Treatise on INVERTEBRATE PALEONTOLOGY *Moore, Editor* (S) Echinodermata 1$^{(2)}$ *Geological Society of America* *University of Kansas*

TREATISE ON
INVERTEBRATE PALEONTOLOGY

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

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

Directed and Edited by
RAYMOND C. MOORE

Part S
ECHINODERMATA 1

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

THE GEOLOGICAL SOCIETY OF AMERICA, INC.
and
THE UNIVERSITY OF KANSAS

1967

Library of Congress Catalogue Card
Number: 53-12913

Text Composed by
THE UNIVERSITY OF KANSAS PRINTING SERVICE
Lawrence, Kansas

Illustrations and Offset Lithography
MERIDEN GRAVURE COMPANY
Meriden, Connecticut

Binding
RUSSELL-RUTTER COMPANY
New York City

Published 1967

Distributed by The Geological Society of America, Inc., 231 East 46 Street, New York, N.Y., 10017, to which all communications should be addressed.

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

[[1]Esso Production Research Company; [2]Oklahoma Geological Survey; [3]The University of Michigan; [4]The University of Kansas; [5]Universität Bonn, deceased]

INTRODUCTION

By Robert O. Fay

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

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

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

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

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

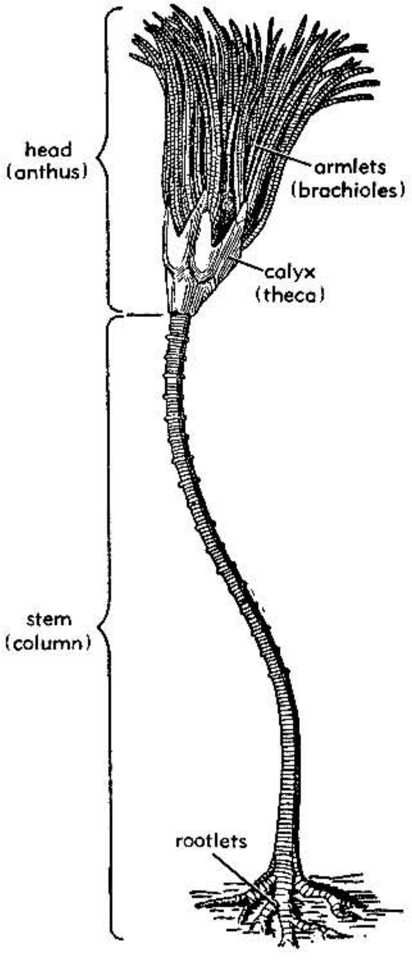


Fig. 177. Reconstruction of entire blastoid (*Orophocrinus,* Miss., N.Am.), showing principal parts (Bather).

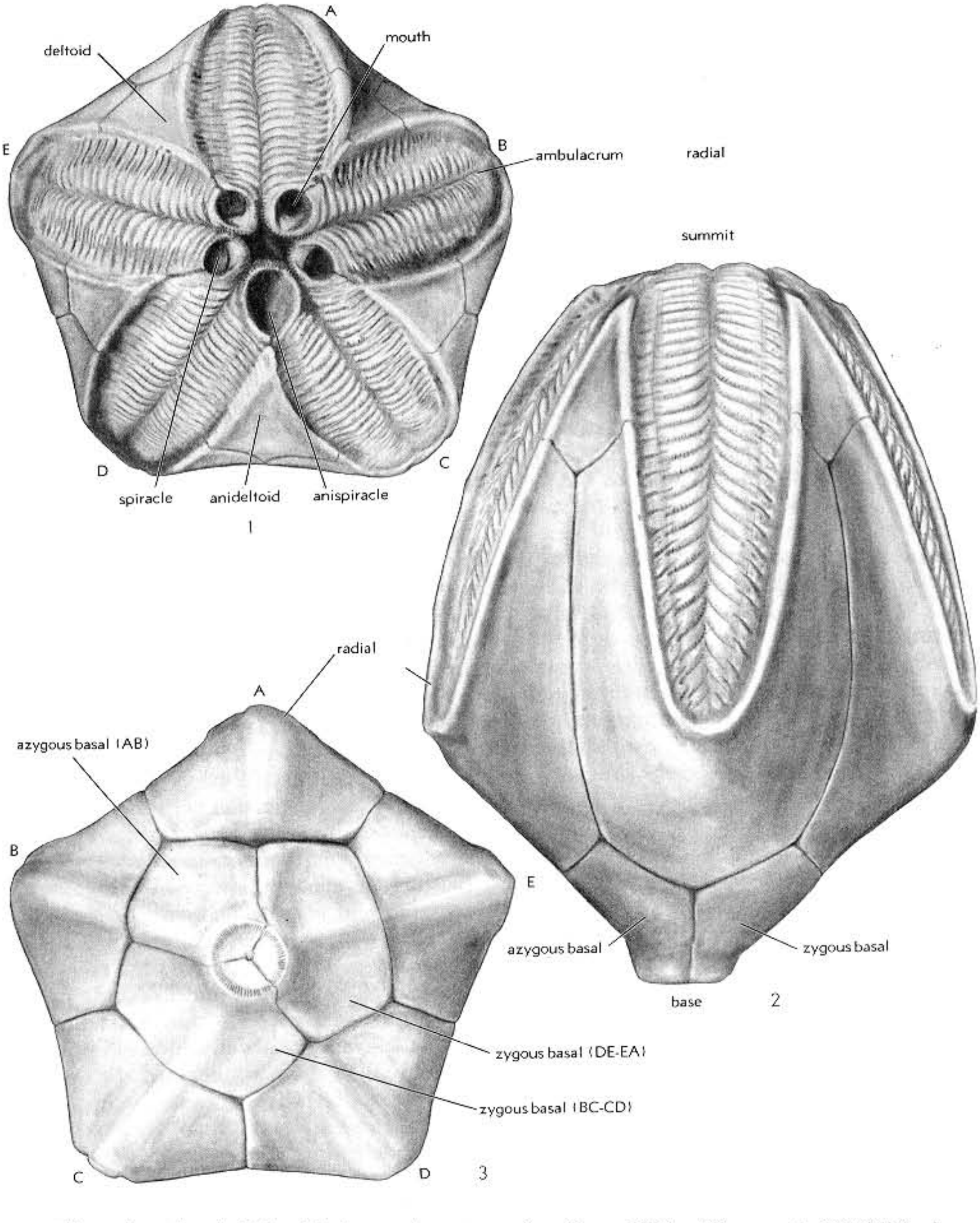


FIG. 178. Calyx of typical blastoid, *Pentremites symmetricus* HALL, U.Miss.(Chesteran), USA(Ill.), showing externally visible parts of theca, ×4.5 (drawings by Roger B. Williams; Beaver, n).——*1*. Summit (oral) view, mouth opening at center surrounded by 4 spiracles (relatively small rounded orifices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

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

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

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

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

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

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

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

MORPHOLOGY

By Harold H. Beaver
[Esso Production Research Company]

COLUMN

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

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

CALYX

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

SHAPE AND SIZE

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

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

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

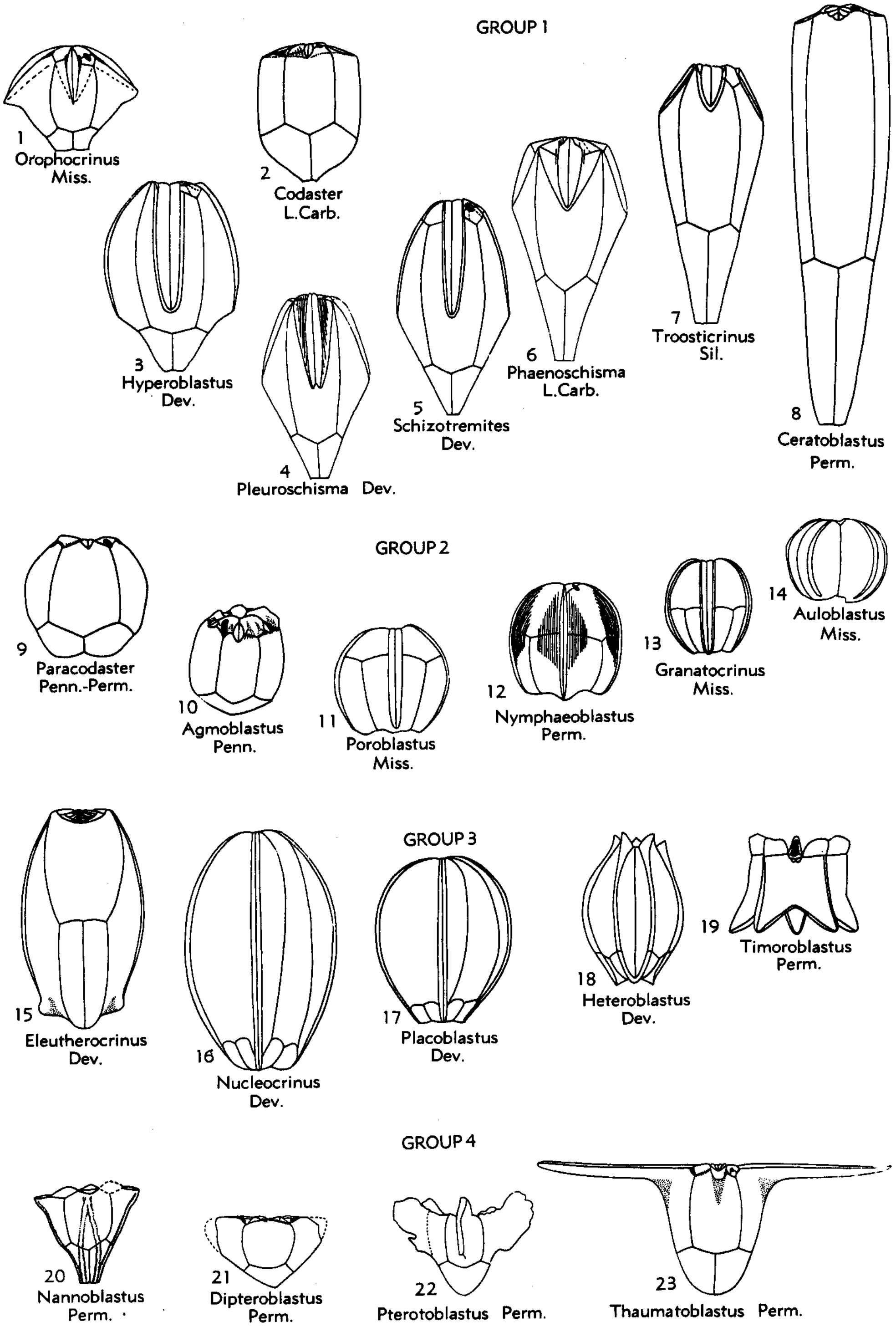


FIG. 179. Shapes of blastoid calyces, shown in lateral views. Groupings are not inferred to delineate phylogenetic assemblages (drawings from Fay, n).

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

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

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

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

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

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

[*See* pages *S*304-*S*305]

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.).

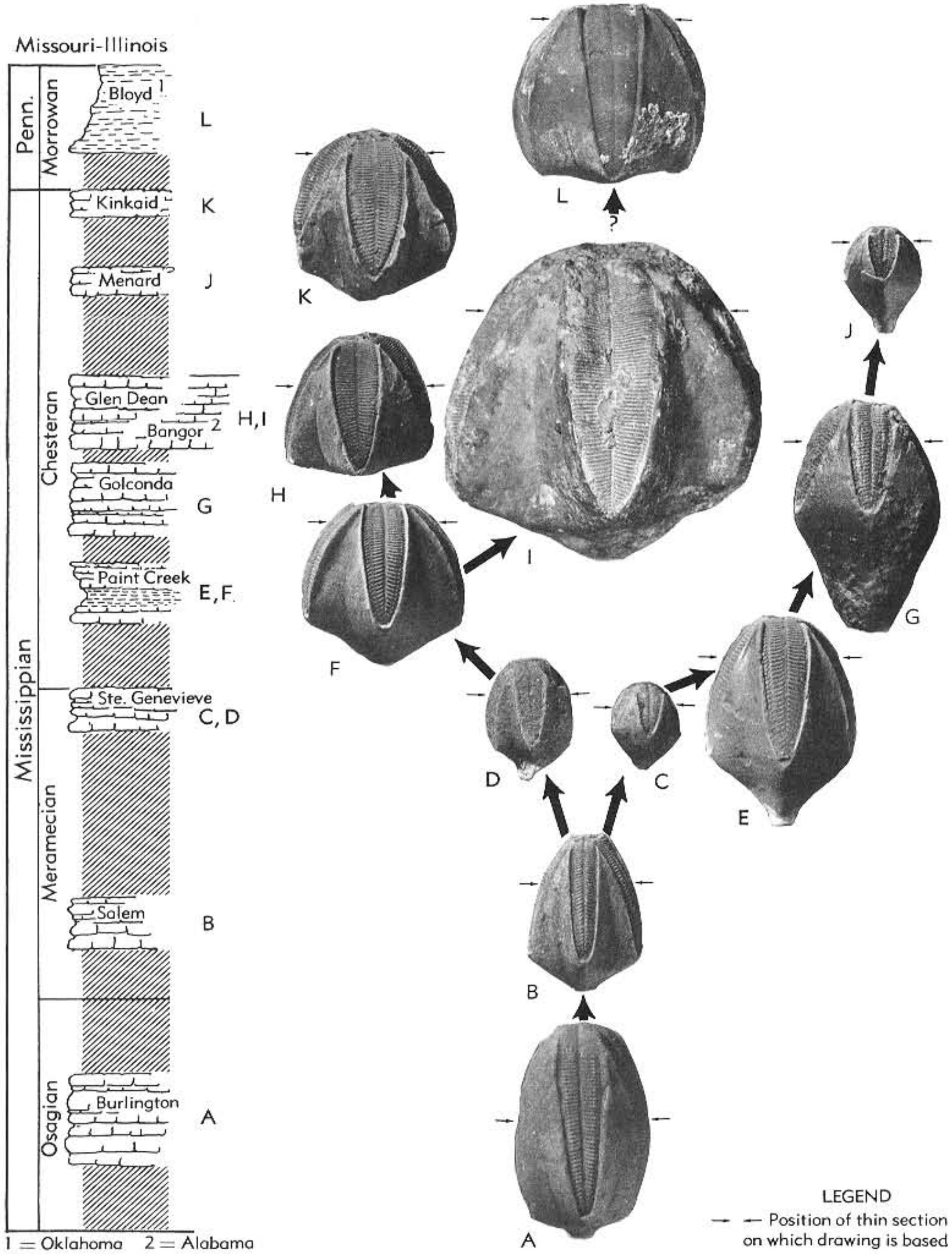


FIG. 180. [*See* page S303 for explanation.]

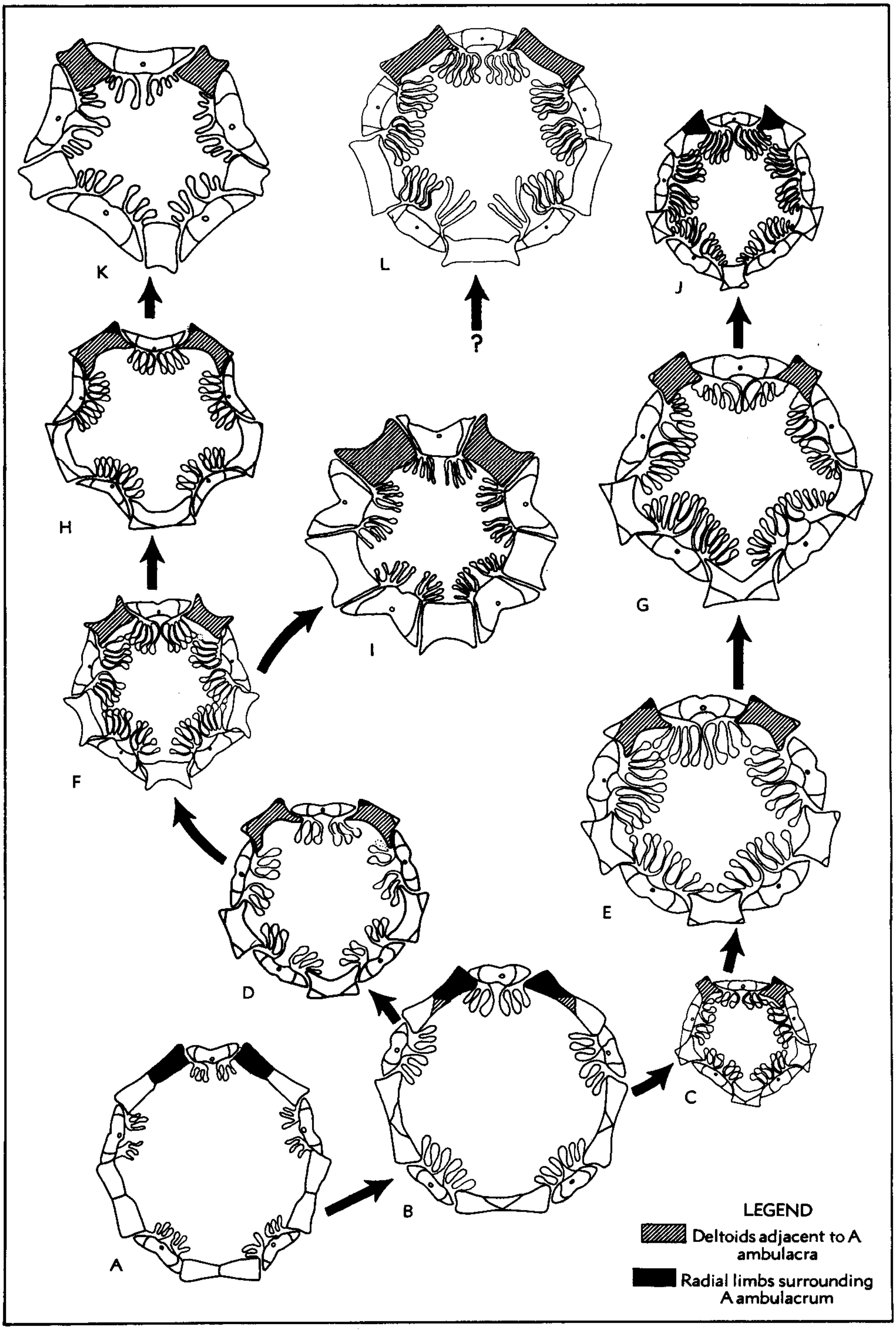


FIG. 180. *(Continued).*

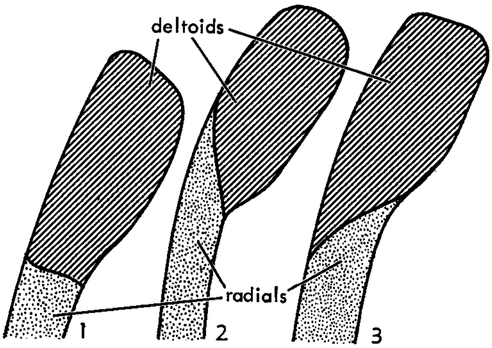


FIG. 181. Radial-deltoid relationships illustrated by diagrammatic sections; *1*, normal abutment; *2*, radial overlap; *3*, deltoid overlap (radials stippled, deltoids oblique ruled, exterior of calyx toward left).

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

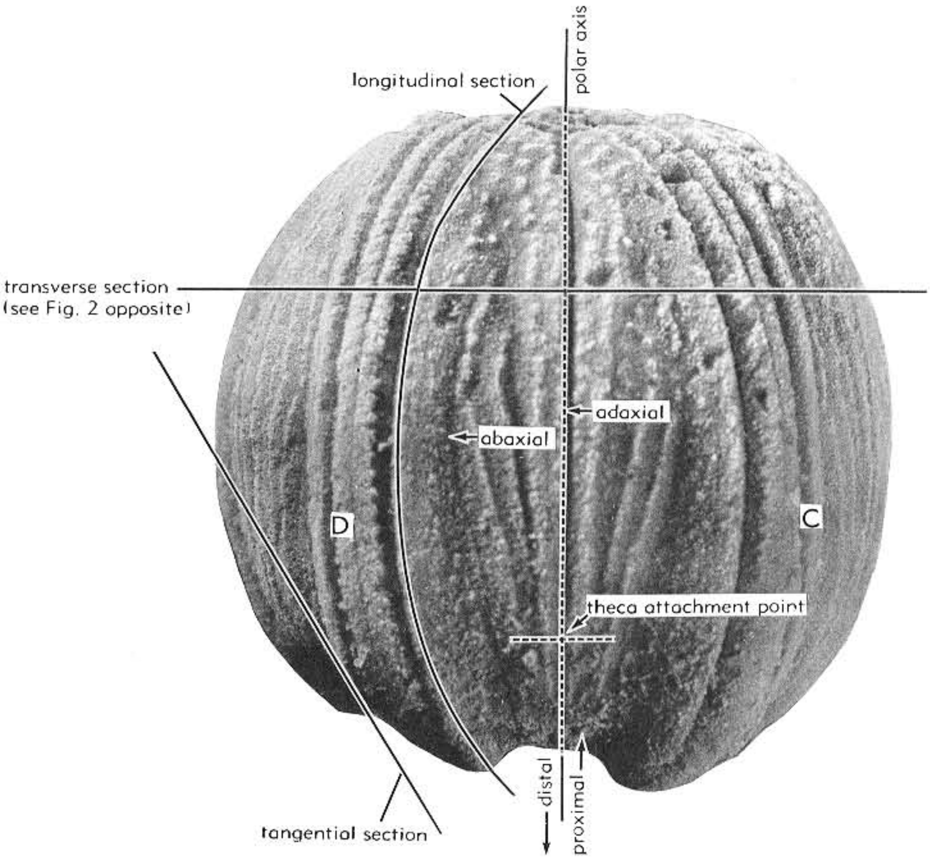


FIG. 182. Terminology related to orientation of blastoid theca illustrated on side view of *Globoblastus norwoodi* (OWEN & SHUMARD), L.Miss.(Burlington Ls.), Burlington, USA (Iowa) (Beaver, n).

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

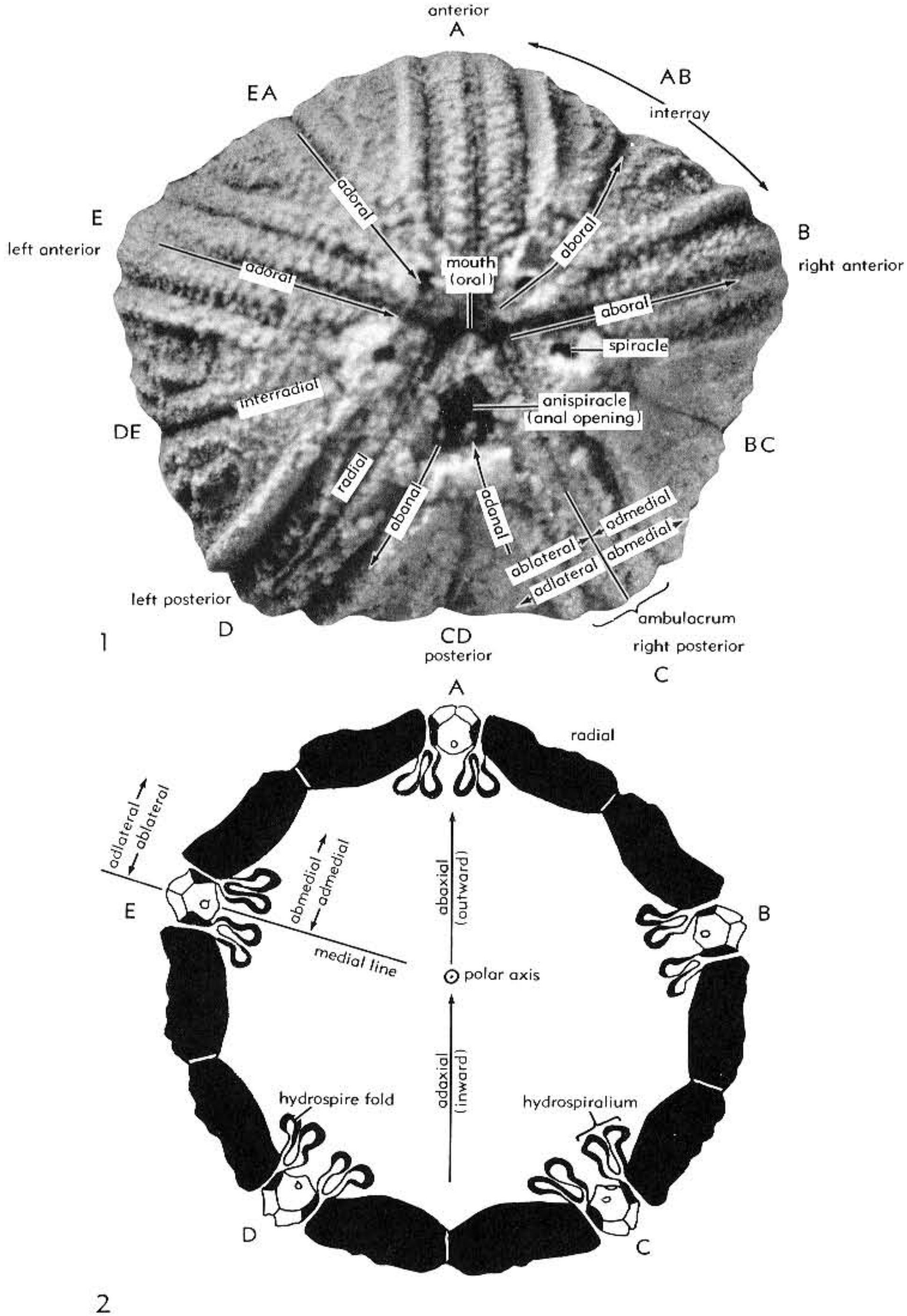


Fig. 183. Terminology related to orientation of blastoid theca illustrated by oral view *(1)* and transverse section *(2)* of *Globoblastus norwoodi* (scale same as in Fig. 193) (Beaver, n).

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 midline of a deltoid is **interradial.**

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

BASALS

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

[*See* pages S310-S311]

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

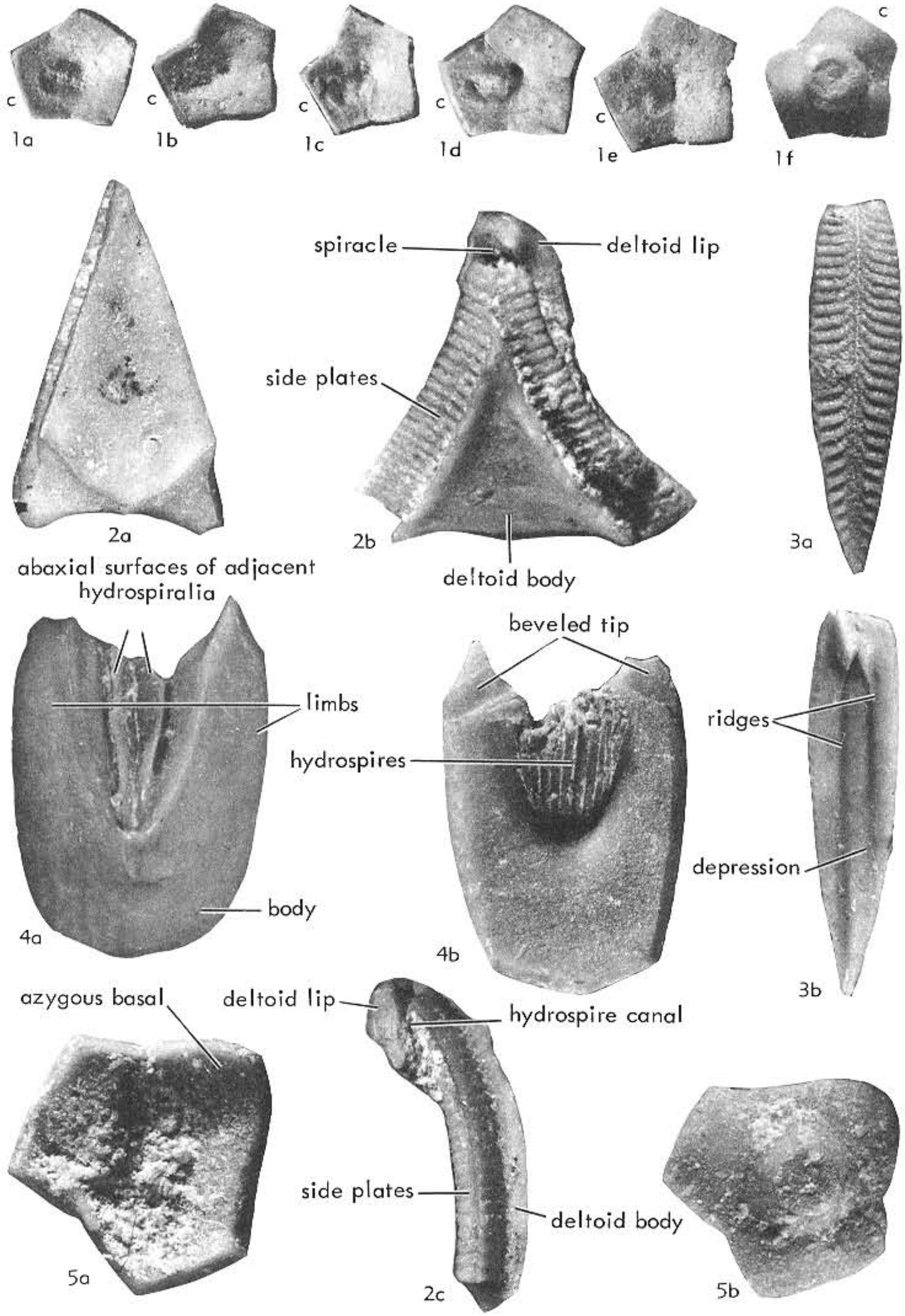


FIG. 184. [*See* page S309 for explanation.]

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

DIMENSIONS

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

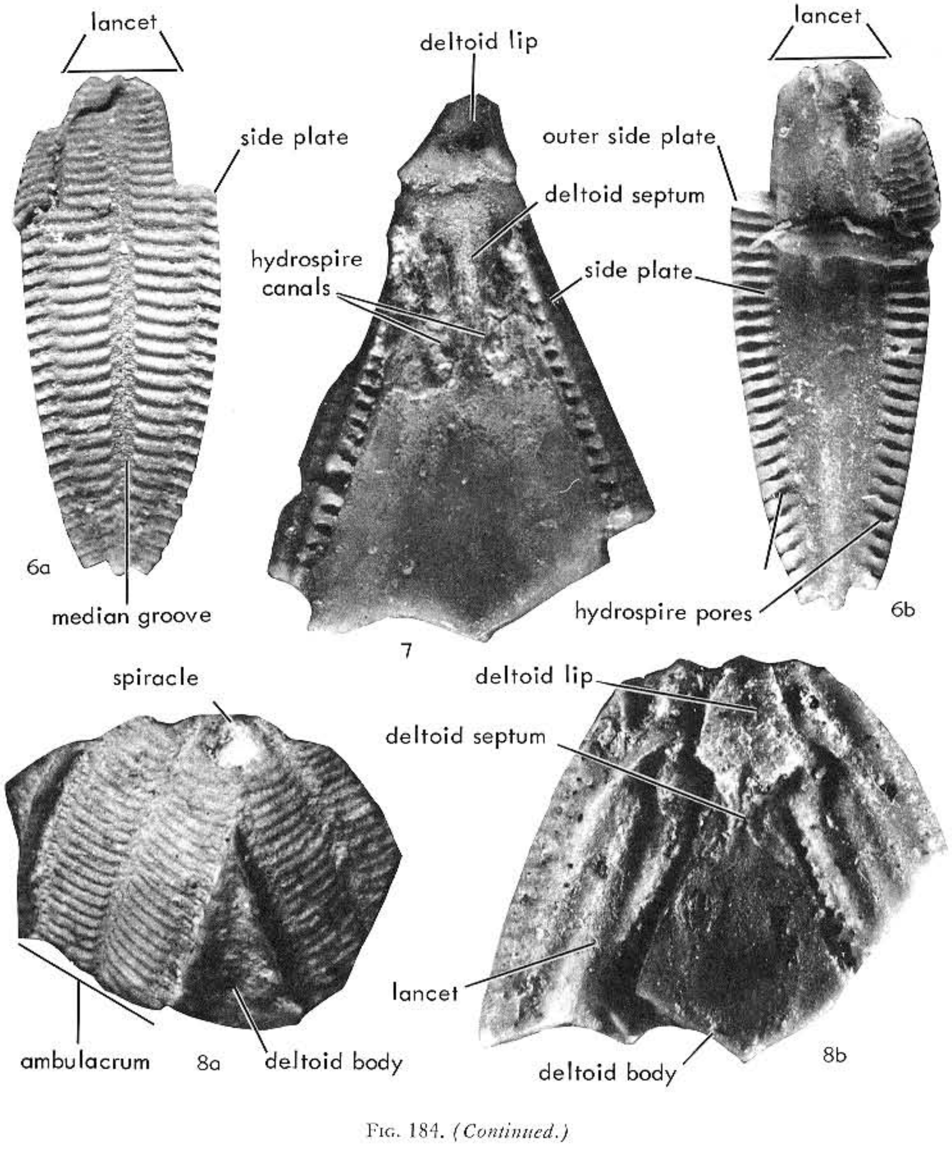


FIG. 184. *(Continued.)*

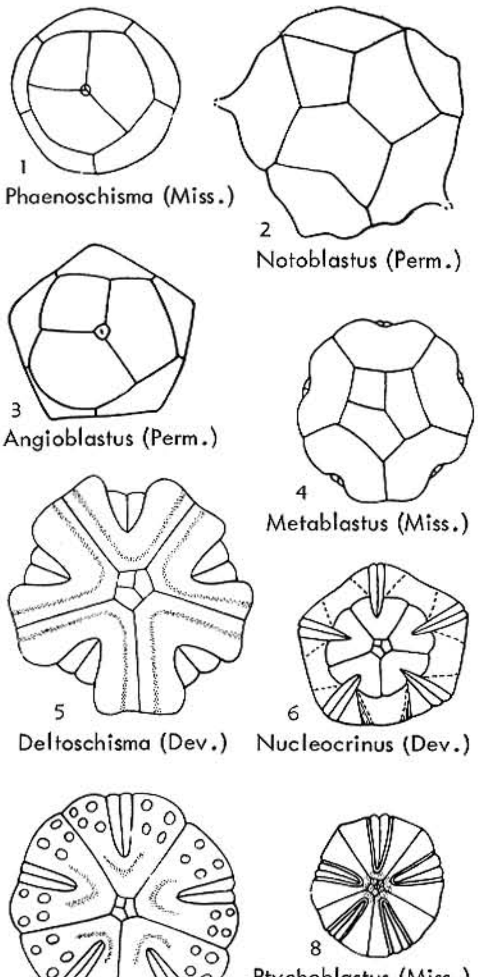


FIG. 185. Aboral views of blastoid calyces showing variation in relationships of basal circlet to adjacent plates of theca; *1-4*, basal circlet relatively large; *5-10*, basal circlet diminutive (not to scale) (Fay, n).

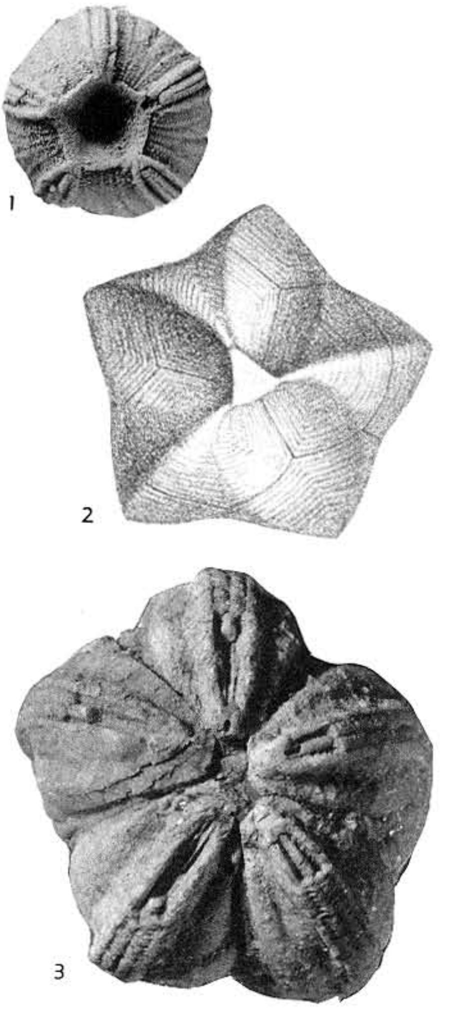


FIG. 186. Aboral views of blastoid calyces showing different types of basal relationships, all ×2.——*1. Globoblastus norwoodi* (OWEN & SHUMARD), L.Miss.(Osagian), Burlington, USA(Iowa) (Beaver, n).——*2. Tricoelocrinus woodmani* (MEEK & WORTHEN), Miss., loc. unknown (Etheridge & Carpenter, 1886).——*3.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

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

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

EXTERNAL FEATURES

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

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

INTERNAL FEATURES

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

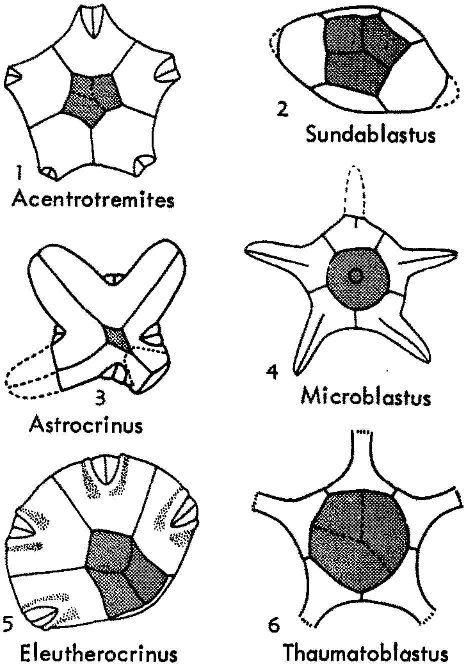


Fig. 187. Aboral views of blastoid calyces showing unusual features or relationships of basal circlets (shaded) (Fay, n).

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

RADIALS

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

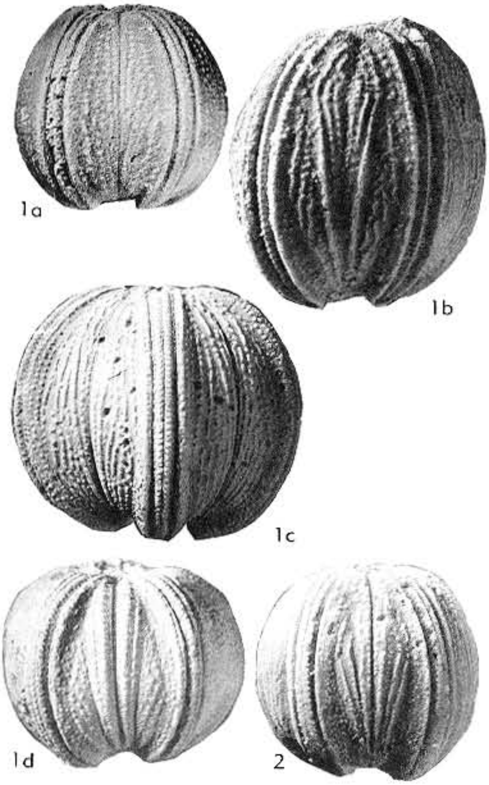


FIG. 188. Variation in ornament of radial plates of *Globoblastus norwoodi* (OWEN & SHUMARD), L. Miss.(Osagian), all ×2; *1a,c,d, 2,* specimens from Burlington Ls., at Burlington, Iowa; *1b,* specimen from Burlington Ls., near Springfield, Mo. (Beaver, n).

SIZE AND SHAPE

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

PORES OR SLITS

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

ORNAMENT

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

DELTOIDS

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

VARIATIONS

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

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

ANAL DELTOIDS

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

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

NOMENCLATURE

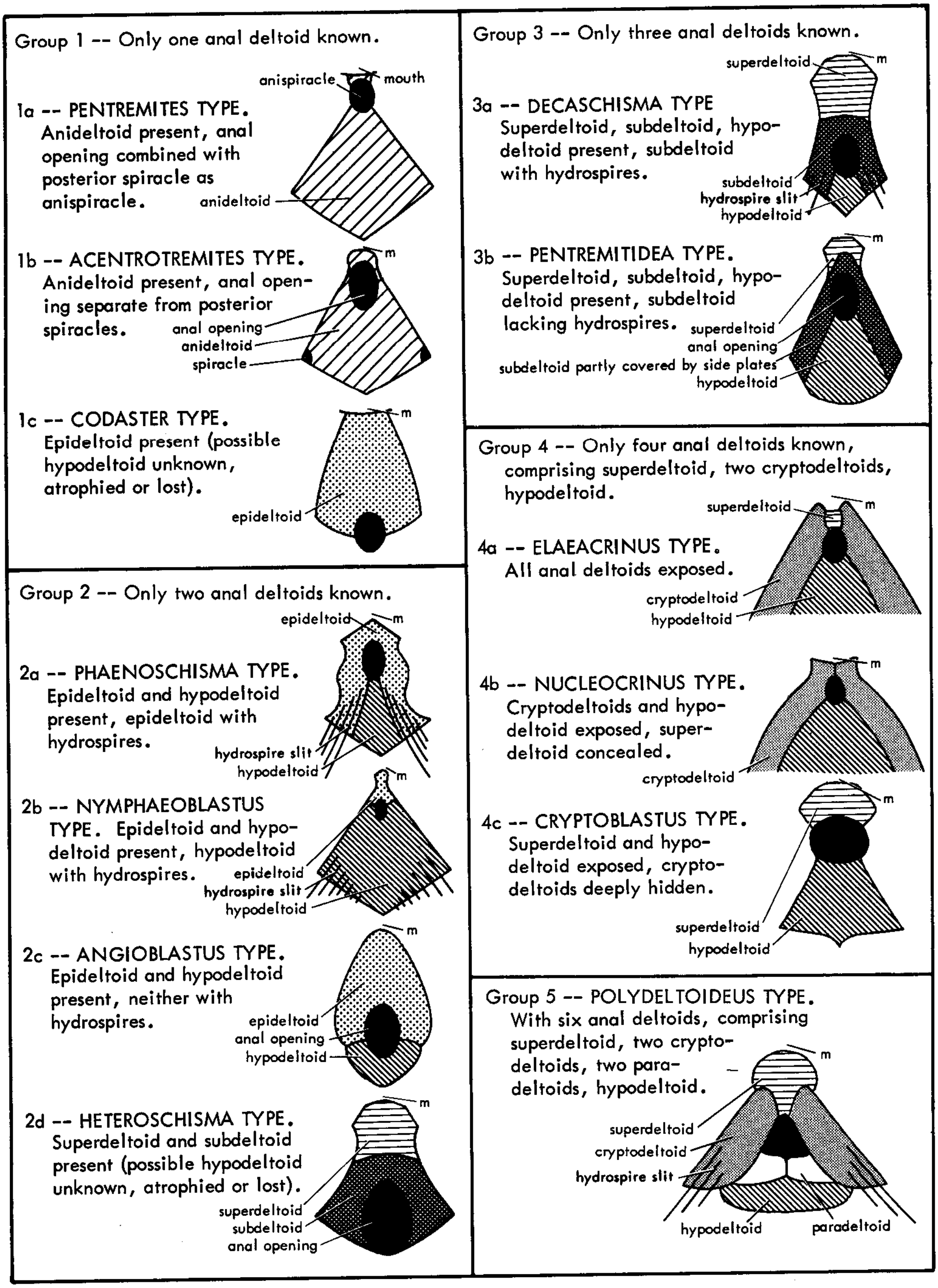
During the past 50 years various names have been introduced for different anal deltoids. The more important of these are **hypodeltoid** and **epideltoid** (Wanner, 1924), **subdeltoid** and **superdeltoid** (Cline & Heuer, 1950), **cryptodeltoids** (Beaver, 1961), and **paradeltoids** (Reimann & Fay,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

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

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

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

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



Group 1 -- Only one anal deltoid known.

1a -- PENTREMITES TYPE. Anideltoid present, anal opening combined with posterior spiracle as anispiracle.

1b -- ACENTROTREMITES TYPE. Anideltoid present, anal opening separate from posterior spiracles.

1c -- CODASTER TYPE. Epideltoid present (possible hypodeltoid unknown, atrophied or lost).

Group 2 -- Only two anal deltoids known.

2a -- PHAENOSCHISMA TYPE. Epideltoid and hypodeltoid present, epideltoid with hydrospires.

2b -- NYMPHAEOBLASTUS TYPE. Epideltoid and hypodeltoid present, hypodeltoid with hydrospires.

2c -- ANGIOBLASTUS TYPE. Epideltoid and hypodeltoid present, neither with hydrospires.

2d -- HETEROSCHISMA TYPE. Superdeltoid and subdeltoid present (possible hypodeltoid unknown, atrophied or lost).

Group 3 -- Only three anal deltoids known.

3a -- DECASCHISMA TYPE Superdeltoid, subdeltoid, hypodeltoid present, subdeltoid with hydrospires.

3b -- PENTREMITIDEA TYPE. Superdeltoid, subdeltoid, hypodeltoid present, subdeltoid lacking hydrospires.

Group 4 -- Only four anal deltoids known, comprising superdeltoid, two cryptodeltoids, hypodeltoid.

4a -- ELAEACRINUS TYPE. All anal deltoids exposed.

4b -- NUCLEOCRINUS TYPE. Cryptodeltoids and hypodeltoid exposed, superdeltoid concealed.

4c -- CRYPTOBLASTUS TYPE. Superdeltoid and hypodeltoid exposed, cryptodeltoids deeply hidden.

Group 5 -- POLYDELTOIDEUS TYPE. With six anal deltoids, comprising superdeltoid, two cryptodeltoids, two paradeltoids, hypodeltoid.

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

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

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

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

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

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

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

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

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

TABLE 1 (continued)

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

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

RELATION OF HYDROSPIRES TO ANAL DELTOIDS

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

TYPES OF BLASTOIDS BASED ON ANAL-DELTOID CHARACTERS

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

Group 1

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

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

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

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

Group 2

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

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

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

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

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

Group 3

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

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

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

Group 4

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

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

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

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

Group 5

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

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

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

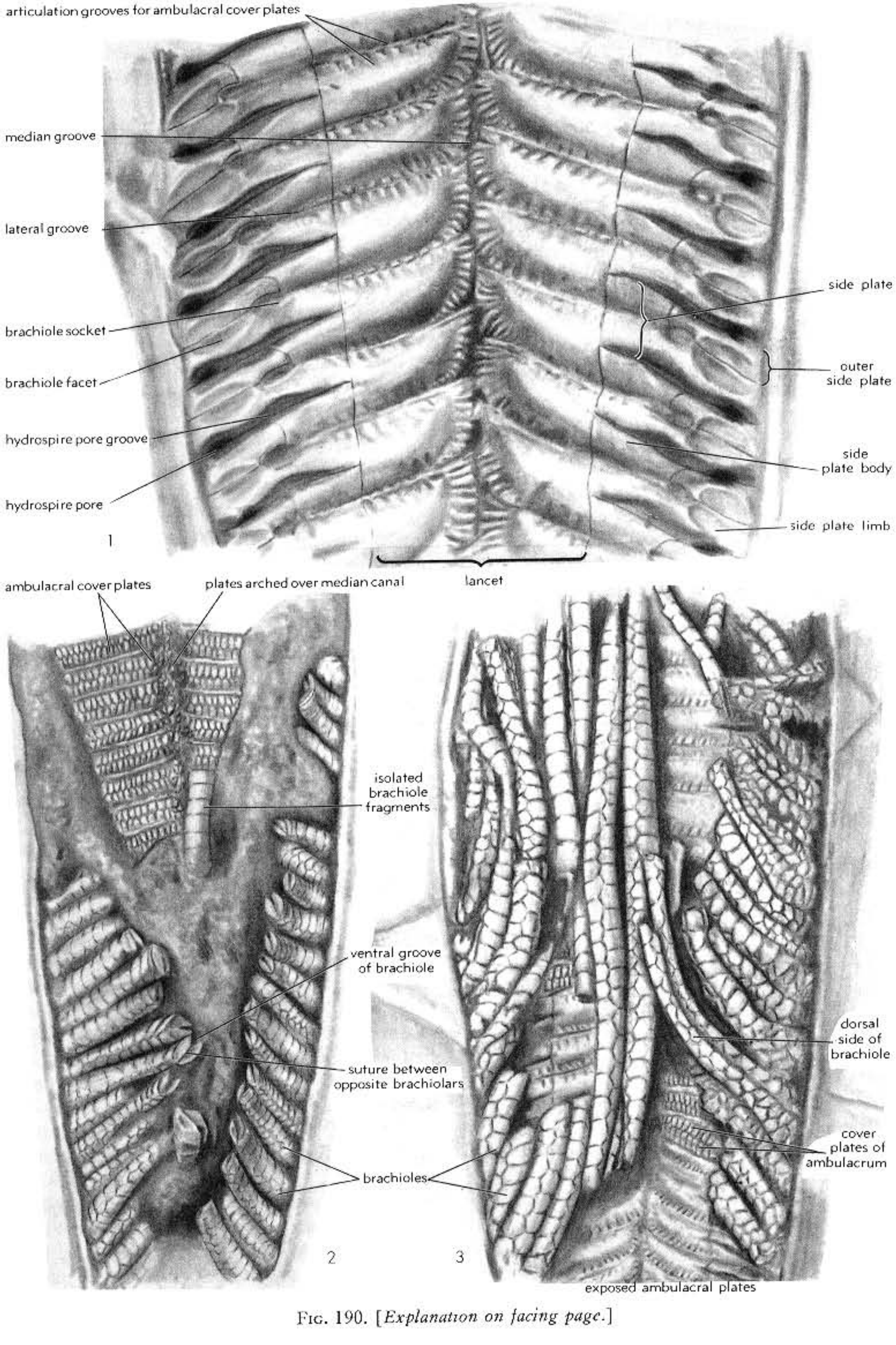


Fig. 190. [*Explanation on facing page.*]

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

AMBULACRA AND AMBULACRAL PLATES

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

MEDIAN AND LATERAL GROOVES

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

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

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

LANCET

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

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

TRANSVERSE SHAPE

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

---

[*See facing page*]

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

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

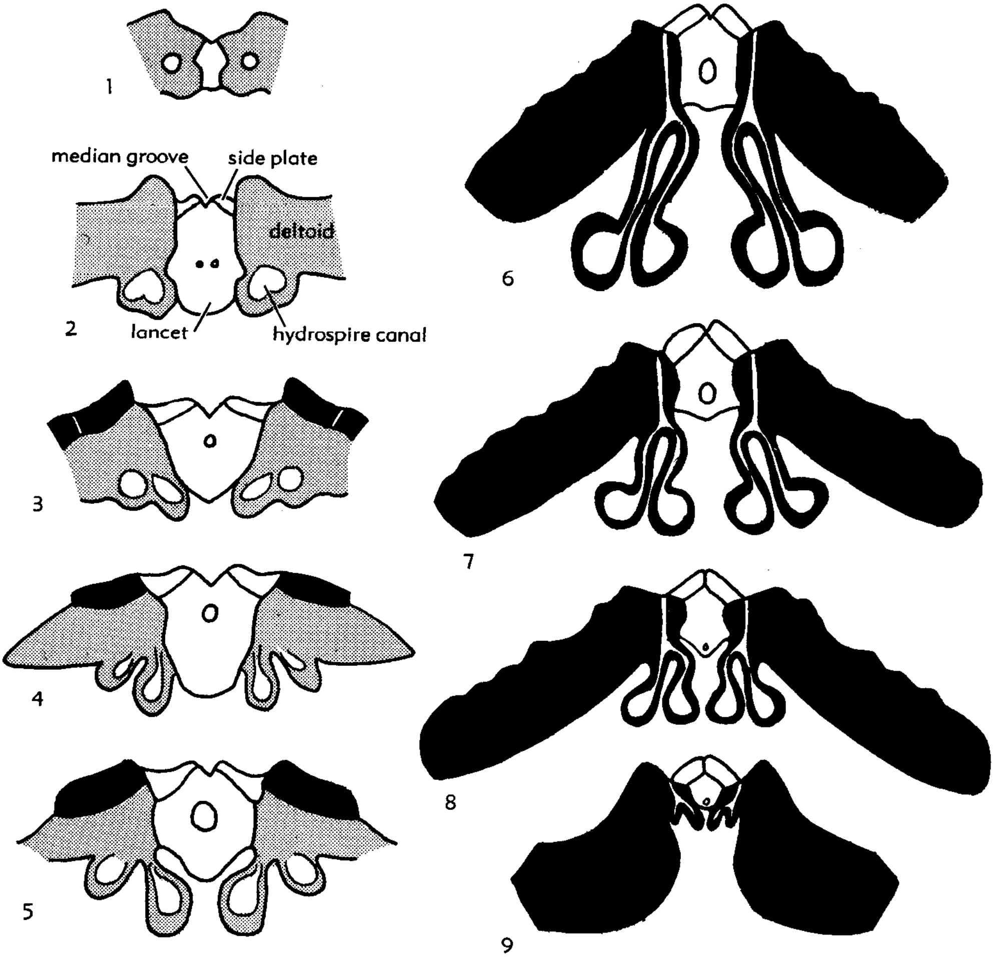


FIG. 191. Lancet and hydrospire structures of *Globoblastus,* L.Miss.(Osag.), USA(Mo.); drawings of thin sections of *G. norwoodi* cut perpendicular to an ambulacrum showing development of hydrospires; (lancet and side plates unshaded, deltoids shaded, radials black), ×8 (Beaver, 1961).——*1*. Section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

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

CANALS

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

"UNDERLANCET"

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

SIDE PLATES AND OUTER SIDE PLATES

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

SIDE PLATES RESTING ON LANCET

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

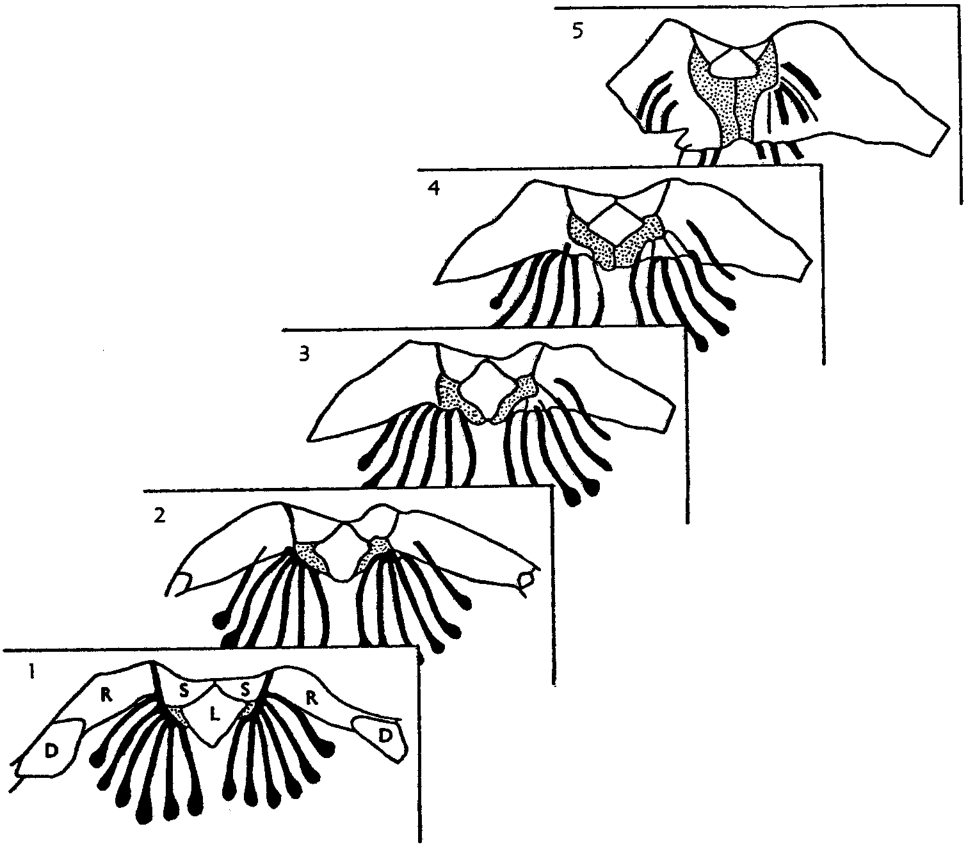


FIG. 192. Serial sections of *Pentablastus supracarbonicus* SIEVERTS-DORECK, U.Carb., Spain, showing hydrospire plates (stippled) coming together admedially beneath lancet to develop so-called "underlancet" in aboral to spiracular slits; section *1* is at level of spiracular slits, whereas section *5*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

SIDE PLATES ABUTTING LANCET

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

---

[*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).

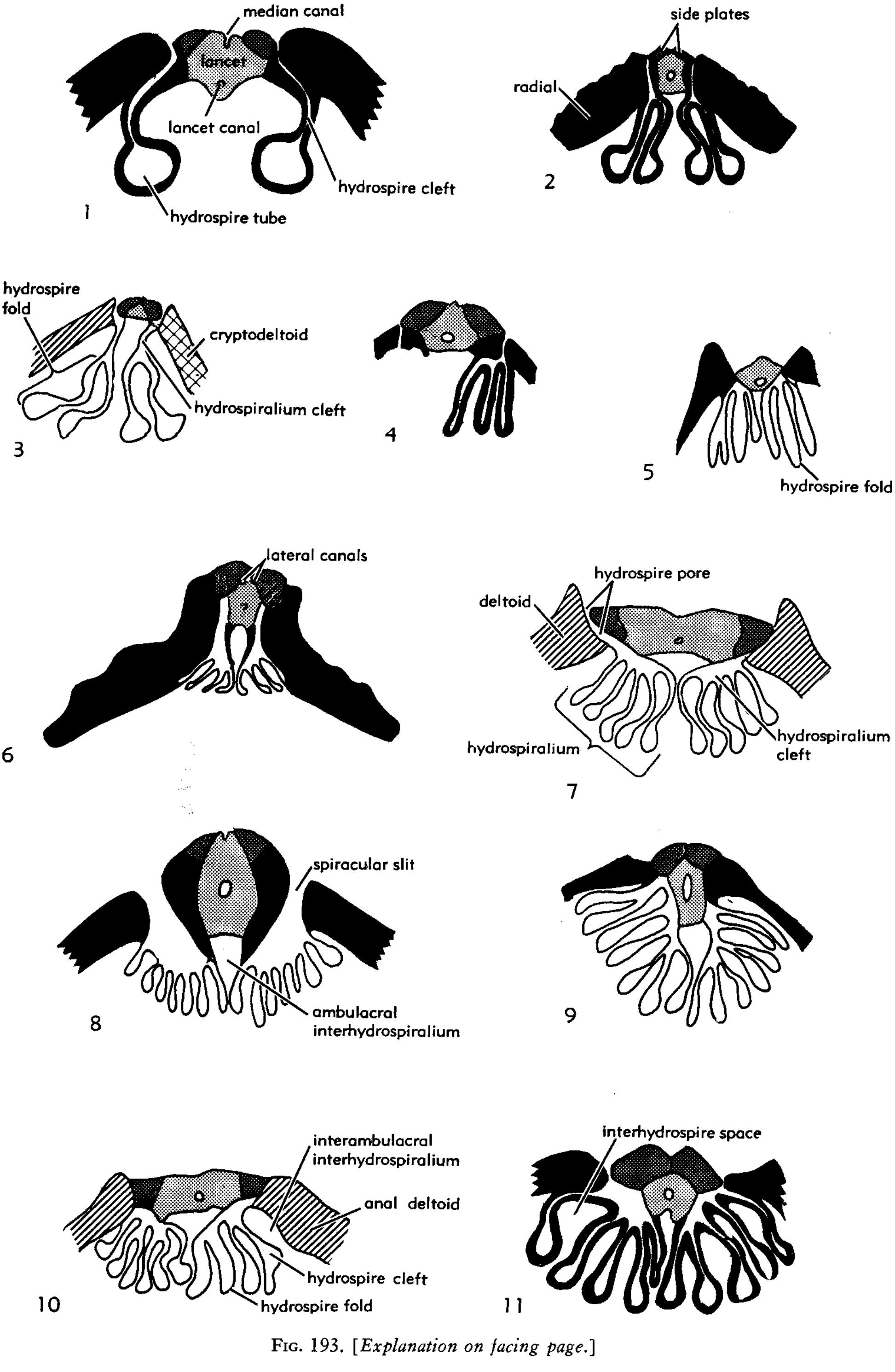


FIG. 193. [*Explanation on facing page.*]

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

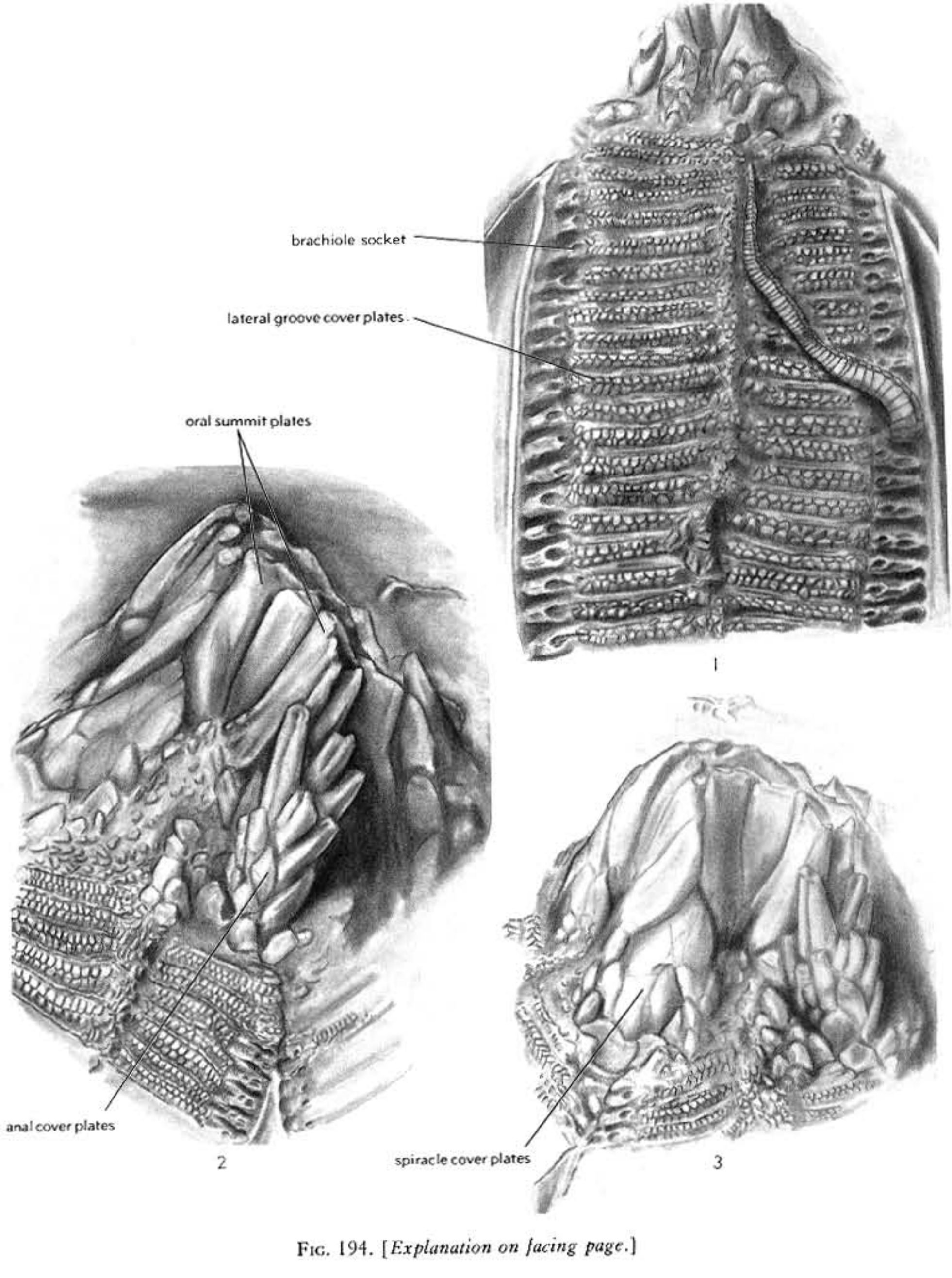


FIG. 194. [*Explanation on facing page.*]

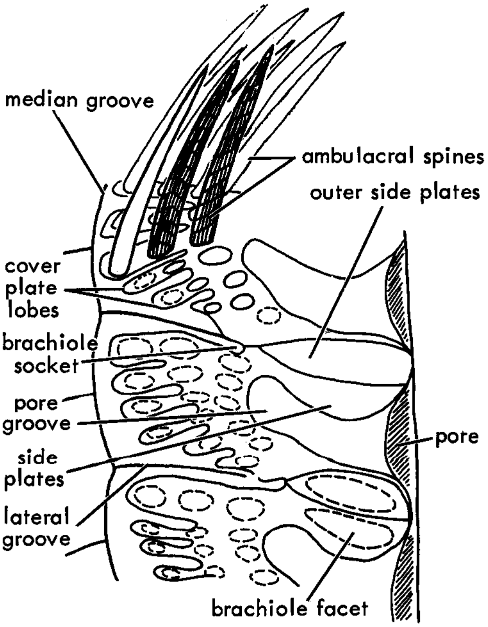


FIG. 195. Composite diagrammatic drawing of side plates in *Hyperoblastus nuciformis* (REIMANN), M. Dev.(Hungry Hollow F., Widder beds), near Thedford, Ontario; showing probable position of ambulacral spines, ×75 (Fay & Reimann, 1962).

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.

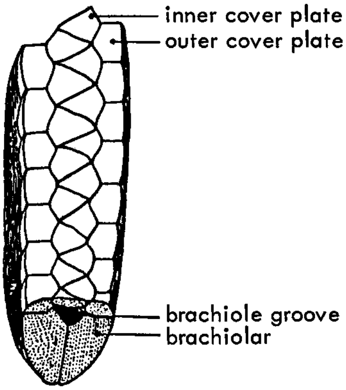


FIG. 196. Diagram of brachiolar fragment *Hyperoblastus nuciformis* (REIMANN), M.Dev., Ontario, showing inner and outer series of brachiole cover plates, ×35 (Fay & Reimann, 1962).

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.

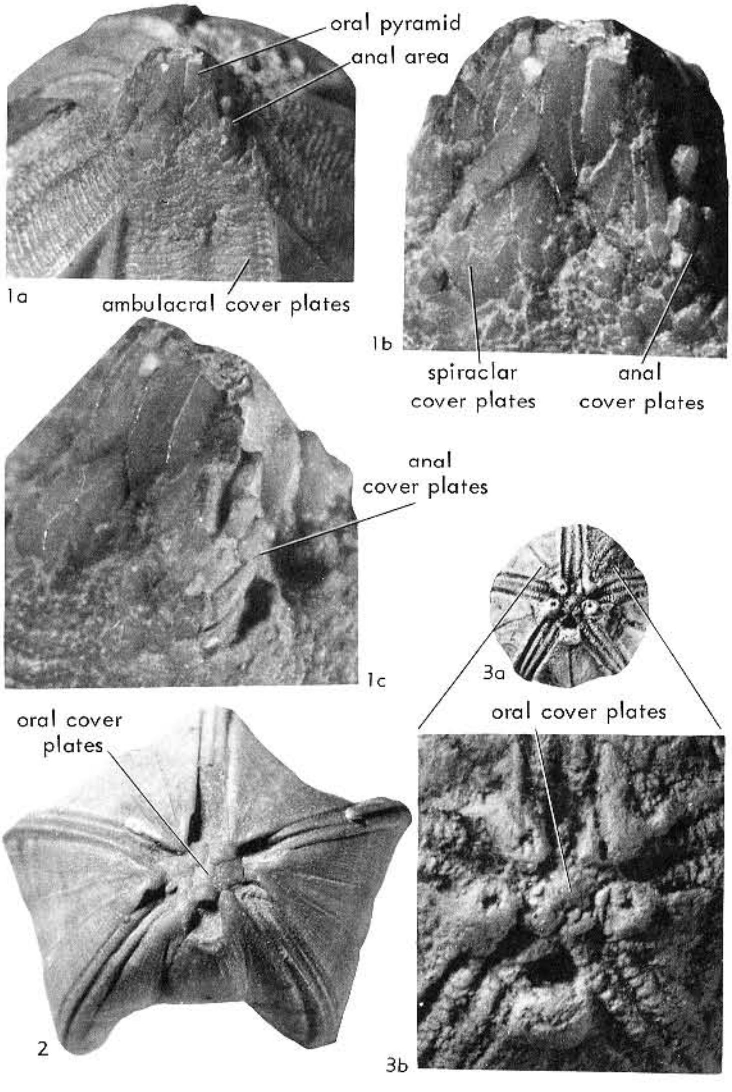


FIG. 197. Types of blastoid summit plates (Beaver, n).——*1. Pentremites godoni* (DEFRANCE), U.Miss. (Chester.), USA(Ill.); *1a*, summit view showing pyramid-like structure over mouth area and ambulacral cover plates, ×6; *1b*, oral pyramid and plates covering spiracle and anal opening, ×15; *1c*, anal 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.

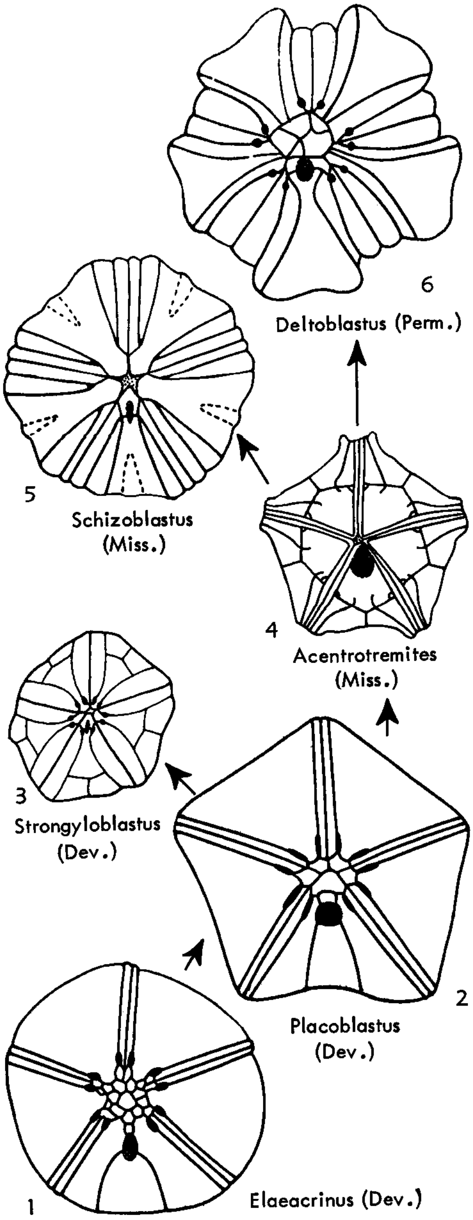


FIG. 198. Variations in spiracles of *Elaeacrinus* type, characterized by 10 spiracles surrounding mouth and separate anus, genetic lineages not implied (drawings from Fay).

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-*

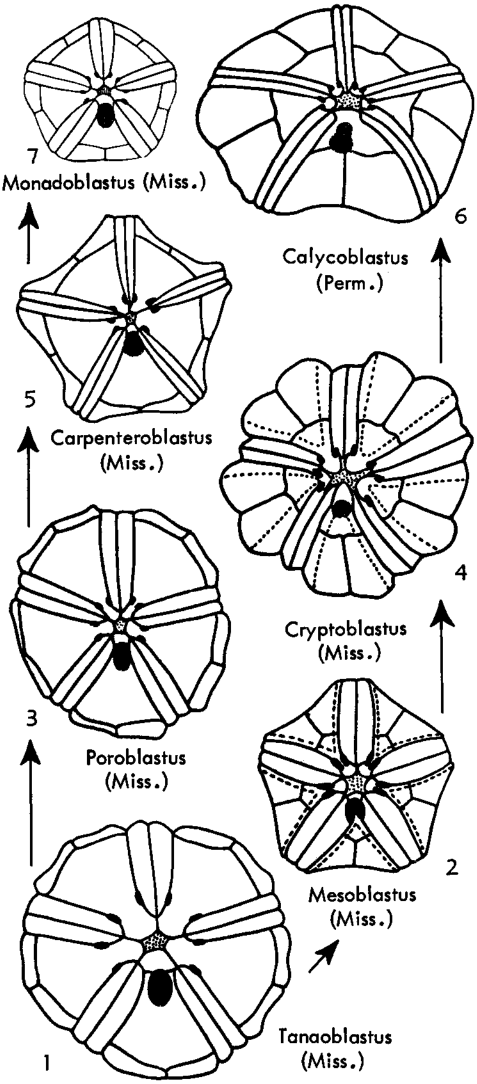


FIG. 199. Variations in spiracles of *Tanaoblastus* type, distinguished by 8 spiracles around mouth and posterior spiracles confluent with anus forming anispiracle, genetic lineages not implied (drawings from Fay).

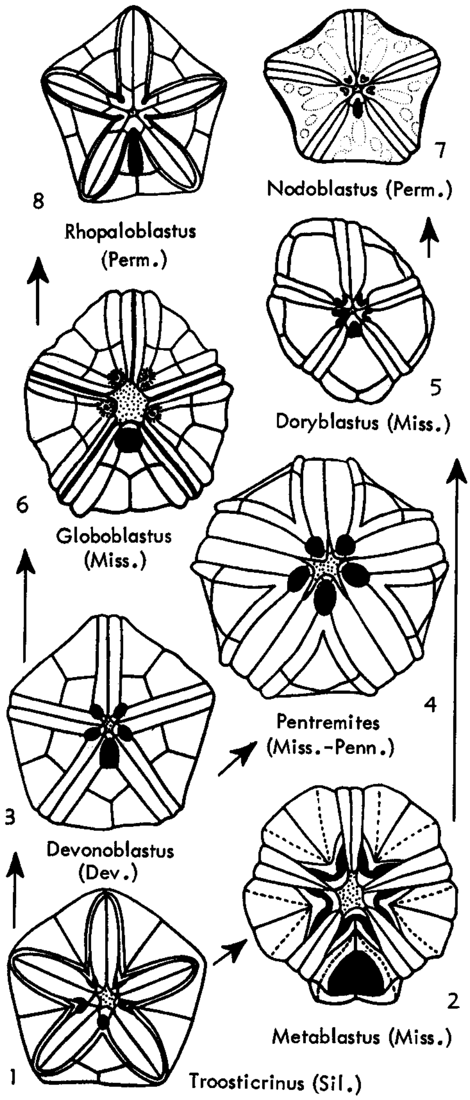


FIG. 200. Variations in spiracles of *Pentremites* type, having four spiracles or four paired spiracles and anispiracle surrounding mouth area, genetic lineages not implied (drawings from Fay).

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

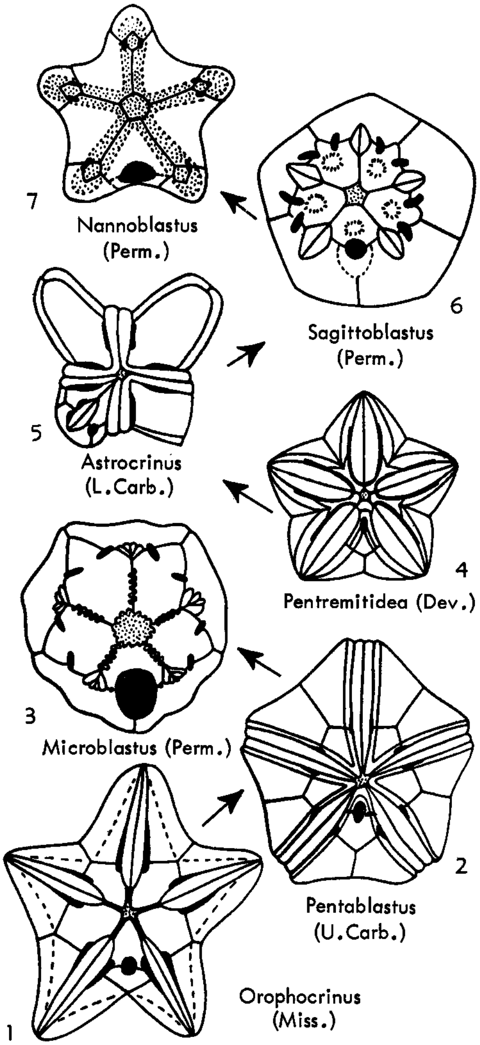


FIG. 201. Variations in spiracular slits. The *Orophocrinus* type is characterized by having 10 slits around mouth and separate anus. The *Sagittoblastus* type differs in that posterior slits are confluent with the anus, resulting in 8 slits and an anispiracle, genetic lineages not implied (drawings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

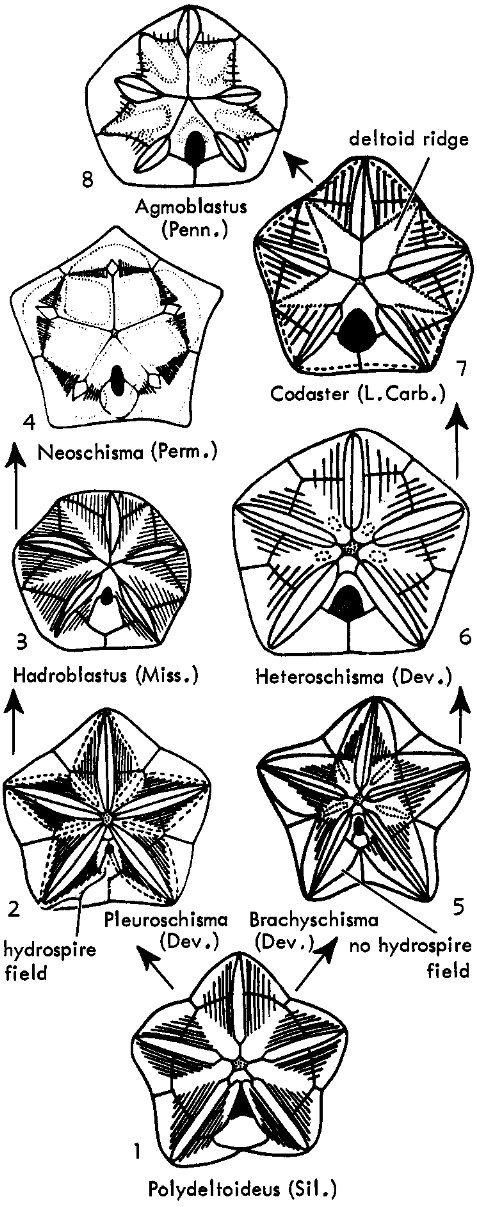


FIG. 202. Variations in hydrospire slits. *1-4*, genera of *Polydeltoideus* type, with slits exposed or partially exposed in 10 fields and separate anus. *5*. *Brachyschisma*, sole representative of *Brachyschisma* type, with nine exposed hydrospire fields and separate anus, slits lacking on left side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

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).

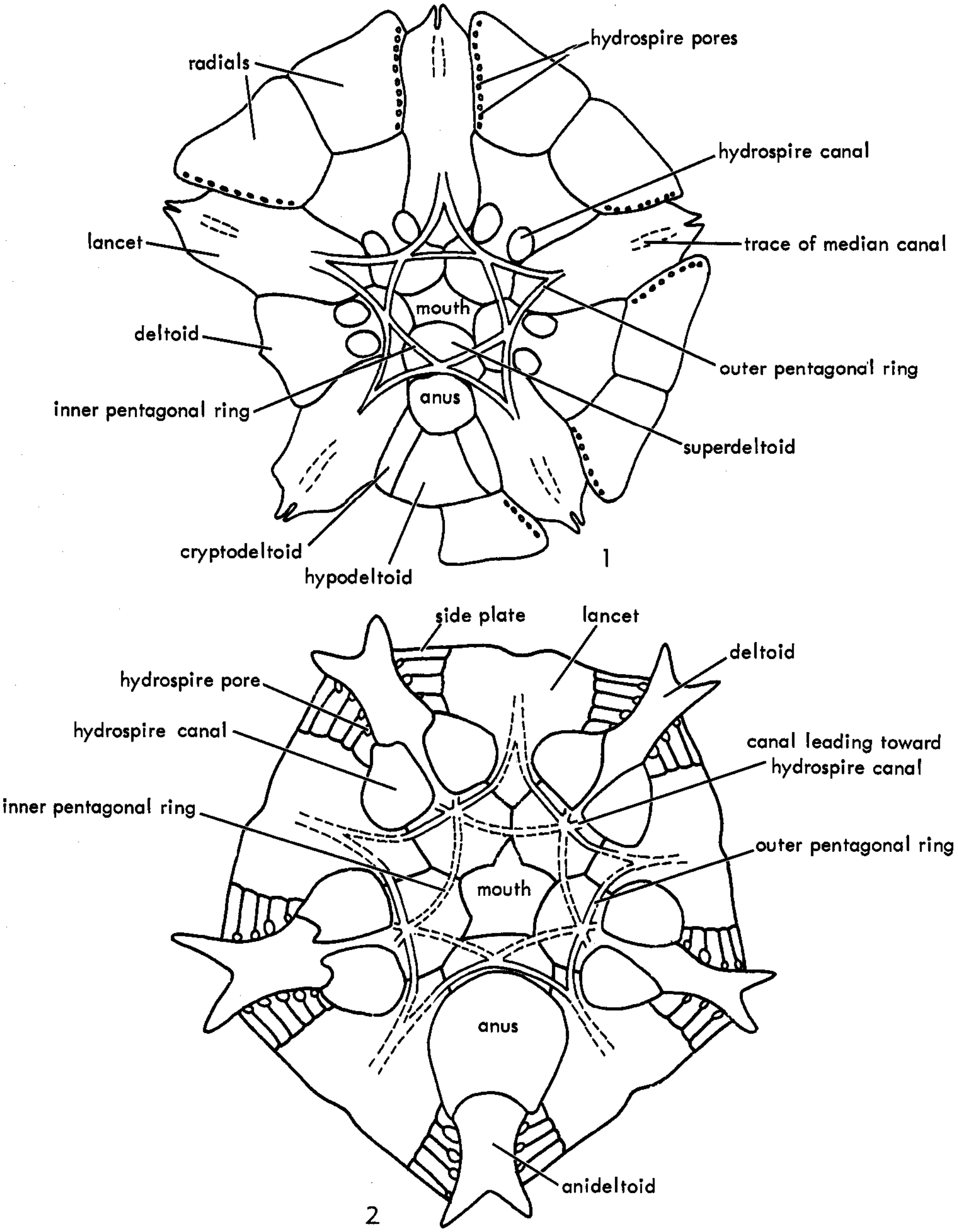


FIG. 203. Drawings based on thin sections of oral ring canal.——*1. Globoblastus norwoodi* (OWEN & SHUMARD), L.Miss.(Burlington Ls.), near Springfield, Missouri; inner and outer pentagonal ring canals, each branch of outer ring connecting aborally with median canal of lancet.——*2. Pentremites godoni* (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-

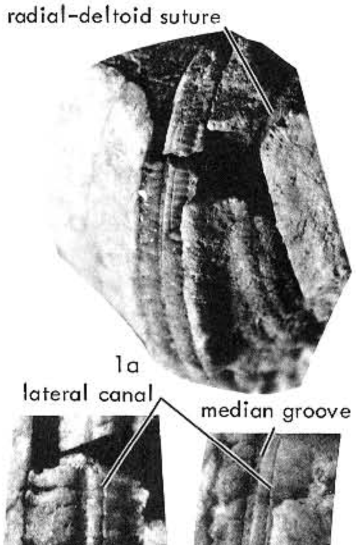


FIG. 204. Lateral canals in *Auloblastus clinei* BEAVER, Miss.(Osag.), near Springfield, Mo.; *A*, ×4; *B,C*, ×10 (*A*, Beaver, n; *B,C*, Beaver, 1961).

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).

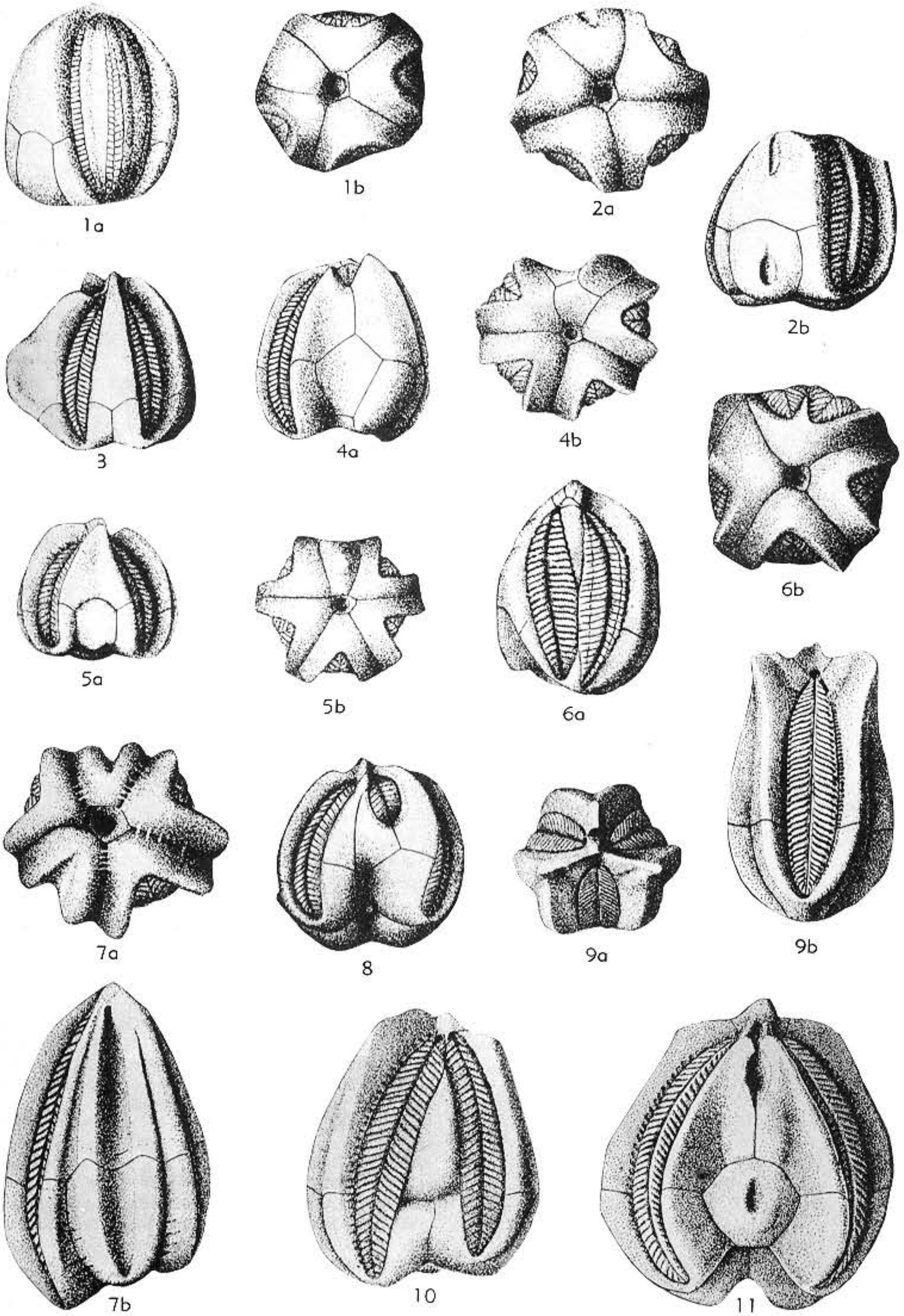


FIG. 205. [*Explanation on opposite page.*]

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.

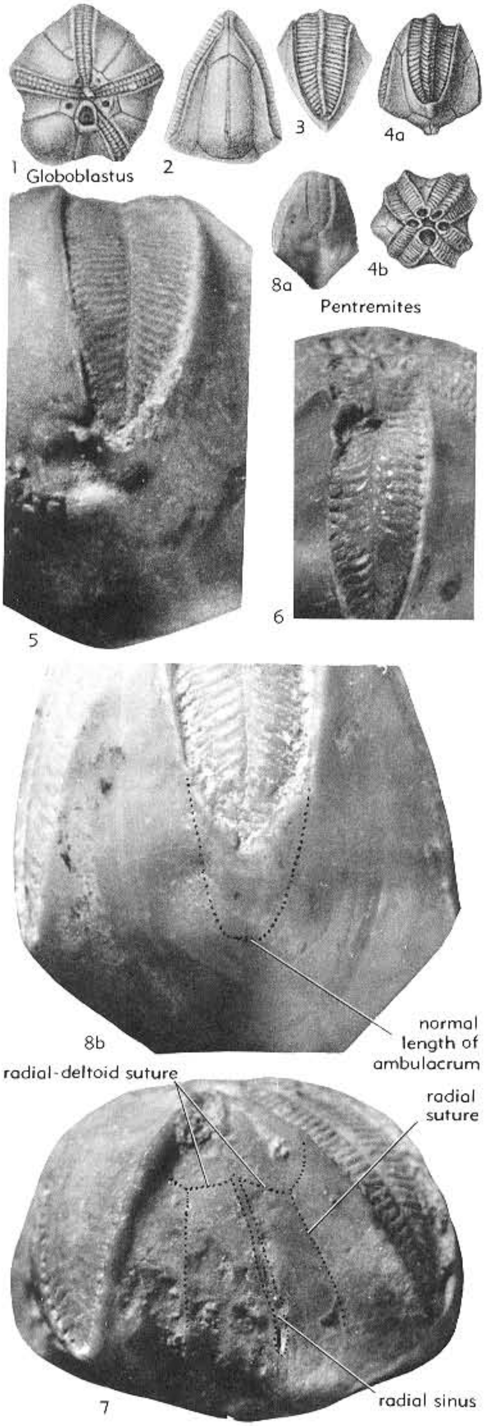


FIG. 206. Abnormal specimens of *Globoblastus (1)* and *Pentremites (2-8)* from Mississippian rocks of Iowa, Illinois, and Alabama.——*1. G. norwoodi* (OWEN & SHUMARD), Iowa; adoral view of specimen with abnormal radials, ambulacrum lacking in *D* ray, ×1.3.——*2-7. P. godoni* (DEFRANCE) from Alabama *(2-4)* 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

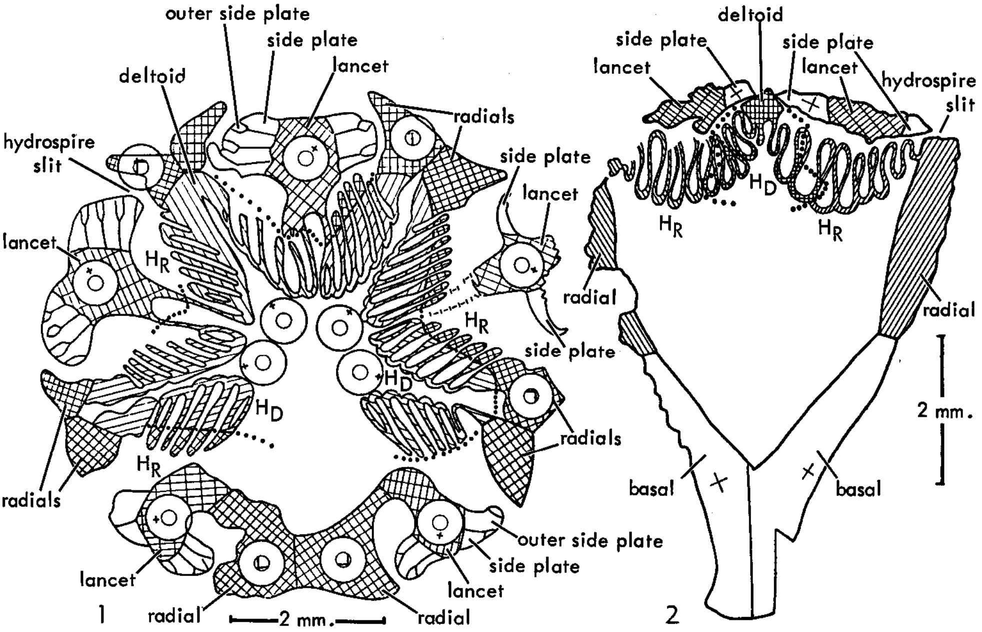


FIG. 207. Optical properties of *Cryptoschisma schultzii* (D'ARCHIAC & DE VERNEUIL).——*1.* Drawing of transverse section in summit area (Lucas, 1953).——*2.* Drawing of slightly inclined longitudinal section through an interray. [H_R, part of hydrospires interpreted to have formed from the radials; H_D, 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-

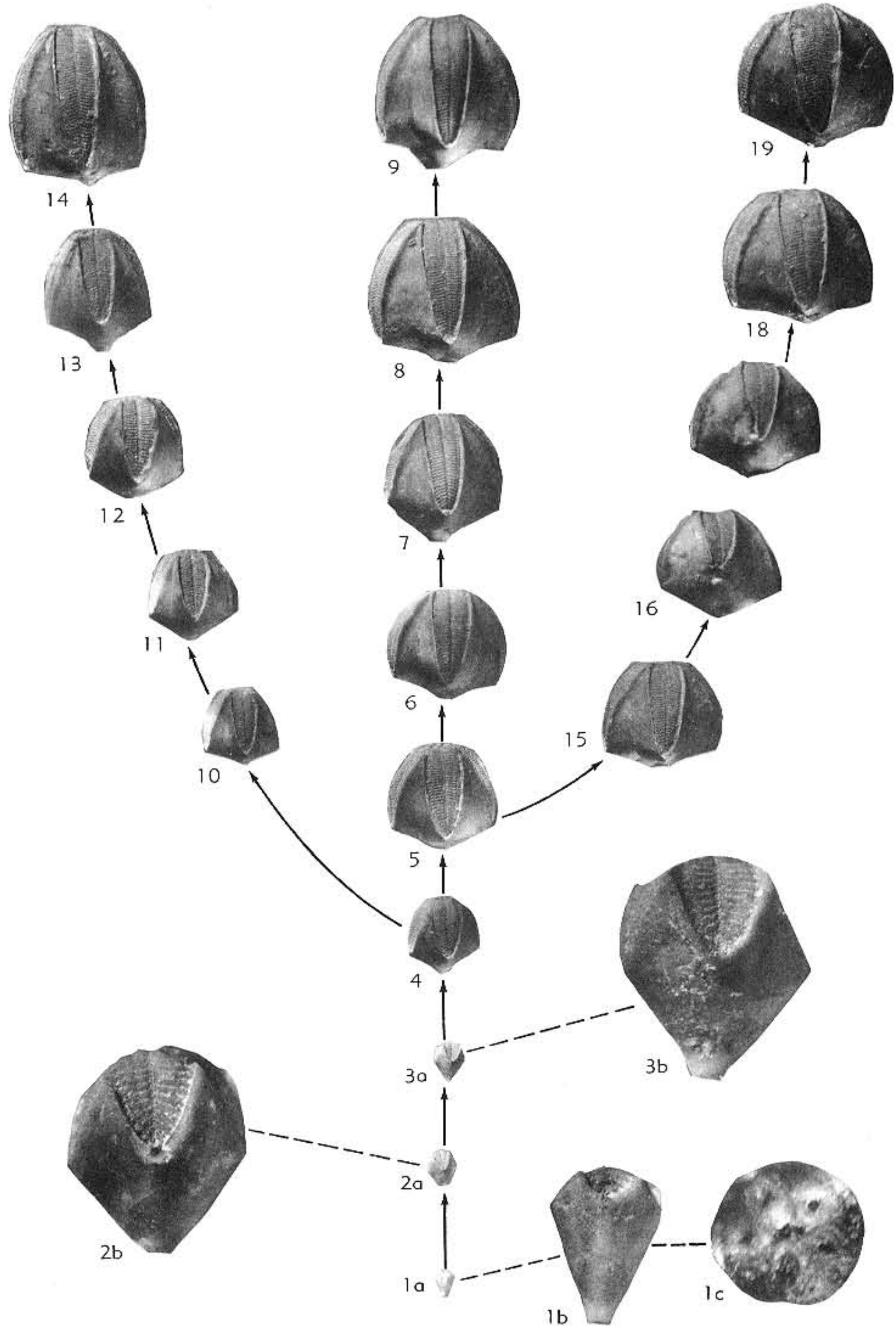


FIG. 208. Growth series of relatively flat-based *Pentremites* calyces (Type 1) represented by *P. godoni* (DEFRANCE), Paint Creek F. (Chester.), near Floraville, Illinois; Subtype 1a, equidimensional, *1-9*; Subtype 1b, slender, *10-14*; Subtype 1c, broad, *15-19*; all figures ×1 except as indicated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

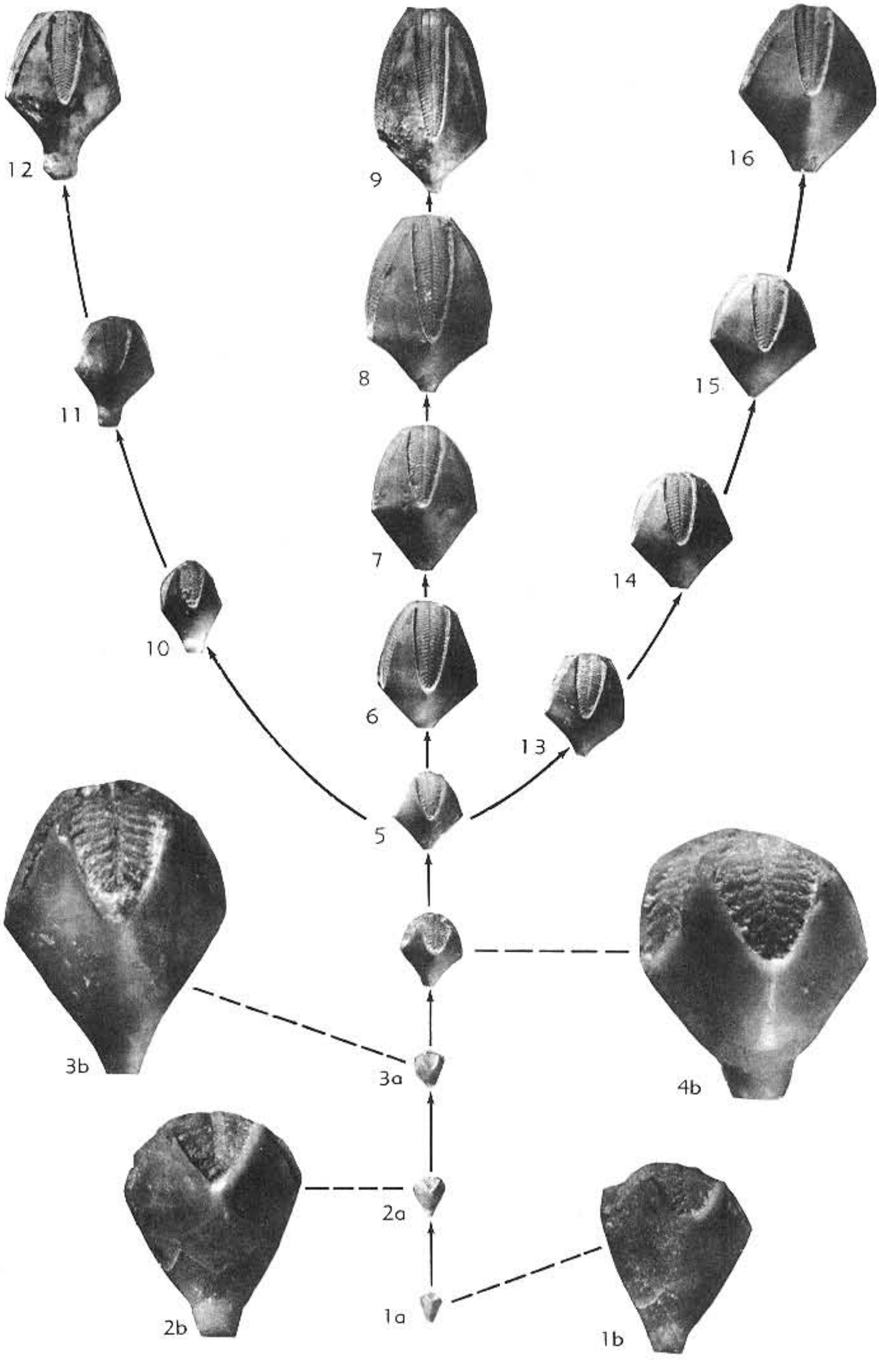


Fig. 209. Growth series of pyriform *Pentremites* calyces (Type 2), all from Paint Creek F. (Chester), near Floraville, Illinois; Subtype 2a, *P. symmetricus* Hall, *6-9*; Subtype 2b, *P. gemmiformis* Hambach, *10-12*; Subtype 2c, *P. pyramidatus* Ulrich, *?13,14-16*; all figures ×1 except as indicated (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.
[Museum of Paleontology, University of Michigan]

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

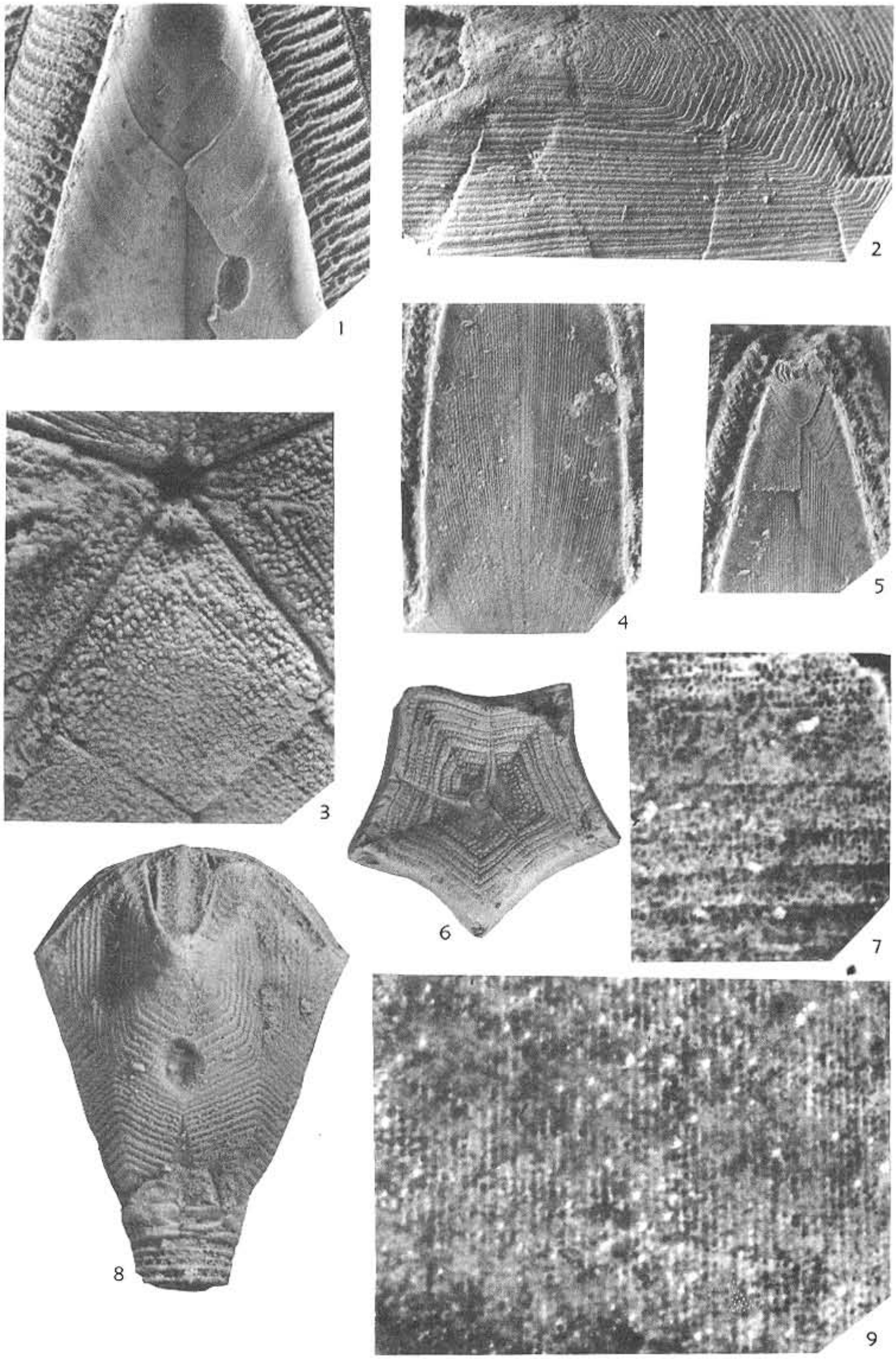


FIG. 210. [*Explanation on facing page.*]

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

---

[See facing page]

FIG. 210. Plate growth in blastoids.

