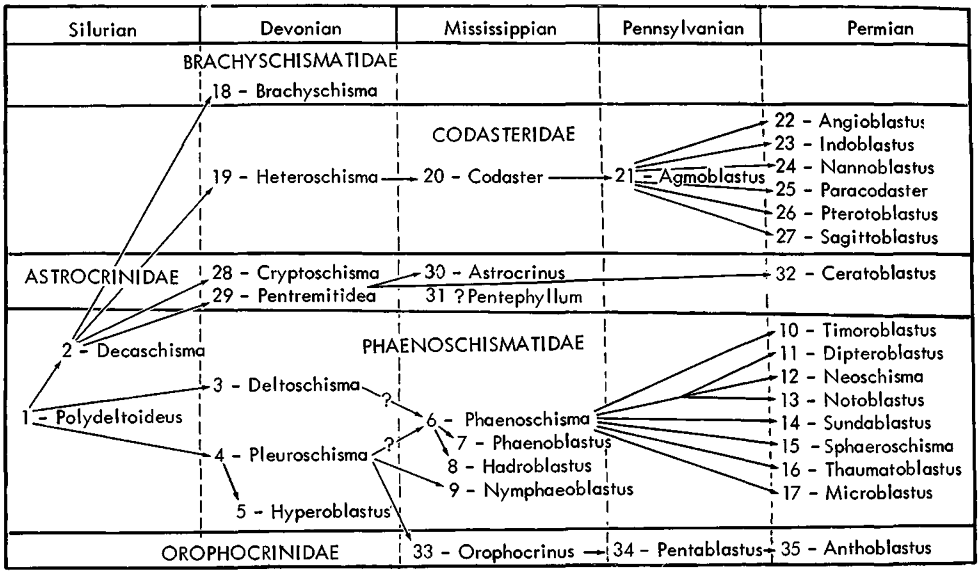
The origin of the Blastoidea is unknown. It has been postulated by Jaekel (1918) and Moore (1954) that this group of echinoderms may have been derived from pore-rhomb cystoids by development of hydrospires through atrophy of the pore-rhombs although this type of atrophy has never been demonstrated. Regnéll (1945) classed the Blastoidea as a subdivision of the Cystoidea, because both groups possess biserial brachioles and pores that pierce the theca. Cline (1944) made no attempt to compare pore-rhombs with hydrospires and was of the opinion that the hydrospires represent successive infolds along ambulacral margins. WANNER (1940) declined to accept homology of pore-rhombs and hydrospires. At present I would agree with WANNER and CLINE, and further, would relate the Blastoidea to the class Edrioblastoidea (FAY, 1961) and suggest that the blastoids were derived from this class. BATHER (1900) presented the concept that the Blastoidea were derived from diplopore cystoids and that each hydrospire fold represents a pore-pair that has become elongated along the ambulacral margins and that hydrospire pores are specialized pore pairs. At the same time, however, BATHER thought that poreless blastoids (Fissiculata) gave rise to pore-bearing blastoids (Spiraculata), thus opposing his own postulate.

The class Edrioblastoidea seems to be the logical group from which the Blastoidea could have developed. The separate orders (in part) of the Blastoidea could have been derived independently from this class, or the order Fissiculata may have descended directly and the order Spiraculata indirectly by development from the Fissiculata. These suggestions are based upon judgment of inferred phylogenetic trends within the Blastoidea, as now understood. A most primitive blastoid is presumed to be similar to *Polydeltoideus,* in which the form of the calyx is conical, with six anal deltoids, ten exposed hydrospire fields (hydrospiralia), and a moderately long lancet plate covered by side plates. An advanced form is one similar to *Pentremites,* in which the calyx is rounded-conical, with a single anideltoid, the sinuses closed to form pores and spiracles, and the lancet plate displaced outward, pushing aside the side plates. If *Pentremites* came from a form ultimately like *Polydeltoideus,* and if one projects this trend backward, he may postulate the type of echinoderm best suited to represent the ancestral stock of the Blastoidea. This echinoderm should have at least six anal deltoids and otherwise possess regular plate symmetry, with random infolds in the thecal plates, a deep lancet (or better, no lancet, since the lancet is interpreted to be a plate secreted around the median canal, having little useful function of protection where deep—hence probably not secreted in a primitive form), five regular, straight ambulacra covered by an alternating biserial set of ambulacral plates, a primitive stem, and possibly primitive brachioles.

The class Edrioblastoidea has these features, except for primitive brachioles, but it is reasonable to postulate that brachioles could have arisen independently when tube-feet became atrophied, and further, that the brachioles of cystoids probably were derived in a similar manner from another class of Echinodermata. One may logically argue that the Edrioblastoidea have a hydropore and that the Blastoidea do not, but it is here interpreted that the hydropore has migrated internally on the anal side in the Blastoidea, and it is quite possible that it was atrophied. FAY (1960) has shown that the radial canal system of blastoids, ending adorally in the circumesophageal ring, is adjacent to the hydrospire canals, and thus it is possible that water entered the radial canal system by diffusion from the hydrospire canals. If this is true, there would have been little need for a hydropore. The canal system is now interpreted to be the main nervous system (because it is a double ring as in Recent echinoderms); so there may not have been a radial canal or water-vascular system in blastoids.

Therefore, the Blastoidea are considered to be a separate class of Echinodermata, closely related to the Edrioblastoidea, and independent of the Parablastoidea. The coronatids have been shown by FAY (1960, 44; 1961, 57; 1962, 66) to belong to the Crinoidea. Blastoid-like forms with pore-rhombs (e.g., *Cystoblastus*) or with diplopores (e.g., *Asteroblastus*) are judged to belong with the Cystoidea, and therefore the groups formerly classed as Protoblastoidea and Asteroblastidae by BATHER (1900), followed by BASSLER & MOODEY (1943), are not recognized as valid categories of the Blastoidea.

The Phaenoschismatidae are considered as the most primitive group of blastoids, from which most others could have been derived (Fig. 232). The ten exposed hydro-



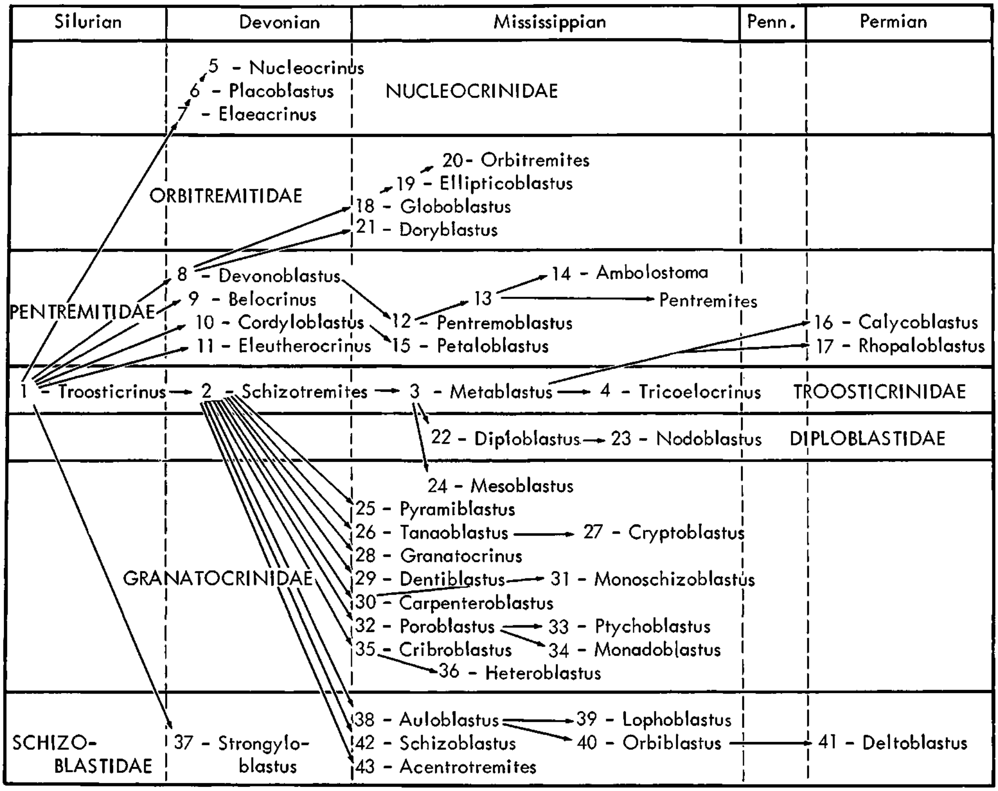
INDEX

Agmoblastus (21)
Angioblastus (22)
Anthoblastus (35)
Astrocrinus (30)
Brachyschisma (18)
Ceratoblastus (32)
Codaster (20)
Cryptoschisma (28)
Decaschisma (2)
Deltoschisma (3)
Dipteroblastus (11)
Hadroblastus (8)
Heteroschisma (19)
Hyperoblastus (5)
Indoblastus (23)
Microblastus (17)
Nannoblastus (24)
Neoschisma (12)
Notoblastus (13)
Nymphaeoblastus (9)
Orophocrinus (33)
Paracodaster (25)
Pentablastus (34)
?Pentephyllum (31)
Pentremitidea (29)
Phaenoblastus (7)
Phaenoschisma (6)
Pleuroschisma (4)
Polydeltoideus (1)
Pterotoblastus (26)
Sagittoblastus (27)
Sphaeroschisma (15)
Sundablastus (14)
Thaumatoblastus (16)
Timoroblastus (10)

FIG. 232. Phylogenetic diagram showing possible or inferred relationships of blastoid genera and families of the order Fissiculata (Fay, n).

spire fields could readily have been reduced to nine, thus forming blastoids classed as genera of the Brachyschismatidae, or to eight hydrospire fields, as observed in the Codasteridae. Another trend is toward closure of the sinuses to form ten spiracular slits (as in the Orophocrinidae), or atrophy of the hydrospire fields on the anal side, with formation of eight spiracular slits (e.g., Astrocrinidae).

The Pentremitidae may be descendants of the Phaenoschismatidae produced by complete closure of the sinuses and formation of gaps (hydrospire pores) between side plates (Fig. 233). This mode of developing hydrospire pores is thought to be probable, and accordingly it seems logical to derive *Devonoblastus* from *Hyperoblastus* and *Pentremites* from *Devonoblastus*. If this is correct, the Troosticrinidae are possible derivatives of the Phaenoschismatidae, though intermediate forms are lacking to prove this; alternatively, the Troosticrinidae may have developed independently from the same stock that gave rise to the Phaenoschismatidae. The Granatocrinidae could have been derived from the Troosticrinidae by outward migration of the deltoid septa, except on the anal side, where the deltoid septa migrated inward. The Schizoblastidae also may have descended from the Troosticrinidae, with outward migration of the deltoid septa, including those of the anal side. The Nucleocrinidae, likewise, are possible derivatives of the Troosticrinidae by outward migration of the deltoid septa and outward-downward migration of the large cryptodeltoids. The Pentremitidae may have come from the Troosticrinidae by internal migration of deltoid septa.



INDEX

Acentrotremites (43)
Ambolostoma (14)
Auloblastus (38)
Belocrinus (9)
Calycoblastus (16)
Carpenteroblastus (30)
Cordyloblastus (10)
Cribroblastus (35)
Cryptoblastus (27)
Deltoblastus (41)
Dentiblastus (29)
Devonoblastus (8)
Diploblastus (22)
Doryblastus (21)
Elaeacrinus (7)
Eleutherocrinus (11)
Ellipticoblastus (19)
Globoblastus (18)
Granatocrinus (28)
Heteroblastus (36)
Lophoblastus (39)
Mesoblastus (24)
Metablastus (3)
Monadoblastus (34)
Monoschizoblastus (31)
Nodoblastus (23)
Nucleocrinus (5)
Orbiblastus (40)
Orbitremites (20)
Pentremites (13)
Pentremoblastus (12)
Petaloblastus (15)
Placoblastus (6)
Poroblastus (32)
Ptychoblastus (33)
Pyramiblastus (25)
Rhopaloblastus (17)
Schizoblastus (42)
Schizotremites (2)
Strongyloblastus (37)
Tanaoblastus (26)
Tricoelocrinus (4)
Troosticrinus (1)

FIG. 233. Phylogenetic diagram showing possible or inferred relationships of blastoid genera and families of the order Spiraculata (Fay, n).

Within each family it is possible to trace certain lineages involving specific morphological parts. These trends appear to be similar in diverse families and therefore are here grouped. For instance, the lancet plate is covered by side plates in primitive forms and the side plates support the main food groove. In advanced forms, the lancet is exposed to the outside and supports the main food groove, or in extremely advanced forms, supports the side food grooves in addition. Thus, linear ambulacra are identified as primitive and petaloid ambulacra as advanced characters. The lancet stipe is adjacent to the mouth in a primitive blastoid and has migrated away from the mouth in an advanced form. There are four or six anal deltoids in a primitive form, and one may trace lineages whereby fusion must have taken place between the two cryptodeltoids to form a subdeltoid and between a subdeltoid and superdeltoid to form a single epideltoid, with consequent atrophy or suppression of the hypodeltoid.

The hydrospire fields (hydrospiralia) become atrophied or the number of hydrospire slits are reduced on the anal side. In the Spiraculata, which possess hydrospires in all ambulacra, certain trends are apparent; the number of hydrospires on each side of an ambulacrum apparently becomes reduced in number by atrophy, from five, to four, to three, to two, and to one in different genera, and the hydrospires on the anal side may differ in number from those of the other ambulacral areas within a single genus. With exception of *Pentremites,* the number of hydrospire folds on each side of an ambulacrum, if less than four, is apparently a stable criterion for differentiation of genera.

Another stable feature is the overlap of radials and deltoids along the radiodeltoid suture, which is constant for each genus and species. A primitive blastoid has short deltoids, overlapped by the radials; an advanced form is one having long deltoids, overlapping the radials. The pelvis is conical in a primitive blastoid, whereas it is rounded or with a concave base in an advanced form.

A blastoid with paired spiracles is considered to be primitive, and owing to migration outward or inward of certain deltoid septa it is possible to have forms with five, nine, or 11 openings around the mouth. Thus, the family Pentremitidae may be polyphyletic, possibly derived from the Phaenoschismatidae and Troosticrinidae.

The blastoid stem could have been derived from fused plates of the base of some Edrioblastoidea, and through time, the stem could have atrophied though disuse in a form like *Eleutherocrinus,* with consequent formation of bilateral symmetry and possible adaptation to swimming habits.

The pores, if formed as simple gaps between side plates, are primitive where one pore occurs between adjacent side plates along the deltoid and radial margins. In advanced forms, the pores evidently migrated laterally into margins of the deltoid and radial plates, and these plates folded along each pore to form multiple pores corresponding to each side plate. In some forms, the pores became atrophied along the deltoid margins and were lost, or the simple pores remained along the deltoid margins, but multiple pores formed along the radial margins (e.g., *Poroblastus*).

The cited features tend to show that although Permian blastoids of Timor and adjacent areas are fissiculate forms, they are highly specialized, advanced forms. Thus, they are not considered to be products of retrogressive evolution. The evolutionary theme in blastoids apparently is one of atrophy through disuse.

The problem of extinction of the Blastoidea is apparently one apart from morphological considerations because blastoids of the Permian possess features that warranted their survival into the Triassic and beyond. Thus, some major external physical change of a radical nature was the probable cause for extinction of the class.

## SYSTEMATIC DESCRIPTIONS

By Robert O. Fay[1] and Johannes Wanner[2]

[[1]Oklahoma Geological Survey; [2]deceased, formerly University of Bonn]

The present classification is that adopted by Fay, but many ideas expressed on relationships and descriptions of Permian blastoids and most of the Permian tone illustrations are taken from materials submitted by Wanner. Various families, as here defined, would be raised to suborders by Wanner on the basis of greater emphasis given by him to anal and spiracular structures. Many specimens in museums probably belong to new genera, but circumstances have prevented new study of them. Until these specimens are correctly illustrated and described, it is best to retain a rather simple classification of the Blastoidea. The relationships among different genera of many recently recognized structures (e.g., inner side plates, paradeltoid plates, ambulacral spines, double brachiolar cover plates, accessory oral plates, lateral canals, anal cover plates) are not well understood. It is hoped that paleontologists will re-examine specimens in their collections, prepare polished thin sections of them, and publish detailed descriptions, supplemented by photographs and line drawings at ade-

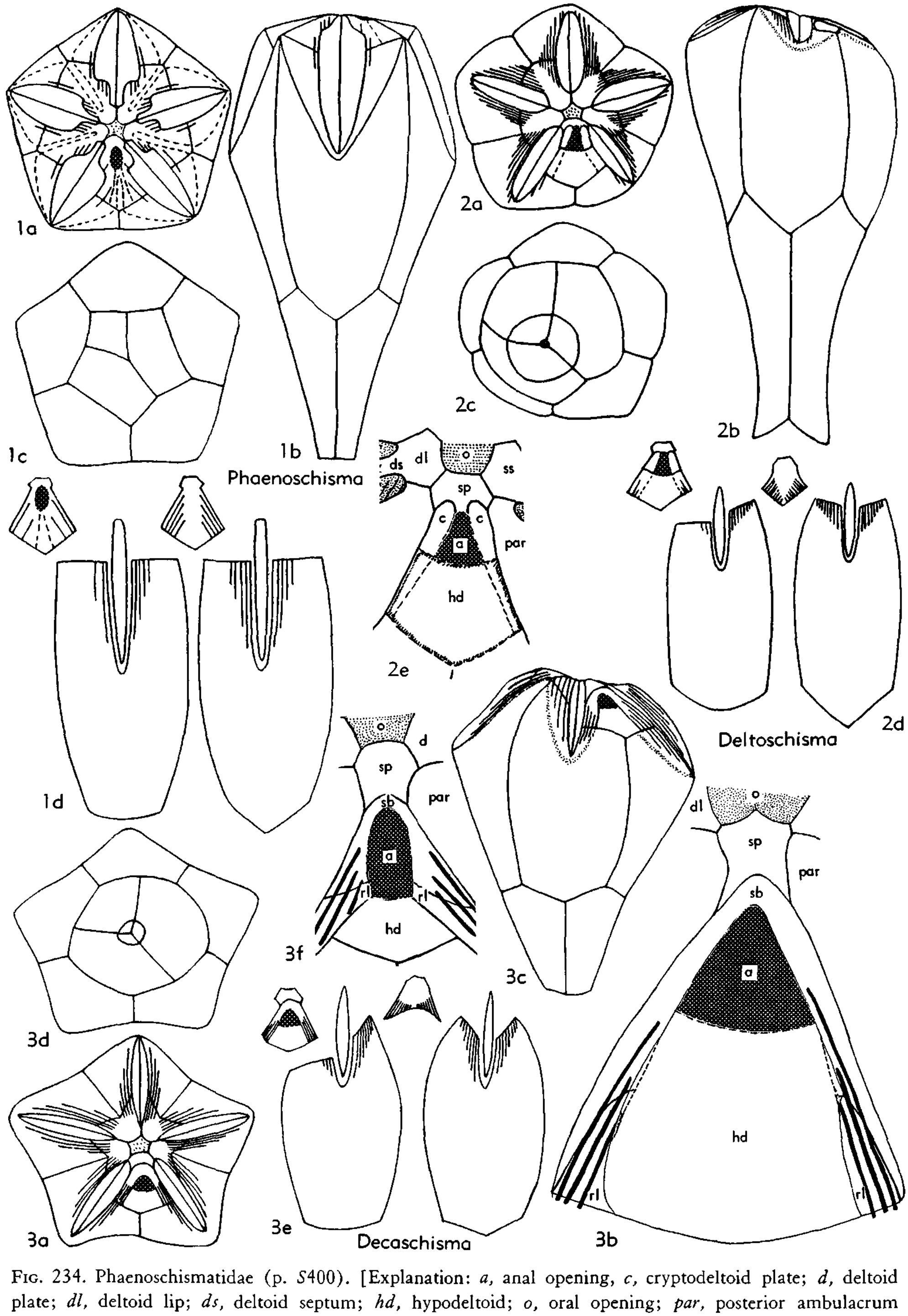


FIG. 234. Phaenoschismatidae (p. S400). [Explanation: *a*, anal opening, *c*, cryptodeltoid plate; *d*, deltoid plate; *dl*, deltoid lip; *ds*, deltoid septum; *hd*, hypodeltoid; *o*, oral opening; *par*, posterior ambulacrum (right); *rl*, radial limb; *sb*, subdeltoid plate; *sp*, superdeltoid plate.]

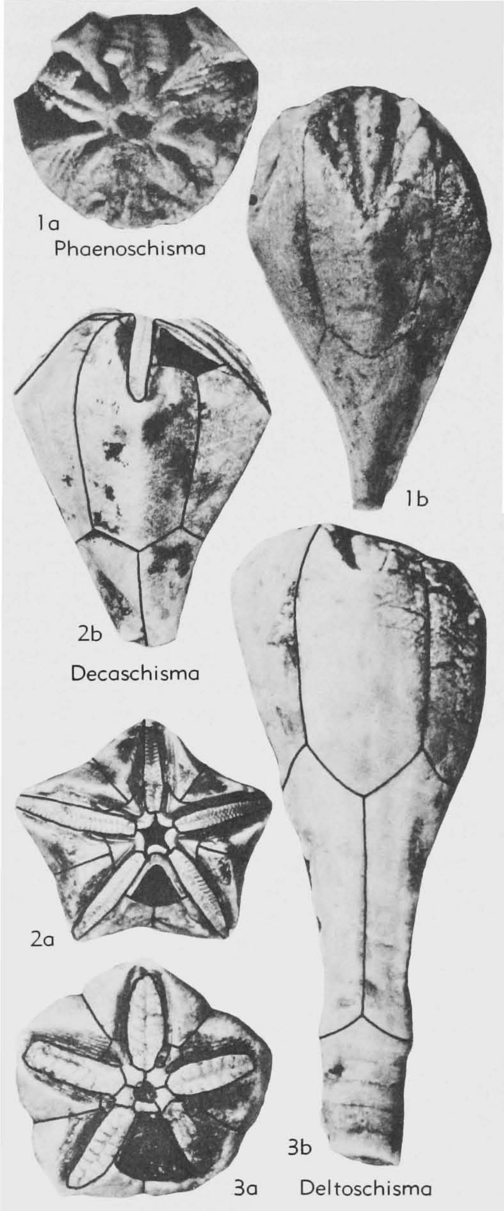


FIG. 235. Phaenoschismatidae (p. S400).

quately large scale. In this manner we may be able to fill in morphologic, stratigraphic, and geographic gaps in knowledge. A somewhat detailed account of previous classifications given in the introduction is not repeated here.

## Class BLASTOIDEA Say, 1825

[Blastoidea SAY, 1825, p. 313 (type, *Pentremites* SAY, 1820, designated by FAY, herein)] [=Eublastoidea BATHER, 1899, p. 920 (type, *Pentremites* SAY, 1820, designated by FAY, herein)]

Hydrospire-bearing, stemmed echinoderms; theca composed of 18 to 21 major plates, which comprise three basals, surmounted by five radials, above which and alternating with them are five deltoids, in addition to five lancet plates in radial position located within radial sinuses; anal side may contain one, two, three, four, or six anal deltoids; hydrospires external or internal; pores and spiracles present mainly in forms with internal hydrospires. Ambulacra bear numerous biserially constructed brachioles. *Sil.-Perm.*

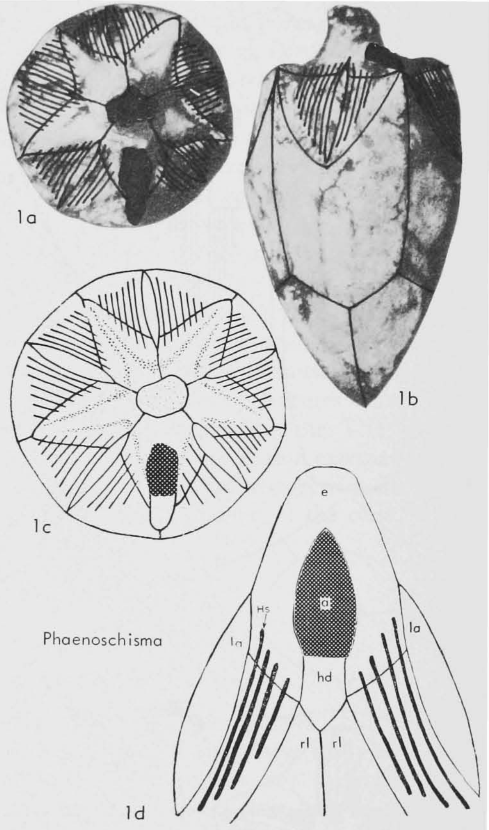


FIG. 236. Phaenoschismatidae (p. S400). [Explanation: *a*, anal opening; *e*, epideltoid plate; *hd*, hypodeltoid; *hs*, hydrospire slit; *la*, lancet plate; *rl*, radial limb.]

## Order FISSICULATA Jaekel, 1918

[Fissiculata Jaekel, 1918, p. 108 (type, *Phaenoschisma* Etheridge & Carpenter, 1882, designated by Fay, herein)] [=Mesoblastida Matsumoto, 1929, p. 28 (type, *Phaenoschisma* Etheridge & Carpenter, 1882, designated by Fay, herein)]

Theca with exposed hydrospire slits or spiracular slits. *Sil.-Perm.*

## Family PHAENOSCHISMATIDAE Etheridge & Carpenter, 1886

[*nom. correct.* Fay, 1961 (60), p. 19 (*pro* Phaenoschismidae Etheridge & Carpenter, 1886, p. 258)] [=Dipteroblastidae Wanner, 1940, p. 234; Neoschismidae (*recte* Neoschismatidae) Wanner, 1940, p. 238; Nymphaeoblastidae Wanner, 1940, p. 237]

Theca with ten exposed or partially exposed hydrospire fields. *Sil.-Perm.*

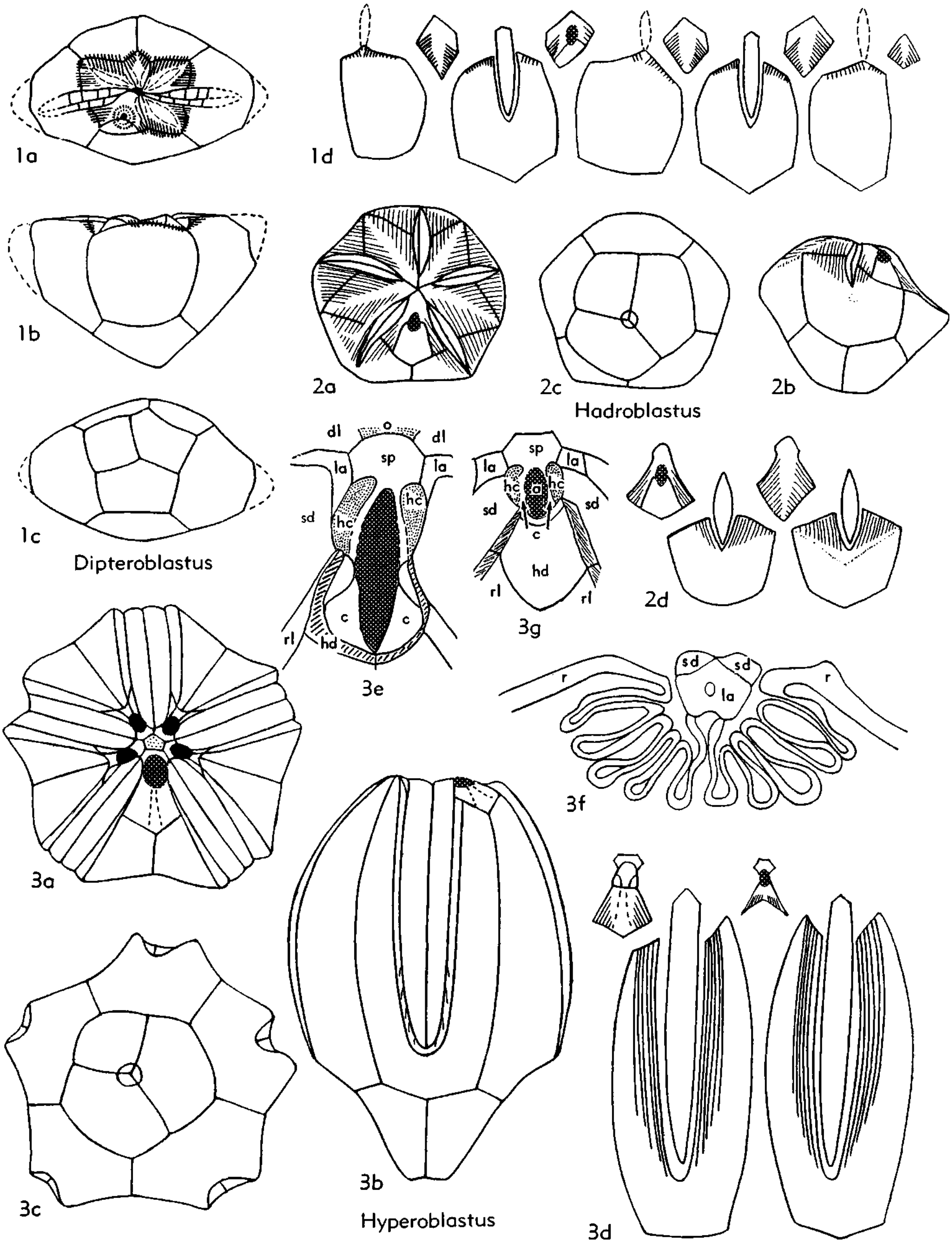


Fig. 237. Phaenoschismatidae (p. S400-S401). [Explanation: *a*, anal opening; *c*, cryptodeltoid plate; *dl*, deltoid lip; *hc*, hydrospire canal; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening; *r*, radial plate; *rl*, radial limb; *sd*, side plate; *sp*, superdeltoid plate.]

**Phaenoschisma** Etheridge & Carpenter, 1882, p. 226 [*emend.* Macurda, 1964 (104), p. 719] [**Pentatremaites acuta* Sowerby, 1834, p. 456; SD Etheridge & Carpenter, 1886, p. 270] [=*Conoschisma* Fay, 1961 (60), p. 23 (type, *Codaster laeviusculus* Rowley, 1900, p. 65)]. Theca biconical with hydrospire fields mostly hidden, but exposed along aboral ends or along outer ambulacral margins; number of hydrospire slits reduced on anal side; anus between epideltoid and hypodeltoid; lancet exposed along median 0.5 of its width; side plates touching deltoid crests, forming 5 teardrop-shaped spiracle-like openings at adoral end. *L.Carb.(Miss.)*, Eu.-N.Am.——Fig. 234,*1*; 235,*1*. **P. acutum* (Sowerby), Eng.; 234, *1a,b*, oral and *D*-ray views, ×4.5 (41); 234,*1c,d*, aboral view and plate layout, ×4.5 (162); 235, *1a,b*, oral and *C*-ray views, ×4, ×4.7 (104).——Fig. 236,*1*. *P. laeviusculum* Rowley, L.Miss. (Burlington Ls.), USA(Mo.); type species of *Conoschisma*, *1a,b*, oral and *D*-ray views, ×4.4 (60); *1c*, oral view, ×5.3 (60); *1d*, plates adjacent to anal opening, ×9 (60).

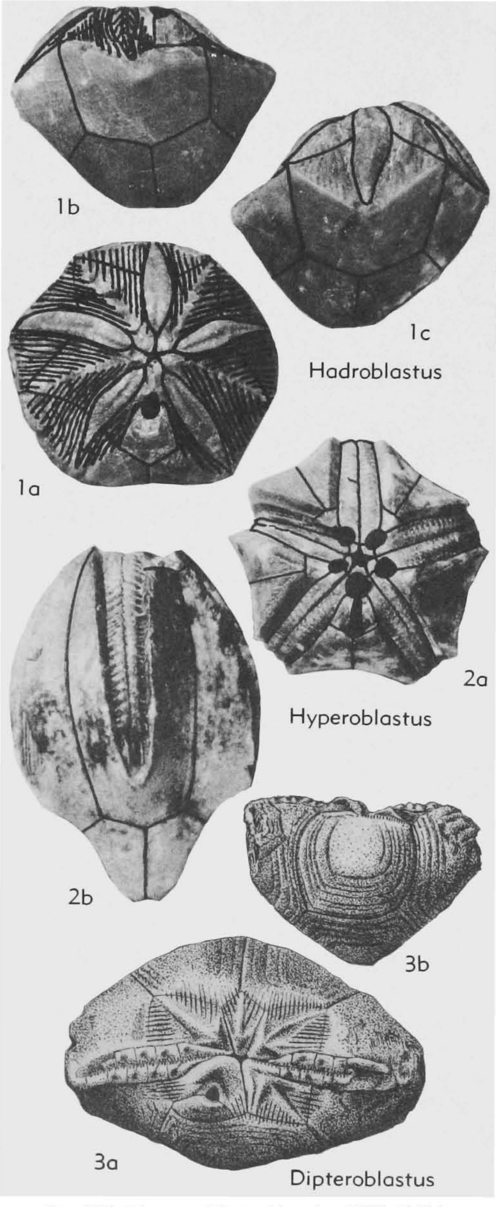


Fig. 238. Phaenoschismatidae (p. *S*400-*S*401).

**Decaschisma** Fay, 1961 (60), p. 27 [**Codaster pentalobus* Hall, 1879, p. 13; OD]. Theca obconical, with well-exposed hydrospire fields; superdeltoid, subdeltoid, and hypodeltoid present; lancet covered by side plates. *Sil.*, USA(Ind.).——Fig. 234,*3a-e*; 235,*2*. **D. pentalobus* (Hall), Niagaran; 234,*3a*, oral view, ×2.6; 234,*3b*, *CD* interray, ×10.1; 234,*3c*, *D*-ray view, ×2.6; 234, *3d,e*, aboral view and plate layout, ×2.7 (all 60); 235,*2a,b*, oral and *D*-ray views, ×2.5 (60).——Fig. 234,*3f*. *D. pulchellum* (Miller & Dyer), Niagaran; plates around anal opening, ×10 (60).

**Deltoschisma** Fay, 1961 (60), p. 29 [**Phaenoschisma archiaci* Etheridge & Carpenter, 1882, p. 229; OD]. Theca conical, with exposed hydrospire fields; strongly pentalobate in top view; with superdeltoid, 2 cryptodeltoids, and hypodeltoid, cryptodeltoids partly visible externally, partly hidden by hypodeltoid; number of slits reduced on anal side; lancet covered by large side plates. *Dev.*, Spain.——Fig. 234,*2*; 235,*3*. **D. archiaci* (Etheridge & Carpenter); 234,*2a-d*, oral, *D*-ray, aboral views, and plate layout, ×4.4; 234,*2e*, anal area, ×9.9; 235,*3a,b*, oral and *D*-ray views, ×4.7 (all 60).

**Dipteroblastus** Wanner, 1940, p. 249 [*emend.* Breimer & Macurda, 1965, p. 212] [**D. permicus*; OD]. Theca cup-shaped, with well-exposed hydrospire fields, with 8 to 13 hydrospire slits on *AB*, *BC*, and *DE* deltoids, but 3 to 6 on epideltoid, and 5 on *EA* deltoid; anus separate, between large epideltoid and large hypodeltoid; with 3 short *A*, *C*, and *E* ambulacra and 2 elongate *B* and *D* ambulacra confined to summit; lancet exposed along food groove. *Perm.*, E.Indies(Timor).——Fig. 237,*1*; 238,*3*. **D. permicus*; 237,*1a-d*, oral, *D*-ray, aboral views, and plate layout, ×1.7 (178); 238,*3a,b*, oral and C-ray views, ×2.7, ×1.7 (178).

**Hadroblastus** Fay, 1962 (72), p. 189 [**H. convexus*; OD]. Theca discoidal with rounded summit and base; hydrospire fields each with 11 slits except on anal side where 4 slits occur in each field; anal opening between large epideltoid and equally large hypodeltoid; lancet exposed along middle 0.3 of its width, raised well above broad flat sinus areas and hydrospire fields; ambulacra moderately long, linear, with lancet stipes moderately separated from oral opening; vault

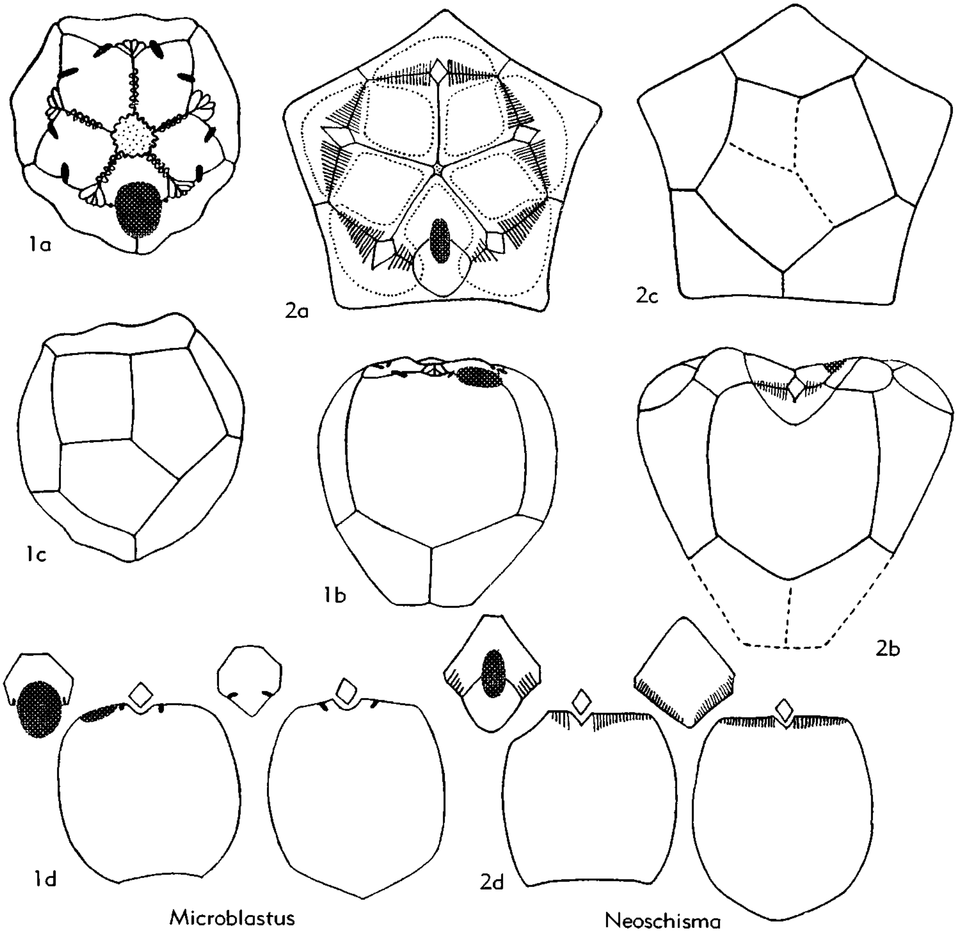


Fig. 239. Phaenoschismatidae (p. S401-S402).

almost equal to pelvic height; basalia large, composed of 3 basals. L.Miss., USA(N.Mex.-Ark.-Okla.).——Fig. 237,2; 238,1. *H. convexus, Osag., N.Mex.; 237,2a-d, oral, D-ray, aboral views, and plate layout, ×2 (72); 238,1a-c, oral, D-ray, and B-ray views, ×2.7 (72).

**Hyperoblastus** Fay, 1961 (60), p. 30 [*Pentremitidea preciosa Reimann, 1945, p. 39; OD]. Theca club-shaped, with aboral ends of outermost hydrospire slits exposed; with pores formed as gaps between side plates; spiracles 5, developed between deltoid lip, deltoid septum, lancet, and side plates on each interambulacrum (including anispiracle on anal side); with superdeltoid, 2 cryptodeltoids, and hypodeltoid; lancet covered by side plates. Dev., N.Am.——Fig. 237,3a-e; 238,2. *H. preciosus (Reimann), Can.(Ont.); 237,3a-d, oral, D-ray, aboral views, and plate layout, ×3.5; 237,3e, anal area, ×10; 238,2a,b, oral and D-ray views, ×2.9 (all 60).——Fig. 237,3f,g. H. filosus (Whiteaves), Can.(Ont.); 3f, cross sec. of ambulacrum, ×8.8; 3g, anal area, ×10.2 (all 60).

**Microblastus** Eykeren, 1942, p. 283 [*M. pocilloformis; OD]. Theca small, cup-shaped, with small restricted hydrospire slits confined to summit; anal opening separate from slits, between large, wide epideltoid and radial limbs, possibly with small ?hypodeltoid on aboral border; ambulacra short, wide, small, well away from mouth, with total of 2 or 3 side plates on each side. Perm., E.Indies (Timor).——Fig. 239,1; 240,1. *M. pocilloformis; 239,1a-d, oral, D-ray, aboral views, and plate layout, ×8.8 (42); 240,1a,b, oral and CD-interray views, ×6 (42).

**Neoschisma** Wanner, 1924 (173), p. 6 [*N. verrucosum; OD]. Theca cup-shaped, with widely exposed hydrospire fields, each with 5 to 18 slits except on anal side where 1 to 5 slits occur on each side of anal opening; anal opening between

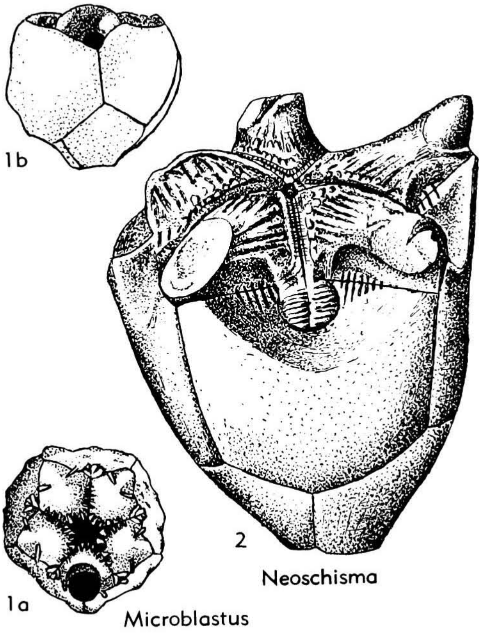


Fig. 240. Phaenoschismatidae (p. S401-S402).

large epideltoid and moderately large hypodeltoid; ambulacra short, wide, small, well away from mouth, confined to summit. *Perm.*, E.Indies (Timor).——Fig. 239,*2*. **N. verrucosum*; *2a-d,* oral, *D*-ray, aboral views, and plate layout, ×2.4 (173).——Fig. 240,*2*. *N. timorense* Wanner, Perm., Timor; *B*-ray view, ×3.3 (178).

**Notoblastus** Brown, 1941, p. 98 [**N. brevispinus*; OD]. Theca discoidal, with widely exposed hydrospire fields, each with 12 to 14 hydrospire slits except on anal side, where slits are few; small anus separate, between large epideltoid and smaller hypodeltoid; ambulacra moderately short, longer than wide, with lancet stipe well away from mouth; radials prolonged into small, short, winglike processes; stem seemingly absent. *Perm.*, E.Australia.——Fig. 241,*4*; 242,*3*. **N. brevispinus*; 241,*4a,b,* oral and *C*-ray views, ×1.3; 242,*3a-d,* oral, *D*-ray, aboral views, and plate layout, ×1.3 (20, 179).

**Nymphaeoblastus** von Peetz, 1907, p. 15 [**N. miljukovi*; OD]. Theca ellipsoidal, with widely exposed hydrospire fields, each containing 10 to 15 slits which extend well down sides of theca; anal opening between small epideltoid and elongate hypodeltoid; lancet apparently covered by side plates; ambulacra long, linear, recurved below; base concave; deltoids almost as long as radials. *L.Carb.*, Eu.(USSR)-Asia(Japan).——Fig. 241,*1*. *N. anossofi* Yakovlev, Tournais., Japan; *1a,b,* oral and E-ray views, ×1.3 (52).——Fig. 242,*1*. **N. miljukovi,* USSR; *1a-d,* oral, *D*-ray, aboral views, and plate layout, ×0.8 (131, 190).

**Phaenoblastus** Fay, 1961 (60), p. 40 [*emend.* Macurda, 1964 (104), p. 723] [**Pentremites*

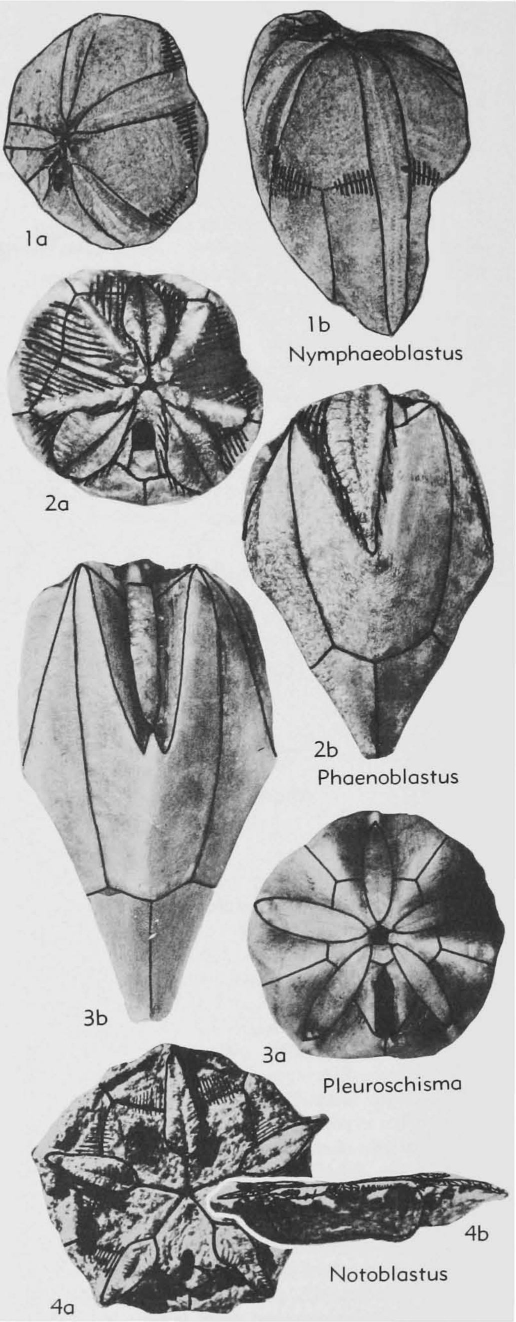


Fig. 241. Phaenoschismatidae (p. S402-S405).

*caryophyllatus* deKoninck & LeHon, 1854, p. 197; OD]. Theca club-shaped with ventral coronal processes; hydrospire fields wide, deeply indented, mostly hidden, each with 7 or 8 slits except on anal side where 4 occur; anal opening between large U-shaped epideltoid and small hypodeltoid; lancet widely exposed throughout its full width, deeply excavated in sinus; side plates large, covering most of slits, adorally forming 4 paired spiracle-like openings and false anispiracle with deltoid crests; ambulacra moderately long, petaloid; vault almost equal to pelvic height; basalia moderately large, composed of 3 basals; radials overlapping deltoids. *L.Carb.*, Eu.——Fig. 241,*2*; 242,*2*. **P. caryophyllatus* (deKoninck & LeHon), Tournais., Belg.; 241,*2a,b*, oral, *D*-ray views,

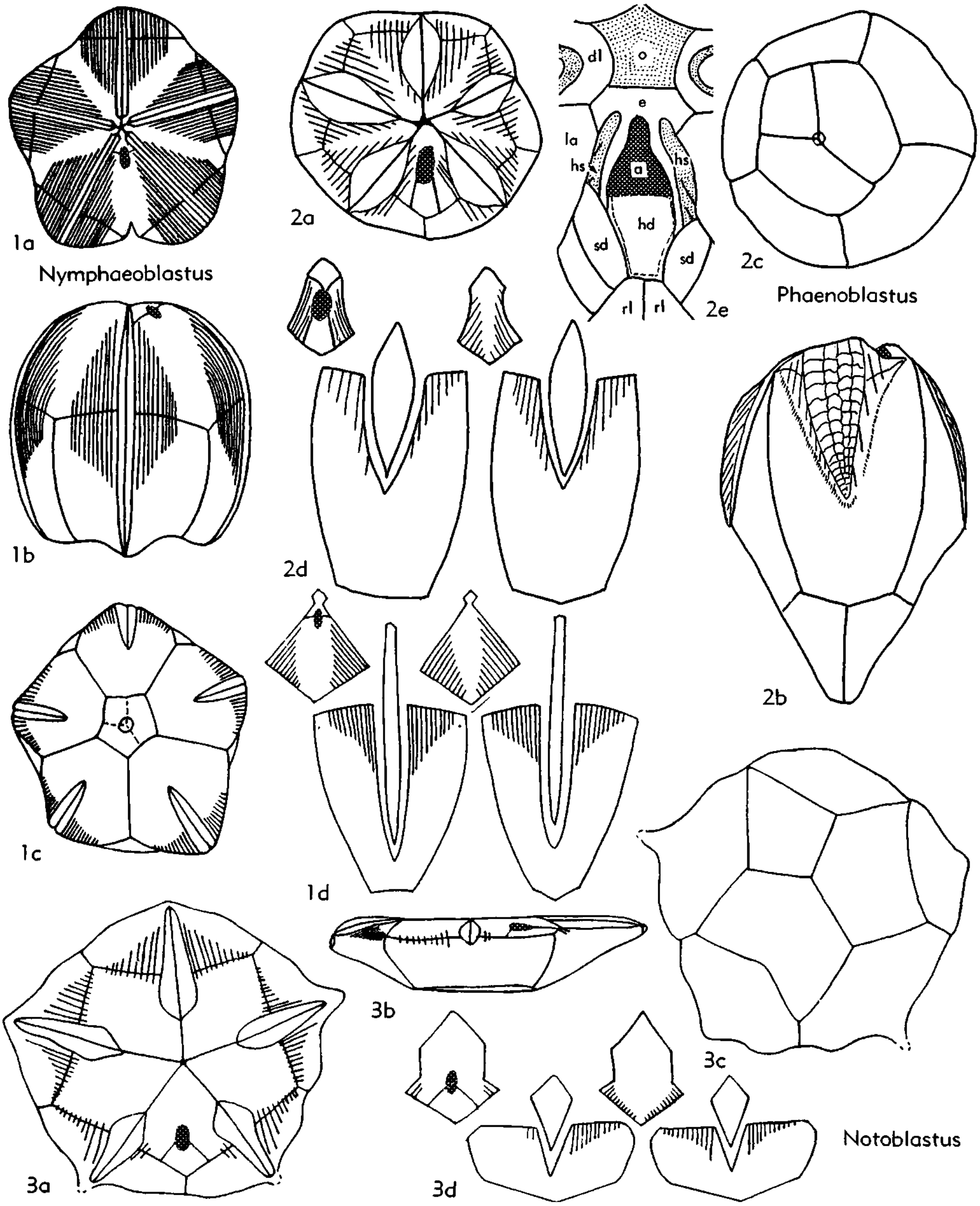


Fig. 242. Phaenoschismatidae (p. *S*402-*S*404). [Explanation: *a*, anal opening; *dl*, deltoid lip; *e*, epideltoid plate; *hd*, hypodeltoid; *hs*, hydrospire slit; *la*, lancet plate; *o*, oral opening; *rl*, radial limb; *sd*, side plate.]

×4; 242,*2a-d,* oral, *D*-ray, aboral views, plate layout, ×4; 242,*2e,* anal view, ×10 (60).

**Pleuroschisma** Reimann, 1945, p. 24 [**Pentremites lycorias* Hall, 1862, p. 151; OD]. Theca club-shaped, with exposed hydrospire fields; superdeltoid, 2 exposed cryptodeltoids, and hypodeltoid present; ambulacra extending downward along theca; lancet completely covered by side plates. *Dev.,* USA(N.Y.)-Can.(Ont.).——Fig. 241,*3*; 243,*1e*. *P. ontario* Reimann, M.Dev., Can.(Ont.); 241,*3a,b,* oral, *D*-ray views, ×6.2; 243,*1e,* anal area, ×10.2 (60).——Fig. 243,*1a-d*. **P. lycorias*

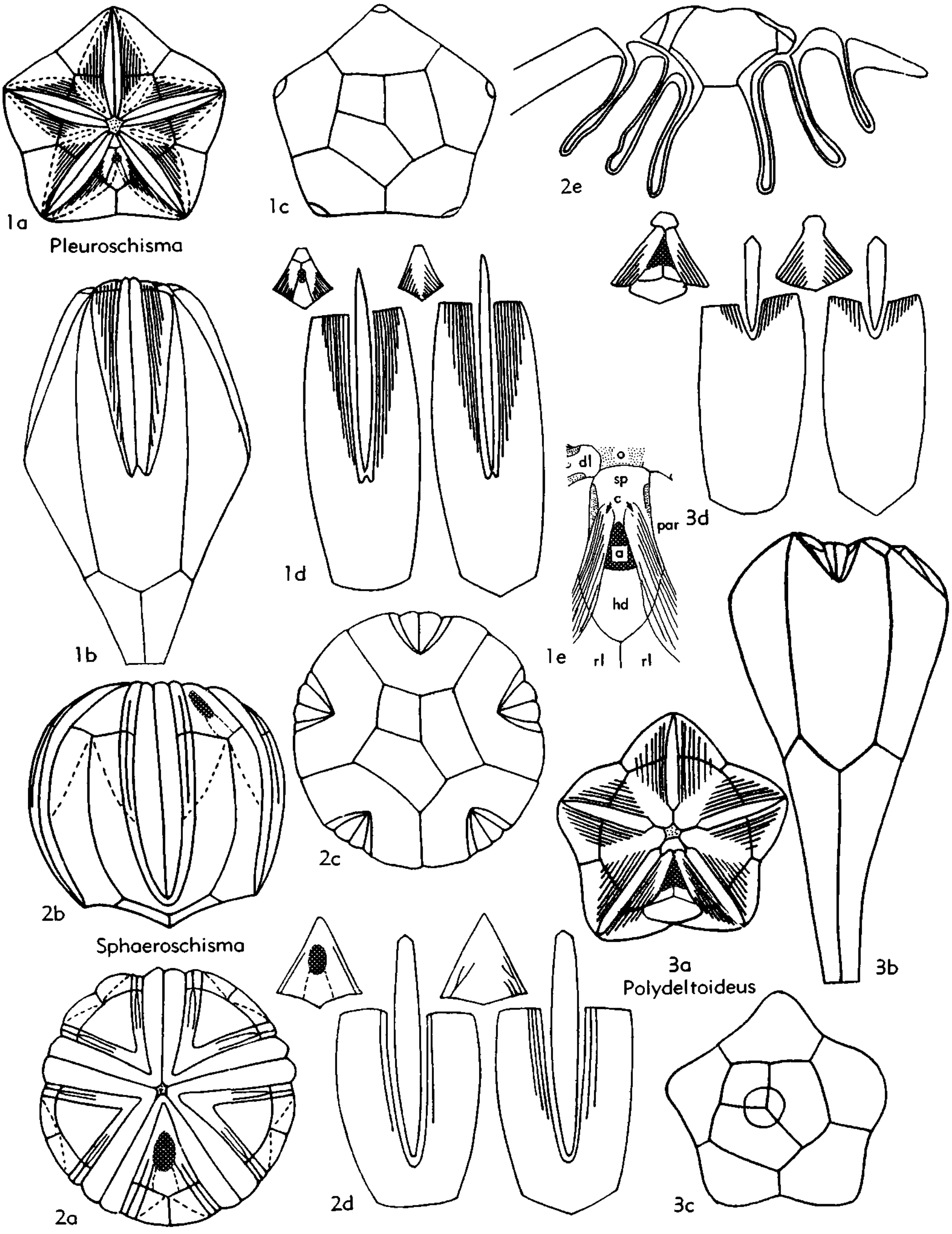


Fig. 243. Phaenoschismatidae (p. *S*404-*S*405). [Explanation: *a,* anal opening; *c,* cryptodeltoid plate; *dl,* deltoid lip; *hd,* hypodeltoid; *o,* oral opening or oral plate; *par,* posterior ambulacrum (right); *rl,* radial limb; *sp,* superdeltoid plate.]

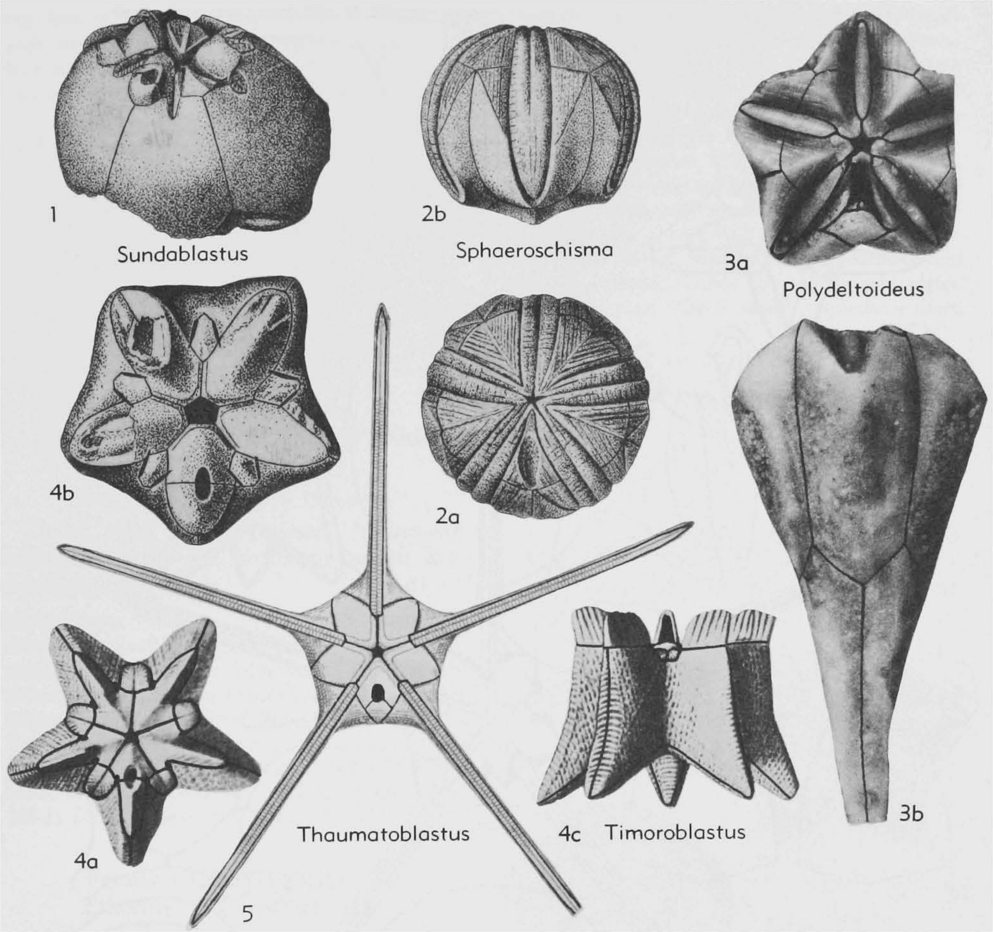


FIG. 244. Phaenoschismatidae (p. *S*405-*S*407).

(HALL), M.Dev., USA(N.Y.); *1a-d,* oral, *D*-ray, aboral views, and plate layout, ×4.4 (83, 139).

**Polydeltoideus** REIMANN & FAY, 1961, p. 86 [**Polydeltoideus enodatus*; OD]. Conical theca with exposed hydrospire fields; superdeltoid, 2 cryptodeltoids, 2 paradeltoids, and hypodeltoid present; ambulacra short, projected laterally, with broad sinuses; lancet covered by side plates; anal opening between superdeltoid, 2 cryptodeltoids, and 2 paradeltoids. *Sil.,* USA(Okla.)-?Czech.——FIG. 243,*3*; 244,*3*. **P. enodatus,* Sil., Okla.; 243,*3a-d,* oral, *D*-ray, aboral views, and plate layout, ×3 (143); 244,*3a,b,* oral, *D*-ray views, ×3 (143).

**Sphaeroschisma** WANNER, 1924 (174), p. 195 [*emend.* BREIMER & MACURDA, 1965, p. 212] [**S. somoholense*; OD]. Theca subglobular, fissiculate with 10 partially exposed hydrospire fields, with 1 to 3 folds per field, partially formed into spiracular slits; one fold is on both sides of *C* ambulacrum and on posterior side of *D* ambulacrum; 2 folds are on left side of *A* ambulacrum and anterior side of *B* ambulacrum, each opening into a spiracular slit; all other hydrospire fields have 3 folds, opening into single spiracular slit on radial limb and into 2 slits on deltoid; anal opening between epideltoid and ?hypodeltoid; deltoids overlap radials; deltoids and slits visible in side view; lancet exposed; ambulacra long, recurved below. *Perm.,* E.Indies(Timor).——FIG. 243,*2*; 244,*2*. **S. somoholense*; 243,*2a-d,* oral, *D*-ray, aboral views, and plate layout, ×3.6; 243,*2e,* cross sec. of *E* ambulacrum, ×13; 244, *2a,b,* oral, *A*-ray views, ×2.7 (174).

**Sundablastus** WANNER, 1924 (173), p. 32 [**S. weberi*; OD]. Theca subglobular, with small restricted hydrospire fields confined to summit; anal opening between large epideltoid and large hypodeltoid; ambulacra short, confined to summit, adjacent to mouth; lancet longer than wide, short, apparently covered by side plates; basals

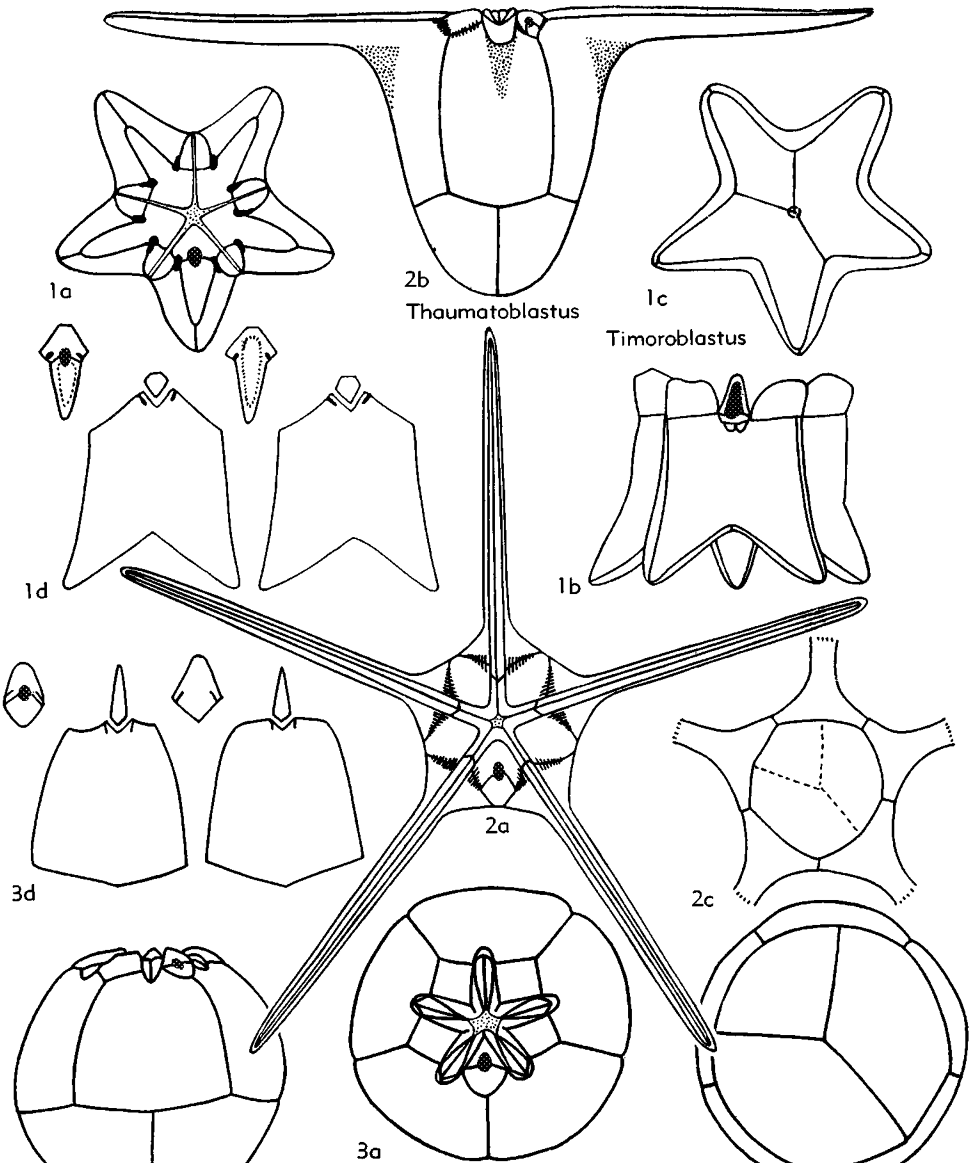


Fig. 245. Phaenoschismatidae (p. S405-S407).

almost equal in size to radials. *Perm.*, E.Indies (Timor).——Fig. 244,*1*; 245,*3*. **S. weberi*; 244,*1*, oblique *C*-ray view, ×1.3; 245,*3a-d*, oral, *D*-ray, aboral views, and plate layout, ×1.18 (173).

**Thaumatoblastus** Wanner, 1924 (174), p. 201 [**T. longiramus*; OD]. Theca cup-shaped, with widely exposed hydrospire fields; anal opening between large epideltoid and large hypodeltoid; slits reduced in number on anal side, but 7 or 8 slits occur in each field of other interambulacra; lancet plates long, extending into winglike extensions of radials; lancets almost completely covered by side plates; base round, summit flat. *Perm.*, E.Indies (Timor).——Fig. 244,*5*; 245,*2*. **T. longiramus*; 244,*5*, oral view, ×0.4; 245,*2a-c*, oral, *D*-ray, aboral views, ×0.44 (174).

**Timoroblastus** Wanner, 1924 (173), p. 14 [**T. coronatus typus*; OD]. Theca star-shaped, with small constricted hydrospire fields confined to summit, each with 1 to 3 hydrospire slits opening into it; one hydrospire slit on each side of anal opening; anus between wide epideltoid and long hypodeltoid; ambulacra short, wide, rounded aborally, well away from mouth; lancet covered by side plates; deltoids and radial limbs flaring outwardly into bluntly rounded winglike processes, with ambulacra in depressed areas between; deltoids projected ventrally into coronal processes; radials projected dorsally into alate processes; base concave. *Perm.*, E.Indies(Timor).——Fig. 244, *4a,c*; 245,*1*. **T. coronatus typus*; 244,*4a,c*, oral, *A*-ray views, ×1.7; 245,*1a-d*, oral, *D*-ray, aboral views, plate layout, ×1.7 (173).——Fig. 244, *4b*. *T. coronatus tesselatus* Wanner, Perm., Timor; oral view, ×2 (173).

## Family BRACHYSCHISMATIDAE Fay, 1961

[Brachyschismatidae Fay, 1961 (60), p. 19]

Theca with nine exposed hydrospire fields; slits atrophied or absent on left side of anal opening. *Dev.*

**Brachyschisma** Reimann, 1945, p. 22 [**Codaster corrugatus* Reimann, 1935, p. 25; OD]. Theca conical, with hydrospire fields well exposed; superdeltoid, subdeltoid, and hypodeltoid present; lancet covered by side plates. *M.Dev.*, USA(N.Y.).——Fig. 246,*1*. **B. corrugatum* (Reimann); *1a-c*, plate layout, aboral, *D*-ray views, ×2.3; *1d*, oral view, ×2.2; *1e*, *C*-ray view, ×2.5; *1f*, oral view, ×2.3; *1g*, anal view, ×8.7 (60, 137, 139).

## Family CODASTERIDAE Etheridge & Carpenter, 1886

[Codasteridae Etheridge & Carpenter, 1886, p. 257]
[=Angioblastidae Wanner, 1940, p. 235]

Theca with eight exposed or constricted hydrospire fields; hydrospire slits lacking on anal side. *Dev.-Perm.*

**Codaster** M'Coy, 1849, p. 250 [**C. acutus*; OD]. Theca conical, with flat summit and rounded base; hydrospire fields well exposed; epideltoid and ?hypodeltoid present; lancet stipe away from mouth; lancet covered by side plates; radials overlapping deltoids. *L.Carb.*, Eu.(Eng.).——Fig. 247,*3*; 248,*1*. **C. acutus*; 247,*3a-d*, oral, *D*-ray, aboral views, plate layout, ×2.2; 248,*1a,b*, oral, *D*-ray views, ×2.1 (10, 41, 60, 100).

**Agmoblastus** Fay, 1961 (59), p. 278 [**Paracodaster dotti* Moore & Strimple, 1942, p. 90; OD]. Form subcylindrical; hydrospire fields moderately exposed, each with 4 to 8 slits excavated in radials and deltoids, slits absent on anal side; anal opening between large U-shaped epideltoid and adjacent radial limbs, or possibly with small hypodeltoid on aboral side (atrophied or ?washed away); deltoids high, wide, arrow-shaped; ambulacra short, well away from oral opening; basals 3, large; lancet covered by side plates. *Penn.*, N.Am.——Fig. 247,*1*; 248,*2*. **A. dotti* (Moore & Strimple), USA(Okla.); 247,*1a-d*, oral, *C*-ray, aboral views, plate layout, ×3.7; 248,*2a,b*, oral, *C*-ray views, ×4.2 (59).

**Angioblastus** Wanner, 1931, p. 53 [**A. variabilis*; OD]. Theca subglobular, with small restricted hydrospire fields confined to summit, with 1 to 4 hydrospire slits in each field; anal opening separate from slits, located between long epideltoid and short hypodeltoid; lancet covered by side plates, with lancet stipe close to mouth; ambulacra short,

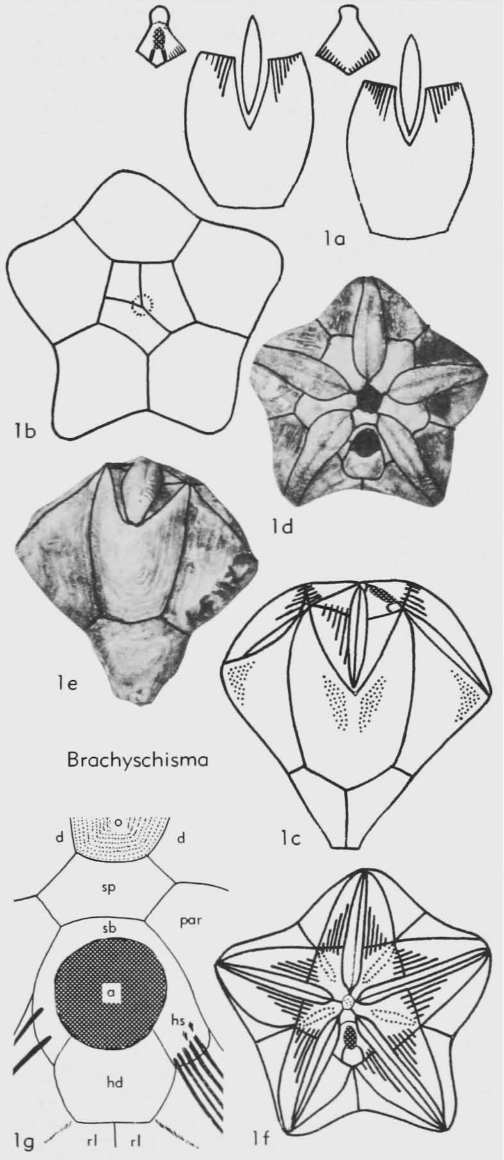


Fig. 246. Brachyschismatidae (p. S407). [Explanation: *a*, anal opening; *d*, deltoid plate; *hd*, hypodeltoid; *hs*, hydrospire slit; *o*, oral opening; *par*, posterior ambulacrum (right); *rl*, radial limb; *sb*, subdeltoid plate; *sp*, superdeltoid plate.]

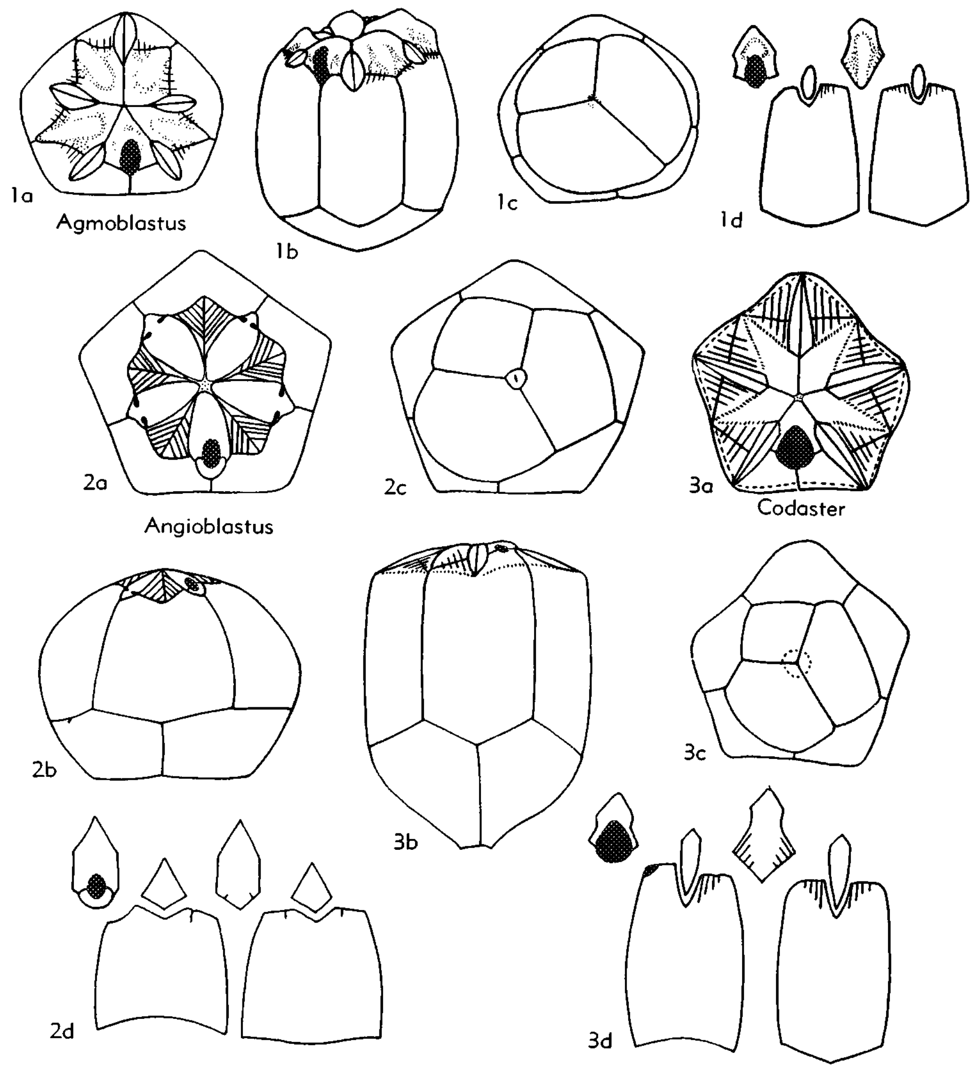


Fig. 247. Codasteridae (p. *S*407-*S*408).

wide, confined to summit; deltoids elongate, narrow. *Perm.*, E.Indies(Timor).——Fig. 247,*2*; 249, *6*. **A. variabilis*; 247,*2a-d*, oral, *D*-ray, aboral views, plate layout, ×3.6; 249,*6a,b*, oral, *CD*-interray views, ×4 (175).

**Heteroschisma** Wachsmuth, 1883, p. 352 [**H. gracile*; OD] [=*Trionoblastus* Fay, 1961 (60), p. 45 (type, *Pentremites subtruncatus* Hall, 1858, p. 485)]. Theca obconical with hydrospire fields well exposed; superdeltoid, subdeltoid, and presumably small ?hypodeltoid on anal side; hydrospire slits absent on anal side; lancet covered by side plates. *Dev.*, N.Am.——Fig. 248,*3a,b*; 250, *1h*. **H. gracile*, M.Dev., USA(Mich.); 248,*3a,b*, *D*-ray view, oral view, ×3.5; 250,*1h*, anal area, ×9.7 (60).——Fig. 250,*1a-e*. *H. subtruncatus* (Hall), USA(Iowa); *1a-d*, oral, *D*-ray, aboral views, plate layout, ×4.4; *1e*, anal view, ×9.7 (60).——Fig. 250,*1f*. *H. pyramidatus* (Shumard), M.Dev., USA(Ohio); anal area, ×7.3 (60).——Fig. 250,*1g*. *H. canadense* (Billings); M.Dev., Can.(Ont.); anal area, ×9.7 (60).

**Indoblastus** Wanner, 1924 (174), p. 28 [*emend.* Breimer & Macurda, 1965, p. 212] [**I. granulatus*; OD]. Theca pear- to cup-shaped, with small restricted hydrospire fields confined to summit; anal opening between large epideltoid and equally large raised hypodeltoid; ambulacra moderately long, mostly confined to summit; lancet covered by side plates, with lancet stipe well away from mouth. *Perm.*, E.Indies(Timor).——Fig. 249,*2*; 250,*2*. **I. granulatus*; 249,*2a,b*, oral, *D*-ray views, ×2,

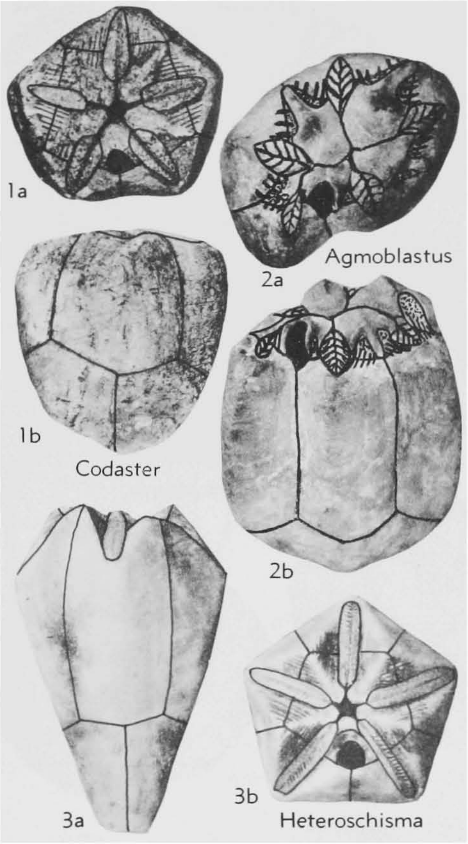


FIG. 248. Codasteridae (p. S407-S408).