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

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

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

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

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

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

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

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

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

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

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

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

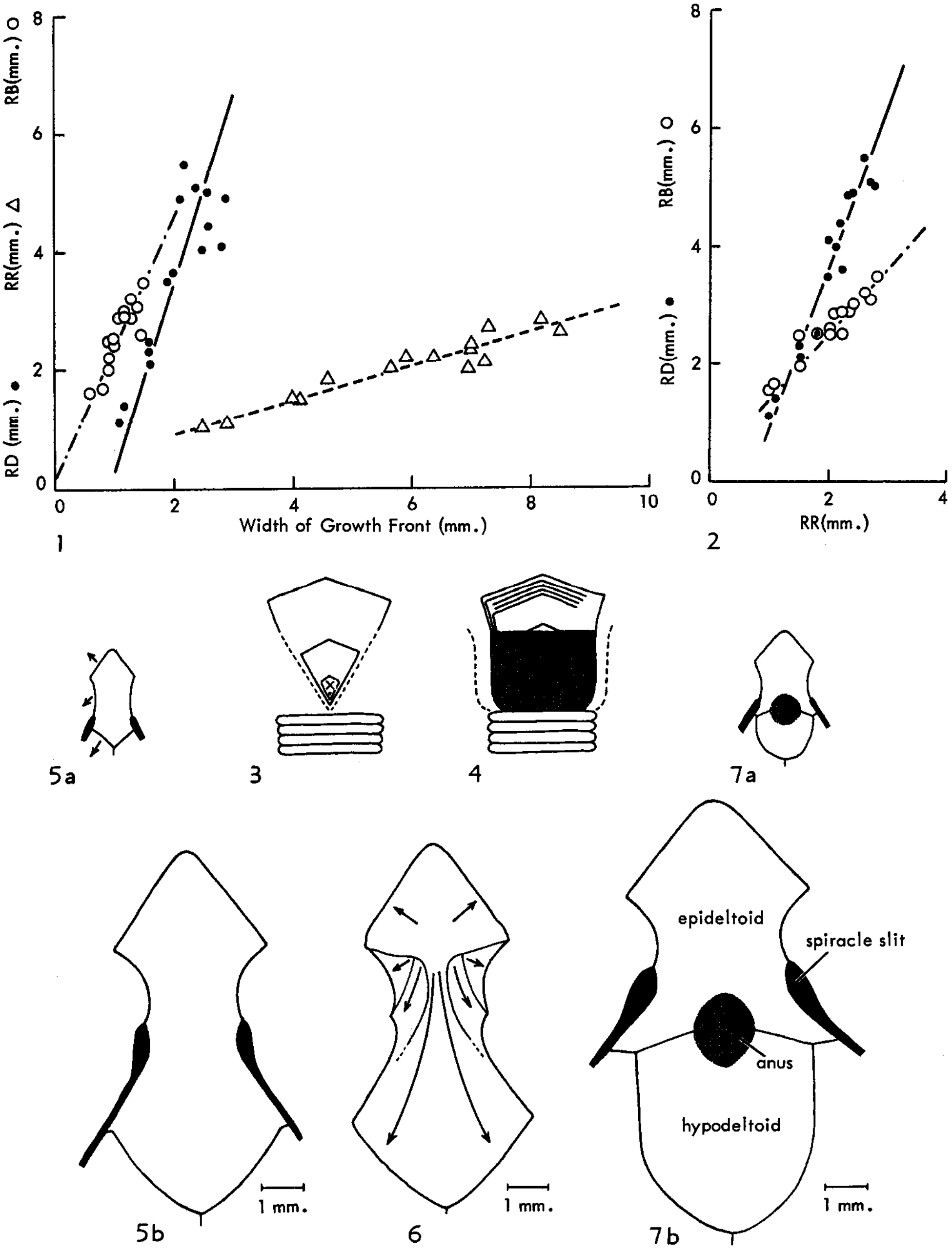


FIG. 212. Growth of radials, basals, and deltoids.

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

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

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

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

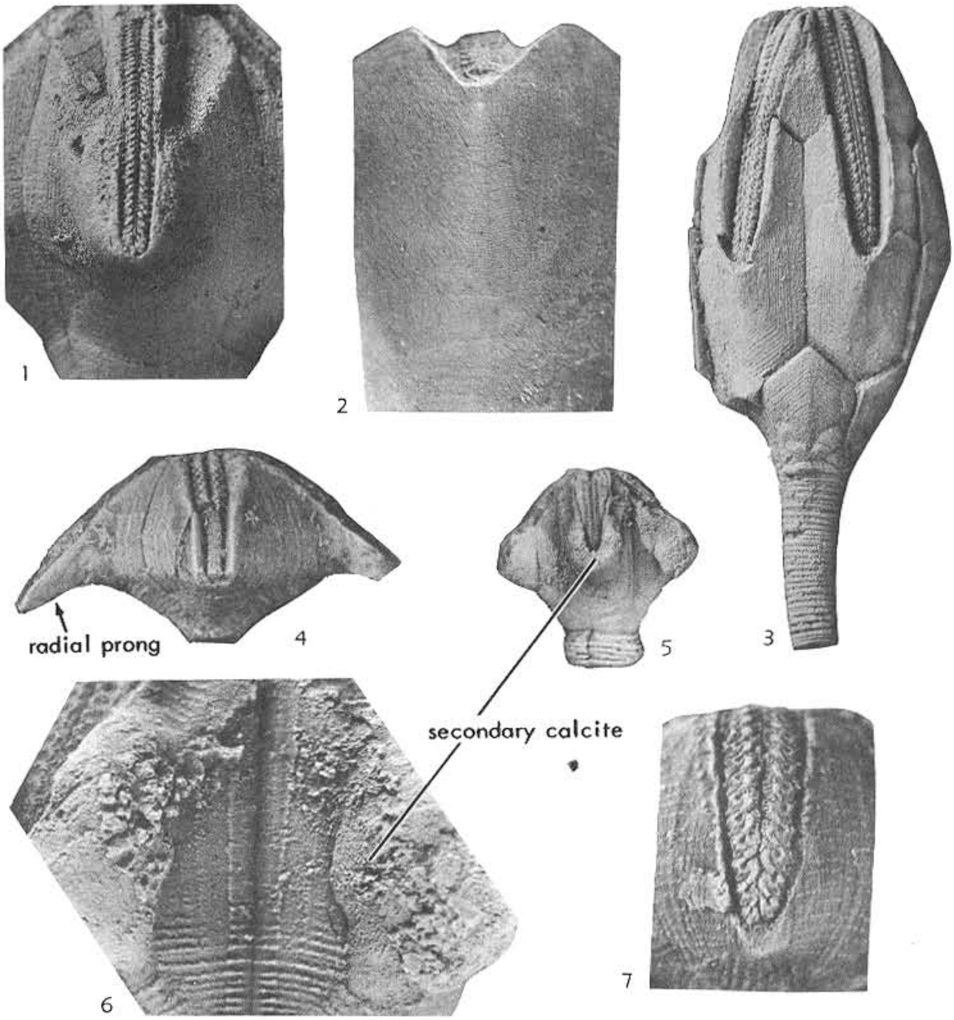


FIG. 213. Growth patterns of radials and secondary calcite deposits.

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

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

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

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

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

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

FIG. 212. (*Continued.*)

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

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

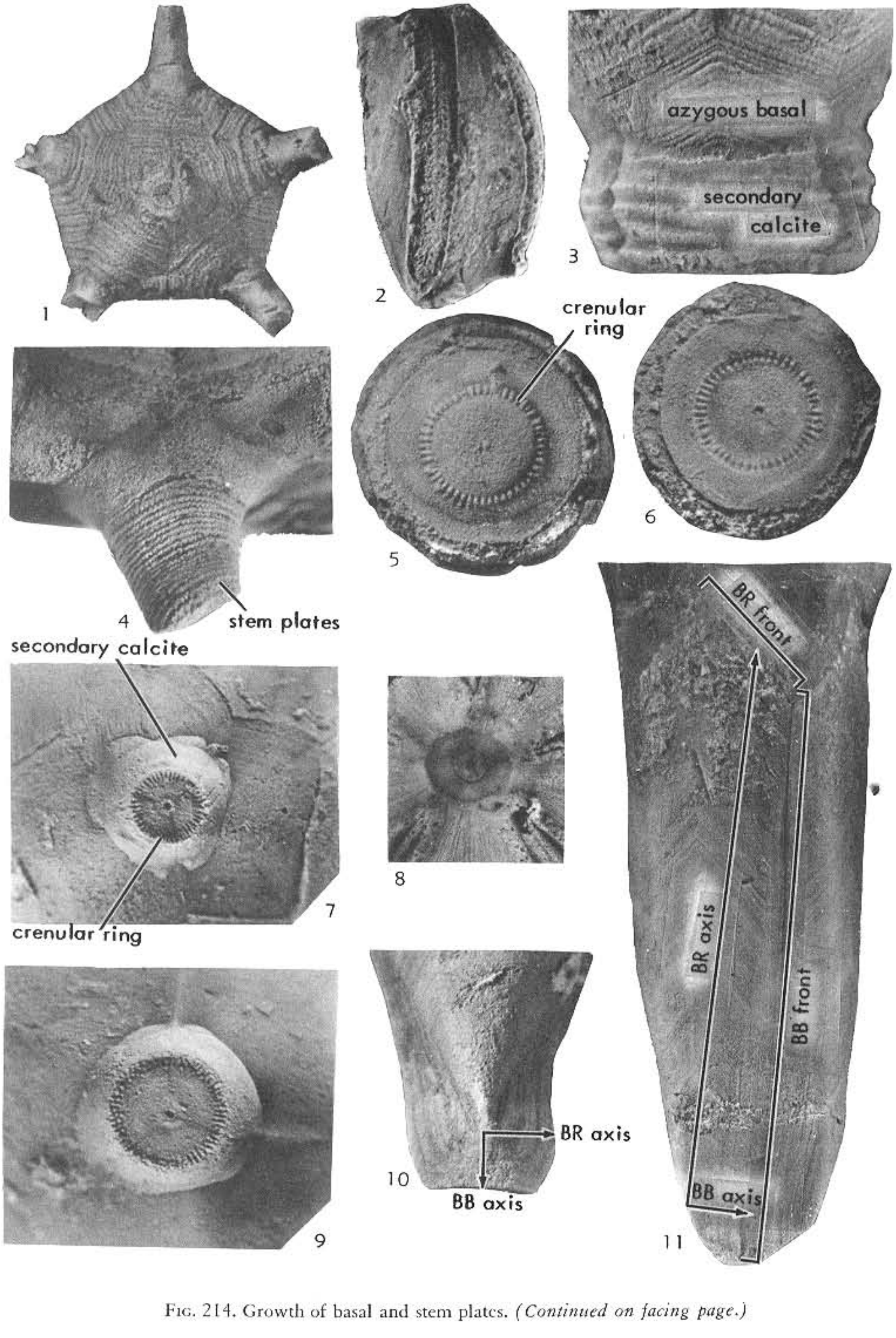


FIG. 214. Growth of basal and stem plates. *(Continued on facing page.)*

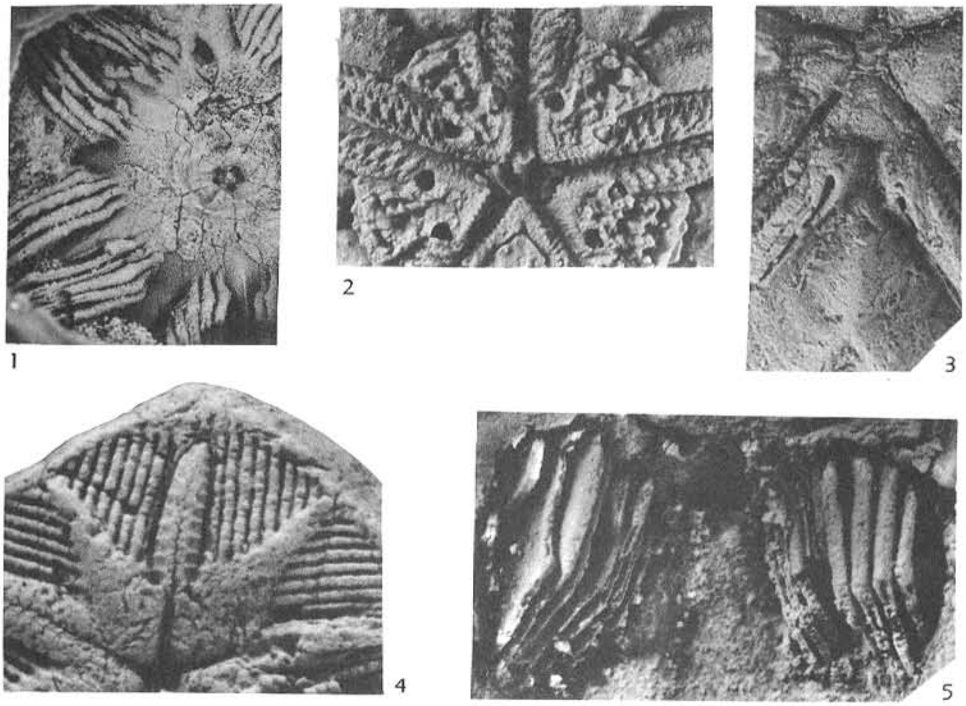


FIG. 215. Deltoids and hydrospires.

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

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

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

The development of the anal deltoids

[*Continued from facing page*]

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

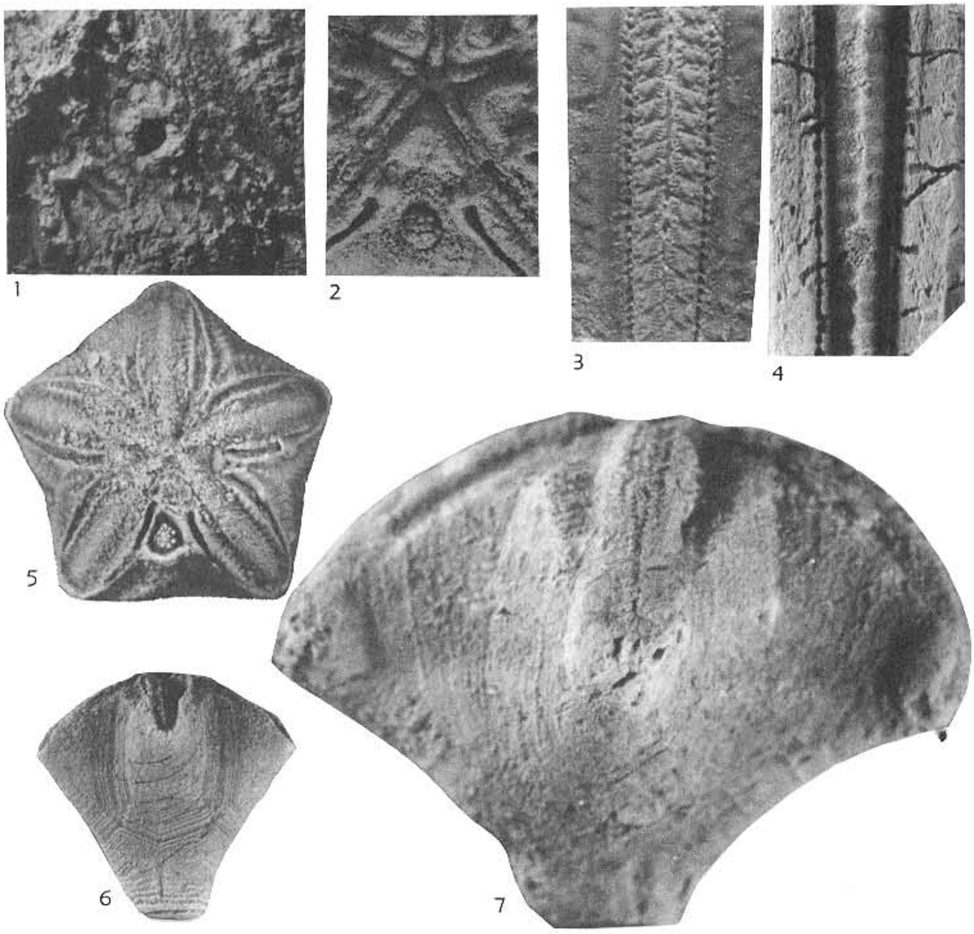


FIG. 216. Cover plates, hydrospire pores, and ontogenetic change in calyx shape.

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

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

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

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

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

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

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

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

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

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

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

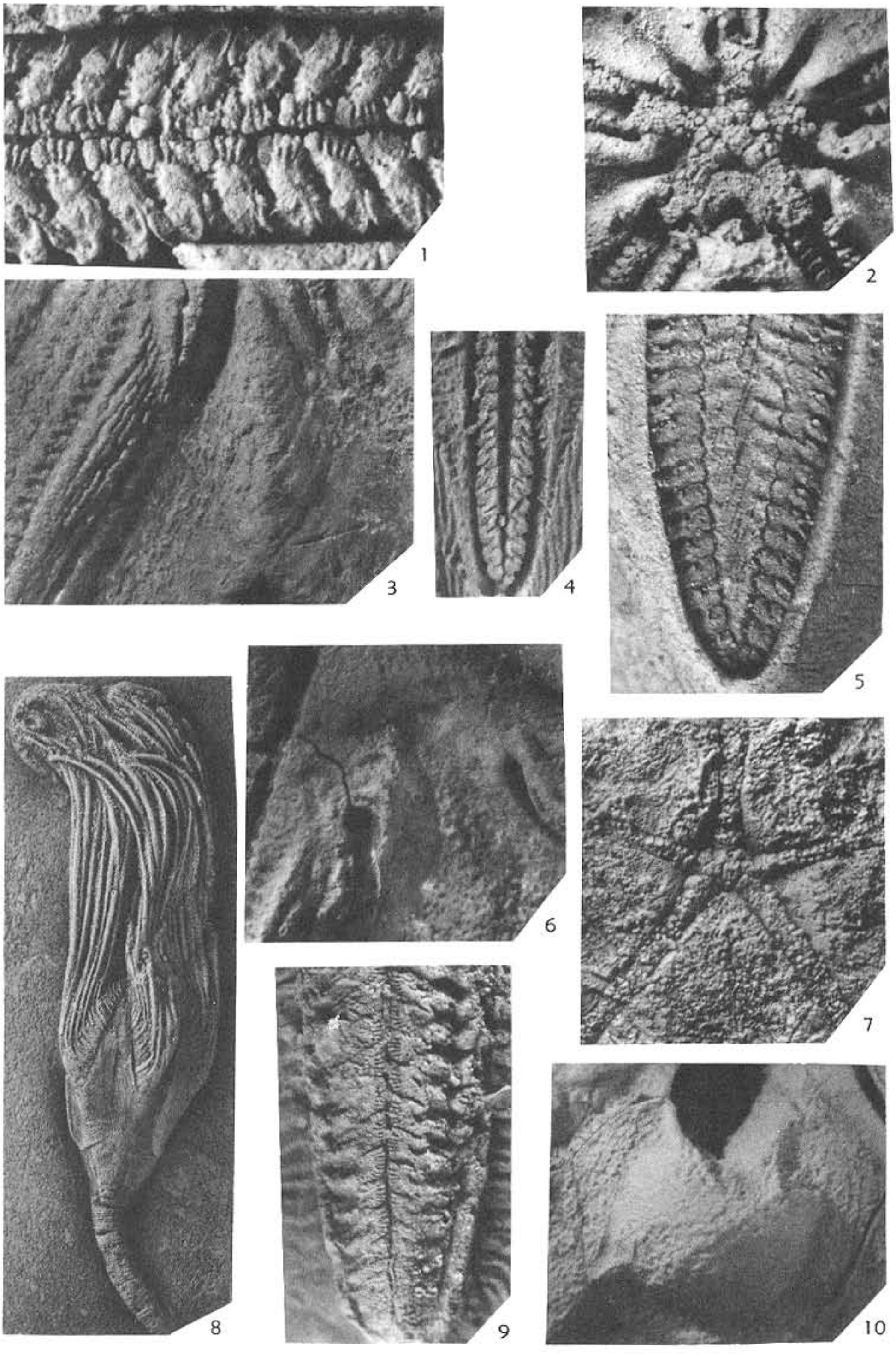


Fig. 217. Ambulacral, anal, and hydrospire structures. *(Continued on facing page.)*

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

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

HYDRODYNAMICS

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

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

---

[*Explanation of Fig. 217, continued*]

1. Brachiolar facets and food grooves, *Rhopaloblastus belfordi* (Crockford & Brown), Perm., Australia, X5 (Macurda, n).

2. Oral cover plates of *Schizoblastus sayi* (Shumard), L.Miss., USA(Ill.), X7.5 (Macurda, n).

3. Growth lines, admedial edge of side plates and deltoid in *Orophocrinus stelliformis* (Owen & Shumard), L.Miss., USA(Mo.), X7.5 (109).

4. Pore furrows and hydrospire pores in *Lophoblastus neglectus* (Meek & Worthen), L.Miss., USA(Mo.), X7.5 (Macurda, n).

5. Lancet and hydrospire pores of *Pentremites* sp., U.Miss., USA(Ill.), X7.5 (Macurda, n).

6. Growth lines bordering spiracle slits in *Orophocrinus stelliformis* (Owen & Shumard), L. Miss., USA(Ill.), X7.5 (Macurda, n).

7. Oral cover plates in *O. stelliformis* (Owen & Shumard), L.Miss., USA(Mo.), X7.5 (109).

8. Brachioles in *Pyramiblastus fusiformis* (Wachsmuth & Springer), L.Miss., USA(Iowa), X3 (105).

9. Lancet and side plates in *Orophocrinus catactus* (Rowley), L.Miss., USA(N.Mex.), X7.5 (Macurda, n).

10. Secondary secretion and trough for extension of anus, *Orophocrinus stelliformis* (Owen & Shumard), L.Miss., USA(Iowa), X7.5 (109).

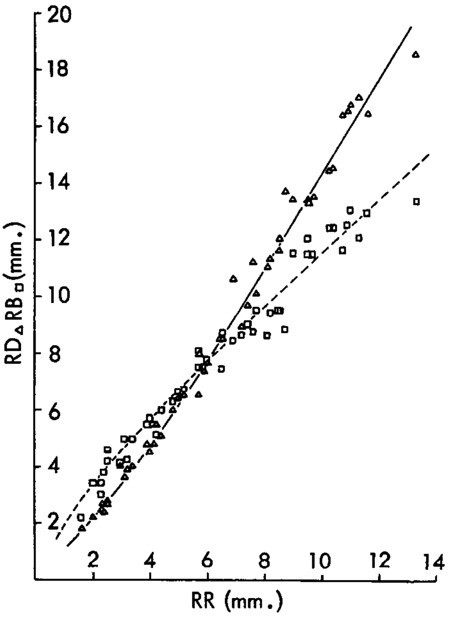


FIG. 218. Growth of *RD* (radial-deltoid) and *RB* (radial-basal) axes of *Orophocrinus stelliformis* (OWEN & SHUMARD) plotted against growth of *RR* (interradial) axis, L.Miss., USA(Iowa-Mo.) (109).

(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-

---

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

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

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

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

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

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

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

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

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

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

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

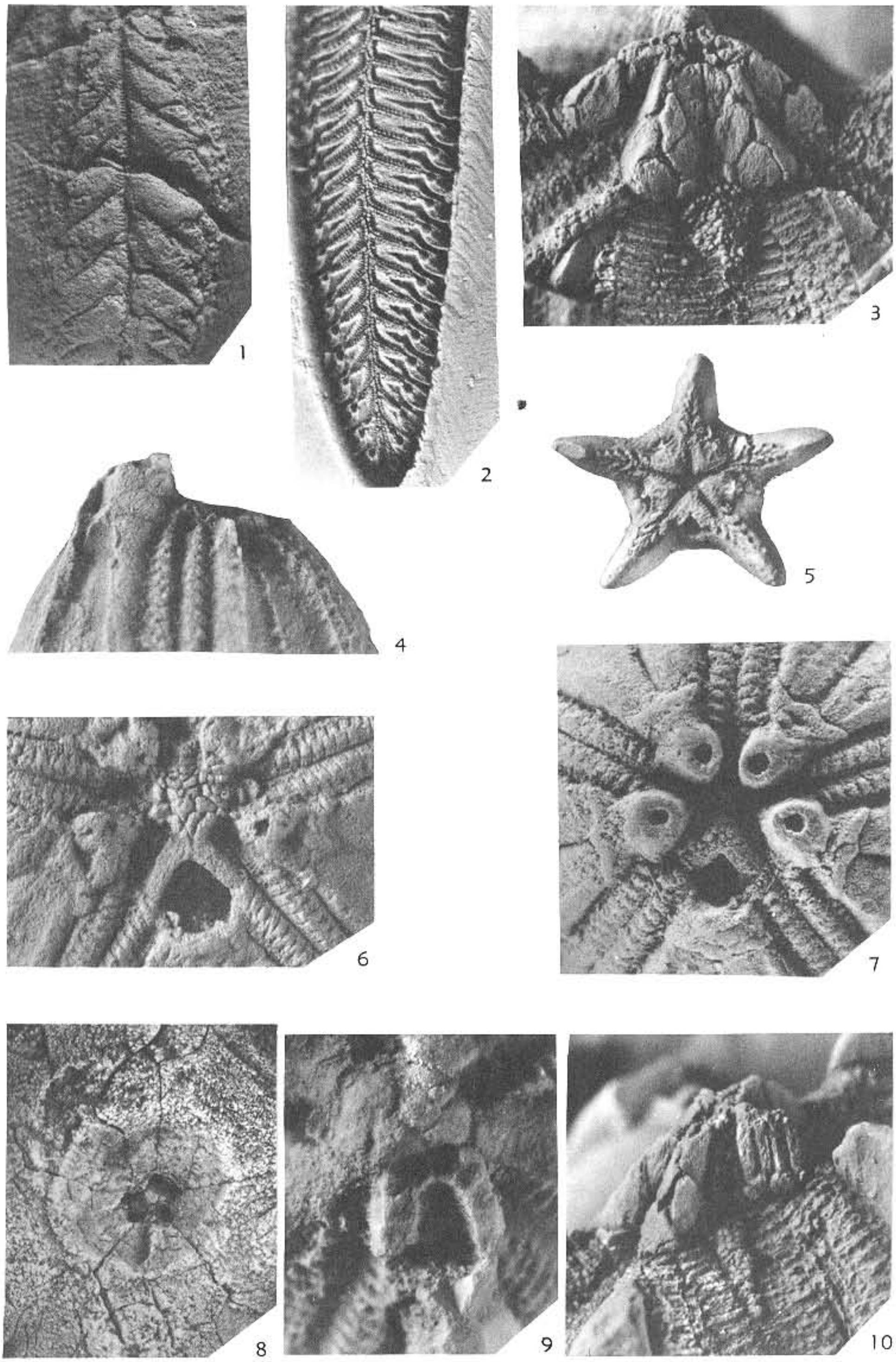


FIG. 219. Ambulacral, oral cover plates, anal, and alimentary canal structures.

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

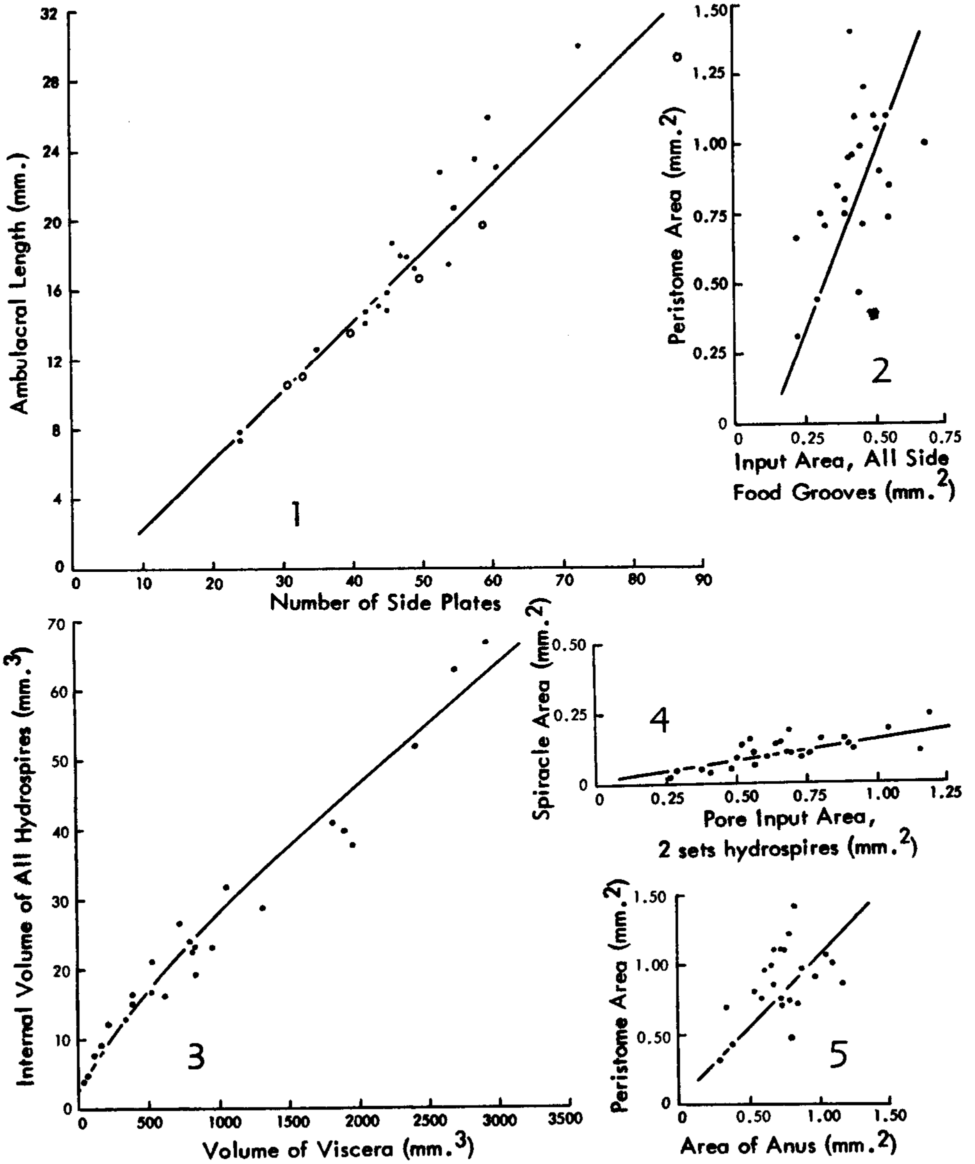


FIG. 220. Hydrodynamics of *Globoblastus norwoodi* (OWEN & SHUMARD), L.Miss., USA(Iowa), throughout an ontogenetic series (108).

1. Ambulacral length plotted against number of side plates on side of ambulacrum.
2. Area of peristome plotted against cross-sectional input area of side food grooves on all ambulacra.
3. Total internal volume of all hydrospires plotted against volume of viscera.
4. Area of one spiracle plotted against input area of pores associated with two sets of hydrospires with which former connects.
5. Area of peristome plotted against cross-sectional area of anus.

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

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

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

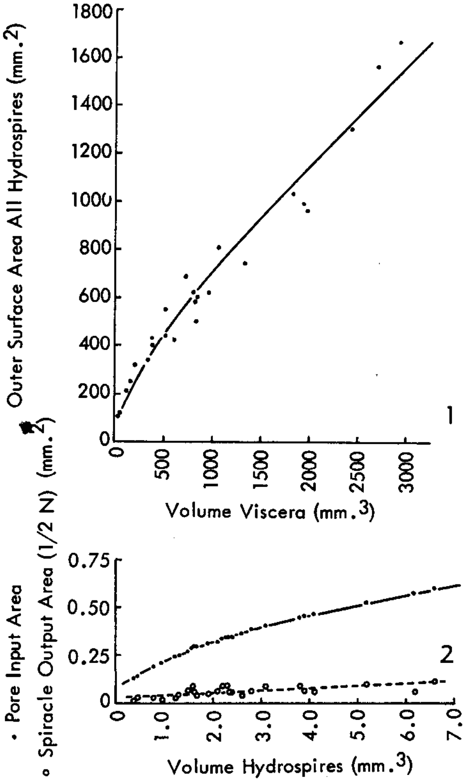


Fig. 221. Hydrodynamics of *Globoblastus norwoodi* (Owen & Shumard), L.Miss., USA(Iowa), throughout ontogenetic series (108).

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

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

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

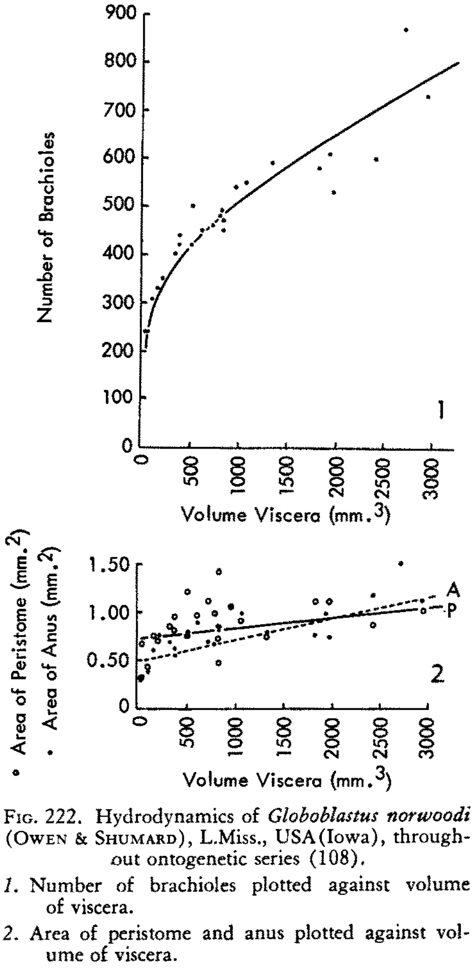


FIG. 222. Hydrodynamics of *Globoblastus norwoodi* (OWEN & SHUMARD), L.Miss., USA(Iowa), throughout ontogenetic series (108).

1. Number of brachioles plotted against volume of viscera.

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

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

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

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

[*Explanation of Figure 223*]

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

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

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

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

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

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

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

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

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

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

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

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

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

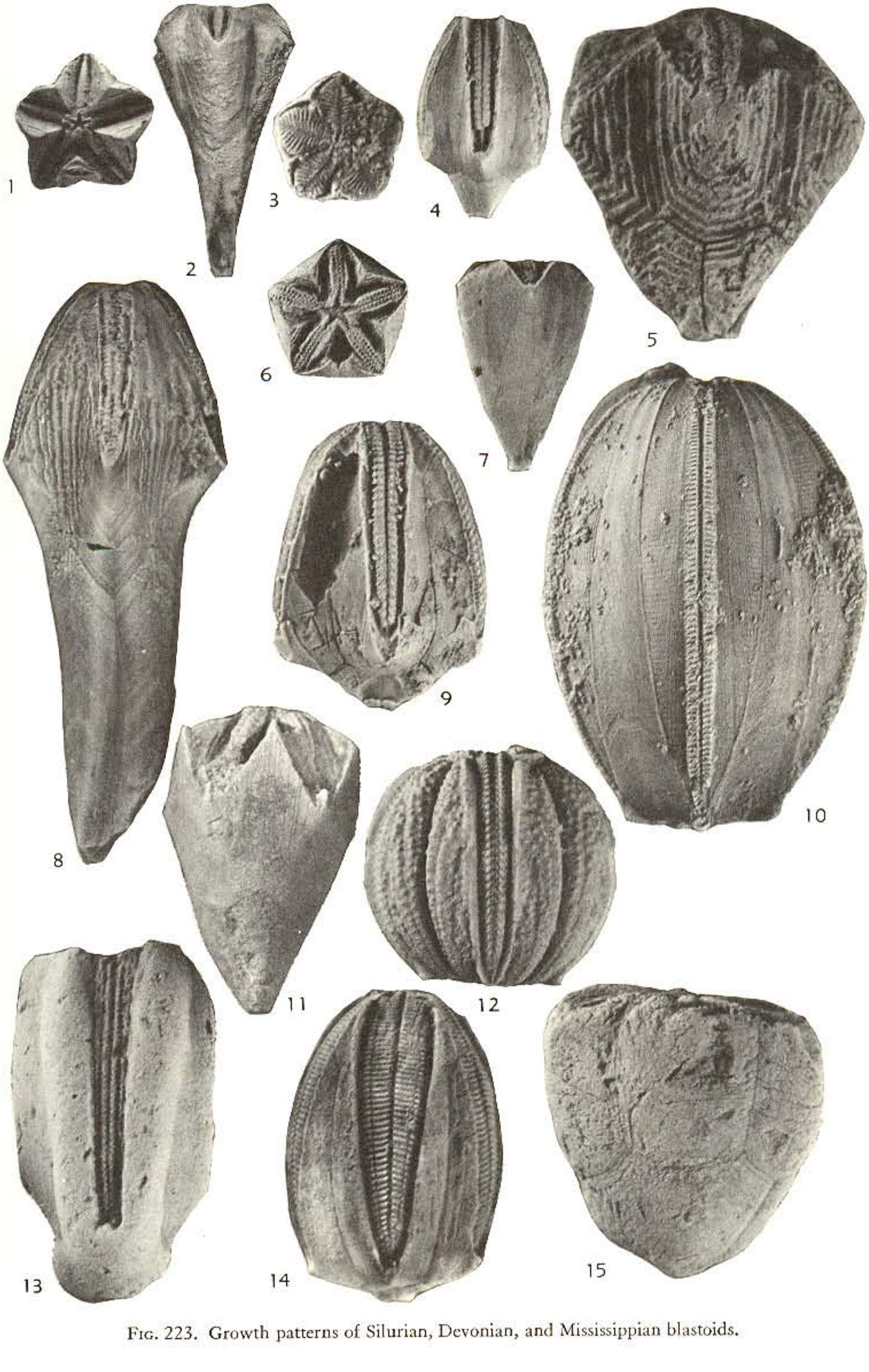


FIG. 223. Growth patterns of Silurian, Devonian, and Mississippian blastoids.

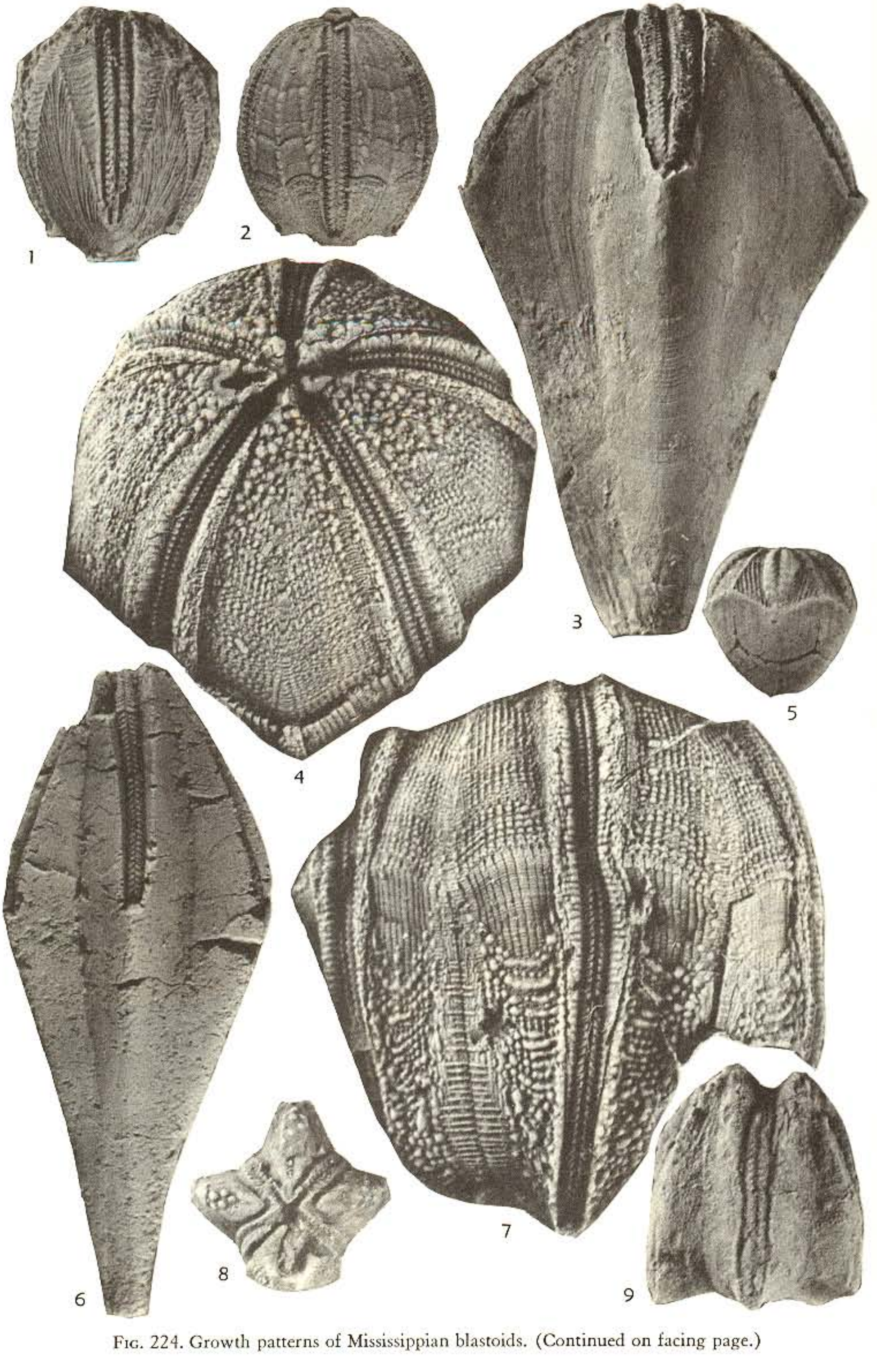


Fig. 224. Growth patterns of Mississippian blastoids. (Continued on facing page.)

TEMPORAL DISTRIBUTION OF GROWTH PATTERNS IN BLASTOIDS

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

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

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

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

[*Explanation of Figure 224, continued*]

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

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

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

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

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

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

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

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

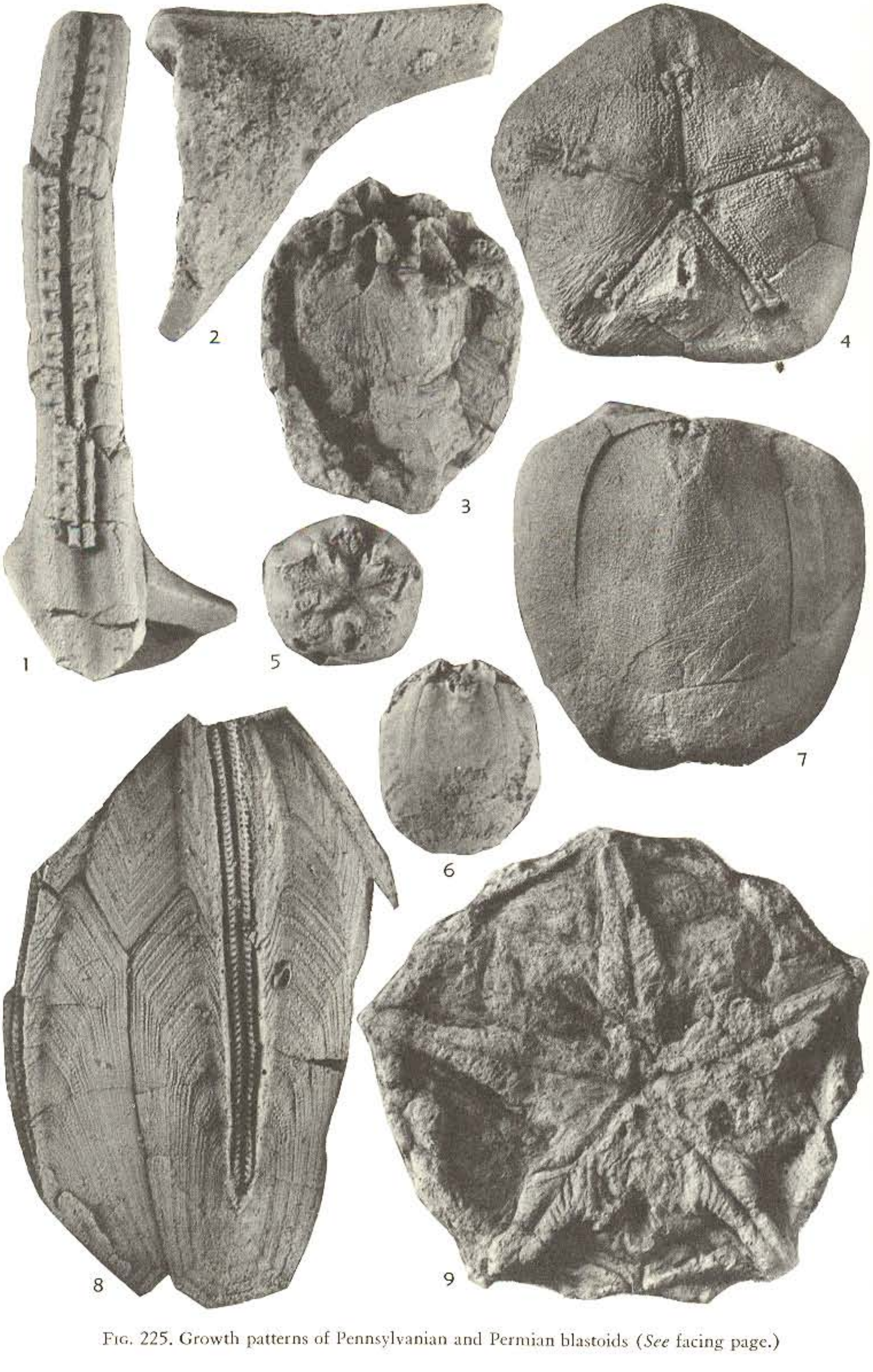


FIG. 225. Growth patterns of Pennsylvanian and Permian blastoids (*See* facing page.)

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

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

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

[*Explanation of Figure 225, continued*]

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

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

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

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

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

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

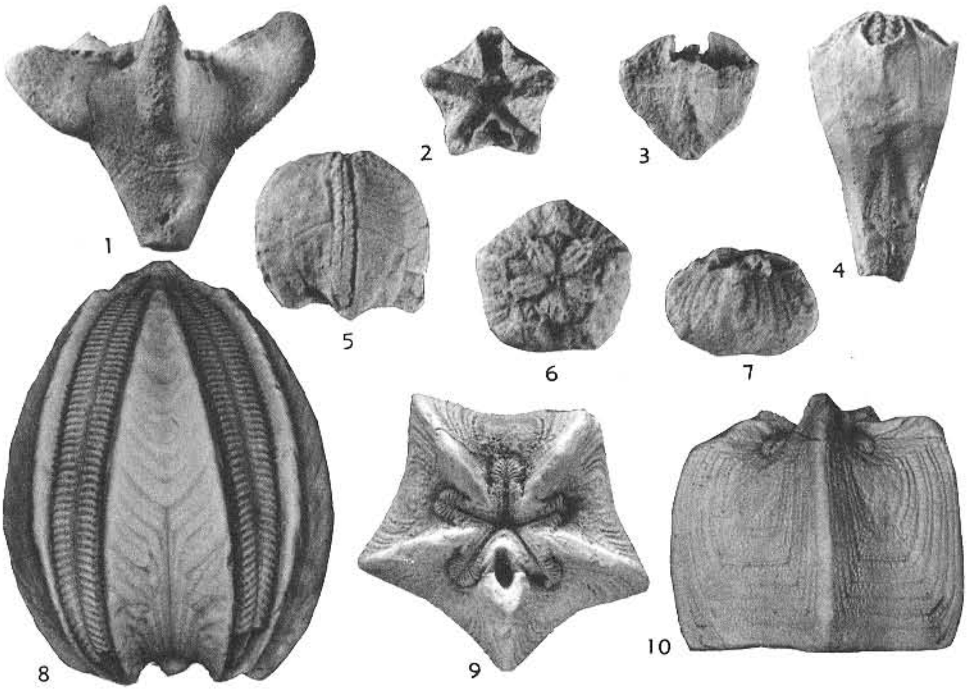


FIG. 226. Growth patterns of Permian blastoids.

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

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

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

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

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

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

PALEOECOLOGY

By Harold H. Beaver

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

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

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

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

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

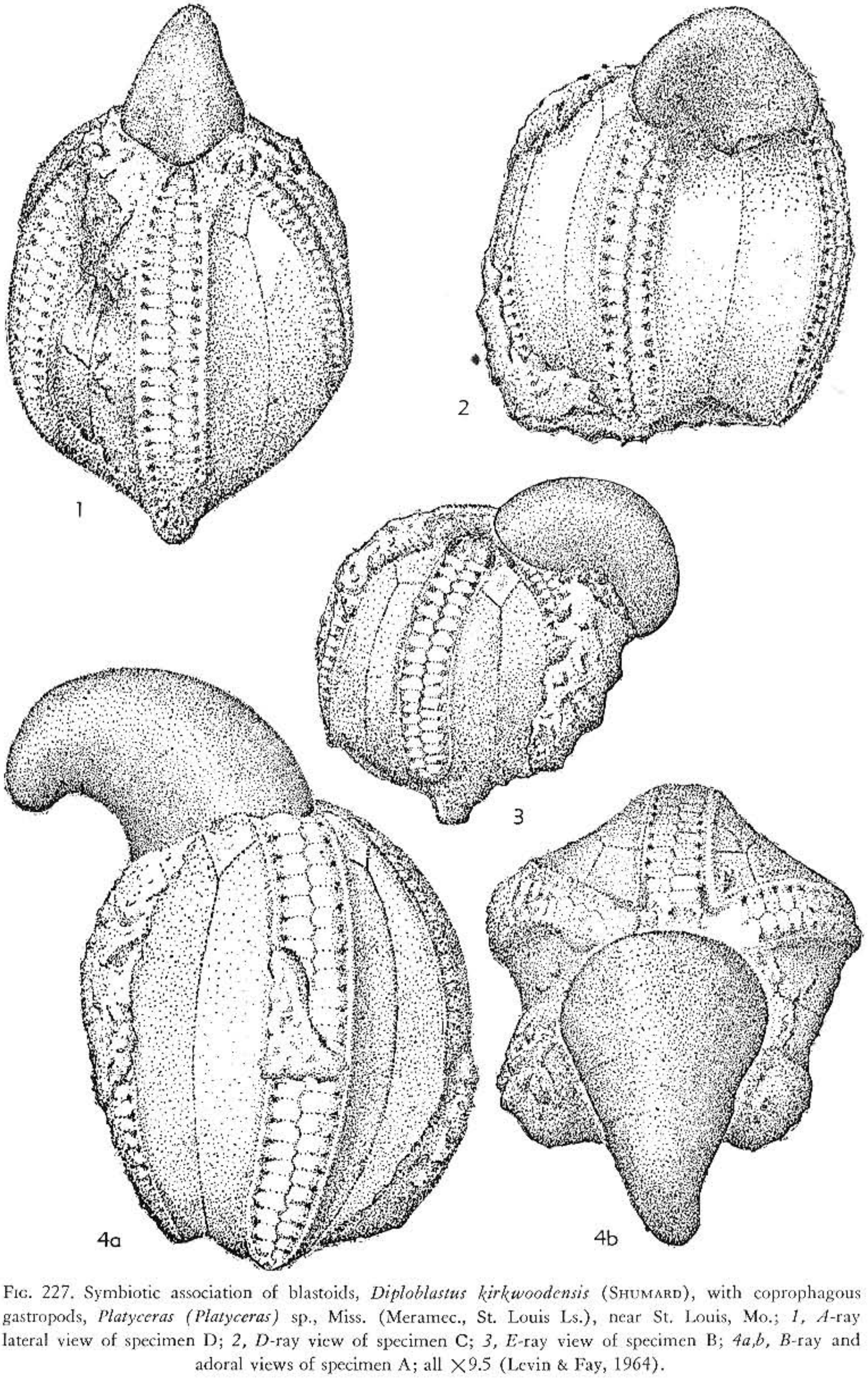


FIG. 227. Symbiotic association of blastoids, *Diploblastus kirkwoodensis* (SHUMARD), with coprophagous gastropods, *Platyceras (Platyceras)* sp., Miss. (Meramec., St. Louis Ls.), near St. Louis, Mo.; *1, A*-ray lateral view of specimen D; *2, D*-ray view of specimen C; *3, E*-ray view of specimen B;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

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

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

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

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

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

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION

By DONALD B. MACURDA, JR.

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

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

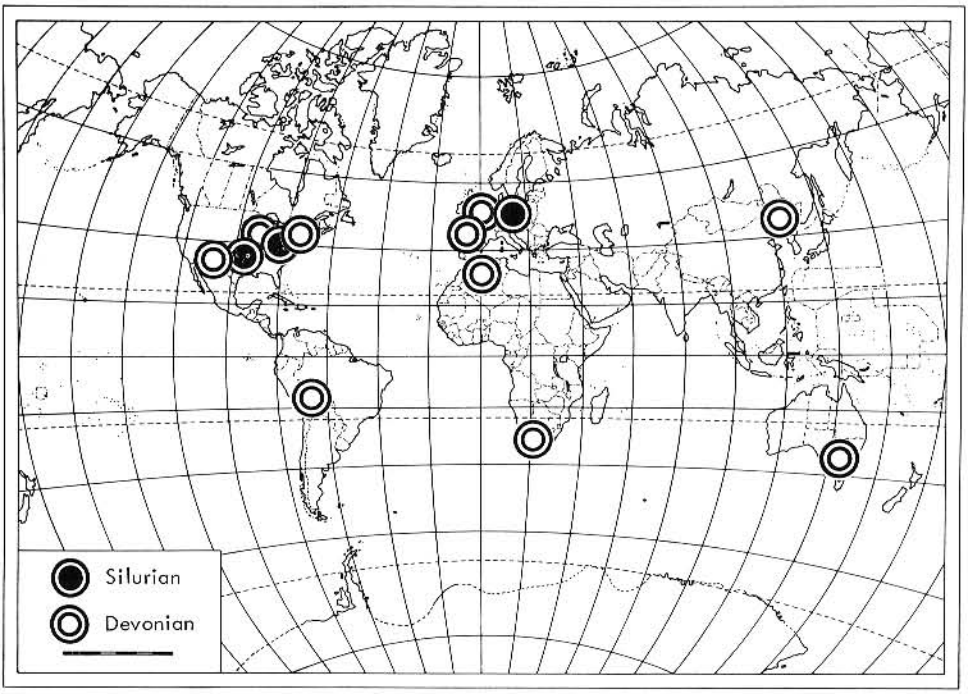


FIG. 228. Geographic distribution of Silurian and Devonian blastoids (Macurda, n).

---

[1] Australian "blastoids" now are judged to be inadunate crinoids (J. SPRINKLE, personal communication).

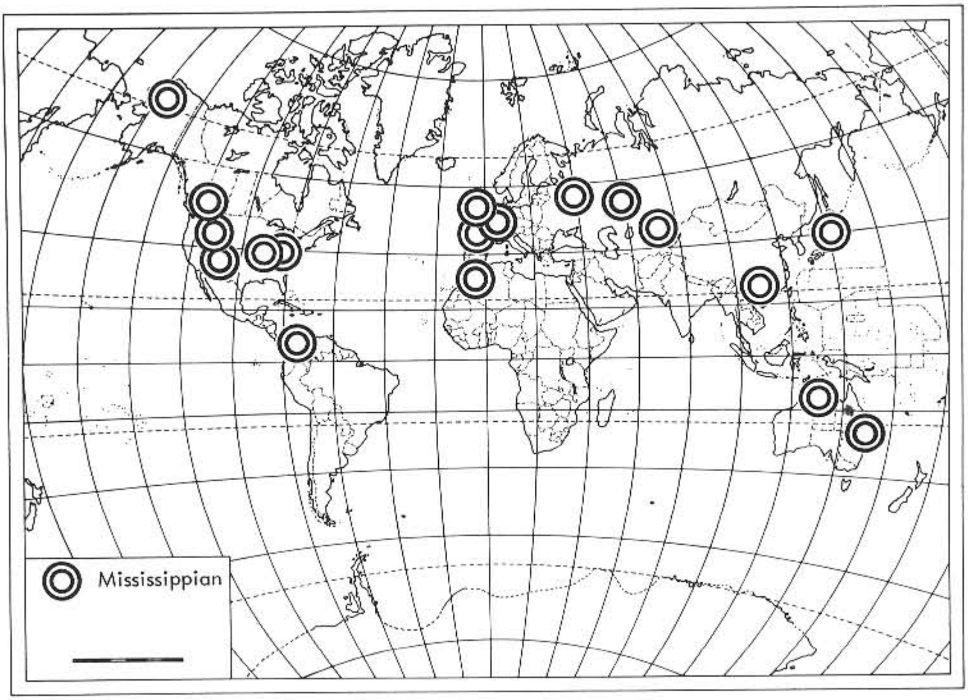


FIG. 229. Geographic distribution of Mississippian blastoids (Macurda, n).

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*

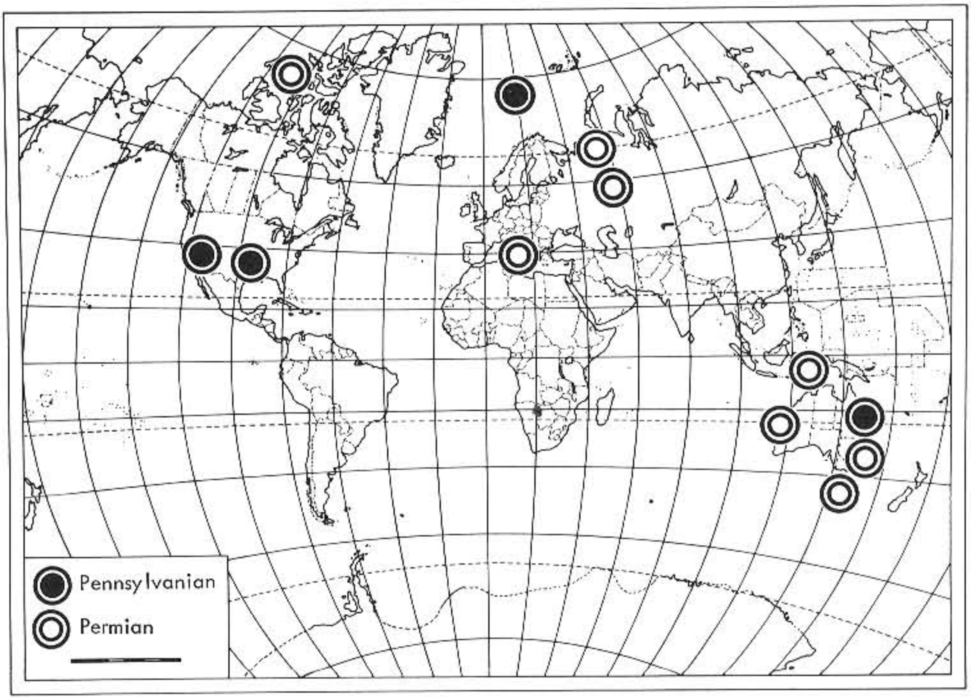


FIG. 230. Geographic distribution of Pennsylvanian and Permian blastoids (Macurda, n).

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

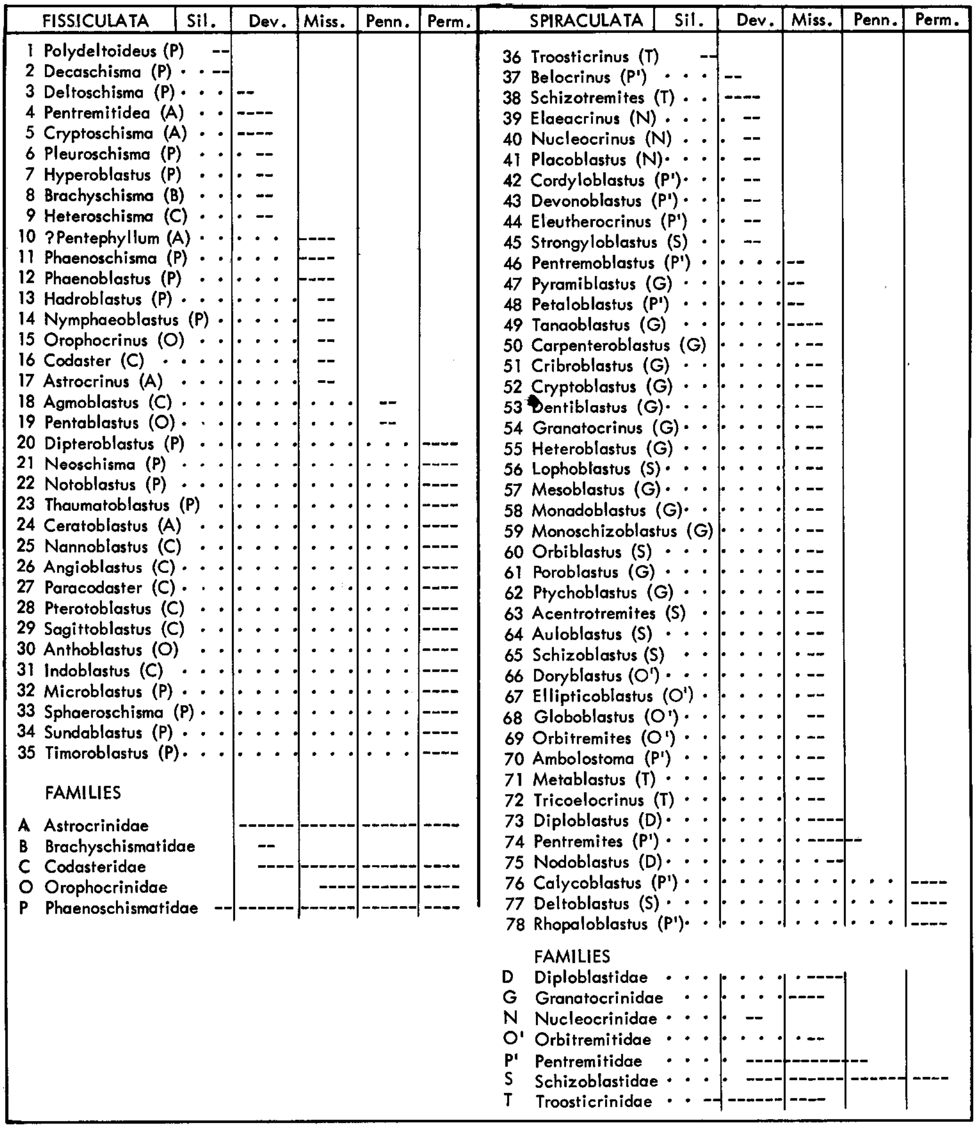


FIG. 231. Stratigraphic distribution of blastoid genera. The letter symbols after the generic names refer to the families in which they are classified, with familial names listed at bottom of chart (Moore & Fay, n).

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

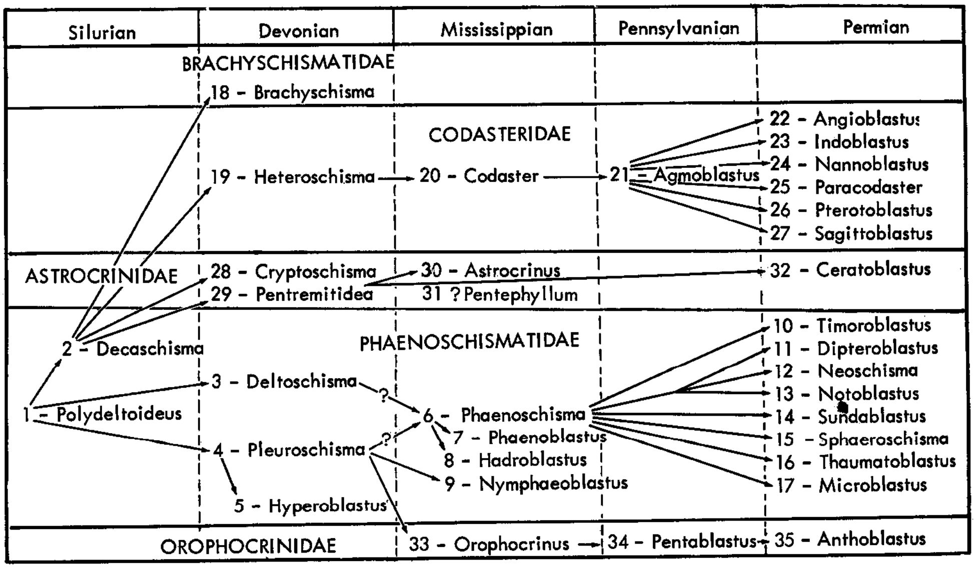
The origin of the Blastoidea is unknown. It has been postulated by Jaekel (1918) and Moore (1954) that this group of echinoderms may have been derived from pore-rhomb cystoids by development of hydrospires through atrophy of the pore-rhombs although this type of atrophy has never been demonstrated. Regnéll (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-



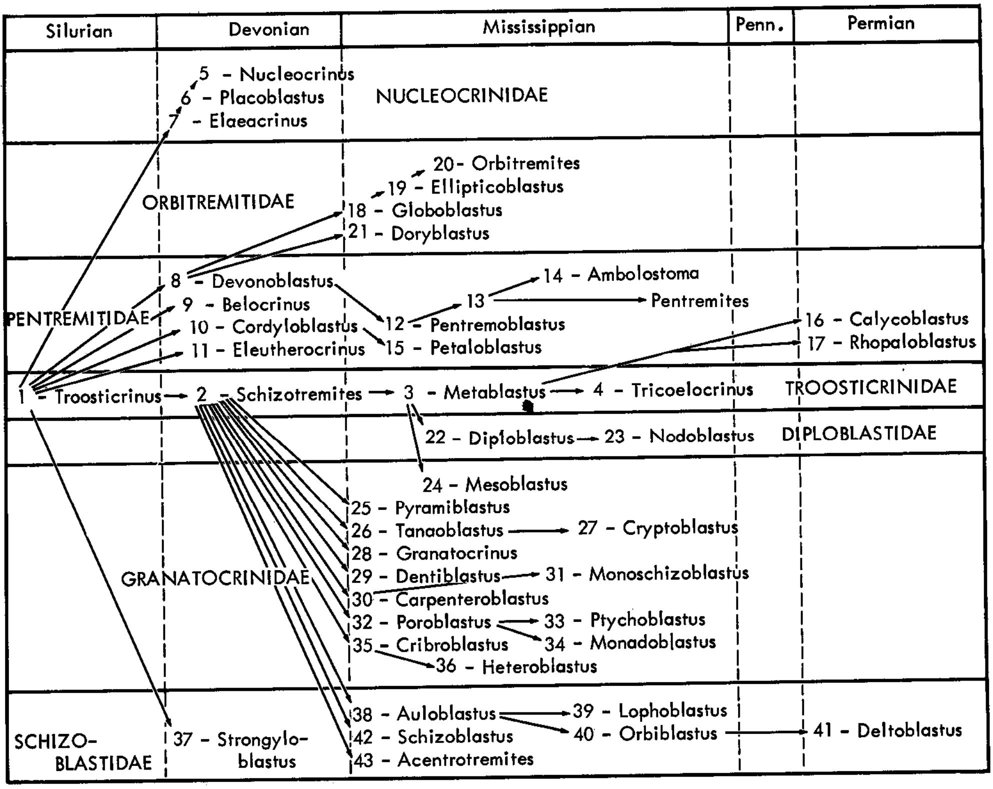
INDEX

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 ot blastoid genera and families of the order Spiraculata (Fay, n).

Within each family it is possible to trace certain lineages involving specific morphological parts. These trends appear to be similar in diverse families and therefore are here grouped. For instance, the lancet plate is covered by side plates in primitive forms and the side plates support the main food groove. In advanced forms, the lancet is exposed to the outside and supports the main food groove, or in extremely advanced forms, supports the side food grooves in addition. Thus, linear ambulacra are identified as primitive and petaloid ambulacra as advanced characters. The lancet stipe is adjacent to the mouth in a primitive blastoid and has migrated away from the mouth in an advanced form. There are four or six anal deltoids in a primitive form, and one may trace lineages whereby fusion must have taken place between the two cryptodeltoids to form a subdeltoid and between a subdeltoid and superdeltoid to form a single epideltoid, with consequent atrophy or suppression of the hypodeltoid.

The hydrospire fields (hydrospiralia) become atrophied or the number of hydrospire slits are reduced on the anal side. In the Spiraculata, which possess hydrospires in all ambulacra, certain trends are apparent; the number of hydrospires on each side of an ambulacrum apparently becomes reduced in number by atrophy, from five, to four, to three, to two, and to one in different genera, and the hydrospires on the anal side may differ in number from those of the other ambulacral areas within a single genus. With exception of *Pentremites,* the number of hydrospire folds on each side of an ambulacrum, if less than four, is apparently a stable criterion for differentiation of genera.

Another stable feature is the overlap of radials and deltoids along the radiodeltoid suture, which is constant for each genus and species. A primitive blastoid has short deltoids, overlapped by the radials; an advanced form is one having long deltoids, overlapping the radials. The pelvis is conical in a primitive blastoid, whereas it is rounded or with a concave base in an advanced form.

A blastoid with paired spiracles is considered to be primitive, and owing to migration outward or inward of certain deltoid septa it is possible to have forms with five, nine, or 11 openings around the mouth. Thus, the family Pentremitidae may be polyphyletic, possibly derived from the Phaenoschismatidae and Troosticrinidae.

The blastoid stem could have been derived from fused plates of the base of some Edrioblastoidea, and through time, the stem could have atrophied though disuse in a form like *Eleutherocrinus,* with consequent formation of bilateral symmetry and possible adaptation to swimming habits.

The pores, if formed as simple gaps between side plates, are primitive where one pore occurs between adjacent side plates along the deltoid and radial margins. In advanced forms, the pores evidently migrated laterally into margins of the deltoid and radial plates, and these plates folded along each pore to form multiple pores corresponding to each side plate. In some forms, the pores became atrophied along the deltoid margins and were lost, or the simple pores remained along the deltoid margins, but multiple pores formed along the radial margins (e.g., *Poroblastus*).

The cited features tend to show that although Permian blastoids of Timor and adjacent areas are fissiculate forms, they are highly specialized, advanced forms. Thus, they are not considered to be products of retrogressive evolution. The evolutionary theme in blastoids apparently is one of atrophy through disuse.

The problem of extinction of the Blastoidea is apparently one apart from morphological considerations because blastoids of the Permian possess features that warranted their survival into the Triassic and beyond. Thus, some major external physical change of a radical nature was the probable cause for extinction of the class.

SYSTEMATIC DESCRIPTIONS

By Robert O. Fay[1] and Johannes Wanner[2]

[[1]Oklahoma Geological Survey; [2]deceased, formerly University of Bonn]

The present classification is that adopted by Fay, but many ideas expressed on relationships and descriptions of Permian blastoids and most of the Permian tone illustrations are taken from materials submitted by Wanner. Various families, as here defined, would be raised to suborders by Wanner on the basis of greater emphasis given by him to anal and spiracular structures. Many specimens in museums probably belong to new genera, but circumstances have prevented new study of them. Until these specimens are correctly illustrated and described, it is best to retain a rather simple classification of the Blastoidea. The relationships among different genera of many recently recognized structures (e.g., inner side plates, paradeltoid plates, ambulacral spines, double brachiolar cover plates, accessory oral plates, lateral canals, anal cover plates) are not well understood. It is hoped that paleontologists will re-examine specimens in their collections, prepare polished thin sections of them, and publish detailed descriptions, supplemented by photographs and line drawings at ade-

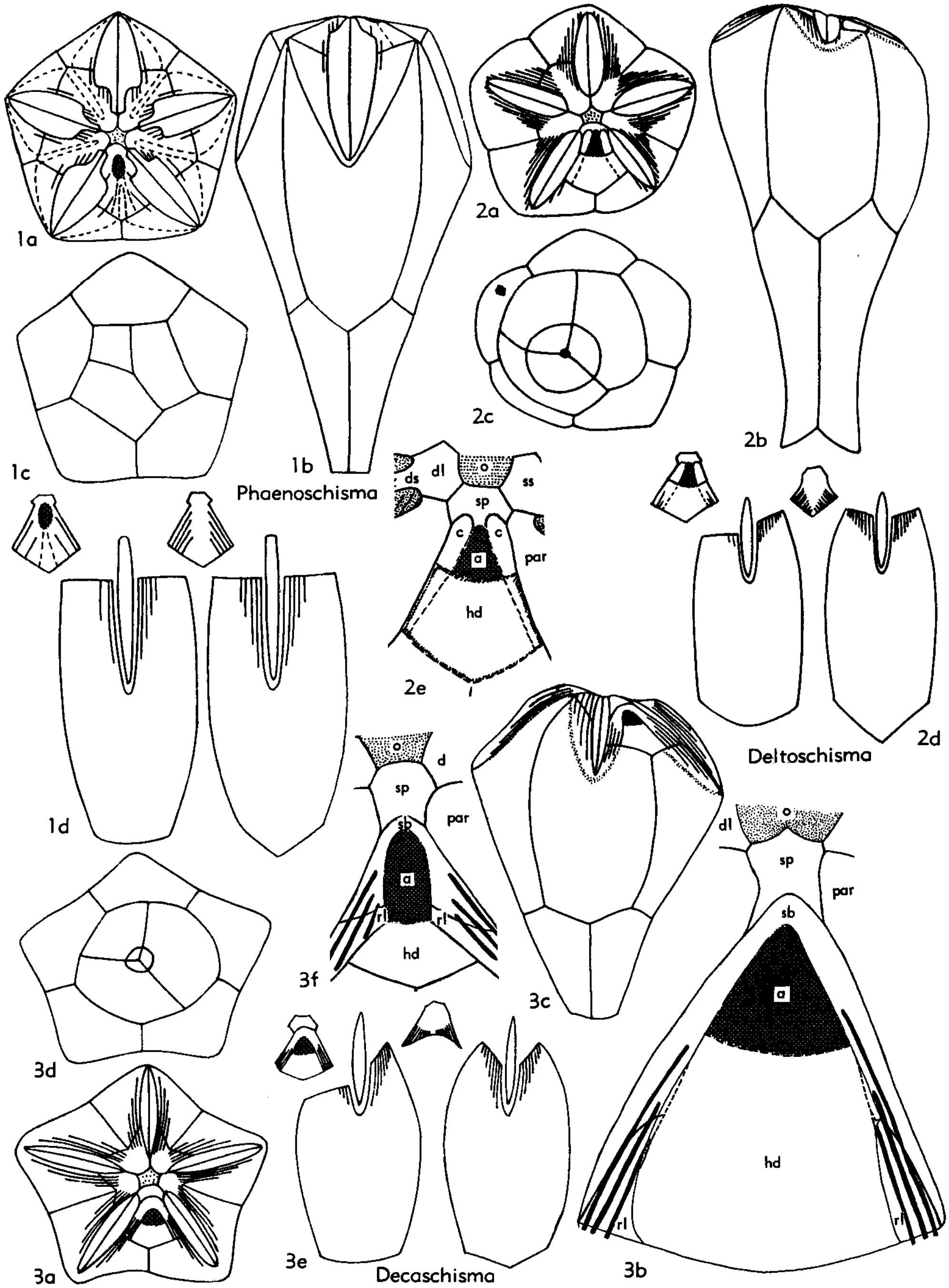


FIG. 234. Phaenoschismatidae (p. S400). [Explanation: *a,* anal opening, *c,* cryptodeltoid plate; *d,* deltoid plate; *dl,* deltoid lip; *ds,* deltoid septum; *hd,* hypodeltoid; *o,* oral opening; *par,* posterior ambulacrum (right); *rl,* radial limb; *sb,* subdeltoid plate; *sp,* superdeltoid plate.]

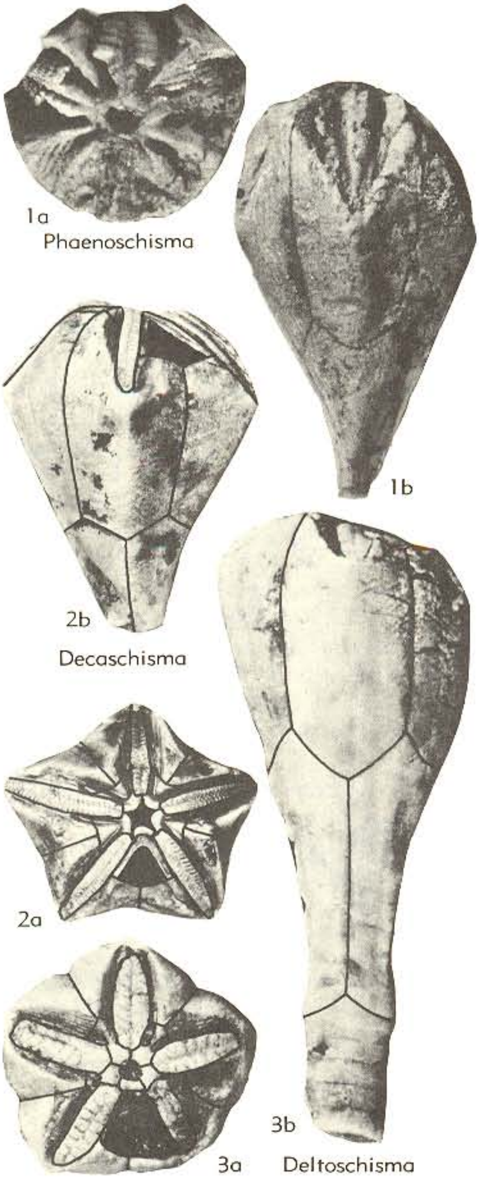


FIG. 235. Phaenoschismatidae (p. S400).

quately large scale. In this manner we may be able to fill in morphologic, stratigraphic, and geographic gaps in knowledge. A somewhat detailed account of previous classifications given in the introduction is not repeated here.

Class BLASTOIDEA Say, 1825

[Blastoidea SAY, 1825, p. 313 (type, *Pentremites* SAY, 1820, designated by FAY, herein)] [=Eublastoidea BATHER, 1899, p. 920 (type, *Pentremites* SAY, 1820, designated by FAY, herein)]

Hydrospire-bearing, stemmed echinoderms; theca composed of 18 to 21 major plates, which comprise three basals, surmounted by five radials, above which and alternating with them are five deltoids, in addition to five lancet plates in radial position located within radial sinuses; anal side may contain one, two, three, four, or six anal deltoids; hydrospires external or internal; pores and spiracles present mainly in forms with internal hydrospires. Ambulacra bear numerous biserially constructed brachioles. *Sil.-Perm.*

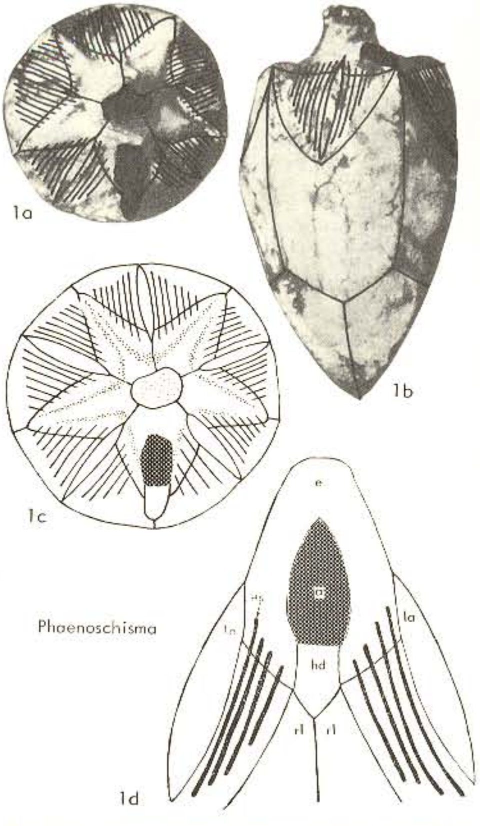


FIG. 236. Phaenoschismatidae (p. S400). [Explanation: *a*, anal opening; *e*, epideltoid plate; *hd*, hypodeltoid; *hs*, hydrospire slit; *la*, lancet plate; *rl*, radial limb.]

Order FISSICULATA Jaekel, 1918

[Fissiculata JAEKEL, 1918, p. 108 (type, *Phaenoschisma* ETHERIDGE & CARPENTER, 1882, designated by FAY, herein)] [=Mesoblastida MATSUMOTO, 1929, p. 28 (type, *Phaenoschisma* ETHERIDGE & CARPENTER, 1882, designated by FAY, herein)]

Theca with exposed hydrospire slits or spiracular slits. *Sil.-Perm.*

Family PHAENOSCHISMATIDAE Etheridge & Carpenter, 1886

[*nom. correct.* FAY, 1961 (60), p. 19 (*pro* Phaenoschismidae ETHERIDGE & CARPENTER, 1886, p. 258)] [=Dipteroblastidae WANNER, 1940, p. 234; Neoschismidae (*recte* Neoschismatidae) WANNER, 1940, p. 238; Nymphaeoblastidae WANNER, 1940, p. 237]

Theca with ten exposed or partially exposed hydrospire fields. *Sil.-Perm.*

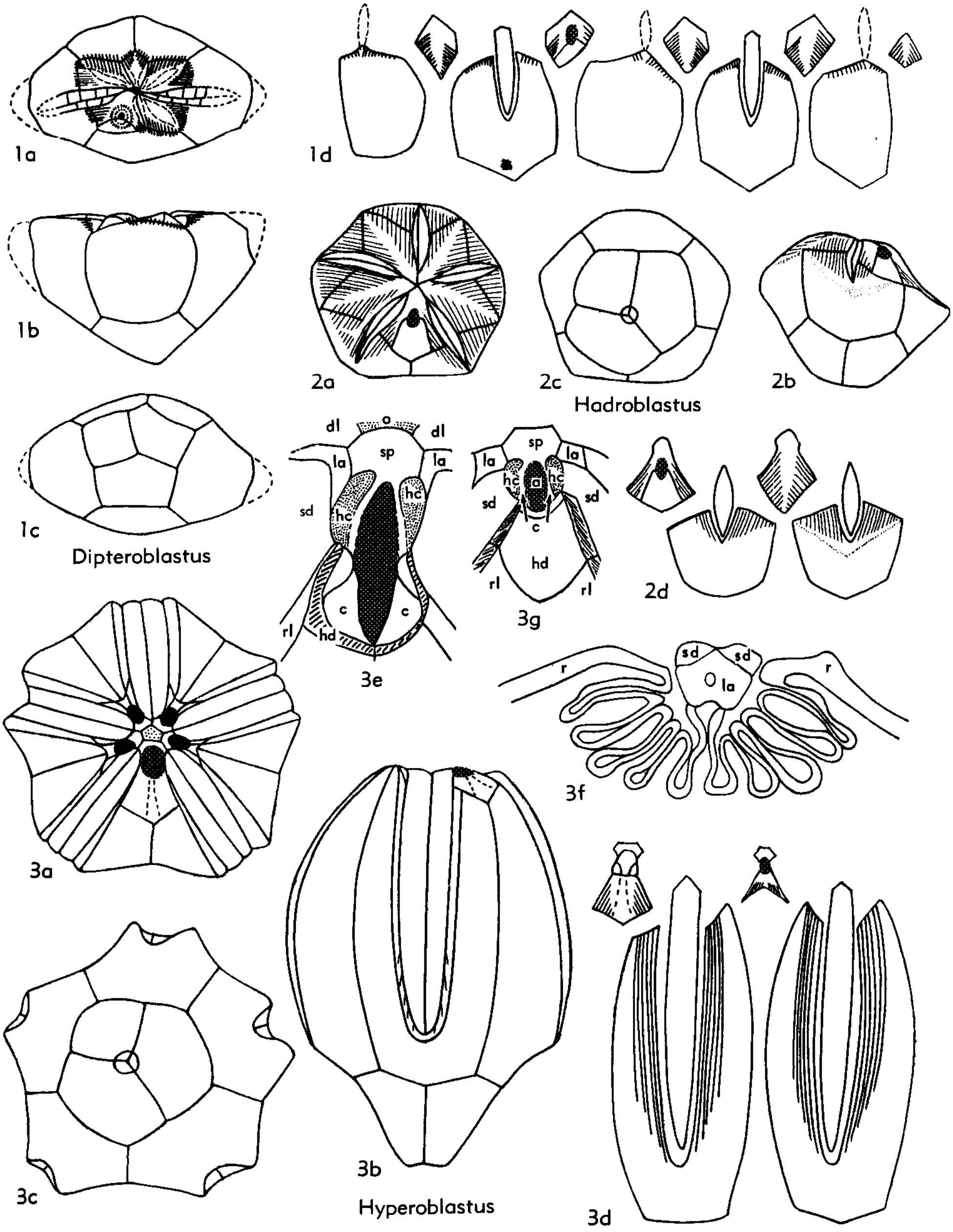


FIG. 237. Phaenoschismatidae (p. S400-S401). [Explanation: *a,* anal opening; *c,* cryptodeltoid plate; *dl,* deltoid lip; *hc,* hydrospire canal; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening; *r,* radial plate; *rl,* radial limb; *sd,* side plate; *sp,* superdeltoid plate.]

Phaenoschisma ETHERIDGE & CARPENTER, 1882, p. 226 [*emend.* MACURDA, 1964 (104), p. 719] [**Pentatrematites acuta* SOWERBY, 1834, p. 456; SD ETHERIDGE & CARPENTER, 1886, p. 270] [=*Conoschisma* FAY, 1961 (60), p. 23 (type, *Codaster laeviusculus* ROWLEY, 1900, p. 65)]. Theca biconical with hydrospire fields mostly hidden, but exposed along aboral ends or along outer ambulacral margins; number of hydrospire slits reduced on anal side; anus between epideltoid and hypodeltoid; lancet exposed along median 0.5 of its width; side plates touching deltoid crests, forming 5 teardrop-shaped spiracle-like openings at adoral end. *L.Carb.(Miss.)*, Eu.-N.Am.——FIG. 234,*1*; 235,*1*. **P. acutum* (SOWERBY), Eng.; 234,*1a,b*, oral and *D*-ray views, ×4.5 (41); 234,*1c,d*, aboral view and plate layout, ×4.5 (162); 235,*1a,b*, oral and *C*-ray views, ×4, ×4.7 (104).——FIG. 236,*1*. *P. laeviusculum* ROWLEY, L.Miss. (Burlington Ls.), USA(Mo.); type species of *Conoschisma*, *1a,b*, oral and *D*-ray views, ×4.4 (60); *1c*, oral view, ×5.3 (60); *1d*, plates adjacent to anal opening, ×9 (60).

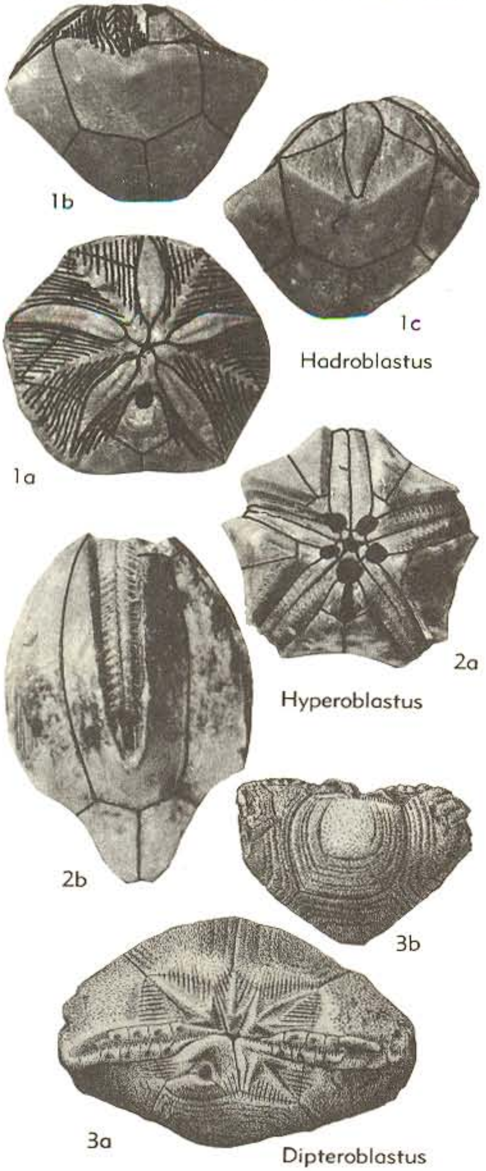


FIG. 238. Phaenoschismatidae (p. S400-S401).

Decaschisma FAY, 1961 (60), p. 27 [**Codaster pentalobus* HALL, 1879, p. 13; OD]. Theca obconical, with well-exposed hydrospire fields; superdeltoid, subdeltoid, and hypodeltoid present; lancet covered by side plates. *Sil.*, USA(Ind.).——FIG. 234,*3a-e*; 235,*2*. **D. pentalobus* (HALL), Niagaran; 234,*3a*, oral view, ×2.6; 234,*3b*, *CD* interray, ×10.1; 234,*3c*, *D*-ray view, ×2.6; 234,*3d,e*, aboral view and plate layout, ×2.7 (all 60); 235,*2a,b*, oral and *D*-ray views, ×2.5 (60).——FIG. 234,*3f*. *D. pulchellum* (MILLER & DYER), Niagaran; plates around anal opening, ×10 (60).

Deltoschisma FAY, 1961 (60), p. 29 [**Phaenoschisma archiaci* ETHERIDGE & CARPENTER, 1882, p. 229; OD]. Theca conical, with exposed hydrospire fields; strongly pentalobate in top view; with superdeltoid, 2 cryptodeltoids, and hypodeltoid, cryptodeltoids partly visible externally, partly hidden by hypodeltoid; number of slits reduced on anal side; lancet covered by large side plates. *Dev.*, Spain.——FIG. 234,*2*; 235,*3*. **D. archiaci* (ETHERIDGE & CARPENTER); 234,*2a-d*, oral, *D*-ray, aboral views, and plate layout, ×4.4; 234,*2e*, anal area, ×9.9; 235,*3a,b*, oral and *D*-ray views, ×4.7 (all 60).

Dipteroblastus WANNER, 1940, p. 249 [*emend.* BREIMER & MACURDA, 1965, p. 212] [**D. permicus*; OD]. Theca cup-shaped, with well-exposed hydrospire fields, with 8 to 13 hydrospire slits on *AB*, *BC*, and *DE* deltoids, but 3 to 6 on epideltoid, and 5 on *EA* deltoid; anus separate, between large epideltoid and large hypodeltoid; with 3 short *A*, *C*, and *E* ambulacra and 2 elongate *B* and *D* ambulacra confined to summit; lancet exposed along food groove. *Perm.*, E.Indies(Timor).——FIG. 237,*1*; 238,*3*. **D. permicus*; 237,*1a-d*, oral, *D*-ray, aboral views, and plate layout, ×1.7 (178); 238,*3a,b*, oral and C-ray views, ×2.7, ×1.7 (178).

Hadroblastus FAY, 1962 (72), p. 189 [**H. convexus*; OD]. Theca discoidal with rounded summit and base; hydrospire fields each with 11 slits except on anal side where 4 slits occur in each field; anal opening between large epideltoid and equally large hypodeltoid; lancet exposed along middle 0.3 of its width, raised well above broad flat sinus areas and hydrospire fields; ambulacra moderately long, linear, with lancet stipes moderately separated from oral opening; vault

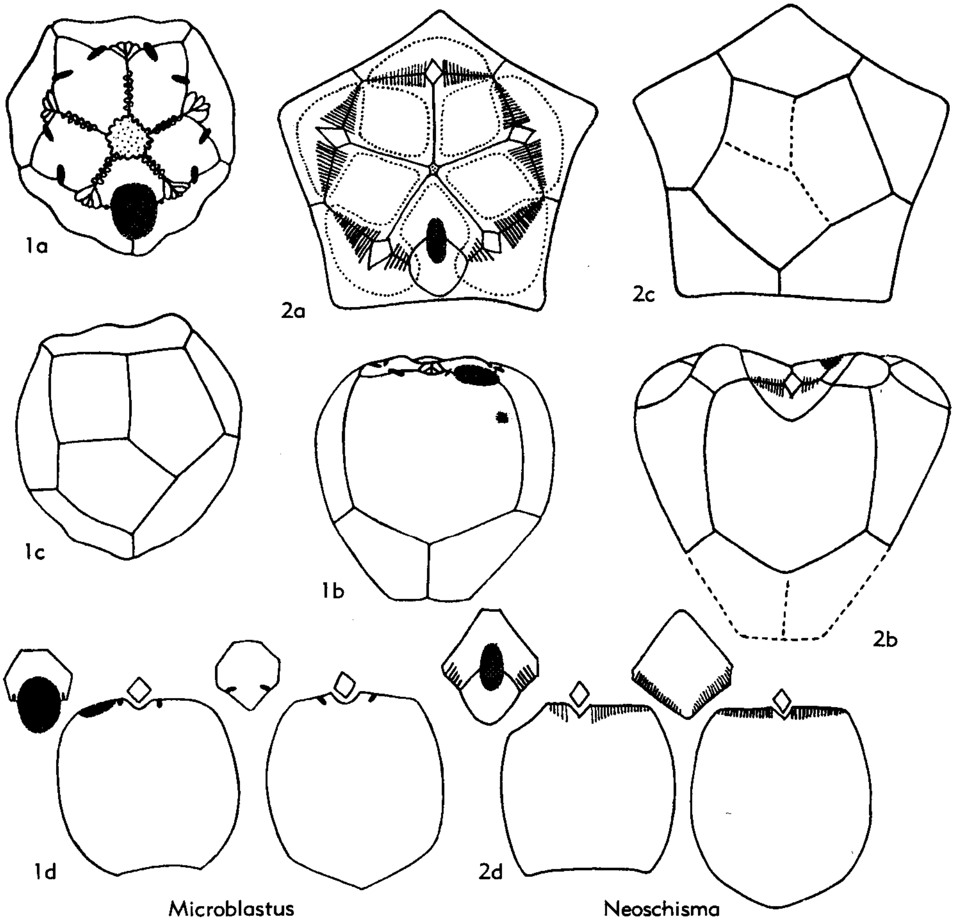


FIG. 239. Phaenoschismatidae (p. S401-S402).

almost equal to pelvic height; basalia large, composed of 3 basals. *L.Miss.*, USA(N.Mex.-Ark.-Okla.).——FIG. 237,*2*; 238,*1*. *_H. convexus_, Osag., N.Mex.; 237,*2a-d*, oral, *D*-ray, aboral views, and plate layout, ×2 (72); 238,*1a-c*, oral, *D*-ray, and *B*-ray views, ×2.7 (72).

Hyperoblastus FAY, 1961 (60), p. 30 [*_Pentremitidea preciosa_ REIMANN, 1945, p. 39; OD]. Theca club-shaped, with aboral ends of outermost hydrospire slits exposed; with pores formed as gaps between side plates; spiracles 5, developed between deltoid lip, deltoid septum, lancet, and side plates on each interambulacrum (including anispiracle on anal side); with superdeltoid, 2 cryptodeltoids, and hypodeltoid; lancet covered by side plates. *Dev.*, N.Am.——FIG. 237,*3a-e*; 238,*2*. *_H. preciosus_ (REIMANN), Can.(Ont.); 237,*3a-d*, oral, *D*-ray, aboral views, and plate layout, ×3.5; 237,*3e*, anal area, ×10; 238,*2a,b*, oral and *D*-ray views, ×2.9 (all 60).——FIG. 237,*3f,g*. *H. filosus* (WHITEAVES), Can.(Ont.); *3f*, cross sec. of ambulacrum, ×8.8; *3g*, anal area, ×10.2 (all 60).

Microblastus EYKEREN, 1942, p. 283 [*_M. pocilloformis_; OD]. Theca small, cup-shaped, with small restricted hydrospire slits confined to summit; anal opening separate from slits, between large, wide epideltoid and radial limbs, possibly with small ?hypodeltoid on aboral border; ambulacra short, wide, small, well away from mouth, with total of 2 or 3 side plates on each side. *Perm.*, E.Indies (Timor).——FIG. 239,*1*; 240,*1*. *_M. pocilloformis_; 239,*1a-d*, oral, *D*-ray, aboral views, and plate layout, ×8.8 (42); 240,*1a,b*, oral and *CD*-interray views, ×6 (42).

Neoschisma WANNER, 1924 (173), p. 6 [*_N. verrucosum_; OD]. Theca cup-shaped, with widely exposed hydrospire fields, each with 5 to 18 slits except on anal side where 1 to 5 slits occur on each side of anal opening; anal opening between

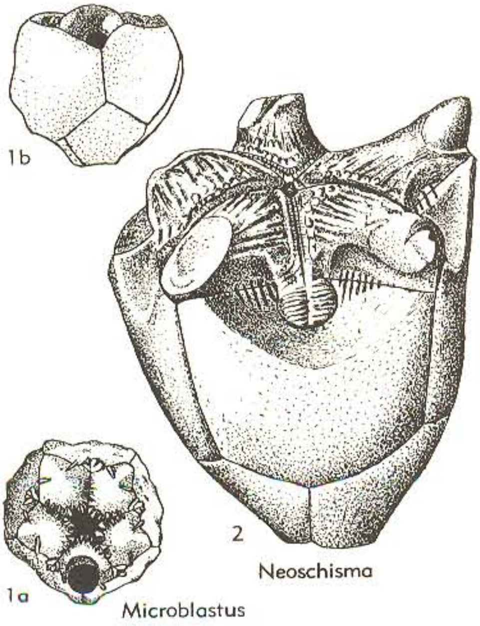


FIG. 240. Phaenoschismatidae (p. *S*401-*S*402).

large epideltoid and moderately large hypodeltoid; ambulacra short, wide, small, well away from mouth, confined to summit. *Perm.*, E.Indies (Timor).——FIG. 239,2. **N. verrucosum*; *2a-d*, oral, *D*-ray, aboral views, and plate layout, ×2.4 (173).——FIG. 240,2. *N. timorense* WANNER, Perm., Timor; *B*-ray view, ×3.3 (178).

Notoblastus BROWN, 1941, p. 98 [**N. brevispinus*; OD]. Theca discoidal, with widely exposed hydrospire fields, each with 12 to 14 hydrospire slits except on anal side, where slits are few; small anus separate, between large epideltoid and smaller hypodeltoid; ambulacra moderately short, longer than wide, with lancet stipe well away from mouth; radials prolonged into small, short, winglike processes; stem seemingly absent. *Perm.*, E.Australia.——FIG. 241,*4*; 242,*3*. **N. brevispinus*; 241,*4a,b*, oral and *C*-ray views, ×1.3; 242,*3a-d*, oral, *D*-ray, aboral views, and plate layout, ×1.3 (20, 179).

Nymphaeoblastus VON PEETZ, 1907, p. 15 [**N. miljukovi*; OD]. Theca ellipsoidal, with widely exposed hydrospire fields, each containing 10 to 15 slits which extend well down sides of theca; anal opening between small epideltoid and elongate hypodeltoid; lancet apparently covered by side plates; ambulacra long, linear, recurved below; base concave; deltoids almost as long as radials. *L.Carb.*, Eu.(USSR)-Asia(Japan).——FIG. 241,*1*. *N. anossofi* YAKOVLEV, Tournais., Japan; *1a,b*, oral and E-ray views, ×1.3 (52).——FIG. 242,*1*. **N. miljukovi*, USSR; *1a-d*, oral, *D*-ray, aboral views, and plate layout, ×0.8 (131, 190).