×1; 250,*2a-d,* oral, *D*-ray, aboral views, plate layout, ×1.18 (173, 178).

**Nannoblastus** Wanner, 1924 (173), p. 24 [**N. pyramidatus*; OD]. Theca widely conical to cup-shaped, with small, short, restricted hydrospire fields confined to flat summit, appearing as 8 small slits; anus separate from slits, located between large epideltoid and small hypodeltoid; lancet covered by 2 or 3 side plates, short, wide, well away from mouth, confined to summit; with small, rounded radial wings. *Perm.,* E.Indies (Timor).——Fig. 249,*1*; 250,*3*. **N. pyramidatus*; 249,*1a-c,* oral view, ×6, oral, *CD*-interray views, ×3.1; 250,*3a-d,* oral, *D*-ray, aboral views, plate layout, ×5.9 (174, 175).

**Paracodaster** Yakovlev, 1940, p. 887 [**P. miloradovitschi*; OD]. Theca subglobular, with moderately exposed hydrospire fields confined to deltoids proper; hydrospire slits absent in anal area; anal opening between large epideltoid and radial limbs, with possible small ?hypodeltoid present; slits and ambulacra short, confined to summit; lancet stipes well away from mouth. *L.Perm.,* Eu. (USSR).——Fig. 249,*4*; 251,*3*. **P. miloradovitschi*; 249,*4*, oral view, ×2; 251,*3a-d,* oral, *D*-ray, aboral views, plate layout, ×1.75 (186, 190).

**Pterotoblastus** Wanner, 1924 (173), p. 9 [**P. gracilis*; OD]. Theca cup-shaped, with moderately exposed to restricted hydrospire fields, each with 2 or 3 wide hydrospire slits; large epideltoid with small anal opening between it and radial limbs, possibly with small ?hypodeltoid; ambulacra moderately short, extended on long winglike projections of radials; lancet well away from oral opening, covered by few large side plates; with 3 basal plates. *Perm.,* E.Indies(Timor).——Fig. 249,*3*; 251,*2*. **P. gracilis*; 249,*3a,* oral view, ×8.2; 249,*3b, CD*-interray, ×2.5; 251,*2a-d,* oral, *D*-ray, aboral views, plate layout, ×1.1 (173, 175).

**Sagittoblastus** Yakovlev, 1937, p. 10 [**Timoroblastus wanneri* Yakovlev, 1926, p. 54; OD]. Theca globular, with small, deep, restricted hydrospire fields on summit, each with 2 or 3 hydrospire slits; deltoids arrow-shaped, wide; large epideltoid, with small anal opening between it and radial limbs, possibly with small ?hypodeltoid (missing) on aboral side of anal opening; with extremely short lancet covered by side plates; lancet well away from mouth. *Perm.,* Eu. (USSR).——Fig. 249,*5*; 251,*1*. **S. wanneri* (Yakovlev); 249,*5*, oral view, ×3.5; 251,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×3.5 (184, 185, 190); 251,*1e,* anal view, ×10 (60).

## Family OROPHOCRINIDAE Jaekel, 1918

[Orophocrinidae Jaekel, 1918, p. 109] [=Anthoblastidae Wanner, 1940, p. 237] [=Pentablastidae Sieverts-Doreck, 1951, p. 113]

Theca with ten elongate spiracular slits bordering ambulacra. *Miss.-Perm.*

**Orophocrinus** von Seebach, 1864, p. 110 [*emend.* Macurda, 1965 (106), p. 1053] [**Pentremites stelliformis* Owen & Shumard, 1850, p. 67; OD] [=*Codonites* Meek & Worthen, 1869, p. 84 (*nec* Audouin, 1826) (type, *Pentremites stelliformis* Owen & Shumard); *Mitra* Cumberland, 1826, *partim,* p. 31 (*non* Martyn, 1784; *nec* Bolten, 1798; Lamarck, 1798; Lesson, 1837; Albers, 1850) (type, *Mitra vera* Cumberland, 1826)]. Theca conical to club-shaped, with 4 to 11 hydrospire slits opening into each spiracular slit; anal opening separate from slits, between epideltoid and hypodeltoid; lancet exposed along main food groove, with lenticular outer side plates between primary side plates, rarely touching abmedial ambulacral margins; thickened radials and deltoids beneath lancet on admedial side of spiracular slits, being termed sublancet or fused hydrospire plate (actually not a separate plate); radials overlap deltoids. *L.Carb.(Miss.),* Eu.-N. Am.——Fig. 252,*2*; 253,*2*. **O. stelliformis* (Owen & Shumard), L.Miss., Iowa; 252,*2a,b,* oral, *D*-ray views, ×1.68 (60); 253,*2a-d,* oral, *D*-ray,

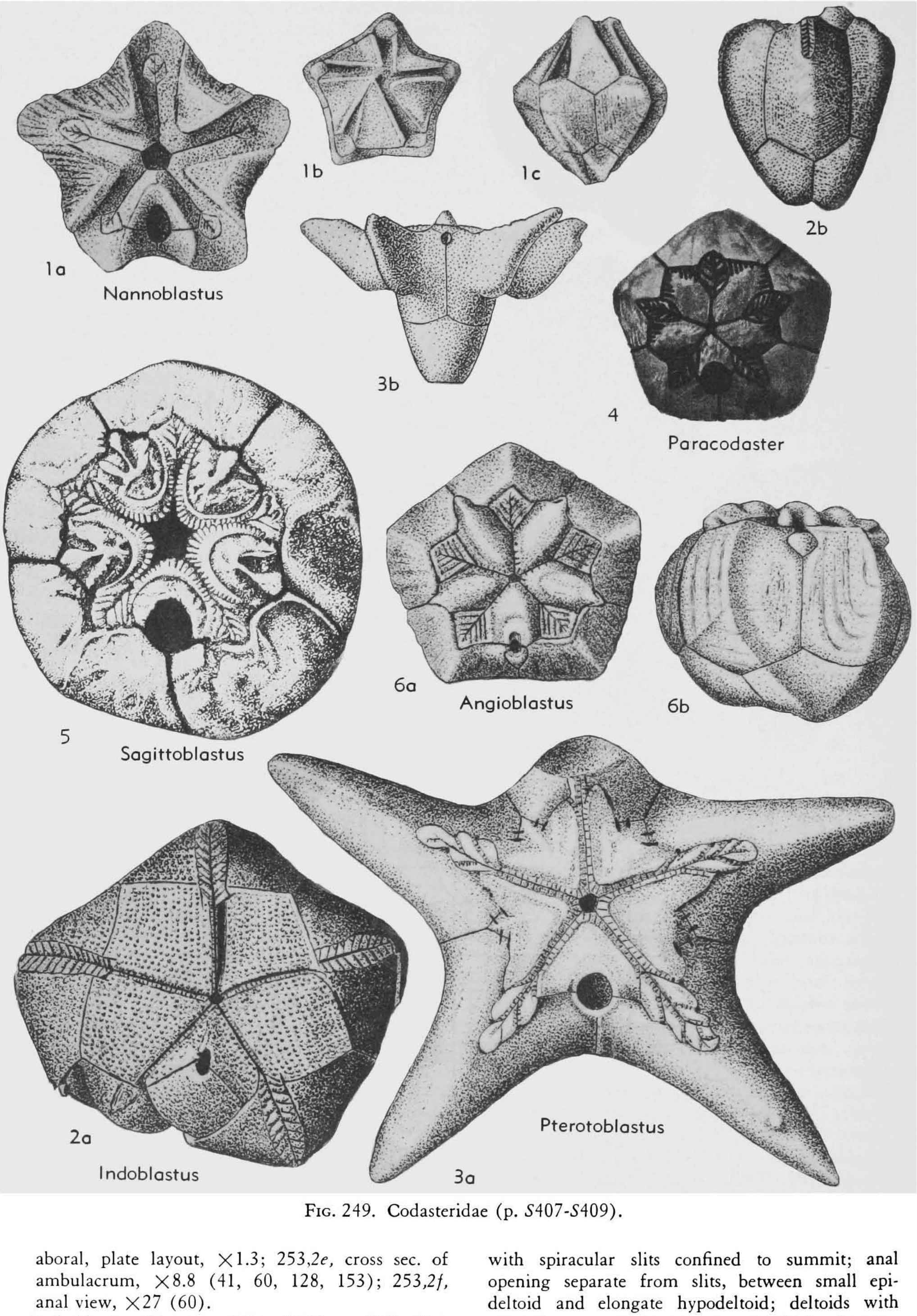


FIG. 249. Codasteridae (p. S407-S409).

aboral, plate layout, ×1.3; 253,*2e,* cross sec. of ambulacrum, ×8.8 (41, 60, 128, 153); 253,*2f,* anal view, ×27 (60).

**Anthoblastus** WANNER, 1924 (174), p. 205 [**A. brouweri*; OD]. Theca conical to club-shaped, with spiracular slits confined to summit; anal opening separate from slits, between small epideltoid and elongate hypodeltoid; deltoids with coronal processes; lancet exposed widely, forming petaloid ambulacra, which extend downward along theca. *Perm.*, E.Indies(Timor).——Fig. 252, *1*; 253,*1*. **A. brouweri*; 252,*1a,b,* oral, *CD*-interray views, ×1.68; 253,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×2.4 (174).

**Pentablastus** Sieverts-Doreck, 1951, p. 113 [**P. supracarbonicus*; OD]. Theca subglobular, with short spiracular slits confined to summit; anal opening separate from slits, which appear to

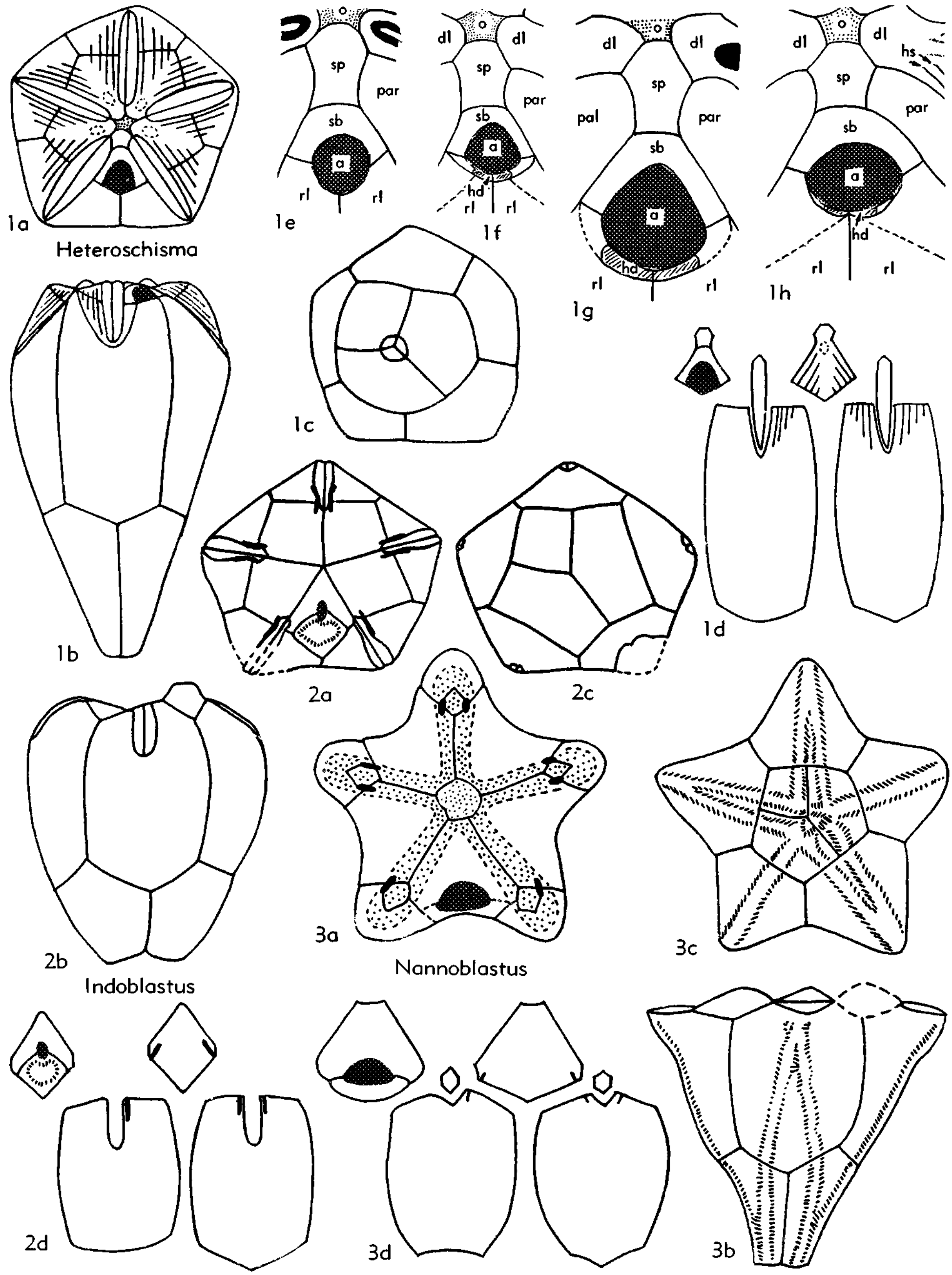


Fig. 250. Codasteridae (p. *S*408-*S*409). [Explanation: *a,* anal opening; *dl,* deltoid lip; *hd,* hypodeltoid; *hs,* hydrospire slit; *o,* oral opening; *pal,* posterior ambulacrum (left); *par,* posterior ambulacrum (right); *rl,* radial limb; *sb,* subdeltoid plate; *sp,* superdeltoid plate.]

terminate in hypodeltoid; anal opening between short epideltoid and long hypodeltoid; hydrospire folds 5 or 6 on each side of an ambulacrum; lancet covered by side plates, linear, slightly recurved below; lancet stipe near mouth; deltoids short, confined to summit; base concave. *U.Carb.*, Spain. ——Fig. 252,*3*; 253,*3*. *_P. supracarbonicus_; 252, *3a,b,* oral, *C*-ray views, ×1.14; 253,*3a-d,* oral,

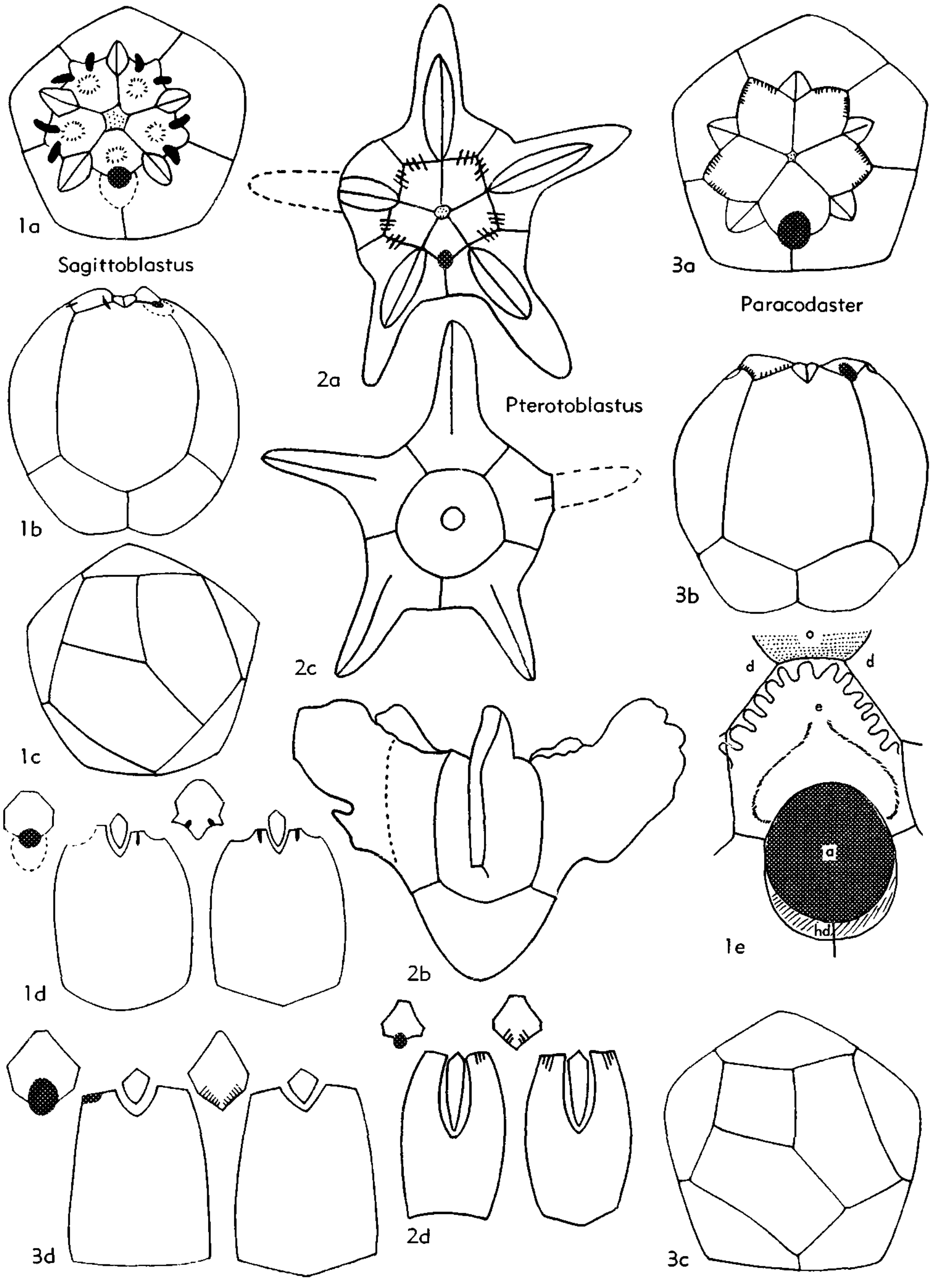


Fig. 251. Codasteridae (p. *S*409). [Explanation: *a,* anal opening; *d,* deltoid plate; *e,* epideltoid plate; *hd,* hypodeltoid; *o,* oral opening.]

*D*-ray, aboral views, and plate layout, ×1.3; 253,*3e*, cross sec. of ambulacrum, ×4.4 (159).

## Family ASTROCRINIDAE Austin & Austin, 1843

[*nom. correct.* Etheridge & Carpenter, 1886, p. 297 (*pro* Astracrinidae Austin & Austin, 1843, p. 205)] [=Pentephyllidae, Zygocrinidae Bather, 1899, p. 920]

Theca with eight spiracular slits along margins of ambulacra; anal side lacking slits. *Dev.-Perm.*

**Astrocrinus** Morris, 1843, p. 49 [**A. tetragonus* Morris, 1843, p. 42 (=*Astrocrinites tetragonus* Austin & Austin, 1843, p. 206, *nom. nud.*); OD] [=*Astracrinites* Austin & Austin, 1842, p. 110 *(nom. nud.)*; *Astracrinites* Austin & Austin, 1843, p. 205 (invalid original spelling); *Astrocrinites* Austin & Austin, 1843, p. 206 (*non* Conrad, 1841, *nec* Mather, 1843, *nec* de Koninck, 1854); *Zygocrinus* Bronn, 1848, p. 1381 (type, *Astracrinites tetragonus*)]. Theca flattened star-shaped, small; epideltoid present, with possible hypodeltoid; ambulacrum *D* short, wide; lancet covered by side plates; single basal plate; theca spinose. *L.Carb.*, Eu.(Eng.-Scot.).——Fig. 254,*3*. **A. tetragonus*, Eng.; *3a-d*, oral, *D*-ray, aboral views, and plate layout, ×5.3 (41).——Fig. 255,*1*. *A. benniei* (Etheridge), L.Carb., Scot.; *1a*, oral view, ×13.8; *1b*, *D*-ray view, ×14.3; *1c*, aboral view, ×14.5 (177).

**Ceratoblastus** Wanner, 1940, p. 245 [*emend.* Breimer & Macurda, 1965, p. 214] [**C. nanus*; OD]. Theca steeply conical, with apparently small spiracular slits confined to summit along ambulacral margins; anal opening separate, between a large epideltoid and small ?hypodeltoid; ambulacra short, wide; lancet covered by side plates, with lancet stipe close to mouth. *Perm.*, E.Indies (Timor).——Fig. 254,*1*; 255,*2*. **C. nanus*; 254, *1a-d*, oral, *D*-ray, aboral views, plate layout, ×13.1; 255,*2a*, oral view, ×7.2; 255, *2b*, *DE* interambulacral view, ×2.25 (178).

**Cryptoschisma** Etheridge & Carpenter, 1886, p. 280 [**Pentremites schultzii* de Verneuil & d'Archiac, 1845, p. 479; OD]. Theca conical with elongate spiracular slits along ambulacral margins, with 9 hydrospire folds opening into each slit; epideltoid and hypodeltoid present; lancet completely exposed, forming petaloid ambulacra. *Dev.*, Spain.——Fig. 254,*2*; 256,*1*. **C. schultzii* (de Verneuil & d'Archiac); 254,*2a-d*, oral, *D*-ray, aboral views, and plate layout, ×3.6 (15, 41, 60); 254, *2e,f*, anal views, ×10 (60); 256,*1a*, oral view, ×4.8; 256,*1b*, *D*-ray view, ×3.5 (60).

**?Pentephyllum** Haughton, 1859, p. 512 [**P. adarense*; OD]. Theca large, cup-shaped or pentalobate, doubtfully fissiculate, perhaps with 8 elongate spiracular slits along ambulacral margins with short ambulacrum *(D?)*, and 4 long, linear ambulacra; thecal plates somewhat irregular, but with 3 large, normally disposed basals, 5 large radials, and 5 short deltoids; anal structures unknown [position uncertain; characters based on interpretations of single cast]. *L.Carb.*, Eire.——Fig. 256,*3*; 257,*2*. **P. adarense*; 256,*3a,b*, oral, *AB?* interambulacral views, ×0.87; 257,*2a-d*, oral, *D*-ray, aboral views, plate layout, ×0.87 (41, 87).

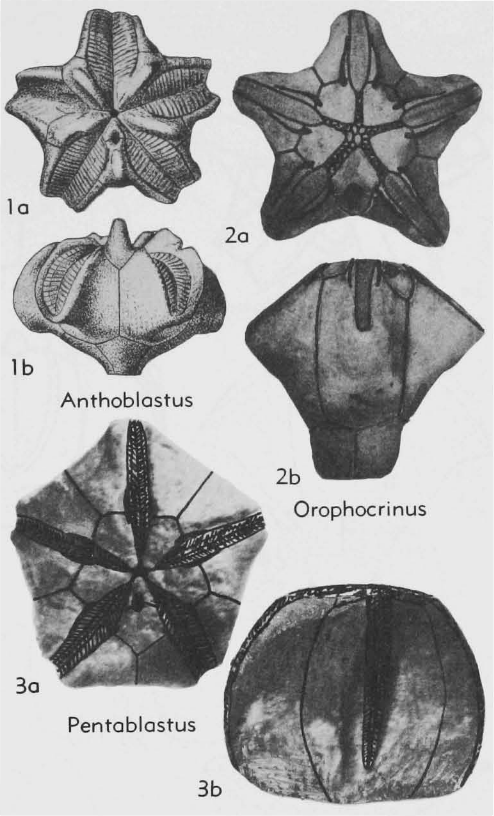


Fig. 252. Orophocrinidae (p. S409-S412).

**Pentremitidea** d'Orbigny, 1850, p. 102 [**Pentremites pailletti* de Verneuil, 1844, p. 213] [=*Pentetrematites* Steininger, 1849, p. 19 *(nom. van.)*; *Pentremitidia* Quenstedt, 1876, p. 718 *(nom. van.)*]. Theca conical, with elongate spiracular slits, each having approximately 8 hydrospire folds; superdeltoids, subdeltoid, and hypodeltoid present; sinuses deep; lancet covered by side plates, with possible inner side plate present. *Dev.*, Spain-?N.Afr.——Fig. 256,*2*; 257,*1*. **P. pailletti* (de Verneuil); 256,*2a*, oral view, ×3.2; 256,*2b*, *D*-ray view, ×3.5 (60); 257,*1a-d*, oral, *D*-ray, aboral views, plate layout, ×3.6 (60, 167, 168); 257,*1e,f*, cross sec. of ambulacrum, anal area, ×10 (60).

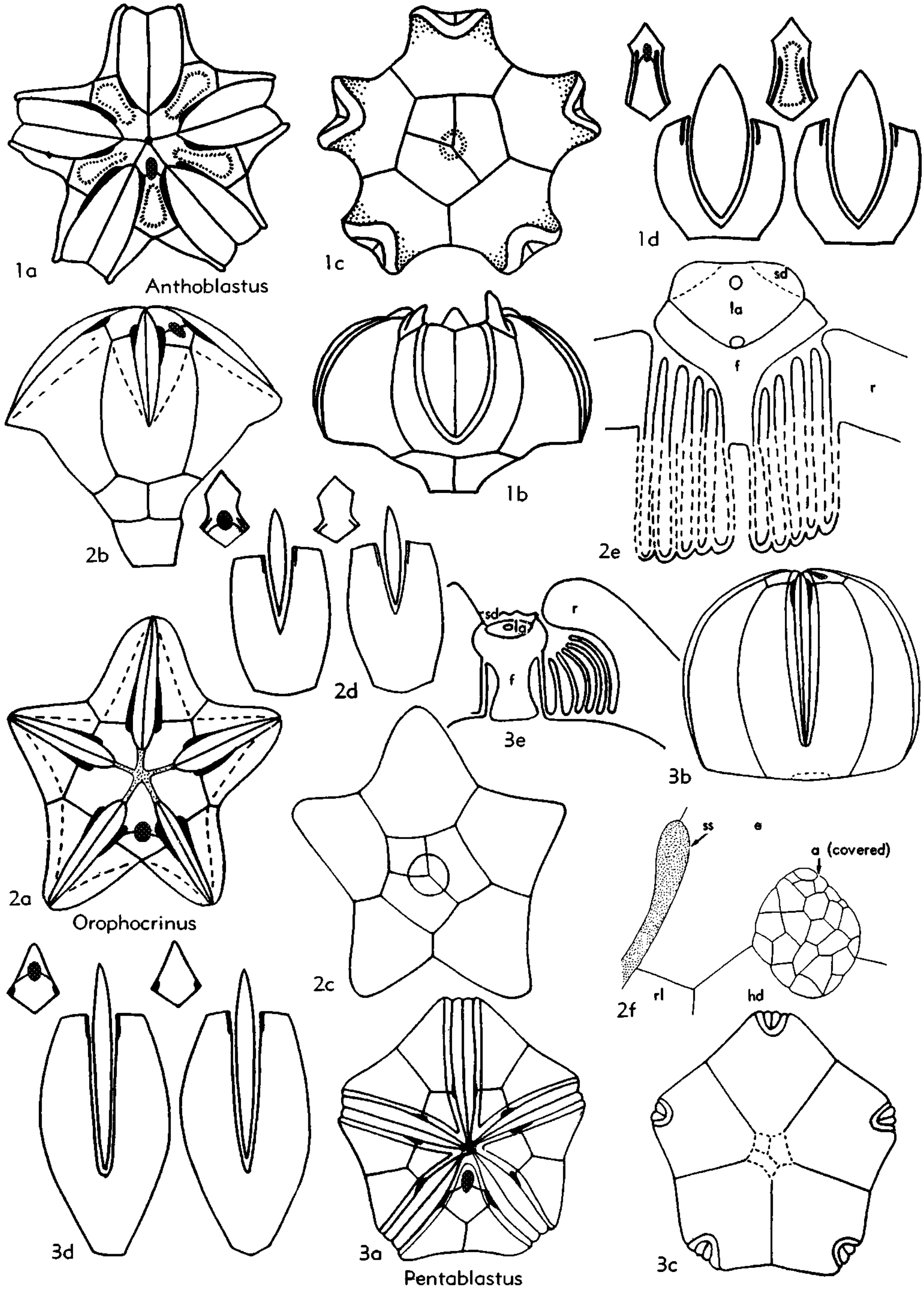


Fig. 253. Orophocrinidae (p. *S*409-*S*412). [Explanation: *a,* anal opening; *e,* epideltoid plate; *f,* fused hydrospire plate; *hd,* hypodeltoid; *la,* lancet plate; *r,* radial plate; *rl,* radial limb; *sd,* side plate; *ss,* spiracular slit.]

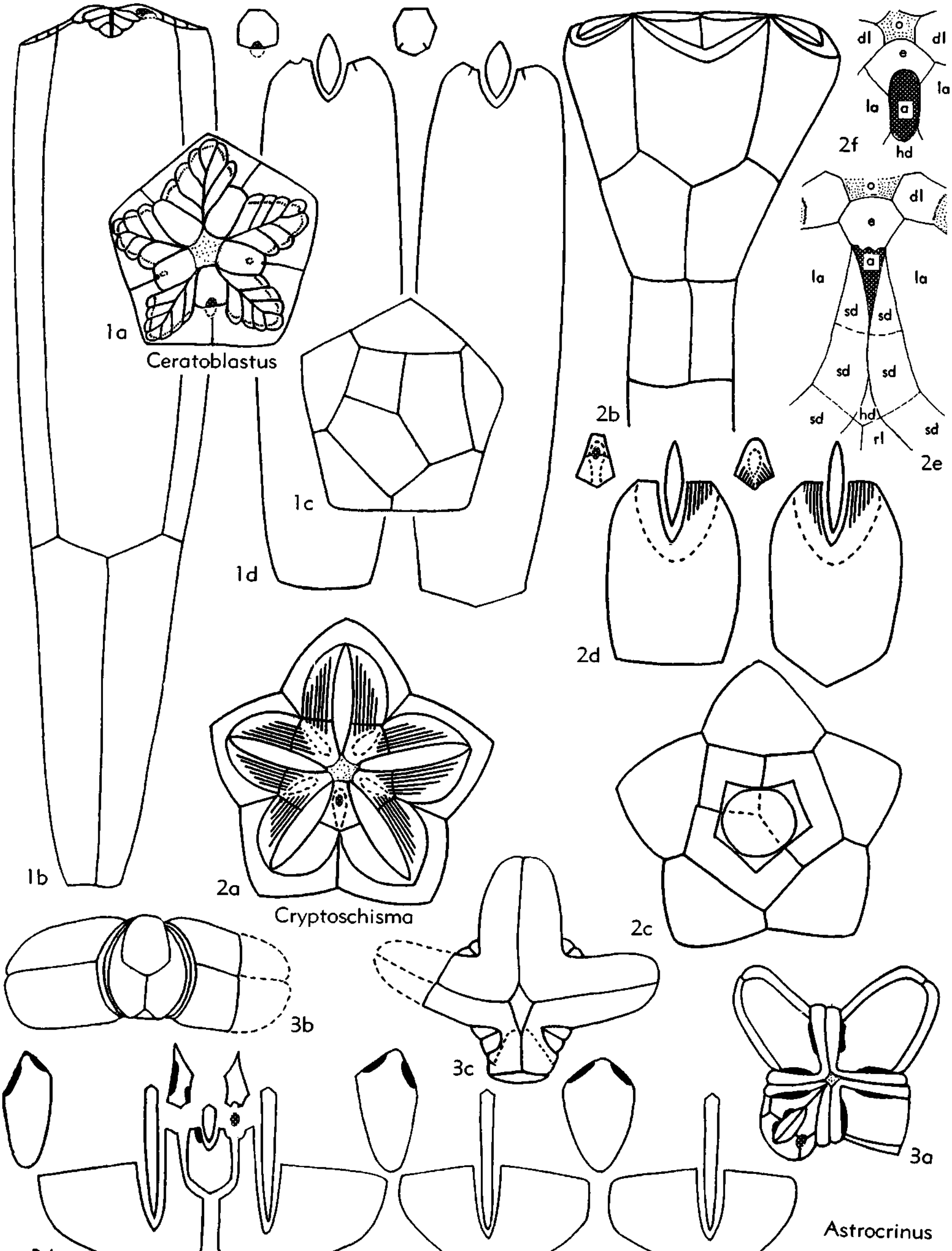


FIG. 254. Astrocrinidae (p. S413). [Explanation: *a*, anal opening; *e*, epideltoid plate; *dl*, deltoid lip; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening; *rl*, radial limb; *sd*, side plate.]

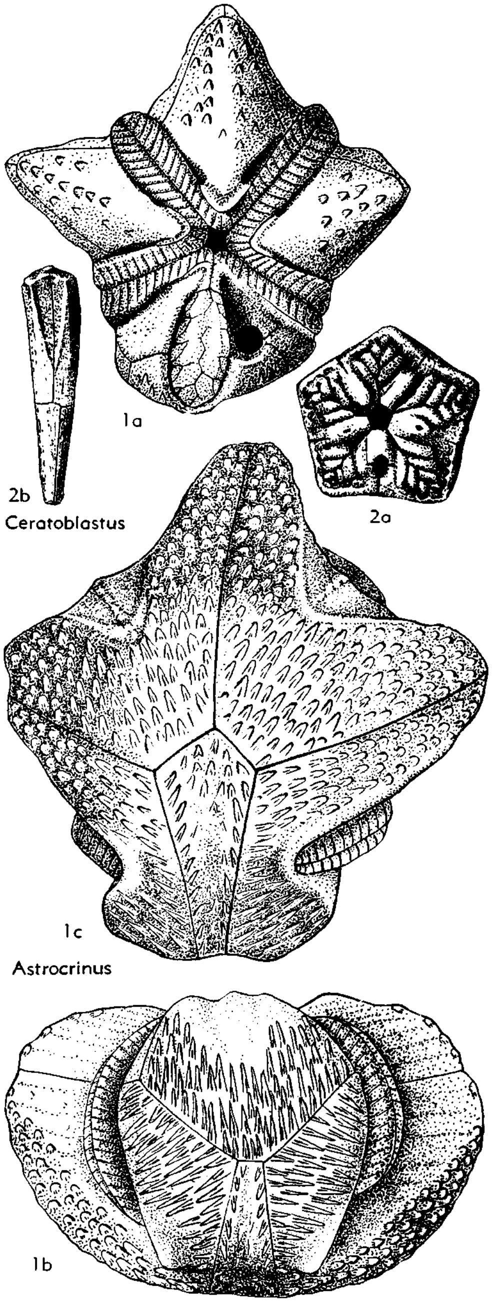


FIG. 255. Astrocrinidae (p. S413).

## Order SPIRACULATA Jaekel, 1918

[Spiraculata Jaekel, 1918, p. 107] [=Eublastida Matsumoto, 1929, p. 28 (type, *Troosticrinus* Shumard, 1866, p. 385, designated by Fay, herein)]

Theca with hidden hydrospire slits that open into hydrospire canals, with definite spiracles and hydrospire pores. *Sil.-Perm.*

### Family TROOSTICRINIDAE Bather, 1899

[*nom. correct.* Bassler, 1938, p. 14 (*pro* Troostocrinidae Bather, 1899, p. 920)] [=Troostoblastidae Etheridge & Carpenter, 1886, p. 190]

Theca elongate conical or obconical with five paired spiracles around mouth. *Sil.-Miss.*

**Troosticrinus** Shumard, 1866, p. 385 [**Pentremites reinwardti* Troost, 1835, p. 224; SD Etheridge & Carpenter, 1882, p. 247] [=*Troostocrinus* Meek & Worthen, 1868, p. 356 *(nom. van.)*; *Clavaeblastus* Hambach, 1903, p. 44 (obj.)]. Theca obconical, with superdeltoid, 2 cryptodeltoids, and hypodeltoid; edges of cryptodeltoids slightly exposed; lancet covered by side plates; one pore between adjacent side plates along ambulacral margins; radials overlapping deltoids; ambulacra short, directed outward and slightly downward; 3 to 5 hydrospire folds on each side of ambulacrum, with thin thecal plates; pelvis long; deltoids not visible in side view, but hypodeltoid visible in side view. *Sil.*, N.Am.——Fig. 258,*1*; 259,*1*. **T. reinwardti* (Troost), Niagaran, USA(Tenn.); 258,*1a*, oral view, ×4; 258,*1b, D*-ray view, ×2.3; 259,*1a-d*, oral, *D*-ray, aboral views, plate layout, ×5.3; 259,*1e,f*, anal views, ×15, ×13 (60, 165).

**Metablastus** Etheridge & Carpenter, 1886, p. 196 [**Pentremites lineatus* Shumard, 1858, p. 241; OD]. Theca conical, with superdeltoid, 2 cryptodeltoids, and hypodeltoid; lancet covered by side plates; one pore between adjacent side plates along radial and deltoid margins; radials overlapping deltoids; 4 to 5 hydrospire folds on each side of an ambulacrum; radial plates thin; pelvis long; ambulacra extended downward aborally; deltoids not visible in side view, but large hypodeltoid visible in side view. *Miss.*, N.Am.(Ill.-Iowa-Ind.-Mo.-Ky.).——Fig. 258,*2a*; 259,*2a-f*. **M. lineatus* (Shumard), M.Miss., Ill.; 258,*2a, CD* interambulacral view, ×1.5; 259,*2a-d*, oral, *D*-ray, aboral views, plate layout, ×3.6; 259,*2e*, cross sec. of ambulacrum, ×7; 259,*2f*, anal view, ×5 (41, 60, 155).——Fig. 258,*2b,c*. *M. wachsmuthi* (Gurley), M.Miss., Ind.; *2b,c*, oral, *D*-ray views, ×1.9, ×1.8 (60).——Fig. 259,*2g*. *M. wortheni* (Hall), M.Miss., Mo.; anal view, ×10 (60).

**Schizotremites** Reimann, 1945, p. 25 [**S. kopfi*;

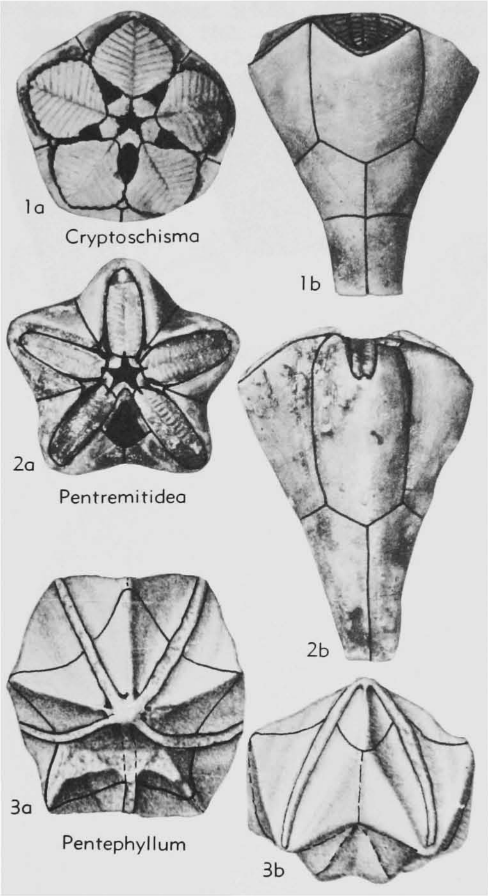


FIG. 256. Astrocrinidae (p. *S*413).