Phaenoblastus FAY, 1961 (60), p. 40 [*emend.* MACURDA, 1964 (104), p. 723] [**Pentremites*

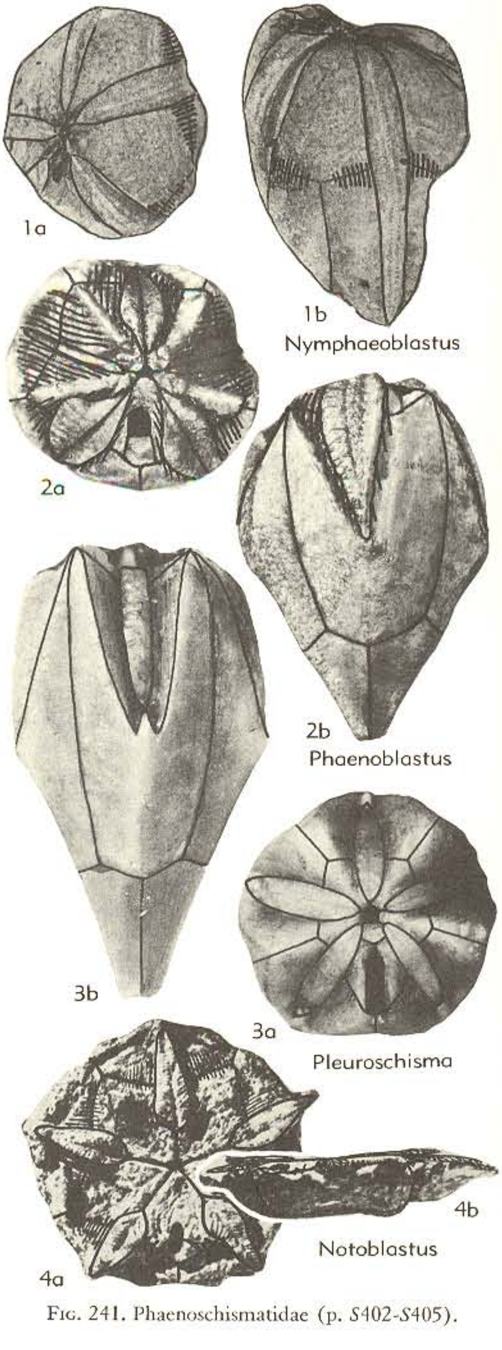


FIG. 241. Phaenoschismatidae (p. *S*402-*S*405).

caryophyllatus deKoninck & LeHon, 1854, p. 197; OD]. Theca club-shaped with ventral coronal processes; hydrospire fields wide, deeply indented, mostly hidden, each with 7 or 8 slits except on anal side where 4 occur; anal opening between large U-shaped epideltoid and small hypodeltoid; lancet widely exposed throughout its full width, deeply excavated in sinus; side plates large, covering most of slits, adorally forming 4 paired spiracle-like openings and false anispiracle with deltoid crests; ambulacra moderately long, petaloid; vault almost equal to pelvic height; basalia moderately large, composed of 3 basals; radials overlapping deltoids. *L.Carb.*, Eu.——Fig. 241,*2*; 242,*2*. **P. caryophyllatus* (deKoninck & LeHon), Tournais., Belg.; 241,*2a,b*, oral, *D*-ray views,

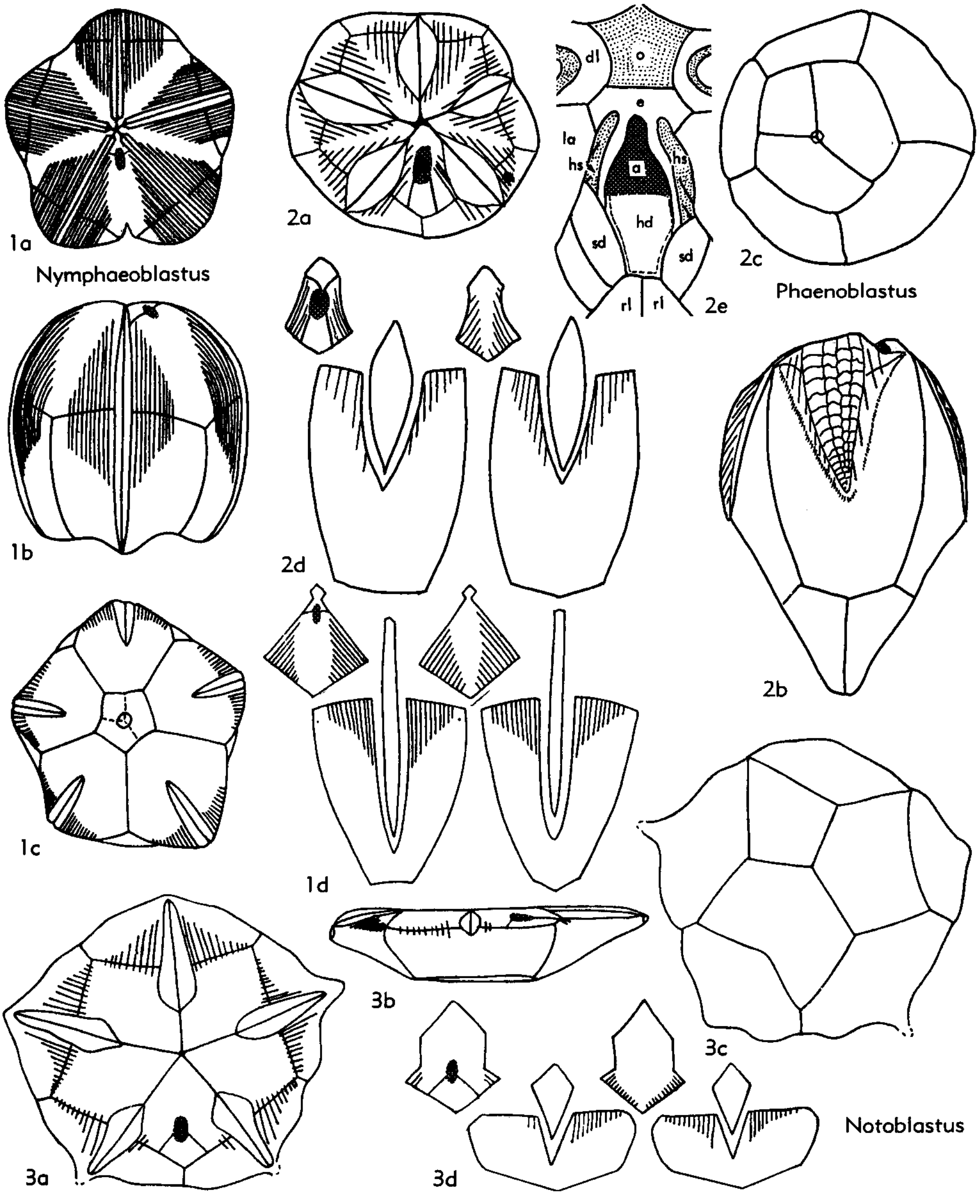


Fig. 242. Phaenoschismatidae (p. S402-S404). [Explanation: *a*, anal opening; *dl*, deltoid lip; *e*, epideltoid plate; *hd*, hypodeltoid; *hs*, hydrospire slit; *la*, lancet plate; *o*, oral opening; *rl*, radial limb; *sd*, side plate.]

×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*

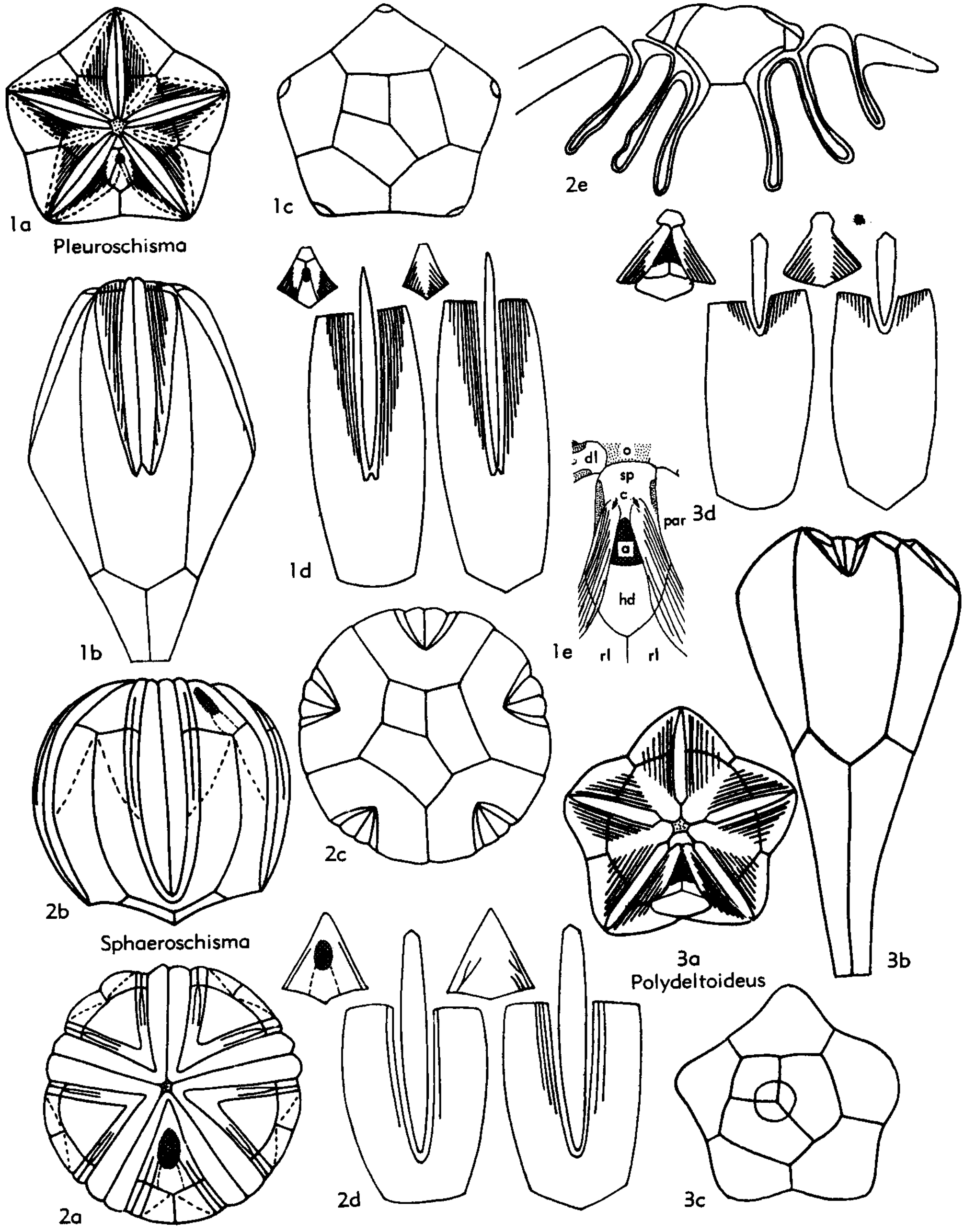


Fig. 243. Phaenoschismatidae (p. S404-S405). [Explanation: *a,* anal opening; *c,* cryptodeltoid plate; *dl,* deltoid lip; *hd,* hypodeltoid; *o,* oral opening or oral plate; *par,* posterior ambulacrum (right); *rl,* radial limb; *sp,* superdeltoid plate.]

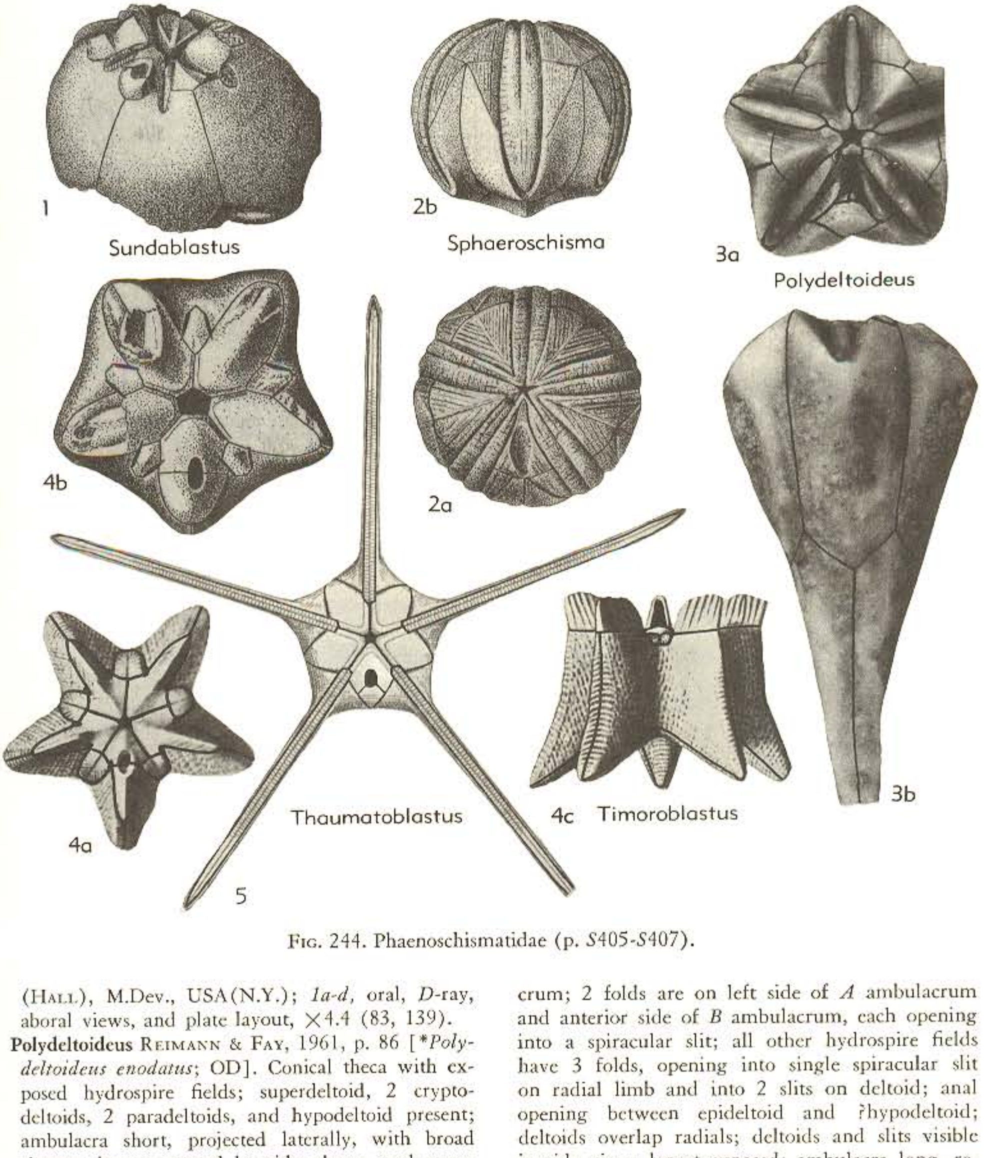


FIG. 244. Phaenoschismatidae (p. S405-S407).

(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

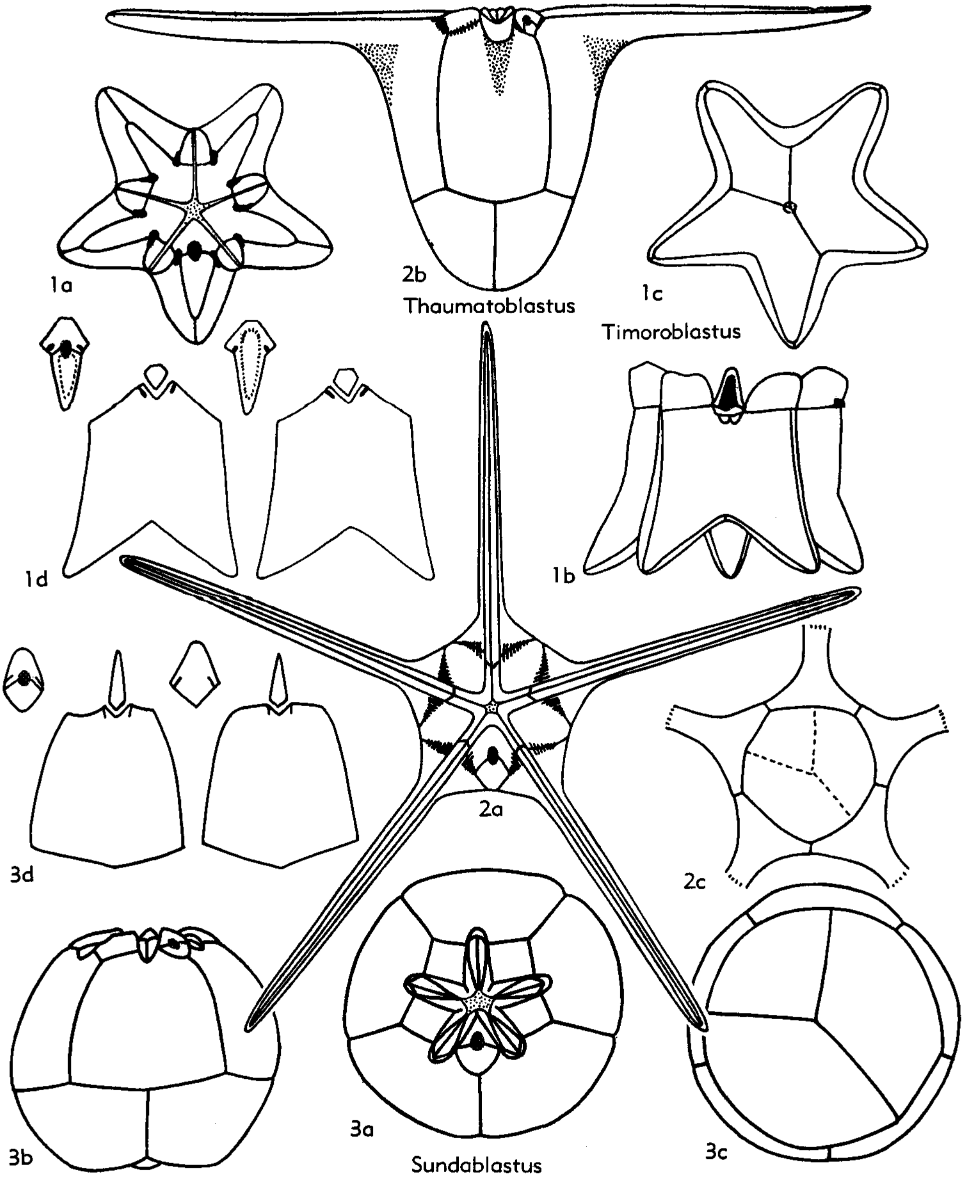


FIG. 245. Phaenoschismatidae (p. S405-S407).

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,

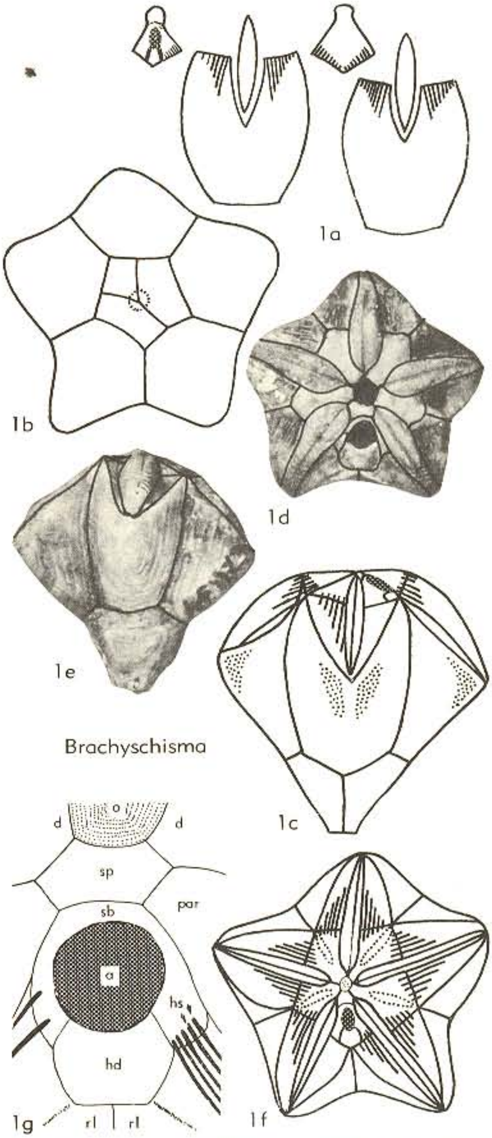


FIG. 246. Brachyschismatidae (p. *S*407). [Explanation: *a*, anal opening; *d*, deltoid plate; *hd*, hypodeltoid; *hs*, hydrospire slit; *o*, oral opening; *par*, posterior ambulacrum (right); *rl*, radial limb; *sb*, subdeltoid plate; *sp*, superdeltoid plate.]

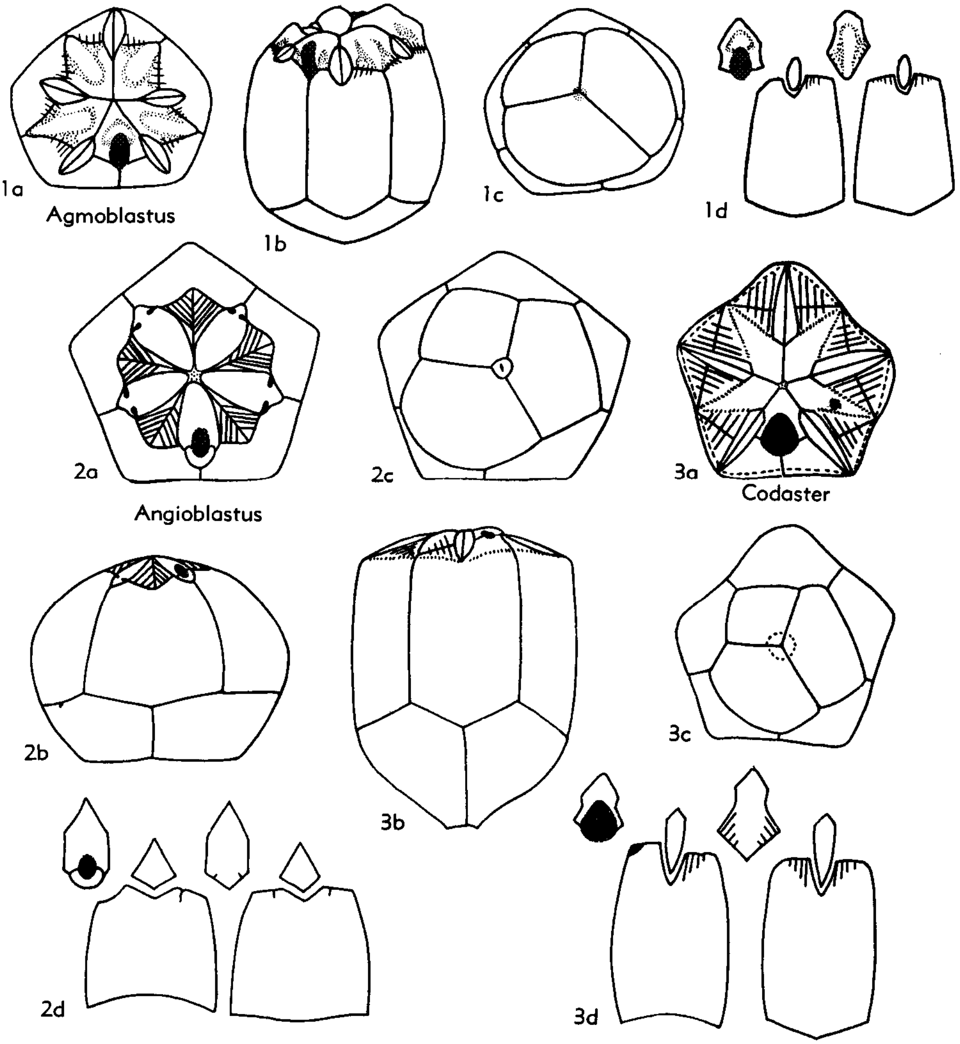


Fig. 247. Codasteridae (p. S407-S408).

wide, confined to summit; deltoids elongate, narrow. _Perm._, E.Indies(Timor).——Fig. 247,_2_; 249,_6_. *_A. variabilis_; 247,_2a-d,_ oral, _D_-ray, aboral views, plate layout, ×3.6; 249,_6a,b,_ oral, _CD_-interray views, ×4 (175).

Heteroschisma Wachsmuth, 1883, p. 352 [*_H. gracile_; OD] [=_Trionoblastus_ Fay, 1961 (60), p. 45 (type, _Pentremites subtruncatus_ Hall, 1858, p. 485)]. Theca obconical with hydrospire fields well exposed; superdeltoid, subdeltoid, and presumably small ?hypodeltoid on anal side; hydrospire slits absent on anal side; lancet covered by side plates. _Dev._, N.Am.——Fig. 248,_3a,b_; 250, _1h._ *_H. gracile,_ M.Dev., USA(Mich.); 248,_3a,b,_ _D_-ray view, oral view, ×3.5; 250,_1h,_ anal area, ×9.7 (60).——Fig. 250,_1a-e._ _H. subtruncatus_ (Hall), USA(Iowa); _1a-d,_ oral, _D_-ray, aboral views, plate layout, ×4.4; _1e,_ anal view, ×9.7 (60).——Fig. 250,_1f._ _H. pyramidatus_ (Shumard), M.Dev., USA(Ohio); anal area, ×7.3 (60).——Fig. 250,_1g._ _H. canadense_ (Billings); M.Dev., Can.(Ont.); anal area, ×9.7 (60).

Indoblastus Wanner, 1924 (174), p. 28 [_emend._ Breimer & Macurda, 1965, p. 212] [*_I. granulatus_; OD]. Theca pear- to cup-shaped, with small restricted hydrospire fields confined to summit; anal opening between large epideltoid and equally large raised hypodeltoid; ambulacra moderately long, mostly confined to summit; lancet covered by side plates, with lancet stipe well away from mouth. _Perm._, E.Indies(Timor).——Fig. 249,_2_; 250,_2_. *_I. granulatus_; 249,_2a,b,_ oral, _D_-ray views, ×2,

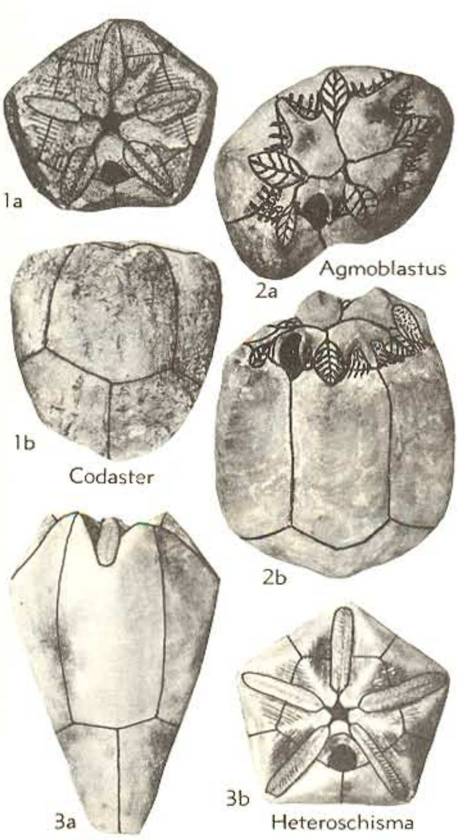


FIG. 248. Codasteridae (p. S407-S408).

×1; 250,*2a-d*, oral, *D*-ray, aboral views, plate layout, ×1.18 (173, 178).

Nannoblastus Wanner, 1924 (173), p. 24 [**N. pyramidatus*; OD]. Theca widely conical to cup-shaped, with small, short, restricted hydrospire fields confined to flat summit, appearing as 8 small slits; anus separate from slits, located between large epideltoid and small hypodeltoid; lancet covered by 2 or 3 side plates, short, wide, well away from mouth, confined to summit; with small, rounded radial wings. *Perm.*, E.Indies (Timor).——Fig. 249,*1*; 250,*3*. **N. pyramidatus*; 249,*1a-c*, oral view, ×6, oral, *CD*-interray views, ×3.1; 250,*3a-d*, oral, *D*-ray, aboral views, plate layout, ×5.9 (174, 175).

Paracodaster Yakovlev, 1940, p. 887 [**P. miloradovitschi*; OD]. Theca subglobular, with moderately exposed hydrospire fields confined to deltoids proper; hydrospire slits absent in anal area; anal opening between large epideltoid and radial limbs, with possible small ?hypodeltoid present; slits and ambulacra short, confined to summit; lancet stipes well away from mouth. *L.Perm.*, Eu. (USSR).——Fig. 249,*4*; 251,*3*. **P. miloradovitschi*; 249,4, oral view, ×2; 251,*3a-d*, oral, *D*-ray, aboral views, plate layout, ×1.75 (186, 190).

Pterotoblastus Wanner, 1924 (173), p. 9 [**P. gracilis*; OD]. Theca cup-shaped, with moderately exposed to restricted hydrospire fields, each with 2 or 3 wide hydrospire slits; large epideltoid with small anal opening between it and radial limbs, possibly with small ?hypodeltoid; ambulacra moderately short, extended on long winglike projections of radials; lancet well away from oral opening, covered by few large side plates; with 3 basal plates. *Perm.*, E.Indies(Timor).——Fig. 249,*3*; 251,*2*. **P. gracilis*; 249,*3a*, oral view, ×8.2; 249, *3b*, *CD*-interray, ×2.5; 251,*2a-d*, oral, *D*-ray, aboral views, plate layout, ×1.1 (173, 175).

Sagittoblastus Yakovlev, 1937, p. 10 [**Timoroblastus wanneri* Yakovlev, 1926, p. 54; OD]. Theca globular, with small, deep, restricted hydrospire fields on summit, each with 2 or 3 hydrospire slits; deltoids arrow-shaped, wide; large epideltoid, with small anal opening between it and radial limbs, possibly with small ?hypodeltoid (missing) on aboral side of anal opening; with extremely short lancet covered by side plates; lancet well away from mouth. *Perm.*, Eu. (USSR).——Fig. 249,*5*; 251,*1*. **S. wanneri* (Yakovlev); 249,*5*, oral view, ×3.5; 251,*1a-d*, oral, *D*-ray, aboral views, plate layout, ×3.5 (184, 185, 190); 251,*1e*, anal view, ×10 (60).

Family OROPHOCRINIDAE Jaekel, 1918

[Orophocrinidae Jaekel, 1918, p. 109] [=Antholblastidae 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,

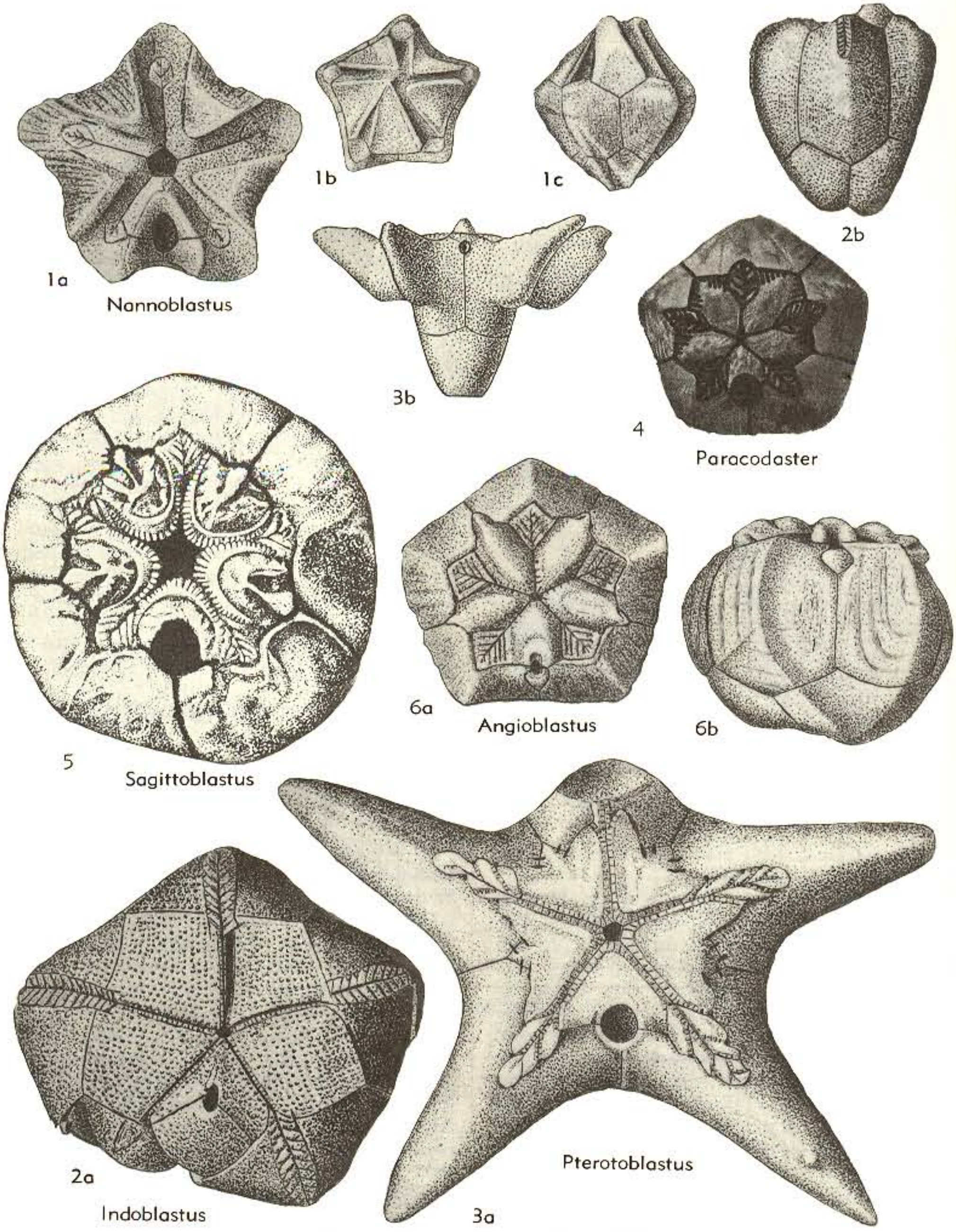


FIG. 249. Codasteridae (p. S407-S409).

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

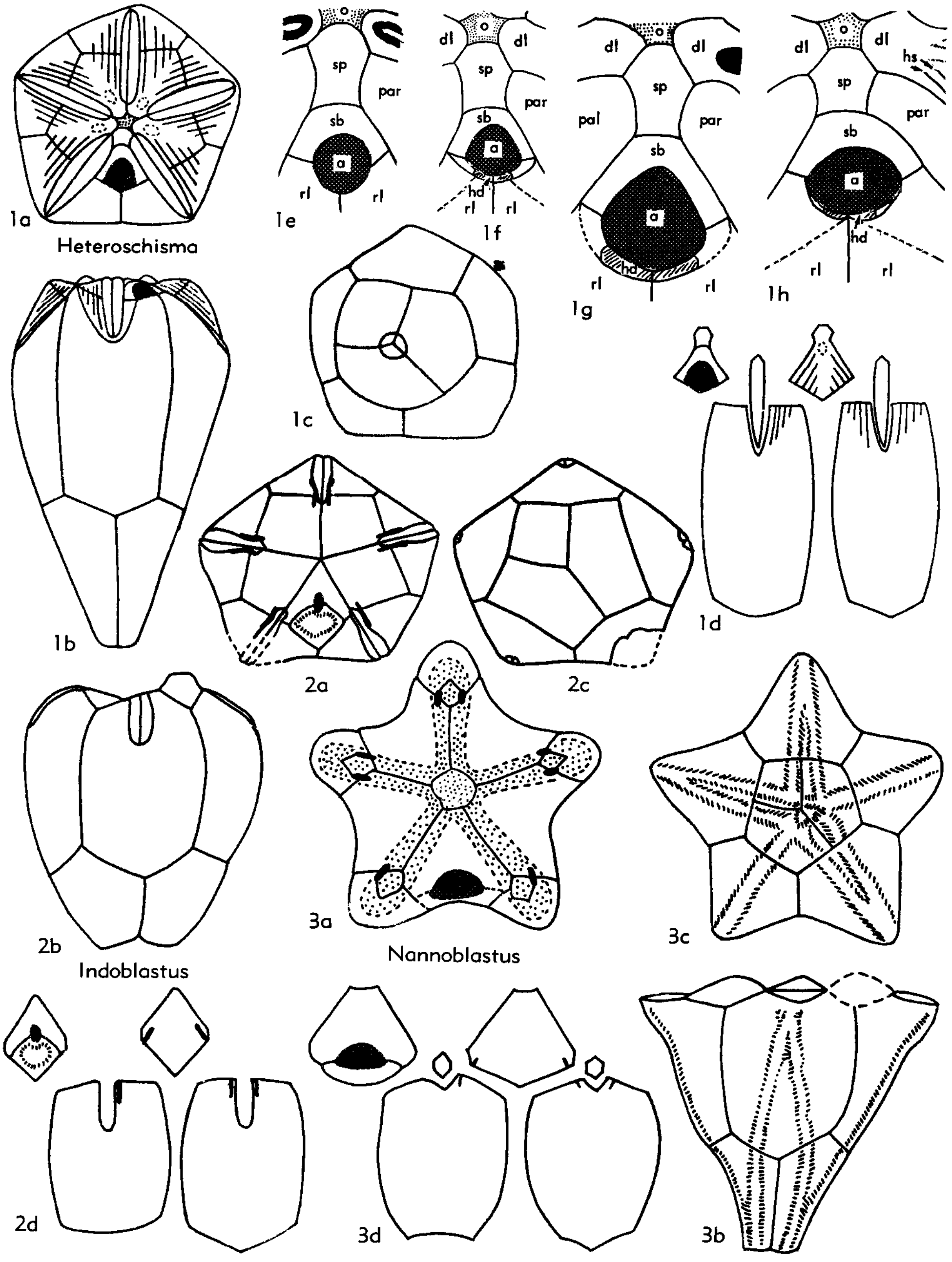


FIG. 250. Codasteridae (p. *S*408-*S*409). [Explanation: *a*, anal opening; *dl*, deltoid lip; *hd*, hypodeltoid; *hs*, hydrospire slit; *o*, oral opening; *pal*, posterior ambulacrum (left); *par*, posterior ambulacrum (right); *rl*, radial limb; *sb*, subdeltoid plate; *sp*, superdeltoid plate.]

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,

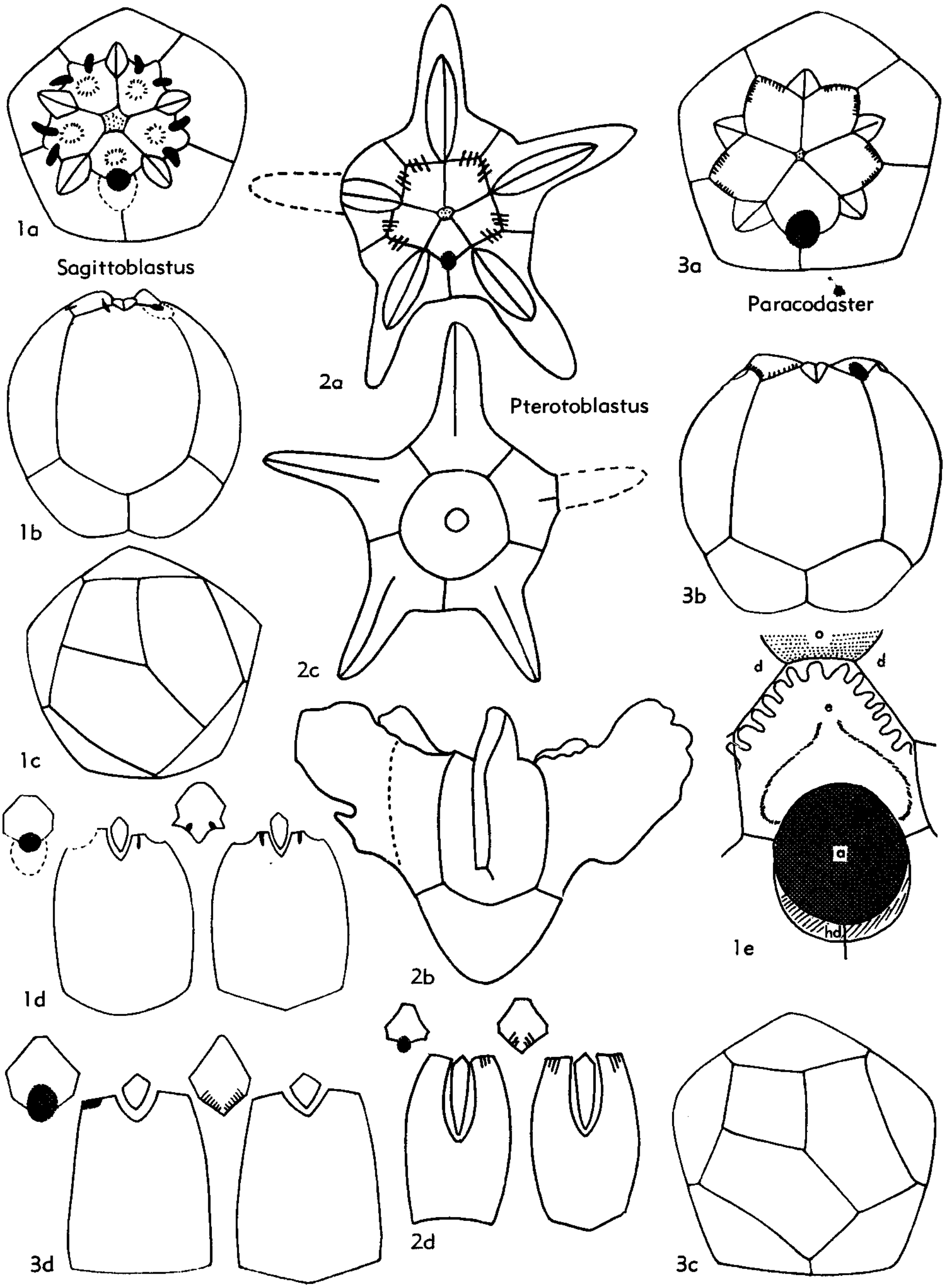


Fig. 251. Codasteridae (p. S409). [Explanation: *a*, anal opening; *d*, deltoid plate; *e*, epideltoid plate; *hd*, hypodeltoid; *o*, oral opening.]

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).

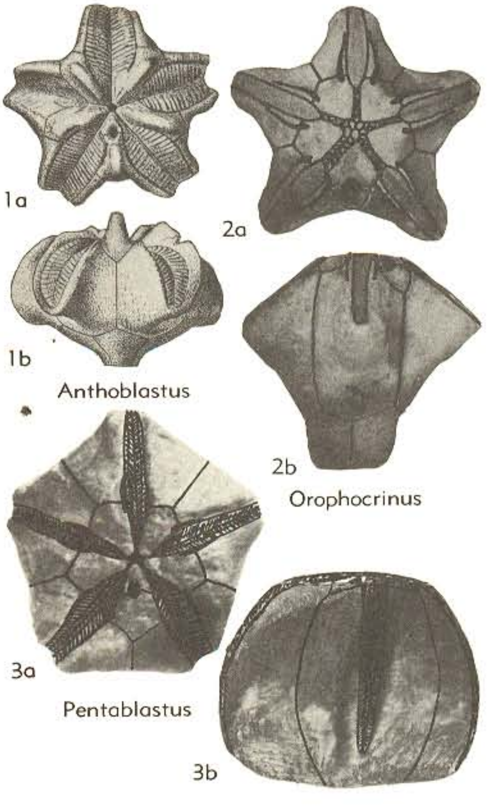


FIG. 252. Orophocrinidae (p. S409-S412).

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).

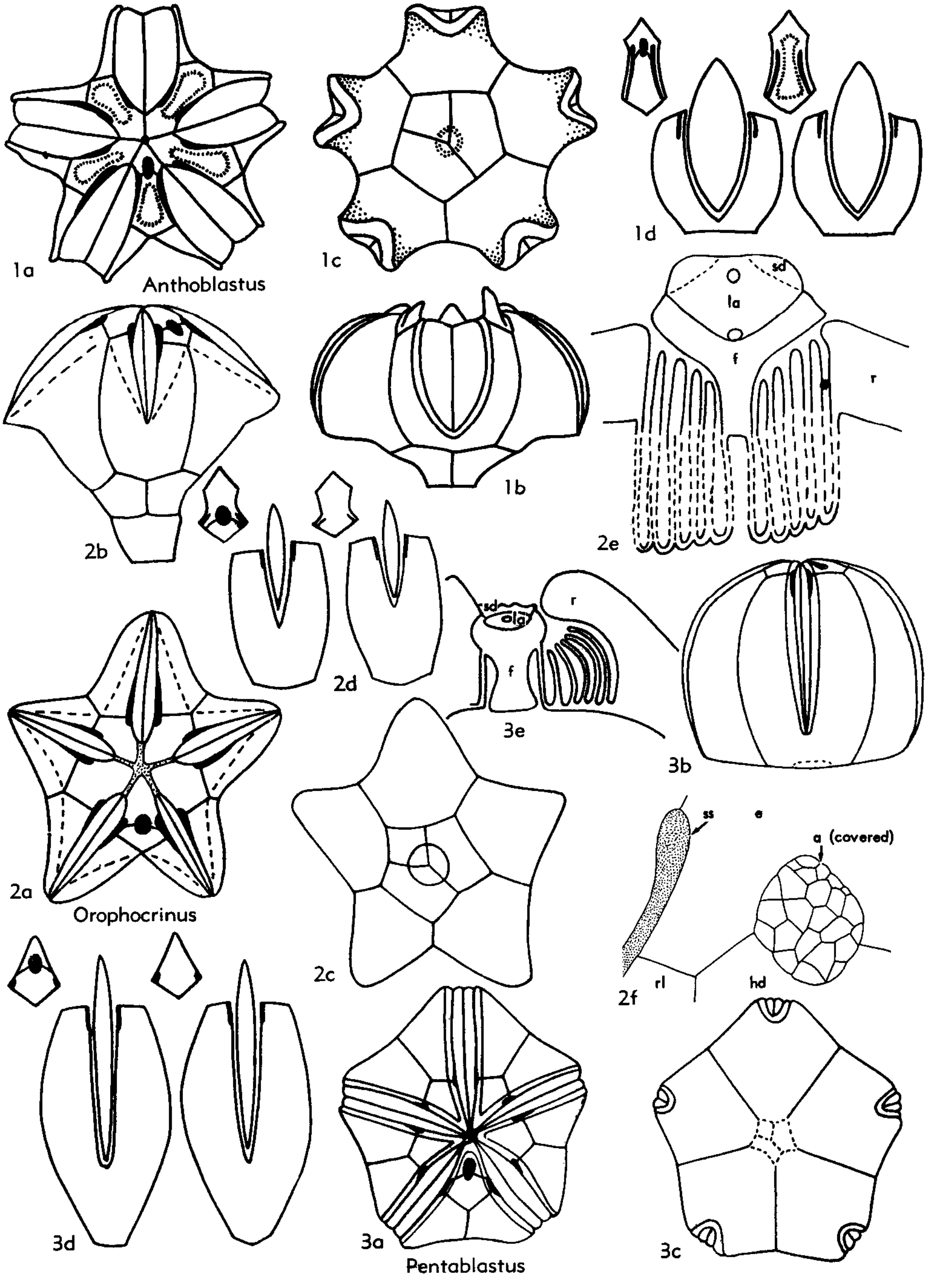


FIG. 253. Orophocrinidae (p. S409-S412). [Explanation: *a*, anal opening; *e*, epideltoid plate; *f*, fused hydrospire plate; *hd*, hypodeltoid; *la*, lancet plate; *r*, radial plate; *rl*, radial limb; *sd*, side plate; *ss*, spiracular slit.]

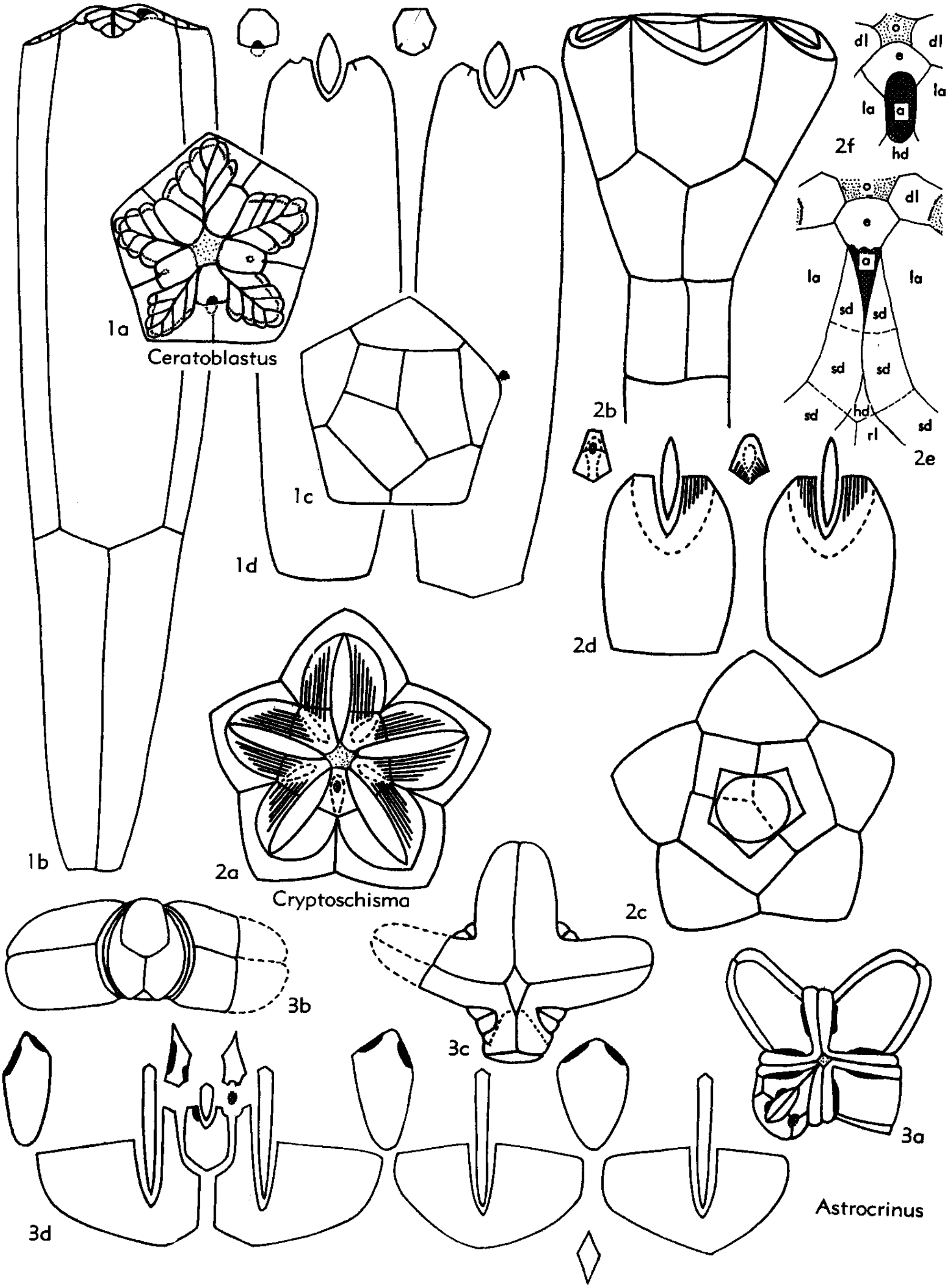


FIG. 254. Astrocrinidae (p. S413). [Explanation: *a*, anal opening; *e*, epideltoid plate; *dl*, deltoid lip; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening; *rl*, radial limb; *sd*, side plate.]

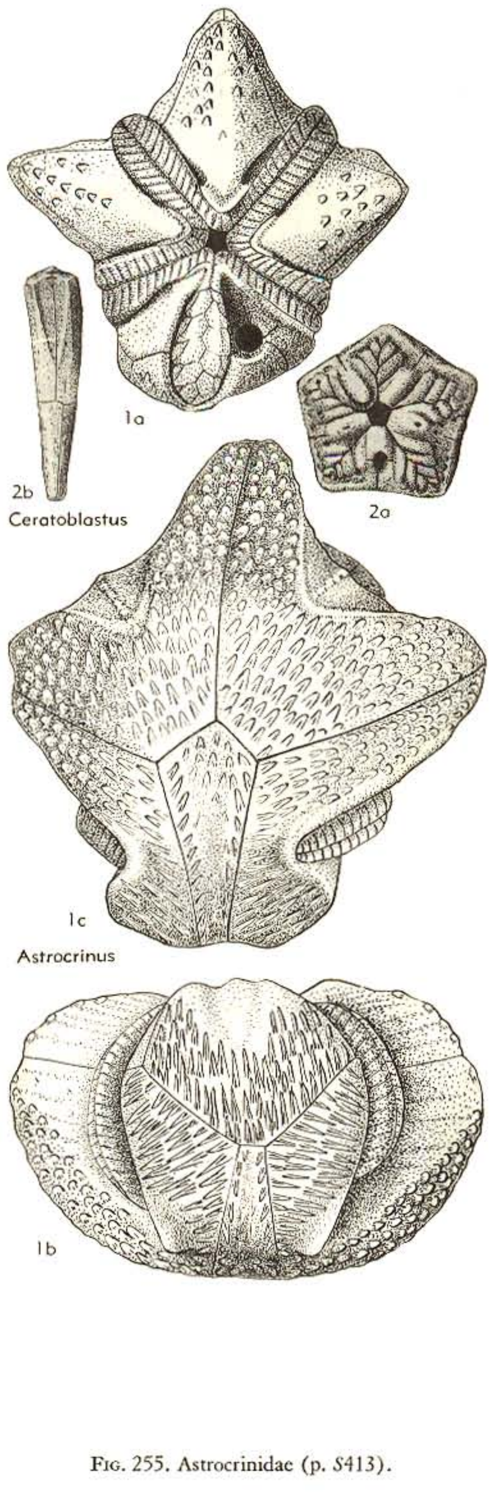


FIG. 255. Astrocrinidae (p. S413).

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*;

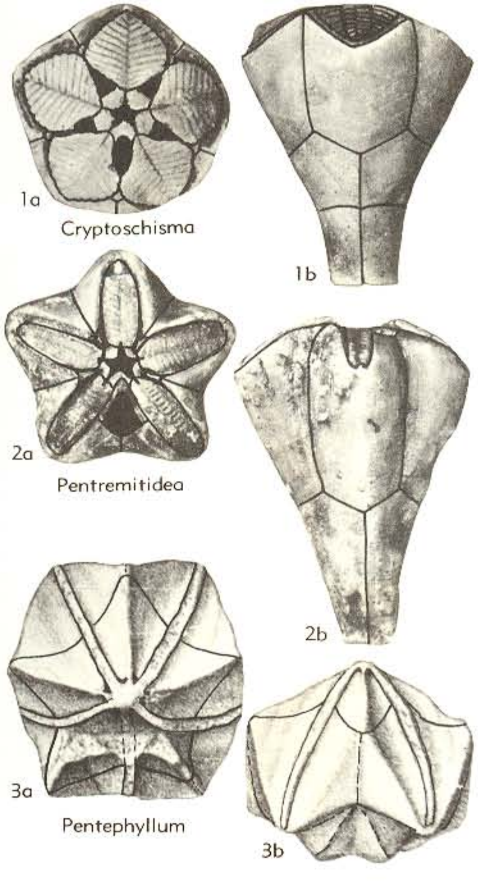


FIG. 256. Astrocrinidae (p. S413).

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-

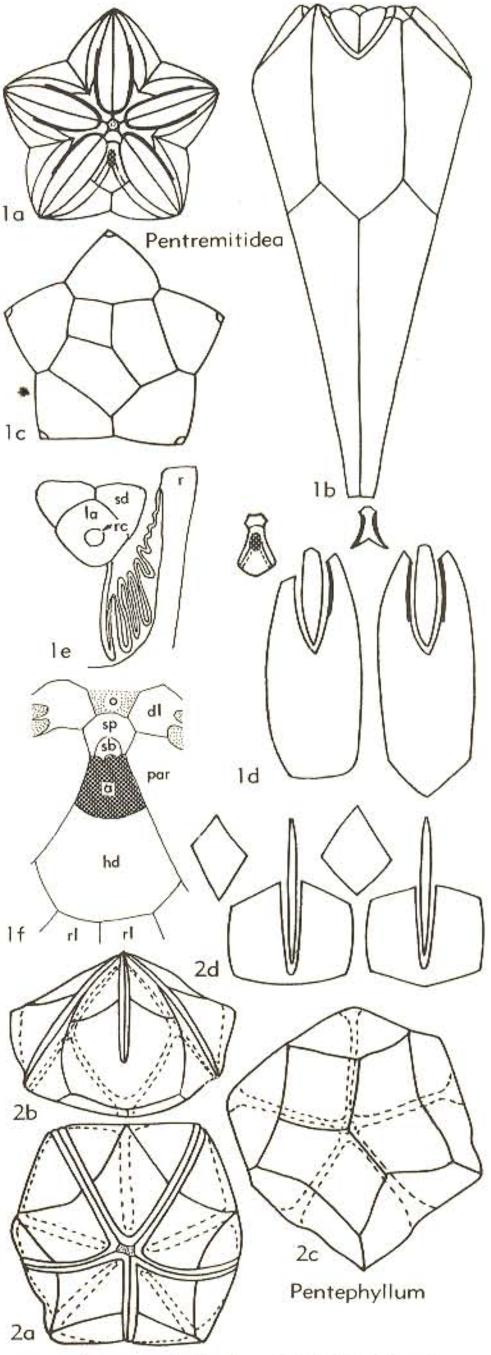


FIG. 257. Astrocrinidae (p. S413). [Explanation: *a*, anal opening; *dl*, deltoid lip; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening; *par*, posterior ambulacrum (right); *r*, radial plate; *rc*, radial canal; *rl*, radial limb; *sb*, subdeltoid plate; *sd*, side plate; *sp*, superdeltoid plate.]

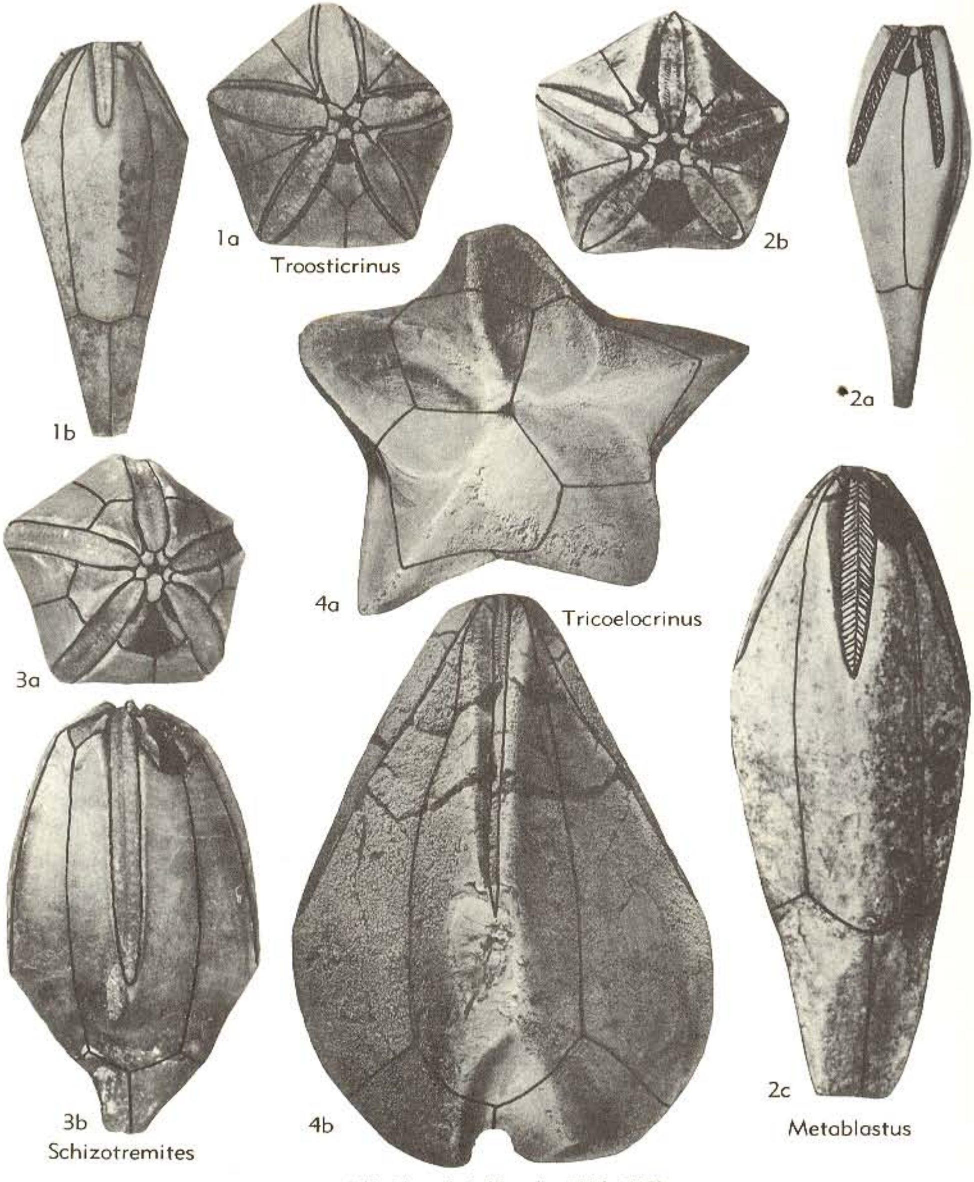


FIG. 258. Troosticrinidae (p. S416-S419).

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.*

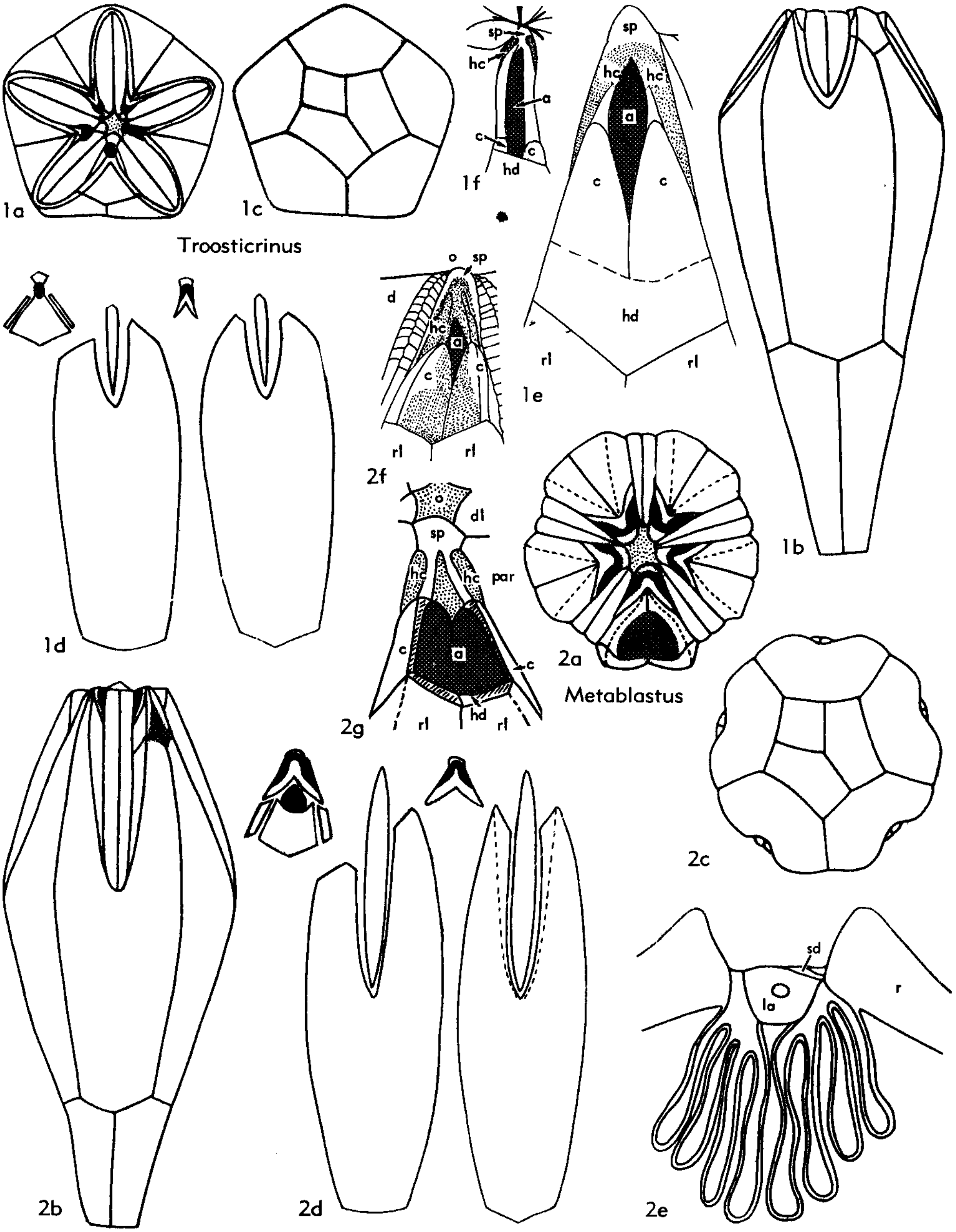


Fig. 259. Troosticrinidae (p. S416). [Explanation: *a*, anal opening; *c*, cryptodeltoid plate; *d*, deltoid plate; *dl*, deltoid lip; *hc*, hydrospire canal; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening; *par*, posterior ambulacrum (right); *r*, radial plate; *rl*, radial limb; *sd*, side plate; *sp*, superdetoid plate.]

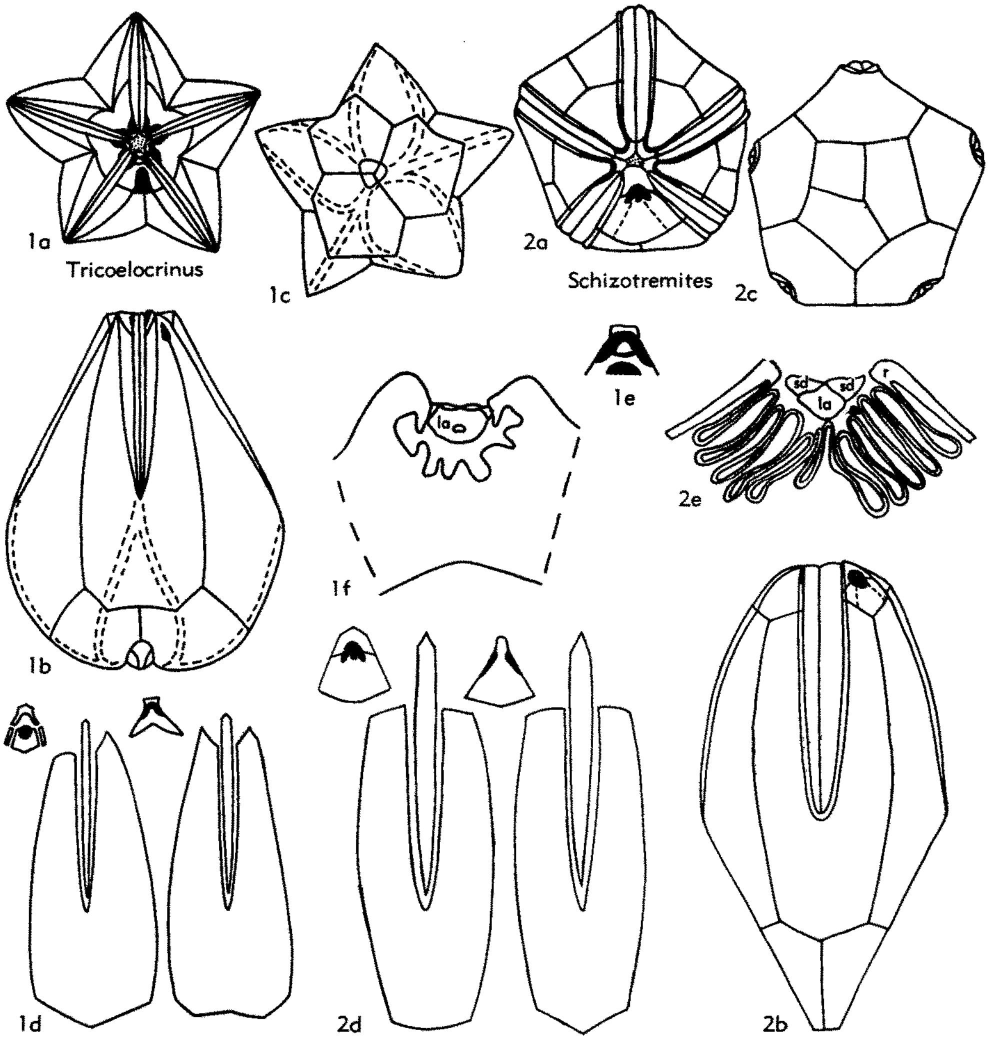


FIG. 260. Troosticrinidae (p. *S*416-*S*419). [Explanation: *la*, lancet plate; *r*, radial plate; *sd*, side plate.]

Diploblastus FAY, 1961 (60), p. 62 [**Granatocrinus glaber* MEEK & WORTHEN, 1869, p. 91; OD]. Theca globular, with superdeltoid, 2 cryptodeltoids, and hypodeltoid; 2 hydrospire folds on each side of an ambulacrum; lancet covered by side plates at aboral end and gradually exposed to 0.3 of its width near adoral end; with one pore between side plates along deltoid and radial margins; radials overlapping deltoids. *Miss.*, N.Am. (Ill.-Mo.-Ky.-Ala.).——FIG. 261,*2*; 262,*1*. **D. glaber* (MEEK & WORTHEN), M.Miss., Ky. (261, 2), Ill. (262,*1*); 261,*2a,b*, oral, *D*-ray views, ×7.5; 262,*1a-d*, oral, *D*-ray, aboral views, plate layout, ×6.3; 262,*1e*, cross sec. of ambulacrum, ×26.5; 262,*1f*, anal view, ×10 (60).

Nodoblastus FAY, 1963, p. 174 [**Schizoblastus librovitchi* YAKOVLEV, 1941, p. 71; OD]. Theca bell-shaped to elliptical, with anispiracle located between short epideltoid and long hypodeltoid; deltoids slightly longer than radials which overlap deltoids; one hydrospire fold on each side of an ambulacrum; hydrospire plate present, with about twice as many pores as side plates; basalia small, in slight basal concavity; deltoids nodose, with medium high deltoid crests. *L.Carb.*, Eu. (USSR).——FIG. 261,*1*; 262,*2*. **N. librovitchi* (YAKOVLEV); 261,*1a,b*, oral, *C*-ray views, ×3.2; 262,*2a-d*, oral, *C*-ray, aboral views, plate diagram, ×3.7; 262,*2e*, transv. sec. of ambulacrum, ×10 (73, 188).

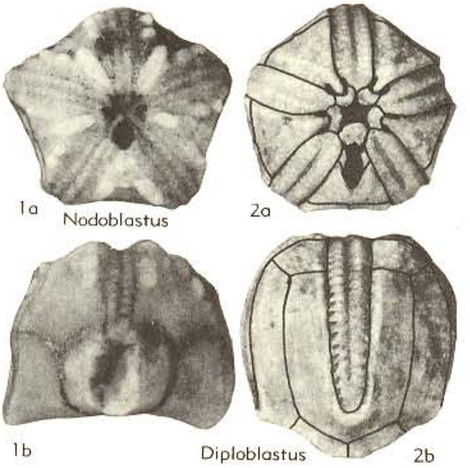


FIG. 261. Diploblastidae (p. S420).

Family GRANATOCRINIDAE Fay, 1961

[Granatocrinidae FAY, 1961 (60), p. 20] [=Granatoblastidae ETHERIDGE & CARPENTER, 1886, p. 237 (invalid, based on nonexistent nominal genus)]

Theca with eight spiracles and anispiracle (or paired anispiracle) around mouth. *Miss.*

Granatocrinus HALL, 1862, p. 146 [**Pentatrematites granulatus* ROEMER, 1851, p. 363; SD SHUMARD, 1866, p. 375] [=*Granatocrinites* TROOST, 1849, p. 420 *(nom. nud.)*; *Cidaroblastus* HAMBACH, 1903, p. 45 (type, *Pentatrematites granulatus* ROEMER)]. Elliptical theca with anispiracle located between epideltoid and hypodeltoid; one hydrospire fold on each side of an ambulacrum; lancet covered by side plates; hydrospire plate present; 2 pores to each side plate along radial and deltoid margins; radials overlapping deltoids; deltoids moderately long. *Miss.*, N.Am.(Ky.-Ind.-Tenn.).——FIG. 263,*1*; 264,*1a-e*. **G. granulatus* (ROEMER), M.Miss., USA(Tenn.); 263,*1a*, oral view,

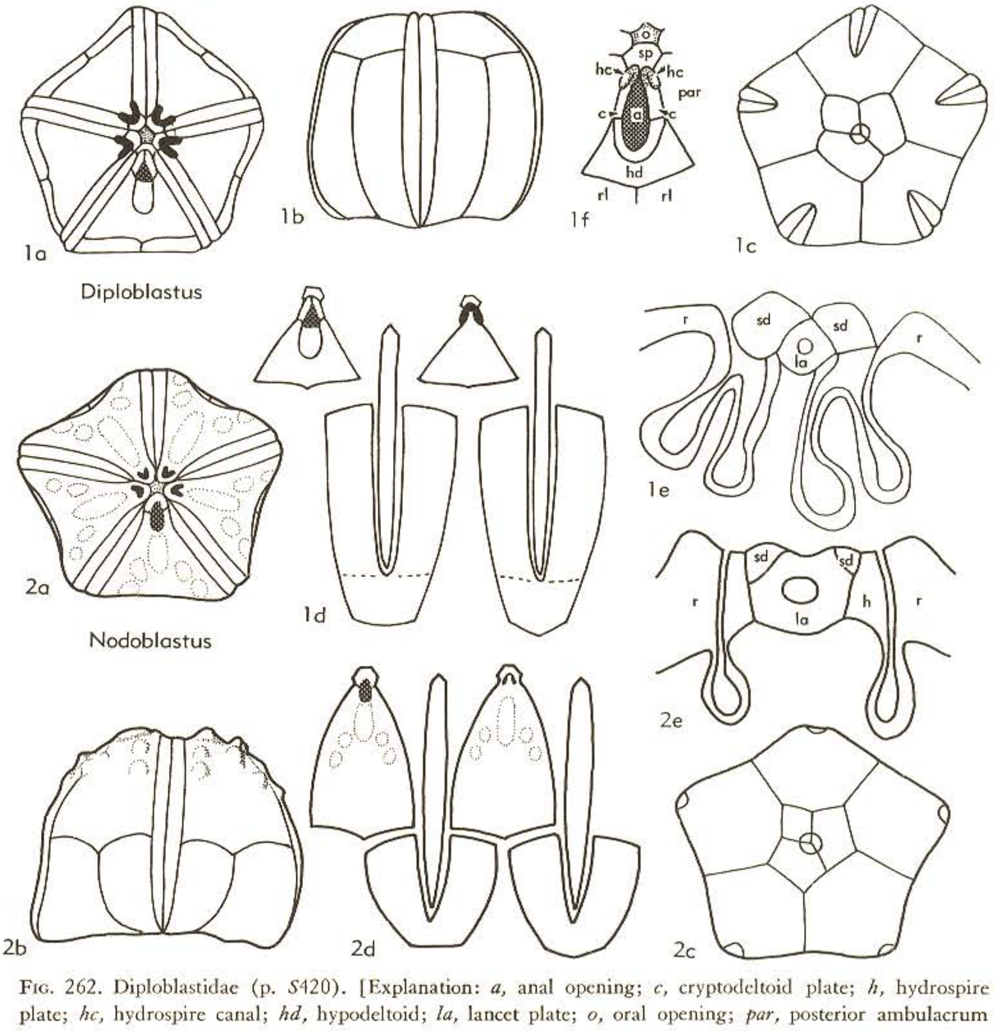


FIG. 262. Diploblastidae (p. S420). [Explanation: *a*, anal opening; *c*, cryptodeltoid plate; *h*, hydrospire plate; *hc*, hydrospire canal; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening; *par*, posterior ambulacrum (right); *r*, radial plate; *rl*, radial limb; *sd*, side plate; *sp*, superdeltoid plate.]

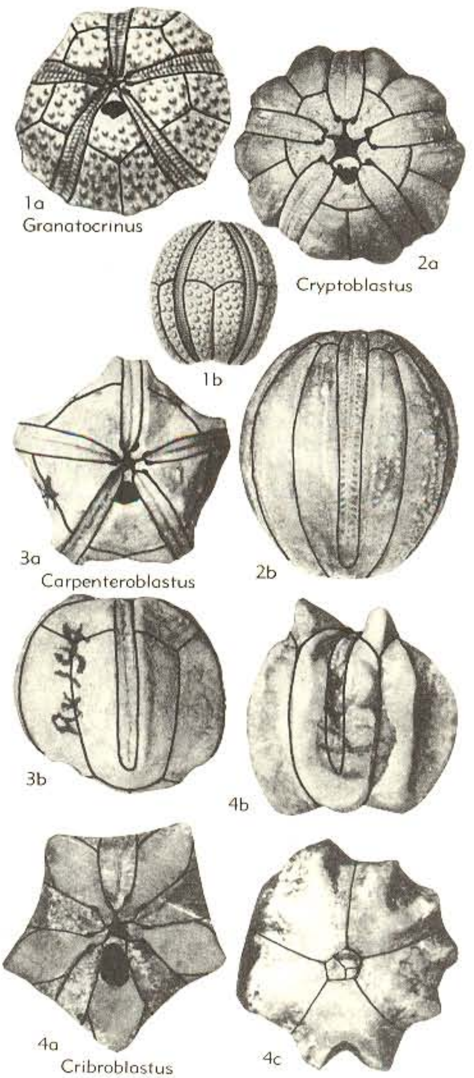


Fig. 263. Granatocrinidae (p. *S*421-*S*422).

×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

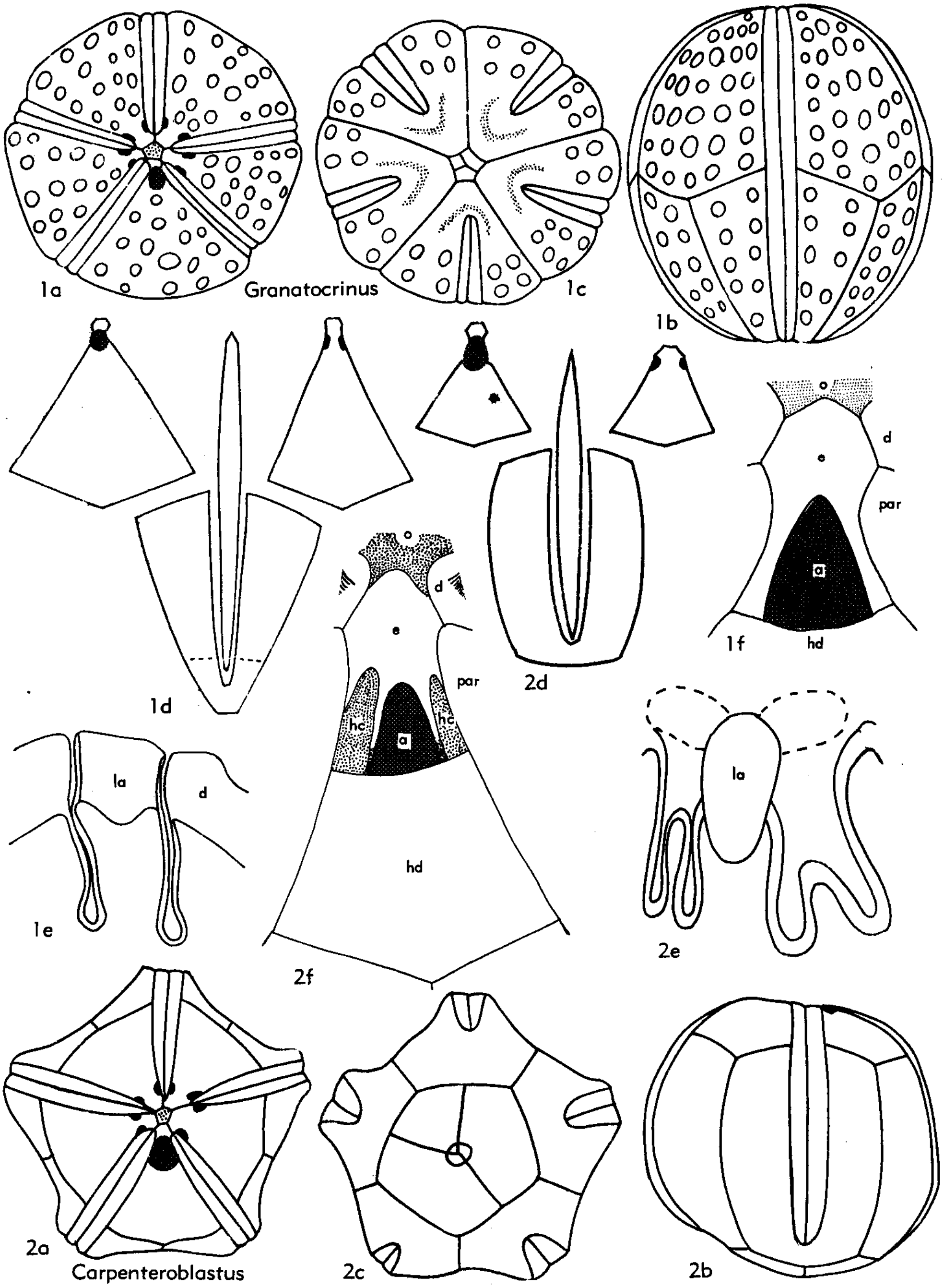


FIG. 264. Granatocrinidae (p. S421-S423). [Explanation: *a*, anal opening; *d*, deltoid plate; *e*, epideltoid plate; *hc*, hydrospire canal; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening; *par*, posterior ambulacrum (right).]

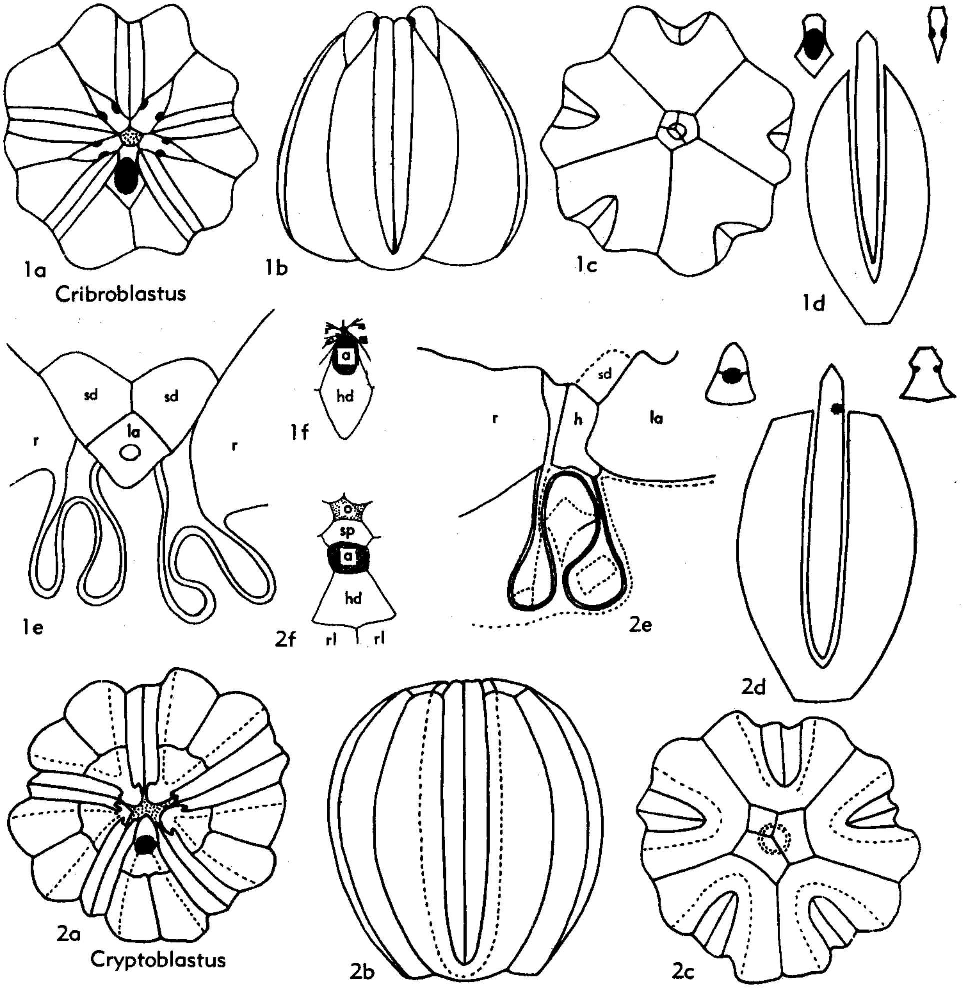


FIG. 265. Granatocrinidae (p. S422). [Explanation: *a*, anal opening; *h*, hydrospire plate; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening; *r*, radial; *rl*, radial limb; *sd*, side plate; *sp*, superdeltoid plate.]

more than one hydrospire fold on each side of an ambulacrum. *L.Carb.*, Eu.(Eng.).——FIG. 267, *1*; 268,*1*. **H. cumberlandi*; 267,*1a,b*, oral, radial views, X3.8; 268,*1a-d*, oral, *D*-ray, aboral views, plate layout, X4.4 (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, X3.2; 268,*2a-d*, oral, *D*-ray, aboral views, plate layout, X5.8; 268,*2f*, anal view, X10 (41, 60).——FIG. 268,*2e*. *M. angulatus* (SOWERBY), Eng.; cross sec. of ambulacrum, X11.8 (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, X6.4; 268,*3a-e*, oral, *D*-ray, aboral views, plate layout, cross sec. of ambulacrum, X8.8 (60).

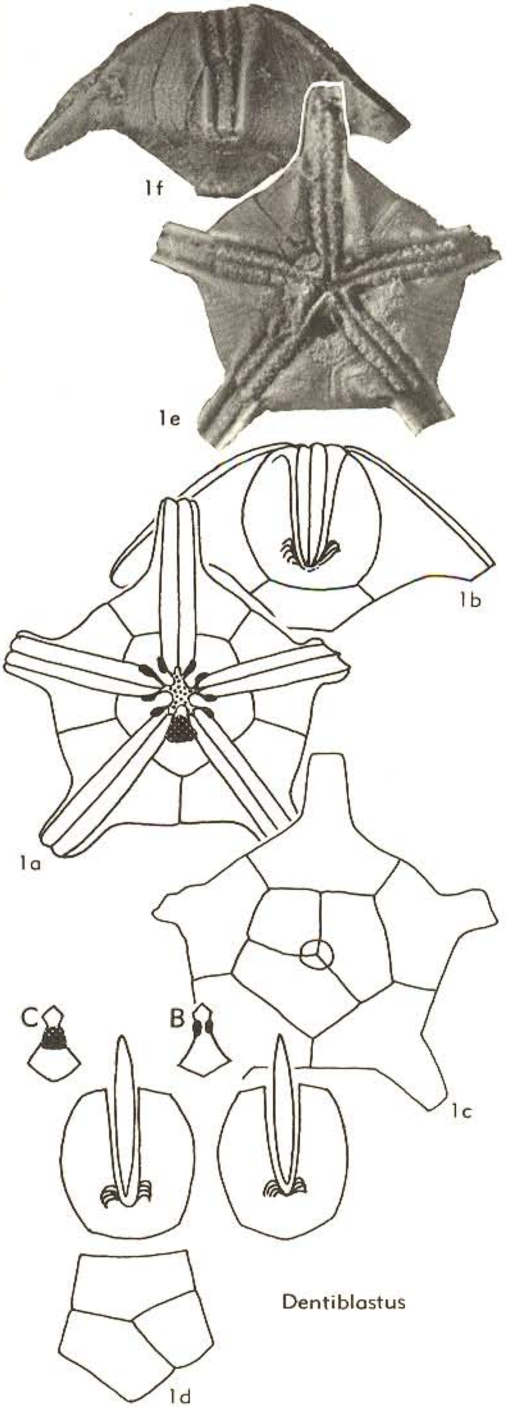


FIG. 266. Granatocrinidae (p. *S*422).

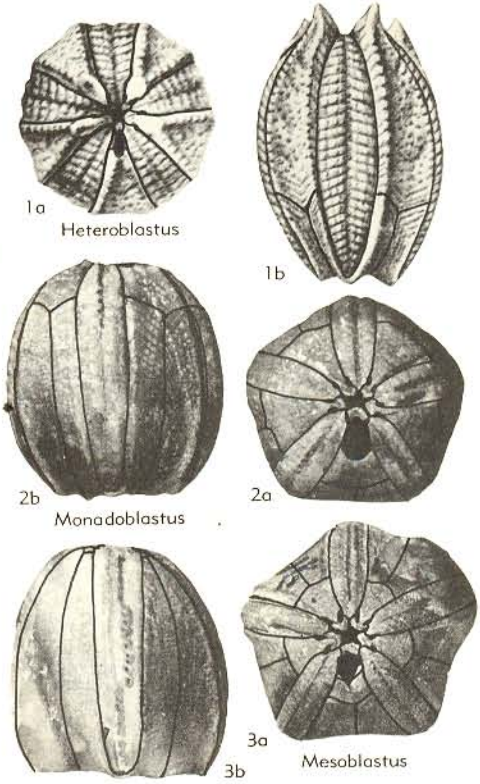


FIG. 267. Granatocrinidae (p. *S*422, *S*424).

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

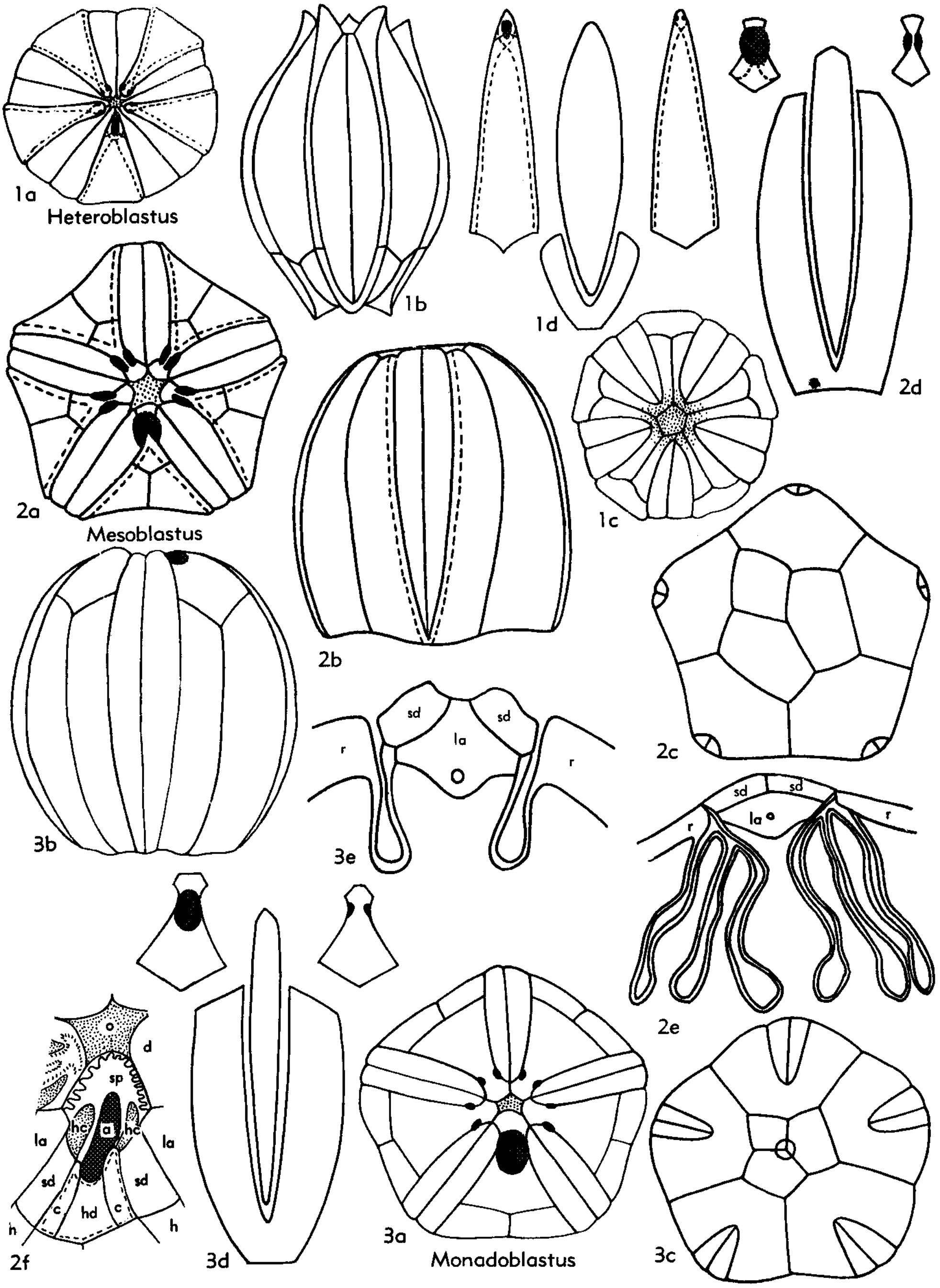


FIG. 268. Granatocrinidae (p. S422, S424). [Explanation: *a*, anal opening; *c*, cryptodeltoid plate; *d*, deltoid plate; *h*, *h*ydrospire plate; *hc*, hydrospire canal; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening; *r*, radial plate; *sd*, side plate; *sp*, superdeltoid plate.]

near adoral end; base concave. *Miss.*, N.Am.(Ill.-Iowa-Mo.).——Fig. 269,2; 270,2. **P. granulosus* (Meek & Worthen), M.Miss., USA(Ill.); 269, *2a,b*, oral, *D*-ray views, ×4; 270,*2a-d*, oral, *D*-ray, aboral views, plate layout, ×4.4; 270,*2e*, cross sec. of ambulacrum, ×26.4; 270,*2f*, anal view, ×10 (60).

Ptychoblastus Fay, 1960 (46), p. 1198 [**P. pustulosus*; OD]. Theca ellipsoidal, with anispiracle between epideltoid and hypodeltoid; radials abutting against deltoids; hydrospire plate present; 2 pores to each side plate along deltoid and radial margins; single hydrospire fold on each side of ambulacra; lancets covered at aboral end, gradually exposed to 0.3 of width near adoral end. *Miss.*, N.Am.(Mo.).——Fig. 269,*3*; 270,*1*. **P. pustulosus*, M.Miss.; 269,*3a-c*, oral, *AE* interambulacral, *D*-ray views, ×3.8 (60); 270,*1a-d*, oral, *D*-ray, aboral views, plate layout, ×5.9; 270,*1e*, cross sec. of ambulacrum, ×17.6 (46).

Pyramiblastus Macurda, 1964 (105), p. 106 [**Orophocrinus fusiformis* Wachsmuth & Springer, 1888, p. 14; OD]. Theca bipyramidal, with paired anispiracle located between superdeltoid, 2 cryptodeltoids, and hypodeltoid; 6 to 8 hydrospire folds on each side of ambulacrum; lancet exposed along 0.3 of its width; single pore between each side plate along radial and deltoid margins; deltoids overlapping radials; deltoids well exposed in side view. *Miss.*, USA (Iowa).——Fig. 271,*1*. **P. fusiformis* (Wachsmuth & Springer), L.Miss., Iowa; *1a-f*, oral, *D*-ray, aboral views, plate layout, side view of holotype, *D*-ray view, ×3 (105).

Tanaoblastus Fay, 1961 (60), p. 101 [**Pentremites roemeri* Shumard *(partim)*, 1855, p. 186, pl. B, fig. 2a only; OD]. Theca subelliptical, with anispiracle located between superdeltoid and hypodeltoid, with 2 hidden cryptodeltoids; deltoids moderately short; radials overlapping deltoids; pores absent along deltoid margins, but 2 pores to each side plate along radial margins; 2 hydrospire folds on each side of ambulacra; lancet exposed along main food groove; interradial sutures even; base flat to convex. *Miss.*, N.Am.(Mo.-Mont.-?Ariz.-Alta.).——Fig. 272,*1a-h*. **T. roemeri* (Shumard), L.Miss., USA(Mo.); *1a*, oral view, ×5.9; *1b*, oral view, ×5.1; *1c*, *D*-ray view, ×5.9; *1d*, *D*-ray view, ×5.1; *1e,f*, aboral view, plate layout, ×5.9; *1g*, cross sec. of ambulacrum, ×11.7; *1h*, anal view, ×10 (60).——Fig. 272, *1i*. *T. concinnulus* (Rowley & Hare), M.Miss., Mo.; anal view, ×10 (60).

Family SCHIZOBLASTIDAE
Etheridge & Carpenter, 1886

[Schizoblastidae Etheridge & Carpenter, 1886, p. 220]

Theca with ten spiracles and separate anal opening around mouth; cryptodeltoids (if present) hidden. *Dev.-Perm.*

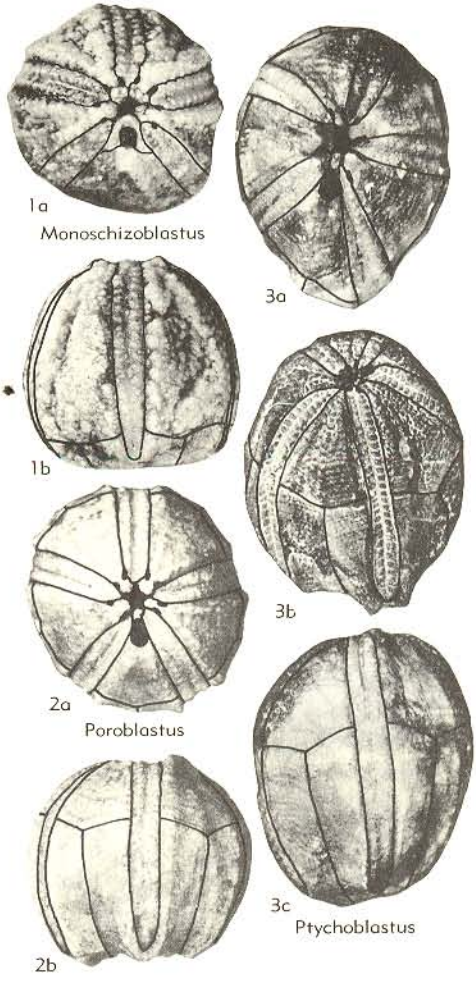


Fig. 269. Granatocrinidae (p. S425, S427).

Schizoblastus Etheridge & Carpenter, 1882, p. 243 [**Pentremites sayi* Shumard, 1855, p. 185; SD Etheridge & Carpenter, 1886, p. 220]. Theca ellipsoidal; anal opening between epideltoid and hypodeltoid; lancet exposed along main food groove; 1 pore between side plates along deltoid and radial margins; deltoids moderately long, overlapping radials; 2 hydrospire folds on each side of ambulacrum; base slightly concave. *Miss.*, N.Am.(Iowa-Mo.-Ill.).——Fig. 273,*2*; 274,*2*. **S. sayi* (Shumard), M.Miss., USA(Mo.); 273,*2a,b*, oral, *A*-ray views, ×2; 274,*2a-d*, oral, D-ray, aboral views, plate layout, ×2.2; 274,*2e*, cross sec. of ambulacrum, ×8.9 (28, 60, 154).

Acentrotremites Etheridge & Carpenter, 1883, p. 232 [**Mitra elliptica* Cumberland, 1826, p. 33;

OD]. Theca bell-shaped, with spiracles adjacent to radials; anal opening excavated in ?single anal deltoid; hydrospire plate present; pores absent along deltoids; deltoids overlapping radials; 4 or 5 hydrospire folds on each side of an ambulacrum; lancet covered by side plates; basalia seemingly fused to form single plate. *L.Carb.*, Eu. (Eng.).——FIG. 273,*3*; 274,*1*. **A. ellipticus* (CUMBERLAND); 273,*3a,b*, oral, *CD* interambulacral views, ×1.3, ×0.7; 274,*1a-d*, oral, *D*-ray, ab-

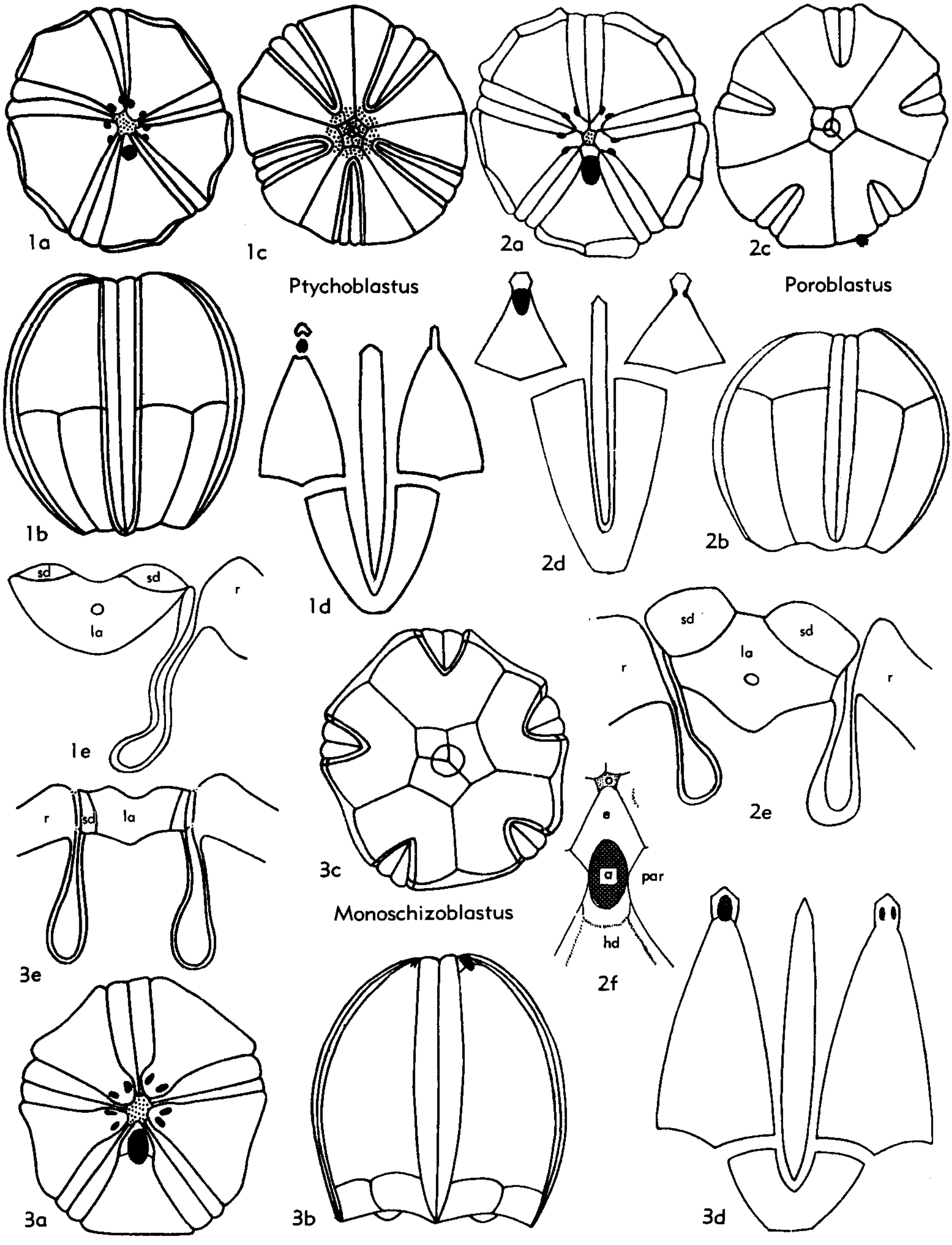


FIG. 270. Granatocrinidae (p. S425, S427). [Explanation: *a*, anal opening; *e*, epideltoid plate; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening; *par*, posterior ambulacrum (right); *r*, radial plate; *sd*, side plate.]