OD] [=?*Pentremitella* LEHMANN, 1949, p. 190 (type, *Pentremitella osoleae*; OD)]. Theca conical, with paired anispiracle located between long hypodeltoid and short superdeltoid, with 2 hidden cryptodeltoids; deltoids moderately long, seen in side view; lancet covered by side plates except near adoral end; one pore between side plates along deltoid and radial margins; 4 to 6 hydrospires on each side of an ambulacrum; radials overlapping deltoids. *Dev.*, N.Am.-?Ger.——FIG. 258,*3*; 260,*2*. **S. kopfi*, M.Dev., USA(N.Y.); 258,*3a,b*, oral, *D*-ray views, ×3.7; 260,*2a-d*, oral, *D*-ray, aboral views, plate layout, ×4.4; 260,*2e*, cross sec. of ambulacrum, ×15 (62, 139).

**Tricoelocrinus** MEEK & WORTHEN, 1868, p. 356 [**Pentremites (Troostocrinus?) woodmani* MEEK & WORTHEN, 1868, p. 356] [=*Saccoblastus* HAM-

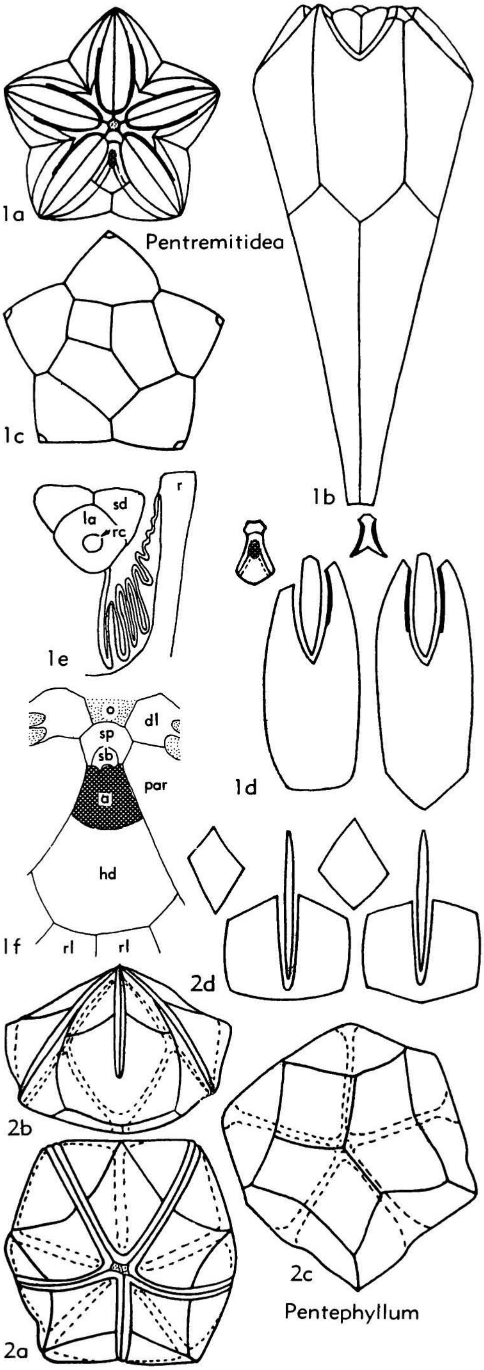


FIG. 257. Astrocrinidae (p. *S*413). [Explanation: *a*, anal opening; *dl*, deltoid lip; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening; *par*, posterior ambulacrum (right); *r*, radial plate; *rc*, radial canal; *rl*, radial limb; *sb*, subdeltoid plate; *sd*, side plate; *sp*, superdeltoid plate.]

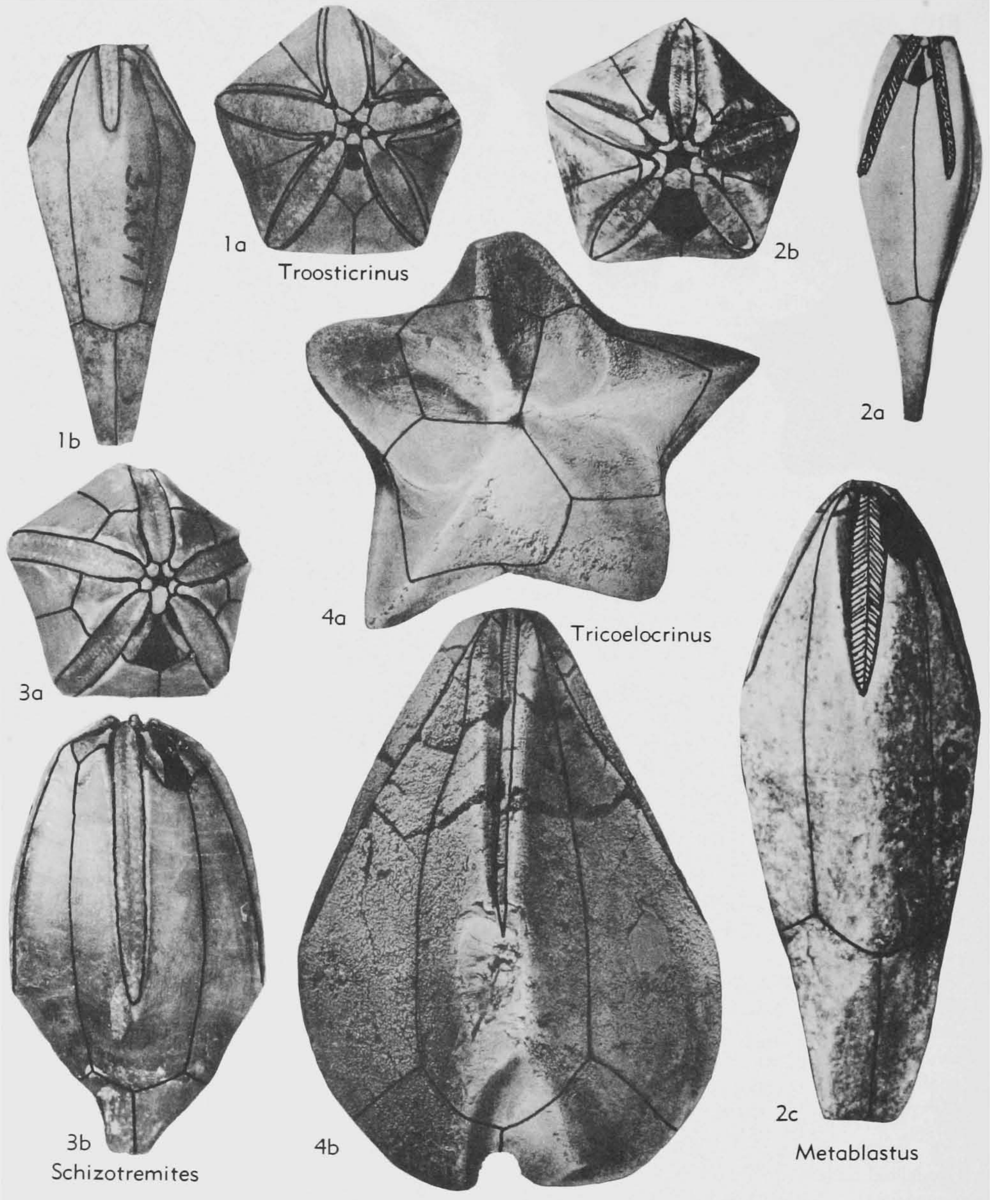


FIG. 258. Troosticrinidae (p. S416-S419).

BACH, 1903, p. 42 (type, *Pentremites bipyramidalis* HALL, 1858, p. 607)]. Theca subpyramidal, with superdeltoid, 2 cryptodeltoids, and hypodeltoid; lancet covered by side plates; one pore between adjacent side plates along deltoid and radial margins; radials overlapping deltoids; with 3 short hydrospire folds on each side of ambulacrum, extending one-half length of ambulacrum, ending within thick radial plate beneath each ambulacrum; pelvis long, widely inflated outward, subrounded below; deltoids not visible in side view, but large hypodeltoid visible in side view. *Miss.*, N.Am.(Ind.-Tenn.-Ky.-Mo.-Ill.).——FIG. 258,*4*; 260,*1a-e*. **T. woodmani* (MEEK & WORTHEN), M.Miss., Ind.; 258,*4a,b,* aboral, *A*-ray views, ×1.3; 260,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×0.86; 260,*1e,* anal area, diagram. (50, 60, 116).——Fig. 260,*1f.* *T. obliquatus* (Roemer), M.Miss., Ind.; cross sec. of ambulacrum, ×4.4 (41).

## Family DIPLOBLASTIDAE Fay, 1964

[Diploblastidae Fay, 1964, p. 84]

Theca globular, with five paired spiracles or four paired spiracles and an anispiracle. *Miss.*

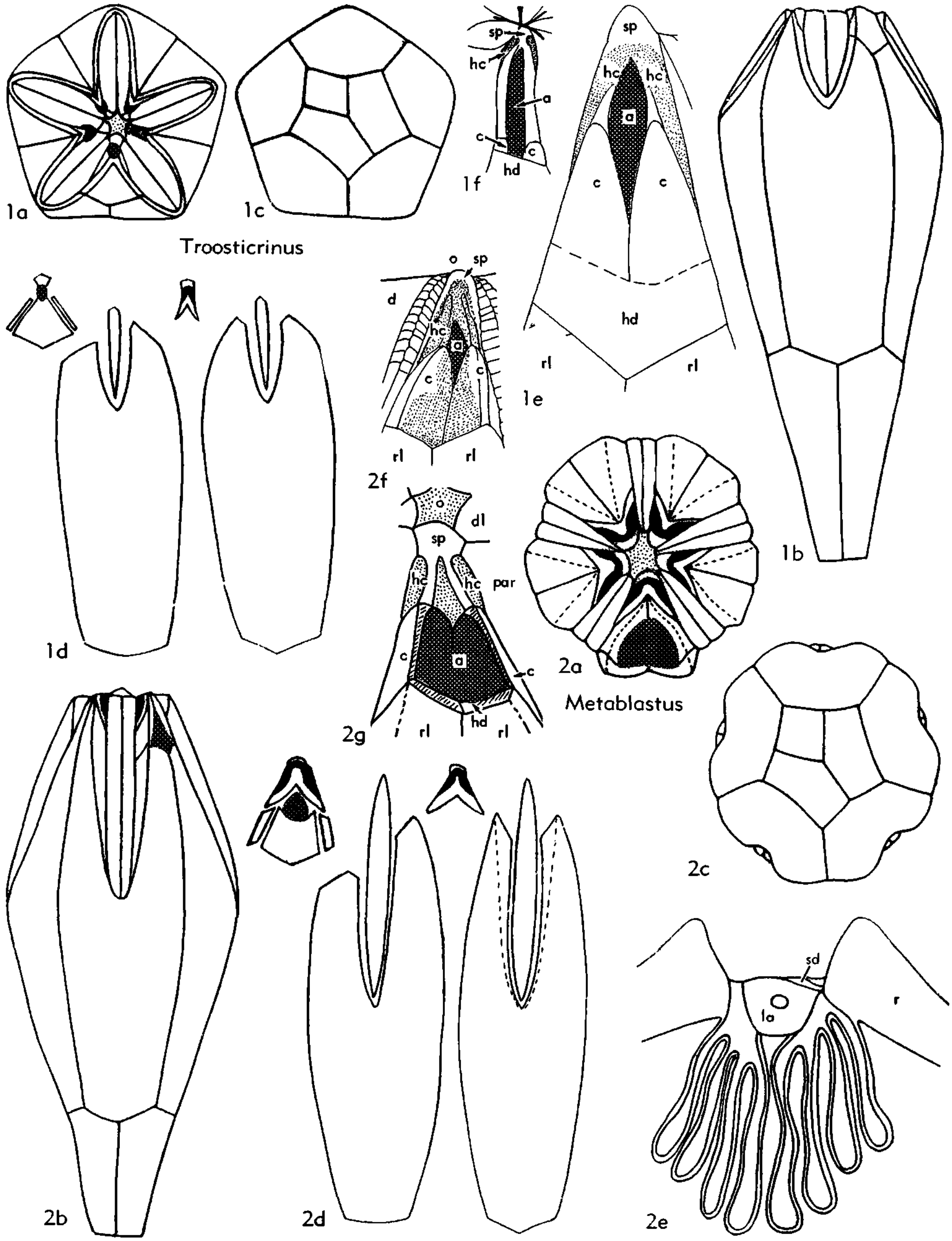


Fig. 259. Troosticrinidae (p. *S*416). [Explanation: *a,* anal opening; *c,* cryptodeltoid plate; *d,* deltoid plate; *dl,* deltoid lip; *hc,* hydrospire canal; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening; *par,* posterior ambulacrum (right); *r,* radial plate; *rl,* radial limb; *sd,* side plate; *sp,* superdetoid plate.]

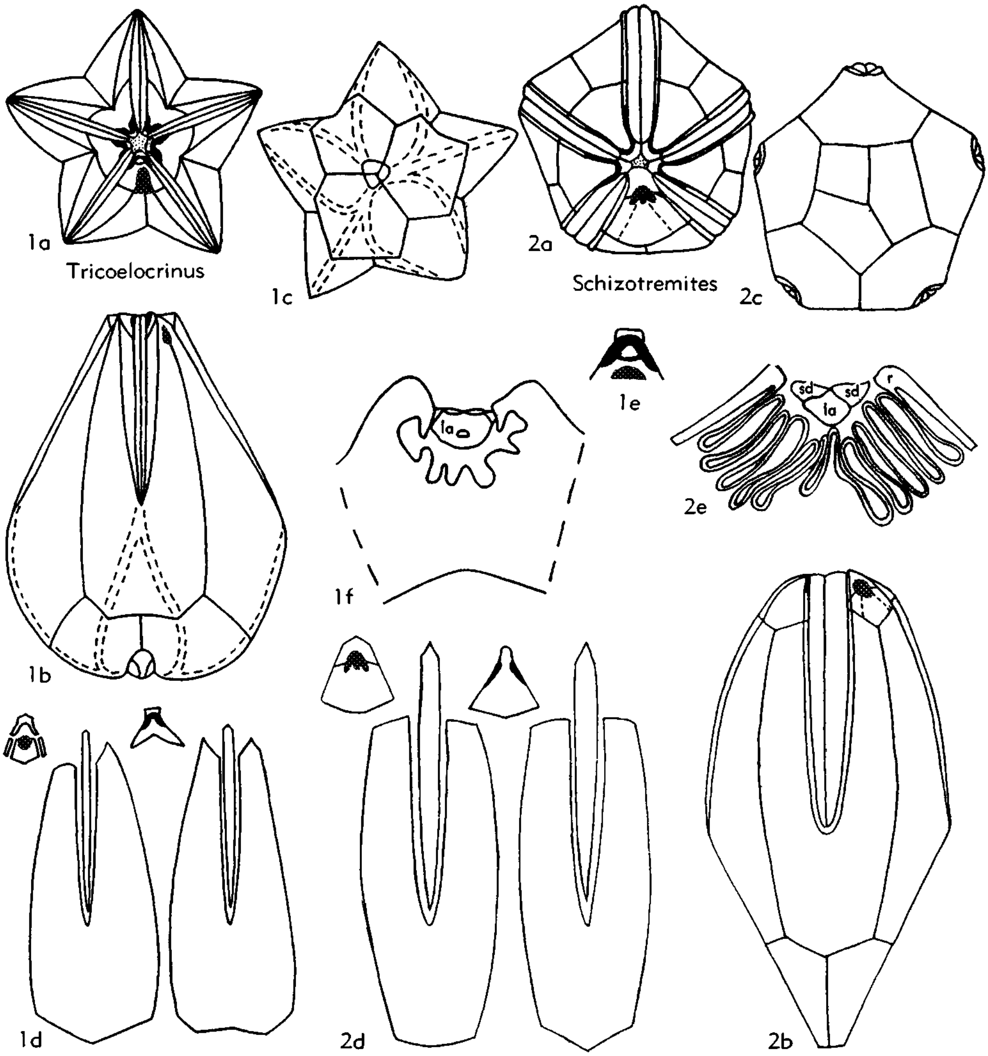


FIG. 260. Troosticrinidae (p. S416-S419). [Explanation: *la,* lancet plate; *r,* radial plate; *sd,* side plate.]

**Diploblastus** FAY, 1961 (60), p. 62 [**Granatocrinus glaber* MEEK & WORTHEN, 1869, p. 91; OD]. Theca globular, with superdeltoid, 2 cryptodeltoids, and hypodeltoid; 2 hydrospire folds on each side of an ambulacrum; lancet covered by side plates at aboral end and gradually exposed to 0.3 of its width near adoral end; with one pore between side plates along deltoid and radial margins; radials overlapping deltoids. *Miss.,* N.Am. (Ill.-Mo.-Ky.-Ala.).——FIG. 261,*2*; 262,*1*. **D. glaber* (MEEK & WORTHEN), M.Miss., Ky. (261, *2*), Ill. (262,*1*); 261,*2a,b,* oral, *D*-ray views, ×7.5; 262,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×6.3; 262,*1e,* cross sec. of ambulacrum, ×26.5; 262,*1f,* anal view, ×10 (60).

**Nodoblastus** FAY, 1963, p. 174 [**Schizoblastus librovitchi* YAKOVLEV, 1941, p. 71; OD]. Theca bell-shaped to elliptical, with anispiracle located between short epideltoid and long hypodeltoid; deltoids slightly longer than radials which overlap deltoids; one hydrospire fold on each side of an ambulacrum; hydrospire plate present, with about twice as many pores as side plates; basalia small, in slight basal concavity; deltoids nodose, with medium high deltoid crests. *L.Carb.,* Eu. (USSR).——FIG. 261,*1*; 262,*2*. **N. librovitchi* (YAKOVLEV); 261,*1a,b,* oral, *C*-ray views, ×3.2; 262,*2a-d,* oral, *C*-ray, aboral views, plate diagram, ×3.7; 262,*2e,* transv. sec. of ambulacrum, ×10 (73, 188).

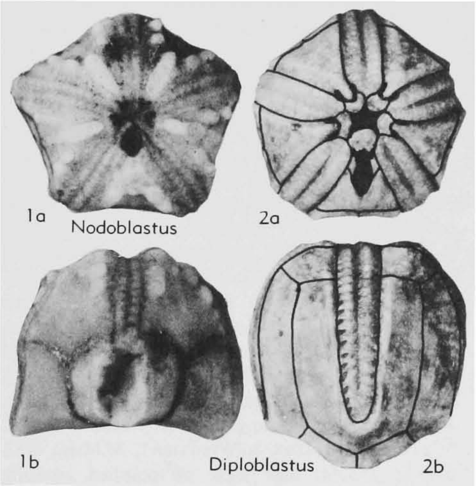


FIG. 261. Diploblastidae (p. S420).

## Family GRANATOCRINIDAE Fay, 1961

[Granatocrinidae FAY, 1961 (60), p. 20] [=Granatoblastidae ETHERIDGE & CARPENTER, 1886, p. 237 (invalid, based on nonexistent nominal genus)]

Theca with eight spiracles and anispiracle (or paired anispiracle) around mouth. *Miss.*

**Granatocrinus** HALL, 1862, p. 146 [**Pentatrematites granulatus* ROEMER, 1851, p. 363; SD SHUMARD, 1866, p. 375] [=*Granatocrinites* TROOST, 1849, p. 420 *(nom. nud.)*; *Cidaroblastus* HAMBACH, 1903, p. 45 (type, *Pentatrematites granulatus* ROEMER)]. Elliptical theca with anispiracle located between epideltoid and hypodeltoid; one hydrospire fold on each side of an ambulacrum; lancet covered by side plates; hydrospire plate present; 2 pores to each side plate along radial and deltoid margins; radials overlapping deltoids; deltoids moderately long. *Miss.,* N.Am.(Ky.-Ind.-Tenn.).——FIG. 263,*1*; 264,*1a-e*. **G. granulatus* (ROEMER), M.Miss., USA(Tenn.); 263,*1a,* oral view,

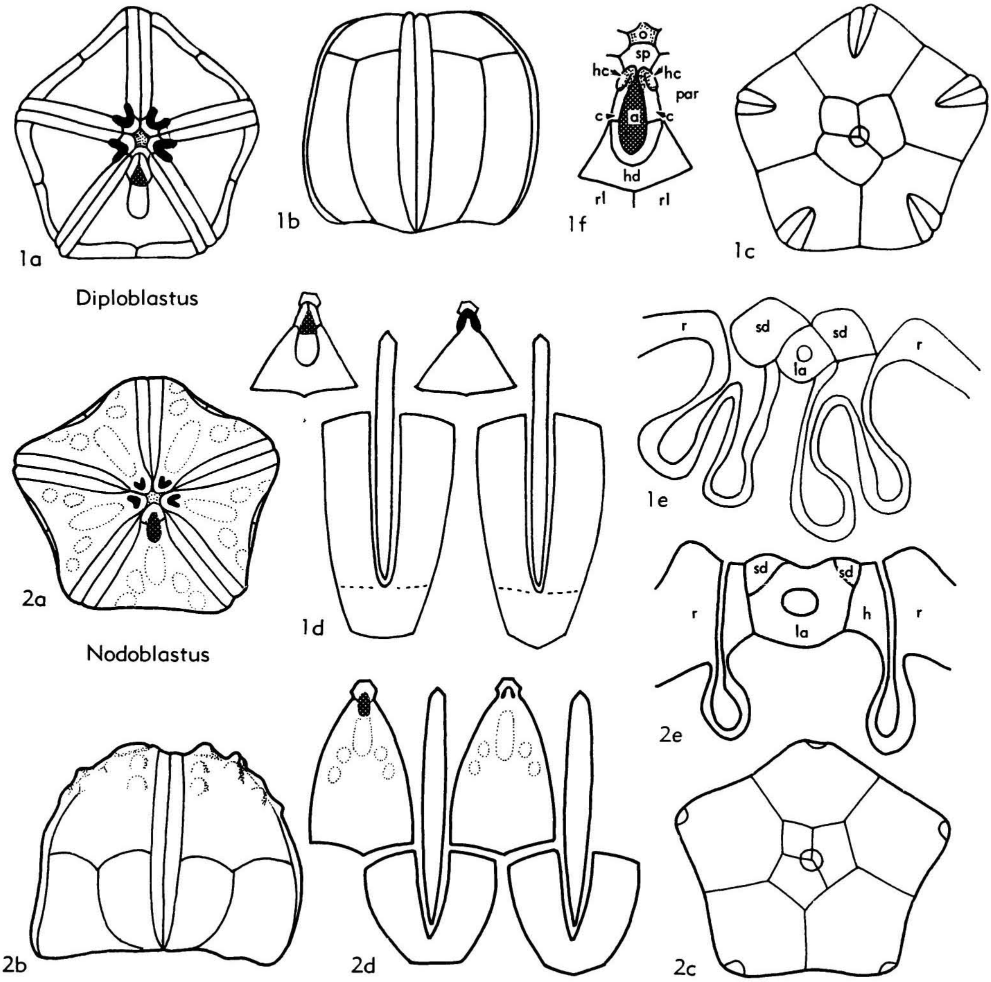


FIG. 262. Diploblastidae (p. S420). [Explanation: *a,* anal opening; *c,* cryptodeltoid plate; *h,* hydrospire plate; *hc,* hydrospire canal; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening; *par,* posterior ambulacrum (right); *r,* radial plate; *rl,* radial limb; *sd,* side plate; *sp,* superdeltoid plate.]

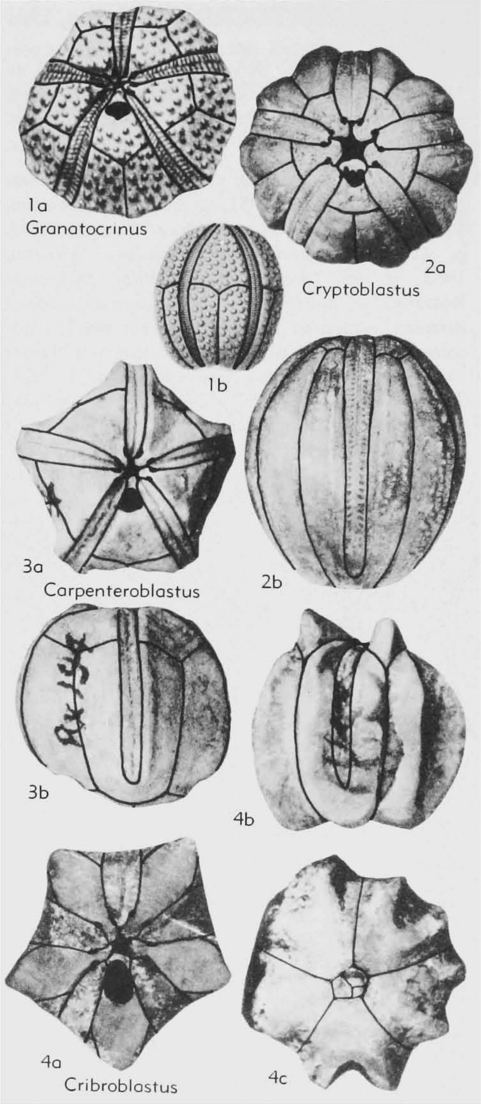


FIG. 263. Granatocrinidae (p. S421-S422).

×1; 263,*1b,* interambulacral view, ×0.5; 264, *1a-d,* oral, *D*-ray, aboral views, plate layout, ×1.3; 264,*1e,* cross sec. of ambulacrum, ×8.7 (60, 86).——FIG. 264,*1f.* *G. kentuckyensis* (CONKIN), M.Miss., Ky.; anal view, ×7.4 (60).

**Carpenteroblastus** ROWLEY, 1901, p. 347 [**Granatocrinus (Schizoblastus) magnibasis* ROWLEY, 1895, p. 220; OD]. Theca conico-elliptical; anispiracle located between epideltoid and hypodeltoid; lancet exposed along food groove proper; with ?2 hydrospire folds on each side of an ambulacrum; one pore between adjacent side plates along deltoid and radial margins; radials overlapping deltoids; base convex. *Miss.,* N.Am.(Mo.-?Ky.).——FIG. 263,*3*; 264,*2*. **C. magnibasis* (ROWLEY), M.Miss., USA(Mo.); 263,*3a,b,* oral, *D*-ray views, ×2.5; 264,*2a-d,* oral, *D*-ray, aboral views, plate layout, ×3.5; 264,*2e,* cross sec. of ambulacrum, ×35.2; 264,*2f,* anal view, ×10 (60).

**Cribroblastus** HAMBACH, 1903, p. 39 [**Pentremites cornutus* MEEK & WORTHEN, 1862, p. 141; SD BASSLER, 1938, p. 75]. Ellipsoidal theca; anispiracle located between epideltoid and hypodeltoid; deltoids short, with high coronal processes; radials overlapping deltoids; lancet covered by side plates, with single pore between side plates along radial and deltoid margins; 2 hydrospire folds on each side of an ambulacrum; hydrospire plate present. *Miss.,* N.Am.(Ill.-Mo.).——FIG. 263,*4*; 265,*1*. **C. cornutus* (MEEK & WORTHEN), M.Miss., USA (Mo.); 263,*4a,* oral view of polished summit, ×5; 263,*4b,* side view, ×2.3; 263,*4c,* aboral view, ×3.1; 265,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×3.6; 265,*1e,* cross sec. of ambulacrum, ×17.9; 265,*1f,* anal view, ×3.8 (60).

**Cryptoblastus** ETHERIDGE & CARPENTER, 1886, p. 229 [**Pentremites melo* OWEN & SHUMARD, 1850, p. 65; OD]. Theca ellipsoidal; anispiracle located between superdeltoid, 2 deep cryptodeltoids, and hypodeltoid; lancet exposed along middle 0.3 of its width except near aboral end; 2 hydrospire folds on each side of an ambulacrum; hydrospire plate present; pores absent along deltoid margins, with about 2 pores per side plate along radial margins; interradial sutures depressed; radials overlapping deltoids except at extreme adoral tip of radial limbs where deltoids project slightly over radials. *Miss.,* N.Am.(Iowa-Mo.).——FIG. 263,*2*; 265,*2*. **C. melo* (OWEN & SHUMARD), M.Miss., USA(Iowa); 263,*2a,b,* oral, *D*-ray views, ×2.6; 265,*2a-d,* oral, *D*-ray, aboral views, plate layout, ×3.6; 265,*2e,* cross sec. of ambulacrum, ×22; 265,*2f,* anal view, ×3.8 (29, 60, 128).

**Dentiblastus** MACURDA, 1964 (102), p. 370 [**Pentremites sirius* WHITE, 1865, p. 20; OD]. Theca oblate spheroidal; with anispiracle located between epideltoid and hypodeltoid; 2 hydrospire folds on each side of ambulacrum; hydrospire plate present; lancet covered by side plates; single pore between adjacent side plates along radial and deltoid margins; deltoids overlapping radials; radials winglike, with ambulacra extending beyond theca proper. *Miss.,* USA(Iowa-Mo.).——FIG. 266,*1*. **D. sirius* (WHITE), M.Miss., Mo.; *1a-f,* oral, *E*-ray, aboral views, plate layout, oral, *E*-ray views, ×6 (102).

**Heteroblastus** ETHERIDGE & CARPENTER, 1886, p. 255 [**H. cumberlandi*; OD]. Theca elliptical; anispiracle seemingly located between epideltoid and hypodeltoid; deltoids long, with high coronal processes; lancet covered by side plates; single pore between side plates along radial and deltoid margins; deltoids overlapping radials; probably

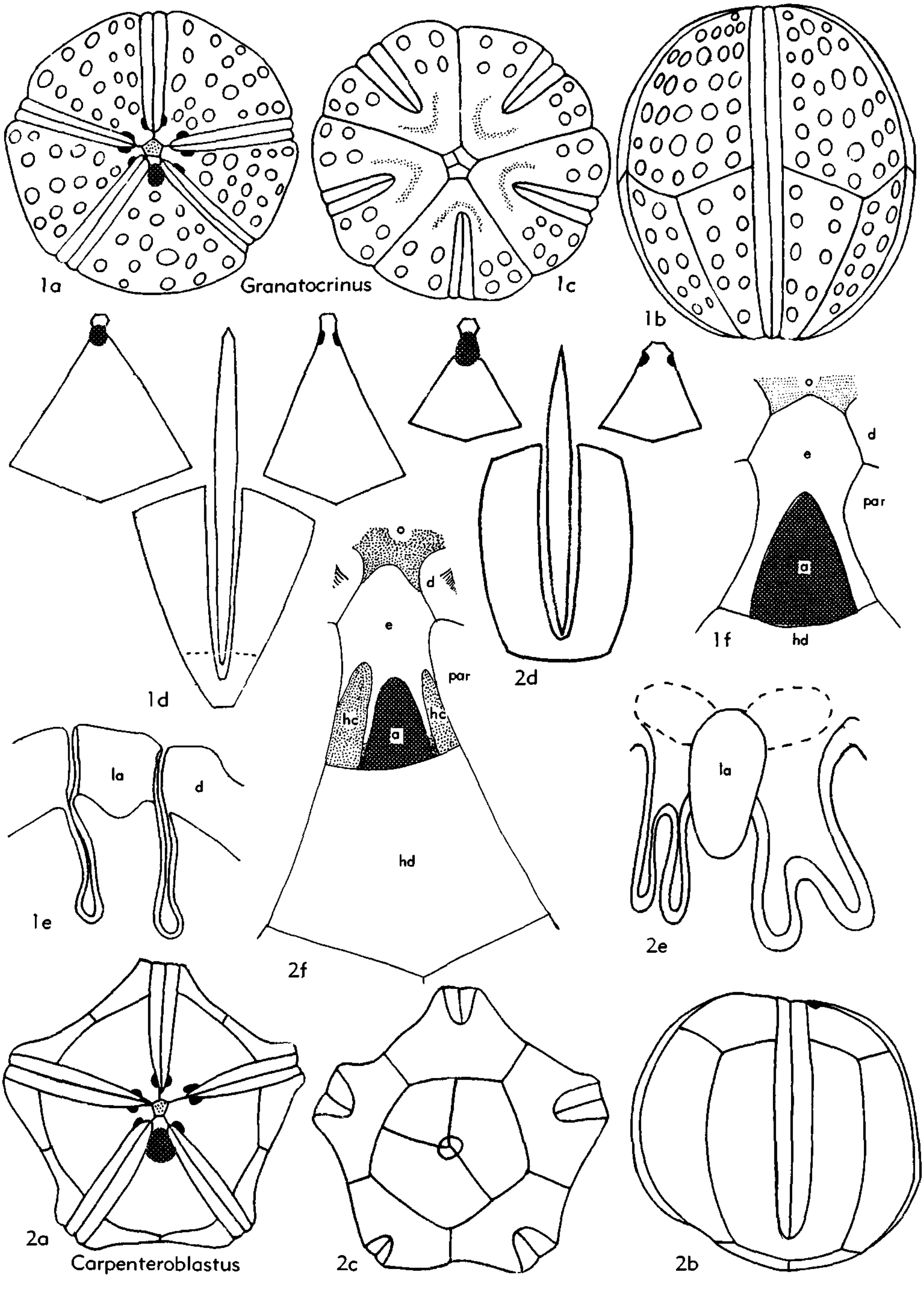


FIG. 264. Granatocrinidae (p. S421-S423). [Explanation: *a,* anal opening; *d,* deltoid plate; *e,* epideltoid plate; *hc,* hydrospire canal; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening; *par,* posterior ambulacrum (right).]

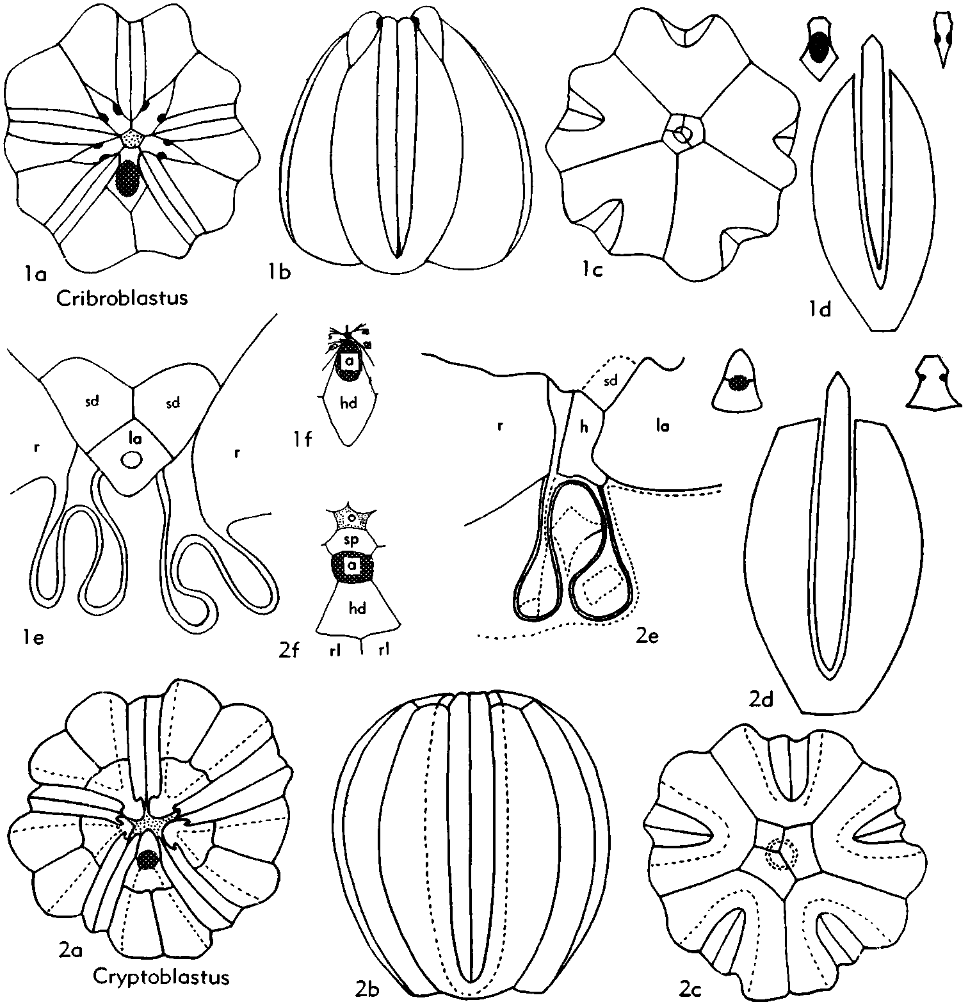


Fig. 265. Granatocrinidae (p. *S*422). [Explanation: *a,* anal opening; *h,* hydrospire plate; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening; *r,* radial; *rl,* radial limb; *sd,* side plate; *sp,* superdeltoid plate.]

more than one hydrospire fold on each side of an ambulacrum. *L.Carb.,* Eu.(Eng.).——Fig. 267, *1*; 268,*1*. **H. cumberlandi;* 267,*1a,b,* oral, radial views, ×3.8; 268,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×4.4 (41).

**Mesoblastus** Etheridge & Carpenter, 1886, p. 181 [**Pentatrematites crenulatus* Roemer, 1851, p. 366; OD]. Theca subglobular; superdeltoid, 2 cryptodeltoids, and hypodeltoid; 3 hydrospire folds on each side of ambulacra; thick hydrospire plate, with approximately 5 pores to each side plate infolded into double row; lancet covered by side plates except at adoral end; pores absent along deltoid margins; radials overlapping deltoids. *L. Carb.,* Eu.(Belg.-Eng.-Ger.)-?China.——Fig. 267, *3*; 268,*2a-d, 2f*. **M. crenulatus* (Roemer), Belg.; 267,*3a,b,* oral, *D*-ray views, ×3.2; 268,*2a-d,* oral, *D*-ray, aboral views, plate layout, ×5.8; 268,*2f,* anal view, ×10 (41, 60).——Fig. 268,*2e*. *M. angulatus* (Sowerby), Eng.; cross sec. of ambulacrum, ×11.8 (41).

**Monadoblastus** Fay, 1961 (60), p. 82 [**M. granulosus*; OD]. Theca elliptical, with anispiracle located between epideltoid and hypodeltoid; hydrospire plate present, and approximately 2 pores to each side plate along radial margins; pores absent along deltoids; one hydrospire fold on each side of ambulacra; lancets covered by side plates except near adoral end; base concave; radials overlapping deltoids. *Miss.,* N.Am.(N.Mex.).——Fig. 267,*2*; 268,*3*. **M. granulosus*; 267,*2a,b,* oral, *D*-ray views, ×6.4; 268,*3a-e,* oral, *D*-ray, aboral views, plate layout, cross sec. of ambulacrum, ×8.8 (60).

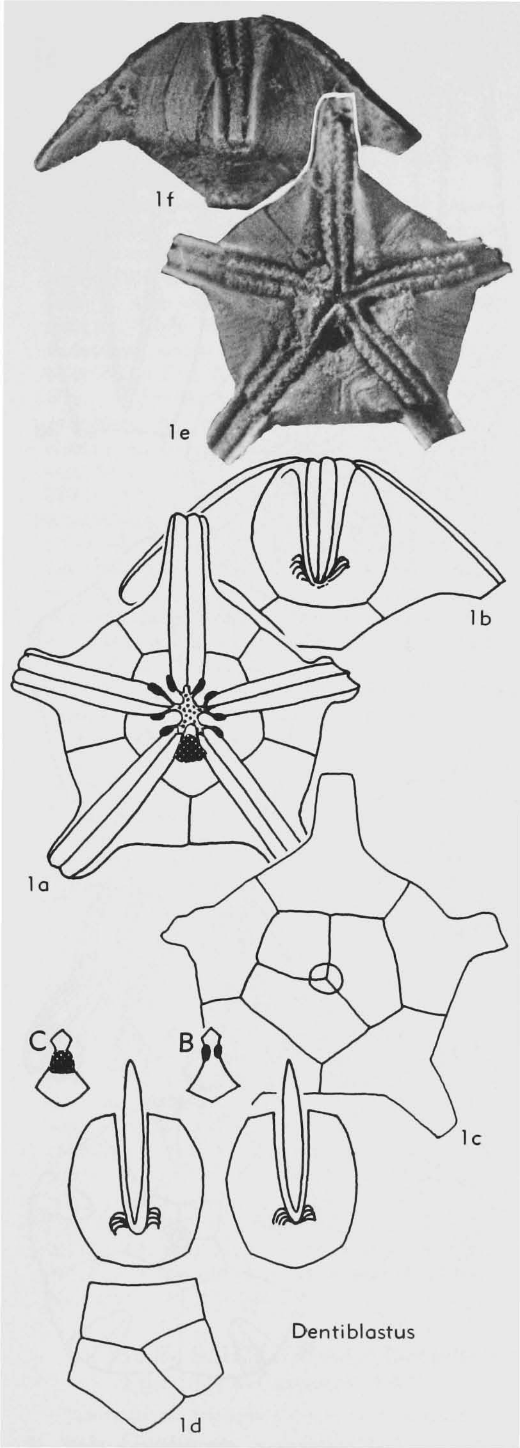


FIG. 266. Granatocrinidae (p. *S*422).

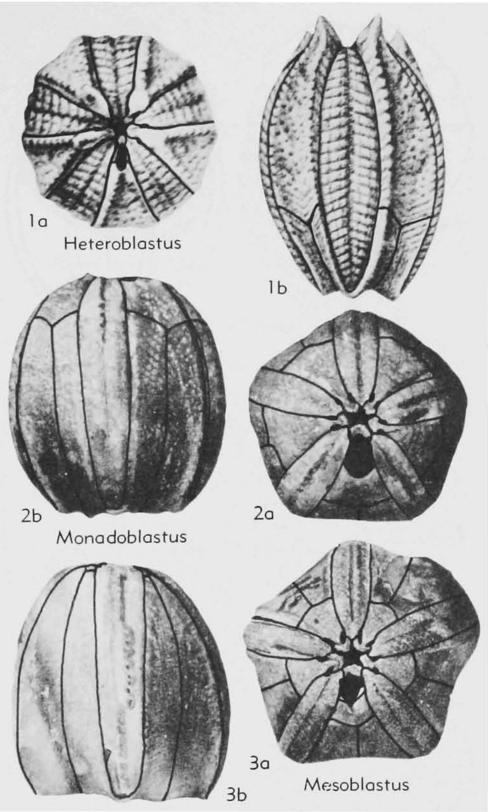


FIG. 267. Granatocrinidae (p. *S*422, *S*424).

**Monoschizoblastus** CLINE, 1936, p. 265 [**Granatocrinus rofei* ETHERIDGE & CARPENTER, 1882, p. 239; OD]. Theca ellipsoidal; anispiracle between small epideltoid and large hypodeltoid; single hydrospire fold on each side of ambulacra; lancet exposed along middle 0.3 of its width; deltoids long, overlapping radials; base concave; with what appears to be single pore between side plates along radial and deltoid margins. *L.Carb.*, Eu.(Eire).——FIG. 269,*1*; 270,*3*. **M. rofei* (ETHERIDGE & CARPENTER); 269,*1a,b,* oral, *A*-ray views, ×4.4; 270,*3a-d,* oral, *D*-ray, aboral views, plate layout, ×7.5; 270,*3e,* cross sec. of ambulacrum, ×13.1 (28, 39, 41, 53).

**Poroblastus** FAY, 1961 (60), p. 97 [**Pentremites (Granatocrinus) granulosus* MEEK & WORTHEN, 1865, p. 165; OD]. Theca ellipsoidal, with anispiracle between epideltoid and hypodeltoid; radials overlapping deltoids; hydrospire plate present; one pore between side plates along deltoid margins but 2 pores to each side plate along radial margins; single hydrospire fold on each side of ambulacra; lancet covered by side plates at aboral end, gradually exposed to 0.3 of its width

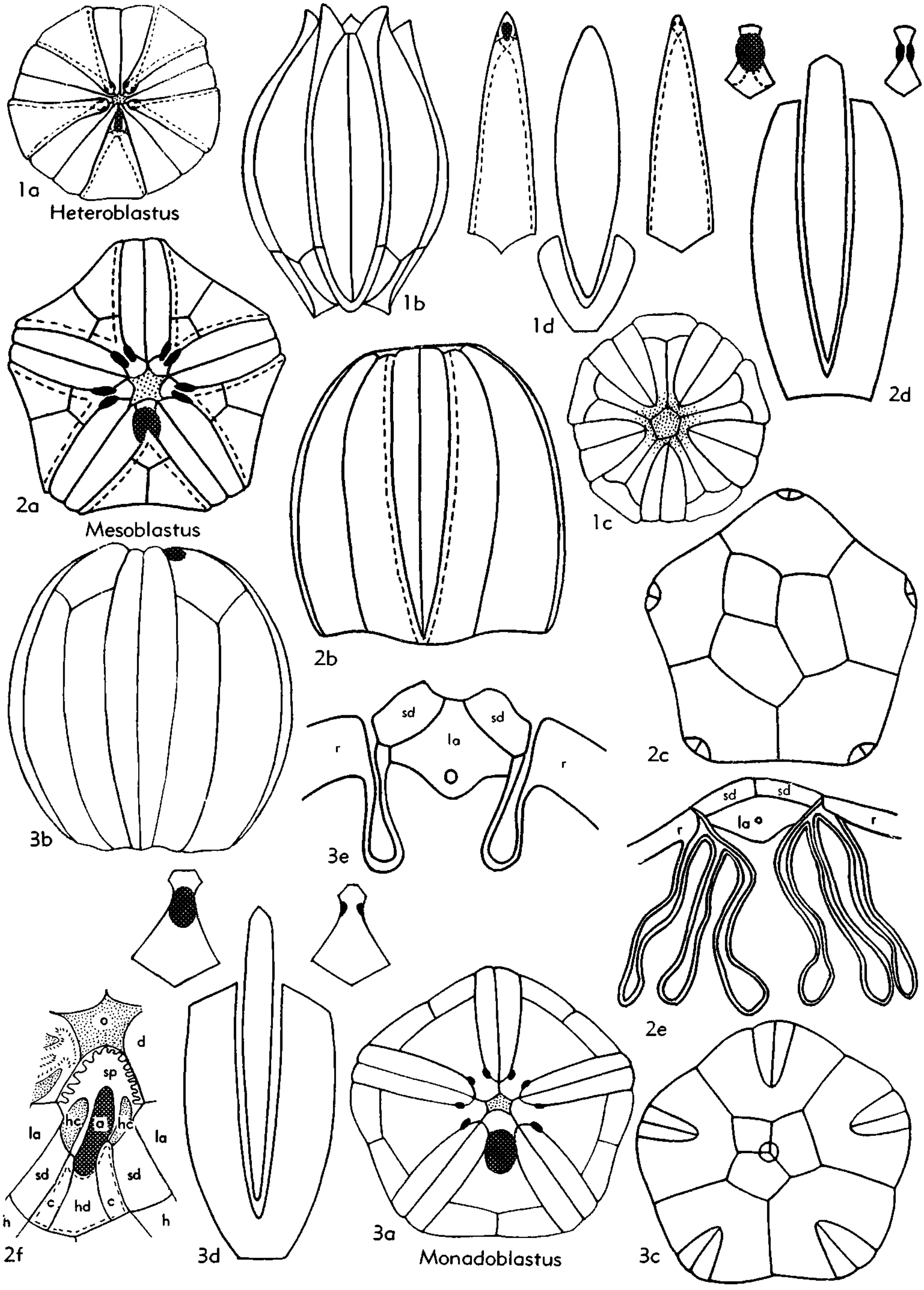


Fig. 268. Granatocrinidae (p. S422, S424). [Explanation: *a,* anal opening; *c,* cryptodeltoid plate; *d,* deltoid plate; *h, hydrospire* plate; *hc,* hydrospire canal; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening; *r,* radial plate; *sd,* side plate; *sp,* superdeltoid plate.]

near adoral end; base concave. *Miss.*, N.Am.(Ill.-Iowa-Mo.).——Fig. 269,*2*; 270,*2*. **P. granulosus* (Meek & Worthen), M.Miss., USA(Ill.); 269, *2a,b*, oral, *D*-ray views, ×4; 270,*2a-d*, oral, *D*-ray, aboral views, plate layout, ×4.4; 270,*2e*, cross sec. of ambulacrum, ×26.4; 270,*2f*, anal view, ×10 (60).

**Ptychoblastus** Fay, 1960 (46), p. 1198 [**P. pustulosus*; OD]. Theca ellipsoidal, with anispiracle between epideltoid and hypodeltoid; radials abutting against deltoids; hydrospire plate present; 2 pores to each side plate along deltoid and radial margins; single hydrospire fold on each side of ambulacra; lancets covered at aboral end, gradually exposed to 0.3 of width near adoral end. *Miss.*, N.Am.(Mo.).——Fig. 269,*3*; 270,*1*. **P. pustulosus*, M.Miss.; 269,*3a-c*, oral, *AE* interambulacral, *D*-ray views, ×3.8 (60); 270,*1a-d*, oral, *D*-ray, aboral views, plate layout, ×5.9; 270,*1e*, cross sec. of ambulacrum, ×17.6 (46).

**Pyramiblastus** Macurda, 1964 (105), p. 106 [**Orophocrinus fusiformis* Wachsmuth & Springer, 1888, p. 14; OD]. Theca bipyramidal, with paired anispiracle located between superdeltoid, 2 cryptodeltoids, and hypodeltoid; 6 to 8 hydrospire folds on each side of ambulacrum; lancet exposed along 0.3 of its width; single pore between each side plate along radial and deltoid margins; deltoids overlapping radials; deltoids well exposed in side view. *Miss.*, USA (Iowa).——Fig. 271,*1*. **P. fusiformis* (Wachsmuth & Springer), L.Miss., Iowa; *1a-f*, oral, *D*-ray, aboral views, plate layout, side view of holotype, *D*-ray view, ×3 (105).

**Tanaoblastus** Fay, 1961 (60), p. 101 [**Pentremites roemeri* Shumard *(partim)*, 1855, p. 186, pl. B, fig. 2a only; OD]. Theca subelliptical, with anispiracle located between superdeltoid and hypodeltoid, with 2 hidden cryptodeltoids; deltoids moderately short; radials overlapping deltoids; pores absent along deltoid margins, but 2 pores to each side plate along radial margins; 2 hydrospire folds on each side of ambulacra; lancet exposed along main food groove; interradial sutures even; base flat to convex. *Miss.*, N.Am.(Mo.-Mont.-?Ariz.-Alta.).——Fig. 272,*1a-h*. **T. roemeri* (Shumard), L.Miss., USA(Mo.); *1a*, oral view, ×5.9; *1b*, oral view, ×5.1; *1c*, *D*-ray view, ×5.9; *1d*, *D*-ray view, ×5.1; *1e,f*, aboral view, plate layout, ×5.9; *1g*, cross sec. of ambulacrum, ×11.7; *1h*, anal view, ×10 (60).——Fig. 272, *1i*. *T. concinnulus* (Rowley & Hare), M.Miss., Mo.; anal view, ×10 (60).

## Family SCHIZOBLASTIDAE

### Etheridge & Carpenter, 1886

[Schizoblastidae Etheridge & Carpenter, 1886, p. 220]

Theca with ten spiracles and separate anal opening around mouth; cryptodeltoids (if present) hidden. *Dev.-Perm.*

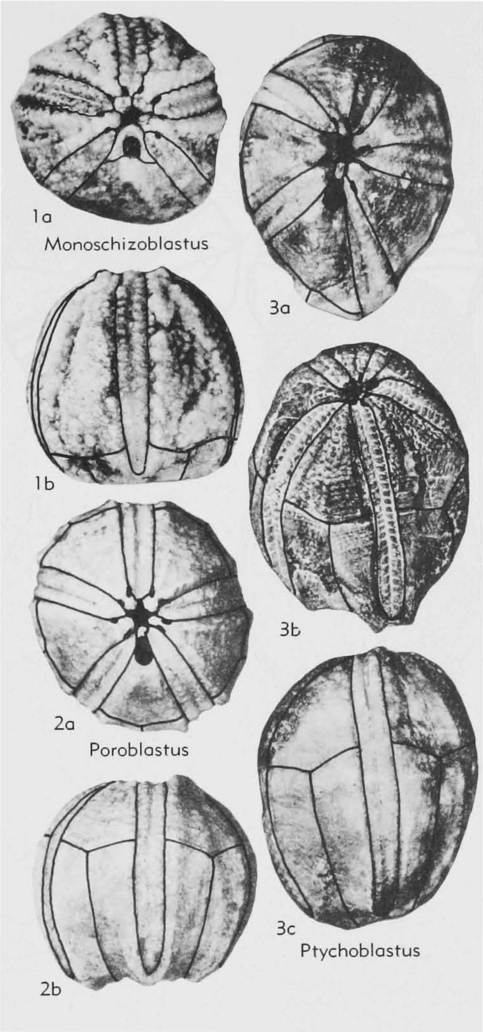


Fig. 269. Granatocrinidae (p. S425, S427).

**Schizoblastus** Etheridge & Carpenter, 1882, p. 243 [**Pentremites sayi* Shumard, 1855, p. 185; SD Etheridge & Carpenter, 1886, p. 220]. Theca ellipsoidal; anal opening between epideltoid and hypodeltoid; lancet exposed along main food groove; 1 pore between side plates along deltoid and radial margins; deltoids moderately long, overlapping radials; 2 hydrospire folds on each side of ambulacrum; base slightly concave. *Miss.*, N.Am.(Iowa-Mo.-Ill.).——Fig. 273,*2*; 274,*2*. **S. sayi* (Shumard), M.Miss., USA(Mo.); 273,*2a,b*, oral, *A*-ray views, ×2; 274,*2a-d*, oral, D-ray, aboral views, plate layout, ×2.2; 274,*2e*, cross sec. of ambulacrum, ×8.9 (28, 60, 154).

**Acentrotremites** Etheridge & Carpenter, 1883, p. 232 [**Mitra elliptica* Cumberland, 1826, p. 33;

OD]. Theca bell-shaped, with spiracles adjacent to radials; anal opening excavated in ?single anal deltoid; hydrospire plate present; pores absent along deltoids; deltoids overlapping radials; 4 or 5 hydrospire folds on each side of an ambulacrum; lancet covered by side plates; basalia seemingly fused to form single plate. *L.Carb.*, Eu. (Eng.).——Fig. 273,*3*; 274,*1*. **A. ellipticus* (Cumberland); 273,*3a,b*, oral, *CD* interambulacral views, ×1.3, ×0.7; 274,*1a-d*, oral, *D*-ray, ab-

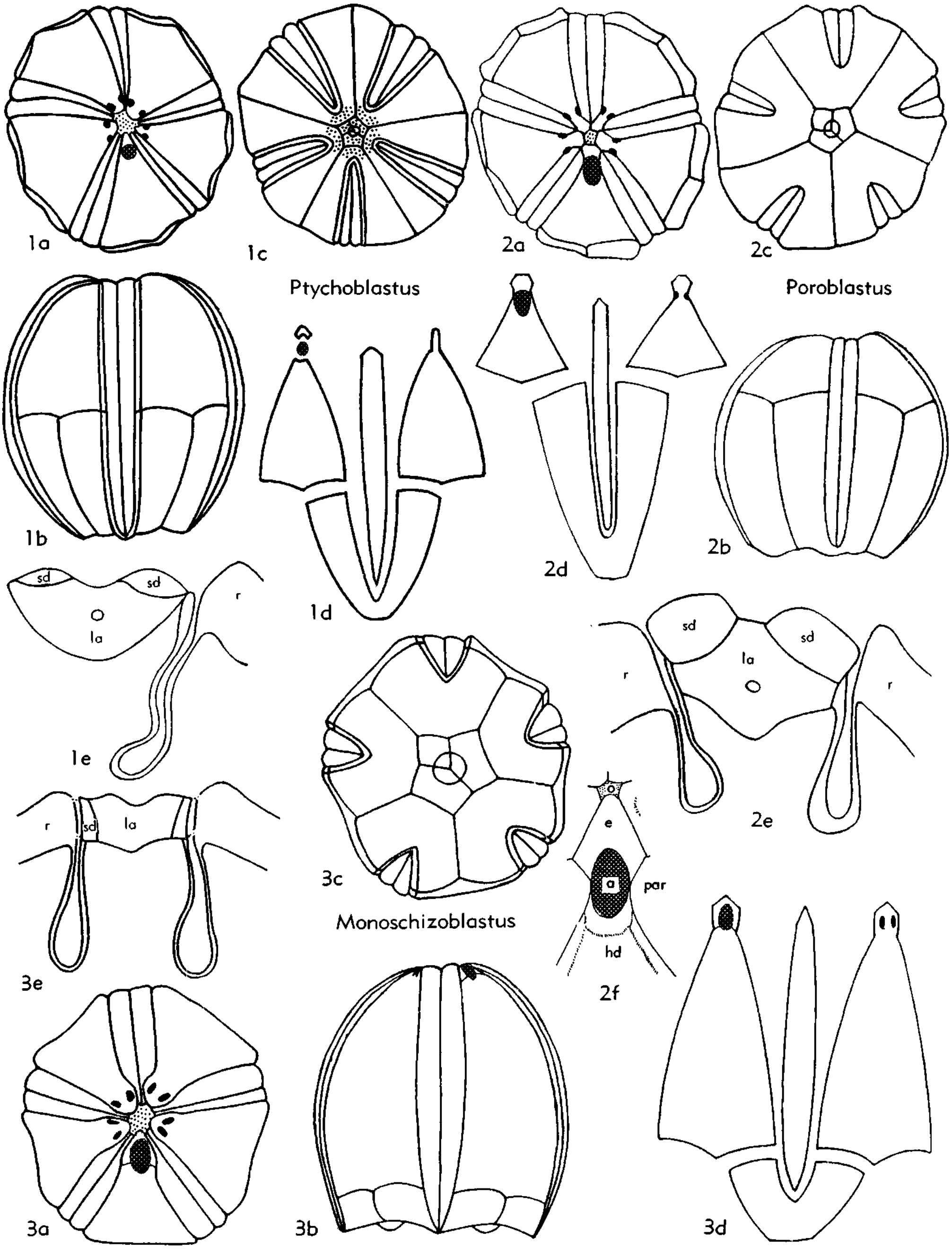


Fig. 270. Granatocrinidae (p. *S*425, *S*427). [Explanation*:* *a,* anal opening; *e,* epideltoid plate; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening; *par,* posterior ambulacrum (right); *r,* radial plate; *sd,* side plate.]

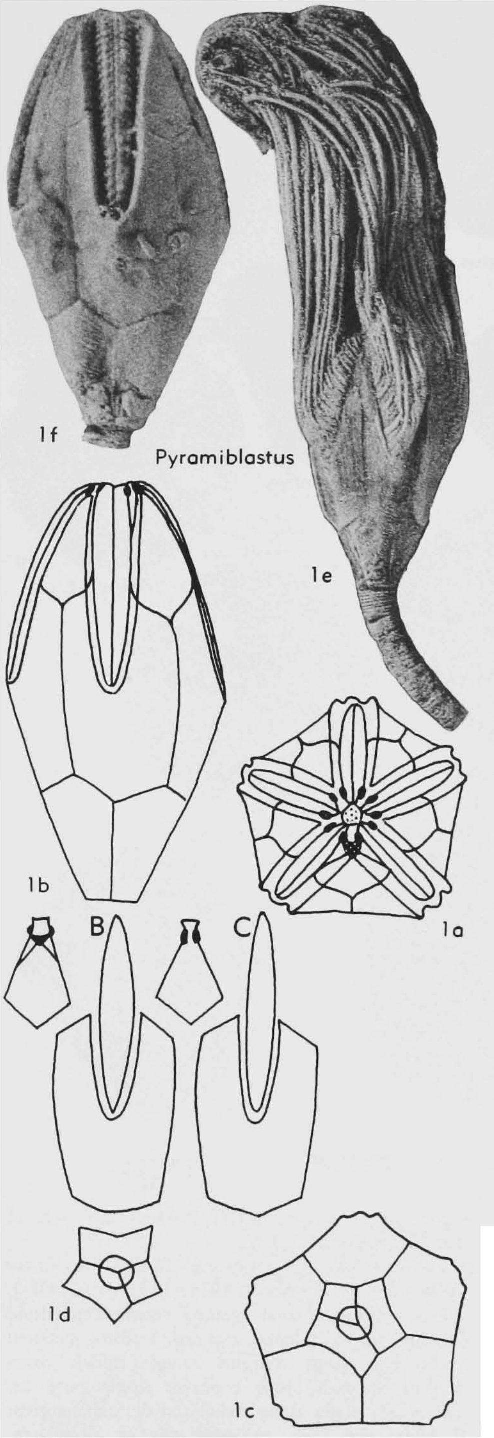


FIG. 271. Granatocrinidae (p. *S*427).

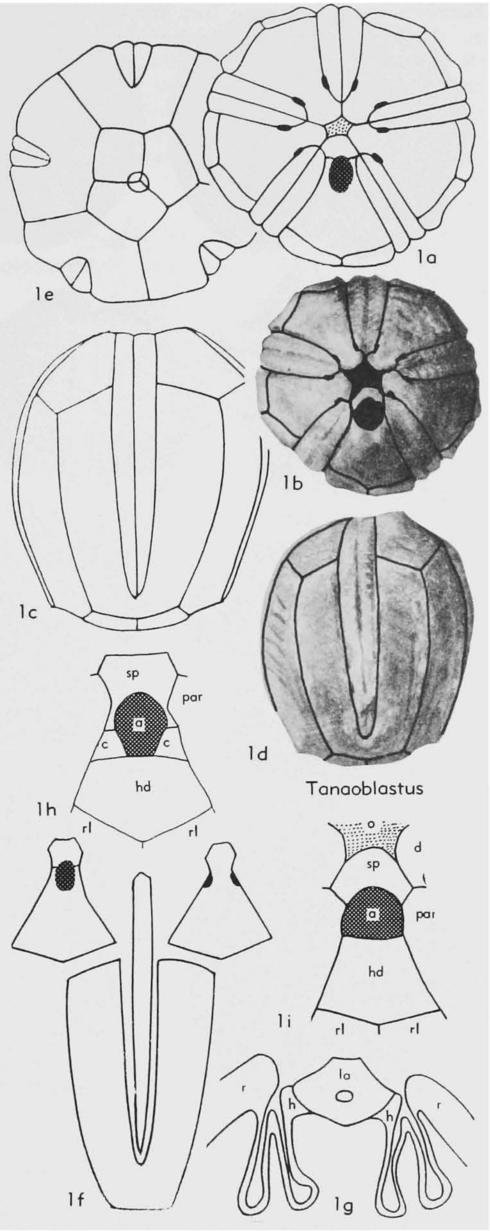


FIG. 272. Granatocrinidae (p. *S*427). [Explanation: *a*, anal opening; *c*, cryptodeltoid plate; *d*, deltoid plate; *h*, hydrospire plate; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening; *par*, posterior ambulacrum (right); *r*, radial plate; *rl*, radial limb; *sp*, superdeltoid plate.]

oral views, plate layout, ×1.3; 274,*1e,f*, cross secs. of ambulacrum, ×3.6 (12, 36, 40, 132).

**Auloblastus** BEAVER, 1961 (14), p. 1113 [**A. clinei*; OD]. Subspherical form with spiracles near sum-

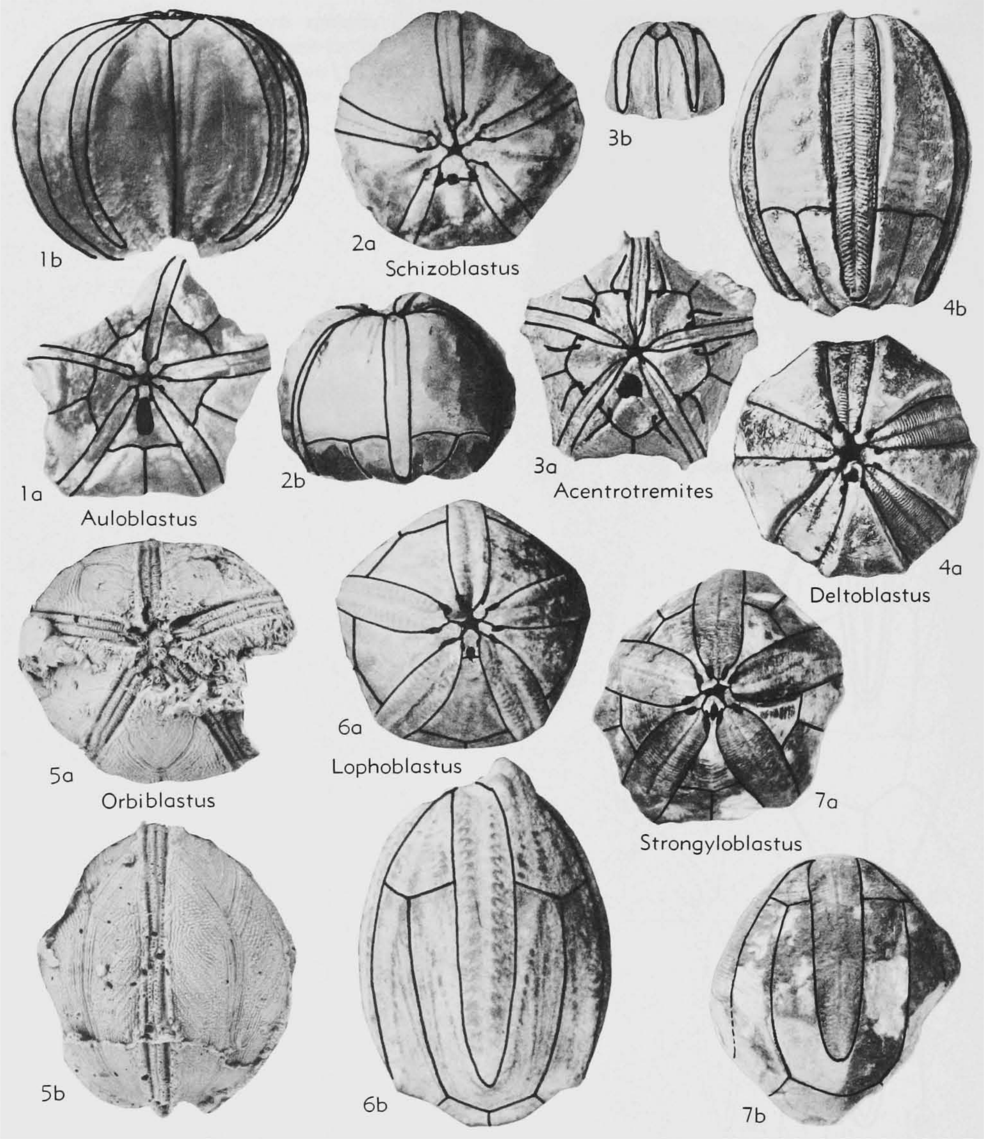


FIG. 273. Schizoblastidae (p. *S*427-*S*432).

mit; anal opening probably separate; basalia small, in concavity; radials long, overlapping deltoids; hydrospire plate absent; single pore between adjacent side plates along ambulacral margins; 4 hydrospire folds on each side of ambulacra; anal opening bordered adorally by superdeltoid, aborally by hypodeltoid, and internally on either side by cryptodeltoids; side plates cover lancets except near adoral tip; lateral canals present. *M.Miss.*, N.Am. (Mo.).——FIG. 273,*1*; 274,*3*. *_A. clinei_, USA (Mo.); 273,*1a,b,* oral, interambulacral views, ×1.3; 274,*3a-d,* oral, interambulacral, aboral views, plate layout, ×1.3; 274,*3e,* cross sec. of ambulacrum, ×10 (14).

**Deltoblastus** FAY, 1961 (49), p. 36 [*_Schizoblastus delta elongatus_ WANNER, 1924 (173), p. 61; OD]. Theca ellipsoidal; anal opening between epideltoid and hypodeltoid; lancet exposed, forming petaloid ambulacra; sinus margins raised; radials overlapping deltoids; base concave; single pore between side plates along radial and deltoid margins; 2 hydrospire folds on each side of ambulacra. *Perm.*, E. Indies(Timor)-?Eu.(?Sicily). —— FIG. 275,*1*. *D. permicus* (WANNER), Timor; 275,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×3.2; 275, *1e,* cross sec. of ambulacrum, ×7.7 (49).——FIG. 273,*4*. *D. timorensis* (BATHER), Perm., Timor; *4a,b,* oral, *B*-ray views, ×1.3 (11).

**Lophoblastus** ROWLEY, 1901, p. 344 [*emend.* MACURDA, 1962, p. 1370] [**Codonites inopinatus* ROWLEY & HARE, 1891, p. 100; OD]. Theca ellipsoidal, with anal opening between epideltoid and hooded hypodeltoid; 3 hydrospire folds on each side of ambulacra; lancet exposed 0.3 of its width; with single pore between adjacent side plates along deltoid and radial margins; deltoids overlapping radials. *Miss.,* N.Am.——FIG. 273,*6*; 276,*3*. **L. inopinatus* (ROWLEY & HARE), M.Miss.,

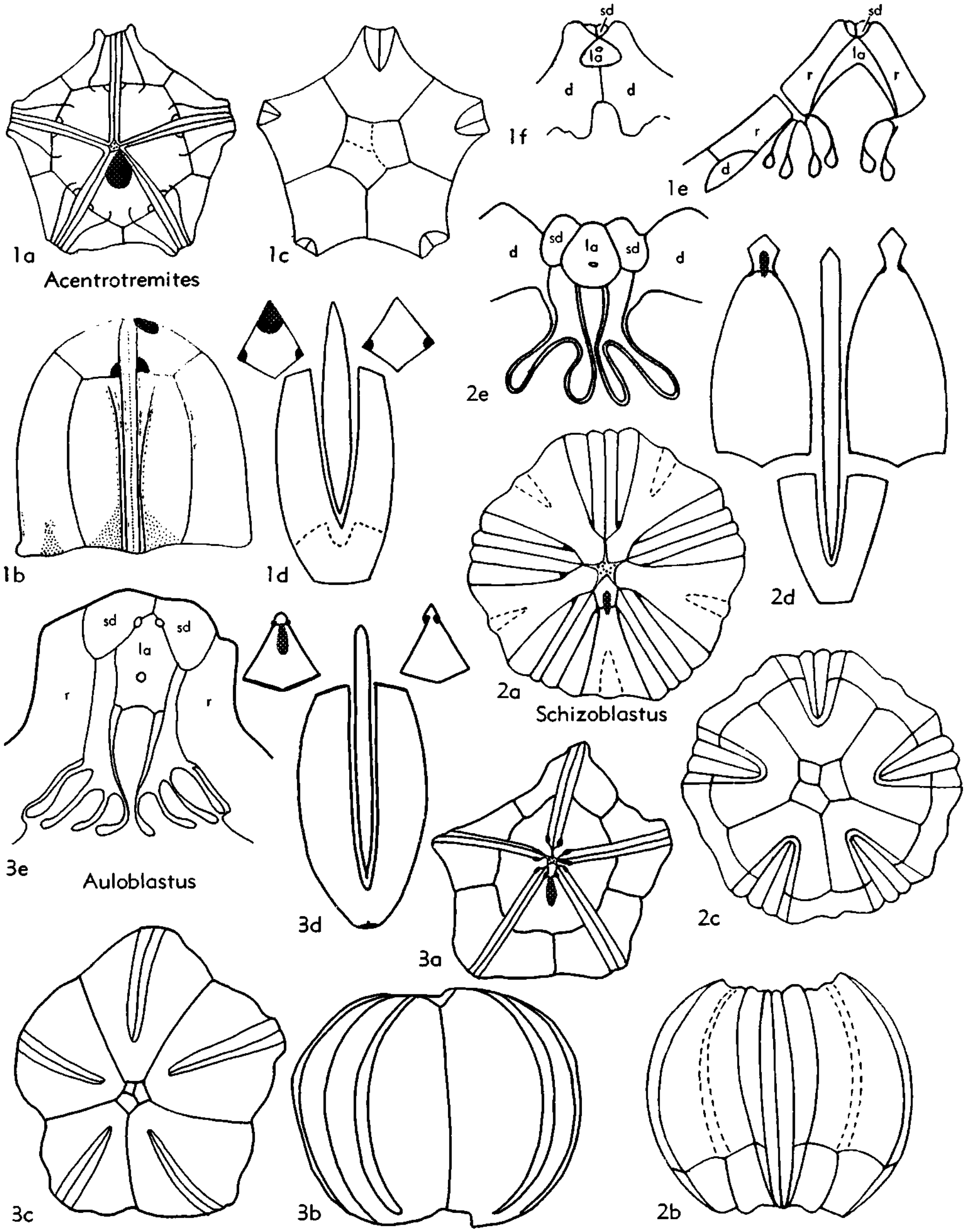


FIG. 274. Schizoblastidae (p. S427-S430). [Explanation: *d,* deltoid plate; *la,* lancet plate; *r,* radial plate; *sd,* side plate.]

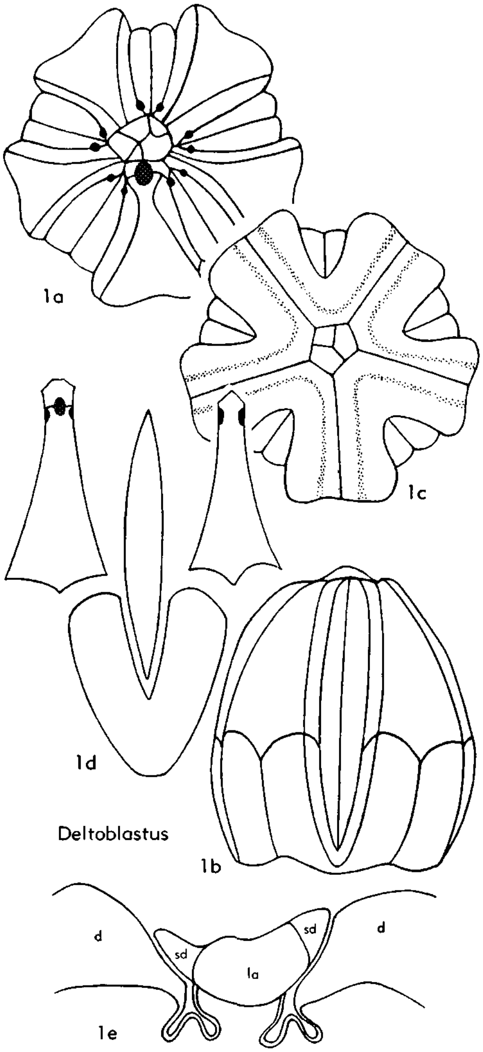


FIG. 275. Schizoblastidae (p. S430). [Explanation: *d,* deltoid plate; *la,* lancet plate; *r,* radial plate; *sd,* side plate.]

USA(Mo.); 273,*6a,* oral view, ×4.2; 273,*6b, D*-ray view, ×5.6; 276,*3a-d,* oral, *D*-ray, aboral views, plate layout, ×5.3; 276,*3e,* cross sec. of ambulacrum, ×13.1; 276,*3f,* anal view, ×10 (60).

**Orbiblastus** MACURDA, 1965 (106), p. 302 [**Orbiblastus hoskynae* MACURDA, 1965 (106), p. 303; OD]. Theca globular, with anal opening between epideltoid and hypodeltoid; 3 hydrospire folds on each side of ambulacra; lancet exposed along main food groove; one pore between each side plate along deltoid and radial margins; radials overlapping deltoids; basalia in basal concavity. *Miss.,* N.Am.(Ark.).——FIG. 273,*5;* 276,*2.* **O. hoskynae,* M.Miss., Ark.; 273,*5a,b,* oral, *D*-ray views, ×1.3; 276,*2a-d,* oral, *D*-ray, aboral views, plate layout, ×1.3 (106).

**Strongyloblastus** FAY, 1962 (68), p. 132 [**Strongyloblastus petalus* FAY, 1962, p. 132; OD]. Theca suboval, with spiracles near oral opening; anal opening between small epideltoid and moderately long hypodeltoid; deltoids visible in side view, overlapped by radials; lancet widely exposed, with single pore between side plates along radial and deltoid margins; 5 hydrospire folds on each side of ambulacra; ambulacra broadly petaloid and moderately long; periphery at radial lips below mid-height; basalia conical, large; theca subrounded pentagonal in top view. *M.Dev.,* USA (N.Y.).——FIG. 273,*7;* 276,*1.* **S. petalus* FAY; 273,*7a,b,* oral, *E*-ray views, ×1.3; 276,*1a-d,* oral, *E*-ray, aboral views, plate layout, ×1.3; 276,*1e,* cross sec. of *D* ambulacrum, aboral view, ×10 (68).

## Family NUCLEOCRINIDAE Bather, 1899

[Nucleocrinidae BATHER, 1899, p. 920] [=Nucleoblastidae ETHERIDGE & CARPENTER, 1886, p. 209 (invalid, based on nonexistent nominal genus); Olivanidae HAMBACH, 1903, p. 48 (invalid, based on nonexistent nominal genus)]

Theca with ten spiracles and anal opening separate around mouth, as in Schizoblastidae, but with two elongate, exposed cryptodeltoids. *Dev.*

**Nucleocrinus** CONRAD, 1842, p. 280 [**N. elegans;* OD]. Theca ellipsoidal; with 5 large oral plates and 3 exposed anal plates, consisting of 2 cryptodeltoids and hypodeltoid; superdeltoid hidden; anal oral abutting against cryptodeltoids; deltoids long, overlapping radials; 2 hydrospire folds on each side of ambulacra, with short hydrospire canal; lancet covered by side plates, with inner side plate present; one large pore between side plates along deltoid and radial margins. *Dev.,* N.Am.(N.Y.-Iowa-Mich.-Ont.).——FIG. 277,*1a-d;* 278,*1.* **N. elegans,* M.Dev., USA(N.Y.); 277, *1a-d,* oral, *D*-ray, aboral views, plate layout, ×2.6 (34, 60, 83); 278,*1a,b,* oral, *D*-ray views, ×5 (43).——FIG. 277,*1e-h. N. meloniformis* (BARRIS), M.Dev., USA(Mich.); *1e,* cross sec. of ambulacrum, ×8.8 (Fay, n); *1f-h,* anal views, ×10 (60).