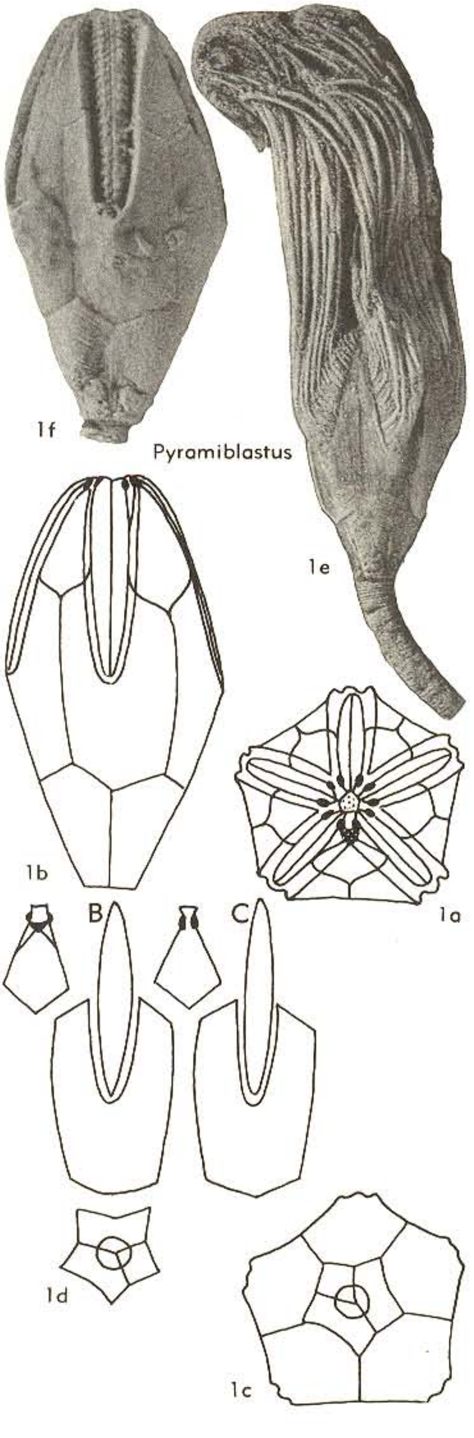


FIG. 271. Granatocrinidae (p. *S*427).

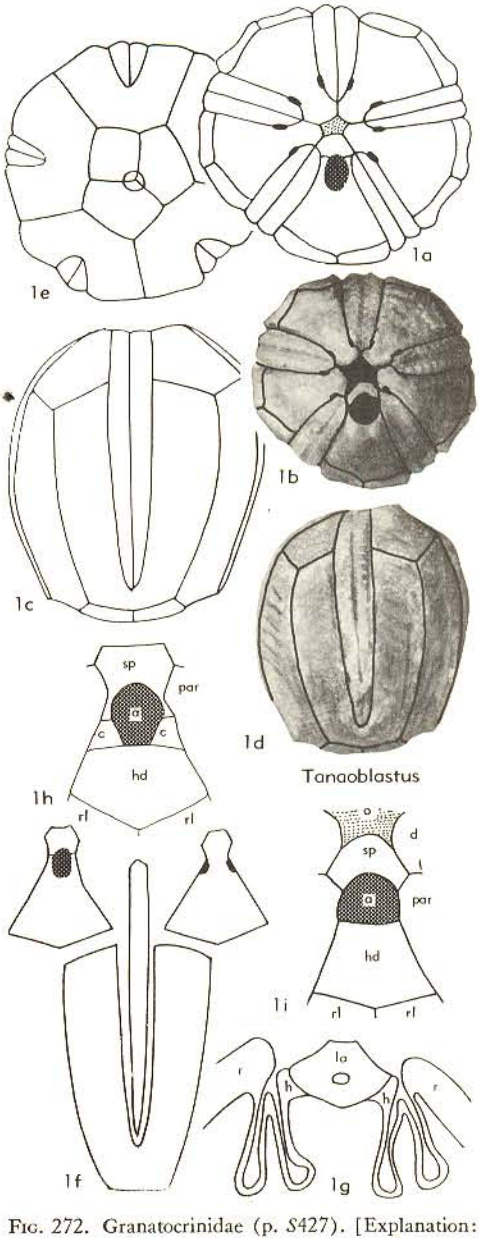


FIG. 272. Granatocrinidae (p. *S*427). [Explanation: *a,* anal opening; *c,* cryptodeltoid plate; *d,* deltoid plate; *h,* hydrospire plate; *hd,* hypodeltoid; *la,* lancet plate; *o,* oral opening; *par,* posterior ambulacrum (right); *r,* radial plate; *rl,* radial limb; *sp,* superdeltoid plate.]

oral views, plate layout, ×1.3; 274,*1e,f,* cross secs. of ambulacrum, ×3.6 (12, 36, 40, 132).

Auloblastus BEAVER, 1961 (14), p. 1113 [**A. clinei*; OD]. Subspherical form with spiracles near sum-

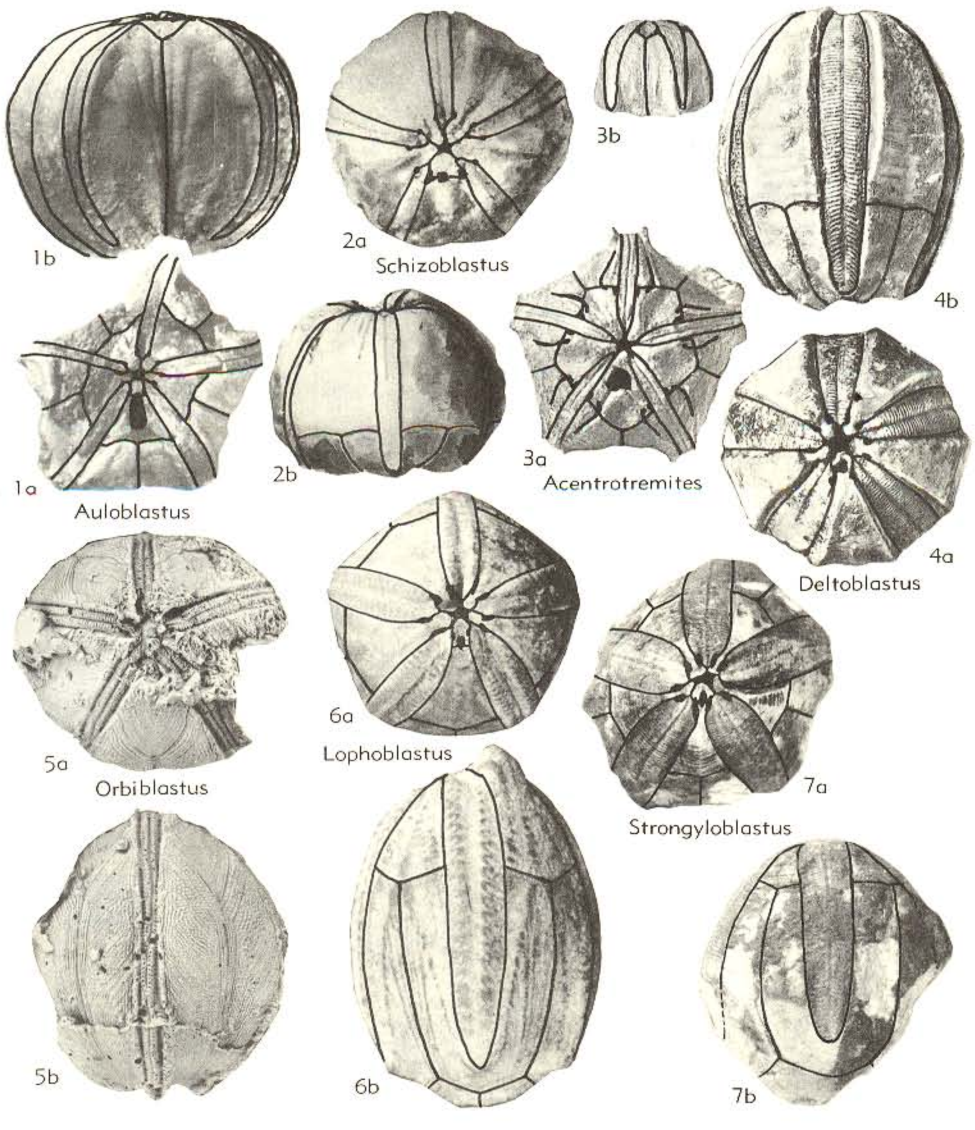


FIG. 273. Schizoblastidae (p. *S*427-*S*432).

mit; anal opening probably separate; basalia small, in concavity; radials long, overlapping deltoids; hydrospire plate absent; single pore between adjacent side plates along ambulacral margins; 4 hydrospire folds on each side of ambulacra; anal opening bordered adorally by superdeltoid, aborally by hypodeltoid, and internally on either side by cryptodeltoids; side plates cover lancets except near adoral tip; lateral canals present. *M.Miss.*, N.Am. (Mo.).——FIG. 273,*1*; 274,*3*. **A. clinei*, USA (Mo.); 273,*1a,b*, oral, interambulacral views, ×1.3; 274,*3a-d*, oral, interambulacral, aboral views, plate layout, ×1.3; 274,*3e*, cross sec. of ambulacrum, ×10 (14).

Deltoblastus FAY, 1961 (49), p. 36 [**Schizoblastus delta elongatus* WANNER, 1924 (173), p. 61; OD]. Theca ellipsoidal; anal opening between epideltoid and hypodeltoid; lancet exposed, forming petaloid ambulacra; sinus margins raised; radials overlapping deltoids; base concave; single pore between side plates along radial and deltoid margins; 2 hydrospire folds on each side of ambulacra. *Perm.*, E. Indies(Timor)-?Eu.(?Sicily). —— FIG. 275,*1*. *D. permicus* (WANNER), Timor; 275,*1a-d*, oral, *D*-ray, aboral views, plate layout, ×3.2; 275, *1e,* cross sec. of ambulacrum, ×7.7 (49).——Fig. 273,*4. D. timorensis* (Bather), Perm., Timor; *4a,b,* oral, *B*-ray views, ×1.3 (11).

Lophoblastus Rowley, 1901, p. 344 [*emend.* Macurda, 1962, p. 1370] [**Codonites inopinatus* Rowley & Hare, 1891, p. 100; OD]. Theca ellipsoidal, with anal opening between epideltoid and hooded hypodeltoid; 3 hydrospire folds on each side of ambulacra; lancet exposed 0.3 of its width; with single pore between adjacent side plates along deltoid and radial margins; deltoids overlapping radials. *Miss.,* N.Am.——Fig. 273,*6*; 276,*3*. **L. inopinatus* (Rowley & Hare), M.Miss.,

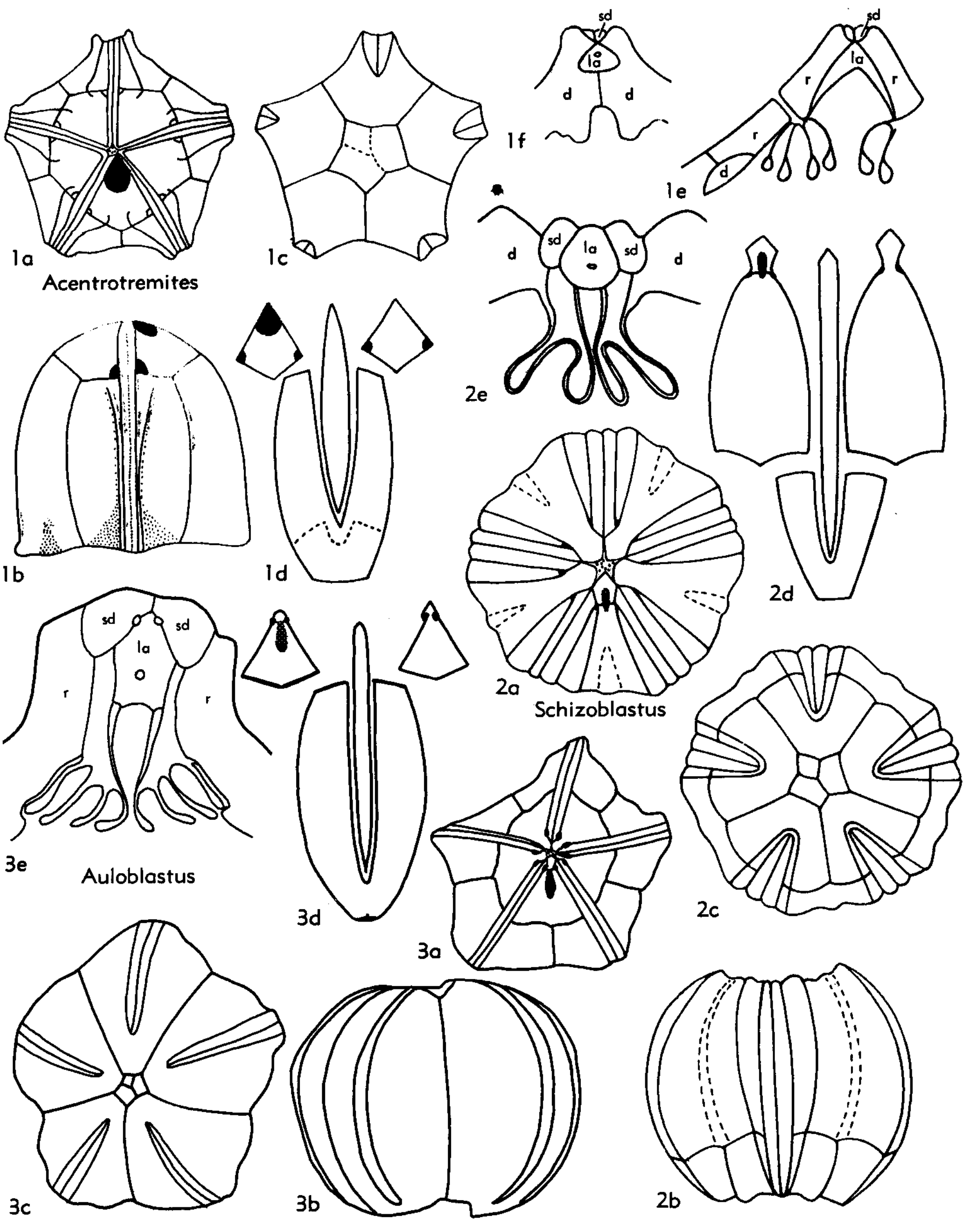


Fig. 274. Schizoblastidae (p. *S*427-*S*430). [Explanation: *d,* deltoid plate; *la,* lancet plate; *r,* radial plate; *sd,* side plate.]

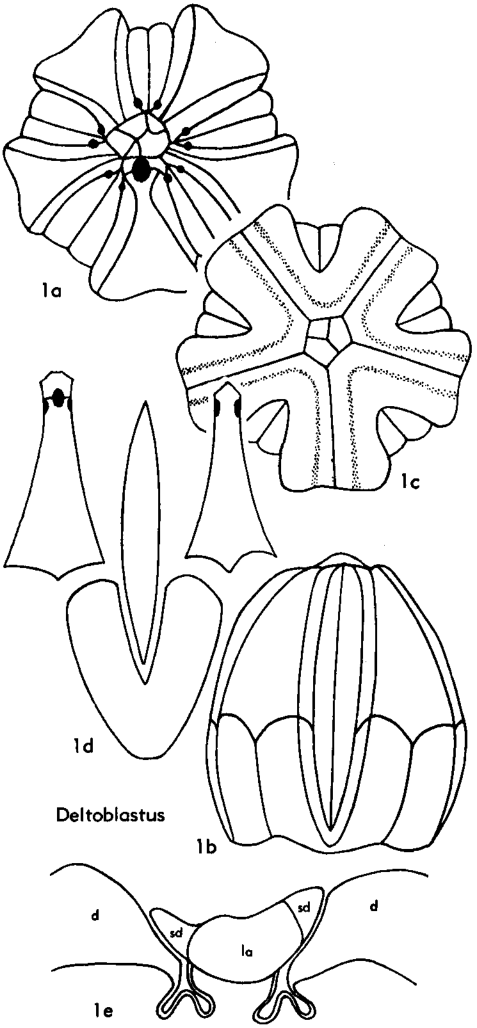


FIG. 275. Schizoblastidae (p. S430). [Explanation: *d*, deltoid plate; *la*, lancet plate; *r*, radial plate; *sd*, side plate.]

USA(Mo.); 273,*6a*, oral view, ×4.2; 273,*6b*, *D*-ray view, ×5.6; 276,*3a-d*, oral, *D*-ray, aboral views, plate layout, ×5.3; 276,*3e*, cross sec. of ambulacrum, ×13.1; 276,*3f*, anal view, ×10 (60).

Orbiblastus MACURDA, 1965 (106), p. 302 [**Orbiblastus hoskynae* MACURDA, 1965 (106), p. 303; OD]. Theca globular, with anal opening between epideltoid and hypodeltoid; 3 hydrospire folds on each side of ambulacra; lancet exposed along main food groove; one pore between each side plate along deltoid and radial margins; radials overlapping deltoids; basalia in basal concavity. *Miss.*, N.Am.(Ark.).——FIG. 273,*5*; 276,*2*. **O. hoskynae*, M.Miss., Ark.; 273,*5a,b*, oral, *D*-ray views, ×1.3; 276,*2a-d*, oral, *D*-ray, aboral views, plate layout, ×1.3 (106).

Strongyloblastus FAY, 1962 (68), p. 132 [**Strongyloblastus petalus* FAY, 1962, p. 132; OD]. Theca suboval, with spiracles near oral opening; anal opening between small epideltoid and moderately long hypodeltoid; deltoids visible in side view, overlapped by radials; lancet widely exposed, with single pore between side plates along radial and deltoid margins; 5 hydrospire folds on each side of ambulacra; ambulacra broadly petaloid and moderately long; periphery at radial lips below mid-height; basalia conical, large; theca subrounded pentagonal in top view. *M.Dev.*, USA (N.Y.).——FIG. 273,*7*; 276,*1*. **S. petalus* FAY; 273,*7a,b*, oral, *E*-ray views, ×1.3; 276,*1a-d*, oral, *E*-ray, aboral views, plate layout, ×1.3; 276,*1e*, cross sec. of *D* ambulacrum, aboral view, ×10 (68).

Family NUCLEOCRINIDAE Bather, 1899

[Nucleocrinidae BATHER, 1899, p. 920] [=Nucleoblastidae ETHERIDGE & CARPENTER, 1886, p. 209 (invalid, based on nonexistent nominal genus); Olivanidae HAMBACH, 1903, p. 48 (invalid, based on nonexistent nominal genus)]

Theca with ten spiracles and anal opening separate around mouth, as in Schizoblastidae, but with two elongate, exposed cryptodeltoids. *Dev.*

Nucleocrinus CONRAD, 1842, p. 280 [**N. elegans*; OD]. Theca ellipsoidal; with 5 large oral plates and 3 exposed anal plates, consisting of 2 cryptodeltoids and hypodeltoid; superdeltoid hidden; anal oral abutting against cryptodeltoids; deltoids long, overlapping radials; 2 hydrospire folds on each side of ambulacra, with short hydrospire canal; lancet covered by side plates, with inner side plate present; one large pore between side plates along deltoid and radial margins. *Dev.*, N.Am.(N.Y.-Iowa-Mich.-Ont.).——FIG. 277,*1a-d*; 278,*1*. **N. elegans*, M.Dev., USA(N.Y.); 277, *1a-d*, oral, *D*-ray, aboral views, plate layout, ×2.6 (34, 60, 83); 278,*1a,b*, oral, *D*-ray views, ×5 (43).——FIG. 277,*1e-h*. *N. meloniformis* (BARRIS), M.Dev., USA(Mich.); *1e*, cross sec. of ambulacrum, ×8.8 (Fay, n); *1f-h*, anal views, ×10 (60).

Elaeacrinus ROEMER, 1851, p. 379 [**E. verneuili*; OD] [=*Olivanites* TROOST, 1849, p. 419 *(nom. nud.)*; *Olivanites* LYON, 1857, p. 487 (type, *Olivanites verneuili* TROOST, 1849); *Eleacrinus* ETHERIDGE & CARPENTER, 1883, p. 228 *(nom. van.)*]. Theca elongate, ellipsoidal; with approximately 18 to 21 oral plates (one of which, however, may be superdeltoid); with 2 prominent, well-exposed cryptodeltoids and hypodeltoid; 1 or 2 anal orals between adoral tips of cryptodeltoids (if 1 it is superdeltoid, and if 2, the aboral one is superdeltoid); deltoids long, overlapping radials; 2 hydrospire folds on each side of ambulacra, with medium-long hydrospire canal; lancet covered by side plates, with inner side plate present; single large pore between side plates along deltoid and radial margins. *Dev.*, N.Am.(Ohio-Ind.-Ky.-Mo.).——FIG. 279,*1a-f*; 280,*1*. **E. verneuili* (TROOST), M.Dev., USA(Ind.); 279,*1a-d*, oral,

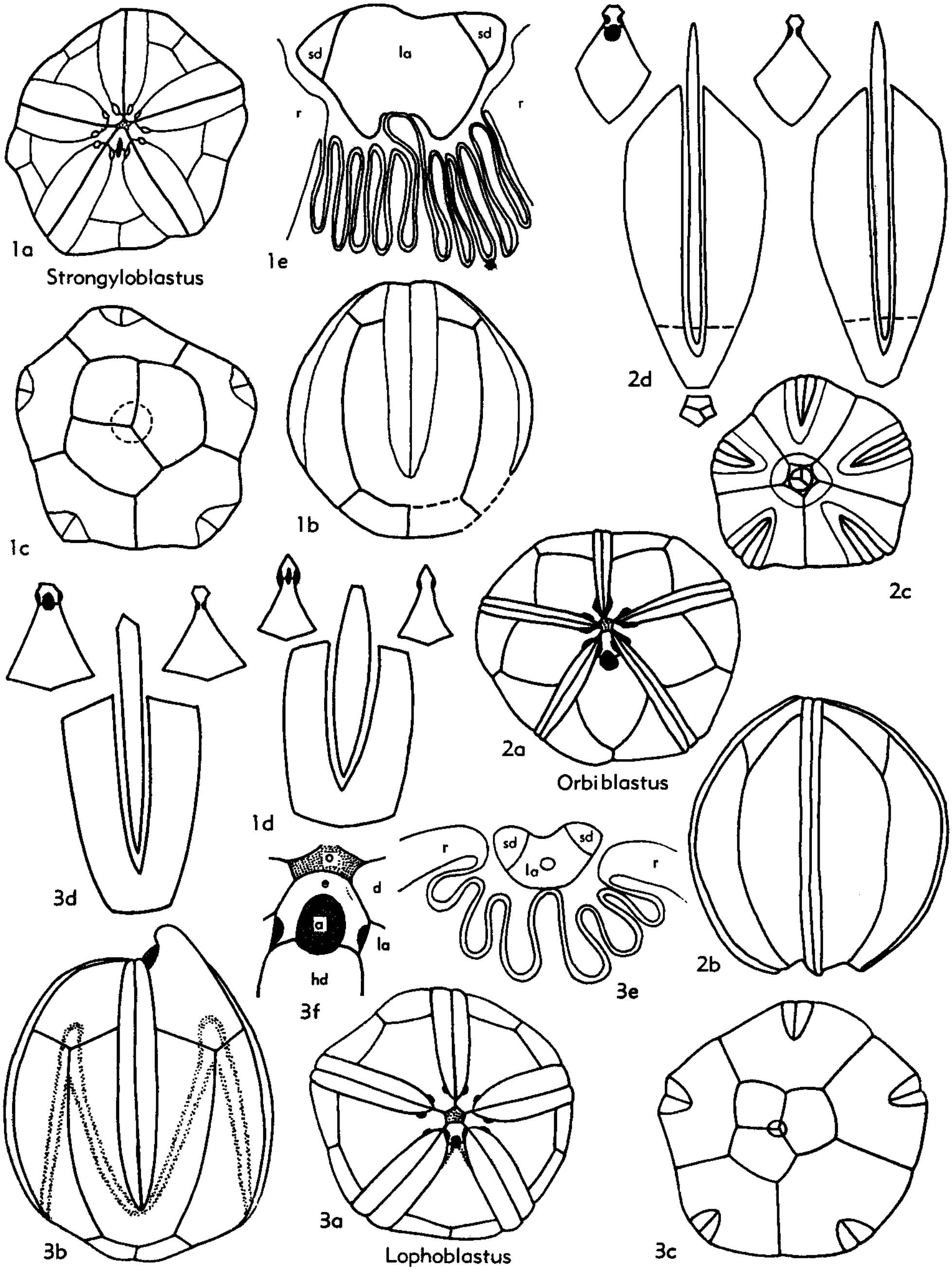


FIG. 276. Schizoblastidae (p. S431-S432). [Explanation: *a*, anal opening; *d*, deltoid plate; *e*, epideltoid plate; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening; *r*, radial plate; *sd*, side plate.]

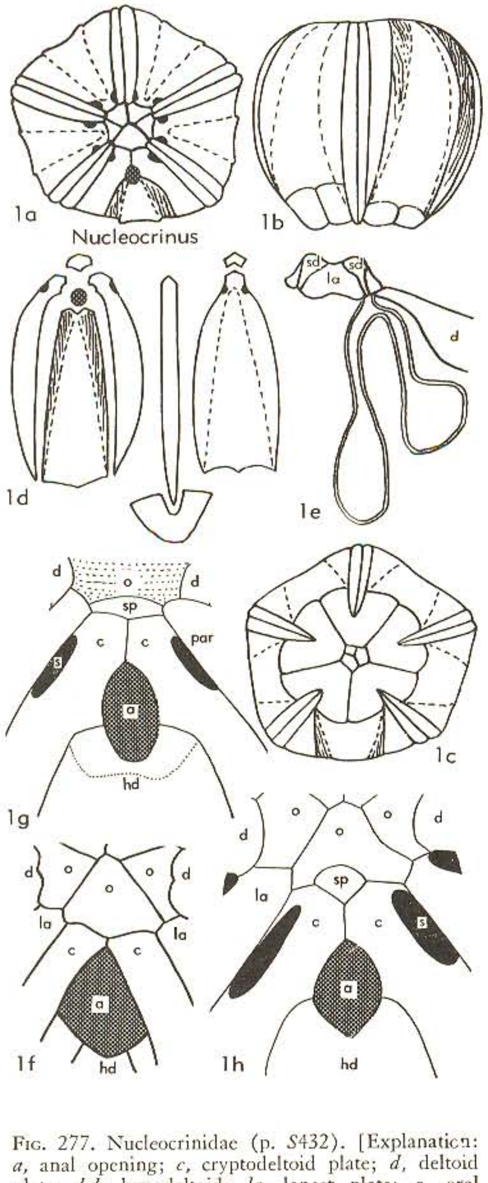


FIG. 277. Nucleocrinidae (p. *S*432). [Explanation: *a*, anal opening; *c*, cryptodeltoid plate; *d*, deltoid plate; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening or oral plate; *par*, posterior ambulacrum (right); *s*, spiracle; *sd*, side plate; *sp*, superdeltoid plate.]

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]

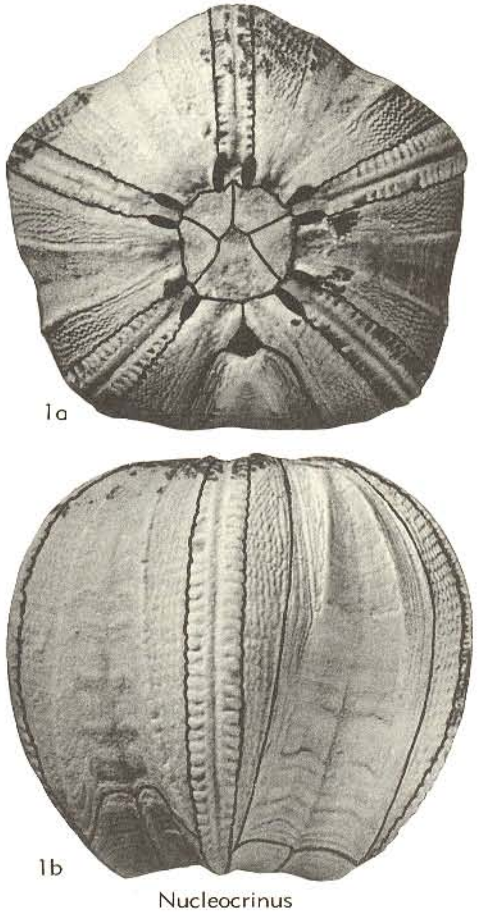


FIG. 278. Nucleocrinidae (p. *S*432).

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).

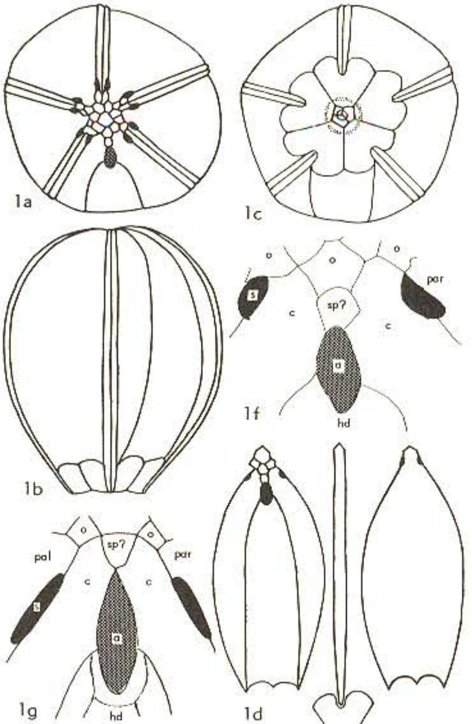


Fig. 279. Nucleocrinidae (p. *S*432-*S*434). [Explanation: *a*, anal opening; *c*, cryptodeltoid plate; *d*, deltoid plate; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening or oral plate; *pal*, posterior ambulacrum (left); *par*, posterior ambulacrum (right); *s*, spiracle; *sd*, side plate; *sp*, superdeltoid plate.]

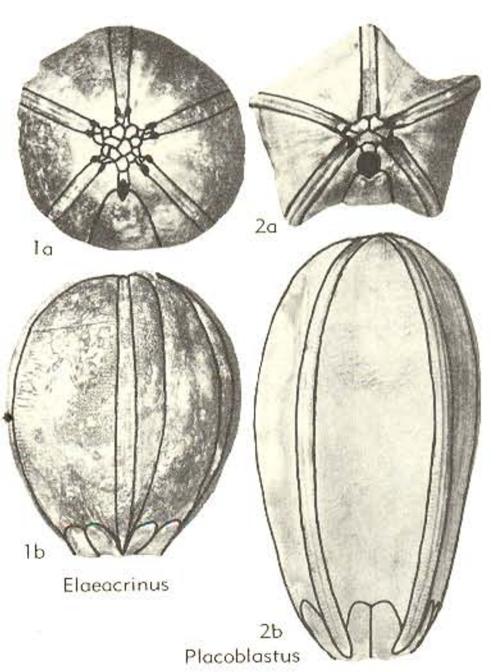


Fig. 280. Nucleocrinidae (p. *S*432-*S*434).

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

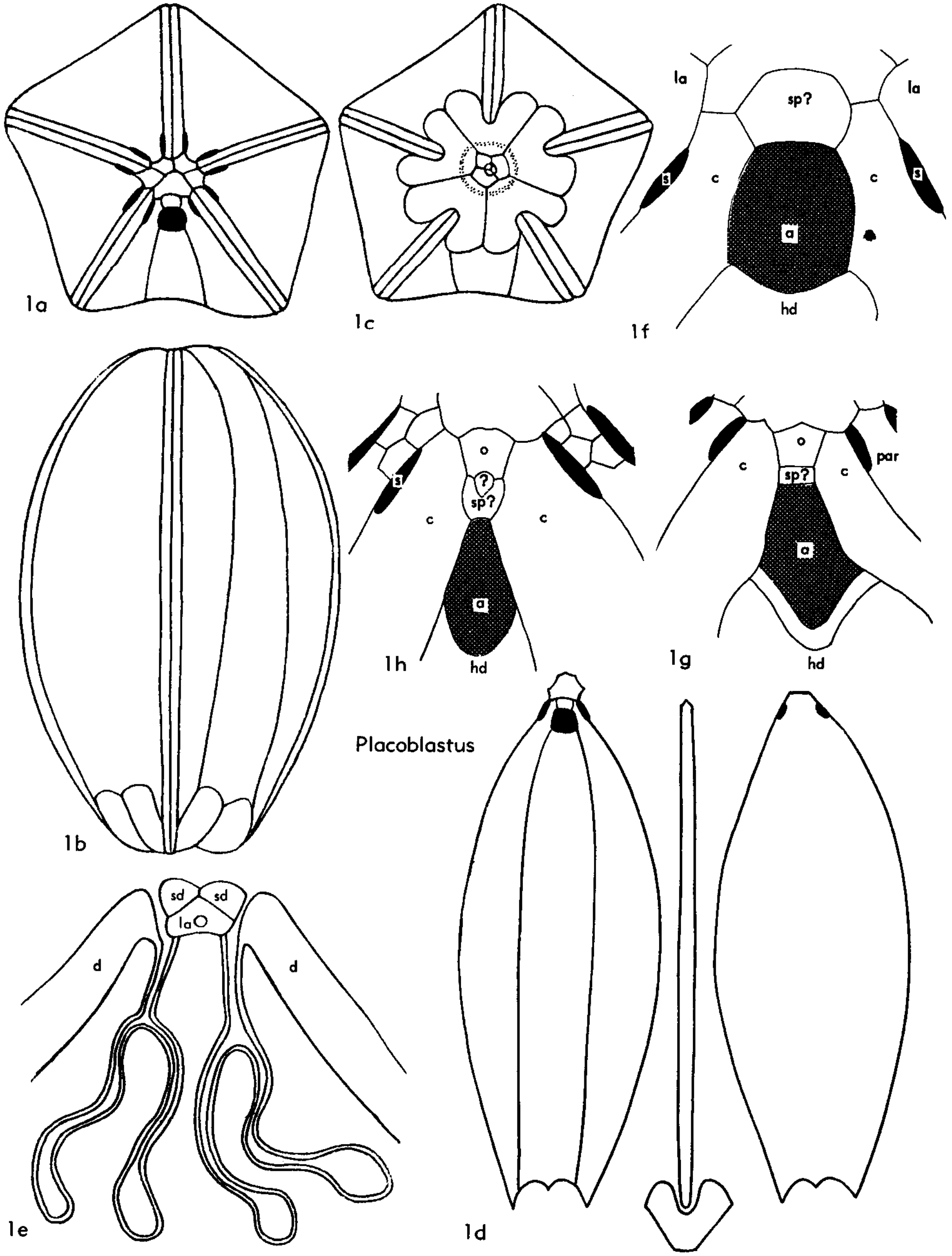


Fig. 281. Nucleocrinidae (p. S434). [Explanation: *a*, anal opening; *c*, cryptodeltoid plate; *d*, deltoid plate; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening or oral plate; par, posterior ambulacrum (right); *s*, spiracle; *sd*, side plate; *sp*, superdeltoid plate.]

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*

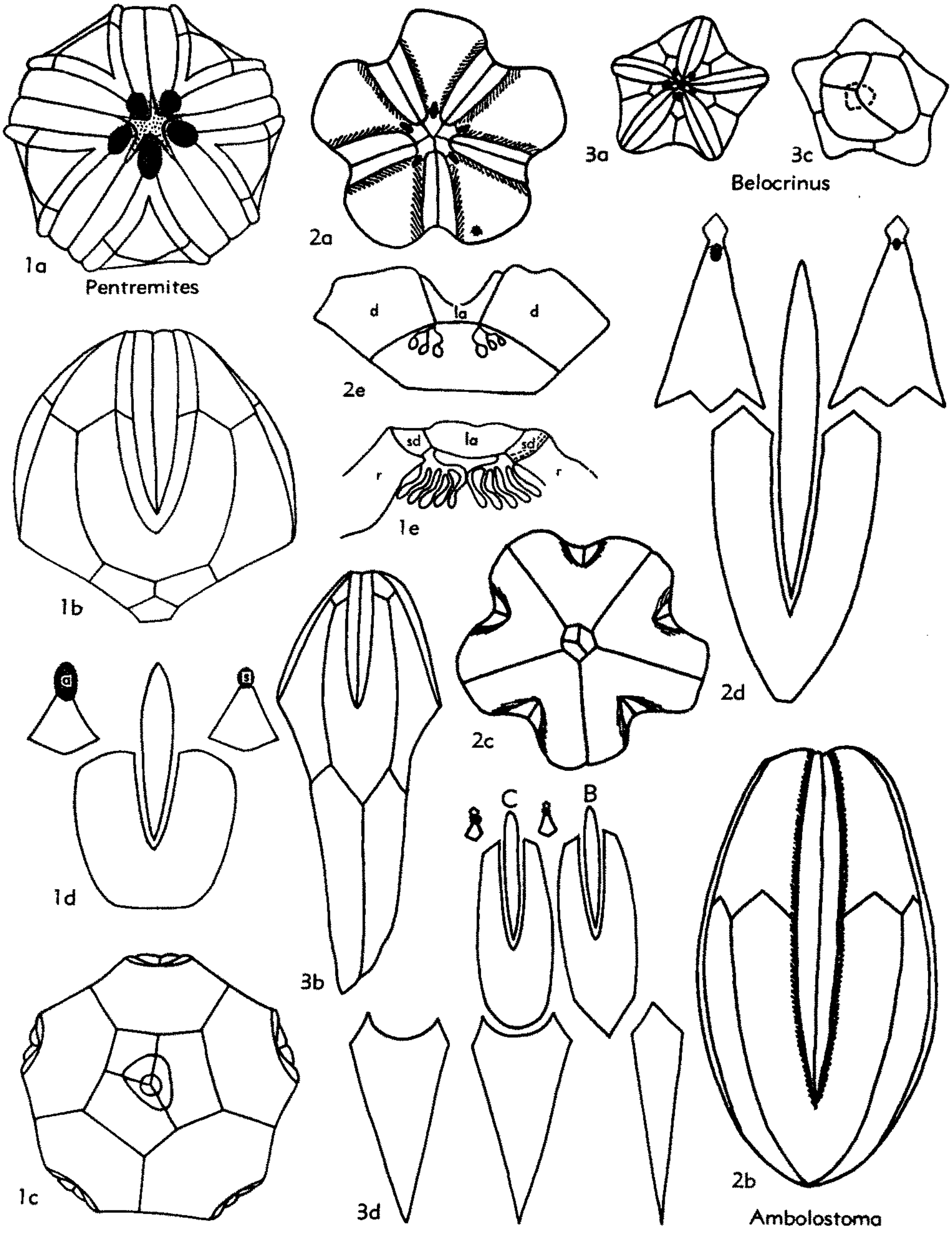


FIG. 282. Pentremitidae (p. S435-S436). [Explanation: *a,* anispiracle; *d,* deltoid plate; *la,* lancet plate; *r,* radial plate; *s,* spiracle; *sd,* side plate.]

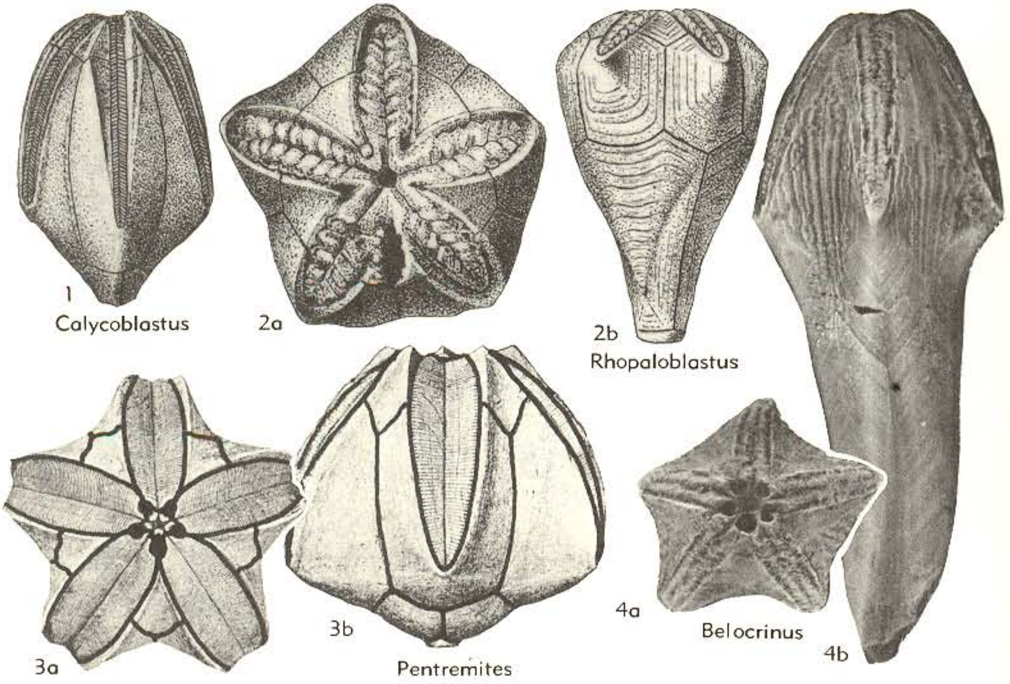


FIG. 283. Pentremitidae (p. S435-S437, S443).

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.

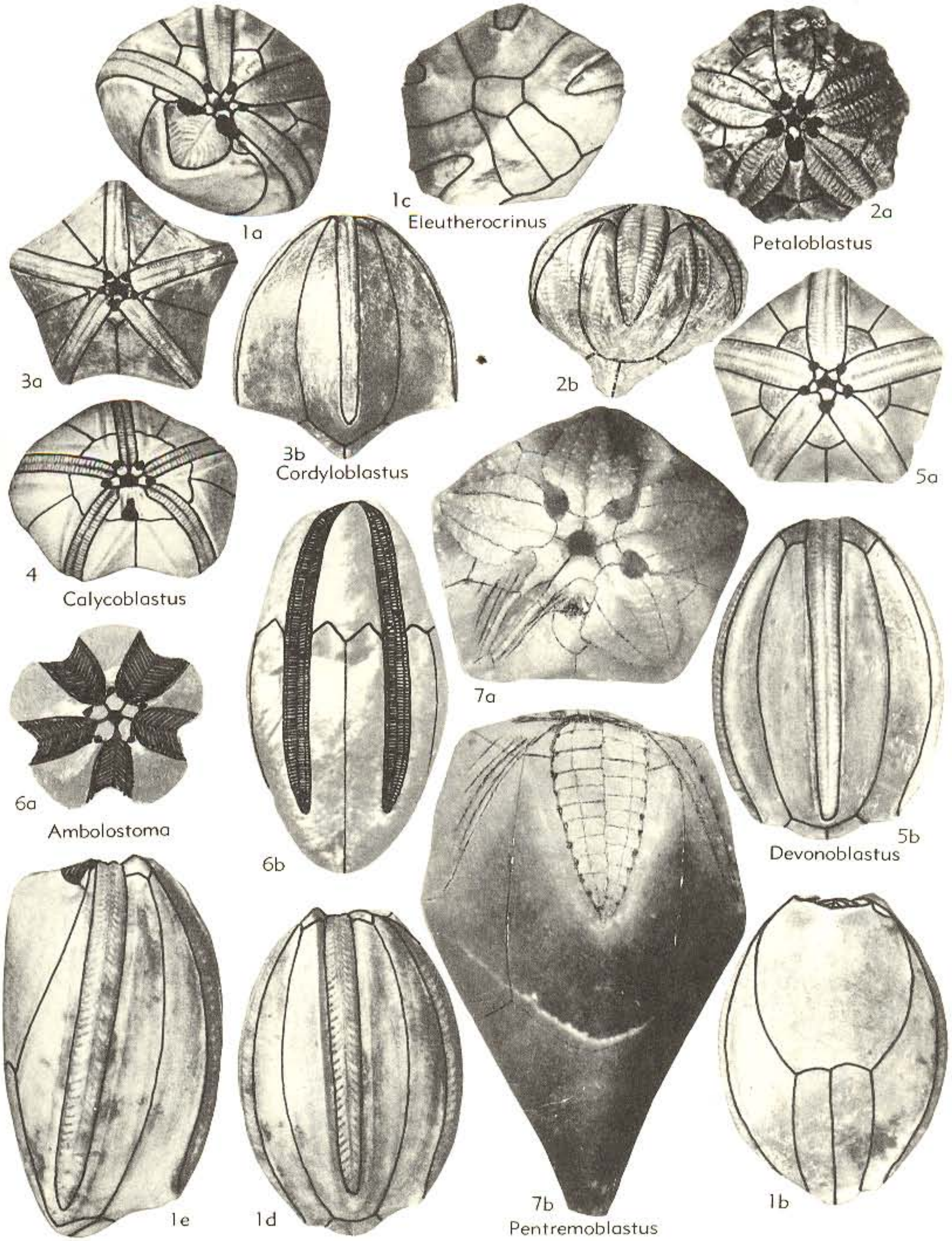


FIG. 284. Pentremitidae (p. *S*435-*S*438, *S*440-*S*443).

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).

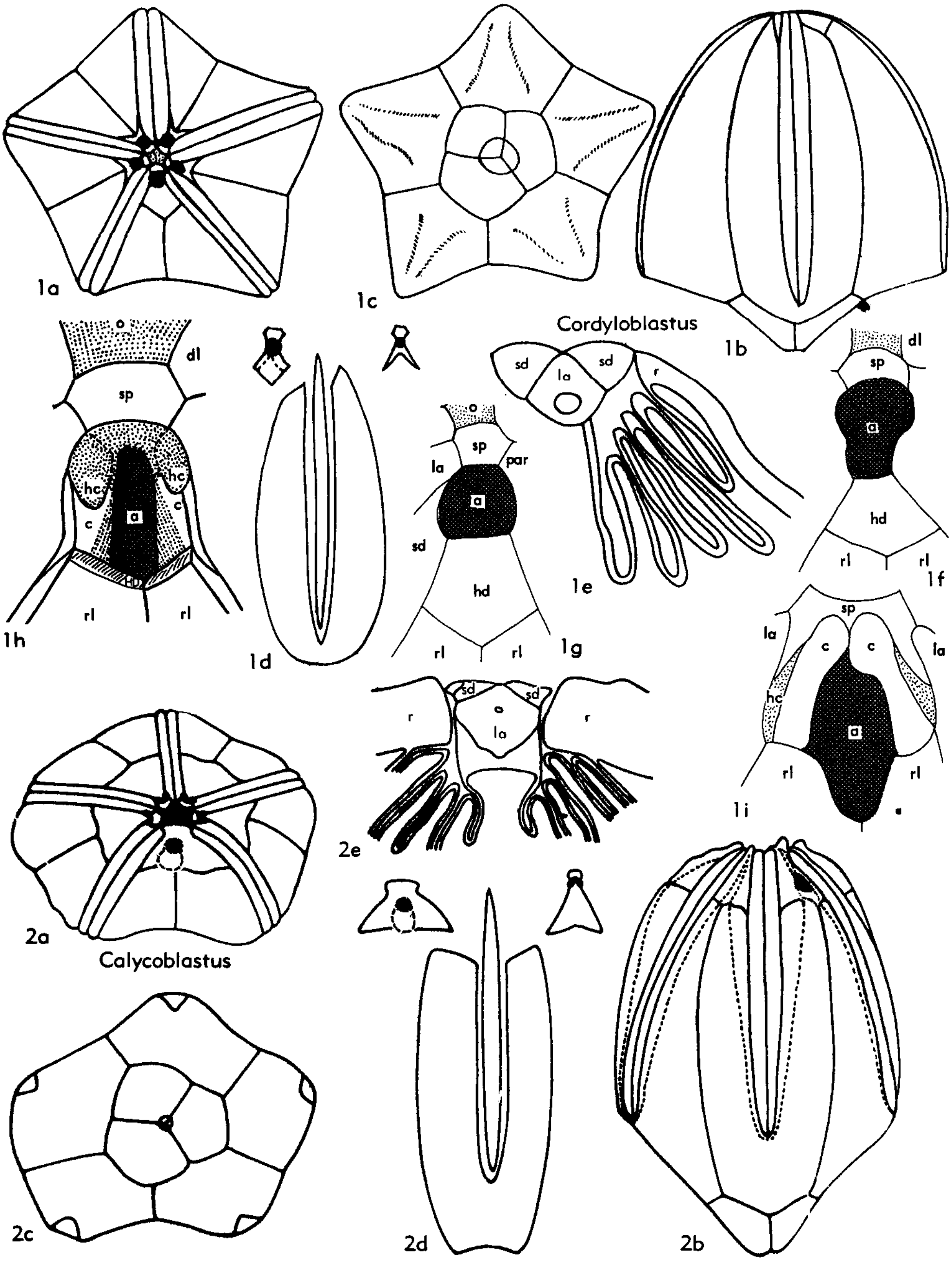


Fig. 285. Pentremitidae (p. *S*436-*S*438). [Explanation: *a*, anal opening; *c*, cryptodeltoid plate; *dl*, deltoid lip; *hc*, hydrospire canal; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening or oral plate; *par*, posterior ambulacrum (right); *r*, radial plate; *rl*, radial limb; *sd*, side 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

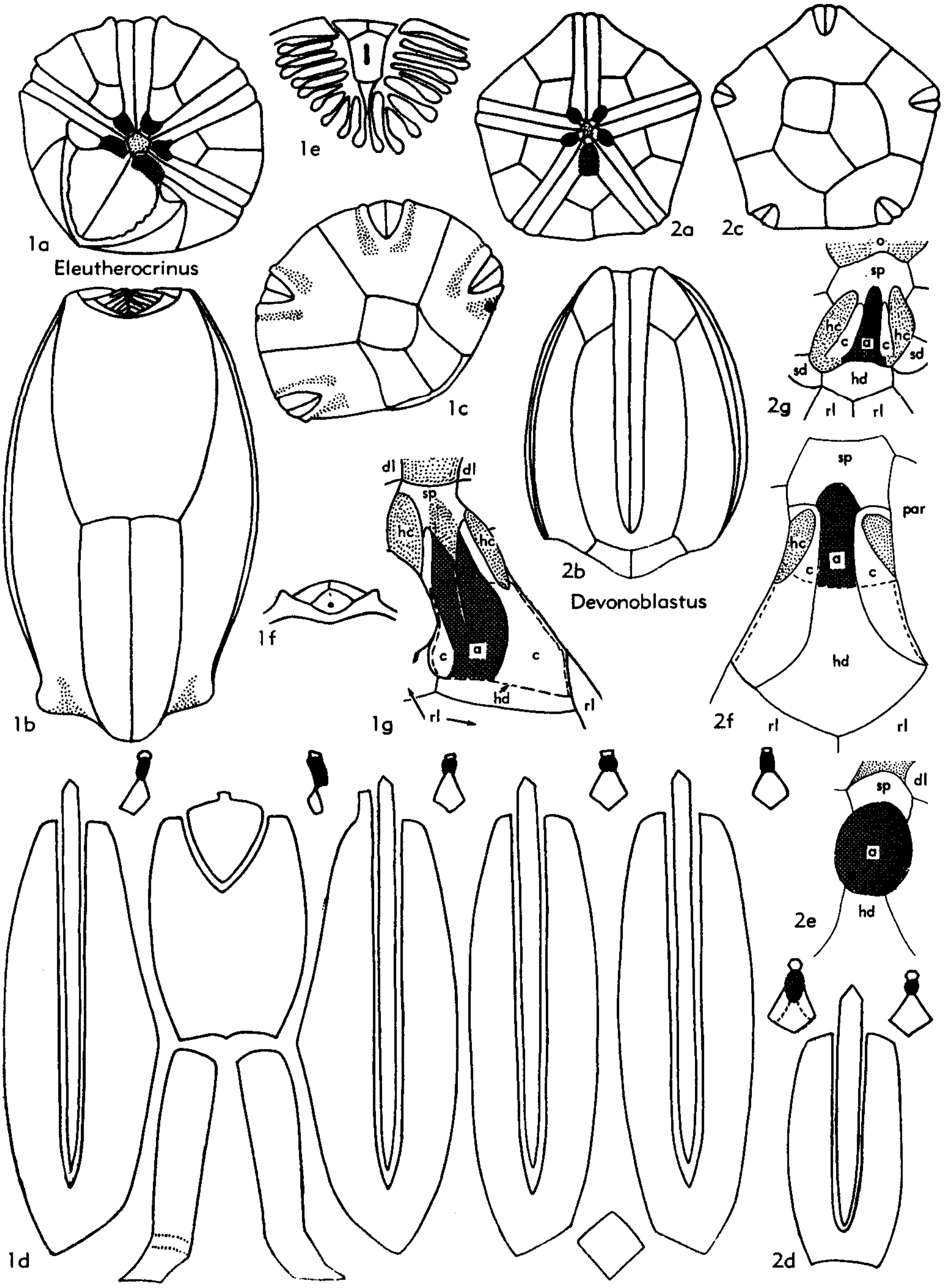


Fig. 286. Pentremitidae (p. S438). [Explanation: *a*, anal opening; *c*, cryptodeltoid plate; *dl*, deltoid lip; *hc*, hydrospire canal; *hd*, hypodeltoid; *o*, oral opening or oral plate; *par*, posterior ambulacrum (right); *rl*, radial lip; *sd*, side plate; *sp*, superdeltoid plate.]

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

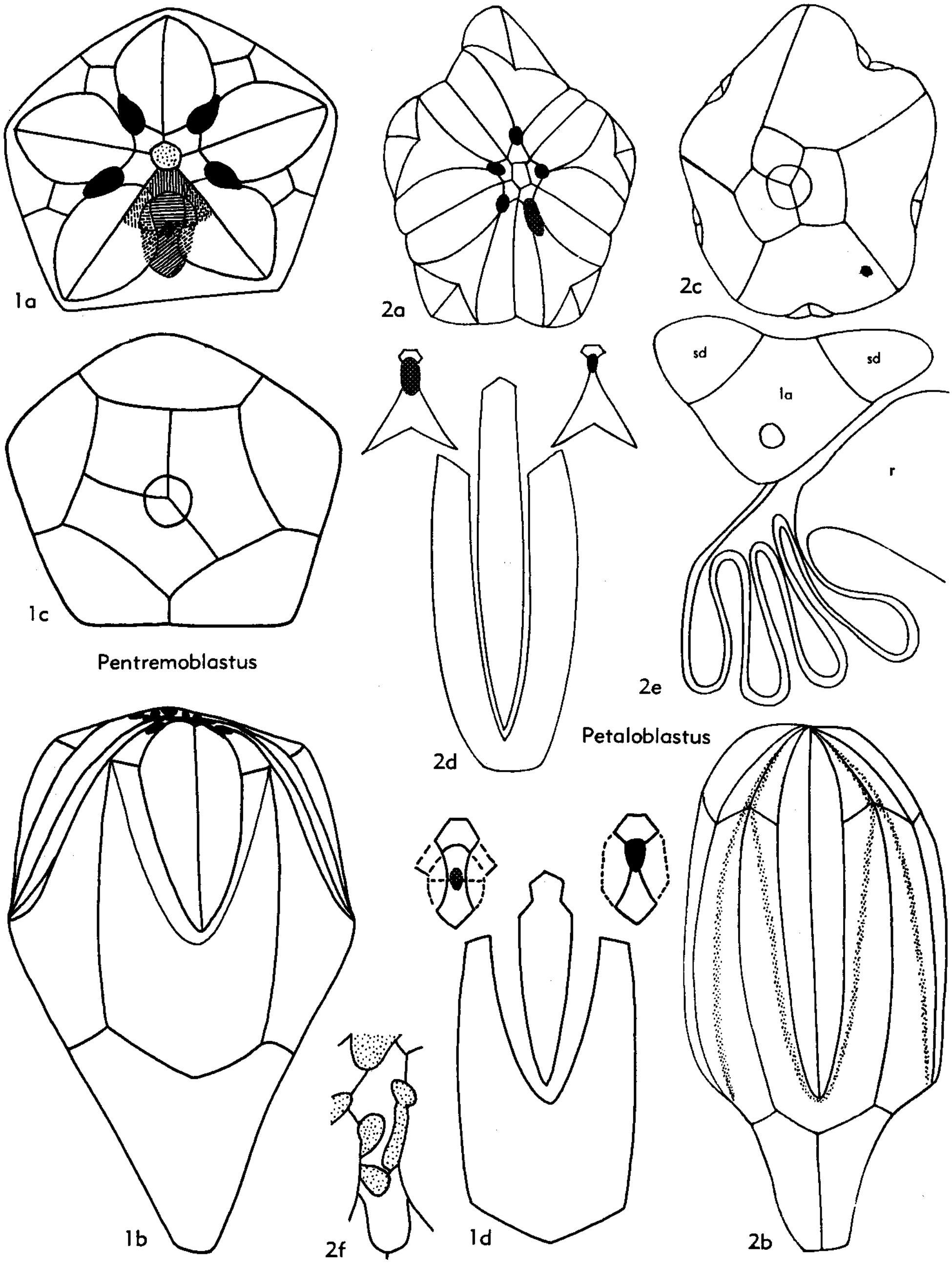


Fig. 287. Pentremitidae (p. S438, S440-S443). [Explanation: *la*, lancet plate; *r*, radial plate; *sd*, side plate.]

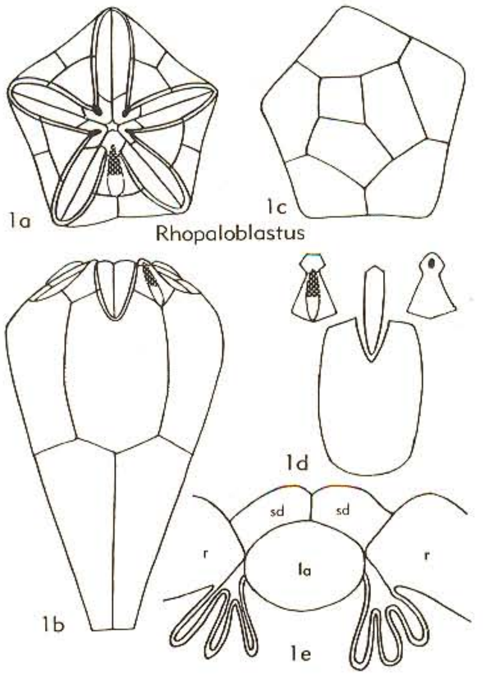


FIG. 288. Pentremitidae (p. *S*443). [Explanation: *la*, lancet plate; *r*, radial plate; *sd*, side plate.]

(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* interray 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-

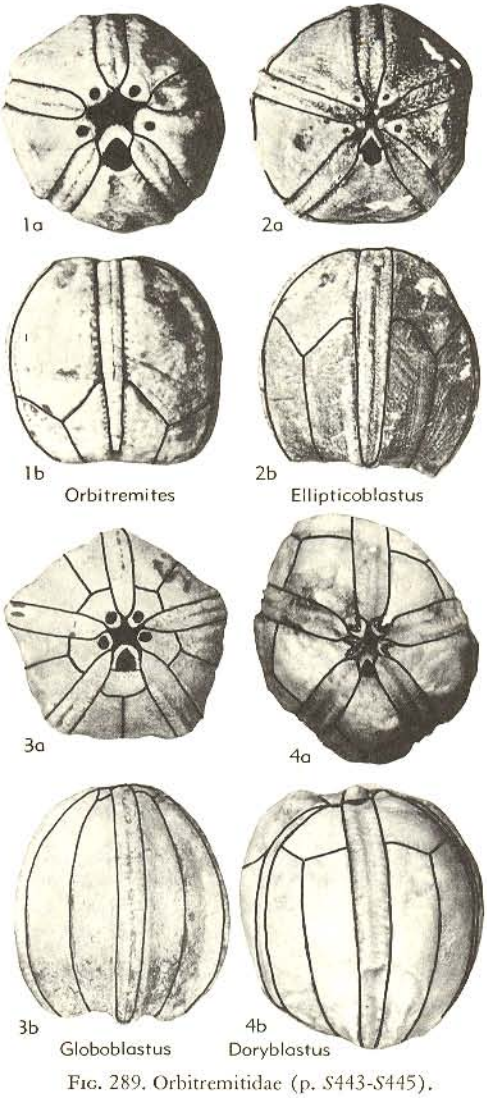


FIG. 289. Orbitremitidae (p. *S*443-*S*445).

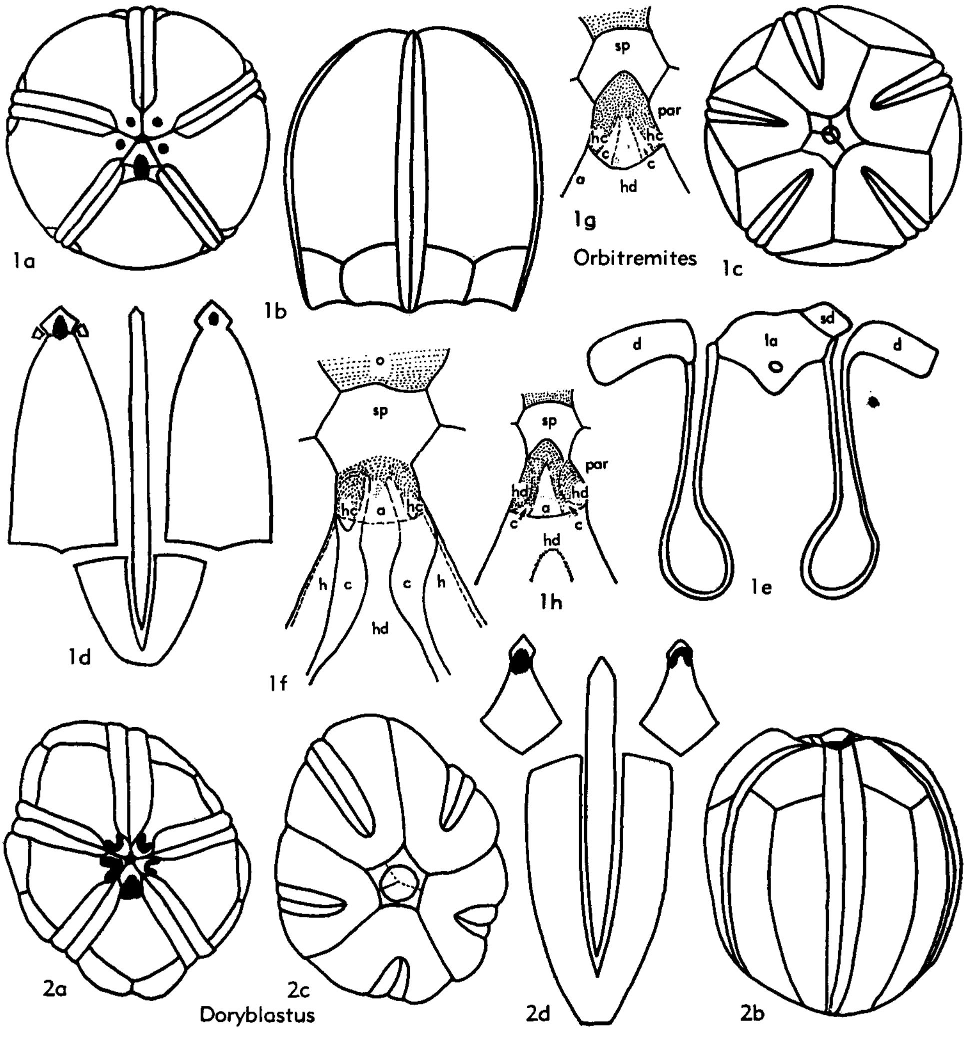


FIG. 290. Orbitremitidae (p. S443-S444). [Explanation: _a_, anispiracle; _c_, cryptodeltoid plate; _d_, deltoid plate; _h_, hydrospire plate; _hc_, hydrospire canal; _hd_, hypodeltoid; _la_, lancet plate; _o_, oral opening; _par_, posterior ambulacrum (right); _sd_, side plate; _sp_, superdeltoid plate.]

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

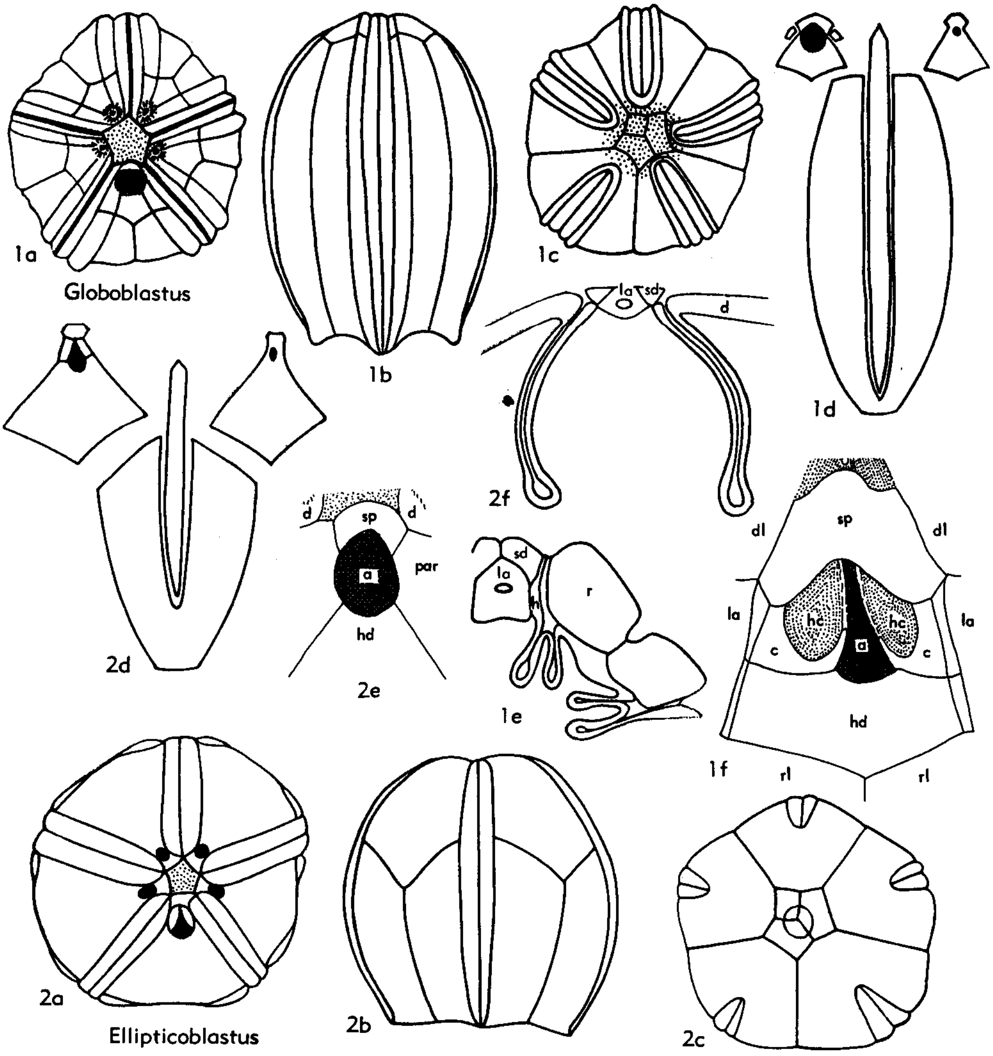


FIG. 291. Orbitremitidae (p. S444-S445). [Explanation: *a*, anispiracle; *c*, cryptodeltoid plate; *d*, deltoid plate; *dl*, deltoid lip; *h*, hydrospire plate; *hc*, hydrospire canal; *hd*, hypodeltoid; *la*, lancet plate; *o*, oral opening or oral plate; *par*, posterior ambulacrum (right); *r*, radial 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 podmosķovnogo ķarbona:* 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, *Morsḳie lilii i blastoidei ḳamennougolnyḳh i permsḳiḳh 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). I. 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

By Georges Ubaghs

[Université de Liège]

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

---

[1] Italicized numbers refer to corresponding numbers in the list of references.

Camerata). Later, in 1918 *(25)*, he introduced for these and a few other genera a new subclass named Eocrinoidea, which he assigned to the class Crinoidea, despite its inclusion with presumed earliest crinoids forms regarded by him as ancestors of the rhombiferan cystoids and diverse others having aberrant features and ephemeral occurrence. RAYMOND C. MOORE has translated this chapter and for this aid the author expresses sincere thanks.

The echinoderm group known as eocrinoids has been treated quite differently by authors in publications issued subsequent to 1918. Although GEKKER (1938, 1940) and more recently NICHOLS (1962) adopted JAEKEL's placement of these forms as a subclass of Crinoidea, such arrangement was rejected by BASSLER (1938) and BASSLER & MOODEY (1943), who distributed the so-called eocrinoid genera among families of cystoids and did not even cite Eocrinoidea in synonymy. CUÉNOT (1953) accepted the group provisionally as an artificial assemblage, mentioned in a chapter on cystoids in the part devoted to rhombiferans, but omitted recognition of it in classification. ZITTEL (1924) ranked the Eocrinoidea simply as an appendage of the Hydrophoridea (=Cystoidea). Finally, REGNÉLL (1945) distinguished the group as an independent class and in this arrangement has been followed by TERMIER & TERMIER (1948, 1954), BASSLER (1950), HARKER & HUTCHINSON (1951), UBAGHS (1953, 1960, 1963), MOORE (1954), GEKKER (1964), and ROBISON (1965).

The essential basis for REGNÉLL's differentiation of the eocrinoids as an acceptable taxonomic group and his advancement of it in rank was judgment that forms composing the assemblage possess a combination of such cystoid features as the presence of brachioles and typical crinoid characters, such as the absence of thecal pores. As matter of fact, UBAGHS (1953, 1963) and ROBISON (1965) subsequently have demonstrated that some eocrinoids do possess thecal pores, but of a sort unlike those of cystoids.

The Eocrinoidea contain the most ancient known representatives of the Crinozoa and together with the Helicoplacoidea and Edrioasteroidea are the oldest of all known echinoderms, for remains attributable to these groups have been found in the lower half of the Lower Cambrian (DURHAM, *13*). Eocrinoids survived into Silurian time when they vanished without having given rise to known descendants. They are relatively uncommon fossils except in a few favored localities. Many are very inadequately known. Their diversity makes it especially difficult to formulate a satisfactory general definition of them. They comprise a heterogeneous assemblage provisionally treated as a class which better acquaintance perhaps will allow to be subdivided.

MORPHOLOGY

GENERAL FEATURES

The skeleton of complete eocrinoids typically consists of three parts—column or stem, theca, and brachioles (Fig. 292)—but a stem may be lacking.

The **column** is a hollow structure more or less differentiated from the theca and serves for temporary or permanent fixation of the organism to the sea bottom.

The **theca** is composed of plates which enclose the visceral mass and as in cystoids contains only orifices of the peristome and periproct, or additionally in some, one to several pores interpreted as hydropore, gonopore, or hydrogonopore openings. Essentially, the plates are solid skeletal elements composed of crystalline calcite. They are imperforate, although along sutures between the plates in numerous genera are aligned pores which probably served for the protrusion of soft organs functioning for gas exchange between the body interior and surrounding sea water.

In many genera no distinct boundary separates the oral and aboral parts of the theca, and accordingly, unlike crinoids, a tegmen and dorsal cup are not recognizable in eocrinoids. A few forms, however, exhibit a vaulted or plateau-like oral surface well differentiated from the remainder of the theca (e.g., *Akadocrinus, Ascocystites, Mimocystites, Lingulocystis*). These somewhat resemble crinoids, but analysis shows that the similarity is superficial and lacking real significance.

The **brachioles** are simple appendages of the theca which invariably lack branches. They are attached to the extremity of the theca opposite to the stem, and being outside of the theca (exothecal), they have a skeletal structure of their own, adapted for the function of transporting food particles to the mouth. Whereas the thecal cavity may be prolonged into the hollow stem, it does not extend into the brachioles.

Eocrinoids are small to medium in size, with height of the theca unknown to exceed 6 or 7 cm.

ORIENTATION AND SYMMETRY

Eocrinoids are radiate, generally pentaradiate, echinoderms. This symmetry may affect not only the ambulacra and oral surface of the theca (e.g., *Columbocystis*[1]) but extend to the dorsal part as well, although radial symmetry never is complete. Oppositely, radial symmetry may be lacking, as in genera with a compressed theca (e.g., *Batherocystis, Lingulocystis, Rhipidocystis*) in which certain rays have become atrophied or possibly never existed; one cannot choose between these alternatives owing to ignorance of the ancestors of these forms.

In a certain number of genera (e.g., *Columbocystis, Cryptocrinites, Mimocystites*) one of the interrays bears an oral element composed of two closely associated plates with a perforated wartlike swelling located on the suture between them, probably marking the position of the hydropore. Furthermore, in relation to this interray the ambulacra are grouped in a bivium (the two ambulacra bordering the interray) and a trivium (the opposite three ambulacra). This arrangement suffices to define a plane of bilateral symmetry which may be designated as the **madreporite plane.** In genera lacking an observed hydropore (e.g., *Rhopalocystis*), the presence of a double oral or occurrence of a bivium and trivium, or both, allow determination of the same orientation with reasonable confidence. In order to employ the Carpenter system of letter designations for the eocrinoid ambulacra, the ray opposite to the interray containing the hydropore is indicated as *A*, and then, viewing the oral surface of the theca,

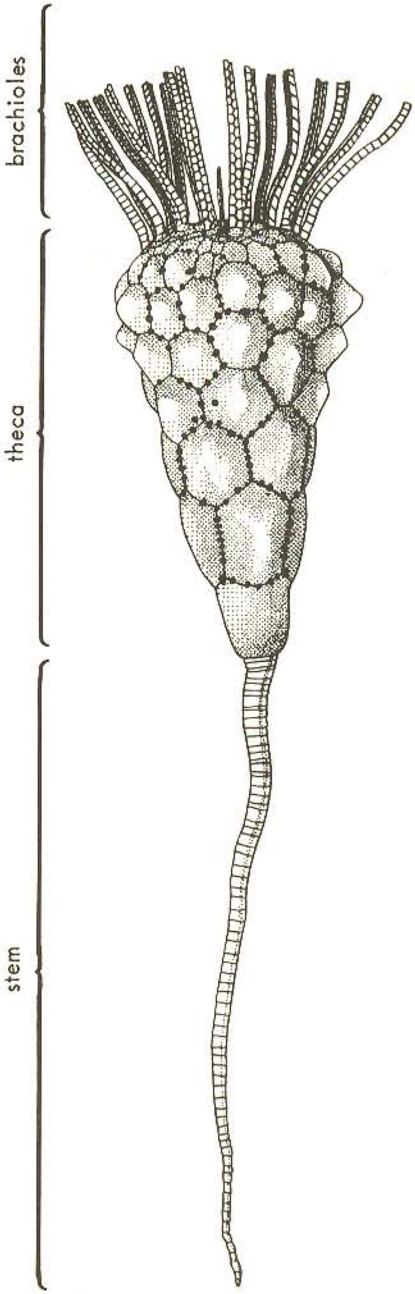


FIG. 292. Entire eocrinoid (reconstr.), showing threefold division of skeleton. *Rhopalocystis destombesi* UBAGHS (Rhopalocystidae), L.Ord., Morocco, ×1 (39).

---

[1] Placement of *Columbocystis* in the Eocrinoidea must remain doubtful until the exothecal appendages of this form have been observed.

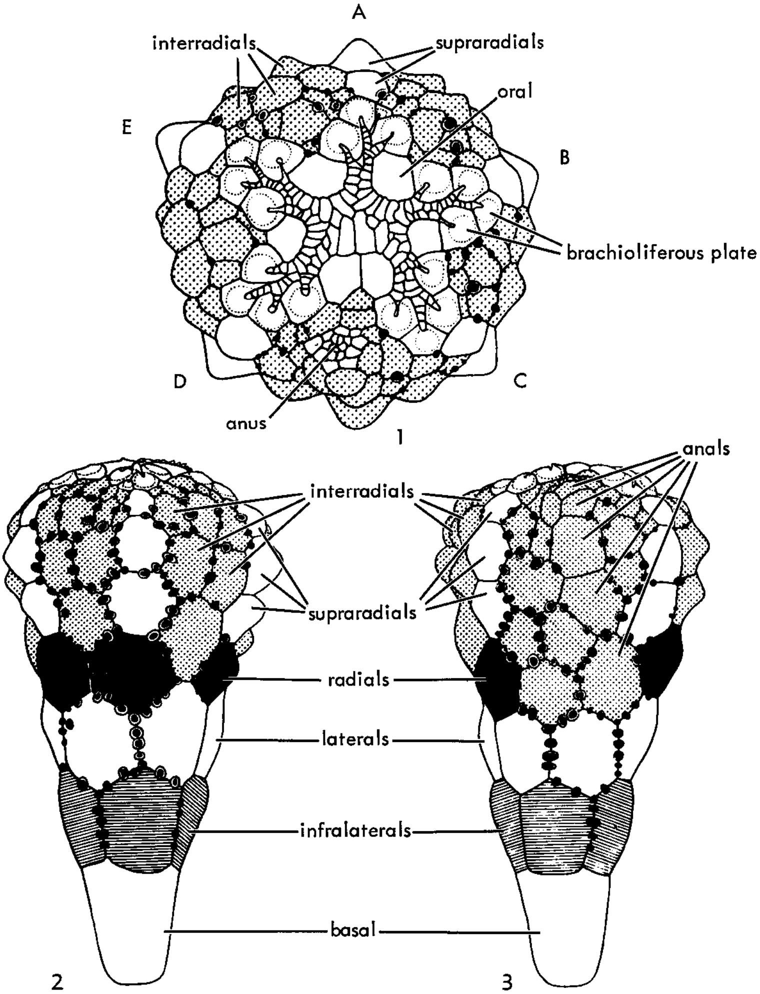


Fig. 293. Morphological features of eocrinoid theca (reconstr.). *Rhopalocystis destombesi* Ubaghs (Rhopalocystidae), L.Ord., Morocco; *1*, oral surface, brachioles lacking, ×2.75; *2,3*, side views of theca from *A*-ray and *CD*-interray sides, ×2 (all Ubaghs, n).

other rays are marked *B, C, D, E* in clockwise succession (Fig. 293,*1*). Interrays are designated by the letters for rays bounding them *(AB, BC, CD, DE, EA)* and thus the hydropore is located in interray *CD*. The anus may occur in interray *CD*, but in several genera it is displaced to a location in *BC*, so that in these forms an anal plane is distinct from the madreporite plane.

The terms **proximal** and **distal** are used as in all Crinozoa, for the skeleton as a whole toward or away from the plane separating theca and stem, and for elements of the oral surface toward or away from the center of this face.

FORM AND COMPOSITION OF THECA

The shape of the theca of eocrinoids may be irregularly spheroidal, ovoid, pyriform, conical, subcylindrical, or combinations of these. Also, it may be laterally compressed so as to offer two flat or weakly convex faces which meet along rounded borders (e.g., *Batherocystis, Cardiocystites, Lingulo-*

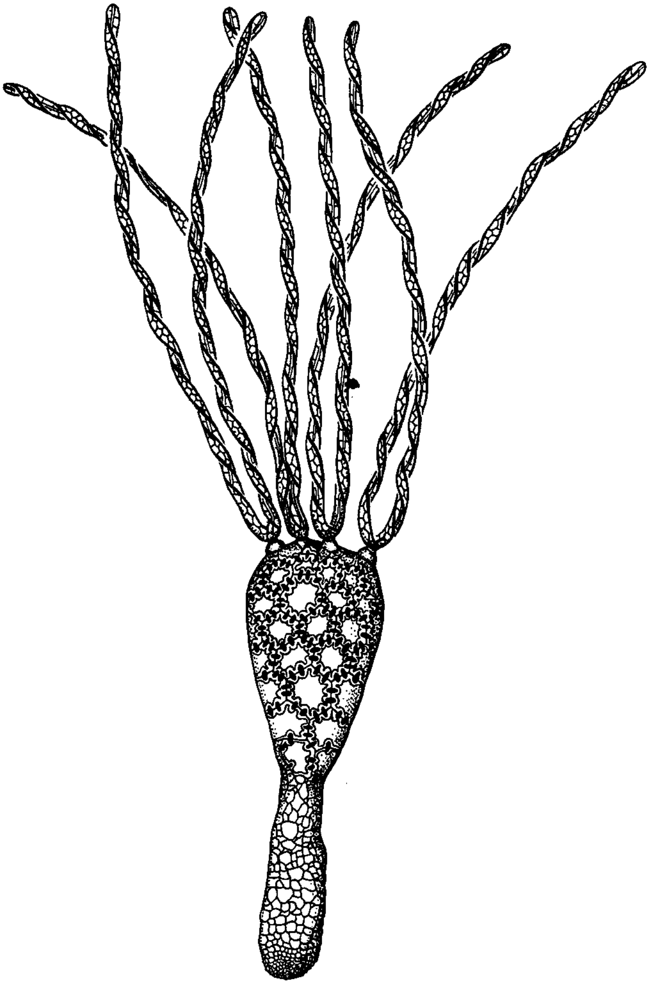


FIG. 294. Entire eocrinoid of rather primitive type (reconstr.), showing dissimilar proximal and distal parts of theca (latter with prominent sutural pores at borders of plates) and helicoidally twisted brachioles, side view. *Gogia spiralis* ROBISON (Eocrinidae), M.Cam., Can.(B.C.), ×2.3 (31).

cystis, Rhipidocystis). Walls of the theca may be flexible (e.g., *Lingulocystis*) but generally they are rigid. They are composed of polygonal plates which vary in number from relatively few (e.g., approximately 20 in *Cryptocrinites*) to extremely numerous (e.g., several hundred in *Lingulocystis*), and in different genera these numbers may be fixed or very indeterminate (e.g., *Gogia, Bockia*). In arrangement the plates may be precisely regular or extremely irregular. Thus several architectural types may be distinguished, furnishing evidence of quite different modes of growth.

Among oldest known eocrinoid genera, such as *Acanthocystites* and *Gogia* (Fig. 294), both from the Middle Cambrian, the theca is formed of ordinarily numerous polygonal plates arranged irregularly. Their number, which varies according to species and even from one individual to another, may range up to 500 in some species of *Gogia (31)*. The plates are joined by straight sutures with aligned pores, but seemingly these thin skeletal elements, strengthened in some forms by radial folds, are readily dissociated after death of the animal. This type of theca, in which neither the number

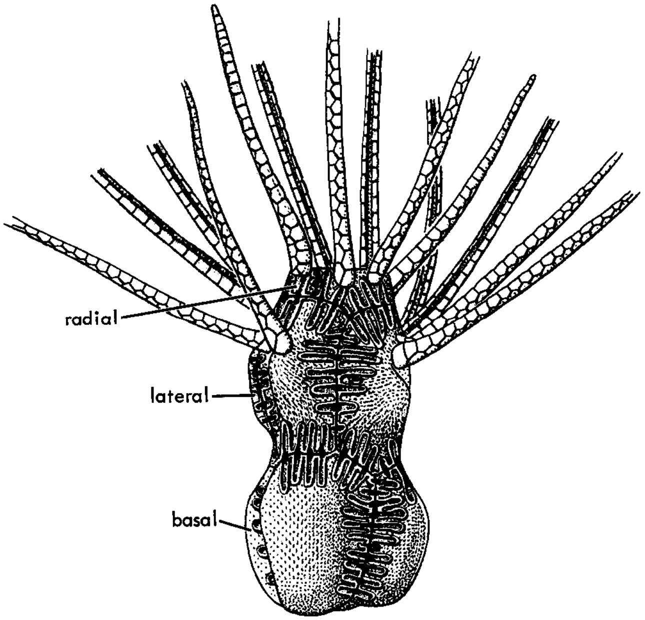


FIG. 295. Entire eocrinoid of type having three circlets of relatively large, regularly arranged thecal plates and well-developed biserial brachioles borne by lateral and radial plates, prominent epispires along sutures between plates (reconstr.). *Lichenoides priscus* BARRANDE (Lichenoididae), M.Cam., Boh., ×3 (Ubaghs, n).

nor disposition of plates is fixed, may represent the most primitive evolutionary stage of the Eocrinoidea.

Another type of thecal structure, which also makes appearance in the Middle Cambrian (e.g., *Lichenoides*), is characterized by arrangement of the plates in successive circlets, as a rule, in alternation. According to their position these plates may be designated by names borrowed from terminology applied to cystoids, that is, from aboral pole to summit 1) a circlet of **basals,** 2) a circlet of **laterals,** and 3) a circlet of **radials** (Fig. 295). In similar manner, a more complex theca may have circlets designated in upward order as 1) basals, 2) **infralaterals,** 3) laterals, 4) radials, and 5) **orals or deltoids** (Fig. 296). Theoretically, each circlet should contain five plates, but there are many exceptions to this rule, because some plates may become divided or new ones come to be inserted, and oppositely because some plates become joined together by fusion or some simply disappear. Examples of these variations can be seen in *Columbocystis, Cryptocrinites, Mimocystites,* and *Rhopalocystis,* in which one of the five oral plates is divided by a suture; in *Mimocystites,* in which the radial circlet contains a supplementary plate; in *Cryptocrinites* and several other genera, in which two of the basals are notably enlarged and modified in shape, seemingly as result of fusion of antecedent pairs of plates; and in *Batherocystis,* in which the two-part base may have originated from elimination of plates. Of course, in none of these examples is the actual mode of plate additions or reductions known.

If the number of plates from circlet to circlet varies somewhat, so that pentameral symmetry of the theca is disturbed, the number of circlets, distribution of plates in different ones, and alternation of plates in contiguous circlets, commonly are far from clearly determinable. As result, a certain amount of transition must be recognized between the thecal organization just described and the preceding one. Moreover, in the course of growth, irregularities commonly tend to be introduced and accentuated. In juvenile individuals of *Bockia,* for instance, plates of the theca comprise a more or less regular pavement, whereas in adults the insertion of new plates between old ones destroys the previous orderly plate

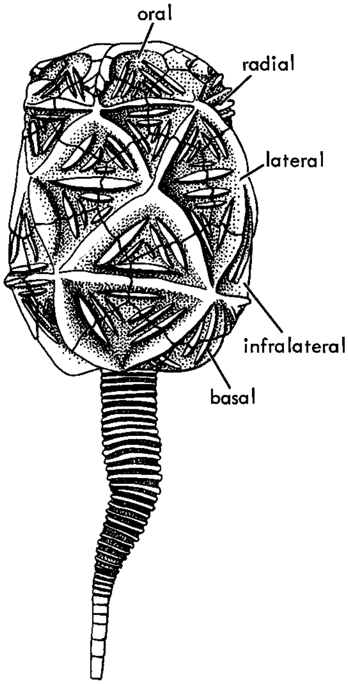


FIG. 296. Side view of theca showing five plate circlets and stem with dissimilar proximal and distal regions, brachioles omitted (reconstr.). *Mimocystites azaisi* THORAL (Macrocystellidae), L.Ord., France, ×2 (Ubaghs, n).

arrangement, making distribution of component thecal elements quite irregular (19).

A third type of thecal construction is encountered in several forms (e.g., *Ascocystites, Palaeocystites, Pareocrinus, Rhopalocystis*) which exhibit disposition of plates throughout a more or less considerable part of the theca no longer in circlets but forming columns or elongate meridional zones. Thus, in *Rhopalocystis* (Fig. 293) the theca is composed of plate circlets from the base to approximately mid-height and then in the upper half exhibits a strongly meridional plate arrangement consisting of five perradial areas (each composed of a **radial** followed by two or three **supraradials**) and five interradial areas (each composed of a much larger number of plates called **interradials,** arranged in four or five successive rows of alternating plates). One of the interradial areas, defined as posterior because of containing the **anus,** is distinguished from others by its greater expanse, by the presence of two plates (instead of one) at its proximal end, and especially by a more or less vertical row of supplementary plates (termed **anals**) distinguished by their large size and conspicuous relief. Such

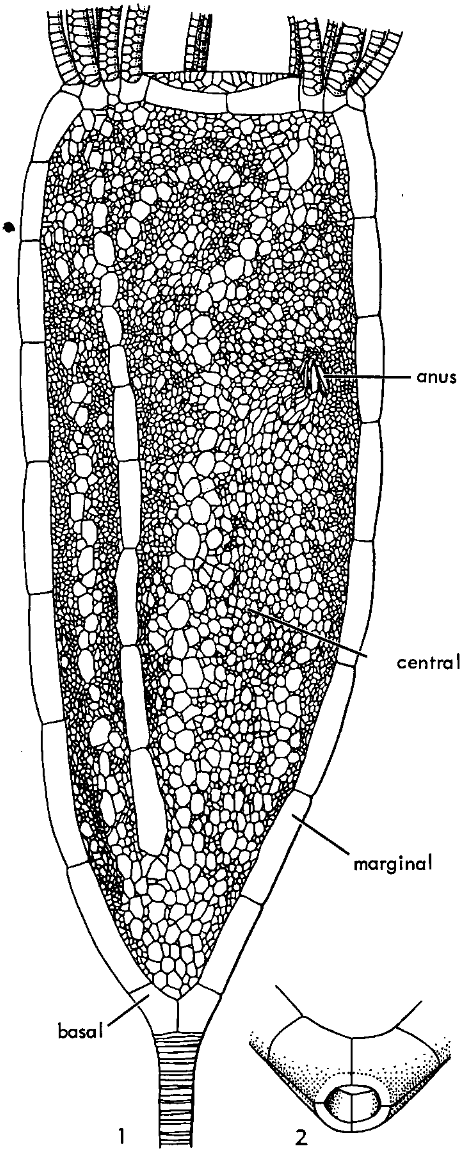


FIG. 297. Eocrinoid with strongly compressed elongate theca rimmed by stout marginal plates and extremely numerous, mostly very minute central plates (reconstr.). *Lingulocystis elongata* THORAL (Lingulocystidae), L.Ord., France; *1,* side view of theca with parts of stem and brachioles, ×4 (38); *2,* oblique view of base, ×6 (38).

organization of the theca in some way resembles that of crinoids, especially that of the Camerata.

Unquestionably, a special place must be reserved for the type of thecal organization seen in compressed forms which rightly or wrongly are included among eocrinoids. A more or less well-differentiated frame accentuates outlines of their theca. It is formed of thick **marginal plates (marginalia).** In *Lingulocystis* (Fig. 297), such plates are elongated, well individualized, and not extended into the pavement of lateral surfaces of the theca. The latter, probably flexible, is composed of innumerable irregular polygonal elements of diminutive size called **centrals (centralia).** In *Rhipidocystis* and *Batherocystis* (see Fig. 318, 319)—perhaps also in *Cardiocystites* (see Fig. 321)—the outer edge of the marginal plates is thickened so as to stand in relief, whereas the remainder of these plates, combined with several central plates, forms a thin but doubtless rigid cover on lateral faces of the theca.

ORAL SURFACE

The region surrounding the peristome in different genera is varyingly distinct from the remainder of the theca. In the Middle Cambrian *Acanthocystites, Gogia,* and especially *Akadocrinus,* it consists of a moderately broad, flat or gently arched area at edges of which the brachioles are attached in bundles, but nothing is known of the structure of this area. In some Ordovician genera (Fig. 298,*1-3*) the peristomial region is formed only by a circlet of **orals,** generally six—each interray having one, except *CD,* which has two, the extra plate considered by YAKOVLEV *(39)* as homologous to the anal plate of crinoids, although this is by no means proved. The brachioles are attached directly to outer edges of the orals (e.g., *Columbocystis,* Fig. 298,*1*) or to pairs of special small plates between the orals which join together beneath them (e.g., *Cryptocrinites,* Fig. 298,*2*).

The oral surface of *Palaeocystites,* from the Middle Ordovician, composed of five orals and five subcircular plates, each serving to support one brachiole, is very little broader than that of the genera previously considered (Fig. 298,*3*). The brachiolar support plates are located along the periphery of the orals and alternate with them. It is unknown whether they rest on other thecal plates or are inserted between them.

In *Rhopalocystis,* from the Lower Ordovician, the oral surface has the form of a slightly raised five-pointed star (Fig. 298,*4*). The interradial areas extend into angles between the perradial branches of the oral surface in such manner that no sharp distinction between oral and aboral parts of the theca exists. Whereas the central disc of the star is composed of six orals grouped around the peristome, each of the branches consists of three to six so-called **brachioliferous plates,** one brachiole being attached to each such plate. The brachioliferous plates are inserted in walls of the theca and take part in forming its inner surface (endothecal condition).

The oral surface attains highest degree of differentiation in *Mimocystites* and *Ascocystites,* both from the Ordovician (Fig. 299,*1,2*). Since the brachioles are attached around its border, a certain analogy with the tegmen of crinoids appears to be offered, but as we shall see later, this resemblance is superficial in nature. The oral surface in these two genera consists of five oral plates *(Ascocystites)* or six *(Mimocystites),* and in addition, a certain number of perradial plates, at outer edges of which the brachioles are attached. The origin of these last plates is unknown. They may be analogous to the brachioliferous plates of *Rhopalocystis.* YAKOVLEV *(43)* called them **adorals.** According to BATHER *(5),* identical plates in *Cheirocrinus* might arise from proliferation of orals themselves, but this is only an hypothesis. The adoral plates of *Mimocystites* rest partly on the orals and partly on the radials, which form a slotlike support to receive them. They do not take part in making the inner surface of the theca. The perradial plates of *Ascocystites* lie on the upper edge of lateral walls of the theca but larger ones may be endothecal in part.

In *Lingulocystis,* finally, the only eocrinoid with compressed theca in which the oral surface is known, this has an elliptical outline with long axis coinciding with the extension plane of the theca (Fig. 299,*3*). At extremities of this axis are concentrated the plates which bear the brachioles, these plates forming part of the frame of marginals bordering the oral surface; they appear to be modified marginal plates, since sporadically these support isolated brachioles.

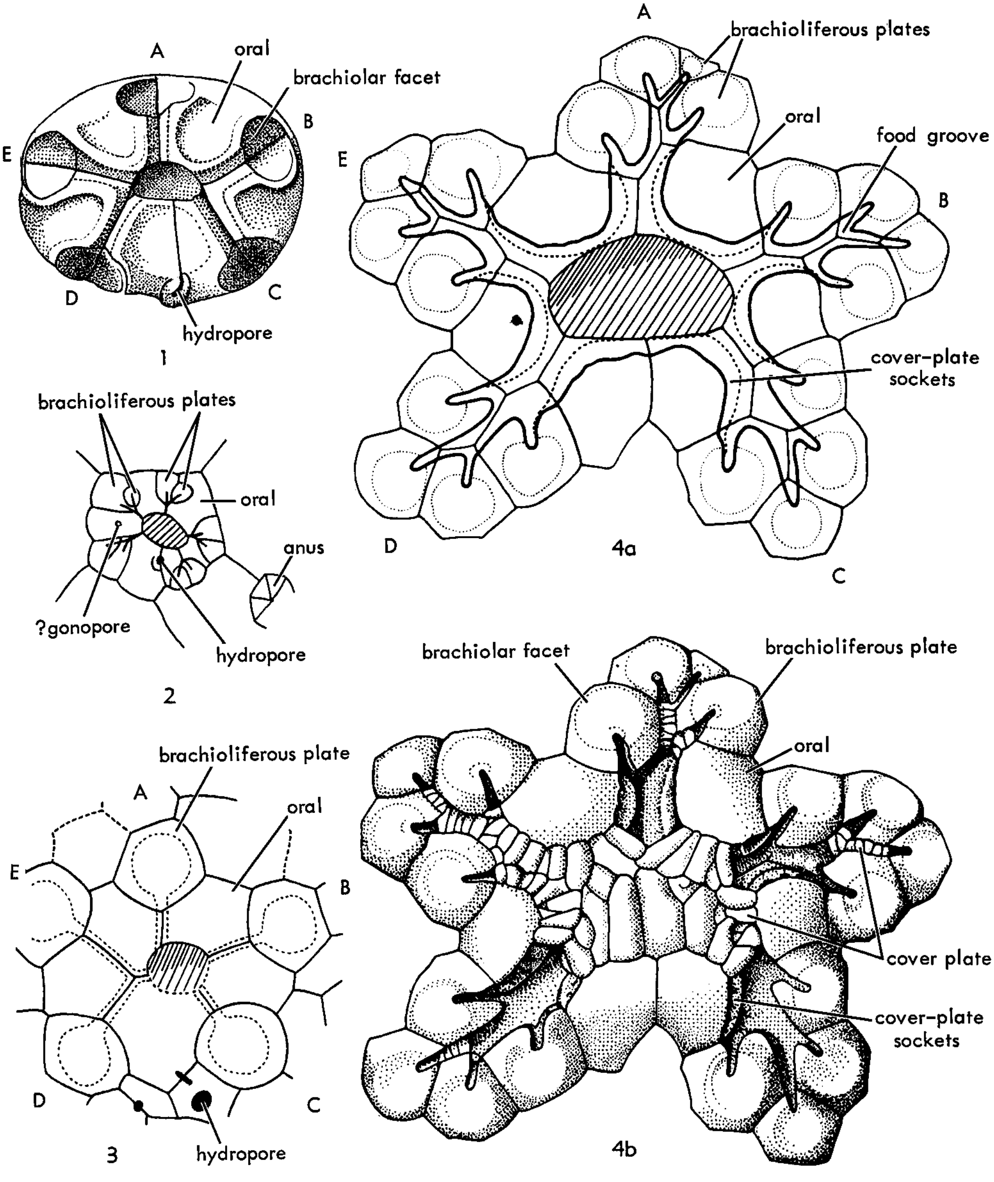


FIG. 298. Morphological features of oral surface of eocrinoid theca.

1. *Columbocystis* BASSLER (?Springerocystidae), M. Ord., N.Am., showing brachiolar facets borne by adjoining pairs of oral plates, ×6 (Ubaghs, n).
2. *Cryptocrinites* VON BUCH (Cryptocrinitidae), M. Ord., E.Baltic, with isotomously branched food grooves leading to pairs of brachioliferous plates, ×4 (Ubaghs, n).
3. *Palaeocystites* BILLINGS (Palaeocystitidae), M. Ord., N.Am., showing short, simple or bifurcating food grooves along interoral sutures, ×7 (22).
4. *Rhopalocystis* UBAGHS (Rhopalocystidae), L.Ord., Morocco, showing heterotomous branching of food grooves leading to clustered brachioliferous plates *(4a)* and cover plates over food grooves *(4b)*, ×10 (39).

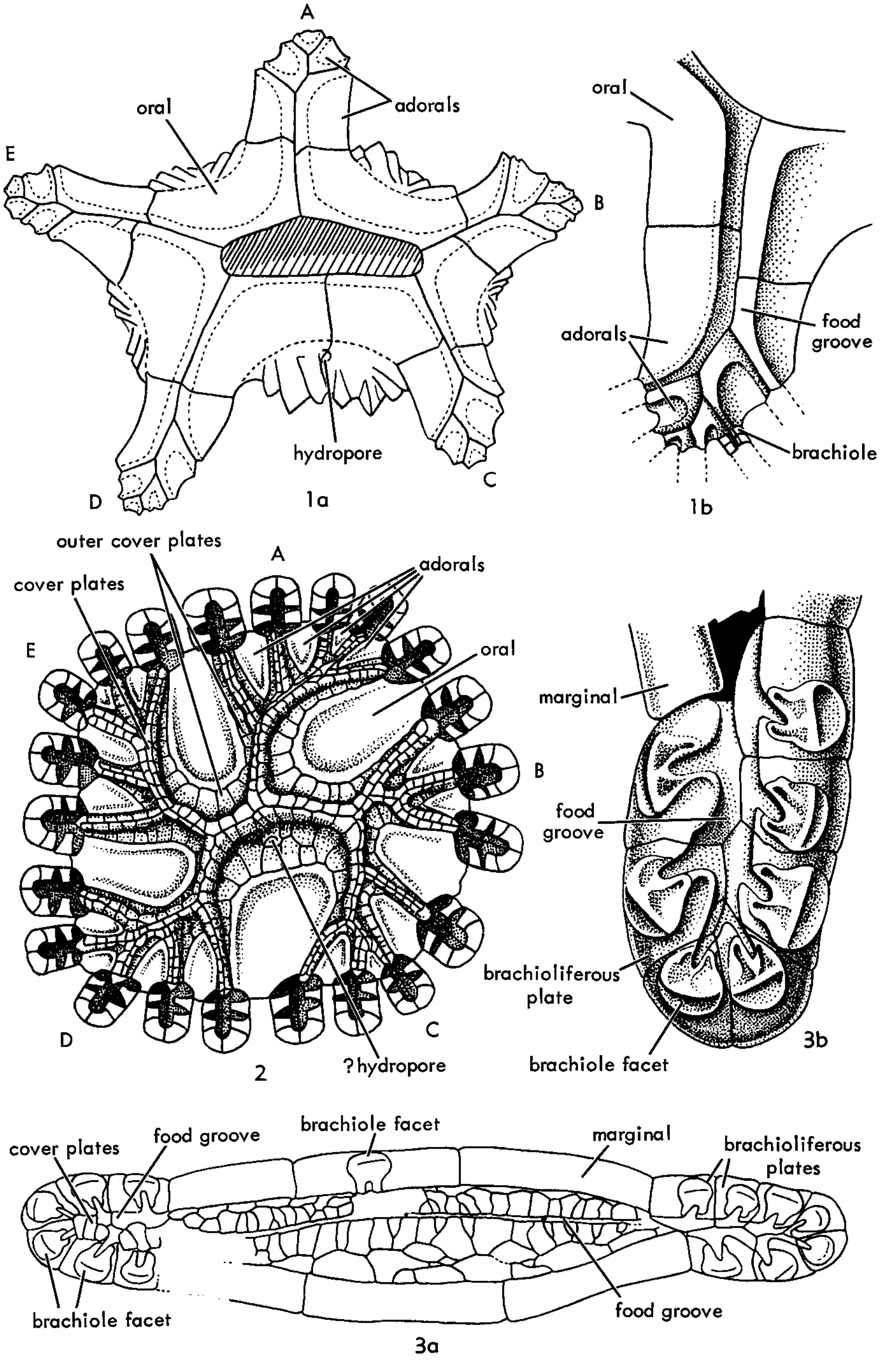


Fig. 299. Morphological features of oral surface of eocrinoid theca.

1. *Mimocystites* Barrande (Macrocystellidae), L. Ord.-M.Ord., Eu.-N.Afr., bifurcations of food grooves distally bunched; *1a,* entire oral surface, ×5; *1b,* single ambulacrum, ×7.5 (both Ubaghs, n).
2. *Ascocystites* Barrande (Ascocystitidae), M.Ord.,

A pavement of irregular platelets extends between the groups of brachioliferous plates, this pavement being limited on the outer side by the marginal plates. The food grooves and peristome (not observed but probably median) are protected by more or less strongly elevated cover plates.

ORIFICES

In addition to sutural pores, if present, the theca of eocrinoids possesses four orifices at most—mouth, anus, probable hydropore, and small opening of indeterminate function (?gonopore).

The **mouth,** which marks the oral pole, generally is surrounded by a moderately large oval or subpentagonal **peristome,** which tends to be elongated transversely to the madreporite plane. In *Lichenoides* (see Fig. 301,*1c*) its inner margin exhibits a rim formed by the thickened adoral edge of the "radials," which in this genus seems directly to bound the peristome, whereas generally the orals have such position. As sometimes seen in fossils and probably invariably present in living eocrinoids, the peristome is covered by plates (**peristomial cover plates**) of the same sort that protect the food grooves (Fig. 298,*4b*; 299,*2*).

The **anus** may be located on the oral surface not far from the peristome (e.g., *Rhopalocystis,* Fig. 293,*1*) but more commonly it occupies a lateral position. As previously stated, it opens in interray *CD* (e.g., *Rhopalocystis*) or *BC* (e.g., *Columbocystis, Cryptocrinites, Mimocystites, Palaeocystites*) but rarely may be found almost on the meridian of ambulacrum *B* (e.g., *Cryptocrinites*). It is covered by an operculum of small triangular plates (**anal pyramid**) (e.g., *Cryptocrinites, Columbocystis*), in some forms (e.g., *Bockia*) enclosed by very diminutive skeletal elements, or it ends as a small cone formed by elongate plates and probably provided with a terminal sphincter (e.g., *Lingulocystis, Mimocystites, Rhopalocystis*). The anus may be surrounded by a large **periproct,** that of *Mimocystites* being developed mainly on flanks of the theca and covered by an integument reinforced by minute plates; the location and other characters of the periproct are identical with those of the cystoid *Cheirocrinus.*

The orifice considered to be a **hydropore** has been observed in only a few genera. In *Columbocystis* (Fig. 298,*1*), *Cryptocrinites* (Fig. 298,*2*), and *Mimocystites* (Fig. 299, *1a*) it consists of a narrow slit or a perforation opening in a small protuberance set astride of the suture between two plates occupying the place of an oral in interray *CD.* In *Ascocystites* (Fig. 299,*2*) I interpret as hydropore a perforated wart borne by a peristomial cover plate in interray *CD.* A plate adjacent to the *CD* oral and brachioliferous plate *C* in *Palaeocystites* (Fig. 298,*3*) shows a large central pore which may be the hydropore or gonopore *(22)* or these two combined. Calling for notice further is the occurrence in *Cryptocrinites* (Fig. 298,*2*) of a second orifice that pierces oral *DE,* interpreted by BATHER *(5)* as a possible excretory pore and by others *(12, 42)* as a gonopore.

SUTURAL PORES AND EPISPIRES

Many eocrinoids (e.g., *Acanthocystites, Akadocrinus, Cigara, Gogia, Rhopalocystis, Lichenoides,* and others) exhibit the presence of **sutural pores,** generally very numerous, distributed along the sutures between nearly all thecal plates. In simplest and probably most primitive examples (e.g., *Gogia, Akadocrinus*) these pores are small in dimensions (greatest diameter 0.15 to 0.5 mm.) and have the form of ellipses disposed transversely with respect to the sutures along which they open. Externally, they are surrounded by a slightly projecting rim (Fig. 300,*1*).

In *Rhopalocystis,* characterized by relatively thick thecal plates, each pore communicates with the thecal cavity by a generally simple canal excavated in walls of the juxtaposed plates, but such conduits may be double, as in the diplopores of cystoids (Fig. 300,*2a-c*). The inner opening of these

FIG. 299. [*Explanation continued from facing page.*]

Boh., showing exotomous branching of food grooves with cover plates flanked by outer cover plates, brachioles sectioned slightly above level of their attachment to oral surface, ×5 (Ubaghs, n).

3. Lingulocystis THORAL (Lingulocystidae), L.Ord., France, showing brachioliferous plates chiefly bunched at opposite extremities of the compressed theca; *3a,* entire oral surface, ×10; *3b,* single ambulacrum, ×20 (38).

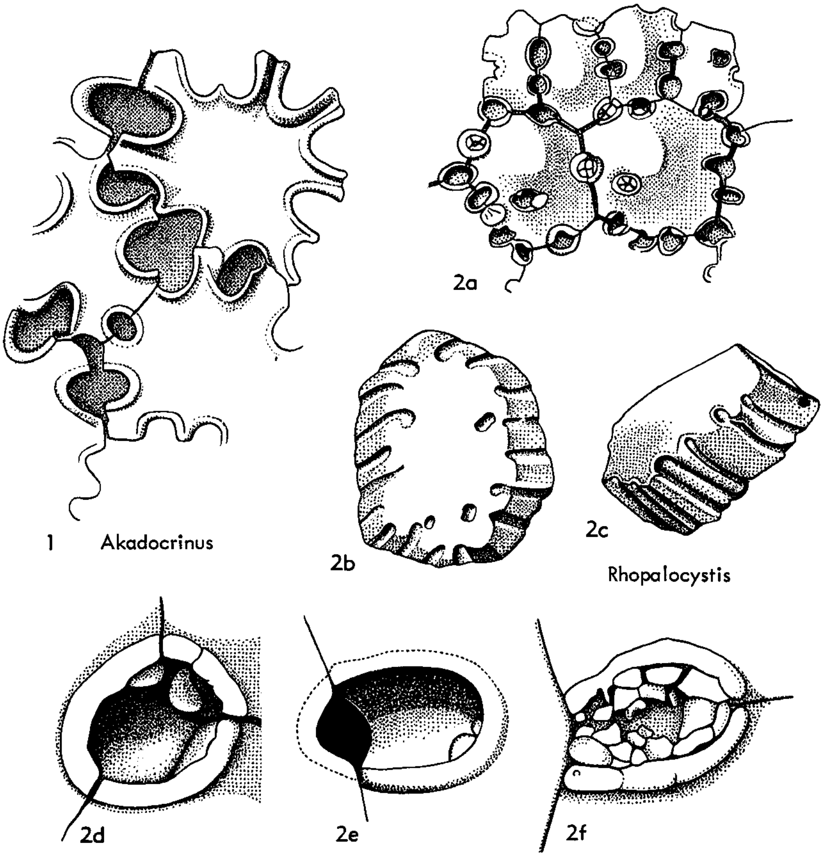


Fig. 300. Morphological features of eocrinoid sutural pores.

1. *Akadocrinus jani* Prokop (Eocrinidae), M.Cam., Boh., showing moderately large sutural pores surrounded by narrow slightly raised rims, ×25 (Ubaghs, n).
2. *Rhopalocystis destombesi* Ubaghs (Rhopalocystidae), L.Ord., Morocco, showing sutural pores bordering several thecal plates; *2a*, exterior of thecal plates with rimmed sutural pores, some penetrating parts of plates at slight distance from sutures and some closed by minute platelets, ×10; *2b*, interior of thecal plate, conduits of pores along sutural faces and inner terminations lacking rims, ×10; *2c*, lateral thecal plate showing sutural pores, ×10; *2d-f*, exterior of sutural pores with more or less numerous cover plates, ×50 (all 39).

canals lacks a rim (Fig. 300,*2b*), whereas the outer opening is located at the bottom of a relatively minute oval basin (maximum diameter 0.25 to 0.35 mm.) which is bounded by a slightly raised edge (Fig. 300, *2e*).

A more complex type of pore apparatus is encountered in *Lichenoides* (Fig. 301, *1a-e*). Here, each sutural pore is prolonged on the outer surface of two juxtaposed thecal plates as an elongated groove bounded by a slightly raised rim, aproximately one-half of the groove being located on one plate and the opposite half in continuation of it on the other plate. Collectively, the grooves tend to produce more or less lozenge-shaped patterns divided by the suture into subequal and symmetrical parts. These occupy nearly the entire surface of the plates, leaving free only median stereomic bosses on the basals and laterals and the brachiolar facets on laterals and radials.

In *Acanthocystites* (Fig. 301,*2a,b*), represented by a single known specimen in which the preservation is much poorer than desirable, the grooves just described appear to have been protected externally by a thin sheet of stereom which covered them com-

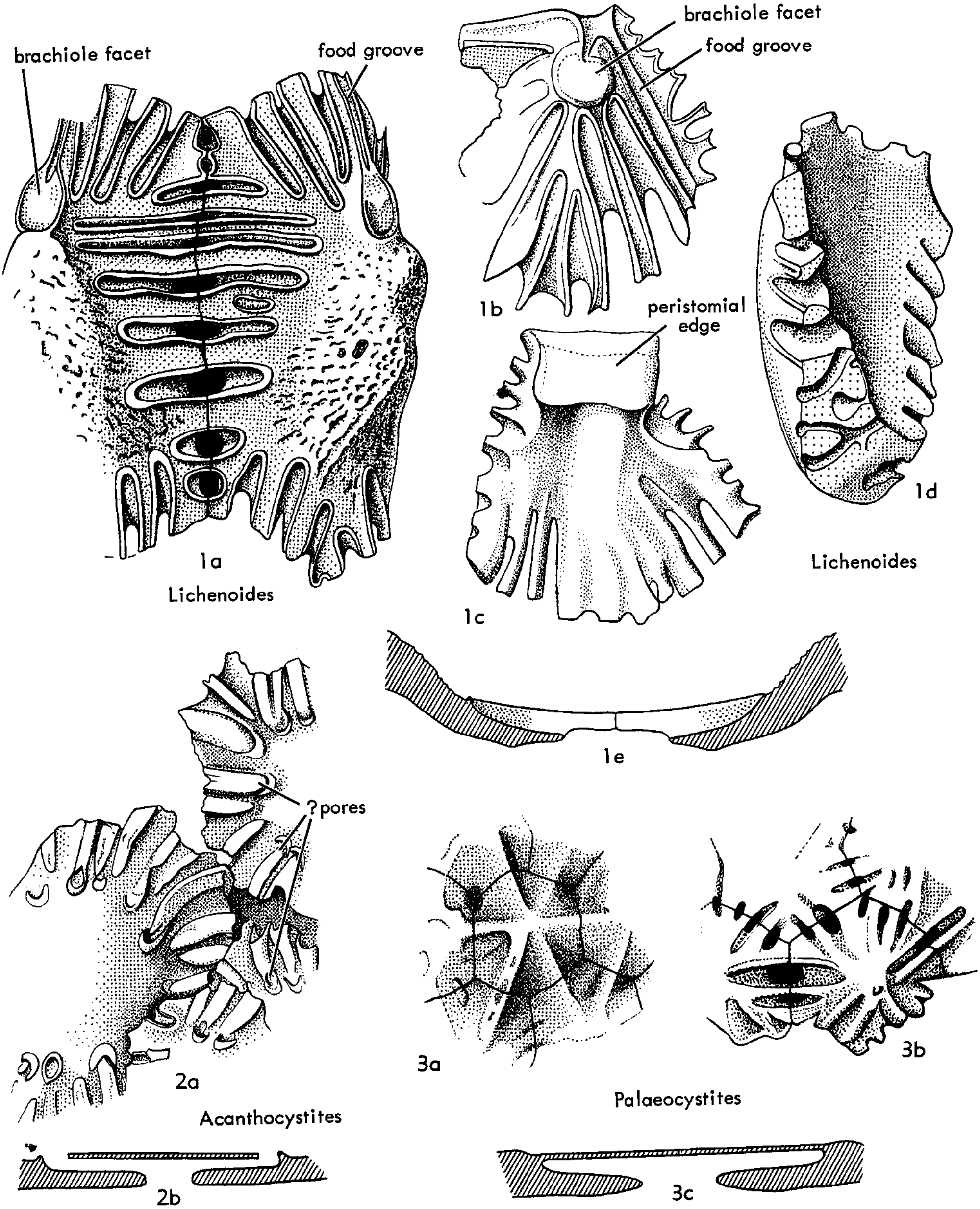


Fig. 301. Morphological features of epispires.

1. *Lichenoides* Barrande (Lichenoididae), M.Cam., Boh.; *1a,* two lateral plates with epispires along sutural margins, also showing brachiolar facets and food grooves, ×9; *1b,c,* exterior and interior of radial plate, ×9; *1d,* oblique view of basal plate, ×9; *1e,* section of epispire transverse to suture, enl. (*1a-d,* Ubaghs, n; *1e,* 37).
2. *Acanthocystites* Barrande (Eocrinidae), M.Cam., Boh.; *2a,* two thecal plates, exterior side, ×10; *2b,* section of epispire transverse to suture, enl. (both Ubaghs, n).
3. *Palaeocystites dawsoni* Billings (Palaeocystitidae), M.Ord., Canada; *3a,* thecal plates showing radially disposed ridges on exterior, ×5 (22); *3b,* thecal plates with hollow folds opening to exterior, ×5 (22); *3c,* section of epispire transverse to suture, enl. (Ubaghs, n).

pletely except for extremities of each where an opening appears to have been maintained. Accordingly, the grooves are interpreted to have been replaced by hollow wrinkles of the plates, communicating with the thecal cavity by pores along the sutures and with the exterior by pores opening at extremities of the wrinkles.

A comparable arrangement is seen in *Palaeocystites* (Fig. 301,*3a-c*), in which the exterior of the theca bears a complex system of radiating hollow ridges and the interior shows numerous sutural pores. However, external openings of the canals lodged within thickness of the plates have disappeared, so that exchanges between sea water and organic structures within the canals could have been effected only through the thin sheet of stereom which covered them (Fig. 301,*3c*).

Finally, it is proper to ask whether the ridges borne by the thecae of *Ascocystites* and *Mimocystites* may not have the same morphological and functional significance as the lozenge-grouped grooves of *Lichenoides* (Fig. 301,*1a*, 302,*1a,b*) and the canals of *Palaeocystites*. Undoubtedly the ridges constitute stiffening ribs that reinforce solidity of the plates (Fig. 302,*3a*). At the same time, along part of their length—precisely that immediately adjacent to the sutures—they are hollow and thus differ from the structures observed in *Palaeocystites* only in lack of a floor interposed between their cavity and the thecal cavity (Fig. 302,*2,3b*).

Despite their diversity, the structures just described have two common features—all are epithecal and all communicate with the thecal cavity by means of sutural pores, conduits hollowed in sutural faces of thecal plates, or internal grooves cut transversely across the sutures. The structures which opened to the exterior possibly were surmounted by vesicles analogous to the papulae of asteroids. Those which were closed must have contained membranous tubules. The hollow ridges on plates of *Ascocystites* and *Mimocystites* could have contained evaginations of coelom or a stroma permeable to organic fluids. At any rate, these structures must have provided circulation that allowed exchange of gases between parts of the animal enclosed by the theca and sea water. The presumed respiratory function and exterior localization of these organs in relation to the theca make appropriate adoption of the name **epispires** for them, as proposed by Hudson *(22)*.

Reported to occur in *Rhopalocystis* are extremely minute platelets which tend to close off the external orifice of numerous sutural pores (Fig. 300,*2d,f*). These minuscule elements may have formed part of the normal equipment of the pores and they could have served to protect papulae. It is possible also, however, that they were secreted as a seal over pores that for one reason or another had ceased to be functional. As matter of fact, all transitions are observed between largely open pores, partially closed pores, completely blocked pores, and nearly effaced pores *(39)*.

It is not uncommon to find that some pores have lost all contact with the suture along which they originated. They penetrate the stereom of a plate in manner suggesting that in the course of growth they had become completely surrounded (Fig. 300,*2a*). Already stated is observation that in *Rhopalocystis* two sutural canals, instead of one, may open into the bottom of an individual external fossette (Fig. 300,*2c*). Such arrangement is reminiscent of the diplopores of the Diploporita among cystoids and perhaps suggests a certain community of origin, or at least a functional analogy between epispires and diplopores. Likewise, the extremely numerous hollow folds crowded together on the plates of some species of *Mimocystites* suggest the striate rhombs of such cystoids as *Cheirocrinus*. Here again, similarity of structures indicative of comparable functions allows us to entertain the possibility of genetic relationships which only future discoveries can verify.

AMBULACRA

The ambulacra of only a few eocrinoids yet have been observed. They number five wherever known, except that in *Lingulocystis* (and probably *Batherocystis* and *Rhipidocystis*) only two ambulacra occur.

Food grooves either run on the surface of thecal plates (Fig. 301,*1b*) or more commonly follow sutures between these plates, the edges of which then are beveled to form the groove (Fig. 298,*1,4a*, 299, *1a,b*). All of

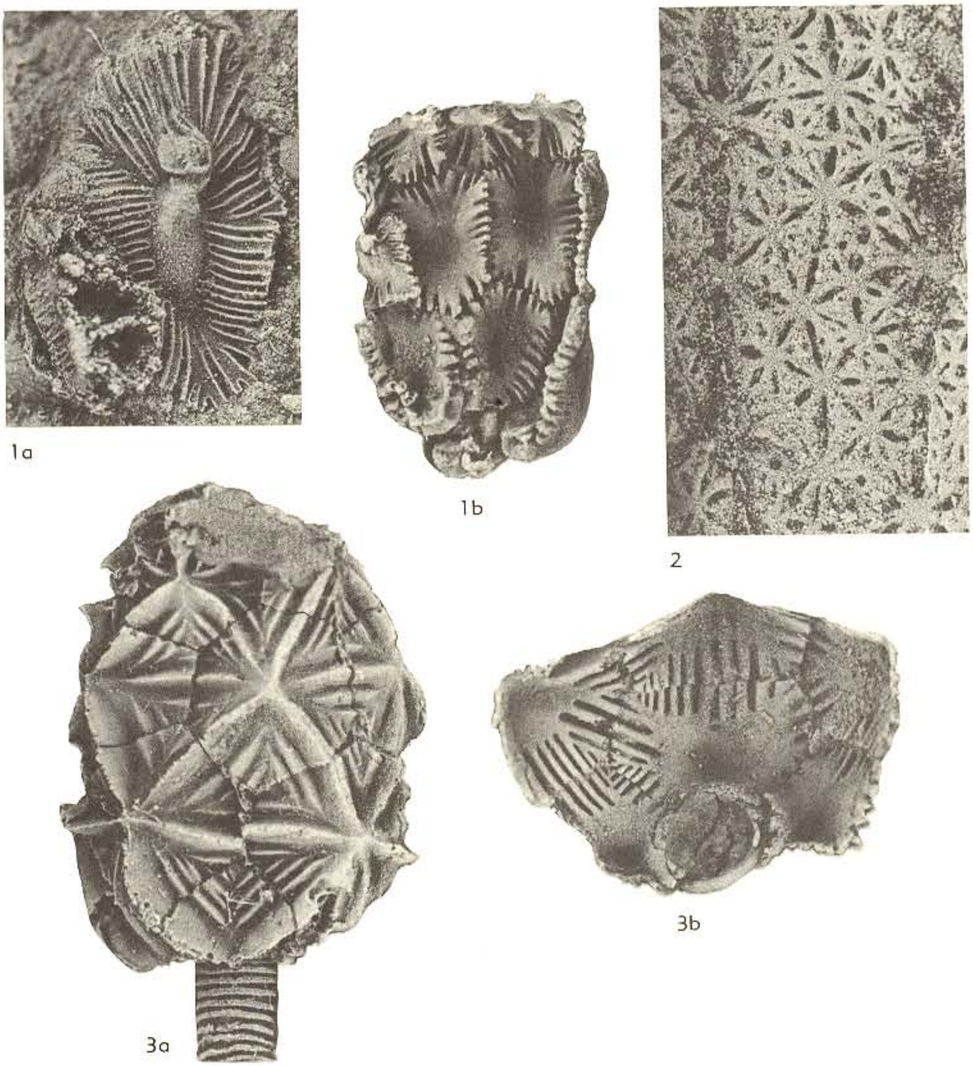


FIG. 302. Morphological features of epispires.

1. *Lichenoides* BARRANDE (Lichenoididae), M.Cam., Boh.; *1a*, external surface of lateral plate showing median boss surrounded by elongate narrow parts of epispires, ×5; *1b*, part of interior of theca showing inner sutural openings, ×3 (both Ubaghs, n).
2. *Ascocystites* BARRANDE (Ascocystitidae), M.Ord., Boh., internal surface of part of thecal wall, ×3 (Ubaghs, n).
3. *Mimocystites azaisi* THORAL (Macrocystellidae), L.Ord., France; *3a*, lateral view of theca and part of attached stem, ×3; *3b*, internal surface of proximal part of theca, ×3 (both Ubaghs, n).

these grooves are short and confined to the oral surface of the theca except in *Lichenoides* where they cross the circlet of radials and descend onto the laterals. They are borne by ordinary thecal plates (orals, radials, laterals, marginals) or by special adoral plates (e.g., *Mimocystites, Ascocystites,* Fig. 299,*1*,*2*), including the brachioliferous plates of *Rhopalocystis* and *Lingulocystis* (Fig. 298,*4a*,*b*; 299,*3a*,*b*).

In general, five food grooves extend directly to edges of the peristome (Fig. 298,*2*) but in some forms two pairs of them next to right and left sides of the madreporite plane came together at a short distance from the peristome border so that only three grooves arrive at this border (Fig. 298,*1,4a*). Exceptionally, four grooves, one of which is bifurcated, reach the peristome (Fig. 298, *3*). The food grooves may be simple unbranched furrows leading directly from a brachiole to the peristome or short secondary furrows may join main ones in treelike manner (Fig. 298,*4a*) or in a bunched pattern at outer extremities of principal grooves (Fig. 299,*1b*). It should be noted that the manner in which secondary food grooves come together or join main ones differs from genus to genus, giving rise to bifurcation patterns which are respectively classifiable as isotomous (branches equal, Fig. 298,*2*), heterotomous (unequal branches alternately meeting from right and left, Fig. 298,*4a*; 299,*3b*), and exotomous (secondary branches all on one side of main groove, this side being interpreted as outer, Fig. 299,*2*). These food-groove patterns provide basis for grouping brachioles in pairs or in larger numbers distributed along branches of a V in each ambulacrum or arranged in a circle around the oral face.

The food grooves were protected by **cover plates** attached on either side generally in alternation, the **cover-plate sockets** appearing as narrow platforms along margins of the grooves (Fig. 298,*4b*). In some forms **outer cover plates** may be interposed between main (or inner) cover plates and edges of the food grooves. In *Ascocystites,* which exhibits very well-developed cover plates of both types, the outer cover plates form a varyingly wide border around the orals with the cover plates raised almost vertically between them (Fig. 299,*2*).

BRACHIOLES

The **brachioles** of eocrinoids are simple exothecal appendages of the theca provided with their own skeleton and excavated on their oral surface are **brachiolar food grooves** which constitute distal extensions of the food grooves on the theca, just discussed. The brachioles are long and narrow—exceptionally slender in some, judging from the size of their facet for attachment. They invariably taper distally and never are branched. They are typically biserial in structure, that is, composed of two rows of alternating diminutive skeletal elements termed **brachiolars,** but a single ossicle may form their proximal extremity and in *Rhipidocystis* the brachioles are uniserial throughout their entire length. *Gogia spiralis* has biserial brachioles twisted on themselves in helicoid spirals (Fig. 294).

The brachiolar food grooves were protected by cover plates, which undoubtedly were capable of being raised. In some the cover plates are so lengthened and so strongly projected above the oral face of the brachioles that they have been misinterpreted as pinnules *(40)* or as structures which could have developed into the pinnules of camerate crinoids *(25)*.

Each brachiole is articulated at its base on a **brachiolar facet** which generally bears weak (probably ligamentary) impressions consisting either of shallow right and left hollows or an aboral depression separated from one or two adoral ones by a faintly marked transverse ridge (Fig. 299,*3b*). However ill-defined the relief of this facet may be, it implies the possibility of at least feeble movements of the brachioles. On the other hand, the great number of sutures between brachiolars must have compensated in some degree the absence of more strongly marked articulations on the facets and it must have rendered the brachioles moderately flexible. On the whole, however, the brachioles of eocrinoids appear to have been rather rigid structures, raised like long spines around the oral pole of the theca (Fig. 295).

It is appropriate to make special mention of the brachioles of *Ascocystites,* in view of their considerable evolutionary modification (Fig. 303). The brachioles of this genus are relatively stout. Each displays a slightly swollen proximal region and a distinctly narrowed distal portion. Their attachments to thecal plates (orals and adorals) are characterized by the presence of deep muscular or ligamentary sockets. Large excavations, especially well developed in the proximal portion of the brachioles, open out between the brachiolars both on aboral and adoral sides. Consequently, each articular face (proximal and distal) of the brachiolars bears two well-marked depressions separated by a transverse fulcral ridge. The depressions evidently served for attachment

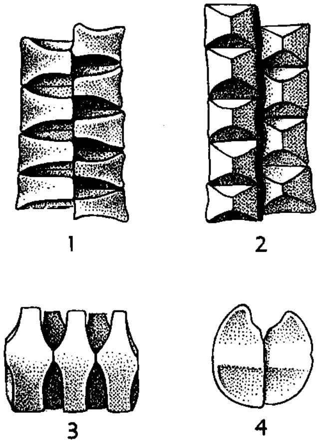


FIG. 303. Brachioles of *Ascocystites* BARRANDE (Ascocystitidae), M.Ord., Boh. (all Ubaghs, n).

1. Dorsal (outer) side of part of brachiole clearly showing biserial arrangement of brachiolars and large excavations between those of each series, ×10.
2. Oral (inner) side of specimen shown in *1*, showing excavations between brachiolars of series on opposite sides of median food groove, ×10.
3. Lateral view of part of brachioles, oral side up, dorsal side down, showing interbrachiolar excavations on each, ×10.
4. Sutural surfaces of pair of brachiolars, oral side up, ×10.

of powerful bundles of contractile or elastic fibers, antagonistic action of which would have produced extension and flexion of the brachioles. Distributed around the circumference of the oral surface of the theca, they must have been able to spread apart and pull toward one another (Fig. 299,*2*).

The number of brachioles varies in different genera and probably also in individuals of different age, as well as in different rays of the same individual. Five brachioles are observed in *Columbocystis,* ten in *Cryptocrinites,* about 15 in *Lingulocystis,* 15 to 30 in *Rhopalocystis,* approximately 23 in *Ascocystites,* and 8 to 22 (or even 44) in *Gogia.*

The brachioles of eocrinoids are attached to the theca in various ways; 1) attachment of each to an individual plate, which may be an ordinary one (radial, lateral, marginal) (Fig. 299,*3a*) or special (adoral, brachioliferous plate) (Fig. 298,*2,3*; 299,*1b,3b*); 2) attachment of two or even three brachioles to a single plate (e.g., laterals of *Lichenoides* with one to three brachioles) (Fig. 295); 3) attachment of each brachiole to a pair of adjoining plates (e.g., two orals, two adorals, an oral and adoral) (Fig. 298,*1*; 299,*1b,2*). To be noted in the third type is the fact that the brachioles are attached to the outer lateral edge of thecal plates and not to their adoral part.

COLUMN

All known eocrinoids possess a column, with exception of *Lichenoides,* which lacks one. Also, the more or less atrophied stem of *Rhipidocystis* and *Batherocystis* appears to be on the way to disappearance.

The most archaic sort of eocrinoid stem appears to be that seen in *Gogia* (Fig. 294), from the Middle Cambrian, in which it is a more or less elongated hollow organ consisting actually of an aboral evagination of the theca. The walls are formed by many irregularly arranged small polygonal plates joined rather loosely together. The most proximal ones may be transitional with plates of the theca, or oppositely, may be very dissimilar in size. The distal extremity of the column may be a narrowly rounded point composed of minuscule platelets or it may become enlarged into a flattened sole.

The structure of the column of *Gogia* possibly explains the origin of the varyingly numerous small plates at the aboral pole of *Lichenoides,* for these correspond rather closely to the skeletal elements of the *Gogia* stem. Indeed, if this indicates their morphological significance, the proximally located small plates of *Lichenoides* may represent a rudimentary stem which never developed. Other hypotheses have postulated that these plates are remnants of an atrophied circlet of thecal plates *(44)* or secondary skeletal elements produced for closure of the axial canal when a supposed peduncle was lost in the course of ontogenetic development *(37).*

The column of *Akadocrinus* (Fig. 304), another Middle Cambrian genus, exhibits structure unlike that of the stem of *Gogia.* Its length is five or six times the height of the theca. Equal to the theca in diameter at its proximal extremity, it progressively diminishes distally to a termination in a probably hollow holdfast disc with upper surface paved by irregular small polygonal

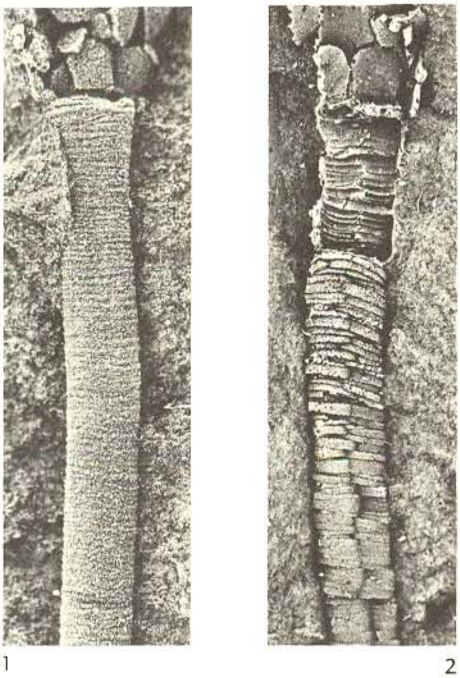


Fig. 304. Morphologic features of eocrinoid stem illustrated by *Akadocrinus nuntius* Prokop (Eocrinidae), M.Cam., Boh. (Ubaghs, n).——*1*. Proximal part of theca and attached stem composed of wide, very short circular columnals, ×5.——*2*. Similar view of specimen showing large hollow interior of stem continuous with thecal cavity, ×5.

plates (Fig. 305) and lower surface unknown. The thin walls of the column are formed by short ossicles unevenly joined together. They enclose a large space which without restriction is continuous with the thecal cavity (Fig. 304,*2*). This broad communication between the stem and thecal cavities is doubtless a primitive characteristic, for it is found also in other eocrinoids, as well as cystoids and archaic crinoids.

Where eocrinoid columns are known in genera not already discussed, they are found to be composed of cylindrical columnals diverse in height (length) and pierced by an axial canal of large diameter, especially in the proximal region. Whether short or moderately long, the stem generally diminishes in diameter distally, terminating or apparently terminating in a point (Fig. 292). Its proximal extremity, attached to the aboral pole of the theca, is well separated from it both by smaller diameter of the column and by nature of the columnals. Commonly, near the theca very short columnals alternate with longer ones but progressively toward the free end of the stem the columnals become elongated and they tend to resemble one another closely. Their articulations, in so far as observed, are indicated by little or no differentiated features of the columnal facets and sutures between columnals are not crenulate.

Longitudinal differentiation of the column in genera of the Macrocystellidae allows distinction of two quite dissimilar regions, joined by a short transitional zone (Fig. 296; see also Fig. 313). The expanded proximal region is characterized by a relatively very large axial cavity which opens broadly into the thecal cavity. It is composed of regularly alternating annular columnals of two different types, one having a strongly salient peripheral flange accompanied internally by a narrow depressed zone which becomes enlarged at two diametrically opposite points where a small protuberance appears (see Fig. 313,*3*), and the other fitting exactly into the depressed zones of the just-described columnals and bearing also a pointed enlargement with small depression corresponding to the small protuberance on the inner side of the first-type columnals *(32)*. The distal part of the column, greatly reduced in diameter, is uniformly built of cylindrical columnals which increase in length while decreasing in width

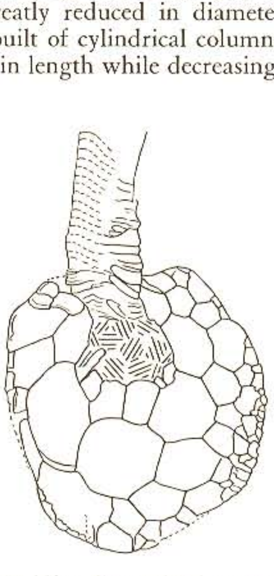


Fig. 305. Holdfast disc at distal extremity of stem of *Akadocrinus nuntius* Prokop, M.Cam., Boh., ×9 (Ubaghs, n).

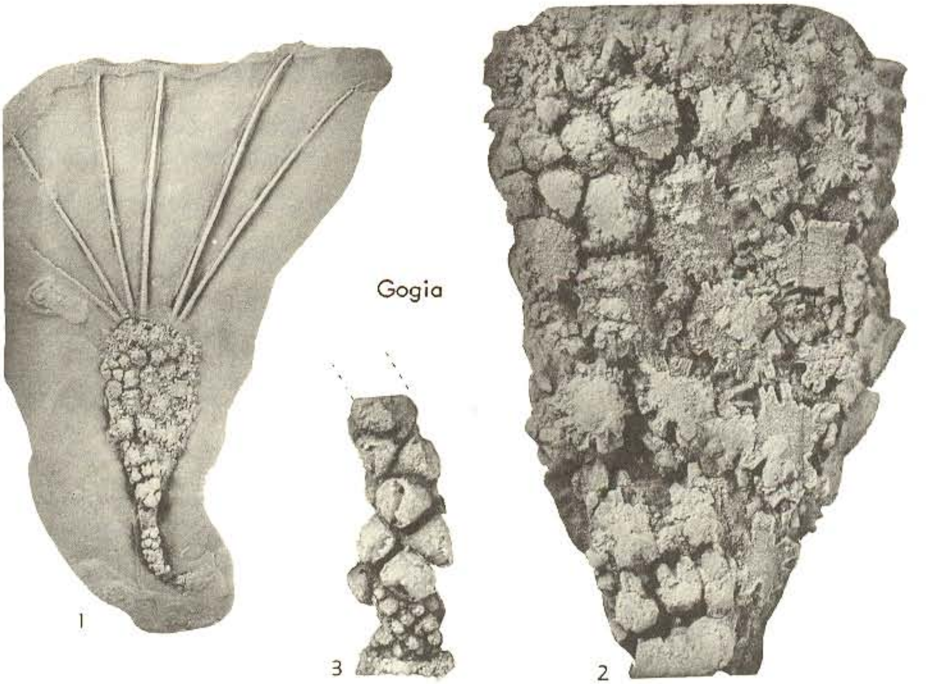


Fig. 306. Eocrinidae (p. S478).

in direction away from the theca (see Fig. 313,*1*).

In the Rhipidocystidae the column appears to be tending toward reduction. That of *Batherocystis* is composed of a few abnormally developed columnals having ovoid or somewhat irregular shape and transversely elliptical section (see Fig. 319,*3*). Perhaps these eocrinoids lived in prone position on the sea floor, like most "carpoids" *(18)*, although similarity of the two opposite flattened faces of the theca does not favor this hypothesis.

In no eocrinoid, other than *Akadocrinus*, has the presence of differentiated anchorage structures been ascertained. Without doubt, the column, implanted in mud or attached to some foreign body by its attenuated and recurved extremity, served to moor the animal at least temporarily. The relatively large hollow stem of *Gogia* may have functioned as ballast to orient the organism in a vertical position; in some individuals the stem is enlarged distally and terminates in a plane surface that may have aided fixation (Fig. 306,*3*). The manner of preservation of several specimens of *Lichenoides* suggests that this stemless form lived in sea-bottom mud implanted by its aboral extremity; also, this extremity, made heavier by its very thick walls, perhaps was utilized as ballast. We may recall that Jaekel *(23)* considered *Cigara dusli, Lapillocystis fragilis,* and *Pilocystites primitivus* as bulbous radicular fragments belonging to eocrinoids (possibly *Acanthocystites*) and interpreted as a hollow root *(Hohlwurzel)* a curious structure found in Middle Ordovician beds containing *Ascocystites (25)*. In fact, *Cigara* comprises the remains of a ?theca prolonged toward the base by a hollow extension (?stem); *Lapillocystis* is an enigmatic, poorly preserved fossil; *Pilocystites* seemingly is not an echinoderm; the presumed *Hohlwurzel* of *Ascocystites* is an object (*?Conularia* shell) to which conical shells (probably brachiopods, perhaps Craniacea) are attached; consequently, the postulate advanced by Jaekel and supported by Ehrenberg that the *Hohlwurzel* represents the most primitive type of echinoderm attachment root seems to lack any basis.

GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO EOCRINOIDEA

adoral. Any plate associated with orals, supporting food grooves on their beveled common edges and carrying brachioles on their outer margin.

ambulacrum. All food grooves, including brachiolar food grooves, of any single ray.

anal. Supplementary plate in *CD* interray.

anal pyramid. Valvular structure of triangular plates serving to close anus.

basal. Any plate of proximal circlet.

brachiolar. Any ossicle of brachiole (exclusive of cover plates).

brachiolar facet. Scarlike area on thecal plate to which brachiole was attached.

brachiolar food groove. Furrow running along oral surface of brachiolar ossicles.

brachiole. Exothecal structure supported by its own endoskeleton and bearing food groove along oral surface.

brachioliferous plate. Special thecal plate bearing brachiole.

column. Stalklike structure attached to aboral pole of theca and presumably used for supporting and anchoring organism.

columnal. Individual ossicle of column.

central. Any plate located in area surrounded by marginal framework on flattened faces of theca in compressed genera.

cover plate. Small plate covering part of food groove.

cover plate socket. Any place of attachment for cover plates.

deltoid. See oral.

epispire. Epithecal structure, open or covered, associated with sutural pore or slit, and presumably serving for respiration.

food groove. Furrow running along adoral surface of brachioles (brachiolar food groove) and on surface of theca to mouth; used for conveying food.

gonopore. Presumed outlet of genital products.

hydropore. Presumed orifice of water-vascular system.

infralateral. Any plate of circlet between basals and laterals.

interradial. Any interray plate above laterals (exclusive of orals).

lateral. Any plate of circlet between infralaterals (or basals, if infralaterals are lacking) and radials.

marginal. Any plate forming framework in compressed genera such as *Lingulocystis* and *Rhipidocystis.*

oral. Any of interradially disposed plates around peristome.

outer cover plate. Any small plate present along food grooves just outside of cover plates.

periproct. Area surrounding anus, covered with anal pyramid or finely plated integument.

peristome. Area surrounding mouth, protected by cover plates continuous with those covering food grooves.

peristomial cover plate. Any small plate participating to covering of peristome.

radial. Any plate of circlet next distal to laterals.

stem. See column.

supraradial. Any plate of meridionally disposed column resting on radial, exclusive of brachioliferous plate.

sutural pore. Any diminutive opening in theca, generally very numerous, distributed along sutures in many eocrinoids.

theca. Plated investment of visceral mass; body exclusive of column and brachiole.

TAXONOMIC POSITION

The problem of the taxonomic position of the Eocrinoidea is made difficult by their diversity, probable heterogeneity of their relationships, and insufficience of knowledge concerning the organization of numerous genera. In order to discuss genetic connections with other echinoderms it is desirable to confine initial consideration to forms in which structural features are reasonably well known and among these chiefly ones judged most suitable to serve as morphological types, later grouping others around them.

The first point that seems to be well established is appurtenance of the Eocrinoidea to the Crinozoa, all diagnostic characters of which are found in eocrinoids—visceral mass enclosed by a calcified theca formed of plates, oral surface typically directed upward, aboral surface resting on the substrate or attached to it permanently or temporarily generally by means of a stem, presence of exothecal processes along which ambulacral grooves designed for collection and transport of food particles to the mouth are developed, and anus located on the adoral half of the theca.

Among crinozoans, the eocrinoids appear to be related most closely to the cystoids. This is true not only of such forms as *Mimocystites* but it applies to the whole eocrinoid assemblage, in which essential features of organization clearly are cystoid-like. Such characters include 1) theca in form of a completely enclosed capsule except for a few openings, 2) absence generally of a true tegmen comparable to that of crinoids, 3) construction of theca similar or identical to that of cystoids, 4) organization of ambulacra as in cystoid ambulacra, 5) presence of true brachioles instead of arms. Only the absence of thecal pores or distinction between the sutural pores of eocrinoids and the diplopores or pore rhombs of typical cystoids allows separation of these echinoderm assemblages, even though morphological intermediates between sutural pores and diplopores are seen *(39)* and though the hollow trans-sutural folds of such eocrinoids as *Mimocystites* undeniably show resemblance to cystoid pore rhombs. Indeed, maximum similarity of the two classes is found in comparing the genus just mentioned with the rhombiferan cystoid *Cheirocrinus*. These forms differ essentially neither in structure of the stem nor in construction of the theca, which has the same number of plates arranged in the same manner, nor in organization of the ambulacra nor in nature and position of the thecal orifices, especially the anus, in both forms located in a wide elliptical finely plated area. Except for the complete lack of thecal pores in one and the presence of pore rhombs in the other, the two genera could easily be confused. Such great similarity in so many characters hardly can be fortuitous. It denotes close relationship in parentage between at least certain eocrinoids, (e.g., Macrocystellidae), and certain cystoids (e.g., Cheirocrinidae), as JAEKEL *(23)* recognized long ago when he interpreted *Mimocystites* (probable synonym of *Macrocystella*) as the immediate ancestor of *Cheirocrinus*. When the general organization of the compared forms is thus nearly identical, one may well ask if the diagnostic importance of the presence or absence of a certain type of thecal pores has not been exaggerated.

Another form particularly cited in considering the relationships of eocrinoids and cystoids is *Cryptocrinites*. As represented by this genus, they are ambiguous, however. If the nature of its ambulacral grooves, the presence of brachioles, the ventrolateral location of the anus, and the discovery by YAKOVLEV *(42)* in a normal specimen of supernumerary plates including one with traces of pore rhombs provide support for arguments favoring genetic relationship with rhombiferan cystoids—indeed, derivation of *Cryptocrinites* from them *(5, 42)*—other characters, such as the tricyclic construction of the theca, the lack of thecal pores, and the morphologic significance attributed by YAKOVLEV *(42)* to plates immediately surrounding the peristome, have suggested to some authors a possible connection with crinoids.

The hypothesis of crinoid affinities, though dependent on very superficial analogies, accords with often expressed opinion that the eocrinoids contain the source of crinoids. JAEKEL *(25)* tested this by study of Middle Cambrian forms such as *Acanthocystites*, in which the still-undifferentiated theca is composed of numerous irregularly arranged plates, with "arms" grouped in five bundles, as if at their level a tendency toward pentamerous division of the body already is manifest. These five arm groups, according to JAEKEL, by influence exerted on the theca, would have led to its progressive differentiation and especially the formation of median columns of thick plates as a kind of vertical ribs suited for support of the arm groups as well as the anal region. A stage illustrated by *Ascocystites* would have preceded appearance of true crinoids, including especially the Camerata. MOORE *(26)* contributed to the problem in undertaking to demonstrate by diagrams that "the respective dorsal-cup patterns of all types of camerate crinoids are directly derivable from eocrinoids, or conceivably from regular rhombiferan cystoids of sorts that belong either to the Cheirocrinidae or Caryocrinitidae; this calls merely for longitudinal shifting of thecal plates in a manner clearly shown within the cystoid assemblage."

It is appropriate to inquire whether these theoretical considerations are confirmed by any facts. Assuredly, many analogies, some of which are very striking, associate the theca of certain eocrinoids, such as *Ascocystites, Palaeocystites, Rhopalocystis,* and *Lichenoides* (termed a "cystocrinoid" by BERNARD, 1895), with that of crinoids. These analogies, never all manifested in a single genus, include 1) division of the theca into a dorsal cup and "tegmen," 2) tricyclic arrangement of dorsal-cup plates in several genera and division of the plates into alternating perradial and interradial meridional zones, 3) presence of supplemental plates interpreted as anals in the posterior interray, 4) more or less pronounced pentameral symmetry, 5) massive and imperforate nature of the plates, and 6) presence of sutural pores and epispires recalling comparable structures in some archaic crinoids.

Analysis indicates that a majority of these resemblances of eocrinoids and crinoids are essentially superficial. Thus, among eocrinoids one cannot find a true tegmen in the crinoid sense of the term, for in crinoids the tegmen is circumscribed by a circle passing through bases of the arms which are supported by plates of the dorsal cup. The brachioles of eocrinoids, which perform the function of the arms of crinoids, are attached to plates that comprise an integral part of the "tegmen" (except in *Lichenoides*) and even in *Ascocystites,* with brachioles distributed in a circle around the "tegmen," these depend entirely on plates (orals, adorals) belonging to it and none on plates belonging to the aboral part of the theca. Accordingly, the "tegmen" of eocrinoids is indicated by its organization, nature of its constituent elements, and relationship with the brachioles to be much more cystoid-like than crinoid-like.

The tricyclic arrangement of thecal plates in a few eocrinoid genera proves nothing as to genetic affinities with crinoids, for such grouping of plates around the visceral mass recurs frequently in the evolutionary history of echinoderms. For the same reason, partition of the theca into alternating perradial and interradial meridional zones lacks significance. Furthermore, the perradial plate columns of eocrinoids are not homologous with those formed by radials and fixed brachials in crinoids, because true arms are nonexistent in eocrinoids. Also, quite unproved is the assumption that supplemental plates of the *CD* interray observed in some eocrinoid genera correspond to anal plates of crinoids. As previously observed, neither in organization of the theca nor in the nature of its component elements is any sure indication found of relationship between eocrinoids and crinoids, and still less of descent of the latter from the former. Finally, the best suggestion of a possible genetic link between the two classes perhaps lies in the absence of thecal pores or the presence of sutural pores and epispires similar to those of archaic crinoids *(37),* although this is far from decisive.

In my view, a main objection to the hypothesis of descent of crinoids from eocrinoids or forms similar to them is the fundamentally different nature of crinoid arms and eocrinoid brachioles. The latter are distinguished from the former 1) in being exothecal appendages, that is, occurring outside of the thecal wall instead of comprising evaginations of it, 2) in lacking any continuity of their skeletal support with plates of the aboral part of the theca, 3) in not being attached to plates homologous with crinoid radials but generally instead to plates of the oral region of the theca, 4) in providing for intercommunication which their soft parts could have with organs and cavities enclosed by the theca by way of the peristome and the epithecal part of the food grooves instead of through an orifice at the base of each brachiole, and 5) in having biserial structure in contrast to the probable initial uniserial nature of crinoid arms. These many profound differences deter guesswork in the present state of knowledge concerning the manner in which one type of appendage could have given rise to the other.

When account is taken of the fact that the eocrinoids most similar to crinoids are contemporaneous with genera of the latter which already exhibit all attributes of this class, it is necessary to admit that the observed resemblances can only signify convergence or evolutionary parallelism, according to judgment that the forms considered are descendants of different or common ancestors. No presently available paleontological evidence allows choice between these alternatives. On the other hand, nothing firmly opposes phyletic relationship between certain cystoids and certain eocrinoids, even though the nature of these relationships cannot yet be specified.

Finally, we may note that some authors (e.g., FELL, *14*; JAEKEL, *25*; NICHOLS, *27*) have assigned to eocrinoids the role of common source of all echinoderms. This entirely speculative concept is denied by the fact that in lowest Cambrian strata such complex forms as *Helicoplacus* and *Stromatocystites* are associated with plates probably attributable to eocrinoids. Also, it is self-evident that no known eocrinoid can represent the ancestral type of *all* echinoderms *(13)*. In addition, how could an echinoderm that had attained the stage of radial symmetry give rise to such forms as the "carpoids," which in all likelihood belong to a preradial-symmetry stage of the phylum? How also could the eocrinoids, already well advanced along the path of the Crinozoa, possibly be ancestors of the Echinozoa? The simple asking of these questions suffices to show the inanity of such suppositions.

CLASSIFICATION

A majority of the genera brought together in the class Eocrinoidea previously have been considered to belong to the Cystoidea *(sensu lato)* and generally classed partly in the Amphoridea and partly in the Aporita. Jaekel *(23)* was first to withdraw this assemblage from the cystoids, later *(25)* grouping them as a subclass of the Crinoidea. Still later, Regnéll *(29)* elevated the subclass to the rank of class.

Again it is Jaekel *(25)* who must be credited for the only published classification of the group, a classification which recognizes four orders, seven families, and 15 genera, with *Amygdalocystites* and *Comarocystites* (now assigned to the Paracrinoidea) provisionally included as an appendix.

Jaekel's first order, named Atava, contained the two families Eocrinidae and Ascocystidae (*recte* Ascocystitidae), intended for inclusion of such forms as *Acanthocystites* and *Ascocystites,* characterized by a theca containing very numerous plates not arranged in circlets and having a flattened upper surface with five attached groups of brachioles. The genus *Eocrinus,* which is a junior subjective synonym of *Gogia (31),* contained in the order, is the type not only of the family Eocrinidae but of the class Eocrinoidea.

The second order, named Reducta by Jaekel, was composed of the families Lichenoidae (*recte* Lichenoididae), Cryptocrinidae (*recte* Cryptocrinitidae), and with reservation, Paractocrinidae. Representatives of the first two families are characterized by a theca composed of only a few circlets, generally with five plates in each, without sharp separation of oral and aboral parts, and with a variable number of brachioles unevenly distributed around the summit. The Paractocrinidae was proposed for three new, rather poorly known genera from Ordovician rocks of the Leningrad region. Since they seem to show greater affinities with crinoids than eocrinoids *(2),* they are omitted from consideration here.

The third order, called Plicata, was erected for the single family Macrocystellidae, in which the theca contains more numerous plate circlets than in the preceding order and five groups of brachioles are supported by plates designated as radials. As indicated by the name of the order, thecal plates are ornamented by a number of folds. The Macrocystellidae were considered as intermediate forms leading directly to the regular cystoids, especially *Cheirocrinus,* which differs from the macrocystellids only in the possession of pore rhombs.

The fourth order, Deviata, was grouped in the Eocrinoidea doubtfully, and Jaekel placed in it the Malocystidae (*recte* Malocystitidae), containing the single genus *Malocystites.* This form now is classed in the Paracrinoidea.

Subsequently to the time of Jaekel's work, several families and numerous genera have been assigned to the Eocrinoidea (*3, 16-18, 28, 38, 39, 46*). Some of these genera (e.g., *Lingulocystis, Rhipidocystis*) originally were thought to be "carpoids" *(17, 18),* but they differ essentially from these echinoderms in having typical brachioles and a stem that is markedly different from the stele of the Homostelea and Homoiostelea. Ubaghs *(38)* recognized that both should be transferred to the Eocrinoidea. *Lepidocystis,* on the other hand, provisionally classified as an eocrinoid by Foerste *(16),* has an organization radically unlike that of this class; since it cannot be attributed to some other known class, perhaps it merits a class of its own. Some genera (e.g., *Columbocystis, Foerstecystis, Springerocystis*), in which the nature of exothecal appendages is unknown, may ultimately prove to belong outside of the Eocrinoidea, though they are included here in the class provisionally.

As delimited in the *Treatise*, the Eocrinoidea contain approximately a score of genera, to which are added a few forms too poorly known for definite classification. In comparing these genera with one another, it is possible to set forth characters found to be present in common and on this basis to recognize families. It is difficult to determine the relative importance of these characters, because their phylogenetic significance is unknown. At any rate, the principal features used in classification of the eocrinoids are 1) number and mode of arrangement of thecal plates, 2) presence or absence of sutural pores (or structures associated with them), 3) symmetry of the theca, and 4) disposition of the brachioles. To be noticed is the relatively large number of monotypic families, though this should not be surprising in view of the probable numerous genera and lineages which are unrepresented in the small fraction of once-living forms now available in fossil collections.

The difficulty in constructing a hierarchy of familial morphological characters indicates that the establishment of systematic categories of superfamilial rank would be highly precarious. They could not be based on criteria other than those having fairly well-established phylogenetic signification. One might, indeed, undertake to distinguish two main groups of eocrinoids defined by possession or lack of possession of sutural pores. Since nothing would prove common origin of families that come to be placed on this basis in either group, it is better not to arrange families in this way. Accordingly, they are here presented in a sequence that takes maximum account of degree of similarities.

SYSTEMATIC DESCRIPTIONS

Class EOCRINOIDEA Jaekel, 1918

[*nom. transl.* Regnéll, 1945 (*ex* subclass Eocrinoidea Jaekel, 1918)] [The term Eocrinites, created but not defined by Jaekel in 1899 (23, p. 174), has no taxonomic status; it served apparently to designate collectively such genera as *Acanthocystites, Eocystites* or *Lichenoides*, which were regarded by him as primitive Cladocrinoidea (=Crinoidea Camerata)]

Extinct, stalked or rarely stemless Crinozoa, with theca closed up to peristome, and with or without tegminal region differentiated from aboral part. Radial (generally pentamerous) symmetry affecting food grooves and (in several families) thecal plates, which are solid, without pores (except tiny pores of stereom meshwork). Sutural pores present in many genera, opening directly to exterior or accompanied by epithecal grooves or covered passageways (i.e., epispires) at right angles to sutures of thecal plates. No true arms, but food grooves extended on exothecal skeletal, unbranched, typically biserial, processes (brachioles), which are inserted either on ordinary thecal plates or on special brachioliferous plates lying outside or between thecal plates. *L. Cam.-Sil.*

Family EOCRINIDAE Jaekel, 1918

[=subfamily Acanthocystida Haeckel, 1896 (invalid family-group name)]

Thecal plates numerous, polygonal, indefinite in number, without any regular arrangement or in many alternating transverse rows, but never in well-defined circlets. Brachioles long, slender, biserial, originating in probably five clusters located at periphery of oral face. Stem enclosing wide central cavity. *M.Cam.*

Gogia Walcott, 1917 [**G. prolifica*; OD] [=*Eocrinus* Jaekel, 1918, type, *Eocystites?? longidactylus* Walcott, 1886]. Theca conical, subspherical or subcylindrical. Plates numerous, polygonal, without any definite arrangement, smooth or ornamented with granules or radiating ridges. Sutural pores rimmed by slightly raised ridges. Brachioles 8 to about 22 and probably as many as 44, twisted in *G. spiralis*, originating in clusters. Stem covered by numerous small irregularly arranged polygonal plates that may be gradational with those of theca or of distinctly different size; distal end of stem characterized by cluster of relatively small plates, which may or may not form an expanded flat-based process. *M.Cam.*, N.Am.——Fig. 306,*1-3*. **G. prolifica*, Can.(B.C.); *1*, lectotype, ×1; *2*, theca of same, ×4; *3*, distal end of stem with expanded, flat-based process, ×6 *(31)*. [See also Fig. 294.]

Acanthocystites Barrande, 1887 [**A. briareus*; OD] [=*Acanthocystis* Bather, 1889 *(nom. van.)*]. Theca elongate, apparently conical. Thecal

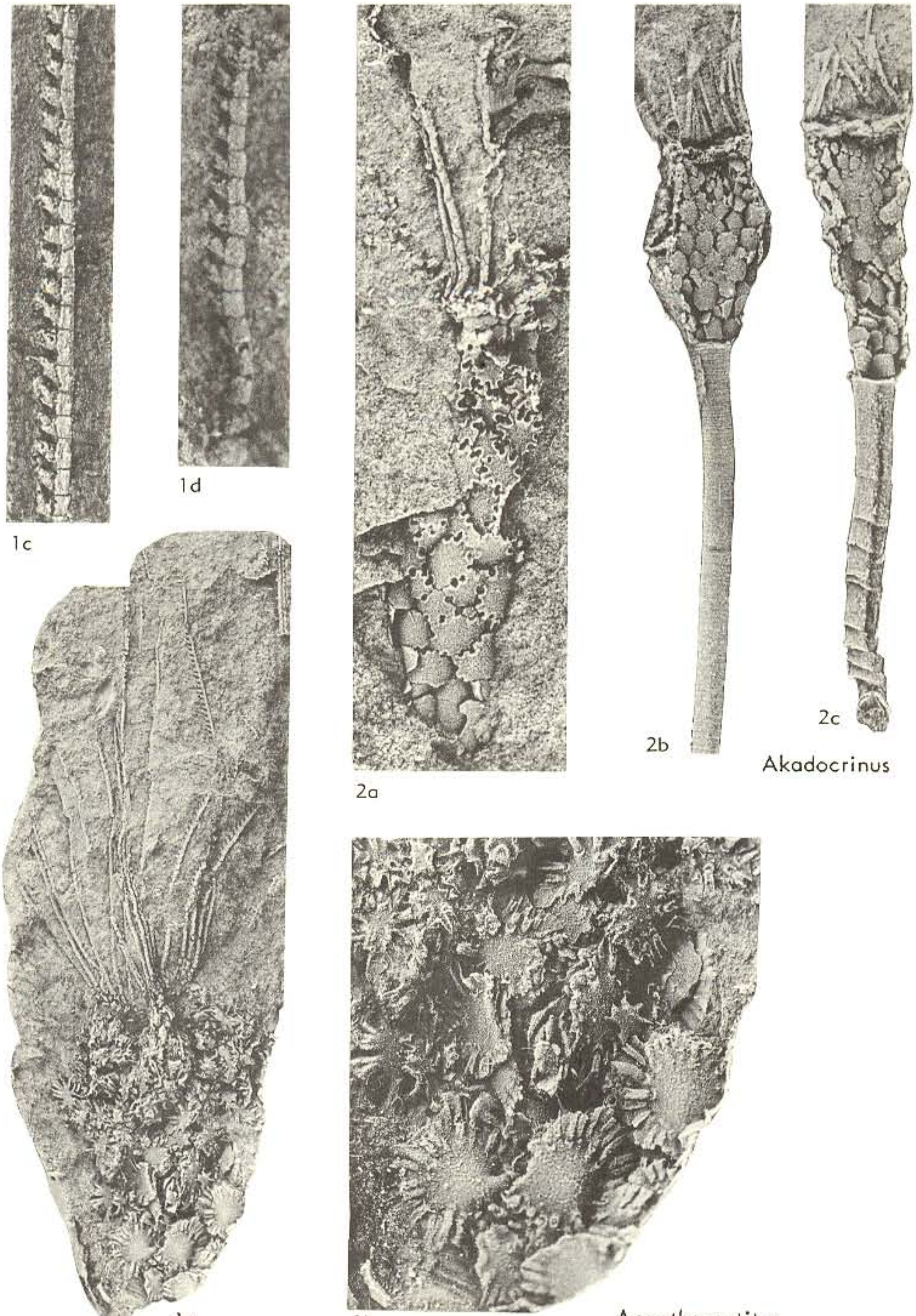


FIG. 307. Eocrinidae (p. *S478*, *S480*).

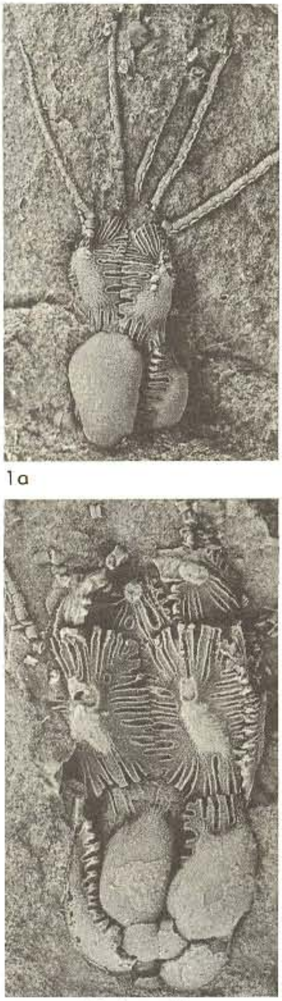


FIG. 308. Lichenoididae (p. S481).

plates thin, irregularly arranged, flat or slightly tumid, ornamented with minute granules; size of plates regularly diminishing in distal direction. Sutural pores leading into covered epispires with seemingly exterior openings at both ends. Cover plates of brachioles relatively large, obliquely protruding, one to each brachiolar ossicle. [Proximal regon of theca and stem lacking in single known specimen.] *M.Cam.*, Boh.——FIG. 307,*1*. **A. briareus*, Jince beds; *1a*, holotype, ×2; *1b*, thecal plates showing covered epispires, ×5; *1c,d*, brachioles, lat. view, ×10 (Ubaghs, n).

Akadocrinus PROKOP, 1962 [**A. jani*; OD] [=*Compsocrinus*[1] ŽELÍZKO, 1911 *(nom. nud.)* (*non* MILLER, 1883)]. Theca relatively small, elongate, bottle-shaped. Oral area between brachiole insertions rather large and flat. Thecal plates irregularly pentagonal or hexagonal, arranged in more or less alternating transverse rows, becoming smaller and more irregular in distal direction. Sutural pores fairly large, rimmed by slightly raised, narrow ridges. Brachioles numerous. Stem long, with proximal diameter as wide as proximal diameter of theca, tapering distally, composed of very low columnals which may meet along irregular zigzag sutures in proximal region. *M.Cam.*, Boh.——FIG. 307,*2a*. **A. jani*, Jince beds; incomplete theca, ×5 (Ubaghs, n).——FIG. 307, *2b,c*. *A. nuntius* PROKOP, Jince beds; *2b*, holotype; *2c*, another specimen, both ×2 (Ubaghs, n).

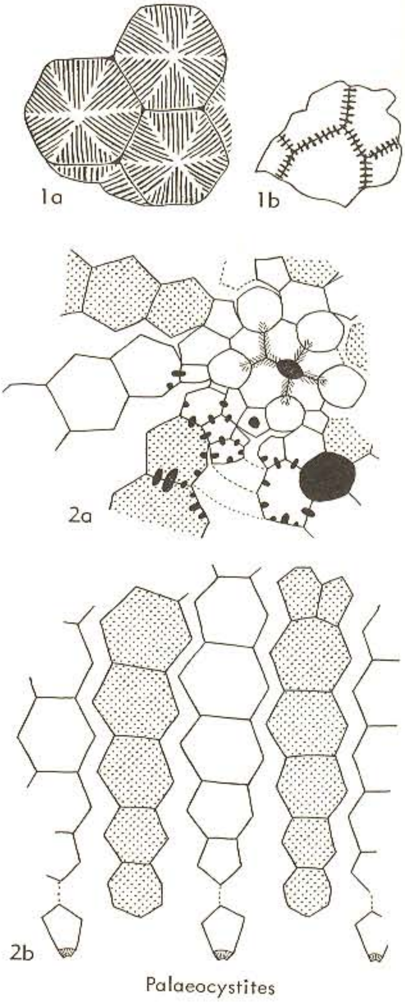


FIG. 309. Palaeocystitidae (p. S481-S482).

---

[1] Name introduced by PERNER in typescript, seemingly first published by ŽELÍZKO in 1911 as *nomen nudum*.

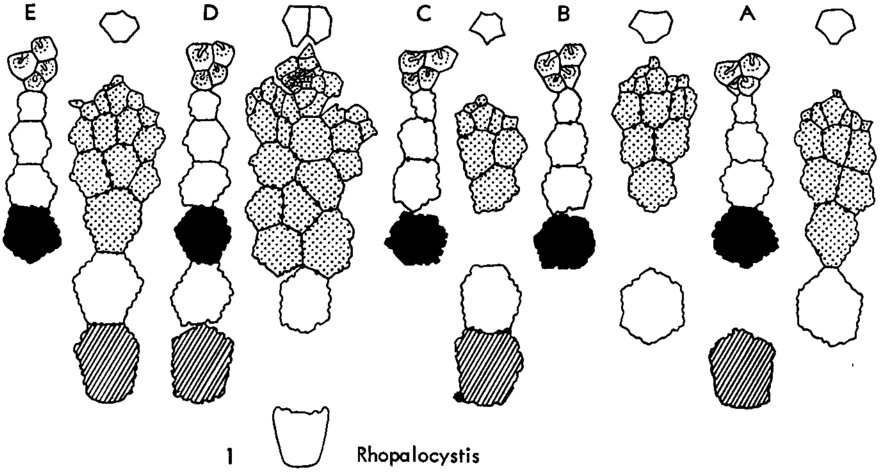


FIG. 310. Rhopalocystidae (p. S481-S482).

Family LICHENOIDIDAE Jaekel, 1918

[*nom. correct.* UBAGHS, herein (*pro* Lichenoidae JAEKEL, 1918)]

Theca composed of three alternating circlets of typically five plates each, plus variable number of small ossicles at aboral pole. Sutural pores numerous, each one passing into an open, well-developed epispire. No "tegmen," but peristome directly surrounded by third circlet of plates (radials). Food grooves epithecal, simple or branching. Brachioles long, biserial, apparently rigid, inserted on second (lateral) and third (radial) circlet of thecal plates. No stem. *M. Cam.*

Lichenoides BARRANDE, 1846 [*L. priscus*; OD] [=*Lichenocystis* HAECKEL, 1896 (*nom. van.*)]. Theca ovoid. Base forming thick-walled cup of large unequal basal plates with their aboral ends partially separated by variable number of small thick ossicles. Middle circlet comprising subpentagonal or subhexagonal lateral plates, largest elements of theca. Upper circlet composed of subpentagonal, rather small radial plates, with thickened inner adoral margin. Epispires rimmed by slightly raised narrow ridges and covering whole surface of plates except brachiole insertions and median stereomic protuberances on basal and lateral plates. Brachioles single or in clusters of 2 or 3 on lateral and radial plates. *M.Cam.*, Boh.——FIG. 308,*1*. **L. priscus,* Jince beds; two specimens; *1a*, ×2; *1b*, ×3 (1). [See also Fig. 295.]

Family RHOPALOCYSTIDAE Ubaghs, new family

Theca divided into 1) proximal part made of single basal ossicle and two alternating circlets of infralateral and lateral plates, 2) middle part composed of five meridional perradial series of plates separated from each other by five interradial plated areas, and 3) oral part comprising circlet of six oral plates and five endothecal ambulacra. Sutural pores numerous, each one opening exteriorly into small depression that is rimmed by narrow ridge. Anus located at adoral end of *CD* interray. Brachioles attached to special plates inserted between other thecal plates. Stem round, progressively tapering distally, composed of low cylindrical columnals. *L.Ord.*

Rhopalocystis UBAGHS, 1963 [**R. destombesi*; OD]. Theca club-shaped, thick-walled. Basal ossicle very thick, cup-shaped; infralaterals 4, pentagonal or hexagonal, largest plates of theca; laterals 6, hexagonal or heptagonal; perradial series of 4 or 5 plates each (one radial and 2 or generally 3 supraradials); interradial areas typically resting on laterals, composed of 4 or 5 rows of interradials; *CD* interray larger than others, asymmetrically divided by a column of extra plates (anals). Peristome central, subpentagonal. Periproct with small anal pyramid. Ambulacra occupying a small stellate area around oral pole, each one composed of 3 to 6 brachioliferous endothecal plates. Brachioles 20 to 30. *L.Ord.*, Morocco.——FIG. 310,*1*. **R. destombesi,* U.Tremadoc, S.Morocco; diagram of theca *(39)*. [See also Fig. 293.]

Family PALAEOCYSTITIDAE Ubaghs, new name (1896)

[=family Palaeocystida HAECKEL, 1896 (invalid family-group name)]

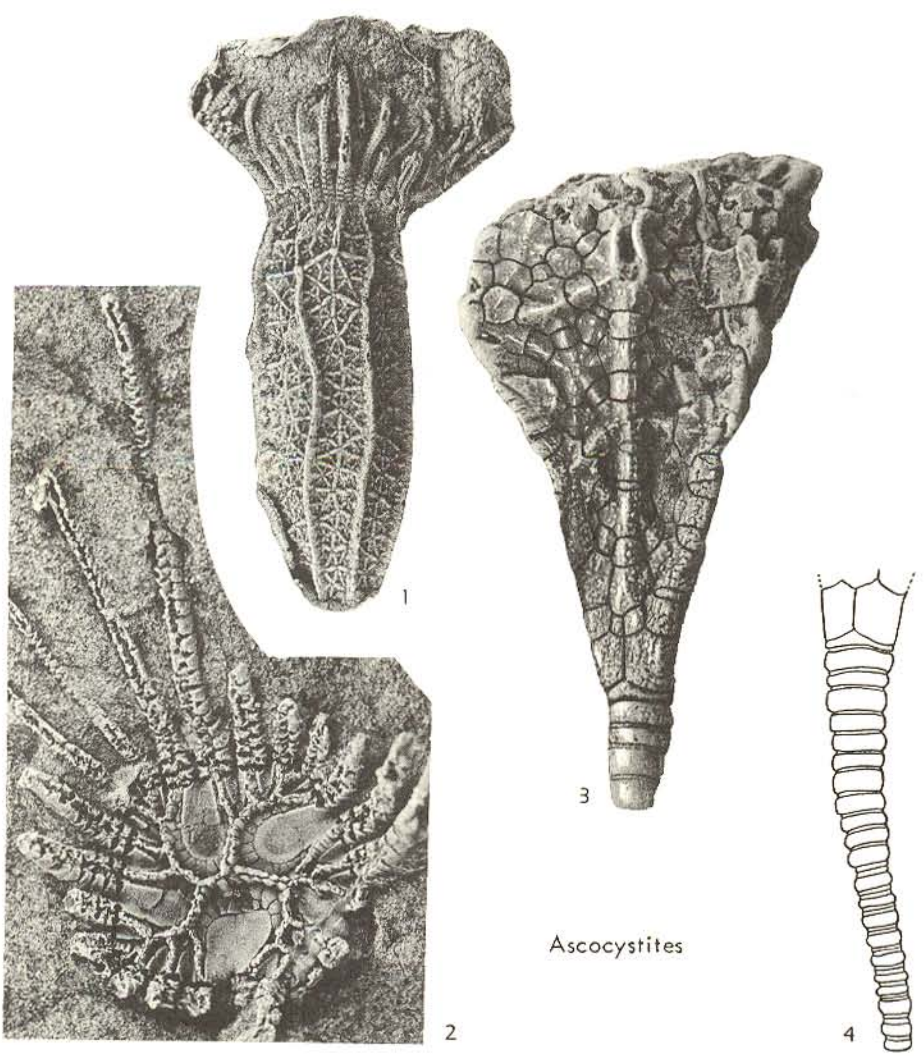


FIG. 311. Ascocystitidae (p. S483).

Theca comprising 1) proximal part of two alternating circlets of five plates each, 2) middle lateral part of ten meridional series of plates, 3) small oral area made of doubled circlet of five orals and five brachioliferous plates, surrounded by more or less complete belt of small irregular plates. Sutural pores opening into covered epispires which externally form elaborate system of strongly raised, radiating ridges. Anus between oral and middle lateral part of theca, in *BC* interray. Pore (?hydropore) in small plate close to oral circlet. Brachioles and stem unknown. *M.Ord.*, N.Am.

Palaeocystites Billings, 1858 [**Actinocrinus tenuiradiatus* Hall, 1847; SD S. A. Miller, 1889] [=*Palaeocystis* Haeckel, 1896 *(nom. van.)*]. Theca elongate, somewhat cylindrical in upper half, conical and proximally tapering in lower half, with hemispherical oral face. Peristome central, rather small. Food grooves along interoral sutures, short, simple or bifurcating into 2 short branches. *M.Ord.*, N.Am.——Fig. 309,*1*. **P. tenuiradiatus* (Hall), Chazyan, USA(N.Y.); *1a,b*, outer and inner sides of thecal plates, enl. *(47)*.——Fig. 309,*2*. *P. dawsoni* Billings, Chazyan, Can.; *2a*, oral area, ×3; *2b*, part of proximal and middle lateral walls of theca, diagram., ×3 *(22)*.

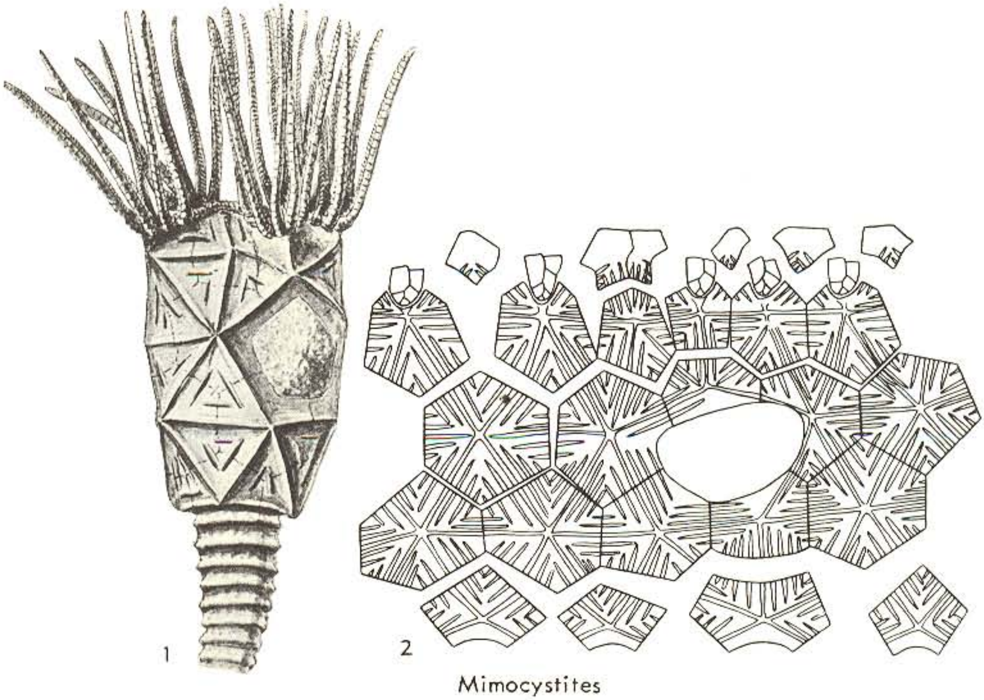


FIG. 312. Macrocystellidae (p. S484-S486).

Family ASCOCYSTITIDAE Ubaghs, new name (1896)

[=family Ascocystida HAECKEL, 1896 (invalid family-group name); Ascocystidae JAEKEL, 1918 (invalid family-group name)]

Theca divided into flat tegmen and elongate aboral part, hexagonal in cross section; aboral part comprising very numerous polygonal plates with subquadrate platelets between them, distributed in six vertical columns and six intermediate fields. No sutural pores, but partially hollow radiating ridges cross sutures. Tegmen composed of five large orals and variable number of adorals. Food grooves exotomously branching. Peristome and food grooves protected by cover plates and outer cover plates. Hydropore? in outer cover plate of *CD* interray. Brachioles 20 to 30, biserial, with deep ventral and dorsal muscle or ligamentary insertions between successive ossicles, forming circle around tegmen; each brachiole inserted on outer edge of an oral and adoral or of two adorals. Anus unknown. Stem round, tapering distally, composed of alternating very thin and thicker columnals. *M.Ord.*

Ascocystites BARRANDE, 1887 [**A. drabowensis*; OD] [=*Ascocrinus* BARRANDE, 1887 (*non* TROMELIN & LEBESCONTE, 1876) (*nom. nud.*); *Ascocystis* BATHER, 1889 (*nom. van.*)]. Thecal plates united by elaborate system of radiating ridges perpendicular to plate sutures and by 6 powerful vertical ridges, running along vertical columns of plates from proximal end to distal margin. *M.Ord.*, Boh.——FIG. 311,*1-4*. **A. drabowensis*; *1*, theca, ×1; *2*, tegmen, ×3; *3*, proximal portion of theca, ×5; *4*, stem, ×5. [The structure figured by JAEKEL [*25*, fig. 9D-F, p. 17] as a hollow root of *Ascocystites* is a foreign body (shell of ?*Conularia*) covered by epizoans (probably brachiopods)] (Ubaghs, n).

Family MACROCYSTELLIDAE Bather, 1899

Theca divided into elongate aboral cup and tegminal portion, and composed of strongly radiately ridged or folded plates, displaying more or less regular pentamerism. Brachioles in five groups. No sutural pores, but radiating hollow ridges cross sutures of thecal plates. Stem round, comprising rapidly tapering proximal region composed of low columnals with wide flange, and gradually tapering distal region composed of long narrow columnals with narrower lumen. *L.Ord.-M.Ord.*

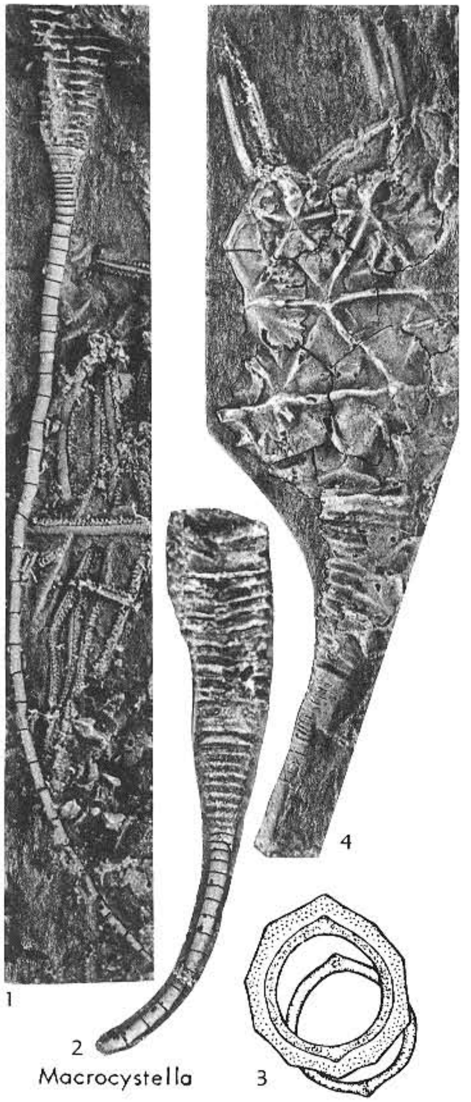


FIG. 313. Macrocystellidae (p. S484).

Macrocystella CALLAWAY, 1877 [**M. mariae*; OD]. Aboral cup showing 4 circlets of plates; those of aboral circlet low, those of 2nd and 3rd circlets relatively large, and of 4th circlet about half size of those in 3rd circlet. Brachioles long, slender, biserial and unbranched, probably inserted on small tegminal elements borne by plates of 4th circlet; cover plates distinct. Aboral thecal plates strongly marked by radiating ridges, which divide surface into triangles, inside of which are smaller folds. [This genus, based on crushed material, is inadequately known; neither the tegmen nor anal side of theca has been observed. The statement by BATHER (5) that each plate of the 4th circlet bears a brachiole, which almost immediately bifurcates, is probably erroneous. So far as determinable from available data, *Macrocystella* does not differ from *Mimocystites,* which is kept apart only provisionally.] *L. Ord.,* Eng.-Ger. (Bavaria)-? Fr.-?Greenl.——FIG. 313,*1-4*. **M. mariae,* Tremadoc, Shineton Shales, Eng.; *1,* almost complete stem, ×3; *2,* proximal and median stem region, ×3; *3,* proximal columns, ×1; *4,* theca, ×3 *(1,2,4,* Ubaghs, n; *3, 32).*

Mimocystites BARRANDE, 1887 [**M. bohemicus*; OD] [=*Mimocystis* CARPENTER, 1891 *(nom. van.)*]. Theca irregularly ovoid, divided into elongate aboral cup and slightly convex oral face, theca composed of 5 circlets of generally alternating plates. Basal circlet of 3 relatively small pentagonal plates and 4th one probably formed by fusion of 2 somewhat larger hexagonal plates. Each of next 2 circlets composed of 5 plates, which are large, theoretically hexagonal or pentagonal, but some variously modified in shape for accommodation of anal area. Plates of 4th circlet relatively small, generally hexagonal, somewhat unequal in size, and distally notched (except one in *CD* interray) for reception of ambulacra. Fifth circlet of 6 orals (2 in *CD* interray), relatively

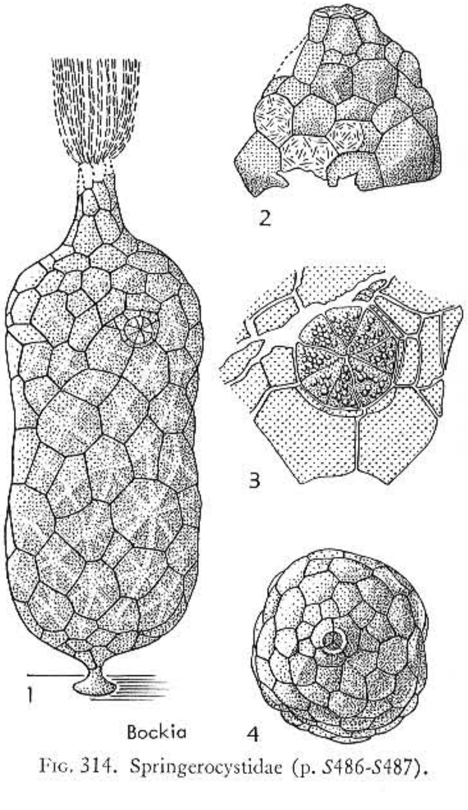


FIG. 314. Springerocystidae (p. S486-S487).

small, lozenge-shaped or subpentagonal in outline, bordering peristome; ambulacra V-shaped, composed of small adorals, bearing brachioles on their outer edge (each brachiole inserted on 2 contiguous adorals). Peristome and food grooves protected by alternating cover plates. Hydropore on suture between orals of *CD* interray. Periproctal area large, oval, lateral, between 2nd and 3rd circlets, filled with small plates and comprising small anal pyramid in *BC* interray. Thecal surface divided into triangles by strongly marked radiating ridges, between which are smaller folds.

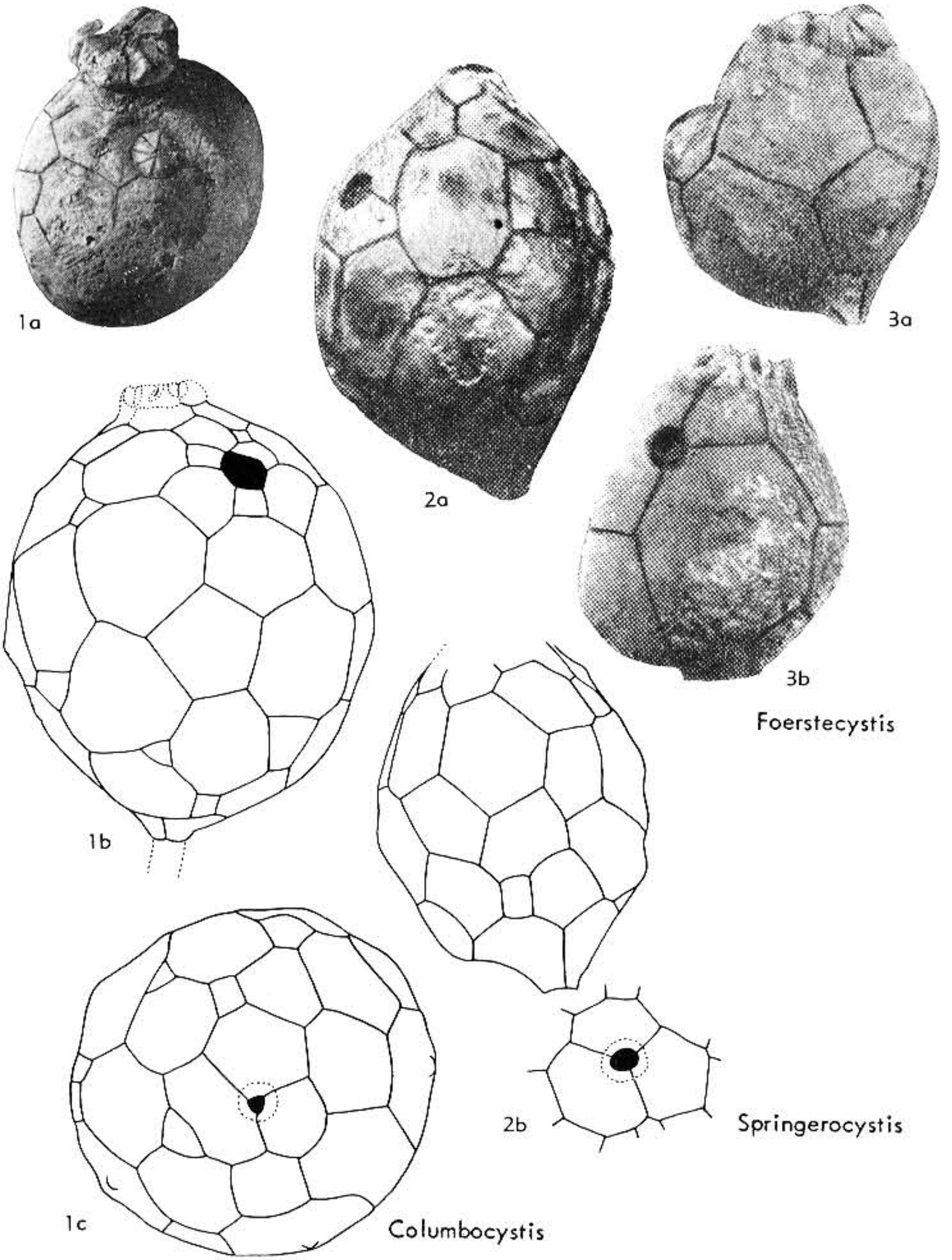


Fig. 315. Springerocystidae (p. *S*486-*S*487).

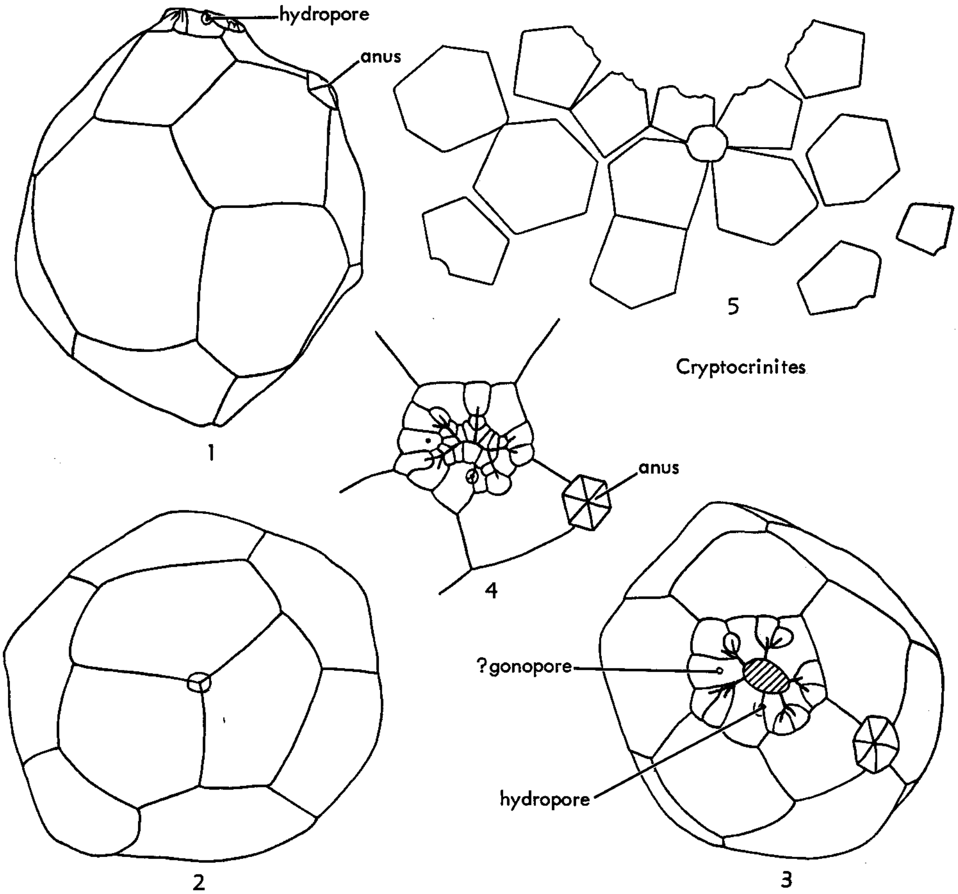


Fig. 316. Cryptocrinitidae (p. S487-S488).

L.Ord.-M.Ord., Boh.-Fr.-Morocco.——Fig. 312,*1*. **M. bohemicus,* M.Ord., Letná beds, Boh.; *1,* restoration by Jaekel *(23),* ×4.——Fig. 312,*2*. *M. azaisi* Thoral, L.Ord.(U.Tremadoc), Hérault, Fr.; diagram of theca *(36).* [See also Fig. 296 and Fig. 299,*1* (oral face).]

Family SPRINGEROCYSTIDAE Bassler, 1950

Thecal plates polygonal, indefinite in number and irregular in shape, size, and arrangement. Basals three, unequal. Theca distally elevated into short protuberance on which are located peristome, food grooves, and brachiole insertions. Anus lateral, with valvular pyramid. Stem facet circular. *L. Ord.-M.Ord.*

Springerocystis Bassler, 1950 [**S. longicollis*; OD]. Theca ovoid or pyriform, proximally produced into short point, distally elevated into tubelike, oral protuberance, upper margin of which is formed by 5 thin oral plates arranged in small circlet. *M.Ord.,* N.Am.——Fig. 315,*2a*. **S. longicollis,* Blackriv., USA(Tenn.); side view of holotype, ×2 *(3).*——Fig. 315,*2b*. *S.* sp., Blackriv., USA(Tenn.); part of lat. view and base, ×3 (Ubaghs, n).

Bockia Gekker, 1938 [**B. neglecta*; SD Gekker, 1940]. Theca elongate, cucumber- or sac-shaped, round in cross section, terminating distally in proboscis-like protuberance, which must have borne oral opening and ambulacral structures. Thecal plates numerous, generally slightly convex, with central umbo and radiating flat ridges, smooth or covered by granules. Anus on upper 3rd of theca, with valvular pyramid. Stem not preserved in connection with theca; discoidal roots found associated with genus may belong to it. *L.Ord.-M.Ord.,* USSR-?Sweden.——Fig. 314,*1-4*. **B. neglecta,* M.Ord., E. Baltic region; *1,* reconstruction, ×1; *2,* distal part of theca, ×1.5; *3,* periproctal area, ×3; *4,* aboral face, ×1.5 *(18).*

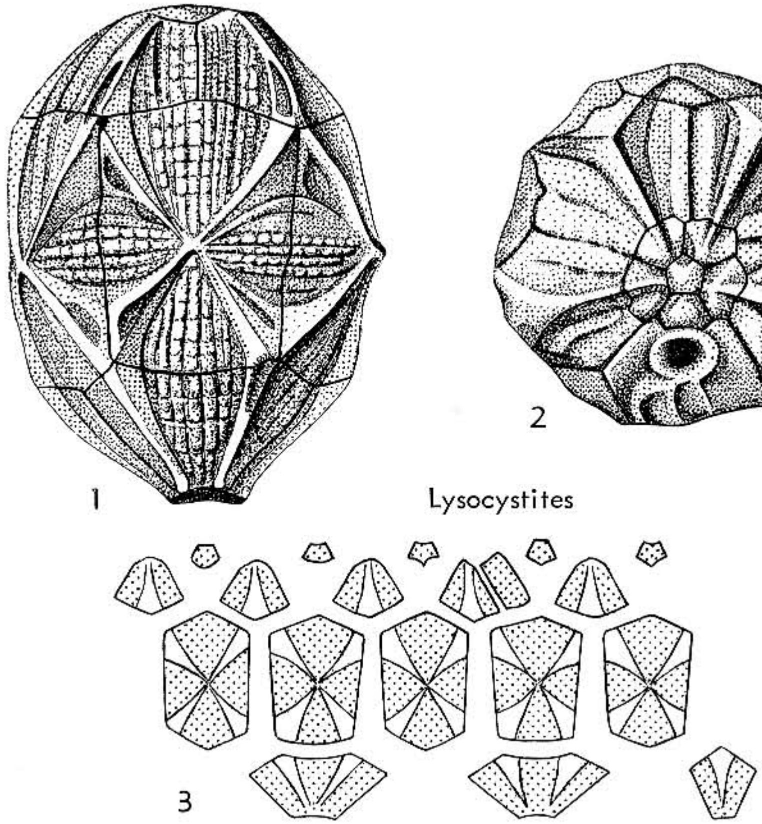


FIG. 317. Cryptocrinitidae (p. S488-S489).

?Columbocystis BASSLER, 1950 [*C. *typica*; OD]. Theca ovoid or subglobose, somewhat asymmetric, with conspicuous oral flattened protuberance composed of 6 thick oral plates (2 in *CD* interray) centering about small peristome. Food grooves on apposed edges of orals. Brachiole facets very large, on outer edge of protuberance, each carried by 2 adjoined orals. Hydropore on suture between 2 orals of *CD* interray. Anus in *BC* interray, protected by anal pyramid. Stem facet small, circular. [Assignment of this genus to Eocrinoidea will be uncertain as long as the "arms" remain unknown.] *M.Ord.*, N.Am.——FIG. 315,*1a*. **C. typica,* Blackriv., USA(Va.); slightly oblique lat. view, ×2 *(3)*.——FIG. 315, *1b,c*. *C. sp.,* Blackriv., USA(Tenn.); side view (*CD* interray) and aboral face, ×2 (Ubaghs, n). [See also Fig. 298,*1*.]

?Foerstecystis BASSLER, 1950 [**F. obliqua*; OD]. Theca irregularly rotund in outline, with anal side very gibbous, especially toward lower end of theca, where it is angularly protuberant in nearly horizontal direction. Thecal plates few. Oral end supporting 5 relatively broad "arms" recumbent on top of theca. [This poorly known genus (no specimen available for study by the present writer) may turn out to belong to another class.] *M.Ord.*, N.Am.——FIG. 315,*3*. **F. obliqua,* Blackriv., USA(Tenn.); *3a,b,* abanal and adanal sides, ×4 *(3)*.

Family CRYPTOCRINITIDAE Bassler, 1938 (1895)

[=Cryptocrinidae ZITTEL, 1895 (invalid family-group name)]

Theca regularly composed of four circlets of plates and more or less completely affected by pentamerous symmetry. Thecal plates in definite number, shape, size, and arrangement; three in basal circlet, unequal, probably produced from five by fusion; five in second circlet; five or six (according to genus) in third circlet; five or six (according to genus) in fourth circlet, which occupies very restricted area around oral pole. No sutural pores. Peristome small. Anus lateral. Brachiole insertions tiny. Stem facet circular. *M.Ord.-Sil.*

Cryptocrinites VON BUCH, 1840 [**C. regularis*

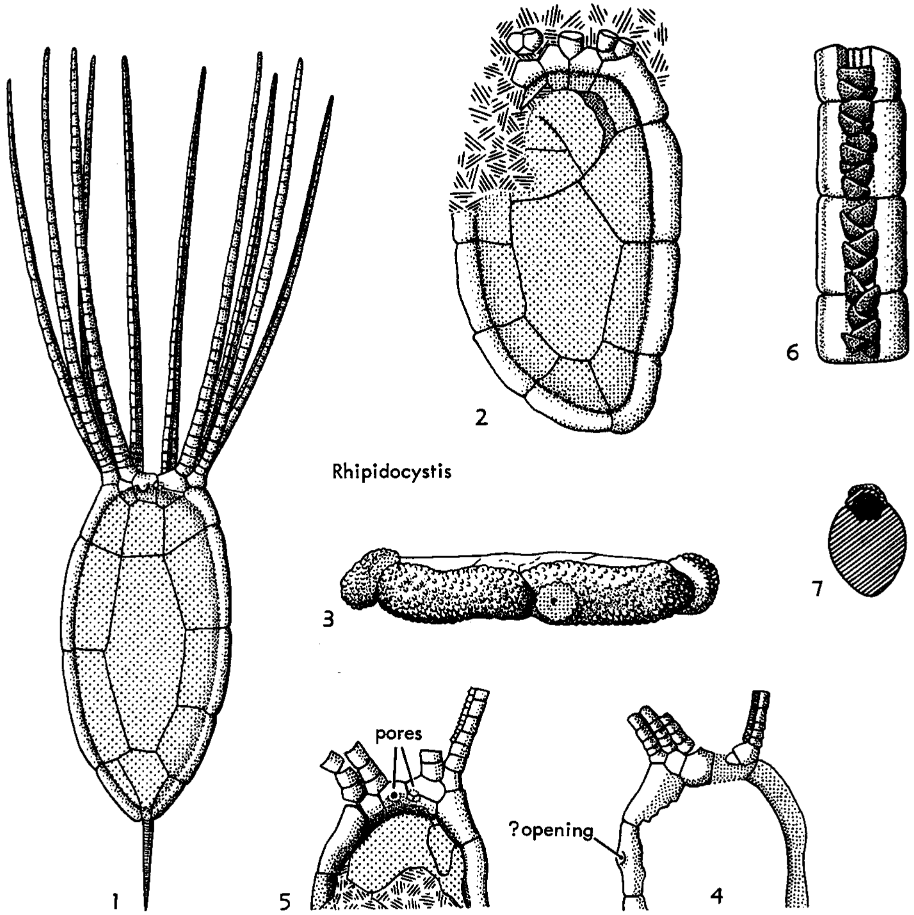
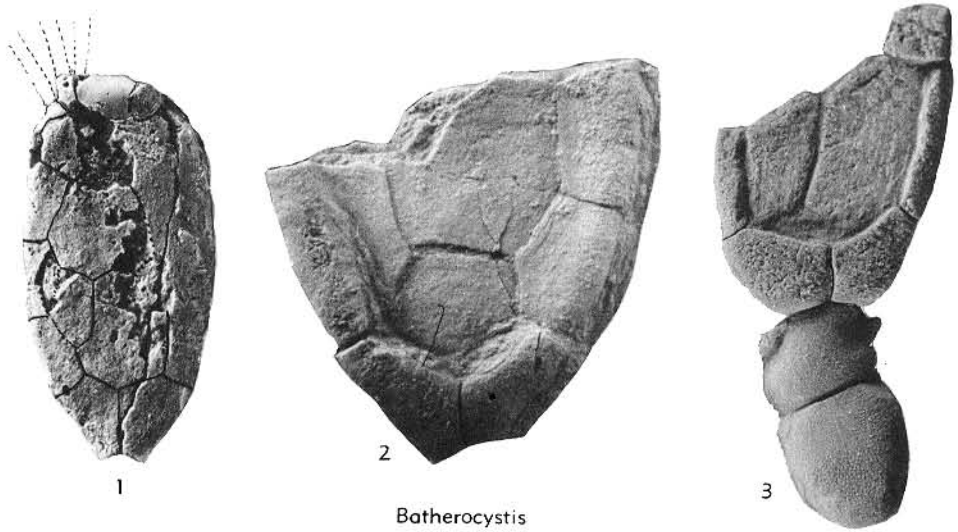


Fig. 318. Rhipidocystidae (p. S489).

(=**Echinosphaerites laevis* Pander, 1830); SD von Buch, 1841] [=*Cryptocrinus* Geinitz, 1846 *(nom. van.)*]. Theca small, irregularly spheroidal. Plates of 2nd circlet large, unequal in size and shape; plates of 3rd circlet 5, smaller, subpentagonal, most of them alternating with plates of preceding circlet; large supplementary plate between 2nd and 3rd circlet; contiguous to periproct; 4th circlet irregularly pentagonal, composed of 6 small oral plates (2 in *CD* interray) surrounding peristome. Food grooves 5, epithecal, very short, on sutures between orals, bifurcating and leading to 10 minute paired brachiole-bearing platelets, which rest on apposed edges of orals. Peristome pentagonal, protected by double series of cover plates (rarely preserved). Periproct hexagonal, with valvular pyramid of 6 plates, located in *BC* interray between 2nd and 3rd circlets of plates. Hydropore on suture between paired orals in *CD* interray; another pore (gonopore?) piercing oral of DE interray. *M.Ord.*, USSR-Sweden. ——Fig. 316,*1-5*. **C. laevis* (Pander), E.Baltic region; *1-3*, lat., aboral, and oral faces, ×4 (Ubaghs, n); *4*, peristome area, cover plates preserved, enl. *(42)*; *5*, diagram of theca, orals excluded (Ubaghs, n).

Lysocystites S. A. Miller, 1889 [*nom. subst. pro Echinocystites* Hall, 1864 (*non* Wyville Thomson, 1861)] [**Echinocystites nodosus* Hall, 1864; OD] [=*Aethocystites* S. A. Miller, 1892; *Echinocystis* Haeckel, 1896 *(nom. van.)*; *Lysocystis* Bather, 1897 *(nom. van.)*; *Scolocystis* Gregory, 1897 (*nom. subst. pro Echinocystites* Hall, 1864); *Aethocystis* Bather, 1900 *(nom. van.)*]. Theca subspheroidal or ovoid. Plates of 2nd circlet very large, elongate, hexagonal; plates of 3rd circlet 6, smaller, pentagonal or quadrate, converging adorally; 4th circlet of 5 very small subtriangular elements enclosing small central peristome, from which shallow and short food grooves extend outward. Anus located near apex of plates of 3rd circlet. Ornamentation consisting of tubular thin-



Batherocystis

FIG. 319. Rhipidocystidae (p. S489-S490).

walled folds surrounding diamond-shaped striated areas. *Sil.*, N.Am.——FIG. 317,*1-3*. *L. sculptus* (S. A. MILLER), Sil.(Niagaran), USA(Ind.); *1*, lat. face showing striation and tubular folds, latter broken in several places, ×1.7 *(33)*; *2*, oral face, ×2.25 *(33)*; *3*, diagram of theca *(15)*.