**Elaeacrinus** ROEMER, 1851, p. 379 [**E. verneuili;* OD] [=*Olivanites* TROOST, 1849, p. 419 *(nom. nud.); Olivanites* LYON, 1857, p. 487 (type, *Olivanites verneuili* TROOST, 1849); *Eleacrinus* ETHERIDGE & CARPENTER, 1883, p. 228 *(nom. van.)*]. Theca elongate, ellipsoidal; with approximately 18 to 21 oral plates (one of which, however, may be superdeltoid); with 2 prominent, well-exposed cryptodeltoids and hypodeltoid; 1 or 2 anal orals between adoral tips of cryptodeltoids (if 1 it is superdeltoid, and if 2, the aboral one is superdeltoid); deltoids long, overlapping radials; 2 hydrospire folds on each side of ambulacra, with medium-long hydrospire canal; lancet covered by side plates, with inner side plate present; single large pore between side plates along deltoid and radial margins. *Dev.*, N.Am.(Ohio-Ind.-Ky.-Mo.).——FIG. 279,*1a-f*; 280,*1*. **E. verneuili* (TROOST), M.Dev., USA(Ind.); 279,*1a-d*, oral,

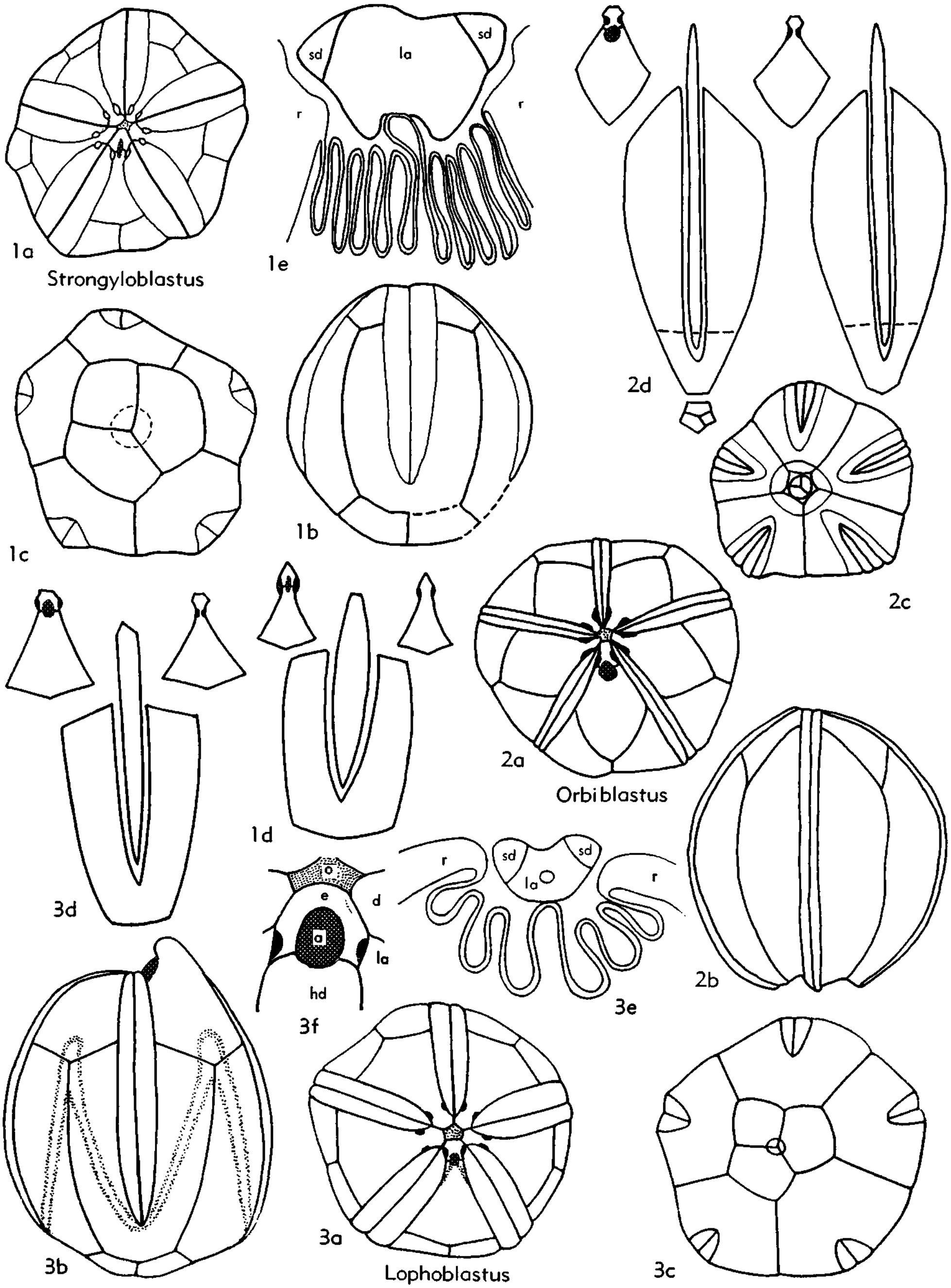


FIG. 276. Schizoblastidae (p. S431-S432). [Explanation: *a*, anal opening; *d*, deltoid plate; *e*, epideltoid plate; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening; *r*, radial plate; *sd*, side plate.]

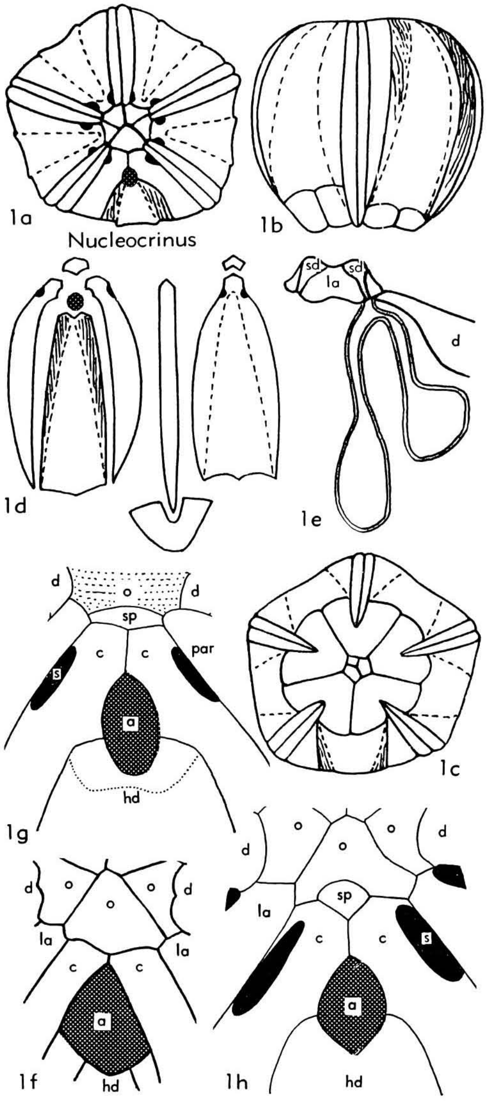


FIG. 277. Nucleocrinidae (p. S432). [Explanation: *a,* anal opening; *c,* cryptodeltoid plate; *d,* deltoid plate; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening or oral plate; *par,* posterior ambulacrum (right); *s,* spiracle; *sd,* side plate; *sp,* superdeltoid plate.]

*D*-ray, aboral views, plate layout, ×1 (60); 279, *1e,* cross sec. of ambulacrum, ×5 (48); 279,*1f,* anal view, ×4 (60); 280,*1a,b,* oral, *D*-ray views, ×1 (60).——FIG. 279,*1g,h. E. venustus* (MILLER & GURLEY), M.Dev., Ohio; *1g,h,* anal views, ×5.7 (60).

**Placoblastus** FAY, 1961 (60), p. 92 [**Elaeacrinus obovatus* BARRIS, 1883, p. 358; OD]. Theca elongate ellipsoidal; with prominent, well-exposed cryptodeltoids and hypodeltoid; 6 or 7 large oral plates, one of which is between aboral ends of cryptodeltoids and may be superdeltoid plate; lancet covered by side plates, with inner side plate present; single large pore between side plates along deltoid and radial margins; deltoids long, overlapping radials; 2 hydrospire folds on each side of ambulacra, with long hydrospire canal. *Dev.,* N. Am.(Iowa-Mich.-N. Y.-Ind.-Ohio).——FIG. 280,*2*; 281,*1a-f.* **P. obovatus* (BARRIS), M. Dev., USA(Mich.); 280,*2a,b,* oral, *EA* interambulacral views, ×1.1; 281,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×1.3; 281,*1e,* cross sec. of ambulacrum, ×13.1; 281,*1f,* anal view, ×7.5 (60).——FIG. 281,*1h. P. angularis* (LYON), M. Dev., N.Y.; anal view, ×7.8 (60).——FIG. 281, *1g. P. lucina* (HALL), M.Dev., N.Y.; anal view, ×10 (60).

## Family PENTREMITIDAE d'Orbigny, 1851

[*nom. correct.* ETHERIDGE & CARPENTER, 1886, p. 148 (*pro* Pentremitidaea D'ORBIGNY, 1851, p. 139)] [=Eleutherocrinidae BATHER, 1899, p. 920; Eleutheroblastidae, p. 50; Pentremidae, p. 35, HAMBACH, 1903]

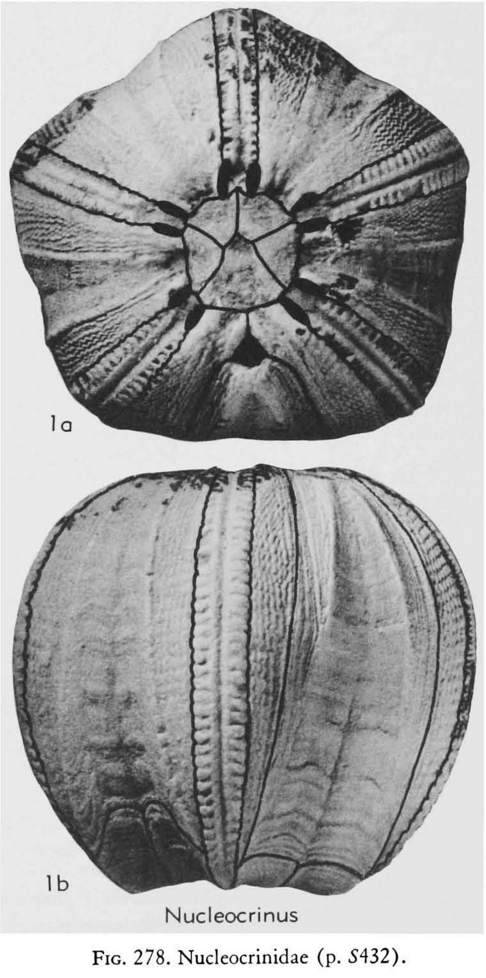


FIG. 278. Nucleocrinidae (p. S432).

Theca subconical or subpyriform with four spiracles and anispiracle around mouth. *Dev.-Perm.*

**Pentremites** SAY, 1820, p. 36 [**Encrina Godonii* DEFRANCE, 1819, p. 467; SD ETHERIDGE & CARPENTER, 1886, p. 157] [*nom. correct.* SOWERBY, 1825, p. 316 (*pro Pentremite* SAY, 1820)] [=*Asterite, Asterial fossil, Encrina, Encrinites, Pentatrematites, Pentatremites,* AUCTT. *(partim)*]. Theca club-shaped to subpyriform; anispiracle excavated in undivided anal deltoid plate; with 3 to 7 or more hydrospire folds on each side of an ambulacrum; oral and anal areas covered by many imbricate plates; one pore between side plates along radial and deltoid margins; lancet widely exposed, forming petaloid ambulacra; radials overlapping deltoids. *Miss.-Penn.,* N.Am.-S.Am.(Colombia).——FIG. 282,*1*. **P. godoni* (DEFRANCE), U.Miss., USA(Ill.); *1a-d,* oral, *D*-ray, aboral views, plate layout, ×2.6; *1e,* cross sec. of ambulacrum, ×5.3 (Fay, n).——FIG. 283,*3*. *P. sulcatus* (ROEMER), U.Miss., Ill.; *3a,b,* oral, side views, ×1 (78).

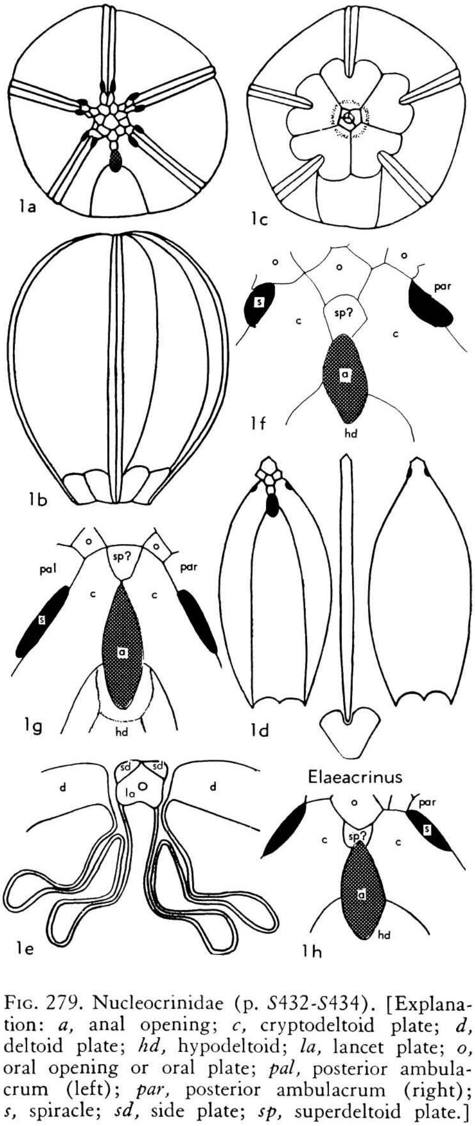


FIG. 279. Nucleocrinidae (p. S432-S434). [Explanation: *a,* anal opening; *c,* cryptodeltoid plate; *d,* deltoid plate; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening or oral plate; *pal,* posterior ambulacrum (left); *par,* posterior ambulacrum (right); *s,* spiracle; *sd,* side plate; *sp,* superdeltoid plate.]

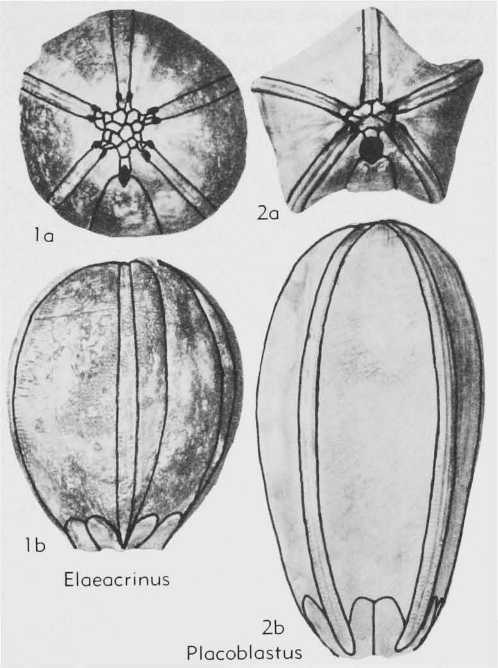


FIG. 280. Nucleocrinidae (p. S432-S434).

**Ambolostoma** PECK, 1930, p. 104 [**A. baileyi*; OD]. Theca ellipsoidal; anispiracle in undivided anal deltoid plate; 5 large oral plates covering summit; lancet completely exposed; one large pore between adjacent side plates along deltoid and radial margins; 3 hydrospire folds on each side of an ambulacrum. *Miss.,* N.Am.(Utah-Alta.).——FIG. 282,2; 284,*6*. **A. baileyi,* USA(Utah); 282,*2a-d,* oral, *D*-ray, aboral views, plate layout, ×0.87; 282,*2e,* cross sec. of ambulacrum, ×17.6; 284,*6a,* oral view, ×1.1; 284,*6b,* interradial view, ×0.8 (130).

**Belocrinus** MUNIER-CHALMAS, 1881, p. 503 [*emend.* MACURDA, 1966 (110), p. 245] [**Belemnocrinus cottaldi* MUNIER-CHALMAS, 1876, p. 105; OD] [=*Belemnocrinus* MUNIER-CHALMAS, 1876, p. 105 (*non* WHITE, 1862)]. Theca club-shaped, with extremely elongate pelvis; spiracles five, simple, with anispiracle between epideltoid? and hypodeltoid (possibly with two deeply hidden cryptodeltoids); deltoids visible in side view, including hypodeltoid; lancet covered by side plates, with one pore between adjacent side plates along radial and deltoid margins; number of hydrospires unknown but in ten groups or fields. *L.Dev.*, Eu. (NW.Fr.).——FIG. 282,*3*; 283,*4*. **B. cottaldi* (MUNIER-CHALMAS), Eu.(NW.Fr.); 282,*3a-d*, oral, *A*-ray, aboral views, plate layout, ×1.3; 283,*4a,b*, oral, *A*-ray views, ×2 (110).

**Calycoblastus** WANNER, 1924 (173), p. 35 [*emend.* BREIMER & MACURDA, 1965, p. 215] [**C. tricavatus*; OD]. Theca subpyramidal, with anispiracle between epideltoid and hypodeltoid; radials overlapping deltoids; 5 hydrospire folds on each

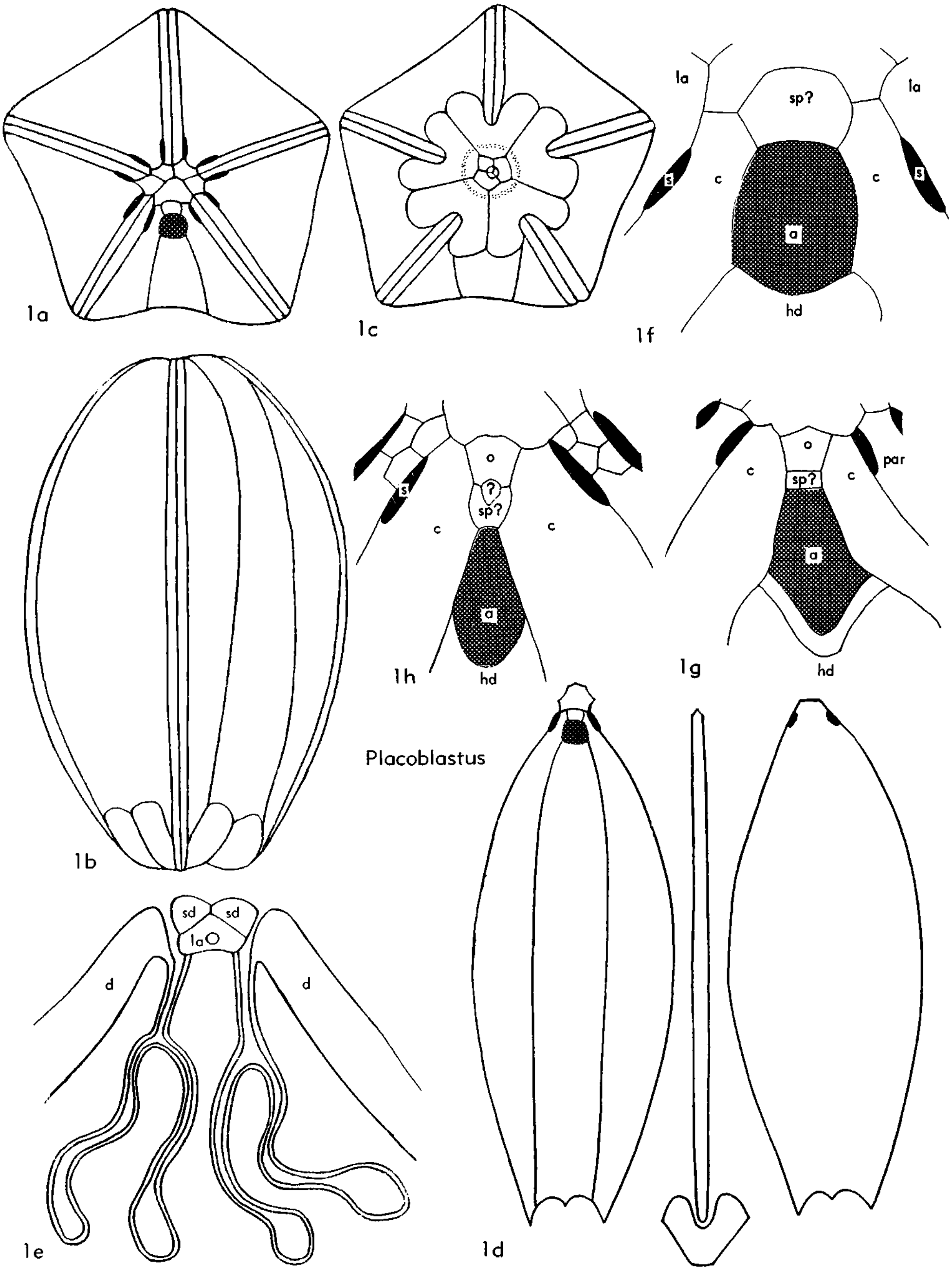


FIG. 281. Nucleocrinidae (p. S434). [Explanation: *a*, anal opening; *c*, cryptodeltoid plate; *d*, deltoid plate; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening or oral plate; par, posterior ambulacrum (right); *s*, spiracle; *sd*, side plate; *sp*, superdeltoid plate.]

side of an ambulacrum; sublancet or fused hydrospire plate present; lancet covered by side plates; deltoids visible in side view. *Perm.*, E.Indies (Timor)-Australia(New S. Wales).——FIG. 283, *1*; 284,*4*; 285,*2*. *C. tricavatus, Timor, 283,*1*, *A*-ray view, ×1; 284,*4*, oral view, ×1.3; 285, *2a-d*, oral, *D*-ray, aboral views, plate layout, ×1.8; 285,*2e*, cross sec. of ambulacrum, ×3.8 (173).

**Cordyloblastus** FAY, 1961 (60), p. 52 [*Pentremites

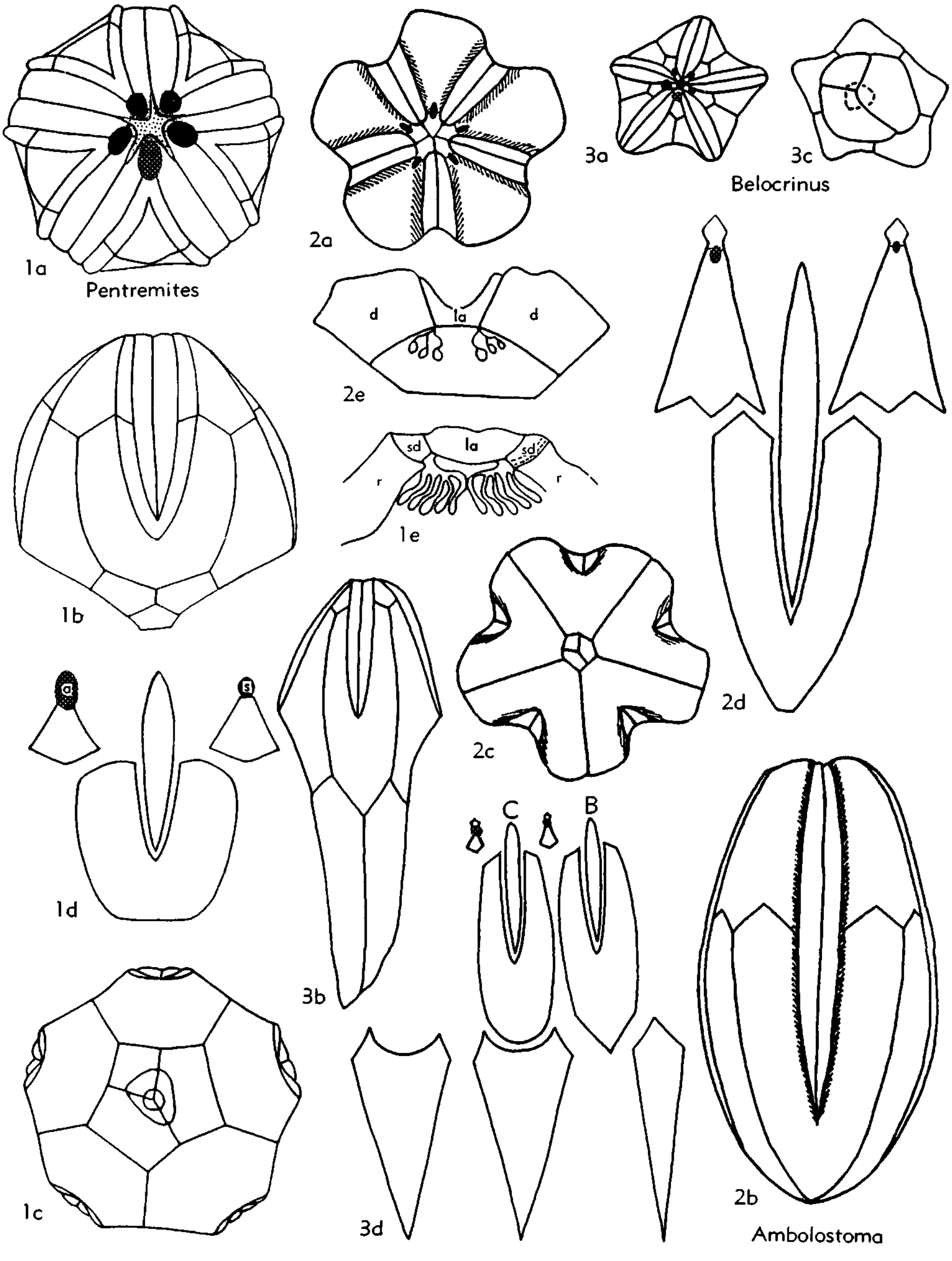


FIG. 282. Pentremitidae (p. S435-S436). [Explanation: *a*, anispiracle; *d*, deltoid plate; *la*, lancet plate; *r*, radial plate; *s*, spiracle; *sd*, side plate.]

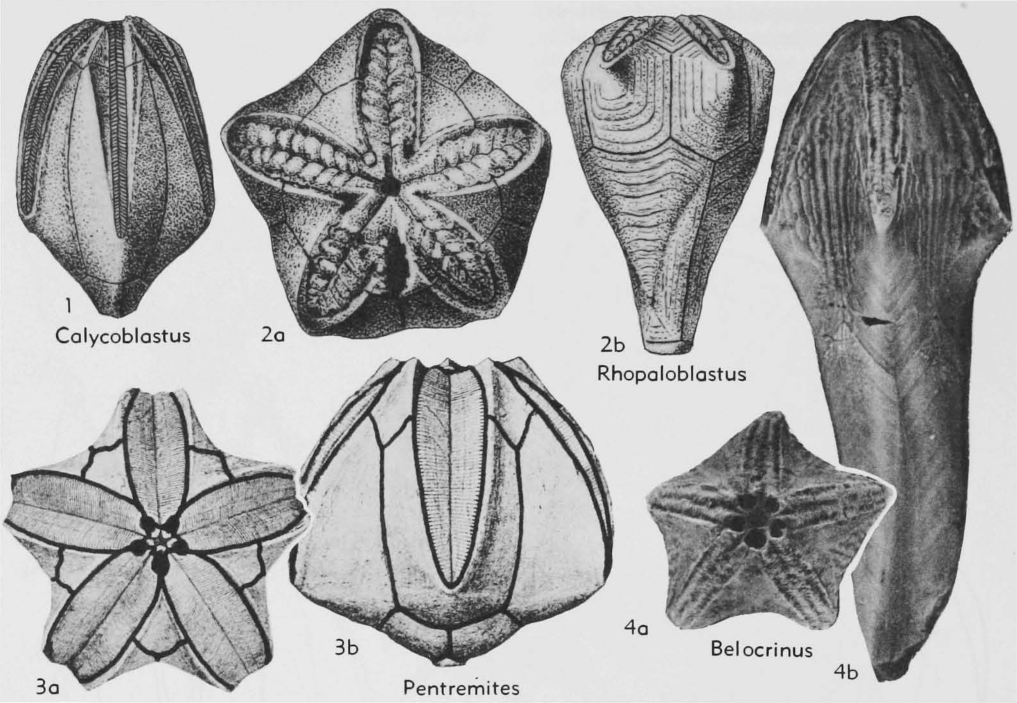


FIG. 283. Pentremitidae (p. S435-S437, S443).

*acutangulus* SCHULTZE, 1886, p. 225; OD]. Theca club-shaped; with anispiracle between superdeltoid and large hypodeltoid, with 2 internal cryptodeltoids; hypodeltoid seen in side view but not other 4 deltoids; radials overlapping deltoids; lancet covered by side plates; one pore between adjacent side plates along radial margins; with 4 to 9 hydrospire folds on each side of an ambulacrum. *Dev.,* Eu.(Ger.-Spain).——FIG. 284,*3*; 285, *1a-f*. **C. acutangulus* (SCHULTZE), Eifel., Ger.; 284,*3a,b,* oral, *D*-ray views, ×1.7; 285,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×1.8; 285,*1e,* cross sec. of ambulacrum, ×13.1; 285,*1f,* anal view, ×10 (60).——FIG. 285,*1g-i*. *C. eifelensis* (ROEMER), M.Dev., Ger.; *1g,* anal view, ×10; *1h,* anal view, ×30; *1i,* anal view, ×10 (60).

**Devonoblastus** REIMANN, 1935, p. 30 [**Pentremites leda* HALL, 1862, p. 149; SD REIMANN, 1942, p. 47]. Theca elliptico-conical; anispiracle between superdeltoid and hypodeltoid, with 2 cryptodeltoids beneath hypodeltoid; 5 hydrospire folds on each side of an ambulacrum; lancet covered by side plates except at adoral end; one pore between side plates along radial and deltoid margins; deltoids visible in side view, overlapped by radials. *Dev.,* N. Am.(N.Y.-?Ind.-Ont.)-?Asia(?China).——FIG. 286,*2a-d*. **D. leda* (HALL), M.Dev., USA (N.Y.); *2a-d,* oral, *D*-ray, aboral views, plate layout, ×2.6 (41, 60, 137).——FIG. 284,*5*; 286,*2e-g*. *D. whiteavesi* REIMANN, M.Dev., Ont.; 284,*5a,b,* oral, *D*-ray views, ×2.2; 286,*2e-g,* 3 anal views, ×10 (60).

**Eleutherocrinus** SHUMARD & YANDELL, 1856, p. 73 [**E. cassedayi*; OD] [=*Eleutheroblastus* HAMBACH, 1903, p. 50 (obj.)]. Theca ellipsoidal, with superdeltoid, 2 cryptodeltoids, and hypodeltoid; short *D* ambulacrum; 6 or 7 hydrospire folds on each side of an ambulacrum; lancet covered by side plates; one pore between adjacent side plates along deltoid and radial margins; radials overlapping deltoids; thecal plates slightly irregular. *Dev.,* N.Am.(Ky.-Ind.-N.Y.-Ont.).——FIG. 284,*1*; 286,*1*. **E. cassedayi,* M.Dev., Can.(Ont.); 284,*1a,* oral view, ×3; 284,*1b, D*-ray view, ×2.8; 284, *1c,* aboral view, ×2.9; 284,*1d, B*-ray view, ×2.9; 284*1e, C*-ray view, ×3.4; 286,*1a-f,* oral, *D*-ray, aboral views, plate layout, cross sec. of middle part of ambulacrum, cross sec. of aboral tip of ambulacrum, ×6.6; 286,*1g,* anal view, ×10 (60, 158).

**Pentremoblastus** FAY & KOENIG, 1963, p. 267 [**Pentremoblastus conicus*; OD]. Theca conical to obconical, with elongate split-elliptical spiracles; anispiracle between superdeltoid, subdeltoid, and hypodeltoid; elongate radials overlap short deltoids along an inverted V-shaped suture; deltoids barely visible in side view; lancet exposed full width, with one pore between side plates; 2 to 3 hydrospire folds on anal side, but 5 hydrospire folds on each side of other ambulacra; stem round.

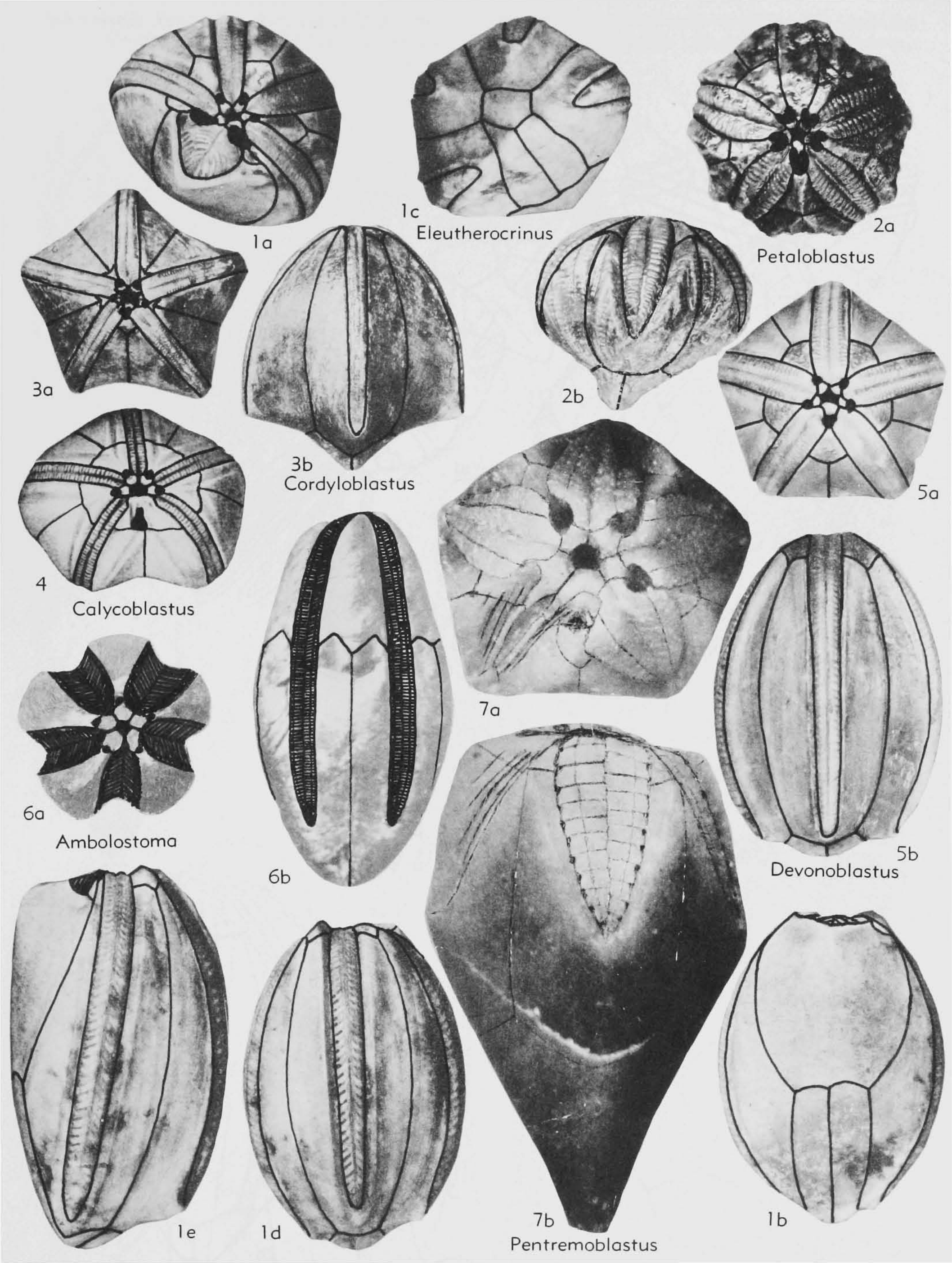


FIG. 284. Pentremitidae (p. S435-S438, S440-S443).

*L.Miss.*, USA(Ill.).——Fig. 284,7; 287,1. **P. conicus*, Kinderhook., Ill.; 284,*7a,b*, oral, *C*-ray views, ×11.4; 287,*1a-d*, oral, *C*-ray, aboral views, plate layout, ×11.4 (75).

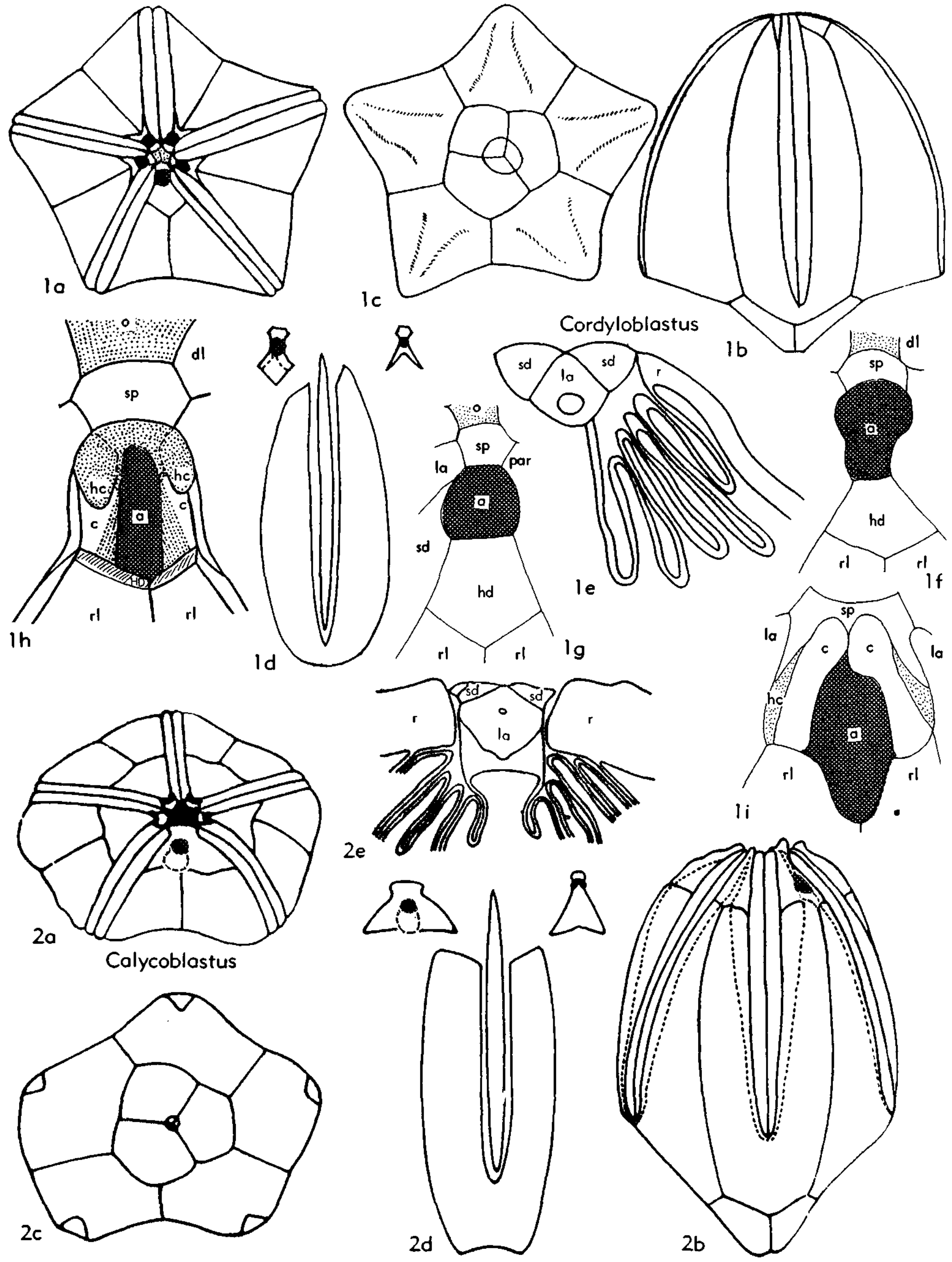


Fig. 285. Pentremitidae (p. *S*436-*S*438). [Explanation: *a*, anal opening; *c*, cryptodeltoid plate; *dl*, deltoid lip; *hc*, hydrospire canal; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening or oral plate; *par*, posterior ambulacrum (right); *r*, radial plate; *rl*, radial limb; *sd*, side plate; *sp*, superdeltoid plate.]