Family RHIPIDOCYSTIDAE Jaekel, 1901

[=Batherocystidae BASSLER, 1950]

Theca elongate, strongly depressed, presenting two flat faces framed by limited number of marginals surrounding relatively large polygonal central plates. Marginals with thickened outer margins and participating more or less in pavement of flat faces. Brachioles on oral margin of both faces. Stem more or less reduced. *L.Ord.-M.Ord.*

Rhipidocystis JAEKEL, 1900, p. 672 [**R. gigas*; SD BATHER, 1913, p. 369]. Theca subelliptical in outline, with blunt oral and tapering aboral ends. Outer edge of marginals massive and raised, forming framework usually quite distinct from flat and relatively thin pavement of 2 main faces. Basal marginals 3, with proximal ends thickened. Central plates large and few. One or 2 tiny apertures (hydropore?) on adoral marginals and single supplementary one or pit in some on one of lateral marginals. Brachioles long, uniserial, unbranched, inserted in 2 series between or upon adoral marginals. Brachiole ossicles long and massive, with alternating cover plates. Stem facet small, circular, borne by generally single and rarely 2 basal marginals. Stem apparently reduced. Axial canal round and narrow. [*Rhipidocystis,* as originally conceived by JAEKEL *(24)*, comprised remains of four genera, belonging to three different classes. It was demonstrated by GEKKER *(17, 18)* that the "cup-plates" of this "genus" partially belong to the ophiocistioid *Volchovia* and partially to the eocrinoid *Bockia*; the "stem-plates" belong to *Dendrocystites kuckersiana* (now *Heckericystis kuckersiana*), of the Homoiostelea; the flat "appendages of the stem" refer to the genus for which GEKKER retained the name *Rhipidocystis*; the "saclike roots" are the thecae of the eocrinoid *Bockia*. *Rhipidocystis* as emended by GEKKER was regarded by him as a "carpoid," for which he proposed the new order Digitata. Later, UBAGHS *(38)* placed it among the eocrinoids.] *L.Ord.-M.Ord.*, USSR.——FIG. 318,*1-3*. *R. baltica* JAEKEL, L.Ord., Leningrad area; *1*, "upper" face (reconstr.), ×0.7; *2*, theca, "lower" face, ×2; *3*, proximal end of theca and stem facet, ×5 *(24)*.——FIG. 318,*4*. *R. öpiki* GEKKER, M.Ord., Estonia; distal part of theca, "lower" face, with (?) opening in one marginal *(17)*.——FIG. 318,*5-7*, *R. sp.* GEKKER, M.Ord., Estonia; *5*, distal part of theca, "upper" face, with pores on adoral margin, ×2; *6, 7*, oral face of a few brachiolars and cross section, ×10 *(18)*.

Batherocystis BASSLER, 1950 [**B. appressa*; OD]. Theca oblong. Basal marginals 2, with common sutures along middle of flat faces. Central plates more numerous than in *Rhipidocystis,* but probably no more than 7 to 10. Anal? opening relatively large, located slightly below distal end of lateral margins, and surrounded by 3 marginals. Prominent pit on one plate of adoral margin. Brachioles unknown, probably inserted on or between adoral marginals. Stem facet elliptical, relatively large, borne by both basal marginals; columnals apparently very few, inflated, ovoid or somewhat irregularly shaped, elliptical in cross section, abnormally large and massive. [I am greatly indebted to R. L. PARSLEY for information concerning this genus.] *M.Ord.*, N.Am.——FIG. 319,*1*. *B. appressa*, Chazyan, USA(Tenn.); holotype ×2 (Parsley, n).——FIG. 319,*2*. *B. sp.*, USA (Ky.); proximal portion of theca, *ca.* ×3 (Ubaghs, n).——FIG. 319,*3*. *B. sp.*, Blackriv., USA (Va.); proximal portion of theca and 2 columnals, ×4 (Parsley, n).

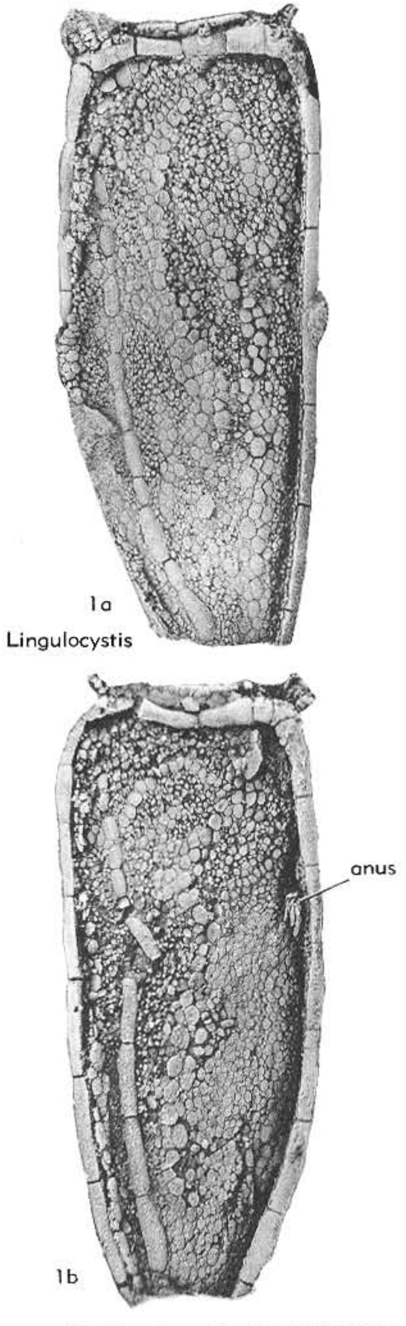


FIG. 320. Lingulocystidae (p. S490-S491).

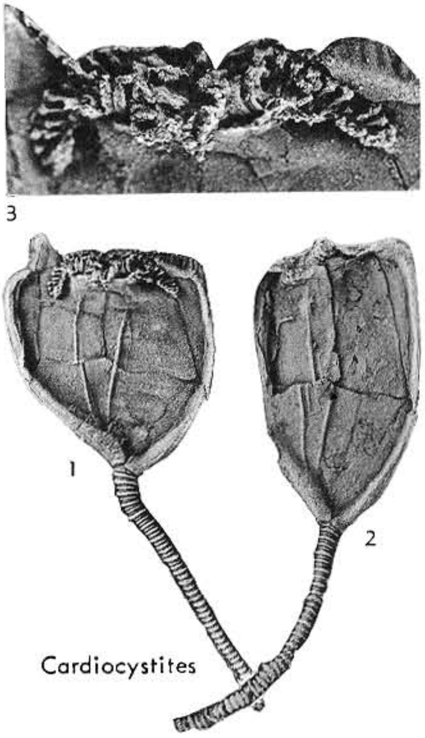


FIG. 321. Unclassified genera (*Cardiocystites*) (p. S491-S492).

Family LINGULOCYSTIDAE Ubaghs, 1960

Theca elongate, depressed, clearly divided into elongate aboral part and low convex oral surface. Marginals numerous, not participating in pavement of flattened faces, which are covered by finely plated integuments. Basals four, equal. Anus lateral. Brachioles carried on special plates inserted in marginal framework at both ends of oral face and in some specimens on ordinary oral marginals. Stem long, round, distally tapering. *L.Ord.*

Lingulocystis THORAL, 1935 [*L. elongata*; OD]. Theca paddle-shaped, probably elliptical in cross section during life. Marginals numerous, elongate, thick and narrow, surrounding both aboral part

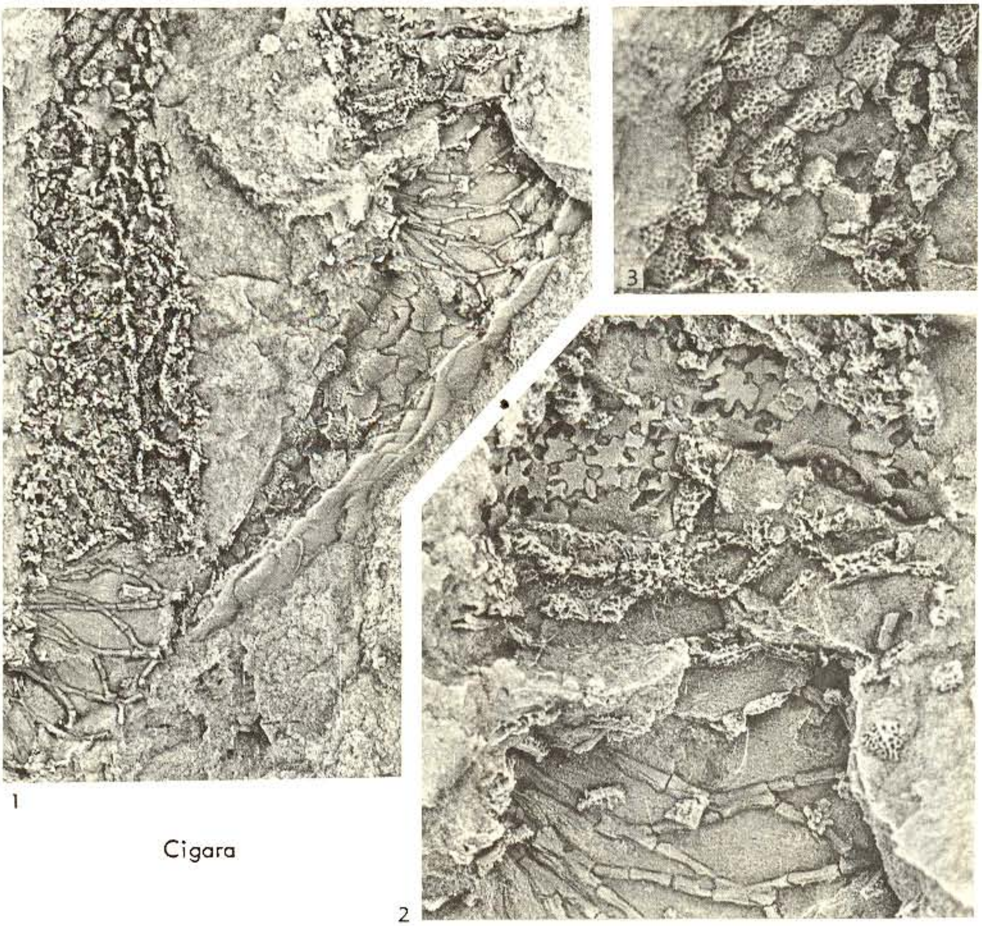


Fig. 322. Unclassified genera *(Cigara)* (p. S492-S493).

and oral surface. Flattened faces apparently pliant, each unequally divided by longitudinal series of relatively large, elongate, slightly convex plates. Anus protected by pyramid of numerous needlelike platelets, located at distal 3rd of theca, near margin. Oral face covered by small plates, with probably subcentral peristome and 2 food grooves leading to clusters of brachioles located at both ends; peristome and food grooves concealed under raised cover plates. *L.Ord.*, France.——Fig. 320, *1*. **L. elongata*, U.Tremadoc-M.Arenig., Hérault; *1a,b*, lectotype, ×3 *(37)*. [See also Fig. 297; 299,*3*.]

UNCLASSIFIED GENERA

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

Cardiocystites Barrande, 1887 [**C. bohemicus*; OD] [=*Cardiocystis* Bather, 1900 *(nom. van.)*]. Theca depressed, moderately elongate, with tapering proximal end and convex lateral margins; distal margin abruptly narrowing and provided on one side with distinct rounded protuberance. Margins strongly thickened and bearing longitudinal groove on large portion of their external face. Theca (only one side known) composed apparently of 2 transverse rows of plates, proximal row of 2 basal marginals and distal row of 2 marginals and probably 2 centrals; admedian parts of marginals and centrals thin. Starting from near proximal end of one of thickened margin, 2 narrow diverging ridges forming V-shaped figure open in distal direction. "Arms" at least 3, apparently short and possibly recumbent, biserial, with sutural faces of successive brachials deeply excavated. Stem long, cylindrical, tapering distally; proximal columnals of unequal height, arranged in more or less regular alternation, each provided with distinct flange; distal columnals higher, all of nearly same size, barrel-shaped and spinose. *M.Ord.*,

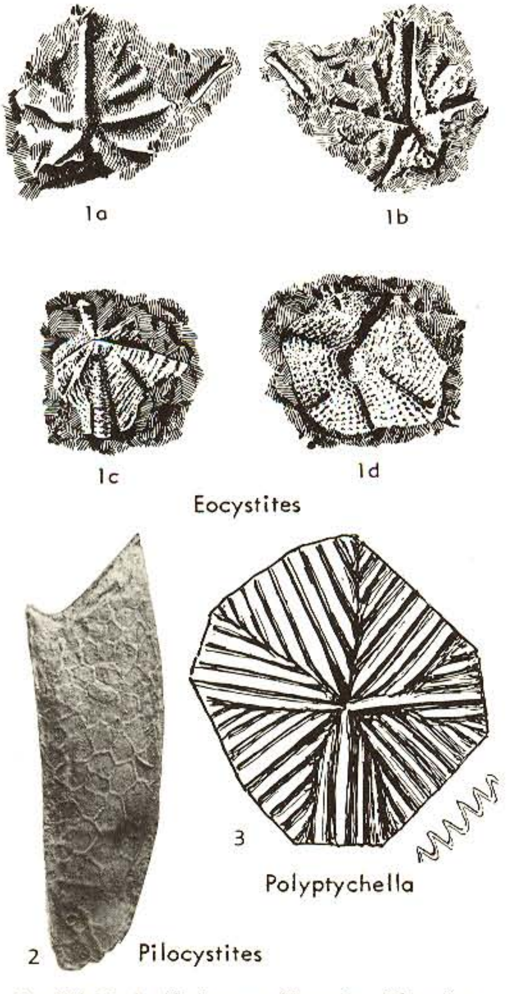


FIG. 323. Unclassified genera *(Eocystites, Pilocystites, Polyptychella)* (p. S492-S493).

Boh.——FIG. 321,*1-3*. **C. bohemicus*; *1,2*, specimens figured by BARRANDE, 1887 (pl. 31, fig. 10-12), ×2; *3*, "arms" of specimen *1*, ×3 (Ubaghs, n).

Cigara BARRANDE, 1887 [**C. dusli*; OD]. Body elongate, composed of 3 regions; 1st or proximal region conical, strongly tapering, covered by thin, polygonal, irregular, and apparently imbricating plates, with delicate radiate ornamentation; middle region characterized by lattice-work of rodlike and X-shaped, exteriorly coarsely ornamented ossicles that enclose diamond shaped, apparently uncalcified or poorly calcified areas; 3rd or distal region slightly tapering distally, composed of numerous, small, stellate plates joining by their ray ends; some plates of distal region distinguished from others by their strongly convex and coarsely pitted outer surface, linked together in such manner as to form irregular, more or less continuous meshwork of ridges, which probably prolong lattice-work of middle region; numerous sutural pores present between all plates of distal region, except most distal ones, which are larger, more convex, and more closely set than others and disposed in oblique, perhaps helicoidal, series. [This enigmatic fossil is represented only by two incomplete specimens on a small slab of shale. BATHER *(5)* thought that it resembles the stem of *Dendrocystites*, in which genus it was placed by BASSLER

FIG. 324. Unclassified genera *(Pareocrinus)* (p. S493).

(2) and by BASSLER & MOODEY *(4)* as a synonym. JAEKEL *(23, 25)* interpreted the proximal region as a stem passing into a saclike hollow root (distal region) and possibly belonging to *Acanthocystites.* These interpretations are unacceptable. The main region (as indicated by the nature of its plates) probably represents a theca prolonged downward by a many-plated extension; such a theca is structurally distinct from that of *Acanthocystites.* No connection with this genus or Homoiostelea are suggested.] *M.Cam.,* Boh.——FIG. 322,*1-3.* **C. dusli,* Jince beds; *1,* specimens figured by BARRANDE (1887, pl. 2. fig. 34), ×2; 2, middle region and proximal part of distal region, showing lattice-work and platelets in outer and inner aspects, ×5; *3,* distal part of distal region, ×5 (Ubaghs, n).

Eocystites BILLINGS, 1868 [**E. primaevus*; OD] [=*Eocystis* BATHER, 1900 *(nom. van.)*]. Genus founded on isolated stellate, probably thecal, plates, having central umbo and variable number of folds which radiate like wheel spokes, most prominent folds reaching umbo and directed toward plate angles. [Discovery of similar plates has been reported from the Middle Cambrian of France, Spain, Morocco, and elsewhere but their assignment to *Eocystites* is uncertain.] *M.Cam.,* N.Am. ——FIG. 323,*1.* **E. primaevus*; *1a,c,* internal, and *1b,d,* external imprints of plates, ×4 *(6).*

Lapillocystites BARRANDE, 1887 [**L. fragilis;* OD] [=*Lapillocystis* BATHER, 1889 *(nom. van.)*]. Body ovoid in outline, composed of many small, irregular, polygonal plates; inadequately known. [According to JAEKEL (23), this fossil comprises the hollow root of an eocrinoid, possibly *Acanthocystites.*] *M.Cam.,* Boh.

Pareocrinus YAKOVLEV, 1956 [**P. ljubzovi*; OD]. Theca small, proximally conical, medially cylindrical, distally truncated by flat oral surface. Cylindrical part composed of 5 or 6 vertical alternating columns of very thin plates, each centrally elevated into conical protuberance. Small circular opening (anus?, hydropore?) at top of one vertical column. Brachioles about 10, slightly longer than theca, attached to elevated processes on margin of oral face. Stem cylindrical, narrow, distally tapering. *M.Cam.* or *U.Cam.,* USSR(Sib.).——FIG. 324,*1.* **P. ljubzovi,* up. M. Cam. or low. U. Cam., E.Sib.; holotype, ×3 *(46).*

Pilocystites BARRANDE, 1887 [**P. primitivus*; OD]. Body elongate, rounded at one end, obliquely truncated at other, divided into polygonal areas by slightly raised limits. [This genus, generally assigned to cystoids, was regarded by JAEKEL *(23)* as a doubtful root fragment of a cladocrinoid but probably it is not even an echinoderm.] *M.Cam.,* Boh.——FIG. 323,*2.* **P. primitivus*; holotype, ×1 (Ubaghs, n).

Polyptychella JAEKEL, 1918 [**P. esthona*; OD]. Genus based on isolated polygonal plates characterized by many radial folds set at right angles to plate sutures. [Placed by JAEKEL *(25)* among Macrocystellidae.] *M.Ord.,* Est.——FIG. 323,*3.* **P. esthona,* Brandschiefer; holotype, enlarged *(25).*

?**Protocystites** HICKS, 1872 [*non* SALTER, 1865 *(nom. nud.)*; =*Protocystis* BATHER, 1900 *(nom. van.), non* WALLICH, 1862].

?**Trachelocrinus** ULRICH, 1929.

REFERENCES

Barrande, Joachim

(1) 1887, *Classe des échinodermes. Ordre des cystidées:* in Système silurien du centre de la Bohême. Part I: Recherches paléontologiques, Ouvrage posthume de feu Joachim Barrande, publié par le Doct. W. Waagen, v. 7, pt. 1, 233 p., 39 pl., Gerhard (Leipzig), Řivnáč (Prague).

Bassler, R. S.

(2) 1938, *Pelmatozoa Palaeozoica (generum et genotyporum index et bibliographica):* Fossilium Catalogus, pt. 1, Animalia, W. Quenstedt (ed.), pars 83, p. 1-194, W. Junk ('s-Gravenhage).

(3) 1950, *New genera of American Middle Ordovician "Cystoidea":* Washington Acad. Sci., Jour., v. 40, no. 9, p. 273-277, fig. 1-19.

——, & Moodey, M. W.

(4) 1943, *Bibliographic and faunal index of Paleozoic pelmatozoan echinoderms:* Geol. Soc. America, Spec. Paper no. 45, 734 p.

Bather, F. A.

(5) 1900, *The Echinoderma. The Pelmatozoa:* in E. R. Lankester (ed.), A treatise on zoology, v. 3, p. 1-216, A. & C. Black (London).

(6) 1918, *Eocystis, I. Eocystites primaevus Hartt.:* Geol. Mag., new ser., dec. 6, v. 5, p. 49-56, pl. 5.

Billings, Elkanah

(7) 1858, *On the Cystideae of the Lower Silurian rocks of Canada:* Canada Geol. Survey, Figures and descriptions of Canadian organic remains, dec. 3, p .9-74, pl. 1-7.

Buch, Leopold von

(8) 1840, *Über Sphaeroniten und einige andere Geschlechter, aus welchen Crinoideen entstehen:* K. Preuss Akad. Wiss. Berlin, Bericht Bekanntmach. geeign., Verhandl., for year 1840, p. 56-60.

(9) 1841, *Beiträge zur Bestimmung der Gebirgsformationen in Russland:* Archiv f. Min., Geogn., Bergbau & Hüttenkunde, for year 1841, p. 3-128, pl. 1-3.

(10) 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.

Choubert, Georges, Termier, Henri, & Termier, Geneviève

(11) 1953, *Presénce du genre Mimocystites Barrande dans l'Ordovicien du Maroc:* Serv. Mines Carte Géol. Maroc, Div. Mines & Géol., Notes & Mém., no. 117, p. 137-143, 7 text fig.

Cuénot, Lucien

(12) 1953, *Classe des Cystidés (Cystidea von Buch 1844):* in Traité de paléontologie, Jean Piveteau (ed.), v. 3, p. 607-628, 31 text fig., Masson et Cie (Paris).

Durham, J. W.

(13) 1964, *The Helicoplacoidea and some possible implications:* Yale Scient. Mag., v. 39, no. 2, p. 24-28, 2 text fig.

Fell, H. B.

(14) 1963, *The evolution of the echinoderms:* Smithson. Inst., Ann. Rept. for 1962, p. 457-490, pl. 1-3.

Foerste, A. F.

(15) 1920, *Racine and Cedarville cystids and notes on other echinoderms:* Ohio Jour. Sci., v. 21, no. 2, p. 33-78, pl. 1-4.

(16) 1938, *Echinodermata:* in C. E. Resser, & B. F. Howell, Lower Cambrian Olenellus Zone of the Appalachians: Geol. Soc. America, Bull., v. 49, p. 195-248, pl. 1-13.

Gekker [Hecker], R. F.

(17) 1938, *Novye dannye o rode Rhipidocystis Jkl (otryad Digitata n. o., klass Carpoidea Jkl) i novyy rod Bockia n.g. (podklass Eocrinoidea Jkl, klass Crinoidea Mill.) iz nizhnego silura Leningradskoy oblasti SSSR i Estonii:* Acad. Sci. URSS, Comptes Rendus, new ser., v. 19, no. 5, p. 421-424, 2 text fig. [*New data on Rhipidocystis Jkl (order Digitata n.o., class Carpoidea Jkl) and on a new genus Bockia (Subclass Eocrinoidea Jkl, class Crinoidea Mill.) from the Ordovician of Leningrad Province, USSR, and Estonia.*]

(18) 1940, *Carpoidea, Eocrinoidea, i Ophiocistia nizhnego silura Leningradskoy oblasti i Estonii:* Acad. Sci. URSS, Travaux (Trudy), Inst. Paléont., v. 9, no. 4, p. 5-82, pl. 1-10. [*Carpoidea, Eocrinoidea and Ophiocistia from the Ordovician of the Leningrad region and Estonia.*] (Russian with German summary.)

(19) 1964, *Klass Eocrinoidea. Eokrinoidei:* in Osnovy Paleontologii, Yu. A. Orlov (ed.), Iglokozhie, gemikhordovye, pogonofory, i shchetinkochelyustnye, p. 52-53, pl. 7, text fig. 46-48. [*Class Eocrinoidea,* in Fundamentals of paleontology, Echinoderms, hemichordates, pogonophores, and chaetognaths.]

Haeckel, Ernst

(20) 1896, *Die Amphorideen und Cystoideen, Beiträge zur Morphologie und Phylogenie der Echinodermen:* Festchr. b. siebenzigsten Geburtstage von Carl Gegenbaur am 21. August 1896, v. 1, p. 1-179, pl. 1-5, W. Engelmann (Leipzig).

Harker, Peter, & Hutchinson, R. D.

(21) 1953, *A new occurrence and redescription of Gogia prolifica Walcott:* Jour. Paleontology, v. 27, p. 285-287, pl. 40.

Hudson, G. H.

(22) 1911, *Studies of some early Siluric Pelmatozoa:* N.Y. State Museum, Bull. 149, p. 195-272, 36 text fig., pl. 1-7.

Jaekel, Otto

(23) 1899, *Stammesgeschichte der Pelmatozoen. 1. Thecoidea und Cystoidea:* 442 p., 18 pl., Julius Springer (Berlin).

(24) 1901, *Über Carpoideen, eine neue Klasse von Pelmatozoen:* Deutsch. Geol. Gesell., Zeitschr., for year 1900, p. 666-677, fig. 1-11.

(25) 1918, *Phylogenie und System der Pelmatozoen:* Paläont. Zeitschr., v. 3, no. 1, p. 1-128, 114 text fig.

Moore, R. C.

(26) 1954, *Status of invertebrate paleontology, 1953. IV. Echinodermata: Pelmatozoa:* Harvard Univ., Museum Comp. Zoology, Bull., v. 112, no. 3, p. 125-149, text fig. 1-8.

Nichols, David

(27) 1962, *Echinoderms:* 200 p., 26 text fig., Hutchinson & Co. (London).

Prokop, Rudolf

(28) 1962, *Akadocrinus nov. gen., a new crinoid from the Cambrian of the Jince area (Eocrinoidea):* Ústřed. Ústavu Geol., Sborník, v. 27 (1960), Odd. paleont., p. 31-39, 3 pl.

Regnéll, Gerhard

(29) 1945, *Non-crinoid Pelmatozoa from the Paleozoic of Sweden:* Lunds Geol.-Mineral. Inst., Medd., no. 108, p. 1-255, pl. 1-15.

(30) 1960, *"Intermediate" forms in early Palaeozoic echinoderms:* Internatl. Geol. Congress, Rept. XXI Session, pt. 22, p. 71-80 (Copenhagen).

Robison, R. A.

(31) 1965, *Middle Cambrian eocrinoids from western North America:* Jour. Paleontology, v. 39, p. 355-364, 3 text fig., pl. 50-52.

Sdzuy, Klaus

(32) 1955, *Cystoideen aus den Leimitz-Schiefern (Tremadoc):* Senckenbergiana Lethaea, v. 35, p. 269-276, text fig. 1-5, pl. 1.

Springer, Frank

(33) 1926, *American Silurian crinoids:* Smithsonian Inst., Publ. no. 2871, p. 1-239, pl. 1-33.

Termier, Henri, & Termier, Geneviève

(34) 1948, *Les échinodermes du Paléozoïque*

inférieur: La Revue Scientifique, v. 86, p. 613-626, text fig. 1-41.

(35) 1954, *A propos de la structure des Eocrinoïdes:* Soc. Géol. France, Comptes Rendus, no. 4, p. 92-94, 5 text fig.

Thoral, Marcel

(36) 1935, *Contribution à l'étude paléontologique de l'Ordovicien inférieur de la Montagne Noire et révision sommaire de la faune cambrienne de la Montagne Noire:* 362 p., 35 pl. (Montpelier).

Ubaghs, Georges

(37) 1953, *Notes sur Lichenoides priscus Barrande, Eocrinoïde du Cambrien moyen de la Tchécoslovaquie:* Inst. Royal Sci. Nat. Belgique, Bull., v. 29, no. 34, p. 1-24, 12 text fig.

(38) 1960, *Le genre Lingulocystis Thoral (Echinodermata, Eocrinoidea), avec des remarques critiques sur la position systématique du genre Rhipidocystis Jaekel:* Ann. Paléontologie, v. 46, p. 81-116, text fig. 1-9, pl. 1-3.

(39) 1963, *Rhopalocystis destombesi n.g., n.sp., Eocrinoïde de l'Ordovicien inférieur (Trémadocien supérieur) du Sud marocain:* Serv. Geol. Maroc, Notes & Mém., v. 23, no. 172, p. 25-40, text fig. 1-9, pl. 1-3.

Walcott, C. D.

(40) 1886, *Second contribution to the studies on the Cambrian faunas of North America:* U.S. Geol. Survey, Bull. 30, p. 727-1095, 33 pl.

(41) 1917, *Cambrian geology and paleontology IV, fauna of the Mount Whyte formation:* Smithsonian Misc. Coll., v. 67, no. 3, p. 61-114, pl. 8-13.

Yakovlev, N. N.

(42) 1918, *Novye dannye o rode Cryptocrinus i svyaze morskikh lilii s tsistoideyami:* Soc. Paléont. Russie, Ann., v. 2 (1917), p. 7-26. [*Some new data on Cryptocrinus and the connection between the Crinoidea and Cystoidea.*]

(43) 1927, *Sur l'homologie dans la structure de la face ventrale du calice de Cystoidea et de Crinoidea:* Akad. Nauk SSSR, Doklady, 1927, A, p. 54-56.

(44) 1928, *Sur quelques collections paléozoïques des musées de l'Europe occidentale:* Comité Géol. Léningrad, Bull., v. 47, no. 1, p. 65-70, 1 text fig.

(45) 1928, *Sur l'évolution discontinue chez les brachiopodes et les échinodermes et l'irréversibilité de l'évolution chez les premiers:* Palaeobiologica, v. 1, p. 371-376.

(46) 1956, *Pervaya nakhodka morskoy lilii v Kembrii SSSR:* Akad. Nauk SSSR, Doklady, v. 108, no. 4, p. 726-727, pl. 1. [*First discovery of crinoids in the Cambrian of the USSR.*]

Zittel, K. A. von

(47) 1924, *Grundzüge der Paläontologie (Paläozoologie)* (Neubearbeitet Ferdinand von Broili): v. 1, edit. 6, 733 p., 1467 text fig., Oldenbourg (München, Berlin).

HOMALOZOANS

By Georges Ubaghs and K. E. Caster

Included in this assemblage are the "carpoid" classes Stylophora, Homostelea, and Homoiostelea, all of which are represented in Cambrian strata but none in post-Devonian deposits.

STYLOPHORA

By Georges Ubaghs

[Université de Liège, Belgium]

[Acknowledgments and cordial appreciation are expressed for assistance furnished by R. C. Moore and K. E. Caster in translations of French text for this chapter. Likewise to officers of various institutions and to other individuals for opportunity to study fossils in their collections, thanks are expressed to *(Austria)* Naturhistorisches Museum, Wien; *(Czechoslovakia)* Národní Museum, Praha; *(France)* R. Courtessole, Gérard Griffe, and Gilbert Griffe, all in Carcassonne; Muséum d'Histoire Naturelle, Paris; Université de Lyon; Université de Montpellier; Université de Rennes; *(Germany)* Ernst Moritz Arndt Universität, Greifswald; Humboldt Universität, Berlin; F. Krantz, Bonn; *(United Kingdom)* British Museum (Natural History), London; Hunterian Museum, University of Glasgow; *(United States of America)* United States National Museum, Washington.]

CONTENTS

INTRODUCTION

The class Stylophora corresponds to the superorder Stylophora (class Carpoidea) proposed by GILL & CASTER (1960, *43*) and embraces the orders Mitrata and Cornuta of JAEKEL (1918,*55*). Forms belonging to these two orders possess the same basic organization, which differs profoundly from that of both Homostelea and Homoiostelea.

Like other "carpoid" echinoderms, stylophorans are asymmetrical flattened organisms which lack any trace of radial symmetry. Their body is composed of a **theca** made of plates, attached to which is a highly characteristic jointed appendage known as the **aulacophore,** here interpreted as a brachial process. Until recently, it was considered erroneously to be homologous to the stele (peduncle) of other "carpoids" *(88)*. The mouth, probably intrathecal, was located at the base of the aulacophore and the anus at or near the opposite extremity of the theca. The placement of these orifices at opposite poles of the theca, combined with presence of an aulacophore, absence of a stele or other sort of peduncular process, and lack of marginal external grooves clearly distinguish the Stylophora from the Homostelea. Stylophorans differ from the Homoiostelea in lacking a stele and in having a brachial process (aulacophore) differentiated into three distinct regions, instead of an arm with the same composition throughout.

In contrast to other "carpoids" so far known, the Stylophora comprise a great diversity of forms. These range from the very peculiar, quite asymmetrical *Cothurnocystis* to genera like *Placocystites* with nearly developed bilateral symmetry. In the Old World stylophorans are known from Middle Cambrian to Middle Devonian, and in the New World from Upper Cambrian to Lower Devonian.

MORPHOLOGY AND FUNCTION

GENERAL CHARACTERS

The skeleton of Stylophora is composed of two parts—a theca that incloses the body, and a unique brachial process termed the aulacophore (Fig. 325). No stele or peduncle is observed. As in other "carpoids," organization of the theca is fundamentally asymmetrical, but several groups, especially within the Mitrata, exhibit a tendency to acquire bilateral symmetry. This is never perfect, however, and must be considered as secondary, since it appears late in the history of the groups.

A stylophoran theca lying flat on a horizontal surface invariably slants downward away from the aulacophore. In the Mitrata

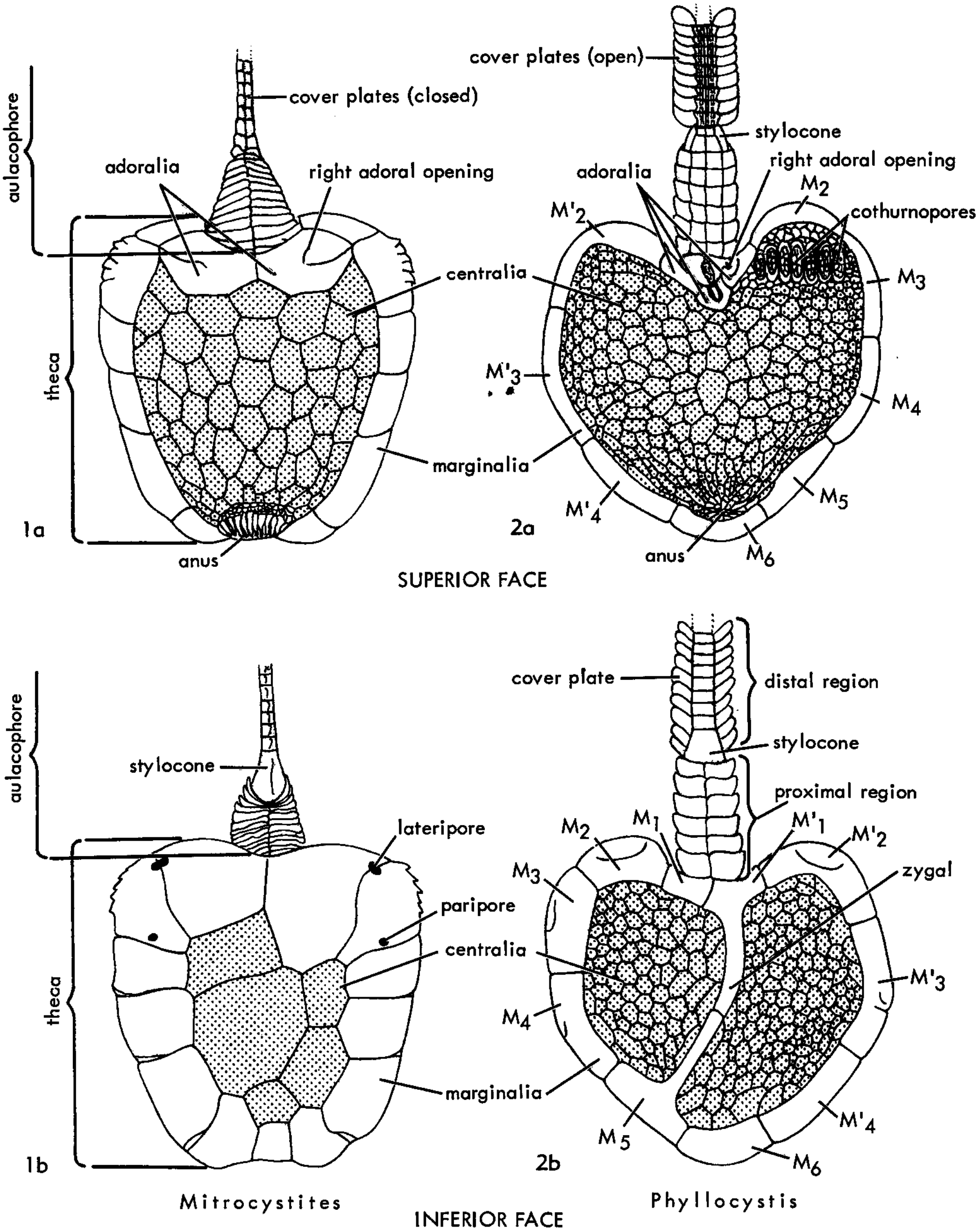


Fig. 325. General features of Stylophora.——*1. Mitrocystites mitra* Barrande, M.Ord., Boh; *1a,b,* superior and inferior faces, ×2.2 (Ubaghs, n).——*2. Phyllocystis blayaci* Thoral, L.Ord., Fr.; *2a,b,* superior and inferior faces, ×1.5 (Ubaghs, n) (M_1-M_6, right marginalia; M'_1-M'_4, left marginalia; centralia stippled).

the theca generally is oval or subrectangular in outline (Fig. 325,*1*); it is somewhat elongate and more or less symmetrical. As a rule, at least one of the faces is covered by large plates. In the Cornuta the theca ordinarily is much more asymmetrical and less regular in shape (Fig. 325,*2*), for instance, with outline resembling that of a pointed boot (e.g., *Cothurnocystis*) or a playing-card heart (e.g., *Phyllocystis*). It may be

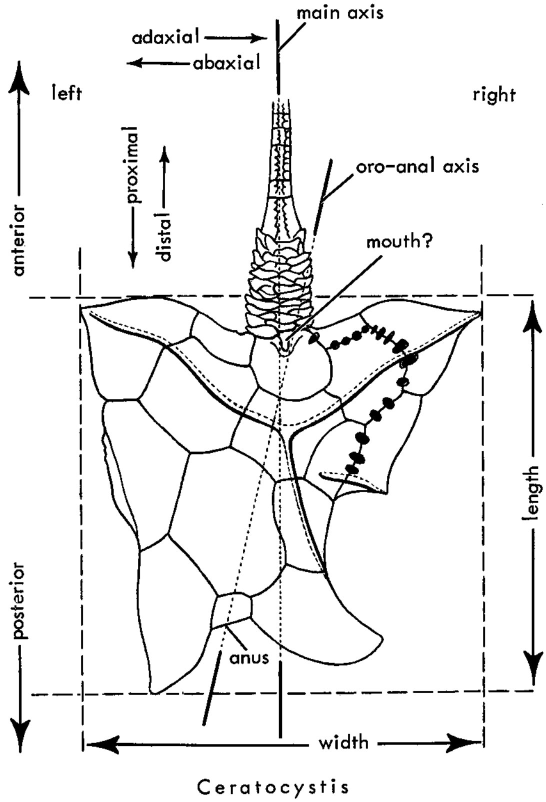


FIG. 326. Orientation of Stylophora. *Ceratocystis perneri* JAEKEL, M.Cam., Boh.; superior face, ×1.8 (Ubaghs, n).

entirely composed of large plates, but more commonly a framework of marginal pieces is sharply set off from sheets of pavement platelets which occupy the two faces. In both groups articulated or fixed appendages may extend outward from the framework, adding to the strange appearance of these creatures.

The two faces of the depressed theca differ in form and composition. The lower one **(inferior face)**, upon which the animal presumably reposed in life, is flat or concave, and the upper one **(superior face)** is convex. The border of the theca consists of a framework of marginal pieces **(marginalia)** which surround a variably large number of plates or platelets **(centralia)** on faces of the theca, those of the lower face being called **infracentrals (infracentralia)** and those of the upper face **supracentrals (supracentralia)**[1] (Fig. 325).

The insertion of the aulacophore is surrounded typically by four or five plates—two marginal plates below and two or three adorals **(adoralia)** above (Fig. 325,*1a,2a*). Some authors have designated these plates erroneously as basals. The adorals form part of the border framework of the theca in Cornuta and generally do not participate appreciably in the covering pavement of the upper face. In the Mitrata, on the other hand, the adorals always occupy part of the upper face and in a few genera (e.g., *Balanocystites*) all of it. According to my interpretation, the two main apertures (mouth, anus) of the body were situated respectively at or near the base of the aulacophore and at the opposite extremity of the theca or in its immediate vicinity. The mouth cannot be observed, however; it is

---

[1] JAEKEL (55) termed these plates hypocentrals and epicentrals, which are hybrid Greek-Latin designations; here all-Latin names are substituted.

judged to have been intrathecal, as in the Homoiostelea.

An orifice called the **right adoral opening,** presumed to be a hydropore (possibly combined with gonopore), is seen in some genera, notching or piercing one of the adoralia (Fig. 325,*1a,2a*). The role of other orifices (e.g., lateripores, paripores, cothurnopores, Fig. 325,*1b,2a*) remains conjectural.

The aulacophore of stylophorans invariably is divisible into three distinct parts (Fig. 325,*2b*). Next to the theca is an inflated hollow **proximal region,** the cavity of which communicates with that of the theca. An intermediate solid piece is termed the **stylocone.** A **distal region** consists of a single series of ossicles placed end to end. The upper face of the stylocone and distal ossicles bears a groove which is interpreted here as an **ambulacral furrow.** It is protected by a double series of **cover plates** which may open and close (Fig. 325,*1a,2a*).

ORIENTATION AND TERMINOLOGY

The major plane of the depressed stylophoran theca has been called the **extension plane** by Bather (1913,*13*) and the **extensiplane** by Gill & Caster (1960,*43*). The two faces of the theca, as previously noted, are the upper or superior (=obverse of Bather, 1913,*13*) and lower or inferior (=reverse of Bather, 1913,*13*); this terminology is based on the inferred natural position of the living animals. In the Mitrata Caster (1925,*25*) has employed carapace for the upper surface of the theca and plastron for the lower one, terms which are very descriptive for this group but ill-suited for application to the Cornuta. Designations such as ventral, dorsal, oral, and aboral have been employed diversely by authors in referring to the two faces of the depressed theca, but use of them is inadvisable because of uncertainty of the implied morphological interpretation. The upper and lower sides of the aulacophore, however, could be differentiated appropriately in this way.

The aulacophore, with the mouth probably located near its base, marks the **anterior extremity** of the body, and opposite to it the margin of the theca adjacent to the anus marks the **posterior extremity** (Fig. 326). By placing the skeleton on its inferior face with the aulacophore directed away from an observer (upward on figures), one can make the conventional distinction between right and left sides.

The aulacophore is bilaterally symmetrical, and the intersection of its plane of symmetry with the extension plane of the theca defines the **main axis** of the body (Fig. 326). The plane through this axis perpendicular to the extension plane is here called the **median plane,** instead of symmetry plane (Bather, 1913,*13*), inasmuch as the never perfectly symmetrical theca is generally very asymmetrical with reference to this plane. The straight line from the aulacophore insertion center, marking the presumed location of the mouth, to the anus defines the **oro-anal axis.** In the mitrates this line approximates or may coincide with the main axis, whereas in the cornutes the two axes generally are quite distinct (Fig. 326). The terms proximal and distal are not useful in describing parts of the theca but may be employed for parts of appendages, then respectively denoting directions toward and away from the insertion. Directions toward and away from the main axis are termed **adaxial** and **abaxial** (Fig. 326).

Length of the aulacophore is measured along the main axis and width perpendicular to this axis in the extension plane; height (or thickness) is determined by measurements perpendicular to the other two lines. Length of the theca is defined as the distance between two lines normal to the median plane and respectively tangent to the most anterior and posterior points (Fig. 326). Width of the theca is the distance between two lines parallel to the median axis and respectively tangent to the right and left sides. Height (or thickness) of the theca is the distance between two planes parallel to the extension plane and respectively tangent to the lower and upper faces.

Individual plates of the marginal framework are distinguished by a conventional system of symbols (Fig. 325,*2a,b*). Marginals on the right side of the oro-anal axis, viewing the superior face of the theca, are indicated from front to back by the symbols M_1, M_2, M_3, etc., and those on the left side similarly by M'_1, M'_2, M'_3, etc. The

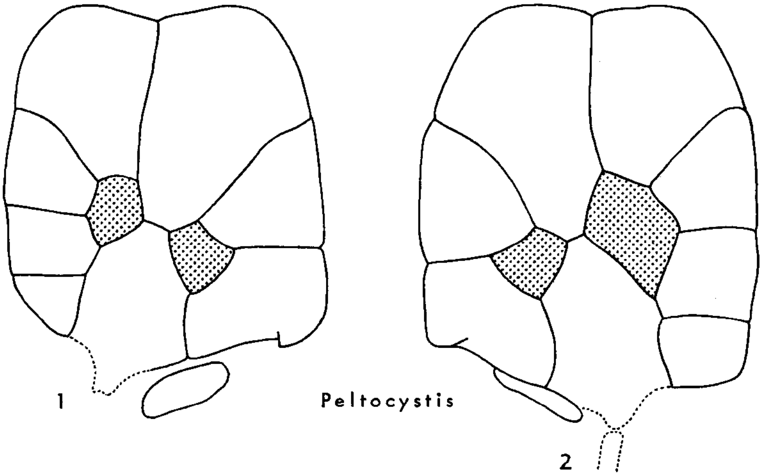


FIG. 327. Reversed asymmetry. *Peltocystis cornuta* THORAL, L.Ord., Fr.; *1,2,* inferior face, of normal and abnormal specimens, ×4.1 (Ubaghs, n).

posterior marginal traversed by the oro-anal axis is arbitrarily attributed to the right-hand series. This method of notation was introduced by JAEKEL (1918,*55*) but here is modified by accepting as anterior what that author considered to be posterior and vice versa.

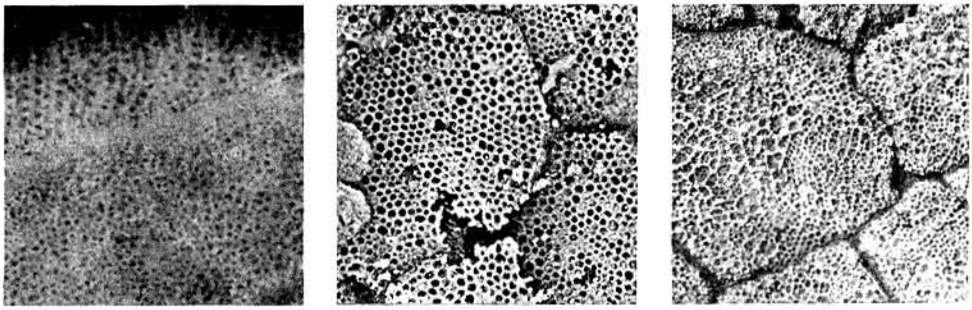
A few other symbols have been found useful, especially for designations of plates shown in figures. Thus, among centralia, *A* identifies the "anomalocystid plate" and *P* the "placocystid plate; the right, median, and left adoralia are respectively marked by *r.ad., m.ad.,* and *l.ad.* Infracentrals (=hypocentrals of JAEKEL) of the Mitrata are individually designated by H_1, H_2, H_3, etc., according to a plan introduced by CHAUVEL (1941,*30*). These notations are preferred rather than more elaborate systems such as have been proposed for the Mitrocystitida by GISLÉN (1930,*45*) and for the Anomalocystitida by CASTER (1952,*25*).

ASYMMETRY

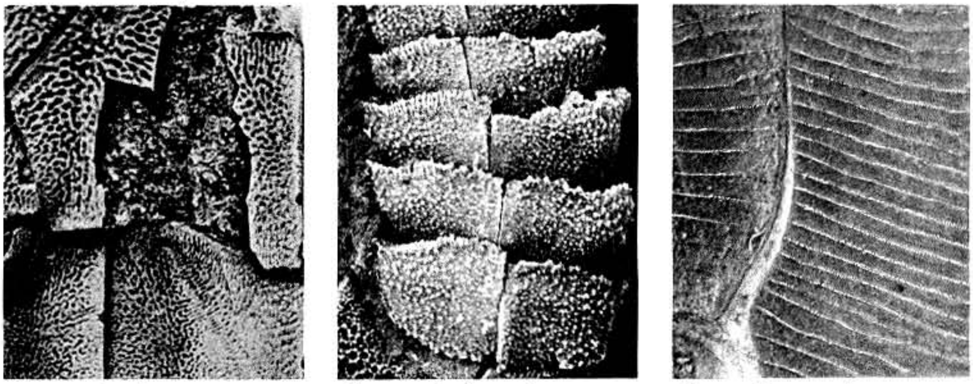
All stylophorans are asymmetrical, though varying in degree. Their asymmetry, more evident in the Cornuta than in the Mitrata, is manifested by (1) outlines of the theca, except in some Anomalocystitida, (2) distribution, form, and dimensions of thecal plates, especially those of the inferior face, (3) almost invariable divergence of the oro-anal axis from the main axis, even though this may be slight, and (4) the presence and location of numerous structures such as the zygal and accessory orifices of the Cornuta, the septum of the Mitrata, and the infundibulum and right adoral orifice of both Cornuta and Mitrata, all of which are placed laterally from the median plane without symmetrical counterparts on the other side of this plane.

The prevalence and diversity of these characteristics indicate that asymmetry is a fundamental attribute of the Stylophora. It is true that the asymmetry often has been considered to be secondary and derived from a perfect bilateral symmetry that is most completely expressed by the aulacophore, erroneously regarded as a stem. The validity of this interpretation is denied by factual observations and especially by the chronologic succession of genera and families. Not only has no fossil trace of a stage with perfect bilateral symmetry been discovered, but the oldest known representatives of the group (e.g., *Ceratocystis, Nevadaecystis, Chinianocarpos, Peltocystis*) are some of the most asymmetrical. Further, genera in which the theca is most nearly symmetrical (e.g., *Australocystis, Basslerocystis, Placocystites, Rhenocystis*) are confined to relatively high stratigraphic levels. They seem to be very specialized forms in which bilateral symmetry, though imperfect, almost surely is a secondary adaptation to some particular mode of life. The bilateral symmetry of the aulacophore probably has no more morphologic and phylogenetic significance than a single crinoid arm or starfish ray.

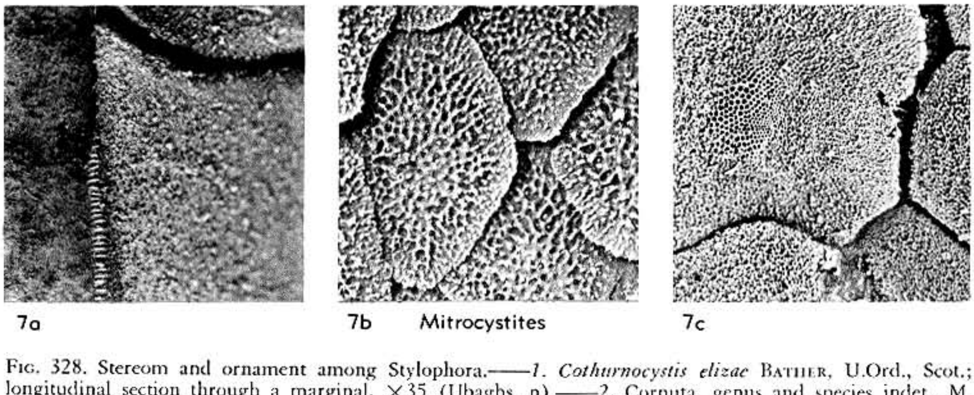
Finally, the occurrence of **inverted asymmetry** should be mentioned, although examples of it are rare (Fig. 327). Some abnormal individuals show all characters



1 Cothurnocystis 2 Cornuta- genus undet. 3 Cornuta- genus undet.



4 Enoplouro 5 Phyllocystis 6 Plococystites



7a 7b Mitrocystites 7c

FIG. 328. Stereom and ornament among Stylophora.——*1. Cothurnocystis elizae* Bather, U.Ord., Scot.; longitudinal section through a marginal, ×35 (Ubaghs, n).——*2.* Cornuta, genus and species indet., M. Ord., Boh.; external surface of supracentralia, ×15 (Ubaghs, n).——*3.* Cornuta, genus and species indet., L.Ord., Fr., ornamentation of supracentralia, ×15 (Ubaghs, n).——*4. Enoploura popei* Caster, U.Ord., Ohio; ornamentation of part of lower face, ×8.3 (25).——*5. Phyllocystis* sp., L.Ord., Fr.; proximal region of aulacophore, inferior face, ×15 (Ubaghs, n).——*6. Placocystites forbesianus* de Koninck, Sil., Eng.; ornamentation of part of superior face, ×8 (Ubaghs, n).——*7. Mitrocystites mitra* Barrande, M.Ord., Boh.; *7a,* striated edge of a marginal, inferior face, ×14; *7b,* ornamentation of supracentralia, ×15 (Ubaghs, n); *7c,* special reticulated subcentral area on infracentral (holotype of *M. latus* Jaekel, considered as syn. of *M. mitra*), ×12 (Ubaghs, n).

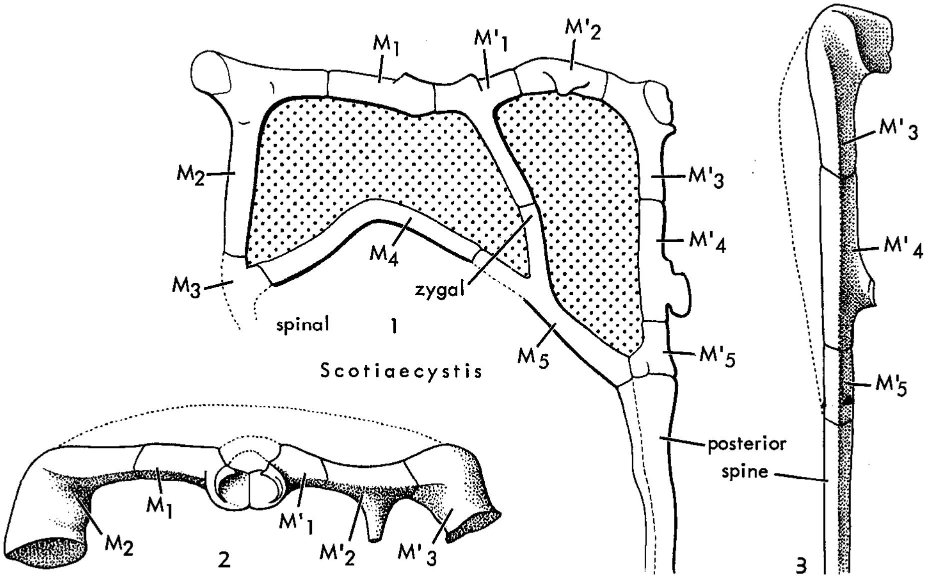


FIG. 329. Marginal frame of a cornute Stylophora.——*1-3, Scotiaecystis curvata* (BATHER), U.Ord., Scot.; inferior, anterior, and right lateral faces, ×3 *(M_1-M_5,* right marginalia; *M'_1-M'_5,* left marginalia) (Ubaghs, n).

transposed to the opposite side of the median plane, as compared with normal individuals.

STEREOM AND ORNAMENT

Little is known as to histology of the stylophoran skeleton, for most commonly fossil specimens consist of natural molds. It is certain, however, that their hard parts were composed, as in other echinoderms, of calcareous stereom with included organic stroma. The characteristic reticulation of echinodermal skeletal elements often is clearly recognizable in stylophoran fossils (Fig. 328,*1,2*). The stroma occupied meshes of the calcareous network. In some specimens (e.g., *Paranacystis*) it appears to have filled a labyrinth of minute canals extending from one plate to another and opening externally in microscopic pores (CASTER & EATON, 1956,*28*).

Ornament of the stylophoran skeleton is varied (Fig. 328). A particularly characteristic pattern on the surface of thecal plates consists of equidistant fine wrinkles, sinuous and parallel, disposed transversely or obliquely to plate margins (Fig. 328,*6*). This type of ornament strikingly resembles the terrace lines of trilobites or markings on machaeridian plates (e.g., *Turrilepas*). It is commonly seen in genera of the Anomalocystitida, rarely in other Mitrata, and never in Cornuta.

Various types of spines have been observed in Stylophora, articulated with marginals or central plates. Some are inconspicuous, being carried probably by tiny tubercles *(89)*. Others, of hairlike appearance, form a sort of brush along margins of an undescribed Lower Ordovician representative of the Scotiaecystidae. In new Lower Ordovician Cornuta, club-shaped spines cover the entire upper surface of the theca in one species and flattened elongate spines are aligned on the marginal framework of two others.

MARGINALIA

The plates which form the marginal framework of the theca are termed marginals (or **marginalia**) (Fig. 325). In all representatives of the Cornuta, save *Ceratocystis,* they are clearly distinct from plates of the pavements which cover the two thecal faces and they barely participate as skeletal elements of these faces (Fig. 325, *2a,b*). They are elongate, relatively narrow and thick pieces which typically are constant in number and position within a given species but may vary somewhat within a genus. Generally they are U-shaped in cross section and have a rounded lower external edge. Some genera (e.g., *Ceratocystis, Phyllocystis, Scotiaecystis, Bohemiaecystis*) have ten marginals; in *Cothurnocystis* their number is ten or 11 (exceptionally 12).

Certain marginals of the cornute Stylo-

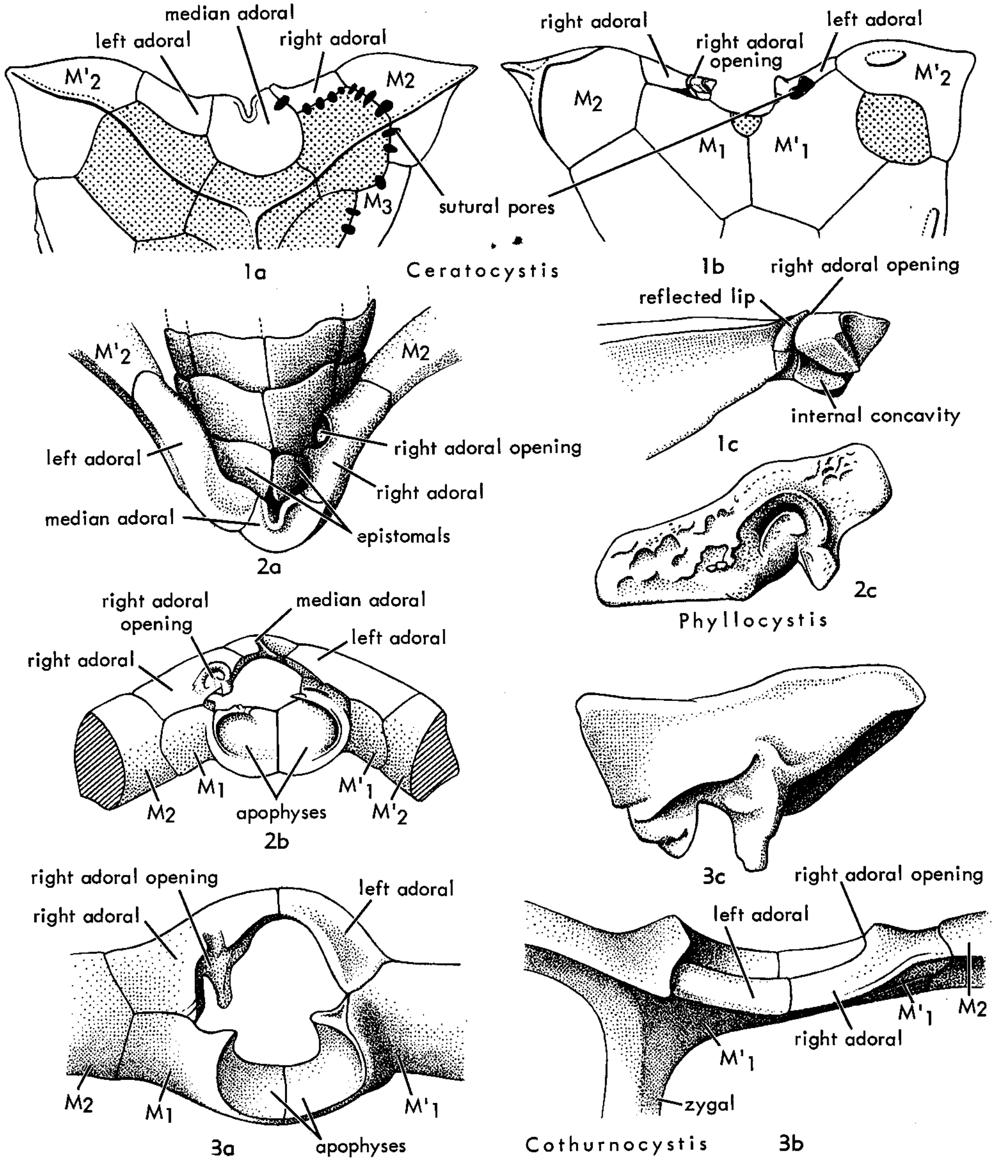


FIG. 330. Adoralia among cornute Stylophora.——*1. Ceratocystis perneri* JAEKEL, M.Cam., Boh.; *1a,b,* superior and inferior faces, ×2.2; *1c,* adaxial part of right adoral, inferior face, ×8.3 (Ubaghs, n).——*2. Phyllocystis crassimarginata* THORAL, L.Ord., Fr.; *2a,b,* superior and anterior faces, ×5; *2c,* right adoral, anterior face, ×12 (Ubaghs, n).——*3. Cothurnocystis elizae* BATHER, U.Ord., Scot.; *3a,b,* anterior and superior faces, ×5; *3c,* right adoral, anterior face, ×10 (Ubaghs, n). (M_1, M_2, . . . , right marginalia; M'_1, M'_2. . . , left marginalia).

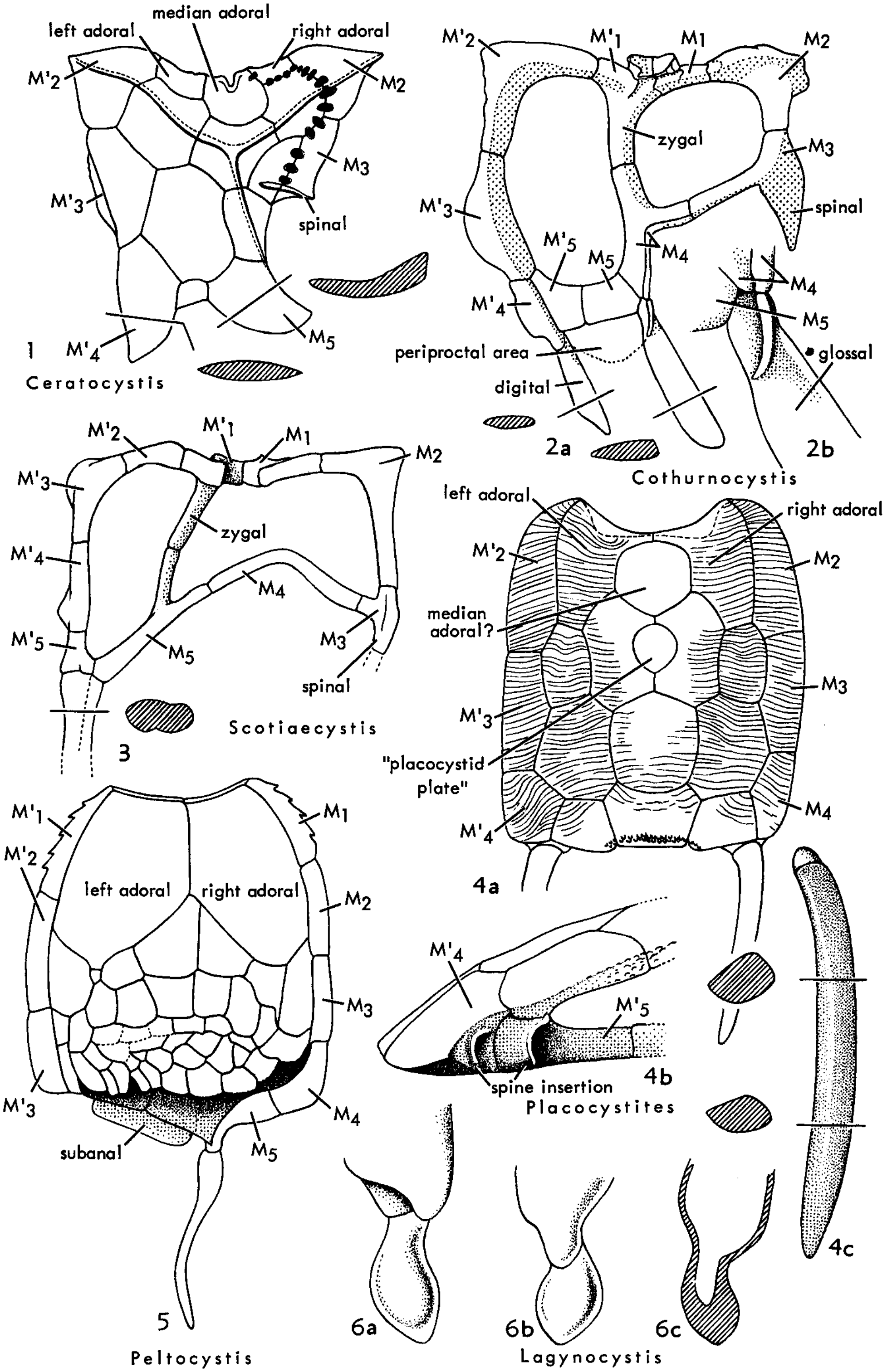


FIG. 331. [*Explanation on facing page.*]

phora generally bear protuberances on their lower side (Fig. 329). These project more or less obliquely or at right angle to the extension plane. Some are simple or denticulated knobs. Others consist of rather long spines which are pointed, truncated, or spatulate in form, depending on the species, nature of the immediate environment, or location on the frame. Typically, the protuberances occur at main angles of the frame on the anterior half of the theca, probably serving for its support and maintenance of balance of the whole body. Also they doubtless prevented displacement of the theca by currents and by movements of the aulacophore. In species provided with flexible integuments, they raised the theca above the sea floor enough to allow the inferior face to take advantage of its flexibility *(13, 14)*.

The two median anterior marginals of the Cornuta (M_1, M'_1) call for special notice in that (1) they form part of the thecal frame only on the inferior face (Fig. 325,*2b*), being covered by adorals on the superior face (Fig. 325,*2a*); (2) the inner side of each bears a powerful apophysis on which proximal muscles of the aulacophore were inserted (Fig. 330,*2b,3a*); and (3) the left marginal (M'_1) sends off a backwardly directed long process which is fused to a similar process generally borne by a marginal on the opposite side of the oro-anal axis.[1] This last-mentioned structure, termed the **zygal** by UBAGHS (1963,*89*) (=strut, BATHER, *13*), is restricted to the inferior face of the theca and divides it into two unequal fields (Fig. 325,*2b*; 329,*1*). It is observed in all cornute stylophorans except *Ceratocystis* and apparently *Nevadaecystis*. Probably the zygal served to brace the theca, impeding distention or rupture of the inferior face integument resulting from pressures exerted by thecal contents and providing a place for attachment of internal organs *(13, 14)*. In several Lower Ordovician species of *Cothurnocystis* the marginal that furnished the posterior branch of the zygal is formed by two superposed pieces which join along a horizontal suture, suggesting a possible double origin for the marginal. The zygal process originates entirely from the lower piece (Fig. 331,*2a*).

The marginals form a less obvious frame in the Mitrata than in the Cornuta. On the upper side of the mitrate theca they typically form only a narrow border which is interrupted for insertion of the aulacophore and generally also for the area around the anus (Fig. 325,*1a*). In *Chinianocarpos*, however, the two most posterior marginals are extended on the upper face enough to cover the entire posterior area. On the lower side of the theca the marginals generally cover a relatively large part of the surface (Fig. 332) and in some genera (e.g., *Lagynocystis*) almost the whole area (Fig. 332,*10*). The plates are generally V- or J-shaped in cross section and in some genera are more or less thickened along their lower external edge, which may be either sharp or blunt. As in the Cornuta, the two median anterior marginals carry a powerful apophysis on their inner side for attachment of the proximal muscles of the aulacophore; manifestly the mitrate M_1 and M'_1 are homologous to similarly designated marginals of the Cornuta. *Mitrocystites* and *Mitrocystella* (Fig. 332,*2,3*) have 12 or 13 marginals, most Anomalocystitida (Fig. 332,*4-7*) 11, *Australocystis* (Fig. 332,*8*) ten, *Chinianocarpos* (Fig. 332,*1*) nine, *Peltocystis* (Fig. 332,*9*) eight, *Lagynocystis* (Fig. 332,*10*) seven, and *Balanocystites* and *Anatiferocystis* (Fig. 332,*11, 12*) only two. If only

---

[1] In a new undescribed genus from the Lower Ordovician of France, the posterior part of the zygal is not a process borne by a marginal but an independent ossicle united to the marginal framework by a distinct suture.

FIG. 331. Marginal appendages among Stylophora.——*1. Ceratocystis perneri* JAEKEL, M.Cam., Boh.; superior face, ×1.6 (Ubaghs, n).——*2. Cothurnocystis primaeva* THORAL, L.Ord., Fr.; *2a*, superior face of whole frame, ×3.4; *2b*, proximal part of glossal, superior face, enl. (Ubaghs, n).——*3. Scotiaecystis curvata* (BATHER), U.Ord., Scot.; superior face, ×2.5 (Ubaghs, n).——*4. Placocystites forbesianus* DE KONINCK, Sil., Eng.; *4a*, superior face of theca, ×2; *4b*, left half of posterior face of theca, ×4; *4c*, posterior spine, superior face, ×4 (Ubaghs, n).——*5. Peltocystis cornuta* THORAL, L.Ord., Fr.; superior face, ×3.8 (Ubaghs, n).——*6. Lagynocystis pyramidalis* (BARRANDE), M.Ord., Boh; posterior appendage, *6a,b*, lower and upper side; *6c*, longitudinal section, ×5.4 (Ubaghs, n) (M_1, M_2 . . . right marginalia; M'_1, M'_2 . . . left marginalia).

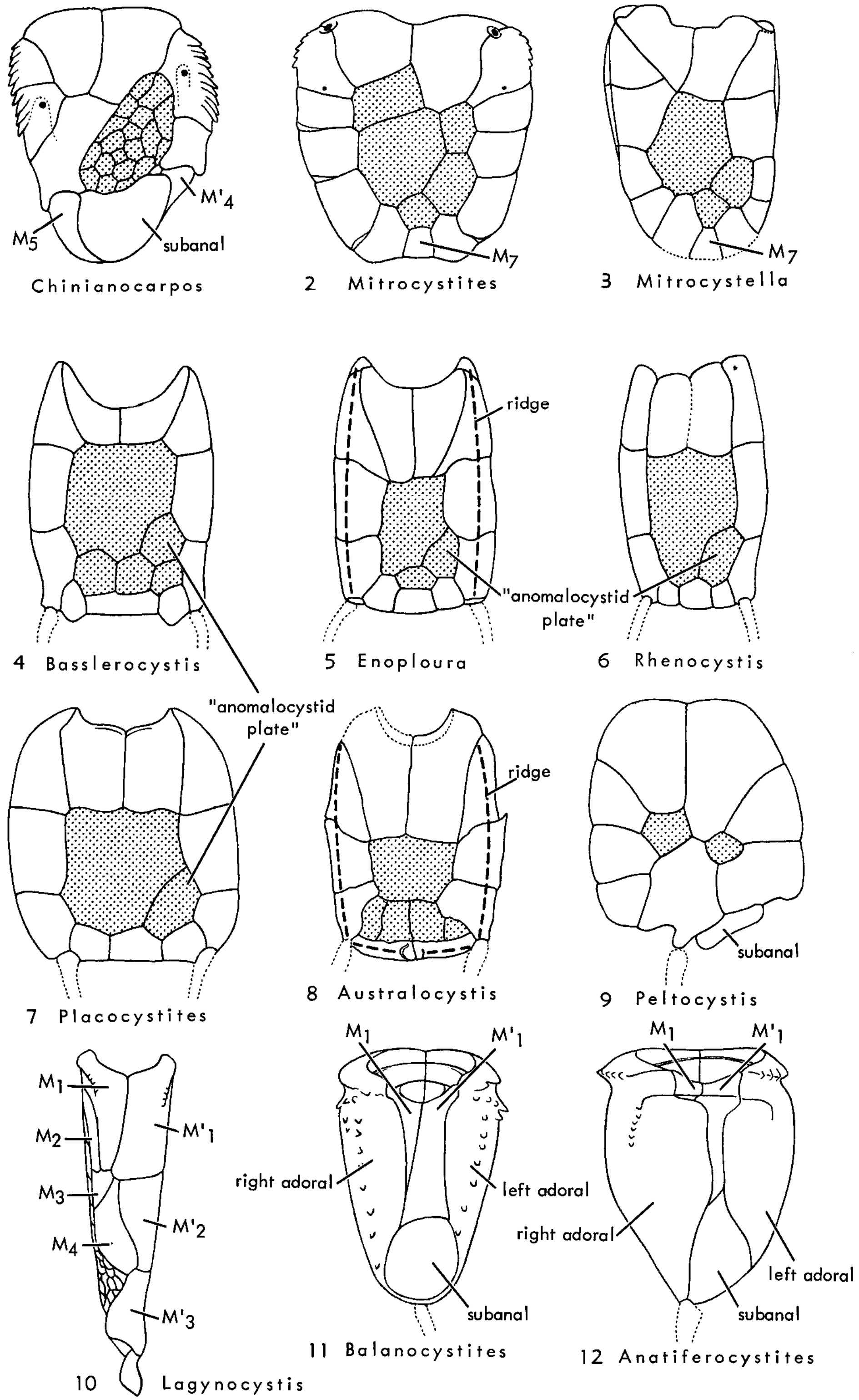


FIG. 332. [*Explanation on facing page.*]

two marginals are present, these are M_1 and M'_1, identified by their location and role for insertion of the aulacophore.

Marginals of the Mitrata never develop protuberances analogous to those of the Cornuta, although their lateral inferior borders may be produced downward as prominent rounded edges which support the theca on flat surfaces (e.g., *Enoploura, Basslerocystis*). A similar ridge occurs along the posterior margin of *Australocystis.* The theca of *Lagynocystis* and *Placocystites* was partially raised above the bottom by a median longitudinal keel extending rearward from the front margin. The marginals of some Mitrata (e.g., *Chinianocarpos, Mitrocystites*) may have a lower denticulated external edge (Fig. 325,*1a,b*) or a narrow striated border (Fig. 328,*7a*) or a flat thin flange stretched out in the extension plane, serving apparently to prevent sinking of the theca into a particularly soft bottom (Chauvel, *30*).

MARGINAL APPENDAGES

Stylophoran marginalia commonly bear fixed or articulated appendages. As previously noted, the marginals of many Cornuta carry knoblike or spinose processes on their lower side. The exaggerated growth of such a protuberance on the "toe" of the boot-shaped theca of *Cothurnocystis* and *Scotiaecystis* produces the long point or blade termed **spinal** (Jaekel, *55*) (=toe spine, Bather, *13*) (Fig. 329,*1*; 331,*2a,3*). The spinal of *Ceratocystis* is a triangular projection extending from the middle of the right lateral margin and from its summit a short transverse ridge runs onto the upper surface (Fig. 331,*1*). The two posterolateral marginals (M_5, M'_4) in this genus have the form of horns, which are fixed and partly hollow. In *Cothurnocystis* corresponding horns are massive spines of unequal size and dissimilar form, designated by Jaekel *(55)* respectively as **digital** (=tag, Bather, *13*) and **glossal** (=tongue, Bather, *13*) (Fig. 331,*2a*). The glossal is joined to the marginals by two sutures, one at a distinct angle to the other, indicating that the spine possibly could be lifted or lowered but not displaced laterally. The digital seems to have been more freely articulated on the framework of the marginals and probably movable in almost any direction. Instead of these two appendages, *Scotiaecystis* has a single long process joined by sutures to the posterior left truncated corner of the theca (Fig. 329; 331,*3*). The presence of longitudinal grooves on its upper and lower sides suggests that the process was formed by union of two pieces.

Among the Mitrata, a single posterior appendage characterizes the Lagynocystida. It is short, somewhat inflated, and partially hollow in *Lagynocystis,* with cavity apparently communicating with the interior of the theca (Fig. 331,*6a-c*). In *Peltocystis* it is long, narrow, seemingly massive, and probably articulated on a posterior thecal prominence (Fig. 331,*5*). The process was rather long and variously shaped in *Balanocystites* and *Anatiferocystis,* articulating with the lower side of the posterior corner of the theca. All Anomalocystitida possess two movable spines (variously called arms, brachial arms, buccal arms, brachioles, tentacles, etc.), symmetrically placed at the two ends of the posterior margin, with attachment by highly differentiated articulations (Fig. 331,*4a-c*). Bases of the spines are constricted and proximally rounded; in *Placocystites* their evenly convex lower face and asymmetrically angulated upper face

---

Fig. 332. Marginalia, infracentralia and subanal among mitrate Stylophora. [All figures show inferior faces.] ——*1. Chinianocarpos thorali* Ubaghs, L.Ord., Fr.; ×3.5 (Ubaghs, n).——*2. Mitrocystites mitra* Barrande, M.Ord., Boh.; ×1.6 (Ubaghs, n).——*3. Mitrocystella barrandei* Jaekel, M.Ord., Boh.; ×1.5 (Ubaghs, n). ——*4. Basslerocystis disparilis* (Hall), L.Dev., N.Y.; ×2.3 *(25)*.——*5. Enoploura popei* Caster, U.Ord., Ohio; ×1.4 *(25)*.——*6. Rhenocystis latipedunculata* Dehm, L.Dev., Ger.; ×1.4 *(25)*.——*7. Placocystites forbesianus* de Koninck, Sil., Eng.; ×1.6 (Ubaghs, n).——8. *Australocystis langei* Caster, L.Dev., Brazil; ×2.6 *(27)*.——*9. Peltocystis cornuta* Thoral, L.Ord., Fr.; ×2.6 (Ubaghs, n).——*10. Lagynopyramidalis* (Barrande), M.Ord., Boh.; ×1.8 (Ubaghs, n).——*11. Balanocystites lagenula* Barrande, M.Ord., Boh.; ×2.5 (Ubaghs, n).——*12. Anatiferocystis barrandei* Chauvel, M.Ord., Boh.; ×2.4 (Ubaghs, n) (M_1, M_2 . . . right marginalia; M'_1, M'_2 . . left marginalia).

meet in a rather sharp edge (Fig. 331,*4c,* cross sections). They have no communication with the thecal cavity and musculature controlling their movements was external.

Spines of this sort in *Enoploura* were supposed by Pope *(70)* to be enveloped by "cover plates" identical to the scales of the machaeridian *Lepidocoleus,* but this has not been confirmed by examination of other anomalocystids. In *Paranacystis* and the Mitrocystitidae no exothecal process of any sort is seen, but the posterior thecal plates of *Paranacystis* form a subtriangular projection interpreted as an ostial cover by Caster *(26).*

All stylophoran thecal appendages are directly related to the marginals, or even considered to be modified marginal plates themselves (Kirk, *56*). Certainly, this applies to the two posterior "horns" of *Ceratocystis.* Probably the processes evolved independently in different lineages and, in view of the diversity of their shapes, it is very likely that they served diverse functions. All of them probably contributed to anchoring the animal and their localization at the posterior extremity of the body suggests that they were a counterweight to the aulacophore.

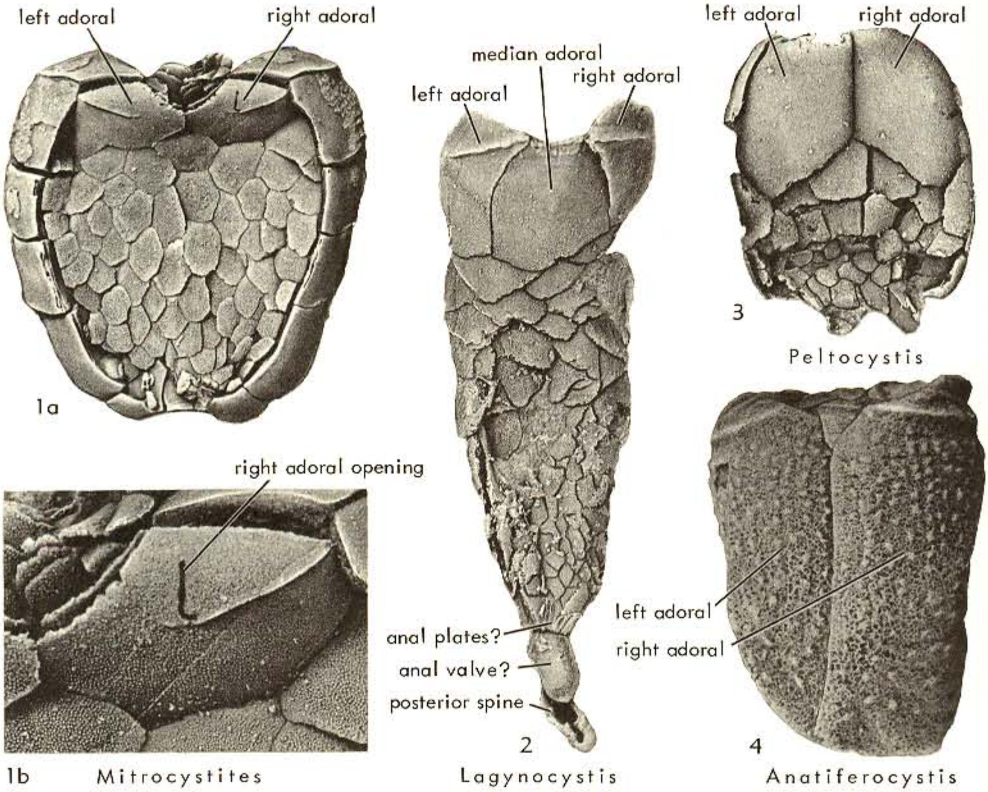


Fig. 333. Adoralia among mitrate Stylophora.——*1. Mitrocystites mitra* Barrande, M.Ord., Boh.; *1a,* superior face of theca, ×2.2; *1b,* right adoral, ×6 (Ubaghs, n).——*2. Lagynocystis pyramidalis* (Barrande), M.Ord., Boh.; superior face of theca, ×3 (Ubaghs, n).——*3. Peltocystis cornuta* Thoral, L.Ord., Fr., superior face of theca, ×4.1 (Ubaghs, n).——*4. Anatiferocystis punctata* (Bassler), M.Ord., Tenn.; superior face of theca, ×7 (Ubaghs, n).

ADORALIA

Plates here designated as adorals are those which in combination with the median anterior marginals (M_1, M'_1) frame the insertion of the aulacophore.[1] They correspond to the *épibasales* of CHAUVEL *(30)* and adcolumnals of CASTER *(25)*. In *Ceratocystis* (Fig. 330,*1a,b*) they are represented by three plates, those at right and left contributing to formation of the anterior thecal border on upper and lower faces equally and the middle one pertaining only to the upper face. The lower surface of the right adoral bears a narrow slit which is a distinct aperture (*see* right adoral orifice, p. S515). The median plate, which is relatively large, has a V-shaped re-entrant bordered by an elevated lip on its anterior margin. The adorals of all other Cornuta, where known, form part of the frame and are restricted to the superior face of the theca (Fig. 330,*2,3*). Whether two or three in number, they form a broad arc with ends resting on the two median anterior marginals (M_1, M'_1). The lower edge of the right adoral is notched by an orifice (Fig. 330,*2b,c, 3a,c*). The middle plate seems to be regressive, being present (though small) in Lower Ordovician forms but unknown in the Upper Ordovician. In *Phyllocystis* (Fig. 330,*2a*) this plate shows a median depression provided with a slightly projecting rim, probably homologous with the notch that is seen in the median adoral of *Ceratocystis*.

At first glance, adorals of the Mitrata seem quite unlike the similarly designated plates in the Cornuta (Fig. 333). Invariably they are much more developed and either partly or completely cover the superior face. Even so, they are held to be homologous to the adorals of Cornuta, since they have the same relationship to the M_1 and M'_1 plates and the aulacophore and since the right adoral (e.g., in *Mitrocystites*) may be pierced by an unpaired orifice, as in the Cornuta (Fig. 333,*1a,b*). They are two or three in number (Fig. 333,*1,2*). The median plate does not attain the anterior upper margin in some genera (e.g., *Placocystites*, Fig. 331,*4a*), and in others it creases to be distinct from adjacent supracentrals (Fig. 333,*3*) or disappears altogether. The adorals may be small (e.g., *Mitrocystites*, Fig. 333,*1*), intermediate in size (e.g., *Placocystites*), or very large (e.g., *Peltocystis*, Fig. 333,*3*). They completely cover the superior face of *Balanocystites* and *Anatiferocystis* (Fig. 333,*4*) and folding over the lateral borders, they occupy most of the inferior face as well (Fig. 332,*11,12*).

EPISTOMALIA

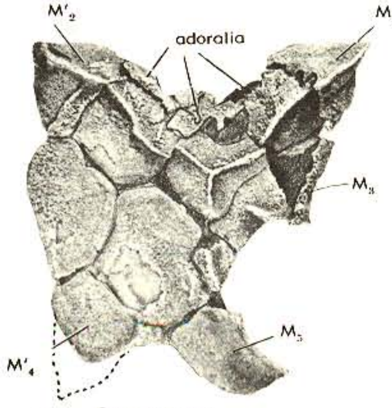
In *Phyllocystis* the triangular space between the adorals and the first skeletal ring segment of the aulacophore is occupied by two small plates which (as they are interpreted as protecting the mouth) are here called **epistomalia (epistomals)** (Fig. 330, *2a*). They are apparently attached to the left and right adorals by their abaxial edges and sutured (or at least contiguous) to the median adoral by their posterior edge, with other margins free. Rarely they join one another along the median plane but more commonly are separated, their adaxial edges prolonging the U-shaped ridge that surrounds the axial depression of the median adoral, this depression thus seeming to be confluent with an empty space between the epistomals. The origin of these plates is obscure, since no equivalents of them have been observed with certainty in other genera. In broad aspect they closely resemble plates which protect the upper face of the proximal region of the aulacophore, but these are parts of skeletal rings, whereas the epistomals are not. Seemingly they could open at least slightly, unlike proximal upper plates of the aulacophore, which always are closed.

CENTRALIA

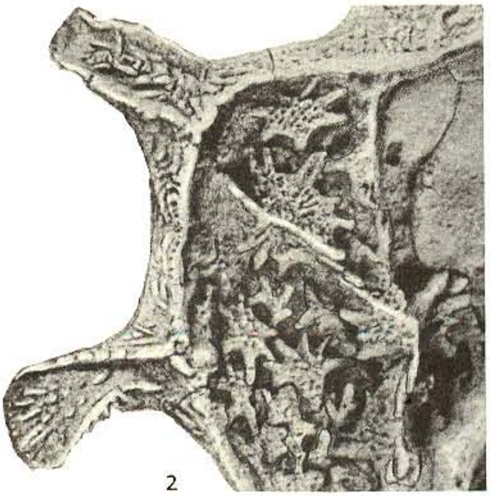
The variably large number of plates or platelets on the superior and inferior faces

---

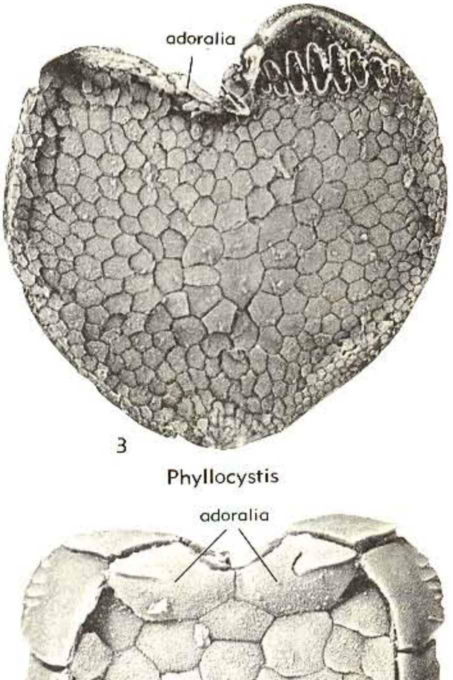
[1] The aulacophore insertion typically is surrounded by four or five plates—M_1 and M'_1 below and two or three adorals above. In *Rhenocystis* and possibly some specimens of *Placocystites* additional marginals (M_2, M'_2) may form part of this anterior ring, bringing to six the number of plates around the base of the aulacophore. Also, the presence of two deltoid "interbasal" plates between the marginals and adorals has been recorded in *Mitrocystella* by CHAUVEL (30) and in *Enoploura* by CASTER (25). Carefully made latex casts of *Mitrocystella*, however, demonstrate that the presumed extra plates are merely reflected downward margins of adorals separated from other adorals by a ridge (see Fig. 340,*3*). The so-called interbasals of *Enoploura*, which admittedly are very small, may be sutural wrinkles. In any case, the "hexabasal" pattern of the anterior ring of plates is no more significant than the "tetrabasal" scheme postulated by JAEKEL (55) as a diagnostic feature of his class Carpoidea.



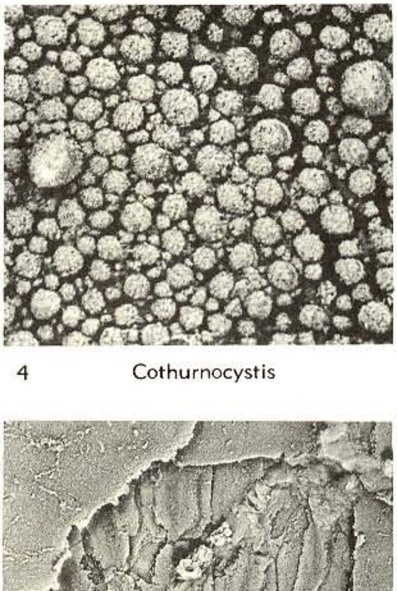
1 Ceratocystis



2 Nevadaecystis



3 Phyllocystis



4 Cothurnocystis

5 Mitrocystites

6 Mitrocystites

FIG. 334. [*Explanation on facing page.*]

of the theca, inclosed by the marginal frame, composes the **centrals (centralia).** In *Ceratocystis,* which is the most ancient known representative (Middle Cambrian) of the Stylophora, centrals are separable from marginals with difficulty, for all are large plates which contribute subequally to formation of the rigid box that surrounded soft parts of the animal (Fig. 334,*1*). On the inferior face are five **infracentrals (infracentralia)** and on the superior face are eight **supracentrals (supracentralia)** (see Fig. 345,*1*,*2*). The upper face of the theca is crossed by a tripartite crest, with branches that meet near the middle.

Morphologically intermediate in some respects between *Ceratocystis* and *Cothurnocystis* is *Nevadaecystis* (Upper Cambrian), which still has large plates on the lower face but numerous stelliform supracentrals on the upper face, joined to one another only at points of their rays so as to leave large oval orifices which doubtless represent uncalcified areas of the integument that served for gaseous exchange between fluids inside and outside of the theca. As in *Ceratocystis,* an apparently triradiate crest (one branch lacking in the only known specimen) may be seen on the upper thecal surface.

The two thecal faces of all other known representatives of the Cornuta are protected by a finely plated, probably flexible integument attached to inner borders of the marginals. Generally the plates are tessellated but in some forms (e.g., *Scotiaecystis*) they appear to be imbricate in many places, possibly owing to defective preservation.

Supracentrals of Cornuta invariably differ from infracentrals in size and commonly also in ornament. The supracentrals may be slightly the larger (e.g., *Phyllocystis*) but in most genera they are ordinarily the smaller. Also, the plating is not the same all over. As a rule, the size of plates decreases toward the periphery and around openings in the integument (Fig. 334,*3*), thus providing greater flexibility of the theca in these regions. The infracentrals next to the zygal in *Bohemiaecystis* and *Phyllocystis* are elongated in a direction parallel to this piece. On the upper face of several species of *Cothurnocystis* (e.g., *C. elizae* in particular), the plating consists of relatively large rounded and swollen plates which in full-grown specimens are surrounded by smaller ones (Fig. 334,*4*). Plates of the left posterior region are more closely set than in other parts of the same side and in some individuals an arcuate row of spines or conical protuberances may be observed at some distance from the upper anterior margin. The supracentrals of *Scotiaecystis* are polygonal plates, each bearing a low, convex-topped spine (see Fig. 348,*2*), and where the spines are contiguous they may form a sort of false test beneath which empty spaces possibly were maintained.

The infracentralia of most Mitrata[1] are large to small plates which are essentially constant in number according to genera and species—four to six in *Mitrocystites* (Fig. 332,*2*), three in *Mitrocystella* (Fig. 332,*3*), two in *Peltocystis* (Fig. 332,*9*), and one to five in Anomalocystitida (Fig. 332, *4-8*). They are entirely lacking in *Lagynocystis, Balanocystites,* and *Anatiferocystis* (Fig. 332,*10-12*) but in *Chinianocarpos* (Fig. 332,*1*) replaced by some 20 platelets in a subcentral elliptical area. Their distribution is almost symmetrical in *Allanicytidium* and *Australocystis* (Fig. 332,*8*) but is very asymmetrical in all other genera. Generally, the center of the inferior face is occupied by a single large plate (two in *Mitrocystites*) in contact with M_1 and M'_1 (in *Mitrocystella* rarely with M'_1 alone). The large infracentral ordinarily is accompanied by smaller plates, one of which designated

---

[1] GISLÉN (1930, 28) designated these according to their position as hypocentral (large middle plate), dextrolaterals (plates on right side) and sinistrolaterals (plates on left side), but orientation used by him is the reverse of that adopted here.

FIG. 334. Supracentralia among Stylophora.——*1. Ceratocystis perneri* JAEKEL, M.Cam., Boh., ×1.5 (Ubaghs, n).——*2. Nevadaecystis americana* (UBAGHS), U.Cam., Nev.; stelliform supracentralia, ×6 (Ubaghs, 1963).——*3. Phyllocystis blayaci* THORAL, L.Ord., Fr.; ×3 (Ubaghs, n).——*4. Cothurnocystis elizae* BATHER, U.Ord., Scot.; ×10 (Ubaghs, n).——*5. Mitrocystites mitra* BARRANDE, M.Ord., Boh.; ×3 (Ubaghs, n).——*6. Mitrocystites mitra hanusi* CHAUVEL, M.Ord., Boh.; internal aspect of supracentralia (center) showing median elevation, ×3 (Ubaghs, n) (M_2, M_3, M_5, right marginalia, 2, 3, and 5; M'_2, M'_4, right marginalia, 2, 4).

as the "anomalocystid plate" by CASTER *(25)* truncates the left posterior corner of the large plate and seems to characterize many Anomalocystitida (Fig. 332,*4-7*). An anomalocystitid plate is lacking in *Australocystis* (Fig. 332,*8*).

Supracentrals of the Mitrata, complemented by adorals, cover the upper thecal surface except for the generally narrow border formed by the marginals. In the Mitrocystida (Fig. 331,*1*; 334,*5*) and some Lagynocystida (Fig. 333,*2,3*) they are rather small, numerous, irregular in outline and arrangement, imbricated or tessellated, and diminishing in size in a backward direction. They are more or less sharply differentiated from the adorals. The integument which they reinforced seems to have been somewhat flexible, rather than rigid. Inner sides of the plates bear median elevations which probably served for attachment of muscle or ligament strands used to control movement of the integument (Fig. 334,*6*). The supracentrals of anomalocystid genera are much larger, fewer, never imbricated, and constant in very symmetrically arranged positions (Fig. 331,*4a*). Together with the adorals, from which they are little distinguished, the supracentrals contributed to a rigid thecal covering for which the term **carapace** (CASTER, *25*) is well suited. A supracentral called the "placocystid plate" by CASTER *(25)*, observed in *Placocystites* (Fig. 331,*4a*) and probably present also in *Rhenocystis,* is remarkable on account of its circular to elliptical outline and smooth (unstriated) outer surface. Earlier (DE KONINCK, *58*; WOODWARD, *95*) this plate was thought to be an anal structure. Supracentrals are entirely lacking in *Balanocystites* and *Anatiferocystis* (Fig. 333,*4*), in which two large adorals completely protect the upper face.

SUBANALIA

The lower face of the theca in some stylophoran genera (e.g., *Chinianocarpos, Balanocystites, Anatiferocystis*) (Fig. 332, *1,11,12*) bears a large subcircular terminal plate, the morphologic and functional meaning of which is obscure. Possibly it is a modified marginal, homologous with the median posterior marginal *(M_7)* that forms the floor of the anal area in *Mitrocystites* and *Mitrocystella* (Fig. 332,*2,3*).

A somewhat different element occurs in *Peltocystis* (Fig. 332,*9*). This is a rectangular plate located beyond the two posterior marginals and thus outside the normal limits of the theca, yet seemingly placed below the anal structures as in the two last-mentioned genera. For all of these similarly located posterior plates of uncertain origin, some perhaps different from others, the designation **subanals (subanalia)** here is adopted.

THECAL ORIFICES

The theca of Stylophora may possess openings of various sorts. For example, four types are observed in *Mitrocystites.* The function of some of these orifices is reasonably certain, whereas the physiological significance of others is entirely conjectural. Names without functional implication should be used for the latter.

MOUTH AND ANUS

The inlet and outlet of the digestive tube in stylophorans are treated together because they are interrelated and because separate consideration of them would be measurably artificial.

Opinions concerning locations of the mouth and anus in the strange echinoderms here discussed are extraordinarily divergent. For the sake of simplicity and avoidance of ambiguity, all references to them are converted to the orientation of Stylophora adopted in the *Treatise,* which requires that the usage of most authors for directional terms (anterior, posterior, right, left) except upper (or superior) and lower (or inferior) must be transposed. Given in these terms, different judgments can be recorded as follows.

(1) Mouth and anus both placed at posterior extremity of the body—BATHER *(11)*, JAEKEL *(54)*, KIRK *(56)*, CASTER *(25)* in *Enoploura,* CUÉNOT *(32)* in all Mitrata, GILL & CASTER *(43)* in *Victoriacystis,* NICHOLS *(68)*.

(2) Single orifice serving as mouth-anus placed at posterior extremity of the body—JAEKEL *(55)*, GISLÉN *(45)*, SPENCER *(80)*. The first two authors postulated that the morphological anus by reason of a com-

plete reversal of food currents in the digestive tube functions also as the physiological mouth. SPENCER thought that the posterior opening of *Cothurnocystis* was the aperture of a vestibule which held both mouth and anus.

(3) Mouth located in anterior position adjacent to the aulacophoral insertion and anus at opposite (posterior) extremity of the body—BATHER *(21)* in *Placocystites,* CHAUVEL *(30)* in Mitrata, TERMIER & TERMIER *(82)* in Mitrata.

(4) Mouth located at or near posterior pole and anus placed variously—HAECKEL *(49),* anus on upper face near right anterior corner of theca in *Mitrocystites* and on mid-line of lower face at base of the aulacophore in Anomalocystitidae; JAEKEL *(54),* anus on right lateral margin of theca in *Ceratocystis*; CASTER *(27),* anus close to the aulacophore insertion in *Paranacystis.*

(5) Anus located on mid-line of superior face, position of mouth indeterminate—DE KONINCK *(58)* in *Placocystites,* SCHUCHERT *(78)* in *Anomalocystites* and *Basslerocystis.*

(6) Anus placed at or near posterior extremity of body and inlets to digestive tube consisting of elliptical organs or sutural pores along the upper right anterior margin of the theca in many Cornuta—BATHER *(13, 14),* CHAUVEL *(30),* DELPEY *(35),* TERMIER & TERMIER *(82),* CUÉNOT *(32).* Also BATHER *(14)* considered that pores on the lower face of *Mitrocystites* served as food intakes.

The extreme diversity of these opinions stems mainly from the absence of any thecal opening in the Stylophora that can be identified with certainty as the mouth. This suggests that the mouth did not open on the outer surface of the theca but probably, as in Homoiostelea, was located inside the theca. Its approximate position may be inferred from the fact that the aulacophore carries a median groove and lateral depressions which are protected by mobile cover plates. Such features in echinoderms are characteristic of ambulacral tracts, and in all Recent and fossil echinoderms these tracts lead to the mouth. Accordingly, if the aulacophoral groove is ambulacral, the mouth of Stylophora must have been placed at or near its proximal end. Several features are possibly related to the presence of this orifice: 1) the presence in *Phyllocystis* of epistomalia which apparently form a protective roof over an aperture (Fig. 330,*2a*), 2) the occurrence in *Phyllocystis* and *Ceratocystis* of a small notch-and-groove on the anterior edge of the median adoral plate seemingly related to an opening just beneath (Fig. 330,*1a,2a*), and 3) the presence of an almost complete separation between the proximal aulacophoral cavity and the thecal cavity in *Lagynocystis,* impeding the passage of a digestive tube (see Fig. 341, *2,3*), and 4) the occurrence of comblike organs on the most anterior part of the theca in this genus, which must have been just in front of the mouth if they functioned as a filter (see Fig. 341,*3,4*).

The anus is placed on the superior face of the theca at or near its posterior extremity in all stylophorans where it has been observed. A radiating arrangement of small plates in this position in *Cothurnocystis* (see Fig. 346,*1*), *Phyllocystis* (Fig. 335,*2a,b*) and *Scotiaecystis* (see Fig. 348,*4*) suggests the presence of an anal pyramid during life. The surrounding thecal integument **(periproctal area)** is judged to have been very flexible and extensible, suggesting that the anal orifice could have been protruded and retracted. The most posterior marginals of *Cothurnocystis* (see Fig. 346,*1*) form a transverse or oblique bar on the lower thecal side only and the periproctal area placed partly on their flattened upper (internal) surface probably extended beyond them into a conical projection. The extension was framed on the left by the proximal part of the digital and on the right by the concave crest of the prolonged upper edge of the adjacent right marginal on the glossal. Retractor and protractor muscles of the anal pyramid could have been attached to all of these skeletal structures (Fig. 331,*2a*).

The upper edge of the posterior marginal of *Phyllocystis* slopes more or less distinctly downward to the level of the periproctal area (Fig. 335,*2a,b*) and the upper (internal) surface of this marginal in some specimens carries two symmetrically placed small knobs which probably provided for insertion of the rectal retractor muscles. In *Scotiaecystis* the anal pyramid was not placed at the apex of the angle formed by marginals M_5 and M'_5 but was shifted toward M'_4 (see Fig. 338,*1a*; 348,*1a*).

The periproctal area surrounding the

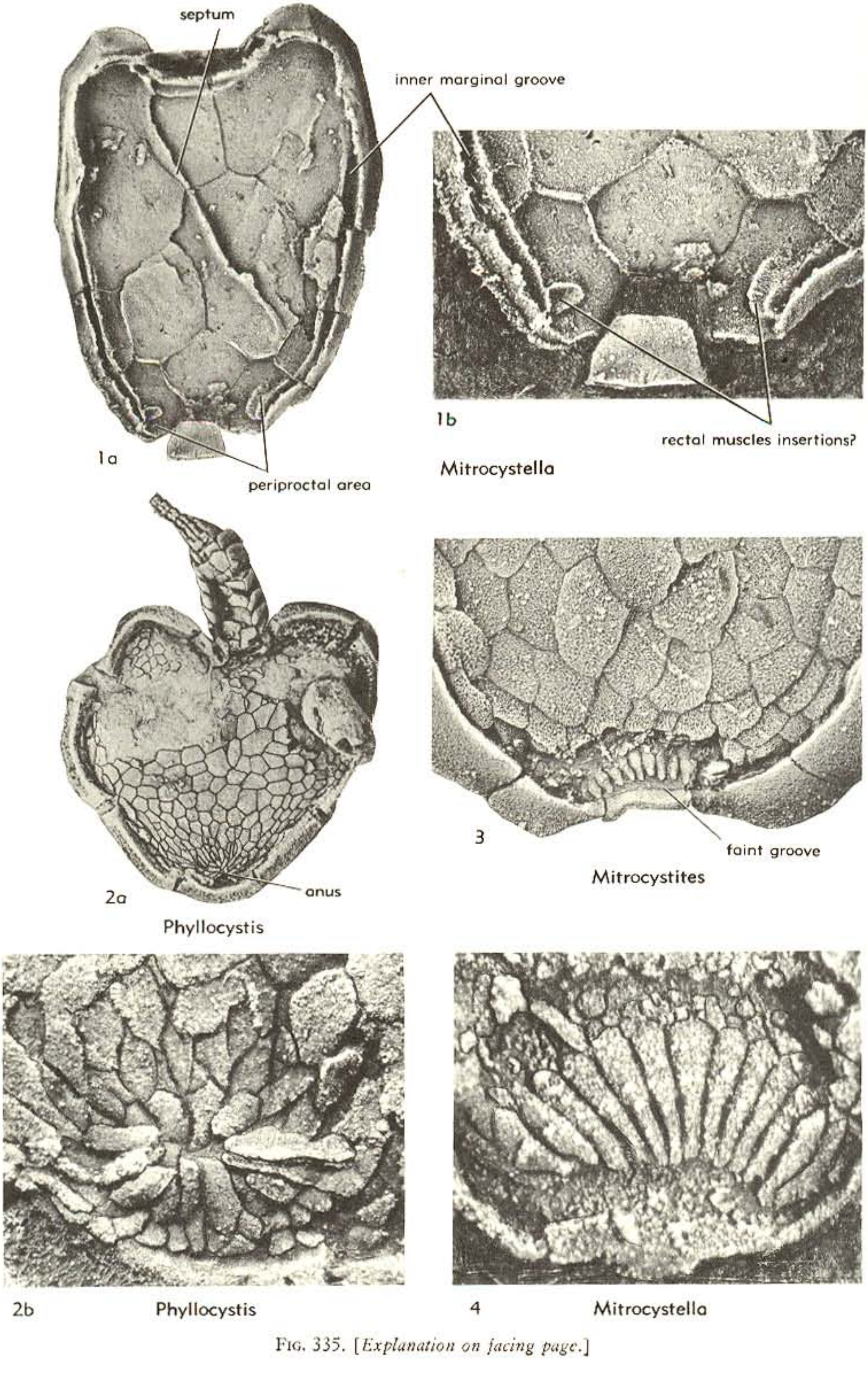


FIG. 335. [*Explanation on facing page.*]

anus in *Mitrocystites* and *Mitrocystella* is limited by a semicircular row of small supracentrals, and the upper edge of the marginal frame slopes downward at its level in manner that interrupts the frame and allows the rectal region to be pushed out and drawn back (Fig. 335,*3,4*). The periproctal area is finely plated and the anus bordered by an arcuate row of toothlike platelets which diminish in size toward both extremities. Each platelet of the row has a somewhat spatulate proximal part in close contact with adjacent ones and a narrower distal part separate from its neighbors by distinct empty spaces (Fig. 335,*4*). The faintly convex proximal regions, made of finely reticulate stereom, probably were embedded in the integument, whereas the more convex distal regions, marked by tiny superficial wrinkles, doubtless protruded at least partly from it. Presumably, the platelets were bound together by transverse fibers, short and elastic between proximal portions, longer and contractile between distal portions. The anal orifice could be opened or closed very readily by opposite action of these fibers. The floor of the periproctal area in these genera, formed by the three most posterior marginals, also deserves attention. In some specimens of *Mitrocystites* the median one carries a faint transverse groove disposed parallel to the posterior margin attachment of the plate, probably marking the attachment of the contractile tissues of the lower lip of the anus (Fig. 335,*3*). Both in *Mitrocystites* and *Mitrocystella,* some portions of the internal surface of the two lateral posterior marginals may be raised into small shelves which apparently served for attachment of muscles or ligaments operating the rectal part of the digestive tube (Fig. 335,*1a,b*).

The anus of *Lagynocystis* is unknown, but a transverse row of very narrow ?anal plates at the posterior end of the supracentral covering abuts against a conical hollow ossicle that may represent a kind of anal valve (Fig. 333,*2*).

The subanals of *Chinianocarpos, Balanocystites,* and *Anatiferocystis* may have served as a floor of the periproctal areas (Fig. 332, *1,11,12*).A small gap at the posterior edge of the subanal should have been sufficient for ejection of excreta. No other indication of an anus is found in these genera.

In at least some Anomalocystitida *(Basslerocystis, Placocystites)* a large transversely elongate opening is observable on the posterior face of the theca (Fig. 331,*4b*). According to SCHUCHERT *(78)* and KIRK *(56),* a sort of trapdoor flap hanging from the upper margin of the aperture apparently served to close the terminal orifice of *Basslerocystis.* In *Placocystites* the orifice is surrounded by a smooth narrow band (bordered on the upper side by a row of small denticles); this band probably marks the attachment of a periproctal membrane. *Victoriacystis* exhibits small plates (termed tegminals by GILL & CASTER, *43*) in series with the supracentrals, geniculated to form a presumed cover surface probably over the anus. CASTER (in *43*) has reported the occurrence of similar platelets in *Enoploura.*

RIGHT ADORAL ORIFICE

A single thecal opening present in *Ceratocystis, Phyllocystis, Cothurnocystis,* and *Mitrocystites* is termed the **right adoral orifice** because invariably it is related to the right adoral plate. It leads more or less directly into a funnel-shaped depression known as the **infundibulum,** which is hollowed out on the internal face of marginal M_1. In *Ceratocystis* this orifice, found on the lower side of the theca, consists of a narrow slit with reflected right margin, followed inside by a concavity which forms a ceiling for the infundibulum (Fig. 330, *1b,c*). The right adoral orifice of *Phyllocystis* and *Cothurnocystis* is located on the anterior thecal margin above the aulacophoral insertion and slightly to the right of it, making a rather deep notch in the lower edge of the right adoral plate (Fig. 330, *2a-c,3a-c*). A somewhat ear-shaped project-

FIG. 335. Anal area among Stylophora.——*1. Mitrocystella incipiens miloni* CHAUVEL, M.Ord., Fr.; *1a,* internal side of inferior thecal face, ×3 (Ubaghs, n); *1b,* posterior part of same, details of floor of anal area, ×6 (Ubaghs, n).——*2. Phyllocystis crassimarginata* THORAL, L.Ord., Fr.; *2a,* superior face of theca, ×3 (Ubaghs, n); *2b,* anal pyramid, ×15 (Ubaghs, n).——*3. Mitrocystites mitra* BARRANDE, M.Ord., Boh.; post. part of superior thecal face, ×6 (Ubaghs, n).——*4. Mitrocystella barrandei* JAEKEL, M.Ord., Boh.; periproctal area, details, ×15 (Ubaghs, n).

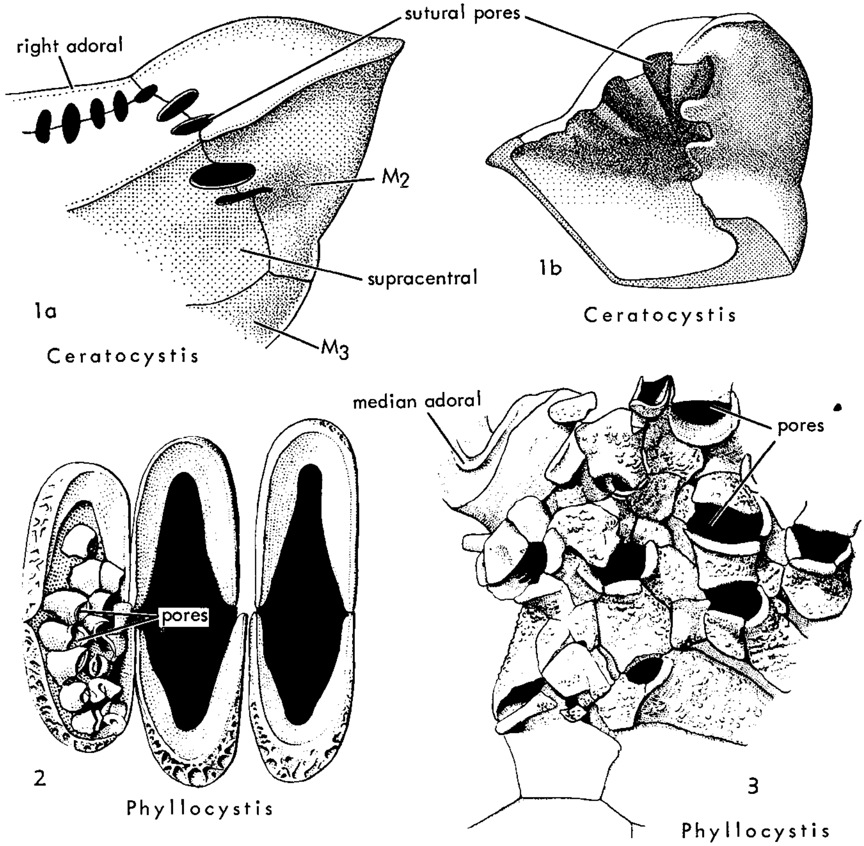


FIG. 336. Sutural pores and cothurnopores among cornute Stylophora.——*1. Ceratocystis perneri* JAEKEL, M.Cam., Boh.; *1a,* right anterior corner of theca, details, X5 (Ubaghs, n); *1b,* right anterior marginal, oblique view showing internal grooves leading to sutural pores, X5 (Ubaghs, n).——*2. Phyllocystis blayaci* THORAL, L.Ord., Fr.; cothurnopores, the left one with platelets preserved, X15 (Ubaghs, n).——*3. Phyllocystis crassimarginata* THORAL, L.Ord., Fr.; sutural pores; X15 (Ubaghs, n) (M_2, M_3, right marginalia).

ing rim borders it above and laterally in *Phyllocystis* but soft tissues must have adjoined it on the lower side. In *Mitrocystites* the upper surface of both adorals shows a fold running transversely from their outer anterior corners to their centers. A narrow slit in the right adoral near the inner (adaxial) end of this fold extends toward the anterior edge of the plate without reaching it (Fig. 333,*1a,b*). As in other genera mentioned, the orifice lies above the infundibulum but seems not to open directly into it, since exfoliated stereomic projections that conceal its inner edge come between it and the depression (see Fig. 340, *2c*). A similar orifice has not been discovered in *Mitrocystella,* although an infundibulum exists, suggesting that the opening was located close to the right adoral plate rather than in it, probably in soft tissues.

The constant relationships of the right adoral orifice to the right adoral plate and infundibulum in all genera where the open-

FIG. 337. Sutural pores and cothurnopores in Cothurnocystidae.——*1. Phyllocystis crassimarginata* THORAL, L.Ord., Fr.; *1a,* theca, superior face; *1b,* upper right anterior area, details, X10 (Ubaghs, n); *1c,* sutural pores, internal aspect, X10 (Ubaghs, n).——*2. Phyllocystis blayaci* THORAL, L.Ord., Fr.; *2a,* theca, superior face, X2 (Ubaghs, n); *2b,* cothurnopores, details, X15 (Ubaghs, n); *2c,* a few cothurnopores, internal aspect, X7.5 (Ubaghs, n).

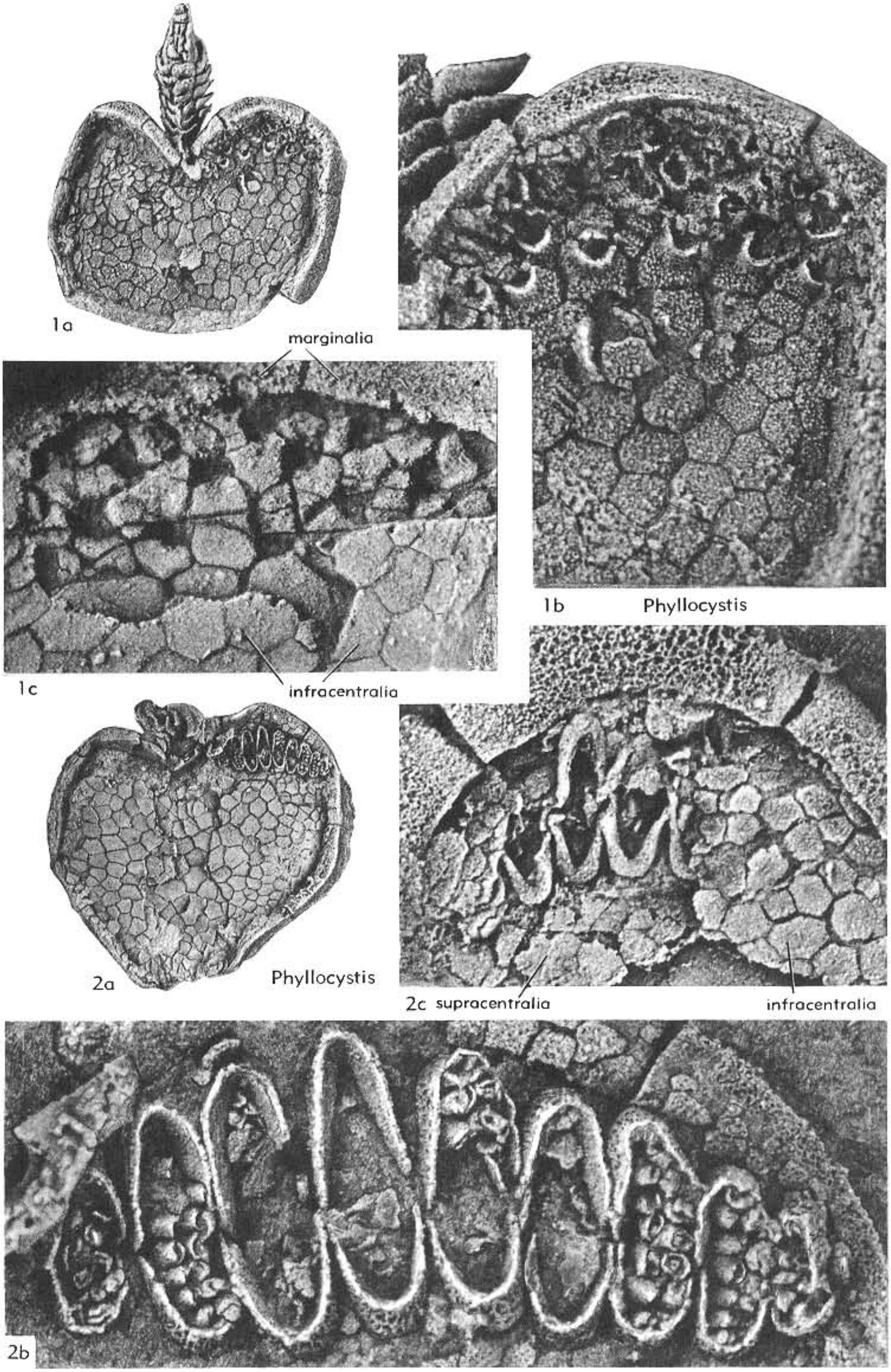


FIG. 337. [*Explanation on facing page.*]

ing has been observed indicates its homology throughout the group. Probably this means that the aperture migrated from an original location on the inferior face of the theca (e.g., *Ceratocystis*) to an ultimate placement on the superior face (e.g., *Mitrocystites*). A similar displacement from one face of the body to the other is seen in the postmetamorphic development of the hydropore in ophiuroids, which migrates from a dorsomarginal to adoral position. Of course, this may be pure analogy, yet it gives hint that the right adoral orifice in stylophorans might represent the hydropore, which is an interpretation supported by its singleness and asymmetrical location in *Ceratocystis* and *Mitrocystites,* as well as its narrowness. In particular, its appearance in *Mitrocystites* (Fig. 333,*1a,b*) is very similar to that of the hydropore groove of some echinoids (e.g., *Cubanaster torrei*). In *Phyllocystis* and *Cothurnocystis* soft tissues must have occupied the triangular space between the lower edge of the right adoral and the upper edge of marginal M_1 (Fig. 330,*2b,3a*), and since the hydropore was located in these soft tissues, we do not know its size and shape. Another possibility is that the hydropore was combined with the outlet for genital products. Close association of hydropore and gonopore in such primitive echinoderms would not be surprising, since the primordium of the gonad in developing individuals of the phylum arises from the wall of one of the coelomic pouches in contact with the complex of organs invariably located in the madreporitic interray.

SUTURAL PORES

All cornute Stylophora, except some undescribed forms, possess orifices in the right anterior part of the superior face of the theca which probably performed similar functions despite their large variety of morphological aspects. One type of these openings consists of rather simple sutural pores, first observed in *Ceratocystis* and called to attention by BATHER *(13)*. In this genus they comprise a series of more or less even-spaced apertures located along sutures that join the median and right adorals and that occur between contiguous supracentrals and the latter, along with marginals M_2 and M_3 (Fig. 330,*1a,b*). The pores vary in size, have rounded edges bent toward the thecal cavity, and lack an external projecting rim (Fig. 336,*1a*). Ordinarily the pores are prolonged by grooves on the inner surface of plates next to them (Fig. 336,*1b*). A single similar orifice is located on the suture between the left adoral and marginal M'_2 at the left anterior margin of the theca and another between the left adoral and M'_1 on the inferior face of the theca (Fig. 330,*1b*). The maximum diameter of the pores is less than 2 mm.

Sutural pores of another sort, in different specimens ranging from a few to more than 50, are seen in *Phyllocystis crassimarginata* THORAL (Fig. 336,*3*; 337,*1a-c*). They open between small supracentrals which have convex corrugated surfaces. Each pore is surrounded by the upturned edges of two or three, or as many as five of these plates. Their maximum diameter is 0.3 to 0.6 mm. As viewed from inside the theca, they appear as subquadrate openings 0.7 in greatest diameter (Fig. 337,*1c*).

COTHURNOPORES

Very curious elliptical structures observed first by BATHER *(13)* on the theca of *Cothurnocystis elizae* and found later by THORAL *(85)* in *Phyllocystis blayaci* are here named **cothurnopores,** as suggested by CASTER (personal communication) (Fig. 336,*2*; 337,*2a-c*). They are present also in several undescribed species of *Cothurnocystis* and in *Nevadaecystis (89),* occupying a tract that extends from the vicinity of the right adoral to the right lateral margin of the frame and projecting slightly above adjacent thecal plates smaller than ordinary supracentrals. The latter suggest a particularly flexible thecal wall. The cothurnopores lie contiguous to one another or nearly so and with diminishing size of individuals toward ends of their tract form a very elongate rhombic figure. They vary in number according to species and size (?reflecting age or growth stage)—eight in *Nevadaecystis,* eight or nine in *Phyllocystis,* and 18 or more in *Cothurnocystis elizae.*

The long axis of each cothurnopore lies approximately at right angle to the adjacent portion of the frame (Fig. 337,*2a*). The elliptical structures are surrounded by a raised rim formed by two unequal U-shaped ossicles, an inner short one and outer long one that meet at their free ends. According to Bather *(13, 14)*, the short U, which borders a semicircular orifice without cover plates, could be bent over on its hinge so as to protect the opening like the hood of a carriage or perambulator. The long U, with sides sloping down to a V-shaped slit, is protected by a double row of alternating cover plates which are similar in appear-

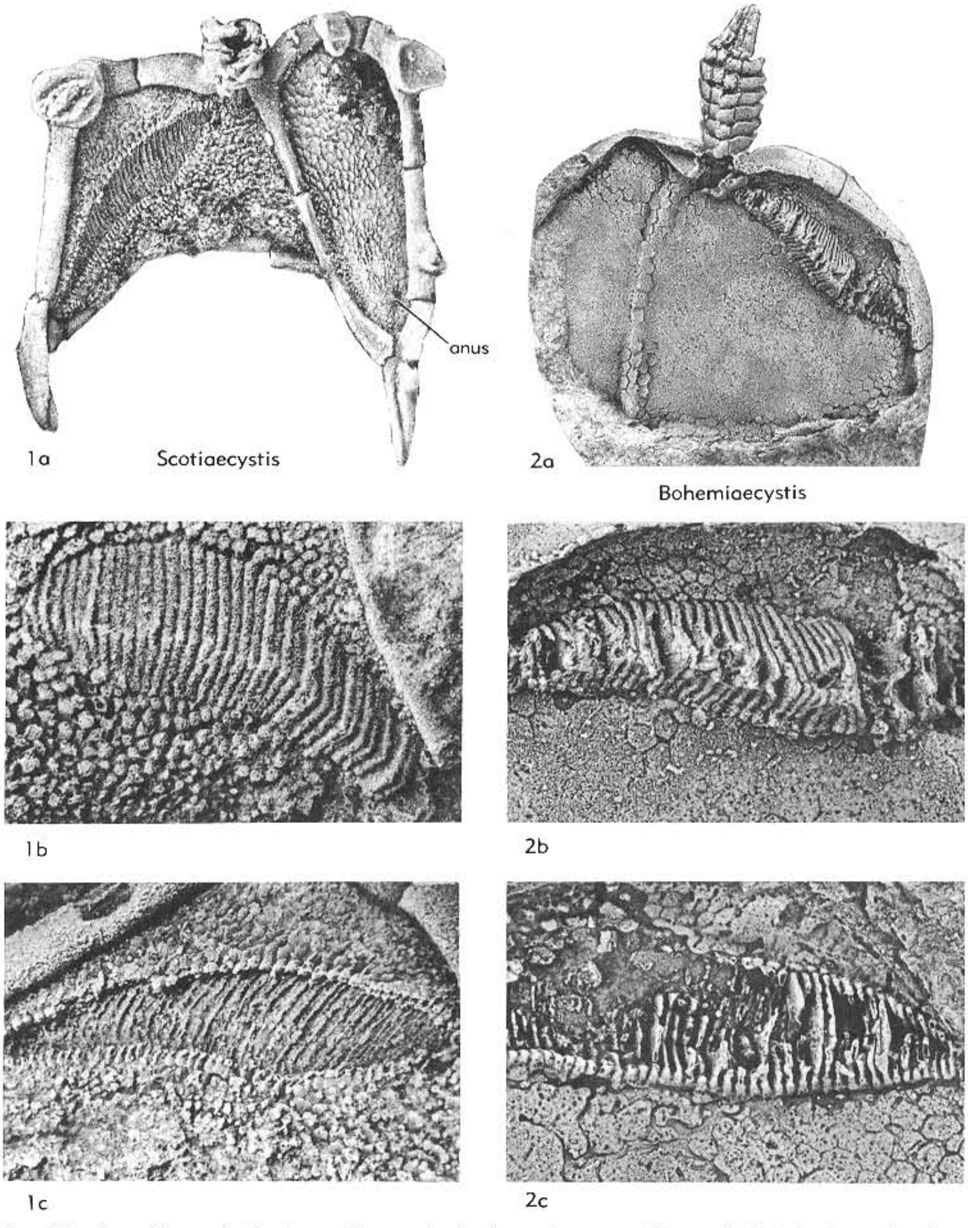


Fig. 338. Lamellipores in Scotiaecystidae.——*1. Scotiaecystis curvata* (Bather), U.Ord., Scot.; *1a,* theca, superior face, ×2.5 (Ubaghs, n); *1b,c,* lamellate organ, external and internal aspects, ×5 (Ubaghs, n). ——*2. Bohemiaecystis bouceki* Caster, n. genus, n. species, M.Ord., Boh.; *2a,* theca, superior face, ×2 (Ubaghs, n); *2b,c,* lamellate organ, external and internal aspects, ×5 (Ubaghs, n).

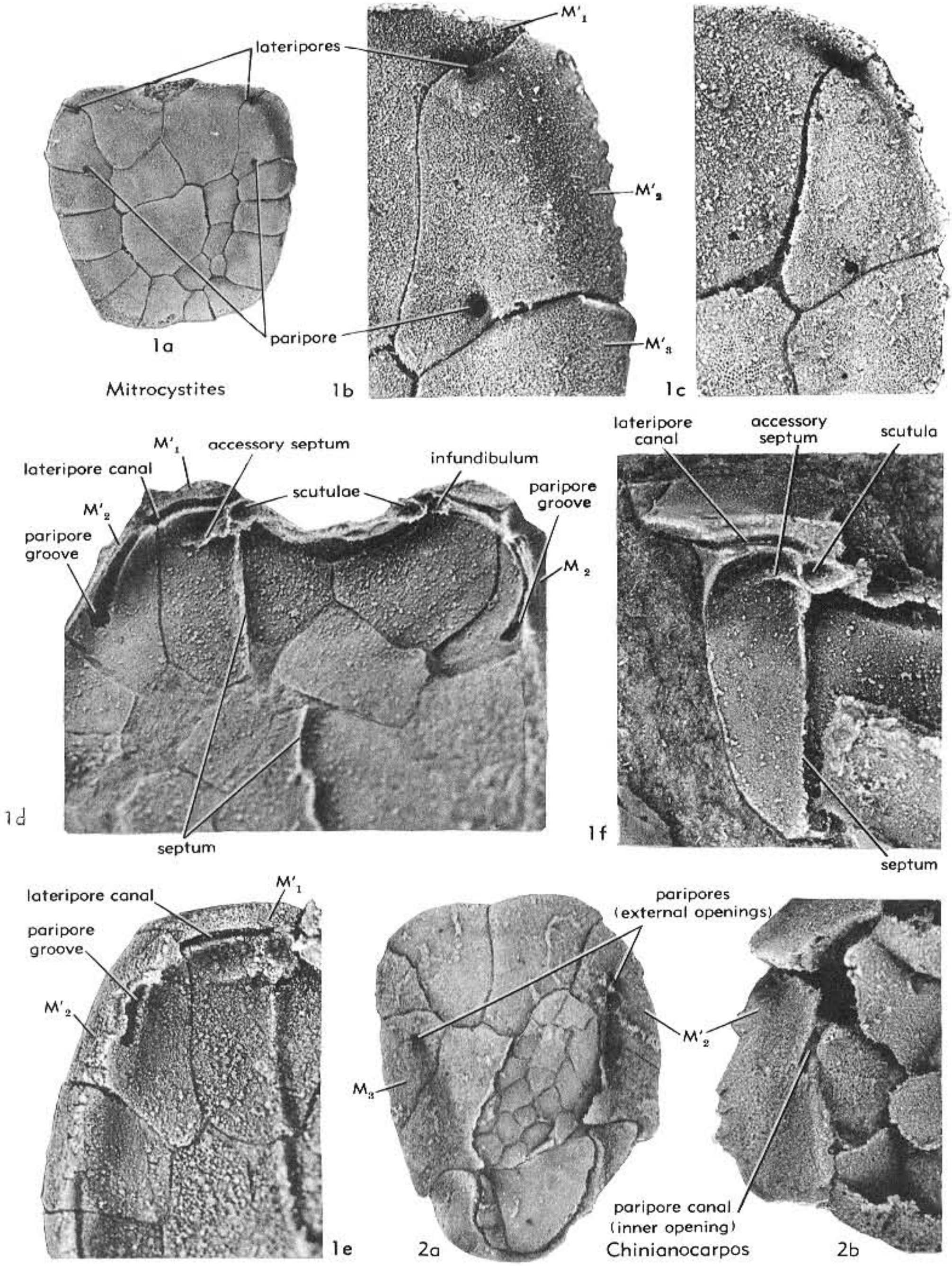


FIG. 339. Lateripores and paripores in Mitrocystidae.——*1. Mitrocystites mitra* BARRANDE, M.Ord., Boh.; *1a,* theca, inferior face (holotype of *M. latus* JAEKEL, considered as syn. of *M. mitra*), ×2 (Ubaghs, n); *1b,* same specimen, detail, ×7.5 (Ubaghs, n); *1c,* another specimen, detail, ×7.5 (Ubaghs, n); *1d,e,* internal side of inferior thecal face, showing canals connected with, respectively, paripores and lateripores, as well as various internal structures, ×5 (Ubaghs, n); *1f,* marginal *M'₁,* internal side, showing inner

ance and probable function to those of ordinary crinozoan food grooves.

Study of specimens of *Phyllocystis blayaci* preserved in matrix finer-grained than that associated with *Cothurnocystis elizae,* supplemented by examination of latex casts, indicates that the true structure of the cothurnopores—at least in *P. blayaci*—differs from the interpretation given by Bather. Neither orifice nor cover plates exist. Instead, the entire space enclosed by the cothurnopore rim is occupied by tiny platelets which are paired to form minute cones, each with a minute apical pore (Fig. 336,*2*; 337,*2b*). Therefore cothurnopores seem to be a very complex type of porous organs having no structural relationship with the subvective system of pelmatozoan echinoderms.

LAMELLIPORES

An additional type of openings occurs on the upper thecal face of *Scotiaecystis* and *Bohemiaecystis* (Fig. 338). It consists of narrow slits between vertical calcareous lamellae, very numerous, closely set, and grouped to form elongate rhombic structures similar to the conjunct pore rhombs of some cystoids. The individual slits here are named **lamellipores** and their combined structure a **lamellate organ.** The outer surface of the organ is slightly ridged, whereas its inner surface is apparently concave in *Scotiaecystis* and strongly convex in *Bohemiaecystis* (Fig. 338,*1b,c, 2b,c*). The internal face of each lamella is prolonged into the thecal cavity *(Bohemiaecystis)* or marked by a median very shallow groove that possibly served for attachment of soft partitions on both lateral edges *(Scotiaecystis).* The entire margin of the lamellate organ of *Scotiaecystis* on its internal side bears curious imbricate platelets, not matched by similar ones in *Bohemiaecystis* (Fig. 337,*1c,2c*). Bather *(13,14)* thought that minute irregular plates covered the slits of *Scotiaecystis,* but study of latex casts indicates that this is a misinterpretation probably based on the coarse appearance of external edges of the lamellae. In neither genus have cover plates actually been detected. In an undescribed species from the Lower Ordovician of France, some lamellae appear to be divided into two subequal parts by a very faint suture; this may suggest that originally at least the lamellipores were sutural pores of some sort.

LATERIPORES

Among accessory orifices in the theca of mitrate Stylophora are two types that first were observed by Jaekel *(55)* on the inferior face of *Mitrocystites* (Fig. 339,*1a*). He termed them *Seitenporen* and *paarige Gruben,* names which here are replaced by lateripores and paripores, respectively.

Lateripores comprise two symmetrically placed openings near the anterolateral angles of the lower thecal face, one striding the suture between marginals M_1 and M_2 and the other that of the suture between M'_1 and M'_2. Each opens on the floor of depressions which vary in depth and span in different specimens (Fig. 339,*1b,c*). The depressions commonly are extended parallel to borders of the theca by shallow furrows, one directed obliquely forward toward the main axis of the body and the other backward. The first of these quickly vanishes, but the second may reach as far as M_3 and M'_3, length varying among individuals, and they may even be absent. The pores themselves indent the edges of the marginals next to them more or less deeply. Each is the external orifice of a vertical canal excavated in the upturned sutural surfaces of the marginals (Fig. 339,*1d-f*; 340,*2b*). At the level of the upper edge of these plates each canal is extended horizontally and adaxially by a furrow on the surface of M_1 or M'_1, that is to say along the border of these marginals which supports corresponding adorals. The canals terminate close to special structures (scutulae, infundibulum, described subsequently) without opening into them.

The occurrence of lateripores in *Mitrocystella* is uncertain. Jaekel *(55)* figured

Fig. 339. [*Explanation continued from facing page.*]

canal from left lateripore, ×5 (Ubaghs, n).——*2. Chinianocarpos thorali* Ubaghs, L.Ord., Fr.; *2a,* theca, inferior face, ×5 (Ubaghs, n); *2b,* inner opening and inner groove of paripore canal on superior edge of marginal M'_2, ×7.5 (Ubaghs, n) (M_2, M_3, right marginals 2 and 3; M'_1, M'_2, left marginals 1 and 2).

them in *M. barrandei,* and CHAUVEL *(30)* thought that probably they were present in *M. incipiens miloni*; but all specimens studied by me show only doubtful indications of them or none at all. On the upper edge of marginal M_1 in two individuals, however, I have observed a furrow comparable to that found in the same posi-

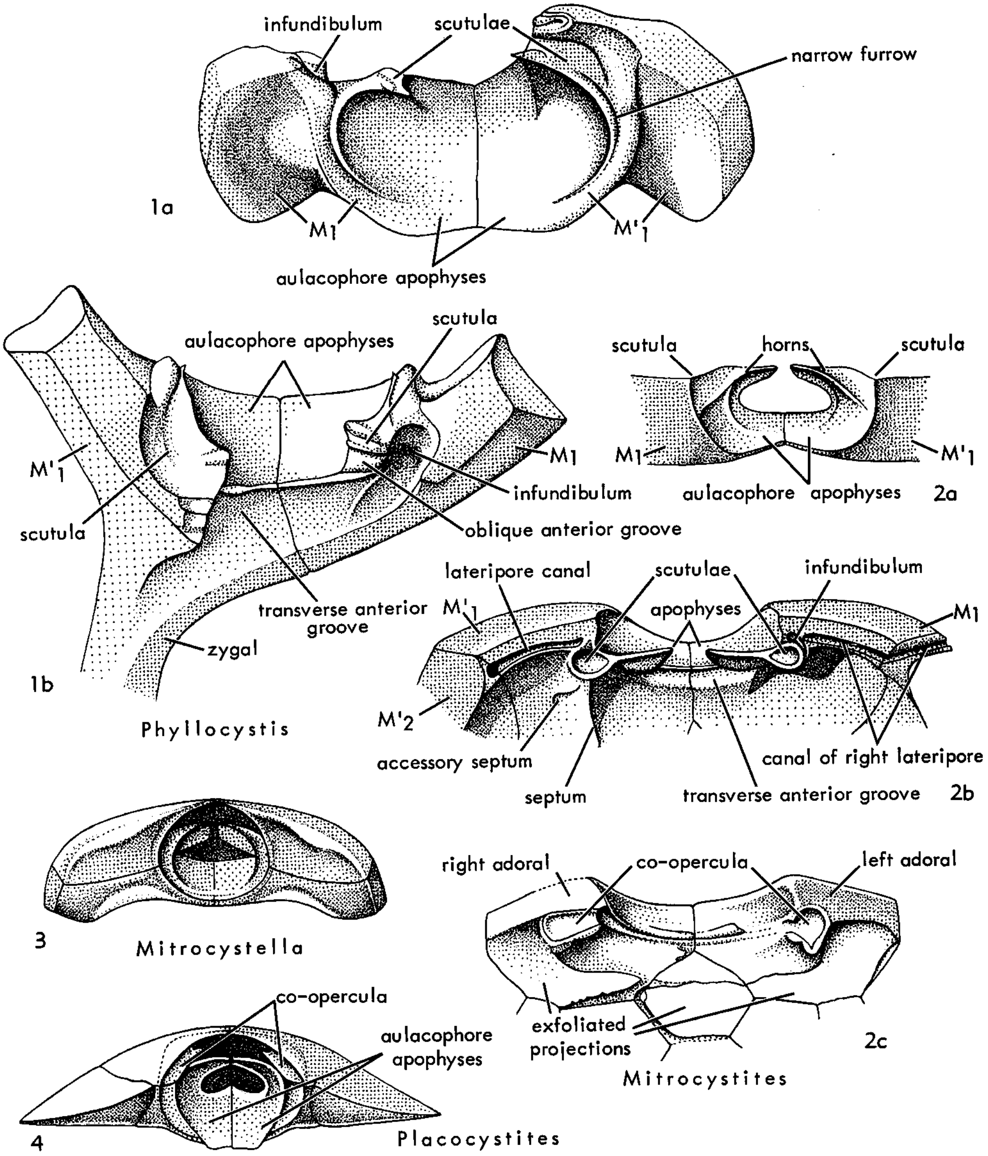


FIG. 340. Internal thecal structures among Stylophora.——*1. Phyllocystis blayaci* THORAL, L.Ord., Fr.; *1a,b,* aulacophore insertion and adjacent structures, in anterior and superior aspects, X16 (Ubaghs, n).——*2. Mitrocystites mitra* BARRANDE, M.Ord., Boh.; *2a,b,* aulacophore insertion and adjacent structures, in anterior and superior aspects, X4.4 (Ubaghs, n); *2c,* adoralia, internal side, X4.4 (Ubaghs, n).——*3. Mitrocystella barrandei* JAEKEL, M.Ord., Boh.; anterior face of theca, X2.5 (Ubaghs, n).——*4. Placocystites forbesianus* DE KONINCK, Sil. (Wenlock Ser.), Eng.; anterior face of theca, X1.6 (Ubaghs, n) (M_1, M'_1, median anterior marginals).

tion in *Mitrocystites* communicating with the right lateripore. Perhaps the lateripores of *Mitrocystella,* if they existed, did not open on the inferior face of the theca but instead opened laterally between the marginals and adorals.

The marginals M_1 and M'_1 of *Lagynocystis* are extended well upward and forward by an incurved hornlike portion which laterally encloses the insertion of the aulacophore (see Fig. 341,*1*). The inner side of this horn is hollowed as a trough and probably this trough opened to the exterior by means of a sutural pore located at the front of the theca (see Fig. 342,*2*), possibly equivalent to a lateripore of *Mitrocystites.*

PARIPORES

Symmetrically placed on opposite sides of the main body axis of *Mitrocystites* and commonly somewhat closer to this axis than the lateripores are two small thecal openings named **paripores.** They are not simple excavations on plates of the inferior face, as JAEKEL's term *Gruben* suggests, but true orifices which pierce marginals M_2 and M'_2 near the posterior sutures of these plates (Fig. 339,*1a-c,2a*). Their nature as pores is demonstrated by their connection with a deeply impressed groove on the inner surface of each marginal (Fig. 339,*1d,e*). The grooves extend from the paripores obliquely forward and upward and terminate on the upper edge of these marginals not far from the sutures between them and M_1 and M'_1. The internal grooves vary in length in different specimens, and in at least a part of their course they seem to be separated from the thecal cavity by a thin wall.

The inferior face of the theca of *Chinianocarpos* shows two pores approximately at the centers of marginals M_3 and M'_2 (Fig. 339,*2a*). They are more or less symmetrical with respect to the axial plane and seem undoubtedly to correspond to the paripores of *Mitrocystites,* even though the inner side of the theca shows neither openings nor grooves associated with these pores. Consequently, the conduits that end in the pores must have been included entirely within the thickness of the thecal wall, a conclusion that seems to be confirmed by the presence of two other pores on the upper edges of M_3 and M'_2, each accompanied by a short forward-trending furrow (Fig. 339,*2b*). The latter pores are presumed to represent internal (intrathecal) orifices of conduits leading to the external orifices identified as paripores.

FUNCTION OF ACCESSORY ORIFICES IN STYLOPHORA

Interpretations of the possible function of the several sorts of accessory orifices seen in the Stylophora differ from one another approximately as much as cothurnopores differ from sutural pores, or lamellipores from lateripores and paripores. Such apertures in the Cornuta were considered by BATHER *(13, 14)* to be inhalant orifices for entrance of food particles which were carried by ciliary currents to an internal mouth and his opinion was accepted by CHAUVEL *(30)*, DELPEY *(35)*, TERMIER & TERMIER *(82)*, and CUÉNOT *(32)*. They were judged by JAEKEL *(55)* to represent genital apertures and by GISLÉN *(45)* to be branchial slits formed by intestinal diverticula which coalesced with the surface of the body and opened upon it, the slits serving to strain off water and allow food particles to remain in the digestive tube. Cothurnopores were thought by SPENCER *(80)* to be respiratory pouches which probably lacked any communication with the alimentary canal and were imagined by NICHOLS *(68)* to house respiratory organs which could be retracted and covered by plates when the animal was disturbed.

The first of these interpretations is the most improbable, if one admits that the food-catching organ of stylophorans is the aulacophore, as all evidence indicates. Then, cothurnopores and analogous orifices were not needed for collecting nutrient particles.

JAEKEL *(55)* suggested that cothurnopores were multiple gonopores but furnished no supporting reasons for such an assumption. BATHER *(14)* rejected this interpretation because their structure, in his view, suggested food-intake organs. GISLÉN *(45)* likewise denied the possibility that cothurnopores could be a series of gonopores, for this would demand a corresponding number of gonads within the theca and call for an extremely improbable segmented body. NICHOLS *(68)* pointed out that gonopores

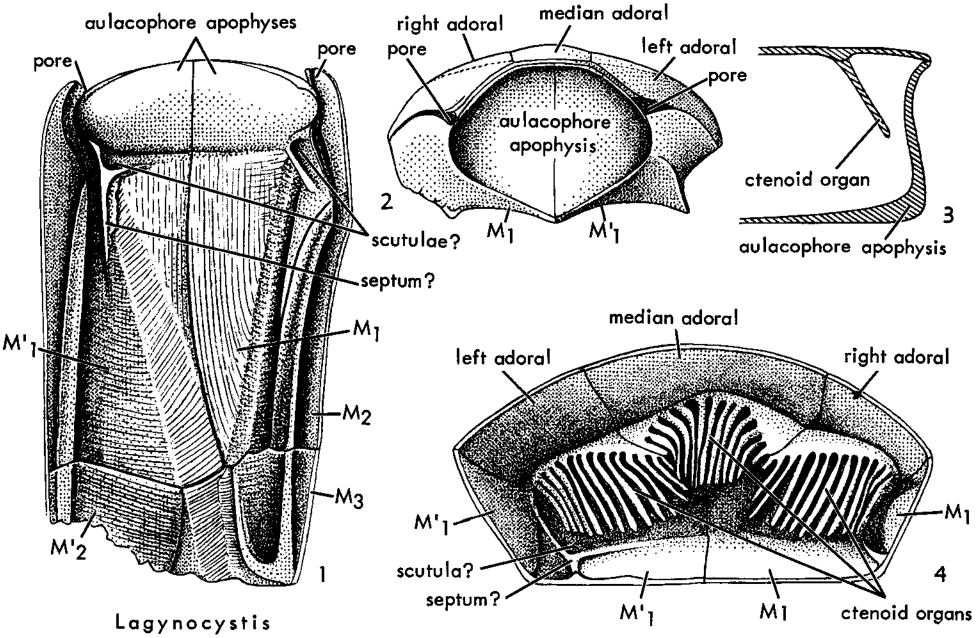


Fig. 341. Morphology of *Lagynocystis pyramidalis* (Barrande), M.Ord., Boh.——*1.* Internal anterior thecal structures of inferior face, ×5 (Ubaghs, n).——*2.* Anterior face of theca, ×5.3 (Ubaghs, n).——*3.* Schematic longitudinal median section through anterior part of theca, ×5.3 (Ubaghs, n).——*4.* Ctenoid organs, posterior face, ×8 (Ubaghs, n) (M_1, M_2, M_3, right marginalia 1, 2, 3; M'_1, M'_2, left marginalia 1, 2).

would not require the complex plate structure of cothurnopores and that multiple gonopores surely would not be needed by Stylophora. Arguments like these do not lead to a definitive judgment, especially since secondary metamerism of gonads is a possibility in archaic echinoderms. It is known in rather primitive Deuterostomia (e.g., Enteropneusta).

The possibility that the stylophoran accessory orifices and structures associated with them served a respiratory function is suggested by their analogy with the hydrospires, pore rhombs, and sutural pores of other primitive echinoderms. It seems hardly conceivable however that in *Nevadaecystis* they were used as simple respiratory pores, for respiratory exchange must have been readily accomplished through the many uncalcified areas between the supracentrals. Furthermore their complex morphology and their narrow location in a definite part of the body suggest that they housed specialized structures or were connected with internal organs such as the alimentary canal. This leads to consideration of the possibility that they were branchial openings related to the pharyngeal part of the digestive tract (and not to the intestinal part, as supposed by Gislén), since they are close to what seems to have been the mouth region. Other deuterostomian invertebrates (e.g., Stomochorda) have developed pharyngotremy. Such a feature might have arisen as means of securing an outlet for the water that entered the pharynx with the food, but it must also have helped to provide respiratory exchange. The accessory pores of Stylophora, however, could not have been gill slits opening directly to the exterior, for the cothurnopores in many specimens of *Cothurnocystis elizae* penetrate so deeply into the posterolateral (spinal) corner of the theca that the digestive tube would have been bent at an acute angle at the end of the branchial region, which is unlikely. Therefore, if they were connected with the alimentary canal, they could only have been external openings of branchial sacs or diverticles. But in such case why did they require the complex plated structure of cothurnopores, why are they so different from one genus to another and even from one species to another species of the same genus, and how it is possible that they are entirely lacking in some species?

Such questions, which remain without satisfactory answers, show that the evidence at hand does not permit elucidation of the real nature of stylophoran accessory orifices. Among various interpretations that have been proposed none seem conclusive and none (except perhaps BATHER's opinion that the cothurnopores were part of a subvective system) can be definitively rejected.

The significance of accessory thecal orifices in the mitrate Stylophora is as difficult to determine as in genera of the Cornuta. For example, both BATHER *(14,19,20)* and GISLÉN *(45)* judged that the morphological attributes and functions of lateripores and paripores in the Mitrata corresponded to cothurnopores and other accessory orifices in the Cornuta. BATHER, however, viewed the pores as entries leading to the digestive tube, passageways to the mouth being invaginated and transformed into a tunnel. GISLÉN interpreted them as branchial orifices produced by coalescence of the body wall with intestinal respiratory diverticula. CHAUVEL *(30)* and CASTER *(26)* have concluded that the small thecal openings in Mitrata cannot be homologized with the complex pore apparatuses of the Cothurnocystidae. Noting that lateripores and paripores are confined to a small number of mitrate forms, CHAUVEL has supposed that they represent organs for optional communication with the exterior or that they could emit their products in diverse ways without need for specialized openings. On the basis of this he developed his hypothesis that lateripores are gonopores and paripores are hydropores, an opinion shared by CASTER *(26)*.

The observed placements of accessory thecal orifices in *Lagynocystis* possibly throws light on the morphologic and functional significance of these pores in the Mitrata generally. On the ceiling of the anterior part of the thecal cavity in this genus are comblike structures (ctenoid organs) so arranged that they could have served to filter water entering the digestive tube (Fig. 341,*3,4*). A sort of entry appears to have been located just in front of the thecal cavity, water entering it by way of the aulacophore and probably escaping from it by sutural pores located at the base of this organ on both sides of its insertion (Fig. 341,*1,2*). Although ctenoid organs have not been found in other genera, it may be assumed that their general organization differed in no essential way from that of *Lagynocystis*. In genera having a single pair of pores, these may be exhalant orifices, as in *Lagynocystis*. Where two pairs of pores are present, an exhalant function is assignable to one of them and a different (?inhalant, ?genital) function to the other pair. We must recognize, however, that this sort of reasoning rests on structural analogies and that the true significance of pores in Mitrata, like those of Cornuta, remains entirely conjectural.

INTERNAL CHARACTERS OF THECA

INSERTION OF AULACOPHORE

The aulacophore is attached to the middle of the anterior face of the theca. Among cornute genera other than *Ceratocystis* its proximal lower edge overlaps against the forward-projecting parts of marginals M_1 and M'_1 (e.g., *Phyllocystis blayaci*) or abuts against it (e.g., *Cothurnocystis elizae*). In *Ceratocystis* and all Mitrata its base penetrates a cavity provided at the front of the theca. Except for this difference, the mode of insertion of the aulacophore is practically the same in the two groups.

On the inner faces of M_1 and M'_1 are two elevations **(aulacophore apophyses)** which plainly serve for attachment of proximal muscles of the aulacophore (Fig. 330,*2b,3a*; 340,*1a,2a,3,4*). These apophyses are somewhat reduced and separated in *Ceratocystis* but strongly developed and closely adjoined in all other genera where they have been observed. Thick at the base, they become slender upward and on internal molds their former presence is shown by a deep incision which CHAUVEL *(30)* named *sillon pédonculaire*. Symmetrical and similar to one another, the apophyses together form a small cup that is directed forward and somewhat upward.

The just-described cup commonly is divided into four unequal concave fields—

two adaxial large ones and two abaxial small ones—separated by a pair of ridges which are raised from the floor of the cup and ascend in a curve parallel to its lateral borders. The upper extremities of the ridges protrude only a little in the Cornuta but are prolonged in the Mitrata into incurved horns with points convergent on one another and by twisting of their axes the horns overhang the cup (Fig. 340, *1a,2a,b,3,4*). The upper surfaces of the horns, which are relatively flat and expanded slightly, furnish attachment and support for the first plate ring of the aulacophore. In the Mitrata the horns divide the passageway between cavities of the aulacophore and theca into lower and upper orifices which are more or less completely separated from each other (Fig. 340, *3,4*). On the other hand, the passage is not divided in the Cornuta and is large, for the adorals above it generally form an elevated arch (Fig. 340,*2b,3a*).

The nature of these features is somewhat different in *Lagynocystis* (Fig. 341,*1-3*). The apophyses of M_1 and M'_1 in this genus have neither ridges nor horns, and they are produced upward to form a wall or diaphragm that separates the aulacophoral and thecal cavities almost completely. The diaphragm is very peculiarly shaped, since its lower half has a median convex portion between two moderately deep concave lateral portions and its upper half is concave, curving forward and down. Communication between the aulacophoral and thecal cavities could have been effected only over the upper edge of the diphragm. Indeed, the internal (posterior) surface of this partition bears an oblique channel descending toward right from the top, possibly representing the path along which water and food particles entered the thecal cavity. The existence of a similar channel descending leftward has not been determined but seems probable.

SCUTULAE

Near the two abaxial extremities of the upper edges of apophyses belonging to M_1 and M'_1 and symmetrically placed with respect to the main body axis is a pair of concave platforms here named **scutulae** (sing., **scutula**), from the Latin for plate or saucer. Among cornute stylophorans they are quite unequal, that on the right side barely developed. The left scutula comprises the floor of a rather large cavity supported by the upper overhanging edge of M'_1 and the adoral above this marginal. Each scutula is prolonged forward (i.e., toward the aulacophore) by a very narrow furrow which descends along one of the two ridges borne by the concave anterior face of the aulacophore apophyses and becomes lost on the floor of these (Fig. 340,*1a*).

The scutulae of mitrate genera are subequal and well developed (Fig. 340,*2b*). Their outline is subtrigonal and their floor rises from a strongly depressed abaxial corner toward the main body axis, merging insensibly with the upper surface of the apophysis horns. It may be noted in passing that on internal molds each scutular depression is marked by a nipple-like protuberance, which CHAUVEL *(30)*, who was first to observe it, called "mamelon" and interpreted as an unpaired feature on the left side of the theca (*Treatise* orientation). In fact, two mamelons are present, one on either side. Scutulae seem to be lacking in *Ceratocystis,* at least in the form which has been described. In *Lagynocystis* a more or less well-marked depression can be seen at left near the base of the diaphragm between the aulacophoral and thecal cavities (Fig. 341,*1*). This depression, matched on the other side by a much more vague concavity, may be the equivalent of a scutula.

CO-OPERCULA

In at least some Mitrata, structures similar to contour to scutulae, with concave surface bounded by a projecting rim, occur in the inner surface of adoral plates and are inferred to correspond to the scutulae. They are here designated as **co-opercula** (sing., **co-operculum**), from the Latin for lid or cap. Undoubtedly, these structures lie above the scutulae and with them contribute to isolating small parts of the thecal cavity more or less completely (Fig. 340,*2c*). Their described placement and nature have been observed in *Mitrocystites* and they probably occur also in *Placocystites* (Fig. 340,*4*). In *Mitrocystella incipiens miloni* one may see identically placed slight prominences from each of which five wrinkles radiate in as many directions *(30)*, and a similar feature occurs in *Paranacystis (26)*. Comparable structures are lacking in *Lagynocystis, Balanocystites*, and *Anatiferocystis*. Their existence in other genera is unknown, but only in rarest circumstances can the inner side of adoral plates be examined.

The role of co-opercula and scutulae is uncertain. CHAUVEL *(30)* postulated that they marked the placement of ganglionic masses from which nerves extended in thickened thecal elements, such as the wrinkles mentioned in *Microcystella incipiens miloni* and *Paranacystis*. The presence of nerve concentrations in this region of the theca seems reasonable in view of the large development and apparently considerable importance of the proximal musculature of the aulacophore. Thus, one is tempted to consider scutulae as possible sites of nerve centers.

INFUNDIBULUM

A depression excavated between the right scutula and upper edge of the inner side of marginal M_1 is here termed the **infundibulum** (Latin, funnel). Its topographic relationships to the right adoral orifice have been noted previously. In *Ceratocystis* the infundibulum is shallow and rounded, but in other Cornuta (e.g., *Cothurnocystis, Phyllocystis*) and the Mitrata (e.g., *Mitrocystites, Mitrocystella*) wherever observable it is deeply impressed in the substance of the plate (Fig. 340,*1b,2b*). A generally well-marked furrow **(transverse anterior groove)** hollowed on inner surfaces of M_1 and M'_1 runs from its base along the posterior face of the aulacophore apophyses, passes beneath the scutulae, and becomes lost either on the inner surface of the zygal (in Cornuta) or at the origin of the septum (in Mitrata), described subsequently. Another furrow **(oblique anterior groove)**, which is much narrower and weaker than the transverse groove, may be seen in some specimens of *Cothurnocystis* and *Phyllocystis*. This leaves the bottom of the infundibulum, rises obliquely, and ends at the summit of the adjacent apophysis just beneath the adaxial angle of the right scutula (Fig. 340, *1b*). Seemingly, it connects the infundibulum with the aulacophore. Finally, in *Ceratocystis* and some specimens of *Phyllocystis* and *Mitrocystella*, a third groove, which generally is very weak, runs from the infundibulum toward the right and disappears on the inner face of the anterior marginals on this side of the theca. Thus it appears that the infundibulum is a sort of center toward which a group of structures converge, and this supports the inference that it exercised a complex role.

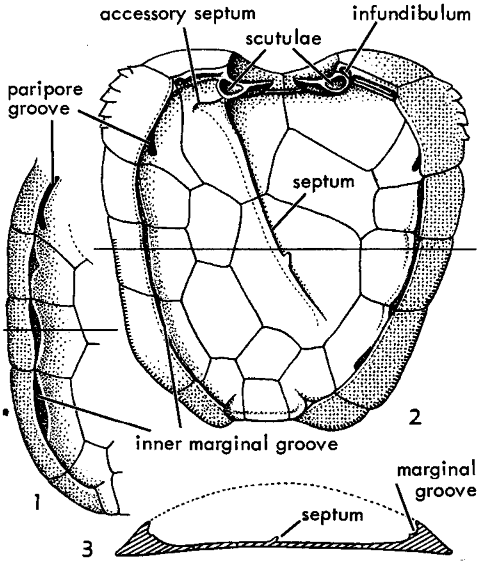


FIG. 342. Internal thecal structures of *Mitrocystites mitra* BARRANDE, M.Ord., Boh.——*1*. Left lateral side of inferior face of theca, slightly oblique view to show inner marginal groove, ×2.2 (Ubaghs, n). ——*2*. Inner side of same, ×2.2 (Ubaghs, n).——*3*. Cross section of theca, ×2.2 (Ubaghs, n).

If, as previously supposed, the orifice by which the infundibulum communicated with the exterior (right adoral orifice) represents a hydropore, possibly combined with a gonopore, the infundibulum should be the seat of a part of what presently constitutes the axial complex of echinoderms. At any rate, it must have inclosed the hydroporic canal, perhaps accompanied by the small ampulla (remnant of the left axocoel) which in modern echinoderms is placed at its junction with the stone canal.

The anterior oblique groove of stylophorans probably inclosed the hydrocoel branch which penetrated into the aulacophore, and the anterior transverse groove may have contained another hydrocoel diverticle passing beneath the esophagus and possibly corresponding to the stone canal and the periesophageal ring of radially symmetrical echinoderms. The transverse groove may also have contained part of the axial sinus. The faint groove on the inner surface of the right anterior marginals perhaps marks the course of the genital rhachis.

SEPTUM

A low wall or ridge observed on the floor of the thecal cavity of most Mitrata is termed the **septum** (Fig. 335,*1a*; 342,*2*,*3*). It originates on the M'_1 marginal slightly below the level of the left scutula and runs obliquely toward the right posterior corner of the theca without reaching it. The course of the septum is slightly irregular and its height is steadily reduced toward the rear. It leans toward the left in its anterior part so as to have an asymmetrical transverse section but straightens up in the posterior part, providing a more symmetrical section. Presence of the septum is marked on internal molds by a very characteristic strong incision, which was clearly illustrated by BARRANDE *(2)* and was called *sillon transversal* by CHAUVEL *(30)*, who was the first to draw attention to its existence.

A small **accessory septum** diverges in a general leftward direction near the anterior extremity of the septum (Fig. 340,*2b*; 342,*2*). Also, a diminutive spur is seen on the right side of the septum in the posterior third of its length in some specimens (Fig. 335,*1a*; 342,*2*).

ZYGAL

Among the Cornuta a septum is lacking, but this structure appears to be replaced by a skeletal bar extending from M_1 to the right posterior margin of the lower thecal face. This bar, named the **zygal** *(89)*, is probably equivalent in function to the septum and perhaps also in morphology. The two structures are closely similar in position and connection with other parts of the theca—for example, with the marginal M_1, the anterior transverse groove, and the left scutula—and they show a like oblique placement with respect to the main axis of the body. A median crest runs on the inner surface of the zygal, serving possibly for attachment of organs or mesenteries, as likewise in the case of the septum. The marginal M'_1 of the mitrate *Anatiferocystis,* which is almost identical in form with that of the equivalent marginal of *Cothurnocystis,* is a thin narrow plate that forms a ridge on the floor of the thecal cavity. This is curiously similar to the zygal of the Cornuta.

Ceratocystis and *Nevadaecystis* seem to have neither a zygal nor a septum. *Lagynocystis* also lacks a septum but has a much shorter ridge parallel to the left border of the theca, and possibly this is homologous to the septum seen in other Mitrata (Fig. 341,*1*). According to CASTER *(26)*, the superior face of the theca of *Paranacystis* has an internal groove that externally is marked by a rounded ridge, and this structure may correspond to the normally developed septum.

FUNCTIONS OF SEPTUM AND ZYGAL

CHAUVEL *(30)* viewed the septum of Mitrata as the place of attachment for a mesenteric membrane that supported one of the loops of the digestive tube. He thought to have discovered traces of two other mesenteries, at right and left, running along the marginals, and assigned to them a comparable role in fixation of the digestive canal. Thus he judged that he could determine the approximate course of this organ, concluding that it turned around like that of crinoids and holothuroids. This interpretation lacks the anatomical foundation inferred by CHAUVEL, for what he

FIG. 343. Morphology of aulacophore in cornute Stylophora.——*1-5. Phyllocystis crassimarginata* THORAL, L.Ord., Fr.; *1,* proximal region, stylocone, and proximal part of distal region, aboral face *(1a)*, oral face *(1b)*, ×7 (Ubaghs, n); *2,* stylocone, oral face *(2a)*, left lateral face *(2b)*, longitudinal median section *(2c)*, ×30 (Ubaghs, n); *3,* ossicles of distal region, oral face *(3a)*, left lateral face *(3b)*, proximal face *(3c)*, distal face *(3d)*, ×30 (Ubaghs, n); *4,* two cover plates, inner or oral face, ×30 (Ubaghs, n); *5,* diagrammatic reconstruction of a portion of distal region, with cover plates widely open and water-vascular organs (in black) (M_1, M_2, right marginalia 1, 2; M'_1, M'_2, left marginalia 1, 2).

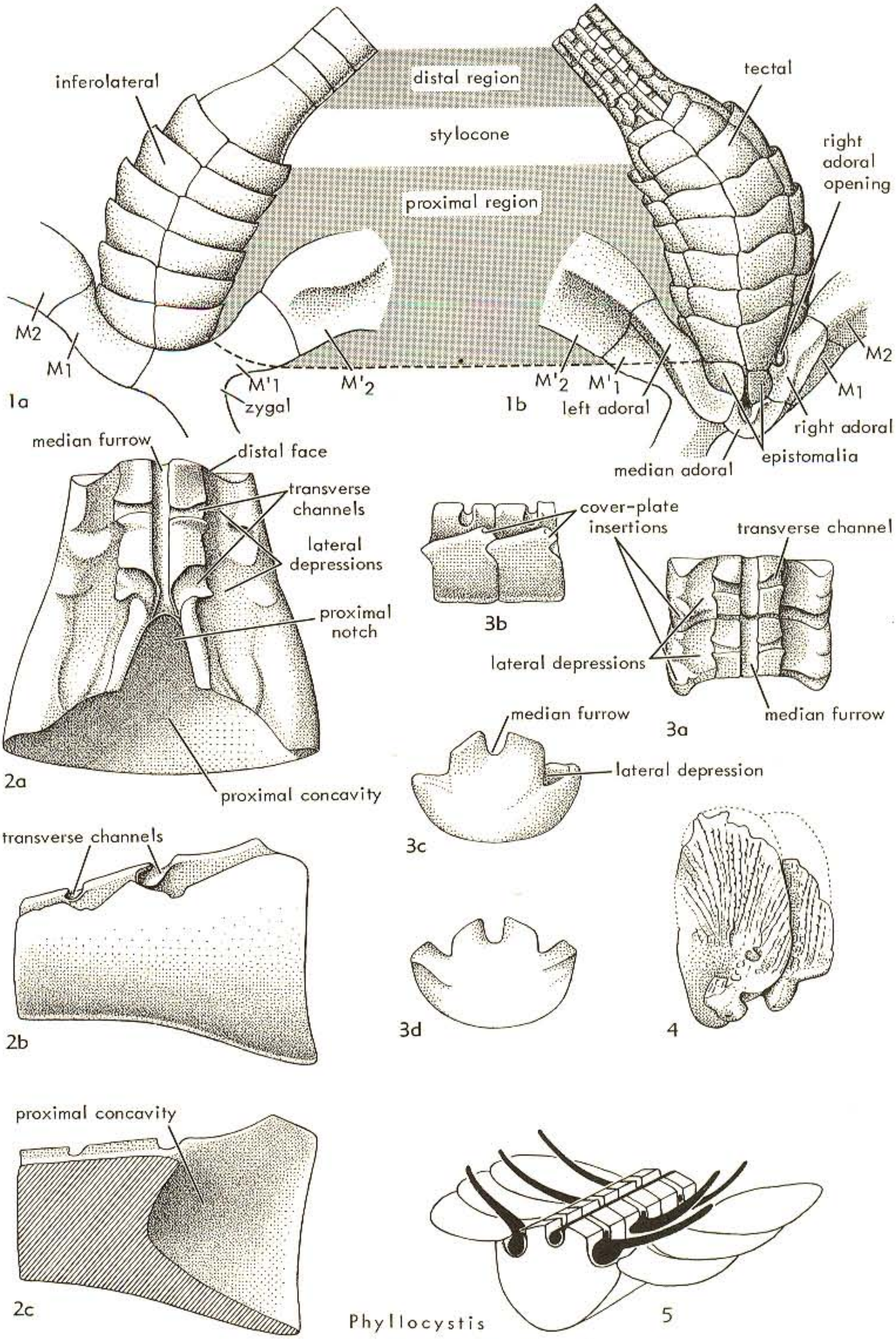


FIG. 343. [*Explanation on facing page.*]

considered to be emplacements of lateral mesenteries in reality represents the projecting adaxial borders of grooves excavated on the inner surface of the lateral marginals (Fig. 335,*1a*). CASTER *(26)*, who inferred a similar function of the septum, arrived at a much simpler course for the digestive tube, almost in a straight line.

Other considerations perhaps allow clarification in some degree of the morphological significance of the septum. We may recall first the close relationships which seem to associate this structure with the anterior transverse groove. This groove leads to the point of origin of the septum (in Mitrata) or to the upper surface of the zygal (in Cornuta), where it disappears.

On the other hand, the transverse groove originates from the infundibulum, which, as discussed previously, could have inclosed certain structures that in living echinoderms are narrowly associated with the aboral part of the axial organ. These anatomical connections seem to indicate that the septum also could be related to the axial organ. It is well known that in larvae the primordium of this organ appears in the accessory mesenteries and that these play an important role in organogenesis. Possibly the septum marks their emplacement in the Stylophora. Doubtless it is not without value to recall here that BATHER *(13)* judged one of the possible functions of the zygal to have been protection of the extensions of a blood plexus and genital rhachis, in addition to a prolongation of a nerve center which he supposed to exist in the opening of the proximal region of the aulacophore—that is to say in summation, a kind of axial complex. Finally, we may point out that a more or less vertical ridge suggestive of the septum in Mitrata occurs on the inner side of the theca in the posterior interray of certain Paleozoic cystoids and crinoids. JAEKEL *(55)*, who drew attention to the presence of this ridge, judged that it had approximately the same trace as that of the vertical mesenteries—accessory mesenteries—in the larva of *Antedon.* For all these reasons we may postulate that the septum of stylophorans served for the attachment of mesenteric membranes, within the thickness of which the axial sinus and axial organ possibly could find lodgment.

INTERNAL MARGINAL GROOVES

In addition to already described stylophoran grooves or canals, such as the paripore grooves, lateripore canals, and transverse anterior groove, some genera of the Mitrata (and possibly Cornuta) possess a pair of furrows on the inner side of the marginals which here are named **internal marginal grooves.** They begin at variable distance from the front of the theca, follow its lateral borders, and disappear in the periproctal region (Fig. 335,*1a*; 342). One is present on the right side and the other on the left. They are constant in *Mitrocystites,* sporadic in *Mitrocystella,* and unknown in other mitrates. [They appear to exist also in an undescribed cornute.] Their somewhat projecting adaxial margins may produce narrow slits on internal molds, called *sillons latéraux* by CHAUVEL *(30)*, who discovered them and interpreted them as traces of mesenteric membranes which with the septum furnished attachment for loops of the digestive tube. In *Mitrocystites* the grooves tend to vanish where they cross intermarginal sutures (Fig. 342,*1*). In opposite manner, they are clearly marked in *Mitrocystella barrandei* only at these crossings. In *M. incipiens miloni* features of the grooves are unmodified where they traverse sutures between the marginals (Fig. 335,*1a*). At their anterior extremity the internal marginal grooves appear to have relationships neither with the lateripores nor the paripores and indeed with no other structures of the theca. They cannot

FIG. 344. Morphology of aulacophore in mitrate Stylophora.——*1. Mitrocystella barrandei* JAEKEL, M.Ord., Boh.; proximal region, stylocone and proximal part of distal region; *1a,* oral face; *1b,* left lateral face, ×7.5 (Ubaghs, n).——*2. Enoploura wetherbyi* CASTER, U.Ord., Ind.; ×1 (90).——*3. Mitrocystites mitra* BARRANDE, M.Ord., Boh.; *3a,* stylocone and three ossicles of distal region, left lateral face, ×15 (Ubaghs, n); *3b,* stylocone, oral face, ×10 (Ubaghs, n); *3c,* stylocone, distal face, ×15 (Ubaghs, n); *3d,* ossicles of distal region, oral face, ×15 (Ubaghs, n).——*4. Peltocystis cornuta* THORAL, L.Ord., Fr.; ossicle of distal region in laterodistal *(4a)*, lateroproximal *(4b)*, and oral *(4c)* views, ×30 (Ubaghs, n); *4d,* diagrammatic reconstruction of two articulated ossicles to show how they can move.

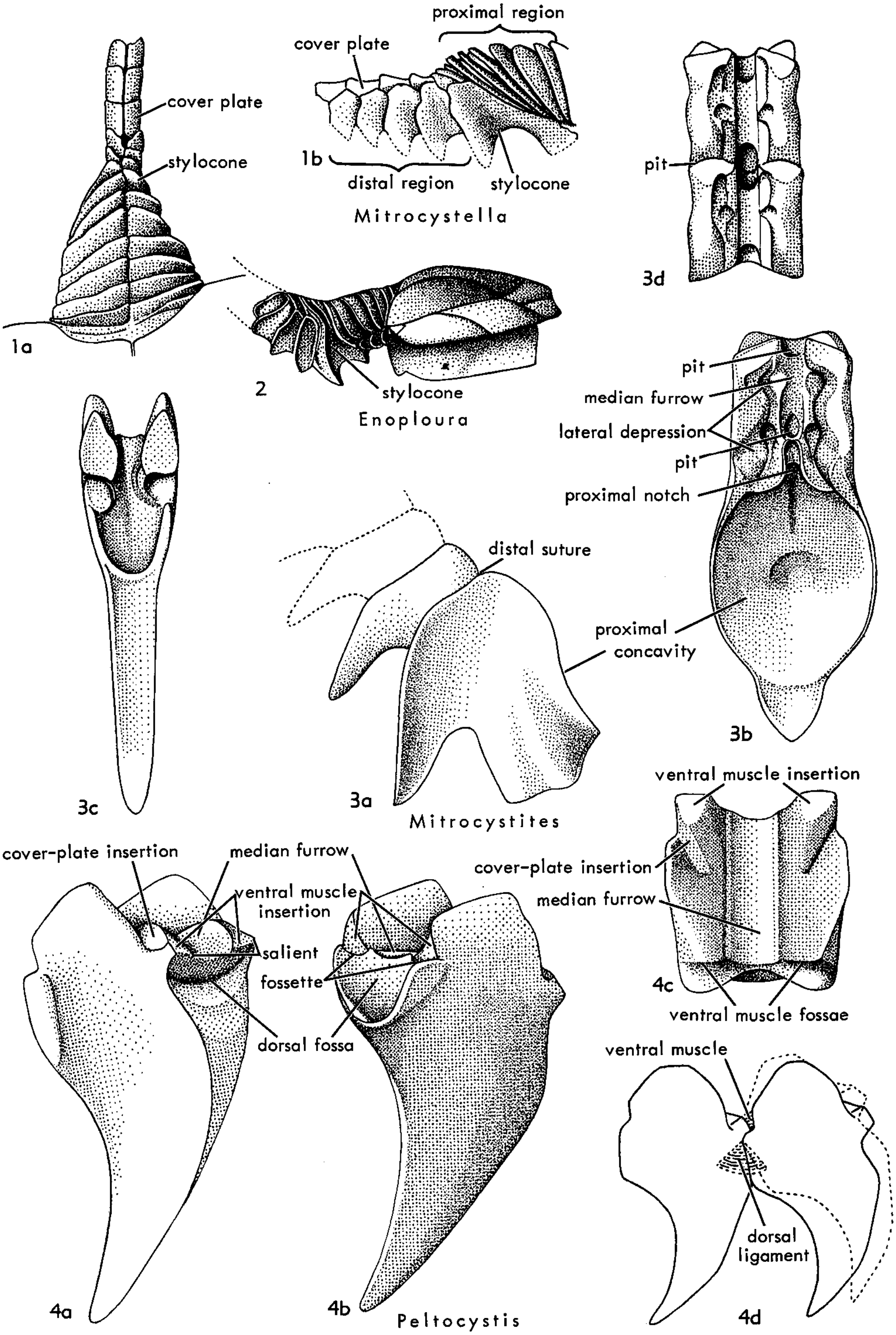


FIG. 344. [*Explanation on facing page.*]

be interpreted reasonably as these invaginated subvective grooves which Bather *(14)* supposed to exist in *Mitrocystites.* Perhaps they are the passageways of nerves leading to the rectum or some other posterior organ. Their actual function is unknown.

CTENOID ORGANS

Structures composed of lamellae in arrangements that resemble the teeth of a comb are here named **ctenoid organs.** They were discovered by Chauvel *(30)* in *Lagynocystis pyramidalis* and as yet are unknown in other stylophoran genera. They occur in three groups, one median and the other two placed laterally (Fig. 341,*4*). Each ctenoid organ is supported by a ridge on the inner surface of an adoral and end to end the three ridges together form an arc which is thin at its center and extremities but thickened at crossings of sutures between the adorals. The lamellae of the organs converge at the same time in three directions—downward, forward, and toward the median axis of the body. Thus they form a sort of grill or filter in the anterior part of the theca. Previously evoked is the possible existence of an atrium in front of the thecal cavity in which a water current charged with food particles must have been induced by the aulacophore, perhaps emerging through exhalant orifices at right and left. The function of the ctenoid organs then would have been to catch food particles suspended in the water, agglutinate them with mucus, and conduct them toward the mouth. The possibility that the organs exercised a respiratory function also is not to be excluded, for they may have served as support for gill structures.

AULACOPHORE

The name **aulacophore** has been introduced by Ubaghs *(88)* for the appendage of Stylophora that formerly was thought to be the same as the stele in Homostelea and Homoiostelea. The designation is morphologically descriptive in indicating that the appendage bears a groove (Greek, *aulacos,* furrow or groove, +*phoros,* bearer). It is in no sense a peduncular process or stem, but is here interpreted as a brachial appendage provided with an ambulacrum. Its unique nature warrants the adoption of a special morphological term.

The aulacophore comprises three parts—(1) a proximal hollow region which is inflated, relatively large, and protected by imbricated plates or by quadripartite rings generally one inserted within another, (2) a massive intermediate piece named the **stylocone,** and (3) a distal region composed of a single series of massive ossicles placed end to end and each provided with a pair of cover plates (Fig. 325; 343,*1a,b*; 344, *1a,b*).

PROXIMAL REGION

Next to the theca is part of the aulacophore defined as the **proximal region.** It encloses a wide hollow space which communicates with the thecal cavity. A covering composed of numerous imbricated scale-like plates is seen in *Ceratocystis* and *Lagynocystis* (see Fig. 345, 354), but in other genera, where known, of a fixed number of four-piece rings which generally are telescoped together, but not invariably so. The ring elements are subequal in the Mitrata, with sutures between them located in mid-superior, mid-inferior, and two mid-lateral positions. The pieces are unequal in size in the Cornuta but symmetrically disposed with respect to the aulacophore plane of symmetry, which coincides with the sutures between plates on the upper and lower sides. Each lateral half ring contains a small plate, above, here called **tectal,** and a large one, below, here termed **inferolateral,** the tectal covering less than half of the mid-part of the upper surface, whereas the inferolateral not only covers an entire half of the lower surface but much of a side as well (Fig. 343,*1a,b*). Each ring was joined to its contiguous neighbor or neighbors by muscles and probably also by ligaments. In addition, powerful muscles attached them in a proximal direction to the inner apophyses of marginals M_1 and M'_1 and in a distal direction to the stylocone. Without doubt, the proximal region of the aulacophore enjoyed great freedom of movement both vertically and laterally and probably it controlled general movements of the whole appendage.

STYLOCONE

The intermediate part of the aulacophore, interposed between its proximal and distal regions, is the unique ossicle named *stylocone*[1] (*Styloconus* or *Styloid* of JAEKEL, *55*). Lengthwise, it is a minor portion of the appendage, though important in reducing within a very short distance the broad width of the proximal region to the narrow diameter of the distal region. Its constant presence and complex nature prove that it must have had considerable functional significance. Its structure is essentially the same in cornute and mitrate Stylophora, thus denying a morphological basis for JAEKEL's *(55)* usage of stylocone for Cornuta and styloid for Mitrata. Nevertheless, the stylocones of the two groups are readily distinguished by external characters, whether viewed from the inferior face or in profile. It appears smooth and regularly rounded in the Cornuta (Fig. 343,*1a,b, 2a-c*), whereas in the Mitrata it bears diverse excrescences—1) a narrow crest in the plane of symmetry, 2) a single long spine incurved toward the theca (e.g., *Mitrocystites, Chinianocarpos*), 3) a series of points (e.g., to six in *Lagynocystis*), or 4) transverse blades resembling plowshares (e.g., *Enoploura*) (Fig. 344,*1-3*). The excrescences just mentioned doubtless served as fulcra for lifting the distal region, which normally was raised at an angle (Fig. 344,*2,3a*). According to CASTER *(43)*, the stylocone blades of *Enoploura* contain coarse radial canals of unknown function and morphological significance.

The stylocone has the general form of a funnel with excavated relatively wide proximal part and narrower semicylindrical distal part. The obliquely chiseled proximal face (more so in Mitrata than Cornuta) is occupied entirely by a deep concavity directed upward and toward the theca (Fig. 343, *2a,c*; 344,*3b*). It served for insertion of the distal extremities of muscles occupying a part of the cavity of aulacophoral proximal region. The distal face of the stylocone in Cornuta is perpendicular to the longitudinal axis of the ossicle, serving for a little or not at all differentiated sort of ligamentary articulation with the proximal plate of the distal region (Fig. 343,*2b*). In the Mitrata this distal stylocone face is oblique and directed upward (Fig. 343,*3a*) and is joined to the first ossicle of the distal region by a very highly differentiated articulation, like those uniting the distal ossicles with one another (Fig. 344,*3c*).

In Mitrata the rather short upper face of the stylocone is framed by steep elevated walls which give it the appearance of a rather narrow throat (Fig. 344,*3b*). The walls are much lower in the Cornuta, being less elevated even than the axial structures which they border on each side (Fig. 343, *2a*). In both Cornuta and Mitrata a deep notch, bordered by raised lips, occurs on the proximal border of the upper face at its middle. This notch leads to a groove **(median furrow)** which extends to the distal extremity of the stylocone, passing there onto ossicles of the distal region. The groove is somewhat raised in the Cornuta and limited by relatively wide rims (Fig. 343,*2a*). It is flanked from place to place by **lateral depressions** and at two points both margins of the groove are generally interrupted by a short **transverse channel** leading to lateral depressions on either side. In Mitrata the median furrow lies in the middle of the throat, which occupies the entire width of the upper face (Fig. 344,*3b*). It is not elevated noticeably and is bordered on each side by a very narrow ridge. The ridges are continuous in some genera (e.g., *Peltocystis*) but interrupted at two points on each side in others (e.g., *Mitrocystites*). Where interrupted, the furrow communicates with small lateral depressions, two on each side, which lie slightly lower than the furrow, but they are not observed in *Peltocystis*. It may be noted also that in some Mitrata (e.g., *Mitrocystites, Mitrocystella*) a small pit or fossa occurs in the floor of the groove at each end, the distal one being divided by the suture between stylocone and first ossicle of the distal region (Fig. 344,*3b*).

The upper face of the stylocone was protected by plates, four pairs of them having been counted in Cornuta. The two proximal pairs closely resemble the median upper plates in rings of the adjacent aula-

---

[1] GILL & CASTER (43) report that the stylocone of *Victoriacystis* has multiple segments. Probably only the most proximal of these represents the real stylocone, others belonging to the distal region. Also, CASTER (43) has described the stylocone of *Enoploura* as composed of several ossicles which become dissociated upon weathering. If correct, this suggests that the stylocone originally was a composite structure resulting from differentiation and fusing of the most proximal ossicles of the distal region.

cophoral proximal region, and they form the ceiling, probably fixed, of the excavated proximal part of the stylocone (Fig. 343, *1b*). The two distal pairs, which overlie the groove and accompanying structures, are mobile plates identical to the cover plates of the aulacophoral distal region (Fig. 343, *4*). A large part of the upper face of the stylocone in Mitrata is covered by rings or half rings of the adjacent aulacophoral proximal region, the remainder being protected by a pair of cover plates (Fig. 344, *1b,2*). This explains why JAEKEL *(55)* thought that the stylocone in the Mitrata was only a half cylinder inserted in the lower face of the organ, and not a solid piece that just as in the Cornuta joins the proximal and distal regions of the aulacophore.

DISTAL REGION

Invariably, the longest and narrowest part of the aulacophore is found in the **distal region.** Its diameter at the extremity nearest to the theca equals that of the distal end of the stylocone. Away from this point it tapers more or less rapidly to its free end. It is entirely composed of semicylindrical, bilaterally symmetrical, very short ossicles which abut end to end and are protected by a pair of cover plates. The ossicles of this region in the Cornuta have rounded inferior and lateral faces (Fig. 343, *3a-d*), whereas their upper face carries an elevated median grove or furrow which generally connects by a short transverse canal with a lateral depression on each side. The median groove is an extension of the similar furrow on the stylocone. The cover plates were movable and each articulated with a salient on the outer margin of the ossicle beneath it. These plates resemble scales strongly imbricated in the distal direction (Fig. 343,*4*).

Ossicles of the aulacophoral distal region of the Cornuta were closely joined by synostosis or by barely differentiated articulations (Fig. 343,*3c,d*). The distal face of each bears two lateral salients which fit into hollowed fossettes on the proximal face of its next-placed neighbor. Slight movement in a vertical plane was permitted by this rudimentary sort of hingement. The distal region must have been relatively rigid and certainly incapable of enrolling on itself.

Construction of the distal-region ossicles is essentially the same in all stylophorans, but in the Mitrata some distinctive traits are seen (Fig. 344,*3d, 4a,b*). Firstly, the lower side of each ossicle bears a spine, point, or blade in the plane of symmetry, ordinarily incurved toward the theca; the projections are most prominent on proximal segments, diminishing and disappearing distally.

Secondly, the upper face of the ossicles, like the upper face of the stylocone, shows 1) a median furrow sunk between high lateral walls and bordered by fine ridges, 2) a shallow short depression on each side of the groove (though seemingly not in all forms), and 3) presence of a fossa or pit in the floor of the groove at the level of each suture, at least in some genera (Fig. 344,*3d*). Thirdly, the cover plates attached at outer borders of the ossicles alternate somewhat with these plates and are not imbricated when the arm was extended (Fig. 344,*1b*). Finally, the ossicles are joined to one another by very well-developed articulations, having on distal faces a pair of salients slightly below the median furrow and on proximal faces corresponding fossettes to receive these projections (Fig. 344,*4a,b*). The salients determine an articulatory axis around which the ossicle could pivot (Fig. 344,*4d*) and above each salient and fossette is a small triangular area which marks the insertion of a flexing **ventral muscle.** A large unpaired concavity **(dorsal fossa)** is seen on both the distal and proximal articular faces of the ossicles below the articulation axis. These concavities doubtless served to accommodate an elastic **dorsal ligament** which operated in opposition to the flexing muscles. The articulations afforded arm movements in a vertical plane. The aulacophore of Mitrata frequently is seen to be recurved toward the superior face of the theca and it may even be enrolled in a spiral, with spines of its inferior face turned outward as though in an attitude of defense.

FUNCTIONS OF AULACOPHORE

How may structures of the aulacophore just described be interpreted? The median furrow, short transverse channels, lateral depressions, and movable cover plates of its upper surface comprise an ensemble nowhere found among echinoderms except in their ambulacra. In living stylophorans, the median furrow must have housed an axial ambulacral canal, and in addition, it probably carried nerve, blood, and coelomic structures such as accompany the canal in living echinoderms. The lateral depressions are presumed to have received tentacles connected to the axial canal by short branches placed in the transverse channels (Fig. 343,*5*). In at least some genera, a distinct widening of the transverse channels at their abaxial extremity (Fig. 343, *2a,3a*) suggests the possible existence of ampulla-like expansions at the base of tentacles such as those present in the podia of some Recent ophiuroids. The sutural pits on the floor of the median groove of some Mitrata could have accommodated saclike expansions of the axial canal, serving as reservoirs lodged in similar hollow cavities of the vertebrae in some living ophiuroids.

The descriptions and discussion which have been given support the following important conclusions. 1) The aulacophore of Stylophora is not a tail, column, or peduncle, for its organization lacks the structures and indicated functions belonging to these morphological features—in particular having nothing in common with the stele of the Homostelea and Homoiostelea. 2) The aulacophore is a mobile brachial process which bears an ambulacrum, and the main function of this ambulacrum can hardly have been other than collection of food particles and transport of them to the mouth. 3) The peculiar structure of the aulacophore and lack of its association with similar appendages borne by any one stylophoran cannot be homologized with the multiple radial brachial processes of other echinoderms. 4) The aulacophore differs structurally from the single arm of the Homoiostelea. 5) The aulacophores of Cornuta and Mitrata are very similar and entirely homologous to one another.

GENERAL ORGANIZATION OF BODY

Information concerning the anatomy of stylophorans derived from study of their skeletal remains evidently is insufficient for reconstruction in detail of the soft parts of these animals. Even so, it may not be too ambitious an undertaking to seek determination of the main divisions of the body and recognition of their morphological significance.

In order to attain these goals, it would be fruitless to depend heavily on comparisons with living adult echinoderms, which by acquisition of radial symmetry have been transformed profoundly and seem to be utterly different. It is permissible, however, to refer to the ontogenetic stages which precede the appearance of this symmetry among them and which, as apparently in the Stylophora, are characterized by pronounced asymmetry in development of their structures.

The skeleton of stylophorans encloses two clearly distinct cavities—that of the theca and that of the proximal region of the aulacophore. It is probable that the first comprised the general body cavity produced by the somatocoels and the second perhaps corresponded to the axocoels and hydrocoel, which in echinoderms always are closely associated. Data supporting this hypothesis are presented in the following paragraphs.

The structure of the aulacophore indicates that this organ served to support a tentacle-bearing diverticle such as only the hydrocoel produces in echinoderms. If this interpretation is correct, the aulacophore diverticle could only depend from the left hydrocoel, for the right one never plays any role in the organogenesis of echinoderms. The aulacophore is fixed to the middle of the front border of the theca, however, and not to its left half. This requires us to suppose that it has migrated, along with the hydrocoel diverticle enclosed by it, so as to become placed in the main axis of the body. Such a movement doubtless represents a phenomenon of secondary symmetrization, comparable to that shown by larvae of modern echinoderms, which, following a stage of asymmetry, tend to develop bilateral symmetry (*sekundär symmetrische Stufe* of HEIDER). It is noteworthy that this tendency toward acquisition of bilateral symmetry with respect to the principal body axis, invariably discernible in the Stylophora, may be very conspicuous (e.g., Anomalocystitida).

Furthermore, the inferred stylophoran hydrocoel appears to have opened outward through an orifice in the right adoral plate. This coelomic compartment, from which the aulacophoral diverticle extended, must have been localized, then, in the immediate vicinity of the attachment of the aulacophore to the theca. In larvae, the hydrocoel lies behind the axocoel and is more or less distinct from it. In adults, the axocoel produces structures (e.g., ampulla at junction of stone canal and hydropore canal, madreporic vesicle, axial sinus) that remain closely associated with unpaired organs (e.g., madreporite, stone canal) of the hydrocoel apparatus. Thus is developed a complex of organs that originates in the anterior and median coelomic compartments of the larva. Perhaps, then, it is not a pure coincidence that the part of the body of stylophorans located in the immediate proximity of the aulacophore attachment is also characterized by a large complex of internal skeletal structures (e.g., infundibulum, anterior transverse groove, origin of septum, scutulae, co-opercula, diverse canals and grooves leading to external orifices or toward posterior regions of the body). This complex, suggestive of that found in the mesosomal region of enteropneusts and pterobranchs, may include (for reasons given in previous chapters) a diversity of organs derived from the two axocoels and left hydrocoel, as well as ganglionic masses needed in particular for control of the aulacophore muscles.

The remaining part of the thecal interior undoubtedly was occupied by the digestive tube, which can be localized with some degree of certainty by the principal thecal orifices, by the gonads, and by the general cavity derived from the larval somatocoels. This cavity must have been divided asymmetrically in diagonal manner, as shown by the course of the septum or zygal, which doubtless furnished attachment for mesenteric membranes and which may have marked, as suggested previously, the position of some elongate unpaired structure such as the axial sinus and axial organ.

We may see, then, that several diverse lines of evidence seem to support the hypothesis initially offered in this discussion. Thus, the two main parts of the body in Stylophora would be axohydrocoelian (in front) and somatocoelian (behind). The first would include the proximal region of the aulacophore and part of the thecal cavity closely adjacent to the aulacophoral attachment, and the second would include the large remaining part of the thecal cavity.

This interpretation allows the fundamental organization of Stylophora to be correlated easily with that of the presumed ancestral echinoderm suggested by embryology. Derived from this ancestor (a least distorted picture of which possibly is offered by the pterobranch *Cephalodiscus*) would be the unattached stylophoran mode of life, the division of the body into two or three successive coelomic regions—separation of the axocoel and hydrocoel is far from well defined in all echinoderms—and the presence of one of an antecedent pair of lophophorian arms, an arm (represented by the aulacophore) which from the outset must have assured nutrition and respiration for the animal. The main transformations marking the passage from this hypothetical ancestor to the Stylophora would be connected with the appearance and accentuation of an asymmetry which would be the same as that demonstrated in the ontogeny of living echinoderms from the beginning of larval development or even from the egg.

Finally, what was the morphological orientation of the body of Stylophora? If attention is directed to the natural position of these organisms during life, distinctions can be made between a superior and inferior face, between an anterior extremity marked by the mouth and a posterior extremity marked by the anus, and between a right side and a left side. These terms evidently have only topographic significance. Orientation in terms of morphology may be very different. If the principal orifices of the theca are adopted for reference, the location of the anus may be considered as posterior, that of the mouth (directed forward and upward) as both anterior and ventral, and that of the hydropore—its most primitive position seemingly observed in *Ceratocystis*—as indicating the dorsal face and left side. From this viewpoint, the conclusion may be reached that the Stylophora reposed on their morphologically dorsal face and that their morphologically ventral surface was directed upward. This conclusion would be permissible if these organisms had maintained the orientation of the bilaterally symmetrical form supposed to exist in echinoderms at their beginning. In fact, the stylophorans are asymmetrical, which proves that their ancestors, like those of other echinoderms, had undergone transformations that could have been accompanied by more or less considerable displacements of the orifices toward faces of the body originally defined as lateral. It follows that their median plane may very well have been newly acquired, not coincident with the ancestral median plane but cutting across it at an indeterminable angle. Likewise, the upper face of stylophorans does not coincide necessarily with the ventral surface of the antecedent primitive form, or the lower face with its dorsal surface. In sum, the problems of morphological orientation of the Stylophora are the same as for other echinoderms and it would be vain to seek in their complex and transformed organization axes of symmetry belonging to the source of the phylum.

GLOSSARY OF MORPHOLOGICAL TERMS USED FOR STYLOPHORA

[Terms considered as synonyms or terms of lesser importance are printed in italics]

abaxial. Directed away from main axis.

aboral. Applied to surface (or structure) of aulacophore situated on face opposite that bearing median groove (*syn.* dorsal, lower, or inferior face of aulacophore).

accessory septum. Small left branch of septum near its anterior extremity.

adaxial. Directed toward main axis.

adcolumnal. See adoral.

adoral (pl., **adorals, adoralia**). One of two or three upper thecal plates which frame aulacophore insertion.

anomalocystid plate. Special infracentral plate truncating left posterior corner of largest infracentral, distinguished by its rather great constancy among Mitrata.

anterior. Applied to part of theca (or thecal structure) located at or adjacent to aulacophore insertion; front of theca; directed toward anterior margin; opposite to posterior.

anterior margin. Part of margin in middle of which aulacophore is inserted.

anus. Vent of alimentary canal.

apophysis (**apophyses**). *See* aulacophore apophysis (apophyses).

aulacophore. Single jointed exothecal appendage, here interpreted as brachial process carrying ambulacrum.

aulacophore apophysis. Inner projection for attachment of aulacophore proximal muscles, carried by each of two median anterior marginals.

carapace. Upper face of theca in Mitrata.

central (centralia). Plate(s) located inside marginal framework either on lower or upper face of theca (*see* supracentral and infracentral).

co-operculum (pl., **co-opercula**). Endoskeletal structure on internal face of adoral plate, serving as partial lid to corresponding scutula; observed in a few mitrates.

cothurnopore. Specialized porous organ in right anterior upper thecal area of *Cothurnocystis* and other Cornuta.

cover plate. One of many small plates which protect oral face of stylocone and ossicles of distal region in aulacophore.

ctenoid organ. Comblike calcareous structure attached to inner side of adorals and protruding into thecal cavity in *Lagynocystis.*

dextrolateral. Infracentral located on right side.

digital. Spine attached to marginal framework directly on left of anal opening of *Cothurnocystis.*

distal. Direction away from insertion in aulacophore or any appendage; opposite of proximal.

dorsal. See aboral.

épibasale. See adoral.

epicentral (epicentralia). See supracentral (supracentralia).

epistomal (epistomalia). Seemingly movable plate(s) in small triangular space between adorals and proximal ring segment of aulacophore.

extension plane. Plane in which theca is depressed (*syn.,* extensiplane).

extensiplane. See extension plane.

frame (framework). Series of plates which constitute margin of theca, i.e., marginals and (in Cornuta) adorals.

glossal. Spine attached to marginal frame directly on right of anal opening in *Cothurnocystis.*

hypocentral (hypocentralia). See infracentral (infracentralia).

inferior. Directed toward inferior face of theca.

inferior face. Flat or concave side of theca, presumably toward sea bottom in life position (*syn.,* lower, reverse).

inferolateral. Lower plate of half ring in proximal region of aulacophore.

infracentral (infracentralia). Plate(s) located inside marginal framework on lower face of theca.

infundibulum. Distinct depression between right scutula and inner upper edge of marginal M_1, located just below and probably related to right adoral opening.

internal marginal groove. Furrow on inner side of lateral marginals in some Mitrata.

lamellate organ. All lamellipores taken together.

lamellipore. Elongated very narrow slit in right anterior upper thecal area in Scotiaecystidae.

lateral depression. Elongate depression on oral face of stylocone and ossicles of distal region of aulacophore in which ambulacral tentacle is presumed to have been located.

lateripore. One of two openings in *Mitrocystites,* symmetrically located on lower thecal face near anterolateral corners, on sutures uniting two first right or left marginals (*syn., Seitenpore*).

left. Referring to side corresponding with left of observer, when theca is placed on its lower face, with aulacophore away; opposite of right.

lower face. *See* inferior face.

main axis. Straight line which corresponds to intersection of extension plane with plane of bilateral symmetry of aulacophore and which is prolonged across theca.

marginal (marginalia). Ossicle(s) of a series framing theca (except adoral).

median groove. Axial furrow along oral surface of stylocone and ossicles of distal region of aulacophore, presumably housing axial ambulacral structures.

median plane. Plane passing through main axis and perpendicular to extension plane (*syn.,* symmetry plane).

mouth. Entrance to alimentary canal, presumably located at or near proximal end of aulacophore inside theca.

oblique anterior groove. Faint groove uniting infundibulum to aulacophore insertion.

obverse. See superior.

oral. Applied to face of aulacophore which carries median groove (*syn.,* ventral, upper or superior face of aulacophore).

oro-anal axis. Straight line from anus to center of aulacophore insertion (presumed mouth position).

paarige Gruben. See paripore.

paripore. One of two openings through marginals M_2 and M'_2 in *Mitrocystites* or marginals M_3 and M'_2 in *Chinianocarpos* symmetrically placed on lower face of theca (*syn., paarige Gruben*).

periproct (periproctal area). Presumed flexible and extensible thecal integument surrounding anus.

placocystid plate. Special supracentral located on mid-line of theca and generally surrounded by its two neighbors, distinguished by its smooth surface and its rounded (rather than polygonal) outline; present in a few Anomalocystitidae (*Placocystites, Rhenocystis*).

plastron. Lower face of theca in Mitrata.

posterior. Applied to part (or structures) of theca located at or adjacent to anal area; direction opposite to anterior; backward.

posterior margin. Opposite to anterior margin.

proximal. Referring to direction toward insertion in aulacophore or any appendage; opposite of distal.

reverse. See inferior.

right. Side of theca corresponding with right of observer when it is placed on its lower face with aulacophore away; opposite of left.

right adoral orifice. Thecal opening which notches or pierces right adoral plate.

scutula (pl., **scutulae**). One of two concave calcareous platforms on internal face of marginals M_1 and M'_1, near abaxial ends of aulacophore apophysis.

Seitenpore. See lateripore.

septum. Calcareous wall on floor of thecal cavity running obliquely from abaxial end of left aulacophore apophysis toward right posterior thecal margin in most Mitrata.

sinistrolateral. Infracentral located on left side.

spinal. Point or fixed spine prolonging right posterior corner of theca in some Cornuta.

strut. See zygal.

stylocone. Cone-shaped ossicle forming middle region of aulacophore (*syn.,* styloid).

styloid. See stylocone.

subanal (subanalia). Special thecal plate(s) in some mitrates located below anal structures.

superior face. Convex side of theca presumably directed upward in life position; opposite of inferior face (*syn.,* upper face, obverse face).

supracentral (supracentralia). Plate(s) located inside marginal framework on superior face of theca.

sutural pore. Pore located on suture between two or several thecal plates.

symmetry plane. See median plane.

tectal. Upper small plate in lateral half ring of proximal part of aulacophore.

tegminal. Supracentral close to posterior margin, possibly serving as cover to posterior opening in some genera.

theca. Body skeleton exclusive of aulacophore.

toe spine. See spinal.

transverse anterior groove. Shallow transverse furrow on internal face of marginals M_1 and M'_1, running from infundibulum to zygal (Cornuta) or septum (Mitrata).

transverse channel. Short groove connecting median furrow with lateral depression on aulacophore.

upper face. *See* superior face.

ventral. See oral.

zygal. Skeletal bar uniting marginal M'_1 with right posterior margin on lower face of most Cornuta.

ONTOGENY

Knowledge of the ontogenetic development of the Stylophora, decidedly meager at best, rests on three sorts of evidence—1) observation of young individuals, 2) study of growth series, and 3) examination of growth lines. All relate to fairly advanced stages, which invariably are subsequent to the metamorphosis.

Chauvel *(30)* has shown that in many species of Mitrocystitidae young individuals differ little from adults, at least in organization of their inferior face, nothing exactly being known about development of the superior face. Growth of the theca is effected not by introduction of new plates but simply by enlargement of existing plates which are constant in number and placement from early youth. Only the proportions and outlines of the theca may be modified.

The number of plates in the frame of the theca in Cornuta likewise seems to have been established at an early growth stage, but the shape and proportions of these plates tend to be altered in the course of development. In a general way, among diminutive individuals the frame seems to be relatively larger than in adults. It seems also that the size of the centralia rather than their number increase with age; if new elements were introduced during growth, it must have been at the periphery where very small plates are generally crowded. The number of cothurnopores or comparable orifices varies among individuals, possibly being greater with age, and their decreasing size toward the two extremities of each series suggests that new pores were introduced in these terminal regions.

Occasionally, striae parallel to edges of plates can be observed on the inner surface of the stylophoran theca. This is especially true of *Lagynocystis* and genera of the Kirkocystidae, in which the inner side of the marginals or adorals bear numerous striae that may be considered as growth lines (Fig. 341,*1*). They show that these plates have undergone changes in proportion in the course of their development.

The mode of growth of the aulacophore is not known. Probably the number and arrangement of plate rings in the proximal region were fixed at a very early age in individuals, but it is very likely that new ossicles were added to the distal extremity of the appendage throughout growth, as in the arms of crinoids.

MODE OF LIFE

LIVING POSITION

Stylophorans lived resting on the sea bottom, as proved by 1) absence of a stem, 2) flattened form of the theca and its lateral extension, 3) marked dissimilarity of the two faces of the theca inferred to be upper and lower, and 4) the presence of one of the thecal faces (lower) in many species of spines or longitudinal ridges which doubtless served to elevate the body and assure equilibrium, as well as eventually for anchoring it.

With respect to the face just referred to, the organism can be oriented unequivocally, for the face that in life was directed upward and accordingly designated as the **superior** face is evidently the one toward which the ambulacral furrow opened. It is also the more convex face and that which generally bears the mouth and anus. It never shows the presence of protuberances and other excrescences of the sort just mentioned as characteristic of the other face.

LOCOMOTION

The absence of a stem and organs comparable to a root indicates that the Stylophora were not sessile animals but rested free on the sea floor or other support. The aulacophore, considered as stem, peduncle, or tail, often has been supposed to be a means of anchorage, operating like the cirrus of a crinoid *(25)*, sinking into clefts or between roots on the substrata *(14)*, or standing vertically on its tapered extremity with the theca extended horizontally in the water *(82)*. The stylocone, especially in the Mitrata, has commonly been considered to be a device for clinging, and Bather *(17)* judged it to be "a support on which the internal muscles could raise the theca as on an elbow, or swivel it round to meet the food-currents." Among other functions which have been assigned to the aulacophore is that of a rudder *(13,25)* and that of a propeller *(49)*. Referring to mitrocystids, Gislén *(45)* thought "that the animal moved itself forward [backward in terms of *Treatise*-adopted orientation] with jerks to the right and left of the strongly muscular proximal part of the stem." Thus the so-called stem would become "a swim tail" *(46)*. Even *Cothurnocystis*—despite its extreme asymmetry, its protuberances, and its long marginal processes—was judged capable of swimming by pirouetting about on itself *(45)*.

Other authors have imagined that stylophorans crawled, using the aulacophore to push themselves backward or pull them forward. KIRK *(56)* described in some detail how the mitrate *Basslerocystis* glided over the sea floor by movement of its aulacophore with the aid of its two posterior spines and CASTER *(25)* explained how *Enoploura* traveled on the sea bottom by "upflexings" of the body at junction of the aulacophore with the theca, in manner recalling the mode of progression of measuring worms.

If, as here interpreted, the aulacophore is not a stem or peduncle but rather a brachial process serving to carry the single ambulacrum of the stylophoran and therefore functioning essentially for capture of food, most of the hypotheses which have been outlined evidently lose all significance. It remains conceivable, however, that the aulacophore, in addition to its function as an organ for obtaining nourishment, could have acted to keep the animal favorably oriented in water currents or to shift them somewhat in case of need. Just as the arms of comatulids enable them to swim or crawl on the sea bottom, the aulacophore of stylophorans, with its powerful proximal musculature, might conceivably have been capable of performing similarly.

Opposed to unqualified adoption of the hypothesis just stated are several anatomical considerations which apply to the Stylophora. 1) The high degree of asymmetry seen in the theca of most Cornuta, and the not uncommon considerable development of their protuberances, spines, and marginal processes make a judgment that these "carpoids" crawled or swam improbable. 2) The rearward thinning down of the theca which is observed in all Stylophora provides a hydrodynamic condition unfavorable for displacement of the body in a backward direction, for very generally aquatic animals move with their big end forward. 3) Similarly the rearward imbrication of the supracentrals of some genera *(Mitrocystella, Lagynocystis)* or of the scalelike covering of the lower face of *Allanicytidium* makes unlikely a backward progression of the organisms. 4) In *Mitrocystites* and *Chinianocarpos* the spines borne by the lateral anterior marginals point obliquely backward and downward in such a way as to impede sliding of the theca sideward and toward the rear. Projections on the lower surface of the stylocone and distal ossicles of the aulacophore in Mitrata have their points generally directed toward the theca—an arrangement that would hinder any propulsive force that movements of this organ could have generated in a posterior direction. Such considerations suggest that the Stylophora either led an essentially static existence, reposing in the same place as long as conditions were favorable, or, if they moved, progressed forward. For moving, they could use their aulacophore to pull them in a manner described by CASTER *(14)* or expel water from the anus, making a jet which served to propel the animal forward. One may here call attention on the occurrence of projections apparently serving for attachment of muscles or ligaments on the inner side of the supracentrals of some Mitrata, suggesting that rhythmical contraction and expansion could have resulted in a bellows-like action of the body wall. In very asymmetrical forms (e.g., *Cothurnocystis*) a forcible expulsion of water from the anus should have induced gyration of the theca, which was probably checked by the protuberances on the lower side of marginals, the spinal and the aulacophore *(13)*. In more symmetrical forms, however, an effective leap forward could probably have been realized in this way. On the other hand, this does not mean that the Stylophora were active swimmers. It seems more likely that they used such possibility occasionally, when, for instance, it was necessary to shift their position. Doubtless JAEKEL *(55)* was right in comparing their behavior to that of holothuroids. One may well imagine that stylophorans lived most of the time in the manner of certain psolid dendrochirotes, which have depressed bodies and cling to the substrate by their flattened ventral sides.