**Petaloblastus** FAY, 1961 (60), p. 90 [**Pentremites ovalis* GOLDFUSS, 1829, p. 161; OD]. Theca ovoid, with anispiracle located between epideltoid and hypodeltoid; radials overlapping deltoids, but

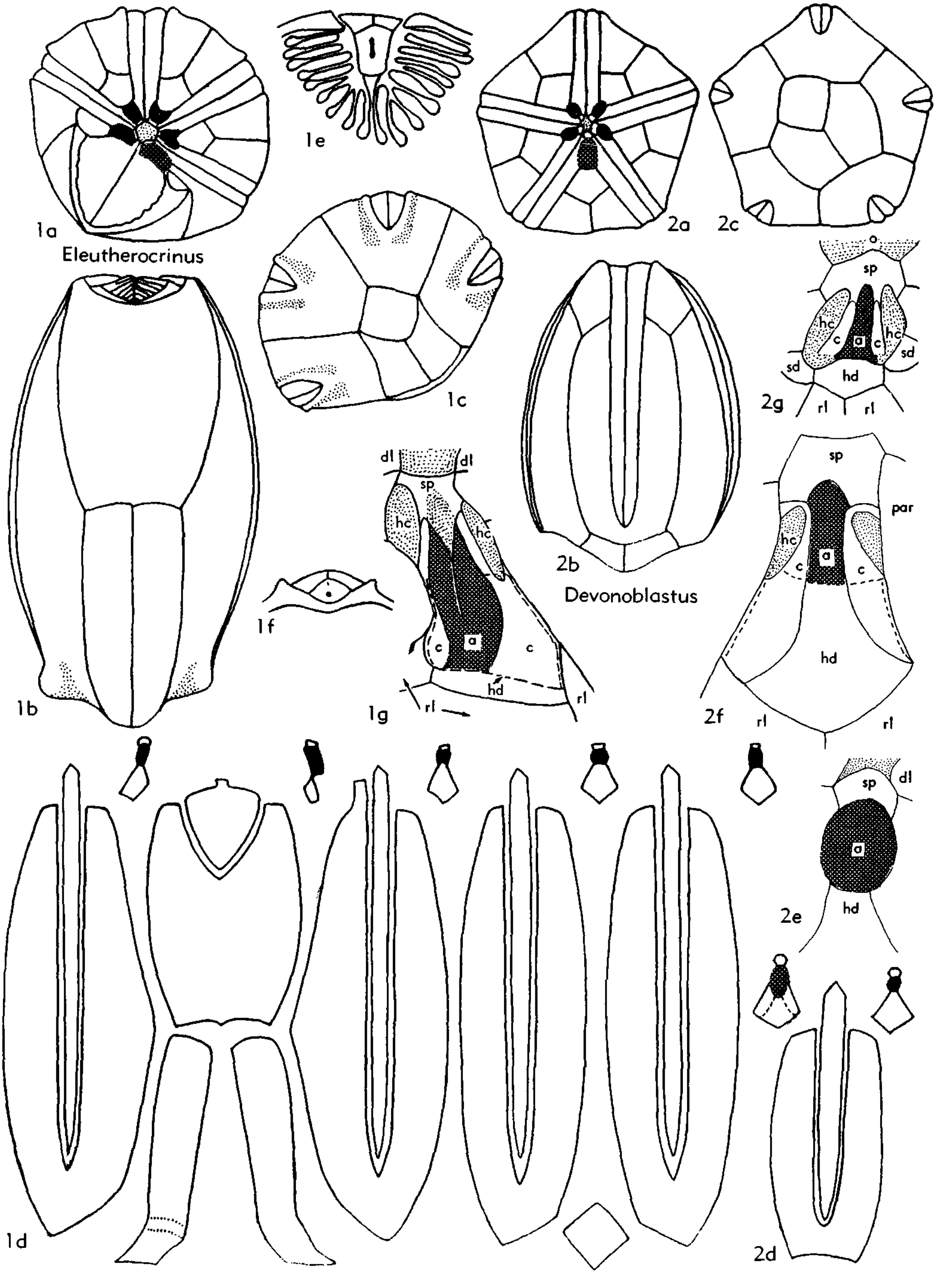


FIG. 286. Pentremitidae (p. S438). [Explanation: *a,* anal opening; *c,* cryptodeltoid plate; *dl,* deltoid lip; *hc,* hydrospire canal; *hd,* hypodeltoid; *o,* oral opening or oral plate; *par,* posterior ambulacrum (right); *rl,* radial lip; *sd,* side plate; *sp,* superdeltoid plate.]

radiodeltoid suture inverted V-shaped (opposite to that seen in *Pentremites*); at least 4 hydrospire folds on each side of an ambulacrum; lancet exposed its full width, forming petaloid ambulacra; one pore between side plates along radial and deltoid margins. *L.Carb.,* Eu.(Ger.).——FIG. 284, *2. P. boletus* (SCHMIDT), L.Miss., Ger.; *2a,b,* oral, *D*-ray views, ×2.9 (63).——FIG. 287,*2.* **P. ovalis*

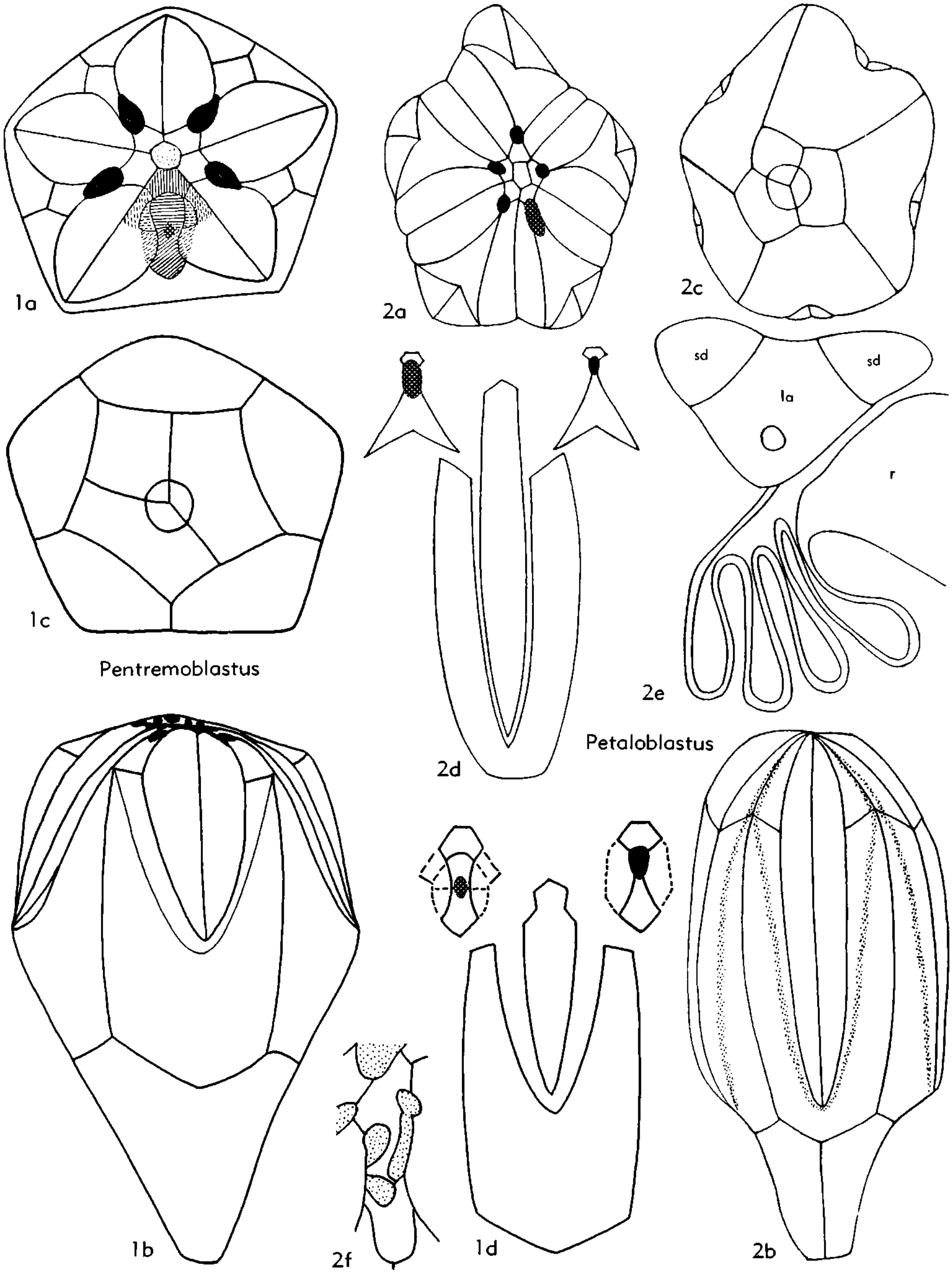


FIG. 287. Pentremitidae (p. S438, S440-S443). [Explanation: *la,* lancet plate; *r,* radial plate; *sd,* side plate.]

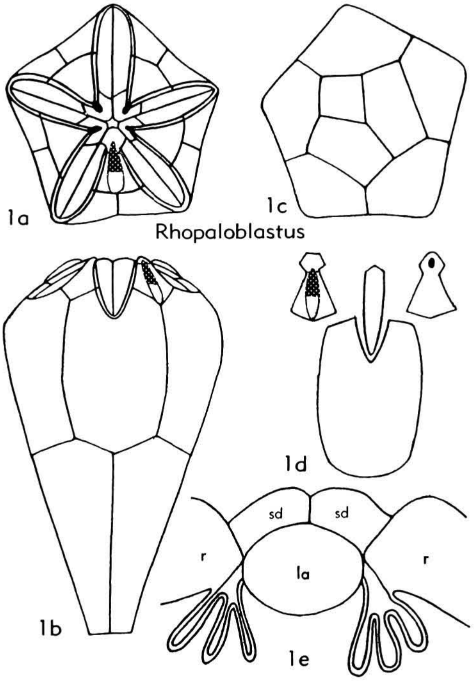


FIG. 288. Pentremitidae (p. *S*443). [Explanation: *la,* lancet plate; *r,* radial plate; *sd,* side plate.]

(GOLDFUSS), Etroeungt.; *2a-d,* oral, *D*-ray, aboral views, plate layout, ×11.1; *2e,* cross sec. of ambulacrum, ×39.5; *2f,* anal view, ×15 (60).

**Rhopaloblastus** WANNER, 1924 (174), p. 215 [*emend.* BREIMER & MACURDA, 1965, p. 216] [**R. timoricus*; OD]. Theca obconical, with 4 spiracles plus anispiracle; anispiracle between a superdeltoid, 2 exposed cryptodeltoids, and a hypodeltoid; one pore between side plates along radial and deltoid margins; ambulacra moderately short, almost confined to summit, with lancet stipe away from mouth; lancet covered by side plates; radials short, basals long; 3 hydrospire folds on each side of an ambulacrum. *Perm.,* E.Indies (Timor)-Australia.——FIG. 283,*2*; 288,*1*. **R. timoricus,* Timor; 283,*2a,* oral view, ×4; 283,*2b, BC* inter-ray view, ×2.5; 288,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×2.6; 288,*1e,* cross sec. of ambulacrum, ×13.1 (174, 178).

## Family ORBITREMITIDAE Bather, 1899

[Orbitremitidae BATHER, 1899, p. 920]

Theca subglobular with five spiracles (including anispiracle) around mouth. *Miss.*

**Orbitremites** AUSTIN & AUSTIN, 1842, p. 111 [**Pentremites derbiensis* SOWERBY, 1825, p. 317; SD BATHER, 1899 (9), p. 24] [=*Orbitremites* GRAY, 1840, p. 12 *(nom. nud.)*]. Theca ellipsoidal; with superdeltoid, 2 cryptodeltoids, and hypodeltoid; hydrospire plate present; approximately twice as many pores as side plates along deltoid and radial margins; one hydrospire fold on each side of an ambulacrum; deltoids overlapping radials; lancet exposed along middle one-third of its width. *L.Carb.,* Eu.(Eng.).——FIG. 289,*1*; 290,*1a-g*. **O. derbiensis* (SOWERBY); 289, *1a,b,* oral, *D*-ray views, ×4.2; 290,*1a-d,* oral, *D*-ray, aboral views, plate layout, ×5.9; 290,*1e,* cross sec. of ambulacrum, ×11.7; 290,*1f,g,* 2 anal views, ×10 (3, 41, 60, 161).——FIG. 290,*1h*. *O. ellipticus* (SOWERBY), L.Carb., Eng.; anal view, ×10 (60).

**Doryblastus** FAY, 1961 (54), p. 194 [**Mesoblastus melonianus* SCHMIDT, 1930, p. 69; OD]. Theca ellipsoidal, with 4 V-shaped spiracles plus anispiracle; anispiracle located between epideltoid and hypodeltoid, possibly with 2 cryptodeltoids be-

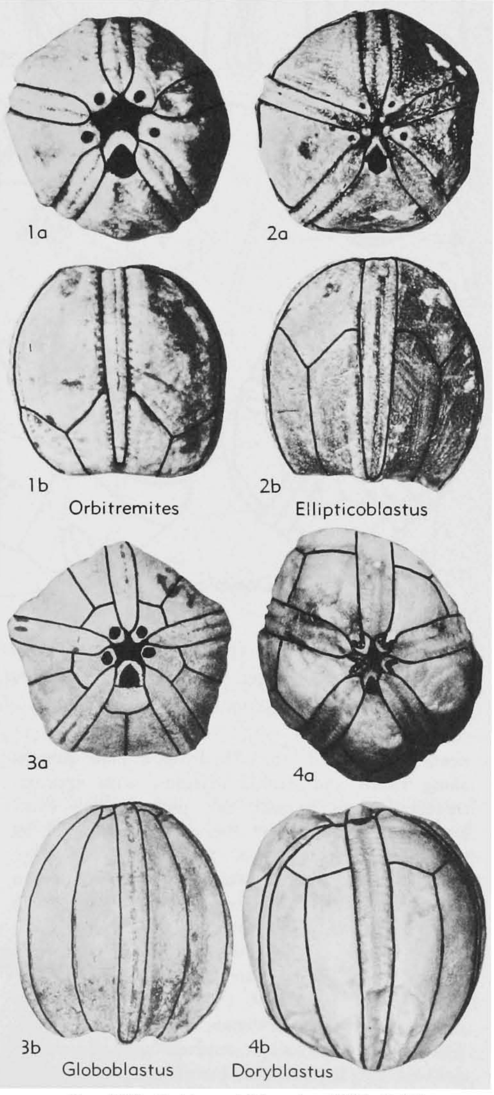


FIG. 289. Orbitremitidae (p. *S*443-*S*445).

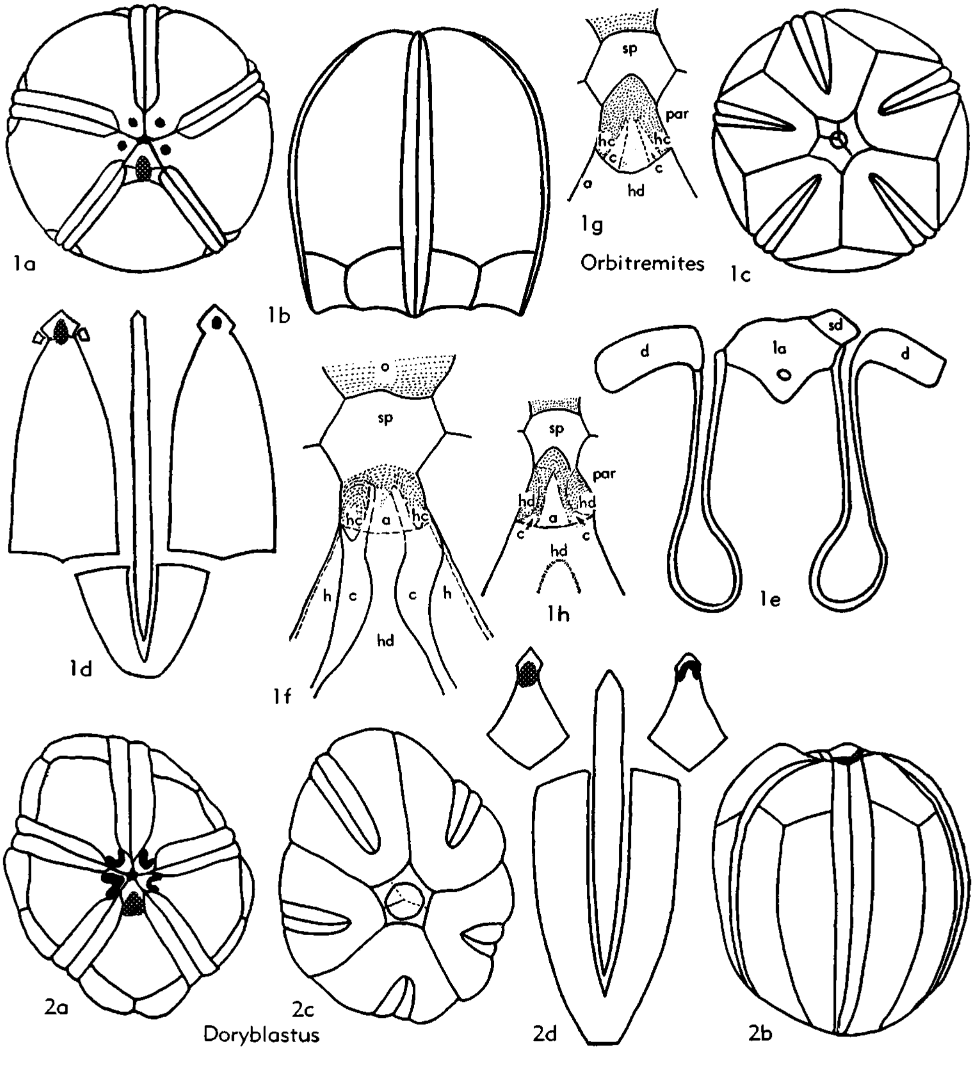


FIG. 290. Orbitremitidae (p. S443-S444). [Explanation: *a,* anispiracle; *c,* cryptodeltoid plate; *d,* deltoid plate; *h,* hydrospire plate; *hc,* hydrospire canal; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening; *par,* posterior ambulacrum (right); *sd,* side plate; *sp,* superdeltoid plate.]

neath hypodeltoid; thick hydrospire plate present along radial and deltoid margins, with approximately 2 pores to each side plate; radials overlapping deltoids; lancet exposed one-third of its width; basalia small, in deep basal concavity; possibly 3 hydrospire folds on each side of an ambulacrum. *M.Miss.,* Ger.——FIG. 289,*4*; 290,*2*. **D. melonianus* (SCHMIDT), U.Tournais., Ger.; 289,*4a,b,* oral, *D*-ray views, ×4.1; 290,*2a-d,* oral, *D*-ray, aboral views, plate layout, ×4.2 (54).

**Ellipticoblastus** FAY, 1960 (47), p. 317 [**Pentatrematites orbicularis* SOWERBY, 1834, p. 456; OD]. Theca elliptical; with superdeltoid, 2 cryptodeltoids, and hypodeltoid; hydrospire plate present; approximately twice as many pores as side plates along deltoid and radial margins; one long hydrospire fold, curved, on each side of an ambulacrum; radials overlapping deltoids; lancet exposed along middle one-third of its width. *L.Carb.,* Eu. (Eng.).——FIG. 289,*2*; 291,*2*. **E. orbicularis* (SOWERBY); 289,*2a,b,* oral, *D*-ray views, ×4.1; 291,*2a-d,* oral, *D*-ray, aboral views, plate layout, ×4.4; 291,*2e,* anal view, ×10 (60); 291,*2f,* cross sec. of ambulacrum, ×6.5 (41).

**Globoblastus** HAMBACH, 1903, p. 46 [**Pentremites norwoodi* OWEN & SHUMARD, 1850, p. 64; OD]. Theca subglobular; with superdeltoid, 2 cryptodeltoids, and hypodeltoid; lancet covered by side

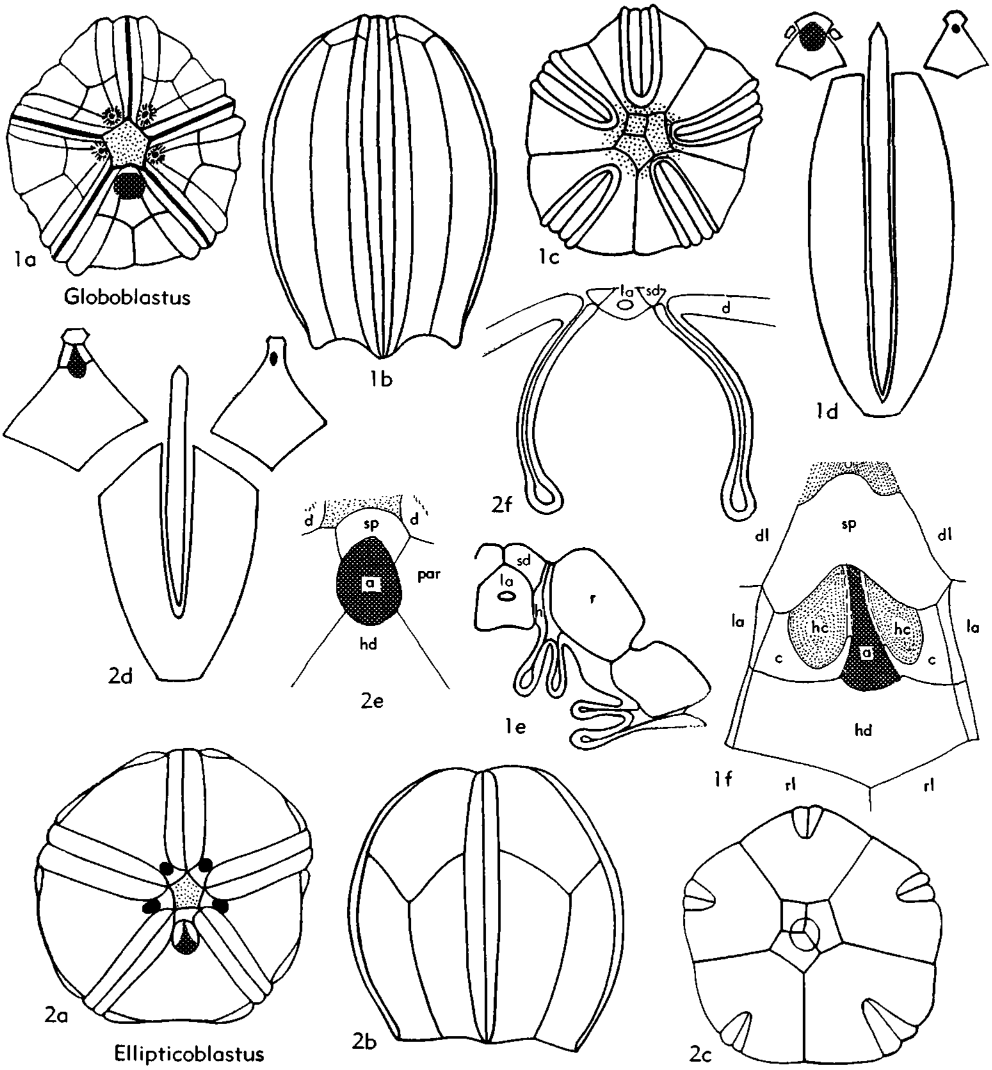


FIG. 291. Orbitremitidae (p. S444-S445). [Explanation: *a*, anispiracle; *c*, cryptodeltoid plate; *d*, deltoid plate; *dl*, deltoid lip; *h*, hydrospire plate; *hc*, hydrospire canal; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening or oral plate; *par*, posterior ambulacrum (right); *r*, radial plate; *rl* radial limb; *sd*, side plate; *sp*, superdeltoid plate.]

plates except near adoral end; radials overlapping short deltoids; hydrospire plate present; 2 hydrospire folds on each side of an ambulacrum; approximately 2 pores to each side plate along radial margins. *Miss.*, N.Am.(Ill.-Iowa-Mo.).——FIG. 289,*3*; 291,*1*. **G. norwoodi* (OWEN & SHUMARD), M.Miss., Iowa; 289,*3a,b*, oral, *D*-ray views, ×2.4; 291,*1a-d*, oral, *D*-ray, aboral views, plate layout, ×3.6; 291,*1e*, cross sec. of ambulacrum, ×8.8; 291,*1f*, anal view, ×11.8 (45, 60, 86, 128).

## REFERENCES

**Allen, A. T., Jr., & Lester, J. G.**

(1) 1953, *Ecological significance of a Mississippian blastoid:* Georgia Geol. Survey, Bull., no. 60, p. 190-199, pl. 1-6. [*Pentremites.*]

**Arendt, Yu. A.**

(2) 1960, *Novyy podvid blastoidey iz podmoskovnogo karbona:* Moskov. Obshch. Ispyt. Prir., Byull., new ser., v. 65, Otdel Geol.,

v. 35, pt. 4, p. 149-150 (Bull. Soc. Impér. Nat. Moscou, new ser., v. 65, Geol. Sec., v. 35). [In Russian.] [*New subspecies of blastoid in Carboniferous near Moscow.*] [*Orbitremites derbiensis musatovi.*]

**Austin, Thomas, & Austin, Thomas, Jr.**

(3) 1842, *Proposed arrangement of the Echinodermata particularly as regards the Crinoidea, and a subdivision of the class Adelostella (Echinidae):* Ann. & Mag. Nat. History, v. 10, no. 63, art. 18, p. 106-113. [*Astracrinites, Orbitremites.*]

(4) 1843, *Descriptions of several new genera and species of Crinoidea:* Same, v. 11, no. 69, art. 33, p. 195-207. [Astracrinidae.]

**Barris, W. H.**

(5) 1883, *Description of some new blastoids from the Hamilton group:* Illinois State Geol. Survey, v. 7, p. 357-364, 3 text fig. [*Nucleocrinus meloniformis, Placoblastus obovatus,* described as now recognized.]

**Bassler, R. S.**

(6) 1938, *Pelmatozoa Palaeozoica: (generum et genotyporum index et bibliographia):* Fossilium Catalogus, pt. 1: Animalia, pars 83, p. 1-194, W. Junk ('s-Gravenhage). [Index of blastoid nominal genera and their type species.]

**———, & Moodey, M. W.**

(7) 1943, *Bibliographic and faunal index of Paleozoic pelmatozoan echinoderms:* Geol. Soc. America, Spec. Paper, no. 45, 734 p. [Lists 350 named species and 50 genera of blastoids, with many subsequent references. This is best bibliographic index at present, but validity of names and dates needs to be checked and used with caution.]

**Bather, F. A.**

(8) 1899, *A phylogenetic classification of the Pelmatozoa:* British Assoc. Adv. Sci., Rept. 68th meeting, p. 916-923. [Lists new families and orders; interprets blastoids as related to diploporitan cystoids.]

(9) 1899, *The genera and species of Blastoidea, with a list of the specimens in the British Museum (Natural History):* x+70 p., 1 text fig. (London).

(10) 1900, *The Echinodermata. The Pelmatozoa:* in A Treatise on Zoology, E. R. Lankester (ed.), pt. 3, 216 p., text fig., Adam & Charles Black (London). [Elaboration of classification (8) with illustrations.]

(11) 1908, *Jüngeres Paläozoicum von Timor, Genus Schizoblastus Etheridge and Carpenter:* in Geologische Mitteilungen aus dem Indo-Australischen Archipel by G. Boehm, Neues Jahrb. Mineralogie, usw., Beil.-Band, v. 25, p. 303-319, pl. 10-11. [*Schizoblastus* described from Permian deposits; now changed to *Deltoblastus.*]

(12) 1912, *Two blastoids (Orophocrinus and Acentrotremites) from Somerset:* Bristol Nat. Soc., Proc., ser. 4, v. 3, pt. 2, p. 47-50, 1 pl. [Verifies occurrence of *Mitra elliptica* Cumberland in Visean (*Dibunophyllum* $D_2$ Zone) at Wrington, England.]

**Beaver, H. H.**

(13) 1961, *Morphology of the blastoid Globoblastus norwoodi:* Jour. Paleontology, v. 35, no. 6, p. 1103-1112, 2 text fig., pl. 129, 130.

(14) 1961, *Auloblastus, a new blastoid from the Mississippian Burlington limestone:* Same, v. 35, no. 6, p. 1113-1116, 1 text fig., pl. 131.

**Bergounioux, F. M.**

(15) 1953, *Classe des Blastoïdes (Blastoidea Say, 1925):* in Traité de Paléontologie, Jean Piveteau (ed.), v. 3, p. 629-650, 36 text fig., Masson et Cie (Paris). [Follows classification of Bassler & Moodey (7), describing *Asteroblastus* and *Blastoidocrinus* as protoblastoids, though in same volume Cuénot (p. 627) classes former as diploporitan cystoid; includes new observations on optic orientation of hydrospires by Gabriel Lucas.]

**Billings, Elkanah**

(16) 1869, *Notes on the structure of the Crinoidea, Cystidea and Blastoidea:* Am. Jour. Sci., ser. 2, v. 48, whole no. 98, no. 142, art. 8, p. 69-83, 12 text fig. [Introduces name hydrospires for infolds in plates of blastoids and other echinoderms.]

**Bond, Geoffrey**

(17) 1949 (1950), *The Lower Carboniferous reef limestones of Cracoe, Yorkshire:* Geol. Soc. London, Quart. Jour., v. 105, p. 157-188, 4 text fig., pl. 7.

**Breimer, A., & Macurda, D. B., Jr.**

(18) 1965, *On the systematic position of some blastoid genera from the Permian of Timor:* [K.] Ned. Akad. Wetensch., Proc., ser. B, v. 68, no. 4, p. 209-217.

**Bronn, H. G.**

(19) 1848, *Handbuch einer Geschichte der Natur. Dritter Band. Erster Abtheilung, erste und zweite Hälfte. III. Theil: Index palaeontologicus, unter Mitwirkung HH.H.R. Göppert und H. von Meyer. A. Nomenclator palaeontologicus:* A-M, 1381 p.; N-Z, 1106 p., E. Schweizerbart (Stuttgart). [*Zygocrinus.*]

**Brown, I. A.**

(20) 1941, *Permian blastoids from New South Wales:* Royal Soc. New S. Wales, Jour. & Proc., v. 75, pt. 3, p. 96-103, text fig. 1-2, pl. 1. [Describes *Notoblastus brevispinus,*

*Calycoblastus casei,* and *Rhopaloblastus(?) belfordi* (formerly *Tricoelocrinus*).]

**Buch, Leopold von**

(21) 1846 (1845), *Über Cystideen eingeleitet durch die Entwicklung der Eigenthümlichkeiten von Caryocrinus ornatus, Say:* K. Akad. Wiss. Berlin, Abhandl. 1844, p. 89-116, pl. 1-2. [Introduces name Cystoidea.]

**Carpenter, P. H.**

(22) 1878, *On the oral and apical systems of the echinoderms:* Quart. Jour. Micro. Sci., Mem., new ser., v. 18, no. 72, p. 351-383, 11 text fig., table.

(23) 1884, *Report upon the Crinoidea collected during the voyage of H.M.S. Challenger during the years 1873-76:* Rept. Scientific Results Explor. Voyage HMS Challenger, Zoology, v. 11, Rept. 2, xi+414 p., 21 text fig., 62 pl.

**Chi, Y. S.**

(24) 1943, *A Lower Carboniferous blastoid from the Tushan district, Kueichou:* Geol. Soc. China, Bull., v. 23, no. 3-4, p. 111-113, 1 pl. [First description of a blastoid *(Mesoblastus tushanensis)* from China (from Kolaoho Series); judging from figures, belongs to some new genus.]

**Clark, A. H.**

(25) 1915, *A monograph of the existing crinoids:* U.S. Natl. Museum, Bull 82, v. 1, pt. 1, 406 p., 122 text fig., 17 pl. [Indicates possible nervous system in blastoids.]

**Clark, H. L.**

(26) 1915, *The comatulids of Torres Strait: with special reference to their habits and reactions:* Carnegie Inst. Washington, Dept. Marine Biology, v. 7, p. 97-125.

**Cline, L. M.**

(27) 1934, *Osage formations of southern Ozark region, Missouri, Arkansas, and Oklahoma:* Am. Assoc. Petroleum Geologists, Bull. v. 18, no. 9, p. 1132-1159, 2 text fig.

(28) 1936, *Blastoids of the Osage group, Mississippian: part I. The genus Schizoblastus:* Jour. Paleontology, v. 10, no. 4, p. 260-281, pl. 44-45. [*Monoschizoblastus* described as new genus.]

(29) 1937, *Blastoids of the Osage group, Mississippian: part II. The genus Cryptoblastus:* Same, v. 11, no. 8, p. 634-649, pl. 87-88.

(30) 1944, *Class Blastoidea:* in H. W. Shimer & R. R. Shrock, Index Fossils of North America, p. 133-137, pl. 50-51, Wiley & Sons (New York). [Describes and figures species of 12 genera without family assignments or stratigraphic arrangement.]

**———, & Beaver, Harold**

(31) 1951, *Observations pertaining to the paleoecology of the blastoids:* National Research Council, Division of Geology and Geography, Report of the Committee on a Treatise on Marine Ecology and Paleoecology 1950-1951, no. 11, p. 62-71.

(32) 1957, *Blastoids:* in Treatise on marine ecology and paleoecology, v. 2. Paleoecology, H. S. Ladd (ed.), Geol. Soc. America, Mem. 67, p. 955-960. [Also 1951, National Research Council, Division of Geology and Geography, Report of the Committee on a Treatise on Marine Ecology and Paleoecology 1950-1951, no. 11, p. 62-71.] [Only serious attempt to compile ecological information about blastoids.]

**———, & Heuer, Edward**

(33) 1950, *The Codaster alternatus—Codaster pyramidatus group of blastoids from the mid-Devonian of North America:* Jour. Paleontology, v. 24, no. 2, p. 154-173, 6 text fig., pl. 27-28, 2 tables. [Describes anal deltoids named superdeltoid and subdeltoid.]

**Conrad, T. A.**

(34) 1842, *Observations on the Silurian and Devonian systems of the United States, with descriptions of new organic remains:* Acad. Nat. Sci. Philadelphia, Jour., v. 8, pt. 2, p. 228-280, pl. 15. [*Nucleocrinus elegans, Stephanocrinus angulatus.*]

**Croneis, Carey, & Geis, H. L.**

(35) 1940, *Microscopic Pelmatozoa: part 1, Ontogeny of the Blastoidea:* Jour. Paleontology, v. 14, no. 4, p. 345-355, 4 text fig. [Analyzes presumed larval stages of *Mesoblastus glaber* and *Pentremites princetonensis* from Chesteran of Illinois.]

**Cumberland, George**

(36) 1826, *Reliquiae Conservatae, from the primitive materials of our present globe, with popular descriptions of the prominent characters of some remarkable fossil Encrinites, and their connecting links:* 8vo., 43 p., 38 text fig., pl. A-C (Bristol). [Describes *Mitra vera, M. depressa, M. eliptica (sic), M. hibernica, M. rugoso, M. quinqueperforata, M. elongata, M. humerostellata.*]

**Defrance, M. J. L.**

(37) 1819, *Encrines:* Dictionnaire Sciences Naturelles, v. 14, EA-EOU, p. 467 (Paris). [Lists *encrina Godonii,* which is first binominal zoological designation for a blastoid species.]

**Etheridge, Robert, Jr.**

(38) 1876, *On the occurrence of the genus Astrocrinites (Austin) in the Scotch Carboniferous Limestone series; with the description of a new species (A.? benniei), and remarks on the genus:* Geol. Soc. London, Quart. Jour., v. 32, pt. 2, no. 126, art. 13, p. 103-115, pl. 12-13.

**———, & Carpenter, P. H.**

(39) 1882, *On certain points in the morphology of the Blastoidea, with descriptions of some new genera and species:* Ann. & Mag. Nat. History, ser. 5, v. 9, no. 52, art. 25, p. 213-252. [Describes *Pentremitidea lusitanica, P. angulata, P. similis, Phaenoschisma acutus* (Phillips), *Ph. caryophyllatus* (de Koninck), *Ph. Archiaci, Ph. Verneuili, Codaster Hindei, Granatocrinus, Schizoblastus, Troostocrinus, Orophocrinus* (names for many of which are now changed).]

(40) 1883, *Further remarks on the morphology of the Blastoidea, with descriptions of a new British Carboniferous genus, and some new Devonian species from Spain:* Same, ser. 5, v. 11, no. 64, art. 31, p. 225-246. [Describes *Acentrotremites, Phaenoschisma nobile, Troostocrinus hispanicus, Pentremitidea Malladae.*]

(41) 1886, *Catalogue of the Blastoidea in the Geological Department of the British Museum (Natural History), with an account of the morphology and systematic position of the group, and a revision of the genera and species:* Brit. Museum Catalogue, xvi+322 p., 8 text fig., 20 pl. (London). [Describes many new genera and species, new morphological parts, and summarizes geographic and stratigraphic information on blastoids. This work has formed the basis for most treatises and textbooks for many years.]

**Eykeren, H.**

(42) 1942, *Microblastus gen. nov. und einige andere neue permische Blastoideen von Timor; in Beiträge zur Paläontologie des Ostindischen Archipels; XVIII:* Neues Jahrb., Geologie u. Paläontologie, Beil.-Band or Abh., Abt. B, v. 86, no. 2, p. 282-298, 5 text fig., pl. 17.

**Fay, R. O.**

(43) 1960, *The type of Nucleocrinus Conrad:* Oklahoma Geol. Survey, Oklahoma Geol. Notes, v. 20, no. 9, p. 236-239, text fig. 1, pl. 1.

(44) 1960, *The "pores" of Stephanocrinus Conrad:* Same, v. 20, no. 10, p. 256-259, pl. 1-2.

(45) 1960, *The type species of Globoblastus Hambach:* Same, v. 20, no. 11, p. 292-299, pl. 1-4.

(46) 1960, *Ptychoblastus, a new Mississippian blastoid from Missouri:* Jour. Paleontology, v. 34, no. 6, p. 1198-1201, text fig. 1.

(47) 1960, *The type species of Orbitremites Austin & Austin, 1842, and Ellipticoblastus, a new Mississippian genus:* Oklahoma Geol. Survey, Oklahoma Geol. Notes, v. 20, no. 12, p. 315-317, pl. 1.

(48) 1961, *The blastoid collection of the Philadelphia Academy of Natural Sciences:* Same, v. 21, no. 1, p. 10-22, pl. 1-4.

(49) 1961, *Deltoblastus, a new Permian blastoid from Timor:* Same, v. 21, no. 2, p. 36-40, pl. 1-2.

(50) 1961, *The type of Tricoelocrinus Meek & Worthen:* Same, v. 21, no. 3, p. 90-94, text fig. 1-3, pl. 1.

(51) 1961, *The type of Devonoblastus Reimann, 1935:* Same, v. 21, no. 4, p. 110-112, pl. 1.

(52) 1961, *Nymphaeoblastus, a Mississippian blastoid from Japan:* Same, v. 21, no. 5, p. 150-153, pl. 1.

(53) 1961, *The type species of Monoschizoblastus Cline, 1936:* Same, v. 21, no. 6, p. 173-175, pl. 1.

(54) 1961, *Doryblastus, a new Mississippian blastoid from Germany:* Same, v. 21, no. 7, p. 194-196, pl. 1.

(55) 1961, *The type of Pentremites Say:* Jour. Paleontology, v. 35, no. 4, p. 868-873, text fig. 1.

(56) 1961, *The type of Pentremitella, a Lower Devonian blastoid from Germany:* Oklahoma Geol. Survey, Oklahoma Geol. Notes, v. 21, no. 8, p. 229-232, pl. 1-2.

(57) 1961, *The type species of Stephanocrinus Conrad:* Same, v. 21, no. 9, p. 236-238, pl. 1.

(58) 1961, *The type of Streptelasma expansa Hall, 1847, an Ordovician Blastoidocrinus fragment from the Chazy Limestone of New York:* Same, v. 21, no. 9, p. 247-248.

(59) 1961, *Agmoblastus, a new Pennsylvanian blastoid from Oklahoma:* Same, v. 21, no. 10, p. 278-280, pl. 1.

(60) 1961, *Blastoid studies:* Univ. Kansas, Paleont. Contrib., Echinodermata, Art. 3, p. 1-147, text fig. 1-221, pl. 1-54. [Reviews development of blastoid knowledge, with revision of most pre-Permian genera and species, key to genera, and tentative classification. New morphological information is presented, 12 new genera described, and enlarged drawings of small features are given. Plates present original photographs. Bibliography containing 811 titles is incomplete. Conclusion is reached that almost all previously reported blastoid species must be examined, illustrated, and described anew.]

(61) 1961, *The type species of Pterotoblastus, a Permian blastoid from Timor:* Oklahoma Geol. Survey, Oklahoma Geol. Notes, v. 21, no. 11, p. 298-300, pl. 1.

(62) 1961, *Type of Schizotremites, a Devonian blastoid from New York:* Same, v. 21, no. 12, p. 331-333, pl. 1.

(63) 1962, *Types of Petaloblastus, a Mississippian blastoid from Germany:* Same, v. 22, no. 1, p. 16-20, text fig. 1, pl. 1-2.

(64) 1962, *Type species of Pleuroschisma, a Devonian blastoid from New York:* Same, v. 22, no. 3, p. 85-88, pl. 1-2.

(65) 1962, *Edrioblastoidea, a new class of Echinodermata:* Jour. Paleontology, v. 36, no. 2, p. 201-205, text fig. 1-3, pl. 34.

(66) 1962, *Ventral structures of Stephanocrinus angulatus Conrad:* Same, v. 36, no. 2, p. 206-210, text fig. 1, pl. 35.

(67) 1962, *Brachyschisma, a Middle Devonian blastoid from New York:* Oklahoma Geol. Survey, Oklahoma Geol. Notes, v. 22, no. 4, p. 103-108, text fig. 1, pl. 1-2.

(68) 1962, *Strongyloblastus, a new Devonian blastoid from New York:* Same, v. 22, no. 5, p. 132-135, pl. 1-2.

(69) 1962, *Mespilocystites, an Ordovician coronate crinoid from Czechoslovakia:* Same, v. 22, no. 6, p. 156-161, text fig. 1-3, pl. 1-2.

(70) 1962, *On Schizoblastus? devonianus from the Onondaga Limestone, New York:* Same, v. 22, no. 6, p. 164-165, text fig. 1.

(71) 1962, *The type of Tricoelocrinus, a correction:* Same, v. 22, no. 7, p. 188.

(72) 1962, *New Mississippian blastoids from the Lake Valley Formation (Nunn Member), Lake Valley, New Mexico:* Same, v. 22, no. 7, p. 189-196, pl. 1-2.

(73) 1963, *Nodoblastus, a new Upper Mississippian (Namurian) blastoid from Russia:* Same, v. 23, no. 7, p. 174-180, pl. 1-3.

(74) 1964, *An outline classification of the Blastoidea:* Same, v. 24, no. 4, p. 81-90.

**———, & Koenig, J. W.**

(75) 1963, *Pentremoblastus, a new Lower Mississippian blastoid from Illinois:* Oklahoma Geol. Survey, Oklahoma Geol. Notes, v. 23, no. 11, p. 267-270, pl. 1.

**———, & Reimann, I. G.**

(76) 1962, *Some brachiolar and ambulacral structures of blastoids:* Oklahoma Geol. Survey, Oklahoma Geol. Notes, v. 22, no. 2, p. 30-49, text fig. 1-4, pl. 1-4.

(77) 1962, *The paradeltoid plates of Polydeltoideus:* Same, v. 22, no. 2, p. 50-52, pl. 1.

**Galloway, J. J., & Kaska, H. V.**

(78) 1957, *Genus Pentremites and its species:* Geol. Soc. America, Mem. 69, ix+104 p., 5 text fig., 5 tables, 13 pl.

**Goldfuss, August**

(79) 1826-1833, *Petrefacta Germaniae:* Theil I, 252 p., 71 pl., Arnz & Co. (Düsseldorf).

**Gray, J. E.**

(80) 1840, *Synopsis of the contents of the British Museum:* 12 mo., 42nd ed., p. 63 (London).

**Gurley, W. F. E. R.**

(81) 1884, *New Carboniferous fossils:* Bull. no. 2, 12 p., private publ. (Danville, Ill.).

**Hall, James**

(82) 1858, *Palaeontology of Iowa:* Iowa Geol. Survey, Rept., v. 1, pt. 2, Palaeontology, p. 473-724, text fig. 53-118, pl. 1-29.

(83) 1862, *Contributions to palaeontology; comprising descriptions of new species of fossils from the Upper Helderberg, Hamilton and Chemung groups; Preliminary notice of some of the species of Crinoidea known in the Upper Helderberg and Hamilton groups of New York:* N.Y. State Cabinet, Ann. Rept. 15, p. 115-153, 2 text fig., 11 pl. (Albany). [Describes *Pentremites calyce, P. leda, P. maia,* (now all *Devonoblastus*), *Pentremites lycorias* (now *Pleuroschisma*), and *Nucleocrinus conradi, N. lucina.*]

(84) 1879, *The fauna of the Niagara group, in central Indiana:* N.Y. State Museum, Ann. Rept. 28, p. 99-203, pl. 3-34 (text printed partly in advance in 1875 or 1876). [Describes *Codaster pentalobus* (now type species of *Decaschisma*).]

**Hambach, Gustav**

(85) 1884, *Notes about the structure and classification of the Pentremites:* Acad. Sci. St. Louis, Trans., v. 4, no. 3, p. 537-547, text fig. 1-6.

(86) 1903, *Revision of the Blastoidea, with a proposed new classification, and description of new species:* Same, v. 13, no. 1, 67 p., 15 text fig., 6 pl.

**Haughton, Samuel**

(87) 1859, *On a new Carboniferous echinoderm, from the county of Limerick:* Dublin Geol. Soc., Jour., v. 8, pt. 2, p. 183-184, pl. 12.

**Hsu, Chen, et al.**

(88) 1957, *Index fossils of China. Invertebrata:* 3 v., illus., in Chinese with English titles; v. 1, p. 1-95, text fig. 1-38, pl. 1-51 (blastoids, p. 87-89, text fig. 23, pl. 51, fig. 10-18), ed. by Paleont. Res. Inst., Academia Sinica, publ. by Geol. Press (Peking). [Lists *Mesoblastus tushanensis* Chi and *Devonoblastus heitaiensis* Mu as only Chinese blastoids described to date. Generic designations may be incorrect.]

**Hudson, G. H.**

(89) 1907, *On some Pelmatozoa from the Chazy limestone of New York:* N.Y. State Museum, Bull. 107, p. 97-152, pl. 1-10. [Describes *Blastoidocrinus* and introduces new class Parablastoidea.]

**Jaekel, Otto**

(90) 1918, *Phylogenie und System der Pelmatozoen:* Paläont. Zeitschr., v. 3, no. 1, p. 1-128, text fig. 1-114. [Later publ. in 1921.] [Proposes blastoid orders named Fissiculata, Spiraculata, and Coronata.]

**Joysey, K. A.**

(91) 1953, *A study of the type-species of the blastoid Codaster McCoy:* Geol. Mag., v. 90, no. 3, p. 208-218, text fig. 1-5, 3 tables.

(92) 1955, *On the geological distribution of Carboniferous blastoids in the Craven area, based on a study of their occurrence in the Yoredale series of Grassington, Yorkshire:* Geol. Soc. London, Quart. Jour., v. 111, p. 209-224, text fig. 1-2, pl. 12.

(93) 1959, *A study of variation and relative growth in the blastoid Orbitremites:* Royal Soc. London, Philos. Trans., ser. B, no. 688, v. 242, p. 99-125, text fig. 1-9, pl. 2.

**———, & Breimer, A.**

(94) 1963, *The anatomical structure and systematic position of Pentablastus (Blastoidea) from the Carboniferous of Spain:* Palaeontology, v. 6, pt. 3, p. 471-490, text fig. 1-5, pl. 66-69.

**Koninck, L. G. de, & LeHon, Henri**

(95) 1854, *Recherches sur les crinoïdes du terrain carbonifère de la Belgique:* Acad. Royale Sci. Belgique, Mém., v. 28, 215 p., text fig., 7 pl. [Describes *Pentremites caryophyllatus* (now *Phaenoblastus*), *P. crenulatus* (now *Mesoblastus*), *P. Puzos, P. Orbignyanus,* and *P. Waterhousianus* (now tentatively referred to *Orophocrinus*). Excellent bibliography contains 350 references to publications dated 1558-1853 (18 pre-1700, 110 pre-1800).]

**Lehmann, W. M.**

(96) 1949, *Pentremitella osoleae n. g. n. sp., ein Blastoid aus dem unterdevonischen Hunsrückschiefer:* Neues Jahrb. Mineralogie, Geologie, Paläontologie, Monatsch., Abt. B, Jahrg. 1949, p. 186-191, text fig. 1-7. [Unrecognizable as to genus but tentatively referred to *Schizotremites.*]

**Levin, H. L., & Fay, R. O.**

(97) 1964, *The relationship between Diploblastus kirkwoodensis and Platyceras (Platyceras):* Oklahoma Geol. Survey, Oklahoma Geol. Notes, v. 24, no. 2, p. 22-29, text fig. 1, pl. 1-3.

**Lucas, M. G.**

(98) 1953, *Étude, au microscope polarisant, des hydrospires des blastoides:* in Jean Piveteau, Traité de Paléontologie (v. 3, 1063 p., 17 pl., 1275 fig.), p. 635-637, text fig. 10-12, Masson et Cie (Paris).

**Lyon, S. S.**

(99) 1857, *Paleontological report. Description of new species of organic remains:* Kentucky Geol. Survey, Rept. 3, p. 465-498, pl. 1-5, maps.

**M'Coy, Frederick**

(100) 1849, *On some new Palaeozoic Echinodermata:* Ann. & Mag. Nat. History, ser. 2, v. 3, p. 244-254, text fig. 1.

**Macurda, D. B., Jr.**

(101) 1962, *Observations on the blastoid genera Cryptoblastus, Lophoblastus, and Schizoblastus:* Jour. Paleontology, v. 36, no. 6, p. 1367-1377, text fig. 1-5.

(102) 1964, *Dentiblastus—a new blastoid genus from the Burlington Limestone (Mississippian):* Same, v. 38, no. 2, p. 367-372, text fig. 1, pl. 58.

(103) 1964, *The blastoid Pentremites Say—a trimerous mutant and some new occurrences:* Same, v. 38, no. 4, p. 705-710, text fig. 1-2, pl. 116.

(104) 1964, *The Mississippian blastoid genera Phaenoschisma, Phaenoblastus, and Conoschisma:* Same, v. 38, no. 4, p. 711-724, pl. 117-118.

(105) 1964, *A new spiraculate blastoid, Pyamiblastus, from the Mississippian Hampton Formation of Iowa:* Univ. Michigan, Museum Paleontology, Contrib., v. 19, no. 8, p. 105-114, text fig. 1.

(106) 1965, *Orbiblastus, a new Mississippian blastoid genus from Arkansas:* Michigan Acad. Sci., Arts, & Letters, Papers, v. 50, pt. 1, p. 299-307, text fig. 1, pl. 1-2.

(107) 1965, *The functional morphology and stratigraphic distribution of the Mississippian blastoid genus Orophocrinus*: Jour. Paleontology, v. 39, no. 6, p. 1045-1096, text fig. 1-16, pl. 121-126.

(108) 1965, *The hydrodynamics of the Mississippian blastoid genus Globoblastus:* Same, v. 39, p. 1209-1217, text fig. 1-4.

(109) 1966, *The ontogeny of the Mississippian blastoid Orophocrinus:* Same, v. 40, no. 1, p. 92-124, text fig. 1-10, pl. 11-13.

(110) 1966, *The Devonian blastoid Belocrinus from France:* Palaeontology, v. 9, pt. 2, p. 244-251, text fig. 1, pl. 39.

**Matsumoto, Hikoschichirô**

(111) 1929, *Outline of a classification of Echinodermata:* Tohoku Imper. Univ., Sci. Rept., ser. 2 (Geology), v. 13, no. 2, p. 27-33.

**Meek, F. B., & Worthen, A. H.**

(112) 1862, *Descriptions of new Paleozoic fossils from Illinois and Iowa:* Acad. Nat. Sci. Philadelphia, Proc. for 1861, p. 128-148.

(113) 1865, *Descriptions of new Crinoidea, etc., from the Carboniferous rocks of Illinois and some of the adjoining states:* Same, Proc. for 1865, p. 155-166.

(114) 1868, *Remarks on some types of Carboniferous crinoids, with descriptions of new genera and species of the same, and of one echinoid:* Same, Proc. for 1868, p. 335-359. [Describes *Tricoelocrinus woodmani.*]

(115) 1869, *Remarks on the Blastoidea, with descriptions of new species:* Same, Proc. for 1869, p. 83-91. [Describes *Codonites* (now *Orophocrinus*), and *Granatocrinus glaber* (now *Diploblastus*).]

(116) 1873, *Descriptions of invertebrates from Carboniferous system:* Illinois Geol. Survey, v. 5, pt. 2, p. 320-619, 32 pl. [Describes and figures *Tricoelocrinus woodmani*.]

**Mitchill, S. L.**

(117) 1808, *Uncommon petrifactions, from Georgia and Kentucky:* Medical Repository, v. 11, p. 415-416, fig. A-C (New York). [One of earliest references and figures of a blastoid (now known as *Pentremites godoni*). The specimens were sent to MITCHILL by DR. SAMUEL BROWN, of Lexington, Kentucky, several years prior to 1808.]

**Moore, R. C.**

(118) 1954, *Status of invertebrate paleontology, 1953, IV. Echinodermata: Pelmatozoa:* Harvard Museum Comp. Zoology, Bull., v. 112, no. 3, p. 125-149, text fig. 1-8.

**———, & Strimple, H. L.**

(119) 1942, *Blastoids from Middle Pennsylvanian rocks of Oklahoma:* Denison Univ. Jour. Sci. Lab., Bull., v. 37, p. 85-91, text fig. 1. [Describes *Paracodaster dotti* (now classed as *Agmoblastus*).]

**Morris, John**

(120) 1843, *A catalogue of British fossils comprising all the genera and species hitherto described; with references to their geological distribution and to the localities in which they have been found:* 8 vo., x+222 p., Van Voorst (London). [Introduces *Astrocrinus tetragonus* for *Astracrinites tetragonus* AUSTIN & AUSTIN.]

**Mu, A. T.**

(121) 1955, *A Devonian blastoid from Kirin:* Acta Palaeont. Sinica, v. 3, no. 2, p. 131-134, 1 pl. [In Chinese, with English summary.] [Describes *Devonoblastus heitaiensis* (Heitai Formation, at Chenchuhoushan near Heitai, Mishan district, Kirin, NE. China). The generic name is misspelled *Devonoboblastus*, and the species may belong to another genus.]

**Munier-Chalmas, E. C. P. A.**

(122) 1876, *Mollusques nouveaux des terrains paléozoiques des environs de Rennes:* Jour. Conchyliologie, ser. 3, v. 16, whole v. 24, no. 1, p. 102-109. [Describes blastoid from Lower Devonian deposits named *Belemnocrinus* (*non Belemnocrinus* WHITE, 1862, crinoid) later renamed *Belocrinus*. Fossil comprises fragmentary basalia and cannot be assigned to another known genus.]

(123) 1881, *Mollusques nouveaux des terrains paléozoiques des environs de Rennes:* Soc. Géol. France, Bull., ser. 3, v. 9, p. 503.

**Nichols, David**

(124) 1962, *Echinoderms:* 200 p., 26 text fig., Hutchinson Univ. Library (London).

**Nissen, H. U.**

(125) 1963, *Röntgegenfügeanalyse am Kalzit von Echinodermenskelleten:* Neues Jahrb. Geologie u. Paläontologie, Abhandl., v. 117, p. 230-234.

**Orbigny, A. D. d'**

(126) 1850, *Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnées faisant suite au cours élémentaire de paléontologie et de géologie stratigraphiques:* 12 mo. with Atlas 4 to.; v. 1, p. lx+394 p., text fig., Masson (Paris).

(127) 1851, *Cours elèmentaire de paléontologie et géologie stratigraphiques:* 8 vo. with plates 4 to.; v. 2, 841 p., 628 text fig., Masson (Paris). [Erects family Pentremitidaea (*sic*), corrected by Etheridge & Carpenter (1886) to Pentremitidae.]

**Owen, D. D., & Shumard, B. F.**

(128) 1850, *Descriptions of fifteen new species of Crinoidea from the sub-Carboniferous limestone of Iowa, collected during the U. S. Geological Survey of Wisconsin, Iowa, and Minnesota in the years 1848-1849:* Acad. Nat. Sci. Philadelphia, Jour., new ser., v. 2, pt. 1, p. 57-70, pl. 7. [Describes species now designated as types of *Cryptoblastus, Globoblastus,* and *Orophocrinus.*]

**Parkinson, James**

(129) 1808, *Organic remains of a former world; The fossil zoophytes:* v. 2, vii+286 p., 19 pl. (London). [Describes and figures what is now *Pentremites godoni,* and is one of the first references to a blastoid.]

**Peck, R. E.**

(130) 1930, *Blastoids from the Brazer limestones of Utah:* Pan-Am. Geologist, v. 54, no. 2, p. 104-108, pl. 1. [Describes and illustrates *Ambolostoma baileyi.*]

**Peetz, H. von**

(131) 1907, *Nymphaeoblastus miljukovi, eine neue Gattung und Art der Blastoidea:* Soc. Impér. Nat. St . Pétersbourg, Tiré des Travaux, Geol. et de Min. Sec., v. 35, liv. 5, p. 15-20, 1 pl.

**Phillips, Winifred**

(132) 1936, *The structure of Acentrotremites:* Swansea Sci. & Field Naturalists' Soc., Proc., v. 1, pt. 10, p. 360-366, text fig. 1-13.

**Quenstedt, F. A.**

(133) 1874-1876, *Petrefaktenkunde Deutschlands:* Abt. 1, v. 4, no. 7-12, 742 p., pl. 90-114.

**Raup, D. M.**

(134) 1959, *Crystallography of echinoid calcite:* Jour. Geology, v. 67, p. 661-674, text fig. 1-7, 1 table.

**Regnéll, Gerhard**

(135) 1945, *Non-crinoid Pelmatozoa from the Paleozoic of Sweden—A taxonomic study:* Lunds Geol.-Mineral. Inst., Medd., no. 108, 255 p., 30 text fig., 15 pl.

(136) 1960, *Données concernant le développement ontogénétique des pelmatozoaires du Paléozoïque (échinodermes):* Soc. Géol. France, Bull., ser. 7, v. 1, no. 7, p. 773-783, text fig. 1-6.

**Reimann, I. G.**

(137) 1935, *New species and some new occurrences of middle Devonian blastoids:* Buffalo Soc. Nat. Sci., Bull., v. 17, no. 1, p. 23-45, pl. 1-4. [Describes *Brachyschisma* and *Devonoblastus.*]

(138) 1942, *"Tully" blastoids in western New York and genotype of Devonoblastus:* Same, Bull., v. 17, no. 3, p. 46-47, pl. 9.

(139) 1945, *New Devonian blastoids:* Same, Bull., v. 19, no. 2, p. 22-42, pl. 5-9. [Describes *Brachyschisma, Pleuroschisma,* and *Schizotremites.*]

(140) 1948, *New genus of blastoids from the Silurian:* Geol. Soc. America, Bull., v. 59, pt. 2, p. 1346 (abstr.). [Describes but does not name a blastoid *(Polydeltoideus)* from the Henryhouse Shale of Oklahoma.]

(141) 1950, *Possible phylogenetic relationships of some early eublastoids:* Jour. Paleontology, v. 24, no. 4, p. 499-500. [Important contribution to phylogeny because it suggests atrophy of skeletal parts in blastoids as fundamental features in evolutionary trends.]

(142) 1961, *A color-marked Devonian blastoid:* Oklahoma Geol. Survey, Oklahoma Geol. Notes, v. 21, no. 5, p. 153-157, pl. 1-2.

**———, & Fay, R. O.**

(143) 1961, *Polydeltoideus, a new Silurian blastoid from the Henryhouse formation of Oklahoma:* Same, v. 21, no. 3, p. 86-89, pl. 1.

**Roemer, C. F.**

(144) 1851, *Monographie der fossilen Crinoidenfamilie der Blastoideen, und der Gattung Pentatrematites in Besondern:* Arch. Naturgesch., Jahrg. 17, v. 1, no. 3, p. 323-397, pl 4-8. [Detailed morphological study in which pores and hydrospires (not then named) were discovered and a classification was presented.]

**Rowley, R. R.**

(145) 1895, *Description of a new genus and five new species of fossils from the Devonian and sub-Carboniferous rocks of Missouri:* Am. Geologist, v. 16, no. 4, p. 217-223, text fig. 1-20. [Type species of *Carpenteroblastus* described as *Granatocrinus magnibasis.*]

(146) 1900, *New species of crinoids, blastoids, and cystoids from Missouri:* Same, v. 25, no. 2, p. 65-75, pl. 2. [Type species of *Conoschisma* (=*Phaenoschisma*) described as *Codaster laeviusculus.*]

(147) 1901, *Two new genera and some new species of fossils from the upper Paleozoic rocks of northeastern Missouri:* Same, v. 27, no. 6, p. 343-355, pl. 28. [Describes *Carpenteroblastus* and *Lophoblastus.*]

**———, & Hare, S. J.**

(148) 1891, *Description of some new species of Echinodermata from the sub-Carboniferous rocks of Pike County, Missouri:* Kansas City Scientist, v. 5, no. 7, p. 97-103, pl. 2.

**Say, Thomas**

(149) 1820, *Observations on some species of zoöphytes and shells principally fossil:* Am. Jour. Sci., v. 2, p. 34-45. [Names *Pentremites,* but spells name as *Pentremite.*]

(150) 1825, *On two genera and several species of Crinoidea:* Acad. Nat. Sci. Philadelphia, Jour., ser. 1, v. 4, pt. 2, p. 289-296. [Proposes name Blastoidea.]

**Schmidt, W. E.**

(151) 1930, *Die Fauna des deutschen Unterkarbons. 1. Teil, Die Echinodermen:* K. Preuss. Geol. Landesanst., Abhandl., new ser., no. 122, 92 p., 20 text fig., 3 pl., tables. [Describes *Pentremites boletus* and *P. ovalis* (now *Petaloblastus*), and *Mesoblastus melonianus* (now *Doryblastus*).]

**Schultze, Ludwig**

(152) 1867, *Monographie der Echinodermen des Eifler Kalkes:* K. Akad. Wiss., Math. Naturwiss. Cl., Denkschr., v. 26, Register-Bd., Abt. 2, p. 113-230, pl. 1-13. [Separates dated 1866 in advance.] [Describes *Pentremites acutangulus* and *P. clavatus* (now *Cordyloblastus*).]

**Seebach, Karl von**

(153) 1864, *Ueber Orophocrinus, ein neues Crinoideen-geschlecht aus der Abtheilung der Blastoideen:* K. Gesell. Wiss. Georg-Augusts-Univ., Nachricht. for 1864, no. 5, p. 110-111.

**Shumard, B. F.**

(154) 1855, *Description of new species of organic remains:* Missouri Geol. Survey, Ann. Rept. 1-2, p. 185-238, pl. A-C; Dr. Shumard's report, p. 147-184, fig. maps. [Describes

*Pentremites sayi* (now *Schizoblastus*) and *Pentremites roemeri* (now *Tanaoblastus*).]

(155) 1858, *Descriptions of new species of Blastoidea from the Palaeozoic rocks of the Western States, with some observations on the structure of the summit of the genus Pentremites:* Acad. Sci. St. Louis, Trans., v. 1, p. 238-248, pl. 9.

(156) 1863, *Descriptions of new Palaeozoic fossils:* Same, Trans., v. 2, no. 1, p. 108-113.

(157) 1865-66, *A catalogue of the Palaeozoic fossils of North America. Part I. Palaeozoic Echinodermata:* Same, Trans., v. 2, no. 2, p. 334-407, publ. in parts at separate times: p. 334-346 (Aug. 24, 1865); p. 347-362 (Sept. 18, 1865); p. 363-378 (Dec. 11, 1865); p. 379-394 (Dec. 5, 1865); p. 395-407 (March 20, 1866). Bound together and published in May, 1866. [Introduces new genus *Troosticrinus* and designates type species of *Granatocrinus.*]

**———, & Yandell, L. P.**

(158) 1856, *Notice of a new fossil genus belonging to the family Blastoidea, from the Devonian strata near Louisville, Kentucky:* Acad. Nat. Sci. Philadelphia, Proc., v. 8, p. 73-75, pl. 2. [Describes and illustrates *Eleutherocrinus cassedayi.*]

**Sieverts-Doreck, Hertha**

(159) 1951, *Echinodermen aus dem spanischen Ober-Karbon:* Paläont. Zeitschr., v. 24, pt. 3/4, p. 104-119, text fig. 1-7, pl. 8. [Describes and illustrates *Pentablastus supracarbonicus.*]

**Smith, E. A.**

(160) 1906, *Development and variation of Pentremites conoideus:* Indiana Dept. Geol. & Nat. Res., Ann. Rept. 30, p. 1219-1242, text fig. 1-3, pl. 43-47.

**Sowerby, G. B.**

(161) 1825, *Note on the foregoing paper, together with a description of a new species of Pentremites:* Zool. Jour., v. 2, no. 7, p. 316-318, pl. 11. [Describes *Pentremites derbiensis* (now *Orbitremites*) and corrects *Pentremite* to *Pentremites.*]

(162) 1834, *On Pentatrematites orbicularis, acuta, and pentagularis:* Same, v. 5, no. 20, art. 62, p. 456-457, pl. 33, suppl.

**Steininger, Johann**

(163) 1849, *Die Versteinerungen des Uebergangsgebirges der Eifel:* Jahresb. über den Schul-Corsus. 1848-49 an dem Gymnasium zu Trier, 4 to., 50 p.

**Termier, Geneviève, & Termier, Henri**

(164) 1950, *Paléontologie Marocaine; II. Invertébrés de l'ère primaire; f. 4, Annélides, arthropodes, échinodermes, conularides et graptolithes:* Service Géol. Maroc, Notes & Mém., v. 79, no. 4, p. 55-105, pl. 207-233. [One of earliest records of blastoids in Africa. Describes and illustrates *Pentremitidea touijinensis* (Strunian) and *Granatocrinus* (Visean) with mention also of *Pentremites* (Visean). These generic assignments may be incorrect.]

**Troost, Gerard**

(165) 1835, *On the Pentremites reinwardtii, a new fossil; with remarks on the genus Pentremites (Say), and its geognostic position in the state of Tennessee, Alabama and Kentucky:* Pennsylvania Geol. Soc., Trans., v. 1, pt. 2, art. 5, p. 224-231, pl. 10. [Describes and illustrates species now designated as type of *Troosticrinus.*]

**Ulrich, E. O.**

(166) 1917 (1918), *The formations of the Chester series in western Kentucky and their correlates elsewhere:* in Mississippian formations of western Kentucky, Kentucky Geol. Survey, iv+272 p., 11 pl.

**Verneuil, Edouard de**

(167) 1844, *Note . . . sur une nouvelle espèce de Pentrémites . . . :* Soc. Géol. France, Bull., ser. 2, v. 1, p. 213-215, pl. 3 [Describes and illustrates *Pentremites pailletti* (now *Pentremitidea*).]

**———, & Archiac, E. J. A. d'**

(168) 1845, *Note sur les fossiles du terrain Paléozoique des Asturies:* Soc. Géol. France, Bull., ser. 2, v. 2, p. 458-482, pl. 13-15. [Describes and figures *Pentremites Pailletti* and *P. Schultzii* (now *Pentremitidea* and *Cryptoschisma,* respectively).]

**Wachsmuth, Charles**

(169) 1883, *On a new genus and species of blastoids, with observations upon the structure of the basal plates in Codaster and Pentremites:* Illinois State Geol. Survey, v. 7, p. 346-357, text fig. 1-2.

(170) 1900, *Class 3, Blastoidea:* in Text-book of Palaeontology, by K. A. von Zittel, transl. by Charles R. Eastman: v. 1, p. 188-198, text fig. 312-325, Macmillan & Co. (London). [Classification follows that of Etheridge & Carpenter (1886).]

**———, & Springer, Frank**

(171) 1879 (1880), *Revision of the Paleocrinoidea:* Acad. Nat. Sci. Philadelphia, Proc., pt. 1, p. 226-378, pl. 15-17.

(172) 1887, *The summit plates in blastoids, crinoids, and cystids, and their morphological relations:* Same, Proc. for 1887, p. 82-114, pl. 4.

**Wanner, Johannes**

(173) 1924, *Die permischen Echinodermen von Timor, Teil II:* Paläontologie von Timor, Lief. 14, Abhandl. 23, 81 p., pl. 199-206,

31 text fig. [Describes and figures 32 new species and varieties of 7 genera (6 new) from Permian marls and tuffs of Timor Island, collected (1909-11) by Jonker, Molengraff, and Wanner. The types are in Delft, The Netherlands, and Bonn, Germany, but those in Bonn were believed to be destroyed during the war but recent-have been found. The fossils came from 38 different localities. Describes *Calycoblastus, Indoblastus, Neoschisma, Pterotoblastus, Sundablastus, Timoroblastus, and Schizoblastus* (now *Deltoblastus*).]

(174) 1924, *Die permischen Blastoiden von Timor:* Mijnwezen Nederland.-Oost-Indië, Jaarb., Verhandl. I, Jaarg. 51 for 1922, p. 163-233, text fig. 1-11, pl. 1-5. [Describes *Anthoblastus, Nannoblastus, Rhopaloblastus, Sphaeroschisma, Thaumatoblastus.*]

(175) 1931, *Neue Beiträge zur Kenntnis der permischen Echinodermen von Timor. VI. Blastoidea:* Wetensch. Meded. no. 16, Dienst Mijnb. Nederland.-Oost-Indië, p. 38-74, 10 text fig., pl. 1-4. [Describes *Angioblastus* (new), *Nannoblastus, Timoroblastus, Pterotoblastus.*]

(176) 1932, *Neue Beiträge zur Kenntnis der permischen Echinodermen von Timor. VII. Die Anomalieen der Schizoblasten:* Same, no. 20, 46 p., 4 pl. [Describes Permian *Schizoblastus* (now *Deltoblastus*).]

(177) 1932, *Über die Blastoideengattung Zygocrinus:* Neues Jahrb. Mineralogie, Geologie u. Paläontologie, Monatsh., B (or Centralbl., Abt. B), no. 9, p. 455-464, text fig. 1-4. [*Zygocrinus* is now *Astrocrinus*; with a spiracular slit along ambulacral margins except in anal region, thus placing genus in Fissiculata.]

(178) 1940, *Neue Blastoideen aus dem Perm von Timor mit einem Beitrag zur Systematik der Blastoideen:* in Geological Expedition of the University of Amsterdam to the Lesser Sunda Islands in the South-Eastern part of the Netherlands East Indies, v. 1, p. 215-277, text fig. 1-2, pl. 1-3. (Amsterdam). [Describes *Ceratoblastus, Dipteroblastus, Indoblastus, Rhopaloblastus.*]

(179) 1951, *Die Analstruktur der Blastoidea:* Neues Jahrb. Geologie u. Paläontologie, Monatsh., Jahrg. 1951, no. 6, p. 170-185, 21 text fig. [A penetrating contribution, showing problems of classification of blastoids when anal plates are used in combination with some other characteristics.]

**Weller, Stuart**

(180) 1920, *The geology of Hardin County:* Illinois Geol. Survey, Bull. 41, 416 p., 30 text fig., 11 pl., 4 tables.

**White, C. A.**

(181) 1863, *Observations on the summit structure of Pentremites, the structure and arrangement of certain parts of crinoids, and descriptions of new species from the Carboniferous rocks at Burlington, Iowa:* Boston Jour. Nat. History, v. 7, no. 4, p. 481-506.

**Whiteaves, J. F.**

(182) 1889, *On some fossils from the Hamilton formation of Ontario, with a list of the species at present known from that formation and province:* Geol. Survey Canada, Contrib. Canad. Paleontology, v. 1, pt. 2, p. 91-125, pl. 12-16. [Describes *Pentremitidea filosa* (now *Hyperoblastus*).]

**Yakovlev, N. N.**

(183) 1926, *O Cystoblastus, Nymphaeoblastus i Acrocrinus:* Vses. Geol.-Razved. Ob'ed. SSSR, Izvestiya (All-Union Geological and Prospecting Institute, Bull.) (formerly Comité Géol., Bull.), v. 45, no. 2, p. 43-49, text fig. 1-4, pl. 1. [In Russian with French summary.] [*On Cystoblastus, Nymphaeoblastus* and *Acrocrinus.*]

(184) 1926, *Fauna Iglokozhikh Permokarbona iz Krasnoufimska na Urale, I:* Same, v. 45, no. 2, p. 50-57, text fig. 1-5, pl. 1. [In Russian with French summary.] [*Fauna of the echinoderms of the Permocarboniferous of the Urals and Krasnooufimsk.*] [Describes *Timoroblastus wanneri* (now *Sagittoblastus*).]

(185) 1937, *Faune des échinodermes du Permo-Carbonifère de l'Oural à Krasnooufimsk, IV:* Vser. Paleont. Obshch., Ezhegod. (Soc. Paléont. Russie, Ann.), v. 11, p. 7-10, pl. 1. [French, with Russian summary.] [Introduces new genus *Sagittoblastus.*]

(186) 1940, *Un nouveau blastoïde du Permien de l'Oural du Nord:* Akad. Nauk SSSR, Doklady (Acad. Sci. URSS, C. R. Doklady), v. 27, no. 8, p. 887-888, text fig. 1. [Describes *Paracodaster miloradovitchi.*]

(187) 1941, *Deux nouveaux échinodermes des dépôts permiens du Timan:* Same, v. 32, no. 1, p. 102-104, text fig. 1-2. [Describes *Codaster barkhatovae,* which appears to belong to a new genus.]

(188) 1941, *Klass Blastoidea:* Atlas of the leading fossil forms of fossil faunas of the USSR, v. 4, 72 p., text fig., 10 pl. (Leningrad). [*Class Blastoidea.*] [Describes *Cryptoblastus submelo, Schizoblastus librovitchi,* and *Nymphaeoblastus kasakhstanensis.* The first two may belong to new genera.]

**———, & Faas, A.**

(189) 1938, *Nuovi echinodermi permiani di Sicilia:* Palaeont. Italica, v. 38, p. 116-126, 1 pl. [*Schizoblastus* cf. *permicus* (now

*Deltoblastus*) reported from Sosio Limestone, Sicily.]

**———, & Ivanov, A. P.**

(190) 1956, *Morskie lilii i blastoidei kamennougolnykh i permskikh otlozheniy SSSR:* Vses. Nauchno Issledov. Geol. Inst., Trudy, v. 11, p. 1-142, text fig. 1-23, pl. 1-21. [*Crinoids and blastoids of the Carboniferous and Permian of the USSR.*] [Summarizes knowledge of blastoids of Russia.]

**Yang, C. C., & Chu, M. T.**

(191) 1965, *A Lower Carboniferous blastoid from Daoxian (Taohsien), Hunan:* Acta Palaeont. Sinica, v. 13, no. 2, p. 370-372, text fig. 1, pl. 1.

**Zittel, K. A. von**

(192) 1903, *Grundzüge der Paläontologie (Paläozoologie). 1. Abteilung: Invertebrata:* 607 p., Oldenbourg (München, Berlin). [Erects the order Hydrophoridae of the class Cystoidea. Regnéll (1945) altered spelling to Hydrophoridea, and raised it to subclass rank.]

# EOCRINOIDEA

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## CONTENTS

## INTRODUCTION

It was Otto Jaekel *(23)*[1] who first proposed, in 1899, to remove from the Cystoidea several genera *(Acanthocystites, Ascocystites, Eocystites, Lichenoides, Macrocystella, Mimocystites, Palaeocystites)* which previously had been included in this assemblage, because he judged them to be classifiable as archaic cladocrinoids (=Crinoidea

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[1] Italicized numbers refer to corresponding numbers in the list of references.