NUTRITION

Interpretation of the aulacophore which has been given indicates that this organ served principally for the collection of nourishment. The nature of the articulations between distal segments of the aulacophore in Mitrata shows that this region was held in a position directed more or less upward. It was inflected or formed an elbow at the level of the stylocone, which served it for support and as a sort of hinge. Many fossils (e.g., *Lagynocystis, Enoploura, Rhenocystis*) show the aulacophore preserved in this bent position. It is not to be doubted that in at least some circumstances this appendage could partially enroll on itself so as to protect soft structures lodged in the furrow of its oral face.

Capability of enrollment assuredly was lacking in the aulacophore of the Cornuta, which was much more rigid, with principal movements, if not only ones, controlled by the proximal region. Even so, it is probable that the aulacophore of these stylophorans did not lie flat on the sea floor, since its aboral surface never is depressed. With little doubt it moved in the water with equilibrium of the body maintained by disposition of the protuberances that served for support of the theca and by the presence of appendages (glossal, digital) or posterior marginal expansions designed to provide a counterweight.

The nature of the median groove and other structures which characterize the oral surface of the stylophoran aulacophore suggest, by analogy with the endoskeletal ambulacral structures of living echinoderms, that these animals were microphagous, capturing minute particles suspended in the sea water or catching tiny prey by play of their tentacles and mucociliary mechanisms. In summation, the nature of the aulacophore furnishes no confirmation at all of hypotheses postulating that these "carpoids" were 1) scavengers *(26)*, 2) sea-bottom mud-swallowers *(56)*, 3) nourished by pumping water inward through the anus *(34,45,46,55)*, and 4) fed through inhalant pores such as cothurnopores, sutural pores of *Ceratocystis*, and lamellipores *(13, 14,32)*.

Among other morphological features that may have been concerned with nutrition are the ctenoid organs of *Lagynocystis*. Seemingly located at the back of an entrance-way atrium, they appear to be adapted for straining out food particles suspended in water currents, embedding them in mucus, and conducting them to the mouth.

RESPIRATION

Respiration of the Stylophora may have been accomplished in various ways—1) directly through the thecal integument when covered by a thin pavement or provided with uncalcified spaces (e.g., *Nevadaecystis*; and according to CASTER *(26)*, very abundant stroma in the plates of *Paranacystis* must have allowed gas exchanges within the skeleton); 2) by extensions of the hydrocoelian apparatus (e.g., tentacles of the aulacophore); 3) through walls of the digestive tube; 4) by introduction and expulsion of water through the anus as in living crinoids and holothuroids *(45,55)*, possibly controlled by pulsations of the upper thecal face when, as seems to have been common in many, it had sufficient flexibility; 5) perhaps by means of specialized organs such as the cothurnopores and lamellipores, if these organs, which in some stylophorans are closely analogous to hydrospires and pore rhombs, actually had a respiratory function; and 6) possibly also through the agency of ctenoid organs (e.g., *Lagynocystis*), which in addition to filtering water from the atrial chamber could have aided aeration of fluids filling the gills that perhaps they supported. It is probable then that, as in other echinoderms, respiration was effected by various means.

ECOLOGY

Little precise information is available as to the environment of living Stylophora. A majority of them appear to have existed in the places where their fossil remains are found, or very close to these places. In view of their relatively large size and delicacy of their complex organization, they could hardly have been transported very far from sites occupied in life to places of burial.

Remains of these animals are found most

commonly in clayey sediments, either on bedding planes of shale or enclosed by siliceous or sand-carbonate concretions occurring in essentially pelitic deposits. Only rarely have they been collected from strongly arenaceous or calcareous formations. This common association of the fossils with argillaceous sediments indicates that most known stylophorans lived in marine environments sufficiently calm to have allowed predominant deposition of clay particles and mica flakes. Although generally true, the stated rule is not universal—for example, dissociated plates of *Enoploura* are found in large numbers in coquinites and calcarenites of the Cincinnati-arch region in Ohio and Indiana, indicating that this mitrate preferred a habitat in which the water was so agitated by waves and currents that clay-size particles could not be deposited but were swept away *(25)*. The diversity in morphology of stylophoran genera and species suggests a corresponding diversity of ecologic niches adapted to each.

Stylophora are rare as fossils. Their rarity may reflect modest size of populations, possibly associated with special ecologic exigencies, but it may mean that they have been neglected by collectors or that conditions of fossilization render finding of them exceptional. Thus, in the Lower Ordovician of southern France (Hérault) in strata which have furnished the most diversified assemblage of stylophorans yet known, only specimens contained in small quartzitic concretions distributed through the shaly mass have a chance of being collected; others which might be found in the shale are entirely irretrievable owing to fracture of the rock into tiny pieces. This may explain why a majority of the species recorded from this region—approximately a dozen—are represented by a single specimen or a small number at most. On the other hand, deposits elsewhere which seem to indicate conditions of fossilization closely similar to those just noted have furnished very numerous stylophoran fossils. Thus, the Šárka Shale, in the Middle Ordovician of Bohemia, has yielded several hundred specimens of *Lagynocystis pyramidalis,* all preserved in siliceous concretions. That this species was especially abundant can hardly be doubted. Another example from the same region is seen in the *Ceratocystis perneri* Zone of the Skryje Shale, Middle Cambrian, which contains heaps of specimens piled together pell-mell. Like many other echinoderms, some stylophoran species must have led a gregarious existence.

It is difficult to determine in what type of sea and under what special conditions a majority of stylophoran species lived, for critical paleoecologic investigations have not been made of any of the deposits that contain these fossils. The few published discussions on this subject relate only to *Cothurnocystis elizae (13), Paranacystis petrii (26), Victoriacystis wilkinsi (43), Dalejocystis casteri (71),* and the genus *Enoploura (25).* No worthwhile synthesis can be offered.

PHYLOGENY

ORIGIN AND RELATIONSHIP OF STYLOPHORA

From the outset of their appearance in Middle Cambrian time the Stylophora display all attributes of their class. Consequently, their source is unknown.

Like other "carpoids," they have long been interpreted and by many still are considered to be modified Pelmatozoa (Crinozoa) which abandoned a fixed mode of life and erect position to assume a partially eleutherozoic habit and a horizontally reclining attitude. No evidence supports this hypothesis, however. On the contrary, the Stylophora display an ensemble of features that oppose them to pelmatozoans. These are: 1) the fundamental asymmetry of their organization and entire absence of radial symmetry; 2) the lack of a peduncle or homologous organ or any means of fixation at all; 3) the presence of a single ambulacrum and hence the probable absence of a hydrocoelian ring and the five primary tentacles which form origins of the rays in other echinoderms; 4) the structure of their aulacophore, which resembles neither a crinoid arm nor a cystoid brachiole; 5) localization of the mouth at the front of the body and the anus at the rear.

All these characters contribute to definition of an organization peculiar to itself, suggesting an independent origin and evolutionary trends unlike those seen in crinoids, cystoids, and sessile echinoderms generally. Moreover, the Crinozoa and pelmatozoic Echinozoa already were represented when the Stylophora first appeared in the Middle Cambrian and no convergence toward a common source is definable among these archaic forms.

Likewise, the stylophorans cannot be placed close to radiate free echinoderms, despite the seeming fact that they never were attached, at least as adults. Indeed, their asymmetrical construction and lack of any mark of radial symmetry, accompanied by their single ambulacrum and morphologic peculiarities of their aulacophore, definitely remove them from echinoderm types such as the Asterozoa and Echinozoa.

What origin is suitable for assignment to this group? In various discussions BATHER *(14,15,20,21)* has outlined an hypothesis according to which the Stylophora could have been derived from a dipleurula attached by its ventral surface rather than by the preoral lobe, in this way acquiring the shape of a Y with the lower part of the letter represented by a stem and the upper part by the body with its mouth at the extremity of one branch of the Y and its anus at the extremity of the other branch. The different types of "carpoids" would have been produced from the Y-shaped form by divergent evolution. CHAUVEL *(30)* accepted the Y plan as fundamental but instead of deriving it from the primitive dipleurula, postulated that it came from a modified one which already had arrived at the generalized sort of pelmatozoic stage approximately represented by the cystoid *Aristocystites*. His concept has a twofold advantage over BATHER's hypothesis in connecting the Stylophora with an ancestor that would be common to all echinoderms and in explaining the asymmetry of stylophorans. It is mistaken, however, in accepting the aulacophore as a stem, which otherwise is unknown in these organisms, and in deriving the Stylophora from an ancestor that already is too far advanced on the path leading to the Crinozoa.

Is it advisable, consequently, to choose BATHER's *(21)* opposed view in affirming that the Stylophora, like other "carpoids," "have never traversed the evolutionary roads followed by the other classes and [that they] do not possess the most familiar characters of the Phylum"? In my opinion, this would be going too far. We have seen that the general organization of stylophorans can be explained in some measure by comparison with the ontogenetic stages which precede the appearance of radial symmetry. Phylogenetically, this indicates that the group must have separated from the remainder of the phylum before radial symmetry was acquired but after asymmetry had become a main echinodermal characteristic. In other words, if they cannot be connected directly with some ancestral dipleurula—any more than can the radial classes—nothing prevents considering them, along with the Homostelea and Homoiostelea, as records of preradial divergences of the echinoderm stock the origin of which doubtless occurred long before the dawn of Cambrian time. In this perspective, the Stylophora and other "carpoids" merit recognition with the Helicoplacoidea as the most primitive echinoderms.

Despite their fundamental archaic nature, the Stylophora exhibit such morphologic and functional specializations that they cannot be considered as possible ancestors of other echinoderms. They became extinct without leaving known descendants.

The hypothesis sometimes has been advanced that the chordates might have been derived from echinoderms similar to the Stylophora. According to GISLÉN *(45)*, the asymmetry of the theca of *Cothurnocystis* and its unique row of cothurnopores may recall a development stage of *Amphioxus*, and the mitrocystids in some respects may resemble the tunicate appendicularians. GREGORY *(48)* has called attention to the astonishing, though possibly superficial, similarity of the theca of *Mitrocystella* or that of *Placocystites* to the cephalothorax of the cyclostome fish *Drepanaspis*. CASTER *(25)* and CASTER & EATON *(28)* have emphasized the analogy which in their eyes exists between the ornament and microstructure of certain stylophoran plates and plates in the exoskeleton of ostracoderms. Such resemblances, however, may be purely accidental and surely do not prove that the

Stylophora had an organization close to that of ancestors of the chordates. At any rate, we know that during the time of their existence vertebrates of already highly organized type lived. If echinoderms are related to chordates, the connection between them must date back so remotely that the fossil record can hardly preserve a trace of it.

In common with the other "carpoids," stylophorans display a depressed body form, presence of a single ambulacrum (bifurcated in the Homostelea), and asymmetry without trace of radial symmetry. As previously suggested, all may belong to an extremely ancient preradial echinoderm radiation, and if this is true, the Stylophora represent an independent branch without known relations to other branches of the radiation. Supposition that *Microcystites* was derived from a form not distant from *Trochocystites (13, 20)* or that the Mitrata and Cincta constitute a morphological series characterized by reduction of ambulacral grooves *(45, 55)* is without foundation. Every comparison between the Stylophora and Homostelea (Cincta) brings essential differences to light. The former are distinguished from the latter by: 1) absence of a stele and in general any peduncular prolongation of the body; 2) presence of the highly organized brachial process termed aulacophore; 3) position of the mouth and anus at opposite poles of the theca; and 4) presence of accessory orifices and such internal structures as the septum, infundibulum, scutulae, and marginal grooves, without known equivalent in *Trochocystites* and its allies.

In equal degree the Stylophora differ from the Homoiostelea, and to some extent in the same ways as from the Homostelea, as shown by: 1) absence of a stele; 2) specialized structure of their aulacophore; 3) constant presence of a framework of marginal plates around the theca; 4) much more pronounced differentiation of the two thecal faces; and 5) presence of internal structures and accessory orifices peculiar to themselves.

These are profound differences and suggest dissimilar general organization. For a given feature, homology cannot be demonstrated. No proof can be found, for example, that the marginal plates of the Stylophora are homologous with those of the Homostelea, since they may have been acquired independently, and likewise the marginals observed in some representatives of other echinoderm classes. In any event they do not correspond exactly either in number, or position, or in relation to the orifices or to other parts of the theca. Further, no form having characters morphologically intermediate between Stylophora, on one hand, and Homostelea and Homoiostelea, on the other is known. For these reasons I concur with CUÉNOT *(32)*, GEKKER *(41)*, and others in judgment that the "carpoids" comprise a heterogeneous assemblage which needs to be separated into three distinct classes.

EVOLUTION WITHIN STYLOPHORA

The Stylophora include two orders, which are named Cornuta and Mitrata. If these orders at first glance seem to be very different, actually they exhibit many strong resemblances, quite in contrast to that shown by comparison of the stylophorans with other "carpoids." Obviously, their fundamental organization is the same, since their body comprises the same parts, disposed in the same way and it has such similarity of plan or identity of connections that homologies cannot be doubted. Particular attention may be directed to the following points: 1) the body is composed in one as in the other of a theca and an aulacophore; 2) it bears no stem or peduncular prolongation; 3) the principal orifices have the same emplacement; 4) the theca and aulacophore possess the same structural elements; 5) attachment of the aulacophore to the theca is effected in the same way; and 6) many internal structures (e.g., muscular apophyses, scutulae, infundibulum) are seen in representatives of both orders. This structural unity seems incontestable and supports the conclusion that the Cornuta and Mitrata are orders derived from a common source.

When they first appear in the stratigraphic records, however, both the Cornuta and Mitrata are seen to be already highly specialized. Their oldest known representatives—*Ceratocystis,* from the Middle Cambrian of Bohemia, of the Cornuta, and

Chinianocarpos and *Peltocystis*, from the Lower Ordovician of Hérault, France, of the Mitrata—are so greatly advanced along lines peculiar to each that it is impossible to ascertain any interrelationships or to determine which of the two groups is the more primitive. Possibly the weak differentiation of the marginals from central plates in *Ceratocystis*, in combination with some other characters, may be identified as archaic traits, but this genus is established as an authentic cornute by the form and composition of its theca, the nature of its orifices, and the structure of its aulacophore. *Ceratocystis* cannot possibly be an ancestor of the Mitrata. On the basis of well-established observations, the Cornuta and Mitrata are recognized as groups having equal phylogenetic values, closely related to one another without doubt but with unknown interrelationships. Their common source must antedate considerably the time represented by the oldest fossils.

The fossil record is much too incomplete to allow steps in the evolution of either order to be followed, though some general trends are discernible by examining the stratigraphic succession of genera. The evolution indicated is difficult to prove, since neither genera nor species are connected by trustworthy lines of descent. However, comparison of *Ceratocystis* with *Nevadaecystis* and other cornute genera suggests that the following changes occurred during history of the group: 1) differentiation of marginal plates in relation to the centrals; 2) appearance of a zygal as reinforcement of the thecal frame and development of various appendages (spinal, glossal, digital) joined to it; 3) fragmentation of the thecal faces into a multitude of platelets, thus providing suppleness to the originally rigid pavements; 4) restriction of the adoral plates to the upper thecal face and gradual integration of them into the marginal framework; 5) regression of the median adoral to its ultimate disappearance; 6) migration of the right adoral orifice from a location on the inferior face to the right anterior edge of the theca; 7) substitution of sutural pores by generally more complex types of openings which retain narrowly localized placement in the upper right anterior area; 8) strengthening of internal structures of the theca, especially the aulacophore apophyses; 9) replacement of imbricated scales, which in *Ceratocystis* enclose the cavity of the aulacophoral proximal region, by a number of quadripartite rings articulating on one another; and 10) enlargement and thickening of the ridges along borders of the median groove of the aulacophore, with associated differentiation of transverse channels and lateral depressions. These alterations, already in progress at the end of Cambrian time (e.g., *Nevadaecystis*), were mostly completed in the Early Ordovician. During this epoch two assemblages became clearly differentiated—the Cothurnocystidae, characterized by the presence of cothurnopores or simple sutural pores, and the Scotiaecystidae, distinguished by the occurrence of lamellipores. They followed parallel lines of evolution until their apparent extinction in the Late Ordovician, for no post-Ordovician cornutes are known.

The Mitrata are represented in the Lower Ordovician by the suborders Mitrocystitida and Lagynocystida. In addition to these, the Middle Ordovician contains representatives of the Anomalocystitida. The Mitrocystitida appear to be the least specialized of the three groups, for they display characters (e.g., arrangement of infracentrals) found to be more or less modified in the other suborders. This does not prove that mitrocystids are the source of other mitrates classed as lagynocystids or anomalocystids or both of them, for all three groups could have been derived from a common trunk or separately descended from different ancestors. Questions of their origin are answerable neither by chronologic nor comparative morphologic evidence.

The Mitrocystitida and Anomalocystitida appear to be homogeneous assemblages, for their most typical representatives, at least, differ from one another respectively only in unimportant ways. The anomalocystids differ from the mitrocystids in having a pair of posterior movable spines and in being much more symmetrically organized with respect to the main axis of the body. As previously emphasized, this bilateral symmetry is superposed on a fundamental asymmetry. It is incomplete and probably denotes a secondary adaptation.

The Lagynocystida, by way of contrast, appear to be more diversified, with constituents modified by several different evolutionary trends. Among these are: 1) appearance of a unique calcareous process at the posterior extremity of the body; 2) retention of thecal asymmetry, or rather an increase of it; 3) reduction in the number of thecal plates; and 4) increase of the adoral plates to the point of hypertrophy. The first three of the cited trends affect all known genera, but in varying degree, and thus indicate the homogeneity of the suborder. The fourth trend is seen only in *Anatiferocystis* and *Balanocystites,* showing that the assemblage as a whole contains some diversification. On this basis two lineages which make appearance in the Middle Ordovician can be distinguished—the Lagynocystidae, containing *Lagynocystis* as its single genus, and the Kirkocystidae, containing *Anatiferocystis* and *Balanocystites* (=*Kirkocystis*). These two families are possibly related to the Peltocystidae, which are less specialized and are already present in the Lower Ordovician.

Finally, a resemblance that seems to relate *Paranacystis* to the Lagynocystida may be noted, though it may be the product of convergent evolution. According to CASTER *(26), Paranacystis,* as well as the Lagynocystida, would have been derived independently from Cambrian or Ordovician Mitrocystitida, considered to be the principal source of the Mitrata. This is agreed to at least provisionally by assigning this genus to the Mitrocystitida because, like representatives of this suborder and unlike the Lagynocystida, *Paranacystis* lacks a posterior exothecal process.

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION

The oldest known stylophoran is the cornute *Ceratocystis perneri* JAEKEL *(54)* from the Skryje Shale, Middle Cambrian, of Bohemia (BATHER, 1913). To find the next representatives of the Cornuta one must go to the uppermost Cambrian of the New World, for Trempealeauan rocks of Nevada contain *Cothurnocystis americana* UBAGHS (=*Nevadaecystis*) and *Phyllocystis* sp. *(89).*

The Lower Ordovician (upper Tremadoc and lower Arenig) of southern France (Hérault) has yielded a highly varied stylophoran fauna *(85)* characterized by: 1) great development of Cothurnocystidae, possibly representing the peak of this family, containing numerous species of *Cothurnocystis*—mostly undescribed—and *Phyllocystis*; 2) first appearance of the Scotiaecystidae, represented by an undescribed species; and 3) first appearance of the Mitrata, represented by two of its three suborders—the Mitrocystitida, with *Chinianocarpos,* and the Lagynocystida, with *Peltocystis.* Fossils identical or closely related to constituents of this fauna have been discovered in the Lower Ordovician of Morocco *(42)* (CHAUVEL, personal communication).

In the Middle Ordovician the Cornuta appear to become more rare, whereas the Mitrata are multiplied in number. The Šárka Shale (Llanvirnian) of Bohemia has yielded many species of *Mitrocystites,* two species of *Mitrocystella,* and one each of *Anatiferocystis, Balanocystites, Lagynocystis,* and *Spermacystis* (new name for *Anomocystis* JAEKEL, 1918, *non* HAECKEL, 1896) *(2,30,54,55).* Llandeilian strata of Brittany, in France, contain a comparable fauna but less rich *(30).* From the Middle Ordovician of the United States, *Anatiferocystis papillata* BASSLER has been recorded in Oklahoma and *Enoploura punctata* BASSLER in Tennessee. In Canada *Ateleocystites huxleyi* BILLINGS is the oldest known representative of the Anomalocystitidae. As for the Cornuta, only *Bohemiaecystis,* of the Scotiaecystidae and two undescribed genera are found in the Šárka Shale and Sv. Dobrotivá Shale of Bohemia.

Only a small number of Stylophora are known from the Upper Ordovician. From Bohemia, BARRANDE *(2)* has described an anomalocystid of uncertain generic affinities, named by him *Anomalocystites bohemicus (25,30).* In Brittany *Mitrocystites riadanensis* CHAUVEL *(30)* has been recorded. The celebrated Starfish Bed (Ashgillian) of Lady Burn, in the Girvan region of Scotland, is the source of two species described by BATHER *(13),* named by him *Cothurnocystis elizae* and *C. curvata,* the latter now designated as the type species of *Scotiaecystis.* These are the last known representatives of the Cornuta. From Ashgillian beds in Yorkshire, England, Marr (1913) has called attention to the occurrence of an undescribed mitrate by him attributed to *Ateleocystites*. Finally, Cincinnatian strata in Ohio and Indiana have yielded five species of *Enoploura (25)*.

From the Silurian onward, only genera of the Anomalocystitidae, Allanicytidiidae, and Paranacystidae are found, with the possible exception of a doubtful form referred to the Mitrocystitidae. From Australia, in beds identified as Lower Silurian, Gill & Caster *(43)* have reported *Victoriacystis* sp. aff. *V. wilkinsi* and from Upper Silurian rocks of the same region they have described *V. wilkinsi*. The Upper Silurian (Wenlock) of England has furnished *Placocystites forbesianus* de Koninck (1869) *(95)*. These species belong to the Anomalocystitidae.

In the Lower Devonian, the Anomalocystitidae are represented by: 1) *Rhenocystis latipedunculata* Dehm *(33, 34)* in Germany; 2) *Anomalocystites disparilis* Hall (1859) *(25, 56, 78)* in Maryland (=*Basslerocystis*); 3) *Anomalocystites cornutus* Hall (1859) *(25, 78)* in New York; 4) *"Placocystites" africanus* Reed *(72)* in South Africa; and 5) *Victoriacystis* sp. aff. *V. wilkinsi* Gill & Caster *(43)* in Victoria, Australia. The Australocystidae contain *Australocystis langei* Caster *(27)* from Paraná, Brazil, and *Placocystella capensis* Rennie (1936, *77*) from South Africa, both from the Lower Devonian. Allanicytidiidae are represented by one genus *Allanicytidium* (herein described) from the Lower Devonian of New Zealand. The Paranacystidae contain the single form named *Paranacystis petrii* Caster *(26)* from the Lower Devonian of Parana, in Brazil. The stylophoran species doubtfully assigned to the Mitrocystitidae is *Mitrocystites? styloideus* Dehm *(34)* from the Bundenbach Shale (Hunsrückian) in Germany.

The geologically latest known member of the Stylophora is the Middle Devonian *Dalejocystis casteri* Prokop *(71)* from Bohemia. Possibly it belongs to the Lagynocystida but here is classified as suborder and family uncertain.

Although the taxonomic diversity of the stylophorans seems to be modest, their geographic range is surprisingly extensive.

SYSTEMATIC DESCRIPTIONS

Class STYLOPHORA
Gill & Caster, 1960

[*nom. transl.* Caster & Ubaghs, herein, *ex* superorder Stylophora Gill & Caster, 1960]

Homalozoa in which the body comprises theca and brachial appendage (aulacophore) but no stele, stem, or peduncle; theca depressed, thickening forward, with very distinct upper and lower faces framed by marginals; mouth intrathecal, at or near proximal end of aulacophore; anus at opposite thecal extremity; aulacophore comprising three parts—a wide hollow proximal region, covered by imbricating scalelike platelets or more generally by tetramerous rings, a median region consisting of a conical reducing piece (stylocone), and a distal region composed of a single series of ossicles; stylocone and ossicles of the distal region carrying a median groove, typically flanked by lateral depressions, groove and depressions being both protected by movable cover plates. *M. Cam.-M.Dev.*

Order CORNUTA Jaekel, 1901

[*nom. transl.* Jaekel, 1918 (*ex* suborder Cornuta Jaekel, 1901)]

Stylophora with asymmetrical outlines; oro-anal axis ordinarily making quite distinct angle with main axis; exothecal processes or some protruding marginals generally present; marginals typically thick and narrow, ordinarily well differentiated from centrals, some of them commonly carrying knobs or spines on lower side; adoralia generally forming part of frame and not markedly participating to covering of both faces; right adoral notched by opening situated on lower face or more typically on anterior margin of theca; pores of various types ordinarily present in upper right anterior area; stylocone with rounded aboral face, without any knob or spine; median furrow of aulacophore raised on median ridge that is flanked by lateral depressions; transverse channels generally connecting median furrow with lateral depressions; cover plates imbricate. *M.Cam.-U.Ord.*

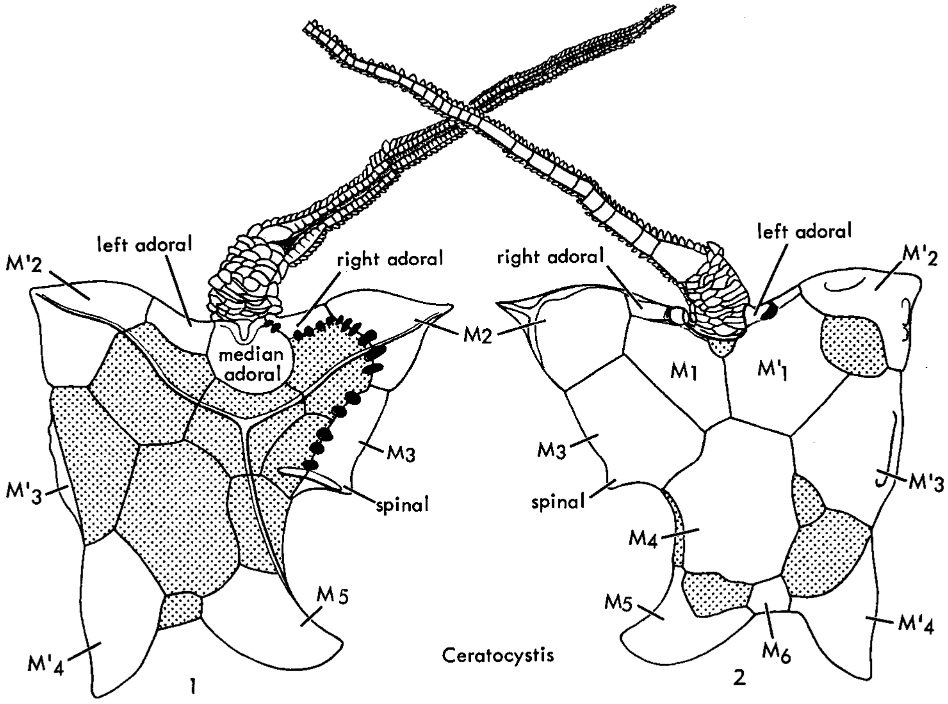


FIG. 345. Ceratocystidae (p. S548).

Family CERATOCYSTIDAE Jaekel, 1901

Theca with outlines not unlike those of pointed shoe; anterolateral corners protruding and thickened; right lateral margin divided by median triangular spinal projection; posterolateral marginals horn-shaped; frame slightly differentiated from central covering; knobs on lower face of M_2, M'_2 and M'_3, M_3 with downward-produced external edge; centrals few and not markedly smaller than marginals; upper thecal face characterized by triradiate ridge and short transverse ridge connected with spinal projection; adoralia 3, left and right, forming anterior thecal margin on both sides of aulacophore insertion and extending on both lower and upper thecal faces into narrow rim; median adoral located on upper thecal face only, its anterior edge with triangular median notch; slitlike opening emarginating lower margin of right adoral; anus unknown, probably located between two posterior horns; pores along sutures joining median adoral with right adoral, and right adoral and marginals M_2 and M_3 with contiguous supracentrals; single similar pore on anterior left thecal margin between M'_2 and left adoral, and on lower face between left adoral and M'_1; proximal region of aulacophore covered by imbricating scalelike platelets; median aulacophore furrow limited by narrow ridge; transverse channels indistinct and lateral depressions slightly marked. *M.Cam.*

Ceratocystis JAEKEL, 1901 [*C. perneri; OD]. Characters of family. *M.Cam.*, Boh.——FIG. 345, *1,2*. *C. perneri, Skryje Sh.; *1*, upper face, ×1.8; *2*, lower face, ×1.8 (Ubaghs, n).

Family COTHURNOCYSTIDAE Bather, 1913

Theca very depressed, boot-shaped or heart-shaped in outline, framed by narrow elongate marginals between which stretch either a pavement of large plates or, more generally, finely plated integuments; lower face typically divided into two unequal parts by a zygal; adorals 2 or 3, resting on M_1 and M'_1, confined to upper thecal side; lower anterior edge of right adoral notched

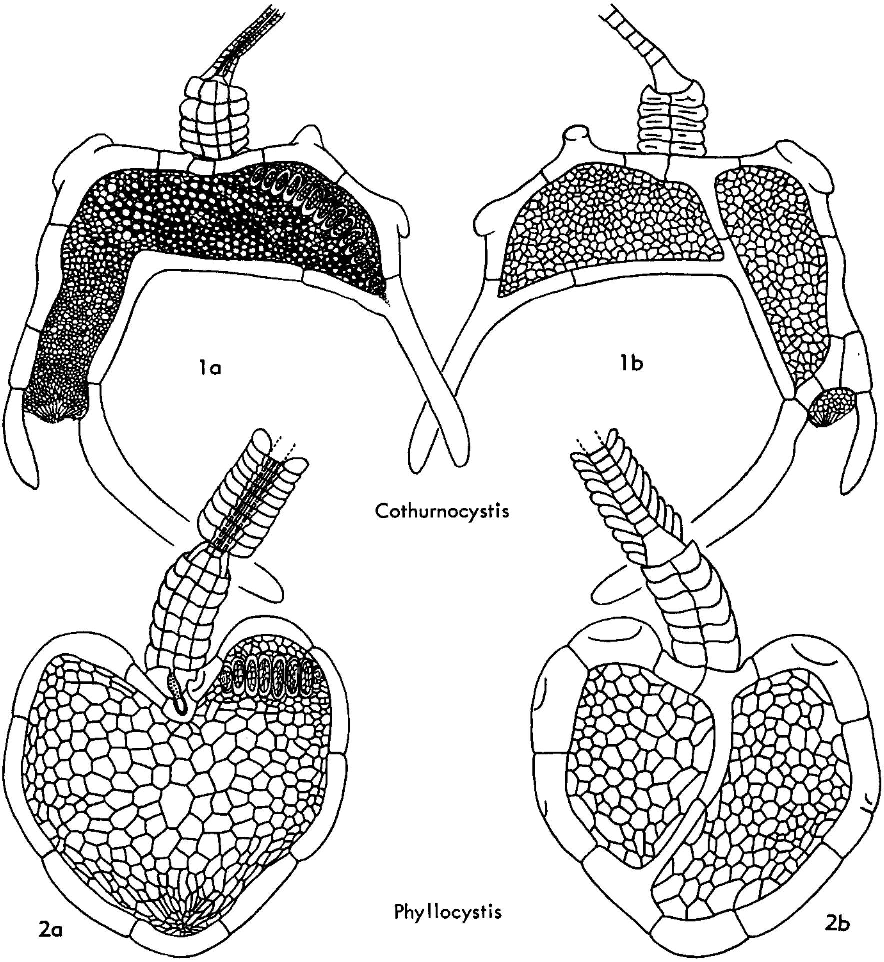


FIG. 346. Cothurnocystidae (p. S549-S550).

by distinct opening; anus terminal at posterior upper end of theca; cothurnopores arranged in row or simple pores scattered between supracentrals in upper right anterior area; proximal region of aulacophore protected by rings, each composed of four unequal plates, two smallest covering mid-part of superior face; median furrow limited by relatively wide rims; transverse channels and lateral depressions well marked. *U. Cam.-U.Ord.*

Cothurnocystis BATHER, 1913 [**C. elizae*; OD]. Theca very asymmetrical, transversely elongate, having boot-shaped outlines; left posterior area forming long narrow protrusion; spinal, glossal, digital, and generally marginal knobs or spines well developed; infracentralia flattened and tessellate; supracentralia generally rounded and slightly swollen; upper integument stretching over 2 most posterior marginals which close frame on its lower side only; cothurnopores arranged in row running from left adoral to spinal corner. *L.Ord.-U.Ord.*, Scot., Fr.——FIG. 346,*1*. **C. elizae,* U. Ord., Ashgill Ser., Girvan, Scot.; *1a,* upper face, ×1.2; *1b,* lower face, ×1.2 (Ubaghs, n).

Nevadaecystis UBAGHS, **new genus** herein [**Cothurnocystis americana* UBAGHS, 1963]. Similar to *Cothurnocystis* but having lower face covered by few large plates and upper face by numerous stellate ossicles with uncalcified areas between their joining rays; no zygal; marginal spine prominent; ridge, probably triradiate, on upper side as in *Ceratocystis*. *U.Cam.*, USA(Nev.).——FIG. 347, *1*. **N. americana* (UBAGHS), Trempealeau; upper face, ×3 (89).

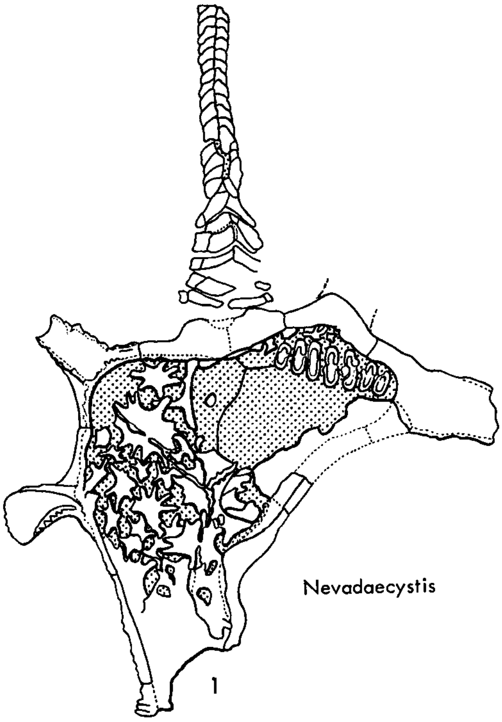


FIG. 347. Cothurnocystidae (p. S549).

Phyllocystis THORAL, 1935 [**P. blayaci*; OD]. Differs from *Cothurnocystis* in having heart-shaped outlines, marginals completely framing theca on both faces, supracentrals as well as infracentrals tessellate, and no exothecal process; simple or denticulate knobs but no spines on lower side of marginals; adorals 3, median one with anterior median notch (as in *Ceratocystis*); row of cothurnopores or numerous scattered openings in upper right anterior area according to species. *U. Cam.-L. Ord.*, USA (Nev.)-Eu.(France)-N. Afr. (Morocco).——FIG. 346,2. **P. blayaci*, L.Ord., France; *2a*, upper face, ×3; *2b*, lower face, ×3 (Ubaghs, n).

Family SCOTIAECYSTIDAE
Caster & Ubaghs, new family

Theca very depressed and asymmetrical, with complicated outlines; frame well distinct from central covering, completely surrounding theca on both sides; marginals narrow and elongate; lower and upper integument finely plated; lamellipores numerous, occupying curved tract between right adoral to near right posterior corner; aulacophore similar to that in Cothurnocystidae. [An undescribed species is known from the Lower Ordovician of France.] *L.Ord.-U.Ord.*

Scotiaecystis CASTER & UBAGHS, **new genus**, herein [**Cothurnocystis curvata* BATHER, 1913; OD]. Theca junk-shaped, transversely elongate; left posterior area not markedly protruding and ending in truncated angle that carries single long posterior spine; spinal short and thick; prominent knobs on lower side of some anterior and lateral marginals; zygal sloping in direction of left posterior corner; infracentrals flattened and tessellate; supracentrals with low convex-topped spines; anus not terminal, but near left posterior margin; lamellae between lamellipores not prolonged into thecal cavity; lower face of ossicles of distal aulacophore region angulate. *U.Ord.*, Scot.——FIG. 348,*1-4*. **S. curvata* (BATHER), Ashgill Ser., Girvan; *1a,b*, upper and lower faces, ×3.3; *2*, supracentrals, ×9; *3*, infracentrals, ×9; *4*, anal area, ×10 (all Ubaghs, n).

Bohemiaecystis CASTER, **new genus**, herein [**B. boučeki* CASTER, **new species**, herein; OD]. Theca sabot-shaped, moderately wide; left posterior end rounded, ?without posterior spine; ?no spinal; simple low knobs on some anterior and lateral marginals; zygal slightly oblique to main axis; supracentrals as well as infracentrals flattened and tessellate; lamellae between lamellipores protruding into thecal cavity. *M.Ord.*, Boh.——FIG. 349, *1,2*. **B. boučeki*, M.Ord., Sv. Dobrotivá and Šárka Shales, Boh.; *1,2*, upper and lower faces, ×1.5 (Caster, n).

Order MITRATA Jaekel, 1918

Stylophora with asymmetrical to bilaterally symmetrical outlines; oro-anal axis approximating or coinciding with main axis; lower thecal face plane or slightly concave; upper thecal face invariably convex; both thecal faces covered by relatively large plates; marginals generally not very distinct from centrals, never carrying knobs or protuberances on their lower side; no zygal, but generally an intrathecal septum in corresponding position on floor of thecal cavity; adorals covering more or less large area on upper surface; right adoral pierced (in *Mitrocystites* only) by slitlike opening; one or two pairs of pores present in some genera on lower or anterior thecal face; stylocone with aboral knob or spine; median furrow in deep groove, with lateral depressions slightly marked, if at all; cover plates not imbricating in extended position of aulacophore. *L.Ord.-M.Dev.*

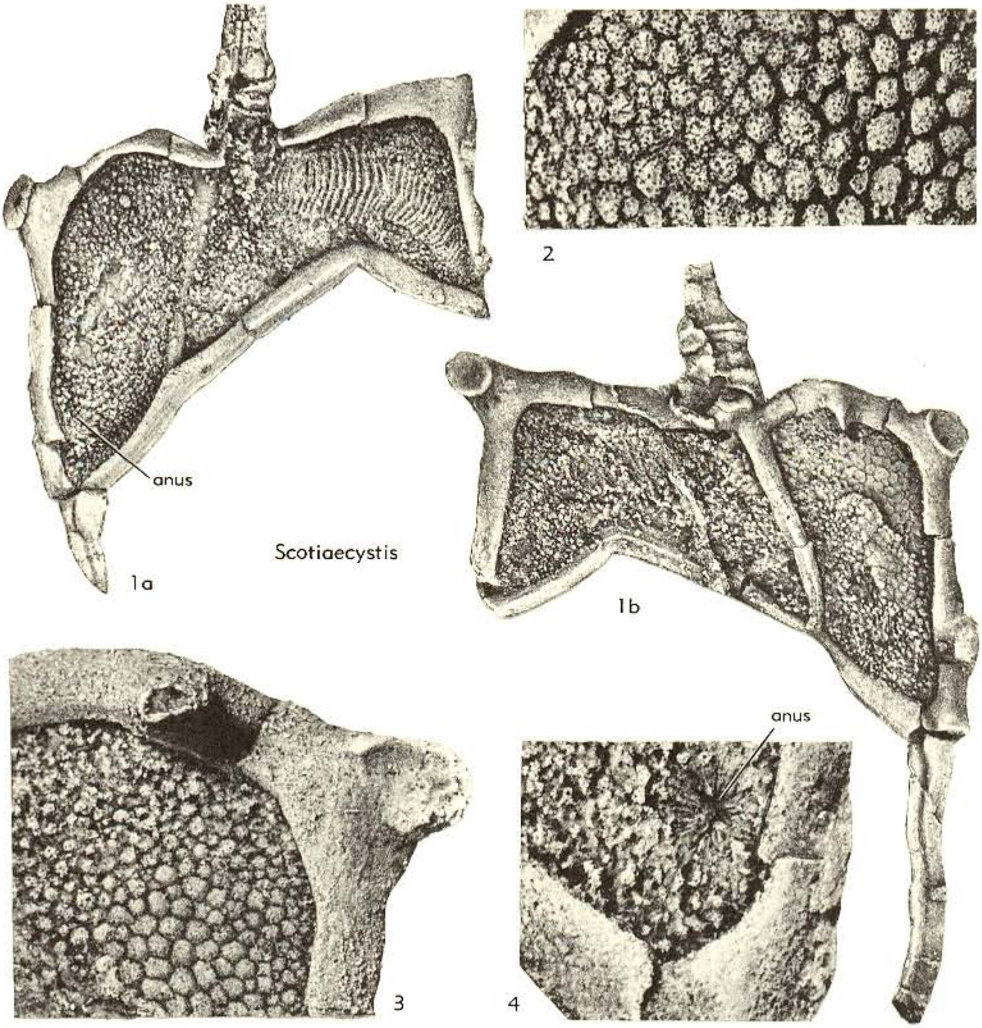


FIG. 348. Scotiaecystidae (p. S550).

Suborder MITROCYSTITIDA Caster, 1952

[*nom. correct.* UBAGHS, herein (*pro* Mitrocystida CASTER, 1952)]

Thecal outlines slightly to moderately asymmetrical; no exothecal posterior process; adorals two. *L.Ord.-L.Dev.*

Family MITROCYSTITIDAE Ubaghs, new family

[=Mitrocystidae JAEKEL, 1901 (invalid family-group name based on *nom. van.*, Code, Art. 11,c)]

Posterior margin evenly arcuate or slightly notched; infracentrals numerous, either small and nearly equal in size, or few and very unequal; adorals moderately developed; supracentrals rather small and more or less numerous; proximal region of aulacophore covered by imbricating quadripartite rings; aboral face of stylocone and following distal ossicles each with strong median curved spine. *L.Ord.-U.Ord.*

Mitrocystites BARRANDE, 1887 [**M. mitra*; OD] [=*Mitrocystis* BATHER, 1889]. Thecal outlines subtrapezoidal or subrectangular, somewhat asymmetrical, slightly notched at both ends; marginals 12 or more, generally 13 (5 or 6 on left side, 7 on right side), relatively thick and folded upward at an acute angle; M'_1 distinctly larger than M_1; lower outer edge of M_2 and M'_2 denticulate;

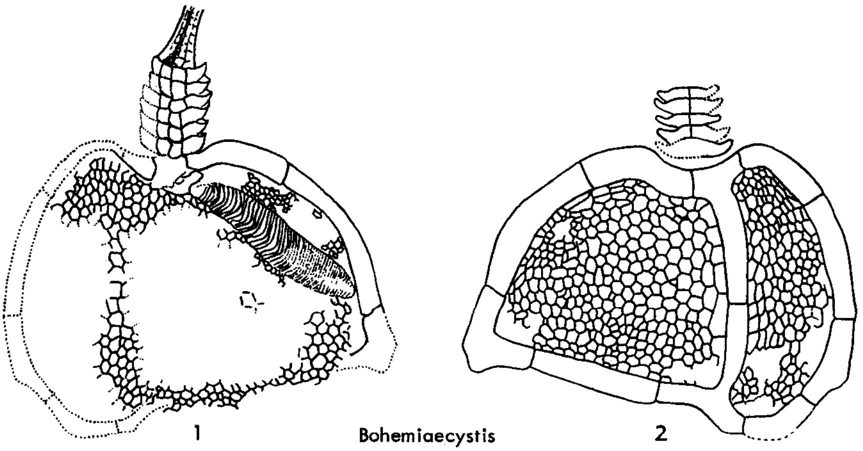


FIG. 349. Scotiaecystidae (p. S550).

infracentrals 4 to 6, largest one subcentral and separated from M_1 by median-sized plate; adorals bearing transverse fold, right one pierced by slitlike opening; supracentrals not imbricate or only slightly so, if at all; periproct semicircular, on upper side, covered by granular integument surrounding perianal row of elongate toothlike platelets; paripores on M_2 and M'_2; lateripores near outer extremity of sutures M_1, M_2 and M'_1, M'_2. _M.Ord.-U.Ord._, Boh.-Fr. [A very doubtful species has been recorded by DEHM (1934) in the Lower Devonian (Hunsrück Sh.) of Germany].——FIG. 350,_1_. *_M. mitra_ M.Ord. (Šárka Shale), Boh.; _1a-c_, lower, upper, lat. faces; _1d_, cross section of theca, ×2 (Ubaghs, n).

Chinianocarpos UBAGHS, 1961 [*_C. thorali; OD_]. Thecal outlines asymmetrical; posterior margin evenly arcuate, anterior margin hardly notched on lower side, moderately so on upper side; no anterolateral lobes; marginals 9 (4 on left side, 5 on right side), relatively thick, folded upward at acute angle, all of them more extended on lower than on upper side, except M'_4 and M_5 which cover whole upper posterior area; lower external border of M_2, M_3 and M'_2 denticulate; M'_1 larger than M_1; M_4 separating M_1, M_2, and M_3 from infracentrals, which are numerous, small, polygonal, subequal, and tessellate, occupying median elliptical area; one large subanal between infracentral area and marginals M_4, M_5, and M'_4; adorals without transverse fold and opening; supracentrals moderately numerous, tessellate; paripores on M_3 and M'_2; periproct unknown. _L.Ord._, Fr.——FIG. 351,_1-4_. *_C. thorali_; _1,2,4_, upper, lower, and lat. faces; _3_, cross section of theca, ×4 (Ubaghs, n).

Mitrocystella JAEKEL, 1901 [*_Anomalocystites incipiens_ BARRANDE, 1887; OD]. Similar to _Mitrocystites_, but theca relatively more elongate and more asymmetrical, rounded or barely notched at posterior end, and with rather deep median embayment between 2 distinct lobes at anterior end; marginals 13 (6 on left side, 7 on right side), relatively thin, folded upward almost at right angle; M_1 and M'_1 about equal in size; infracentrals 2, one of them very large, always in contact with M'_1, and generally also with M_1; adorals without transverse fold and opening, transversely striated in some species; supracentrals apparently imbricate; paripores and lateripores unknown. _M.Ord._, Boh.-Fr.——FIG. 350,_2_. _M. barrandei_ JAEKEL, 1901, Šárka Sh., Boh.; _2a-c_, lower, upper and lat. faces; _2d_, cross section of theca, ×2 (Ubaghs, n).

Family PARANACYSTIDAE Caster, 1954

Posterior margin acute and prominent; infracentrals few, about equal in size, elongate and roughly hexagonal; adorals very large, covering half or more of upper surface; infracentrals few and rather large. _L.Dev._

For this monotypic family alone, CASTER (1954) proposed the new suborder Paranacystida. It does not seem that our present knowledge is sufficient to justify recognition of a higher category than family for this rather admittedly aberrant assemblage of Mitrata.

Paranacystis CASTER, 1954 [*_P. petrii;_ OD]. Theca lancet-shaped to ovate, with nearly vertical lateral surfaces; anterior corners of upper side moderately inflated, produced subangularly; anterior margin more excavated for aulacophore insertion on lower than on upper face; posterior thecal plates seemingly imbricated and prolonged into beak-shaped structure; 2 (possibly 3) marginals on each lateral surface, taking no part in covering of upper side; infracentrals 2 (possibly 3); supracentrals 3 or 4, rather large; anteromedian supracentral quadrangular; aulacophore considerably longer than theca; stylocone 2-bladed, ossicles of aulacophoral distal region with strong median aboral spines. *L.Dev.*, S.Am.(Paraná, Brazil).——FIG. 352,*1-3*. **P. petrii*; *1*, paratype, external mold, upper side, ×10; *2a,b*, holotype, external molds, upper and lower faces, ×5.3; *3*, paratype, external mold, lower face, ×5 *(26)*.

Suborder LAGYNOCYSTIDA Caster, 1952

Thecal outlines moderately to very asymmetrical; a single exothecal posterior process. *M.Ord.*

Family PELTOCYSTIDAE Ubaghs, new family

Thecal outlines moderately asymmetrical, irregularly pentagonal, slightly excavated for aulacophore insertion on both sides; posterior margin unequally divided by marginal protuberance bearing elongate sigmoid spine; marginals eight (three on left side, five on right side), taking almost no part in covering of upper face; lower external edge of M_1 and M'_1 denticulate; infracentrals two, small, not in contact; subanal subquadrangular, outside marginal frame; adorals two, large, extending to mid-length of theca; supracentrals numerous and small, seemingly tessellate; proximal region of

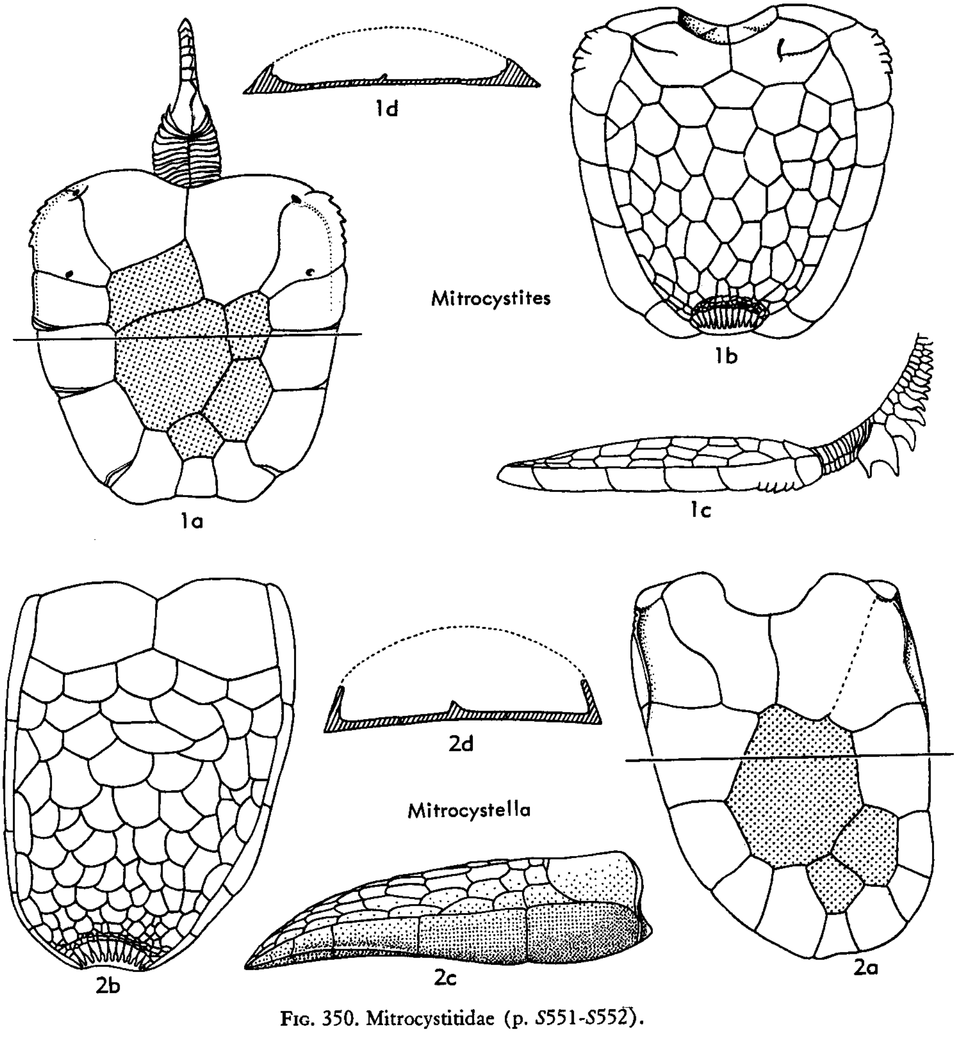


FIG. 350. Mitrocystitidae (p. S551-S552).

aulacophore covered by imbricating tetramerous ring; stylocone and following distal ossicles with strong curved aboral spines. *L.Ord.*

Peltocystis THORAL, 1935 [**P. cornuta*; OD]. Characters of family. *L.Ord.*, Fr.——FIG. 353,*1-4*. **P. cornuta*; *1,3,* interior and exterior of lower face; *2,* upper face; *4,* anterior face; ×3 (Ubaghs, n).

Family LAGYNOCYSTIDAE Jaekel, 1918

Theca elongate, pyramidal, subquadrate in cross section, very asymmetrical; posterior end obliquely truncated, with short hollow calcareous process attached to left posterior corner; left lateral surface higher than right one; lower left lateral edge sharper than right one; no infracentrals, whole inferior face being covered by seven marginals (three on left side, four on right side) and few scalelike platelets in lateral connection with supracentrals; adorals three, moderately large; supracentrals numerous, imbricating; posterior hollow conical piece (?anal valve) terminating upper face; sutural pore on each side of aulacophore insertion; proximal part of aulacophore protected by spinous scalelike imbricated platelets; stylocone elongate, very shallow, with median aboral row of four or five spines; distal region of aulacophore composed of elongate ossicles, each with short distal triangular aboral projection. *M.Ord.*

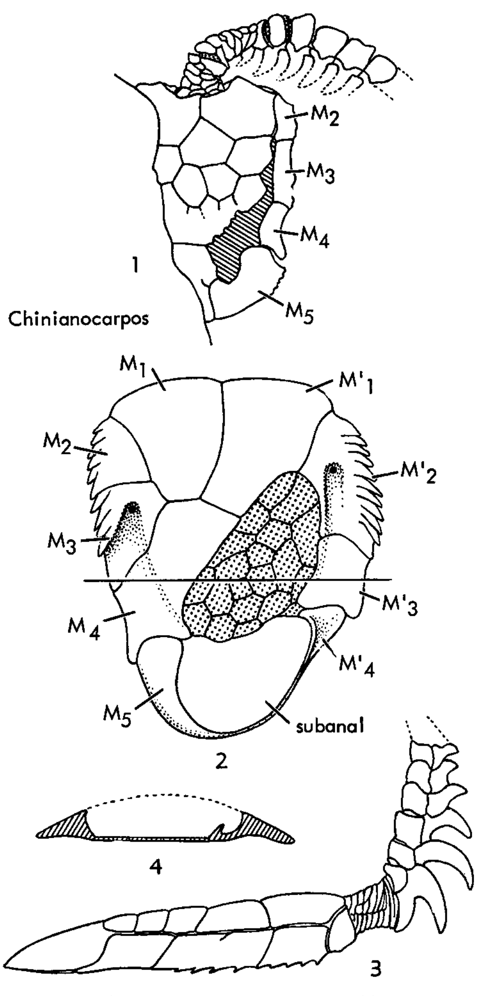


FIG. 351. Mitrocystitidae (p. S552).

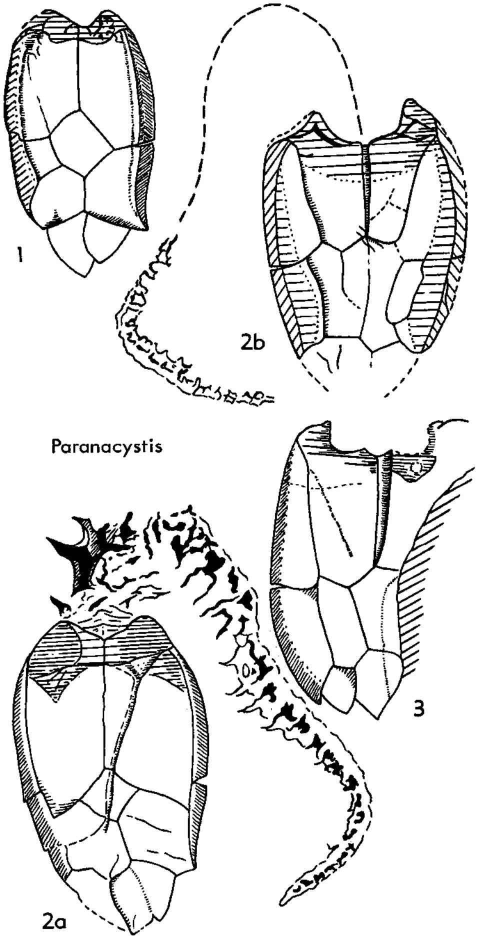


FIG. 352. Paranacystidae (p. S552-S553).

Lagynocystis Jaekel, 1918 [**Anomalocystites pyramidalis* Barrande, 1887; OD]. Characters of family. *M.Ord.*, Boh.——354,*1-5*. **L. pyramidalis* (Barrande), Šárka Sh.; *1-4*, lower, upper, right lateral and ant. faces; *5*, cross section of theca, ×3 (Ubaghs, n).

Family KIRKOCYSTIDAE Caster, 1952

[*nom. transl.* Ubaghs, herein (*ex* Kirkocystinae Caster, 1952)]

Theca plano-convex, asymmetrical, composed of only two adorals, two marginals *(M_1, M'_1)* and one subanal, and with calcareous posterior process; adorals convex, elongate, subequal, very large, covering entire upper face and large part of lower face as well; M_1 and M'_1 more or less reduced, M_1 smaller than M'_1, which touches large subanal inserted between posterior and adaxial lower margins of adorals; proximal region of aulacophore protected by quadripartite rings; stylocone and following distal ossicles each with aboral spine. *M.Ord.*

Balanocystites Barrande, 1887 [**B. lagenula;* OD]. M'_1 relatively large, widening in posterior direction and broadly in contact with subanal; M_1 triangular, extending for some distance along side of M'_1; subanal suparallel to extension plane. *M.Ord.*, Boh.-?Fr.——Fig. 355,*1*. **B. lagenula*, Šárka Sh.; *1a-c*, lower, anterior, upper faces of theca, ×3 (Ubaghs, n).

Anatiferocystis Chauvel, 1941 [**A. barrandei*; OD] [=*Kirkocystis* Bassler, 1950 (type, *Enoploura? papillata* Bassler, 1943)]. M'_1 narrow, in contact with subanal by short suture; M_1 subquadrate, not extending along side of M'_1; subanal oblique to extension plane. *M.Ord.*, Boh.-Fr.-USA (Okla.).——Fig. 355,*2*. **A. barrandei*, Šárka Sh., Boh.; *2a,b*, lower, upper faces, ×3 (Ubaghs, n). ——Fig. 355,*3*. *A. papillata* (Bassler), Blackriv., USA(Okla.); *3a-e*, lower, posterior, upper, right and left lateral faces of theca, ×6 (Ubaghs, n).

Suborder ANOMALOCYSTITIDA Caster, 1952

[*nom. correct.* Ubaghs, herein (*pro* Anomalocystida Caster, 1952)] [=suborder Placocystida Caster, 1952]

Thecal outlines nearly bilaterally symmetrical, with two exothecal posterior spinous processes articulated at base. *M. Ord.-L.Dev.*

The genera classified herein under this suborder were placed by Caster (1952) under two new monotypic suborders—Anomalocystida and Placocystida—under the erroneous assumption that the Anomalocystitida are provided with segmented brachia and the Placocystida with unsegmented rodlike processes. In fact, as demonstrated by Caster (see under *Anomalocystites*), the Anomalocystitida have no jointed brachia at the posterior end of the body. Therefore they do not differ in any essential way from the placocystid genera.

Family ANOMALOCYSTITIDAE Bassler, 1938

[=Anomalocystidae Meek, 1872 (invalid family-group name based on *nom. van.*, Code, Art. 11,e); fam. Anomocystida Haeckel, 1896 (invalid) *(partim)*; subfam. Placocystida Haeckel, 1896 (invalid) *(partim)*; fam. Atelocystida Haeckel, 1896 (invalid) *(partim)*; Placocystidae Caster, 1952 (invalid); Placocystinae Caster, 1952 (invalid); Enoplourinae Caster, 1952; Basslerocystinae Caster, 1952; Placocystitidae Gill & Caster, 1960]

Theca achieving high degree of bilateral symmetry in general outlines, as well as in

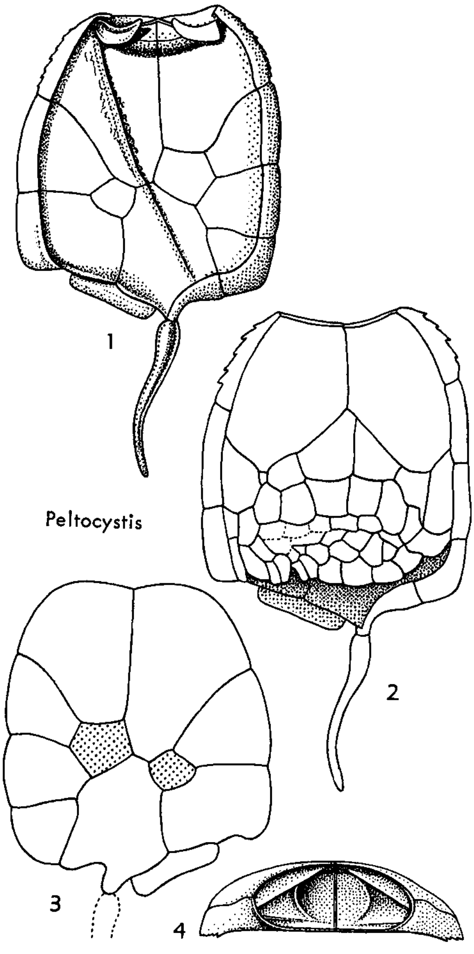


Fig. 353. Peltocystidae (p. S554).

shape and arrangement of plates, particularly on upper face; marginals 11 (two on anterior face, three on each lateral face, and three on posterior face; infracentrals few, including one large plate usually in median position accompanied by small "anomalocystid" plate at its left posterior corner and possibly by one to four additional posteriorly placed small plates; supracentrals tessellate, forming apparently solid pavement; thecal ornament typically consisting of transverse wavy lines. *M.Ord.-L.Dev.*

Partition of the anomalocystitid genera into subfamilies, seems inadvisable to me, at least until better understanding of phyletic relationships has been obtained.

Anomalocystites HALL, 1859 [**A. cornutus*; SD S. A. MILLER, 1889] [=*Anomalocystis* BATHER, 1889 *(nom. van.)*; *Anomocystis* HAECKEL, 1896 *(nom. van.)*] [Diagnosis furnished by K. E. CASTER after study by him of HALL's types.]. Theca subovoid in outline, upper face convex and lower one concave, with lateral rim; lateral faces longitudinally arcuate, posterior and anterior upper margins transversely arcuate, inferior face deeply arcuate for reception of aulacophore. Upper thecal surface composed of 12 laterals, 3 large adorals (median one touching margin), 3 large adprocteals, and 14 supracentrals arranged in 4 transverse rows (3 in proximal row, 5 in 2nd, 4 in 3rd, 2 in 4th). Lower thecal face composed of 6 marginals, 2 large adaulacophorals deeply excavated proximally, 3 adprocteals, and 2 infracentrals. Theca partially ornamented by transverse wavy lines, at distal lateral extremities bearing 2 articulated spines. Aulacophore broad proximally, formed of 8 or 9 telescoping rings which imbricate axially on lower side; styloid with 3 axial elements, short blades; distal part of aulacophore long and narrow, apparently biserial. [According to SCHUCHERT (1904), 2 segmented brachia bearing exothecal ambulacra were inserted on the posterior thecal margin. This conclusion is er-

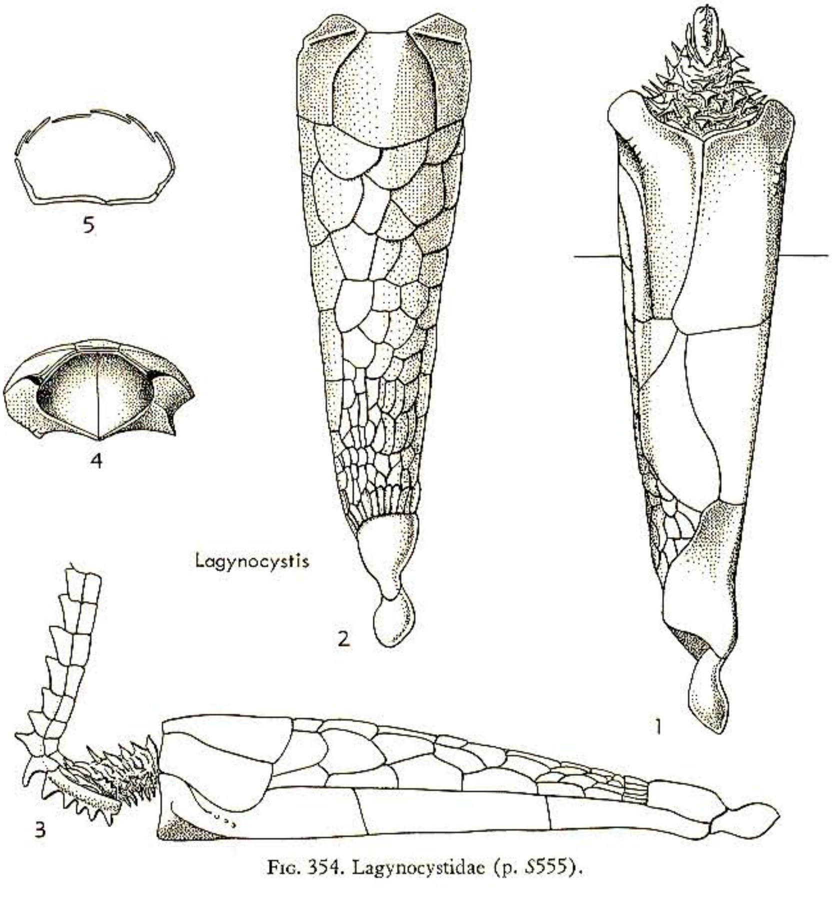


FIG. 354. Lagynocystidae (p. S555).

roneous, for it was based on the distal stele of an adjacent specimen on the same slab (USNM no. 35078). Hall's types preserve the bases of articulated spines in the position of Schuchert's inferred ambulacra.] *L.Dev.*, USA(N.Y.).——Fig. 356,*1*; 357,*1*. _*A. cornutus_; 356,*1a-d*, four of Hall's type specimens (AMNH no. 2288); 356, *1a* (holotype), *1b* (previously unfigured paratype), showing superior face; 356,*1c,d*, paratypes showing inferior face (356,*1c*, figured by Hall, 356,*1d*, previously unfigured); all ×3 (Caster, n); 357,*1a,b*, plate arrangements of superior face (holotype) and inferior face (paratype, ×4.5 (Caster, n).

Ateleocystites Billings, 1838 [_*A. huxleyi_; OD] [=*Ateleocystis* Lindström, 1888 *(nom. van.)*; *Atelecystis* Bather, 1889 *(nom. van.)*; *Atelocystis* Haeckel, 1896 *(nom. van.)*] [Diagnosis furnished by K. E. Caster after study by him of Billings' types]. Small anomalocystitid mitrates

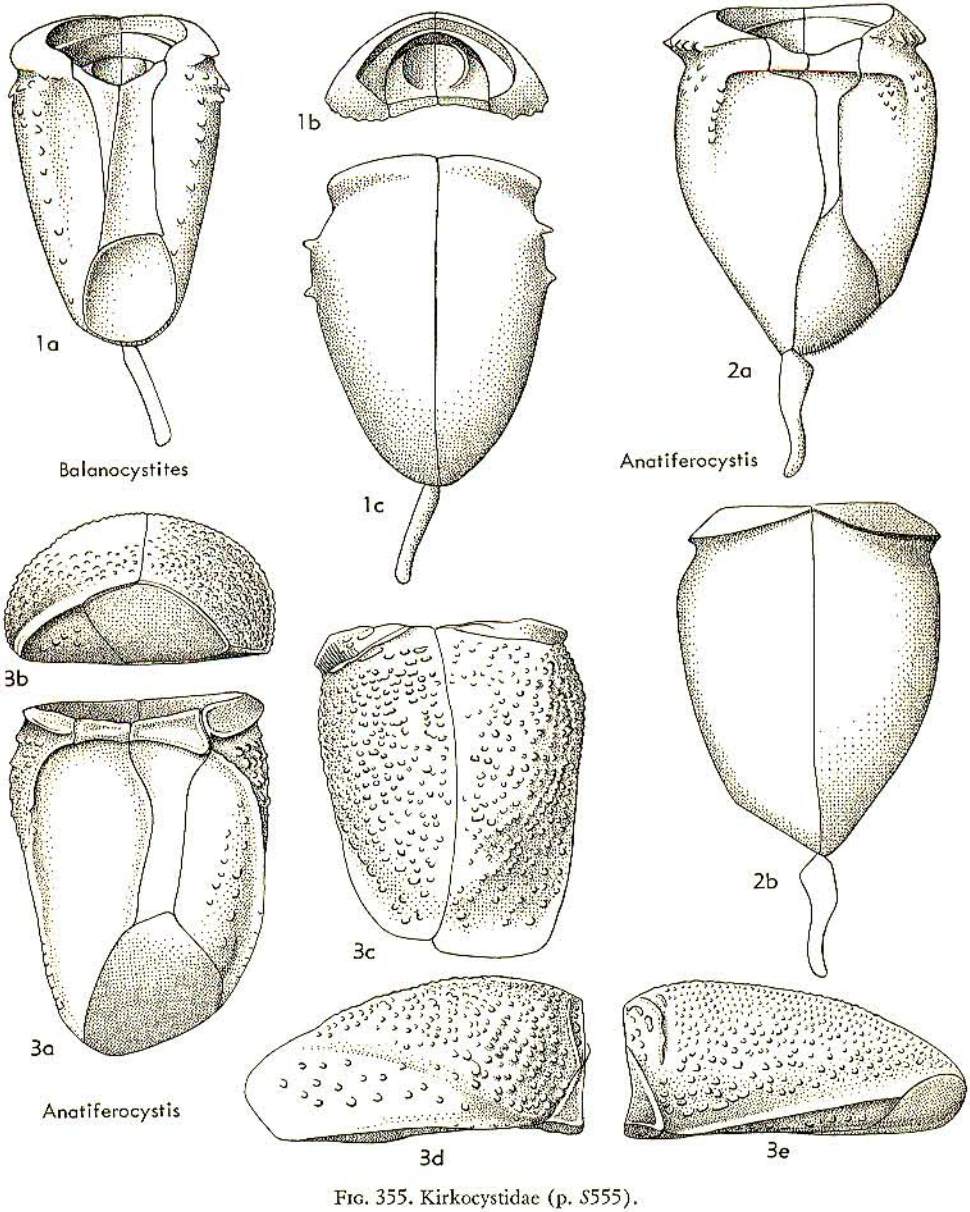
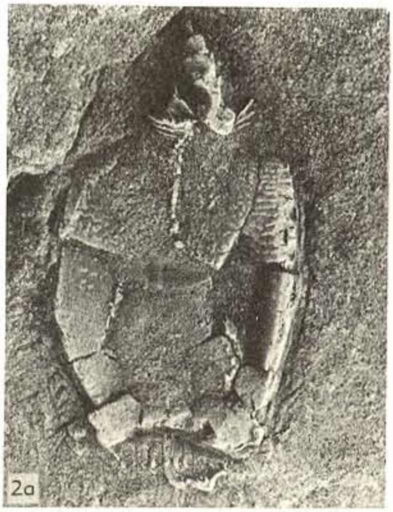
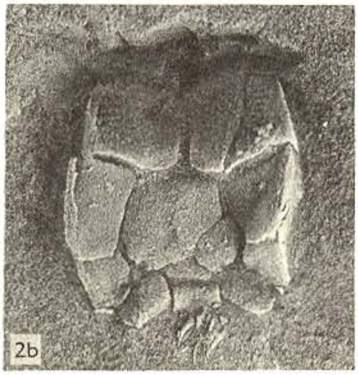


Fig. 355. Kirkocystidae (p. *S*555).

Anomalocystites





Ateleocystites

with inferior (plastron) surface composed of 14 plates, of which 3 are somatic and others marginal, as in *Enoploura*; superior (carapace) surface poorly known, but with more numerous somatic plates and considerably narrower adaulacophore axial plate than in *Enoploura*, superior

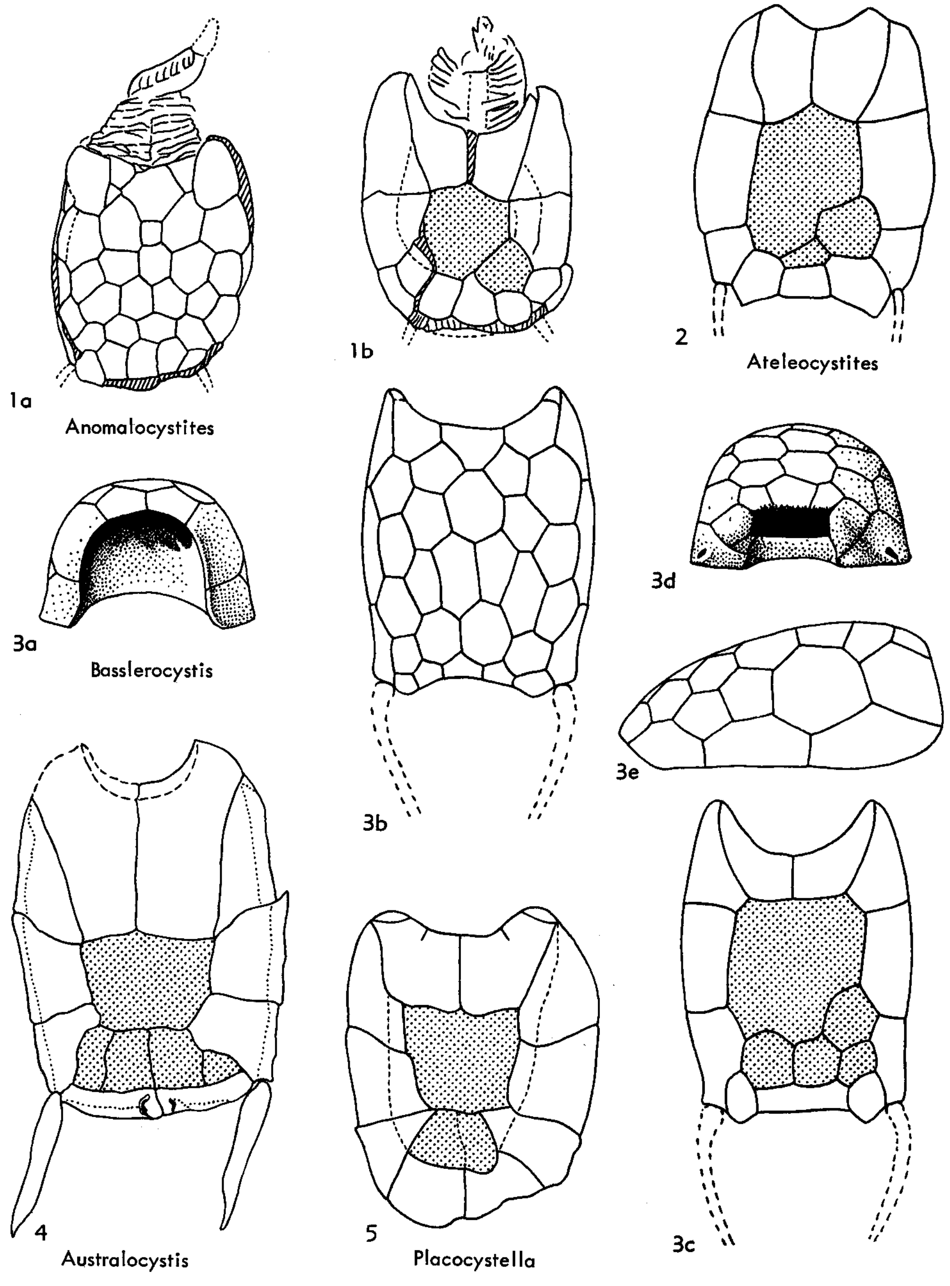


FIG. 357. Anomalocystitidae *(1-3)*; Australocystidae *(4-5)* (p. *S*556-*S*557, *S*559-*S*560).

FIG. 356. Anomalocystitidae (p. *S*556-*S*557, *S*559-*S*560) [*On facing page*].

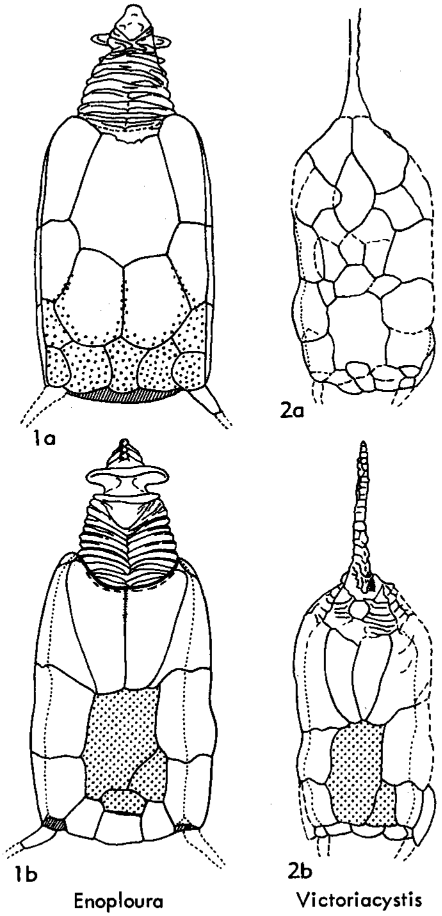


FIG. 358. Anomalocystitidae (p. S560-S561).

face extending posteriorly well beyond inferior margin, this part apparently formed by single thick posterior marginal plate that served as hood over large posterior orifice (?anus), interior surface of this hood bearing prominent rounded longitudinal carinae nodosely expanded distally. Two distal-lateral articulated "arm" spines known mainly from thecal articulatory surface. Aulacophore 3-zoned, proximal region composed of thin-walled smooth tetrameres which imbricate deeply, styloid part massive and bearing 2 short stout blades, distal region apparently dimerous, inferiorly carinate, and probably long and narrow; surface of inferior adaulacophore plates with prominent pseudoimbricating transverse ridges which grade into seemingly imbricated squamae adaxially; ornament apparently overlapping away from aulacophore. *M.Ord.(Trenton.)*, Canada (Ottawa Valley).——FIG. 356,*2*; 357,*2*. **A. huxleyi*; 356,*2a,b*, inferior face of two syntypes (Geol. Survey Canada, nos. 1392A,H) showing longitudinal ridges on posterior, interior of superior (carapace) cover, ×4 (Caster, n); 357,*2*, lower face, ×3.8 (25, mod.).

Basslerocystis CASTER, 1952 [**Anomalocystites disparilis* HALL, 1859; OD]. Theca egg-shaped; lateral faces longitudinally arcuate, more or less steep; lower face concave, with downward produced lateral margins; upper face rather strongly convex; posterior face invaginated for length of quadrate, transverse opening, which apparently could be closed by single, hinged, ?opercular plate; anterior side rather deeply emarginated for aulacophore insertion; infracentrals 5, comprising large central plate and 4 small ones in left posterior and posterior positions; adorals 3; supracentrals numerous. *L.Dev.*, USA(Md.).——FIG. 357,*3*. **B. disparilis* (HALL), Oriskany; *3a-e*, ant., upper, lower, post., and right lat. faces, ×1.4 (*3a,d,e*, Kirk, 1911; *3b,c*, Caster, 1952).

Enoploura WETHERBY, 1879 [**Anomalocystites (Ateleocystites?) balanoides* MEEK, 1872; OD]. Theca subrectangular, larger than wide; lateral faces axially arcuate and nearly vertical, making almost right angle with upper side; anterior margin deeply emarginated for aulacophore insertion, posterior margin slightly arcuate; lower face concave; theca resting on downward-produced edges of lateral marginals; infracentrals 3, one large central plate and two small ones in left posterior and submedian posterior positions; adorals 3, one large median reaching about mid-length of theca and two smaller lateral ones; supracentrals 11; thecal ornament finely granular, coarsely pitted, labyrinthine, or transversely striated. *U.Ord.*, USA(Ohio-Ind.).——FIG. 358,*1*. *E. popei* CASTER, Ohio; *1a,b*, upper and lower faces, ×1.4 (Caster, 1952).

Placocystites DE KONINCK, 1869 [**P. forbesianus*; OD] [=*Placocystis* HAECKEL, 1896 *(nom. van.)*]. Theca flattened subquadrate, somewhat longer than wide; lateral margins slightly arcuate longitudinally; anterior margin deeply emarginated by aulacophore insertion; posterior margin almost straight; lower face slightly concave, upper face moderately convex, both faces joined at acute angle; infracentrals 2, one large central plate and one small one at left posterior corner; adorals 2, moderately developed, almost completely separated by subpentagonal median plate (?third adoral) which does not reach anterior margin; supracentrals 11, in 3 transverse rows, those belonging to most anterior row including median rounded plate ("placocystid plate") generally quite surrounded by its two neighbors; large posterior opening; most thecal plates ornamented with transverse wavy lines on both faces. *U.Sil.*, Eng.-?Gotl.——FIG. 359,*2*. **P. forbesianus*, Wenlock; *2a,b*, upper and lower faces, ×1.5 (Ubaghs, n).

Rhenocystis DEHM, 1932 [**R. latipedunculata*; OD]. Theca subrectangular, elongate, plano- and more probably concavo-convex; lateral margins slightly arcuate longitudinally; posterior margin straight, anterior margin apparently almost entirely occupied by aulacophore insertion; infracentrals 2, large central plate and small one at its left posterior corner; adorals 2, almost completely separated by narrow median plate (?third adoral) which typically does not reach anterior margin; supracentrals 15, in 4 transverse rows; "placocystid plate" narrow, longitudinally elongate; aulacophore very long, ossicles of distal region with long aboral spines. *L.Dev.*, Ger.——FIG. 359,*1*. **R. latipedunculata,* Hunsrück Sh.; *1a,b,* upper and lower faces, ×1.5 (Ubaghs, n).

Victoriacystis GILL & CASTER, 1960 [**V. wilkinsi*; OD]. Theca elongate, with subpentagonal outline; lower face flat or slightly concave; upper face strongly convex; lateral margins nearly vertical; upper anterior border overarching proximal region of aulacophore, lower anterior margin arcuately excavated by wide aulacophore insertion; four most anterior marginals occupying nearly half of lower thecal face; infracentrals 2, moderately large median plate and small one at its left posterior corner ("anomalocystid plate"); adorals 2, small, posteriorly separated by lozenge-shaped plate (?third adoral); supracentrals numerous and rather small, except relatively large one in median posterior position; anterior upper plates ornamented with transverse wavy lines. *U.Sil.*, Australia.——FIG. 358,*2*. **V. wilkinsi*, Victoria; *2a,b,* upper and lower faces, ×1.5 *(43).*

Family AUSTRALOCYSTIDAE Caster, 1954 [1956]

[*nom. transl.* UBAGHS, herein (*ex* Australocystinae CASTER, 1954 [1956])]

Theca achieving high degree of bilateral symmetry in general outlines, as well as in shape and arrangement of plates on both thecal faces; marginals 10, two on anterior face, three on each lateral face, and two on posterior face; infracentrals few, comprising one large subcentral plate and generally some additional smaller ones. *L.Dev.*

Australocystis CASTER, 1954 [1956] [**A. langei;* OD]. Theca subrectangular in outline arcuately excavated for reception of aulacophore on lower face (only one known); lateral and posterior inferior margins raised in prominent rounded flanges; marginals 10 (12 according to CASTER) and infracentrals 5 (3 according to CASTER) almost symmetrically arranged; no "anomalocystid plate"; transverse row of 4 small infracentrals immediately behind large central plate; posterior margin entirely occupied by only 2 massive transversely elongate marginals. *L.Dev.*, S.Am.(Paraná, Brazil). ——FIG. 357,*4*. **A. langei*; lower face, ×3.6 (27).

Placocystella RENNIE, 1936 [**P. capensis*; OD]. Theca apparently cordiform in outline; lower face made of ?12 plates (10 marginals, 2 infracentrals), more or less symmetrically arranged. *L.Dev.*, S.Afr. ——FIG. 357,*5*. **P. capensis,* Bokkeveld Ser.; lower face, ×2.5 (27, modified).

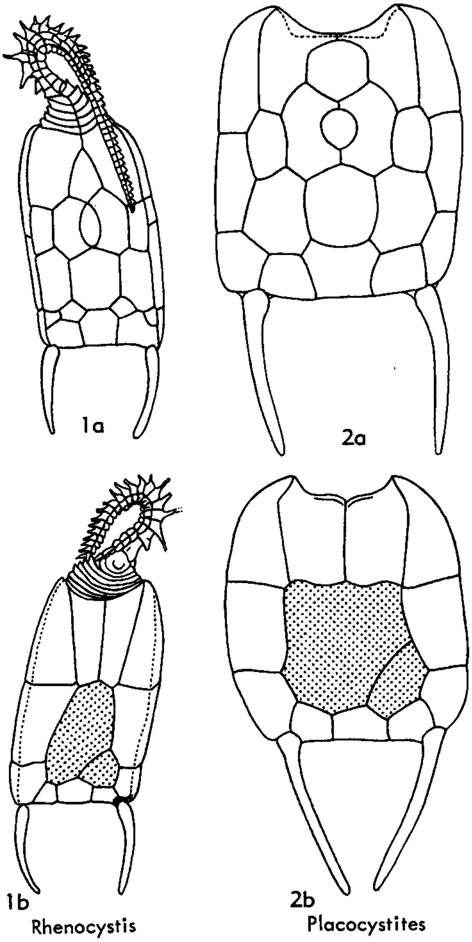


FIG. 359. Anomalocystitidae (p. S560-S561).

Family ALLANICYTIDIIDAE
Caster & Gill, new family

Mitrate, anomalocystid Stylophora of nearly perfect bilateral symmetry both in outline and thecal plate arrangement; with pair of articulated distal lateral spines, articulatory bases for which are seen on thecal corners; one large somatic plate in superior (carapace) face, and two subequal, paired somatics in inferior (plastron) face; aulacophore large, three-zoned, one styloid blade of quite exceptional width. *L.Dev.*

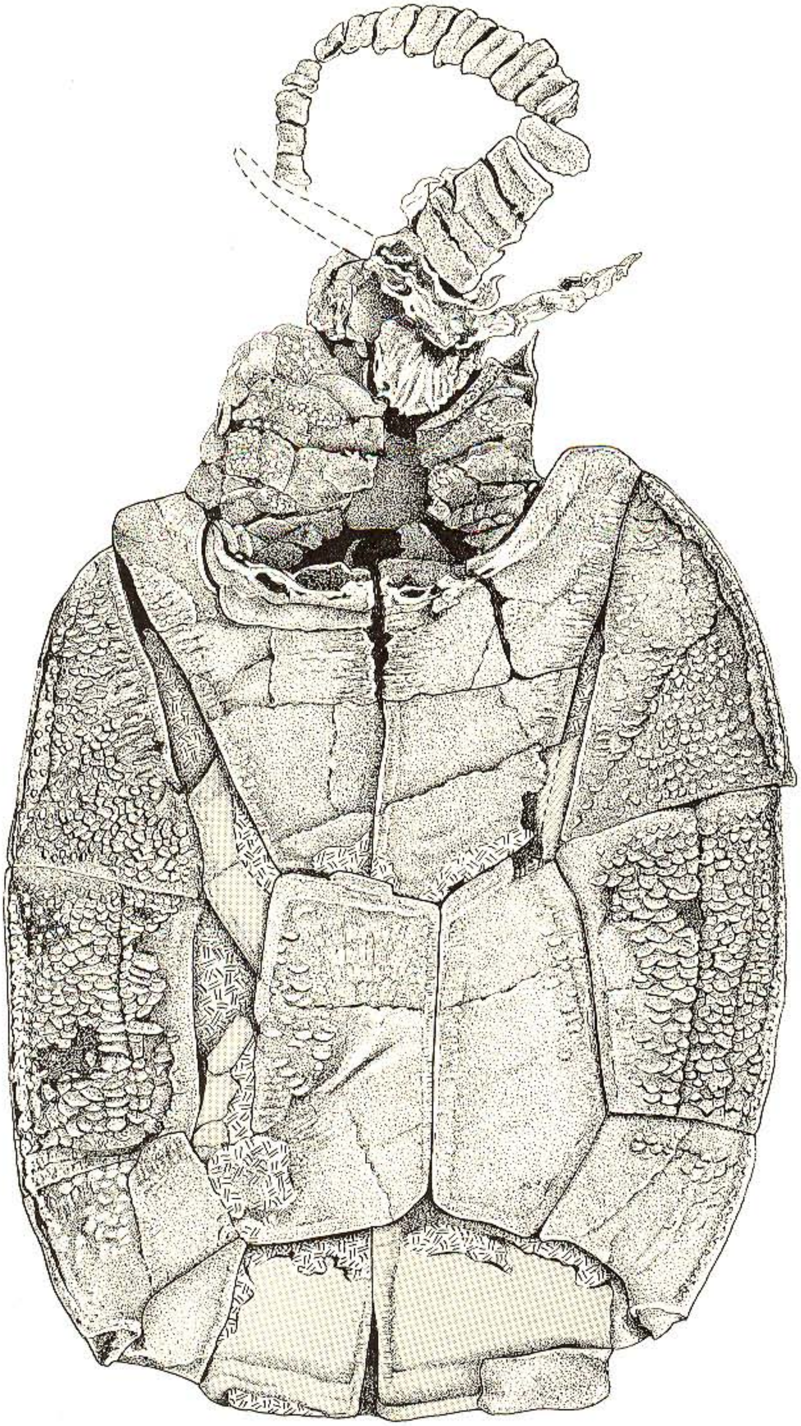


FIG. 360. *Allanicytidium flemingi* CASTER & GILL (Allanicytidiidae) (p. S564).

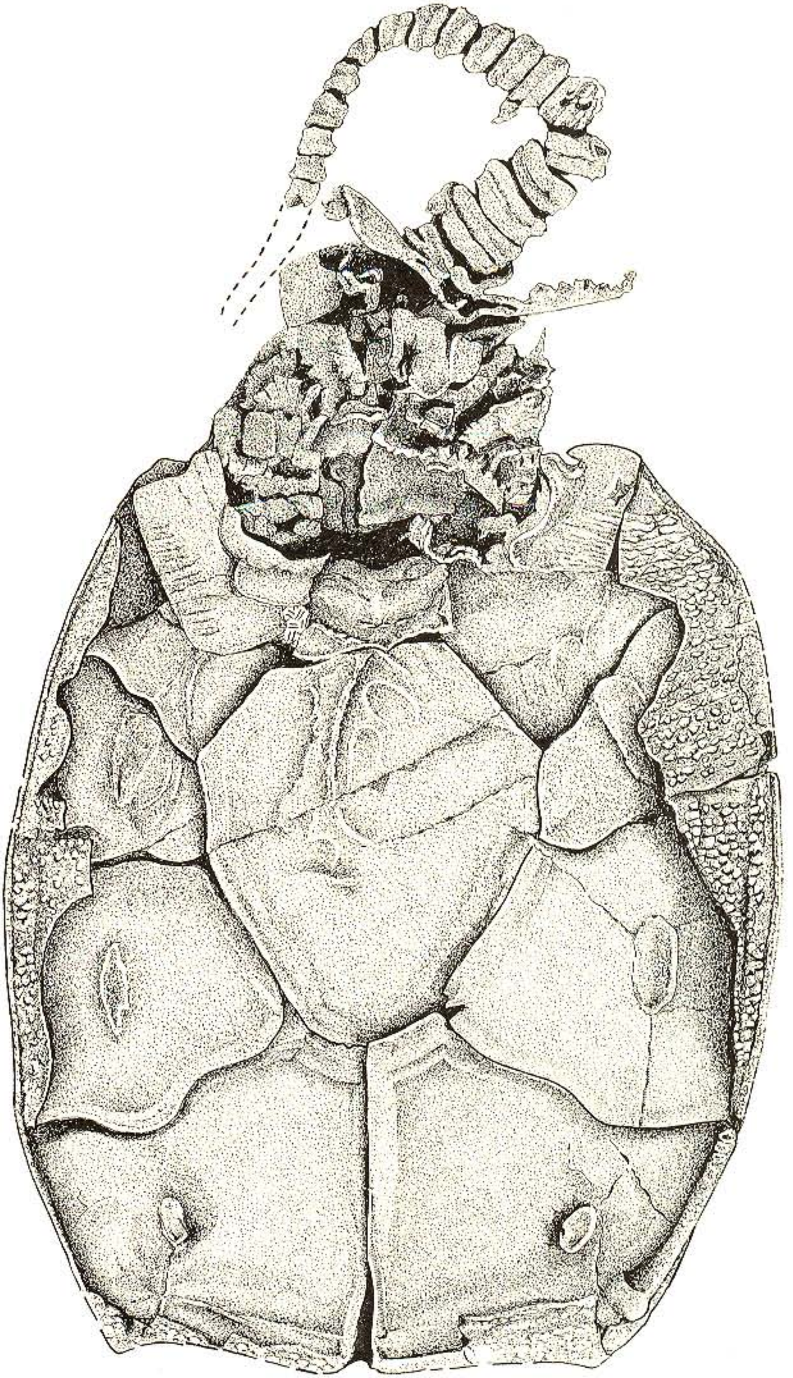


FIG. 361. *Allanicytidium flemingi* CASTER & GILL (Allanicytidiidae) (p. S564).

Allanicytidium Caster & Gill, **new genus,** herein (named for Robin S. Allan; *cytidium,* little box) [**A. flemingi* Caster & Gill, n.sp.; OD]. Large placocystoid, with boxlike theca, tripartite aulacophore and paired, basally articulating distal-lateral spines. Theca quadrately ovoid in plan; broadly convexi-concave in cross section; length to width as 13:11; broad-margined re-entrant of both thecal faces for aulacophore insertion. Surface of thecal plates prominently scaly in appearance, with pseudo-overlap away from aulacophore; imbrice scale aspect merging into typically mitrate transverse ridging on the adaulacophore plates (surface ornament seen so far only on inferior thecal face). Coarse granular ornament on proximal aulacophore tetrameres. Inferior (concave, plastron) thecal surface covered by probably 13 large nonimbricating plates, only 2 of which are somatic. Plates seemingly flexibly united in life (holoperipheral growth lines prominent on interior of plates), except possibly at margins of theca, where either there was fusion of plates of both thecal surfaces, or more likely marginal plates bend laterally so as to form lateral surface and extend onto both thecal surfaces. [For purposes of description here, the marginal plates seen on each surface are treated as though separate plates.] Lateral thecal margin bears narrow, downwardly directed keel; remainder of inferior surface forming broad vault. Holotype has 9 marginal plates but 2 more are reasonably inferred at distal margin; somatic pair are elongate, subequal in size and shape, meeting on axial plane. Right somatic (as seen with theca inverted and aulacophore directed away from viewer) is slightly smaller in area and pentagonal, rather than quadrate. Superior (convex, carapace) thecal surface covered by 9 large plates, only one of which has appearance of being somatic, but in reality is large adaulacophore basal axial plate. (Only the interior surface on the carapace plates is known.) The disposition of the plates and the circumperipheral lines of growth indicate that the plate sutures were flexible and integumentary. Most of the superior plates bear prominent, cuplike calcareous myophores. *L.Dev.,* N.Z.——Fig. 360, 361. **A. flemingi*; Reefton Beds, South Island, N.Z. (Rain Creek, Waitahn); views of holotype (N.Z. Geol. Survey no. 38/370203), 360, 361, inferior (plastron) and superior (carapace) surfaces, ×8 (Gill & Caster, n).

[These new taxa differ markedly from any other Stylophora in nature of the plate arrangement; they are mainly covered by the homologues of marginal plates in other forms; the somatic elements are as a correlate much reduced in number and highly modified. The right somatic of the plastron appears to be the homologue of the small asymmetric "anomalocystid" plate in other mitrates (e.g., *Placocystites, Enoploura*). The central "somatic" of the carapace is a distally migrated and enlarged central basal plate of other forms; in this genus it no longer makes contact with the aulacophore. Only the Australocystidae (*Australocystis,* L.Dev., Brazil; *Placocystella,* L.Dev., S. Afr.) approach the Allanicytidiidae in bilaterality; however, the plate arrangements of the two families are quite different. The new genus, being monotypic, is characterized by large size, pseudosquamose ornament, and extraordinary large styloid blade.]

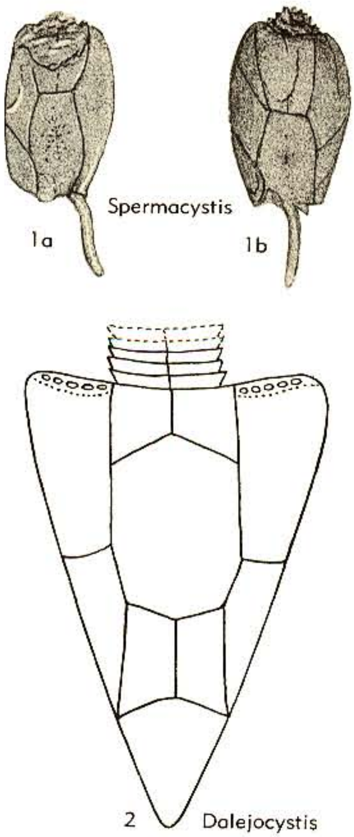


Fig. 362. Stylophora, Suborder and Family uncertain (p. S564-S565).

Suborder and Family UNCERTAIN

Dalejocystis Prokop, 1963 [**D. casteri*; OD]. Theca symmetrical, showing form of rounded isosceles triangle; upper face composed of fairly large symmetrically arranged plates and ending in rounded massive triangular plate; anterior margin bearing row of conical tubercles on both sides of aulacophore insertion; lower face unknown. *M.Dev.,* Boh.——Fig. 362,2. **D. casteri,* Daleje Sh. (Couvinian); upper face, schematic reconstruction, ×6 (71).

Spermacystis Ubaghs, herein [*nom. subst. pro Anomocystis* Jaekel, 1918, p. 122 (*non* Haeckel, 1896)] [**Anomalocystites ensifer* Barrande, 1887; OD]. Thecal outline nearly symmetrical; anterior border emarginated for aulacophore insertion, lateral margins longitudinally arcuate, posterior margin straight; one (possibly 2 according to Barrande) posterior exothecal rodlike process;

number and arrangement of plates, as well as aulacophore, unknown. [This nominal genus, based on scanty and poorly preserved material, was placed among Anomalocystidae by JAEKEL (1918) and CHAUVEL (1941). Possibly it belongs in the Lagynocystida.] *M.Ord.*, Boh.——FIG. 362, *1.* **S. ensifer* (BARRANDE); *1a,b,* different specimens, orientation unknown, ×1.5 (2).

[References for the chapter on Stylophora are included with those for Homostelea and Homoiostelea (*see* p. S624).]

HOMOSTELEA

By GEORGES UBAGHS[1]

[Université de Liège, Belgium]

CONTENTS

INTRODUCTION

The subclass Homostelea, here elevated to class rank, was proposed by GILL & CASTER (1960,*43*) to embrace the two orders Cincta JAEKEL *(55)*[2] and Digitata GEKKER (1938,*39*), which GILL & CASTER included in the class Carpoidea JAEKEL *(54)*. Subsequently, the Digitata were assigned to the class Eocrinoidea by UBAGHS (1950,*86*). Therefore, as here understood, the Homostelea contain only the single order Cincta.

Within the Cincta are placed *Trochocystites* BARRANDE (1887) and a few related genera, all of which belong to the Middle Cambrian of the Old World. That it is appropriate to classify *Trochocystites* in a family group of its own was first recognized by JAEKEL when he defined the Trochocystitidae. At the same time he united this assemblage with the Mitrocystidae *(54)* in a suborder named Marginata of the order Heterostelea (class Carpoidea). The Mitrocystitidae now are recognized as a family of the order Mitrata in the class Stylophora. BATHER *(13)* maintained the Trochocystitidae—incorrectly spelled Trochocystidae, as given by him (BATHER, 1902, in Zoological Record) earlier and generally

---

[1] I am much indebted to KENNETH E. CASTER and RAYMOND C. MOORE for translating my manuscript, and to the following persons for loan of specimens or permission to study collections: Prof. JACQUES AVIAS, Université de Montpellier, France; Dr. ALBERT BREIMER, Vrije Universteit, Amsterdam, Netherlands; Abbé ROBERT COURTESSOLE et M. GÉRARD GRIFFE, Carcassonne, France; Dr. HERMANN JAEGER, Humboldt-Universität, Berlin, Germany; Dr. R. P. S. JEFFERIES, British Museum (Natural History), London, Great Britain; Dr. FERDINAND PRANTL, Národni Museum, Prague, Czechoslovakia; Dr. GERTA WEHRLI-OLBERTZ, Ernst-Moritz-Arndt-Universität, Greifswald, Germany. Photographs, drawings and assemblage of figures have been prepared by Mrs. MARIE MASSON. To all these people I express deep thanks.

[2] Numbers enclosed by parentheses, other than years, indicate serially numbered publications in the list of referenecs at end of this chapter.

accepted by other authors—but rejected the Marginata, assigning the family instead to the suborder Heterostelea of the order Amphoridea (class Cystoidea).

In 1918 Jaekel *(55)* described two new genera of echinoderms more or less similar to *Trochocystites* and grouped all of them together in a new order named Cincta. The genus designated as *Trochocystoides* was placed in the Trochocystitidae and one named *Gyrocystis* in the new family Gyrocystidae.

Other authors generally have treated the genera mentioned as members of a single family of the class Carpoidea *(32,41)* or grouped them with most other "carpoids" as mere so-called cystoids referred to the family Anomalocystidae of Meek (1872) (Zittel, 1895, 1910, 1913; Bather, 1900; Delage & Hérouard, 1903) or its equivalent, correctly designated, Anomalocystitidae Bassler (1938) (Bassler & Moodey, 1943). The Anomalocystitidae now are classified as a family of the Mitrata in the class Stylophora.

The Homostelea have nothing in common with other "carpoids" except the depressed form of their asymmetrical body girdled by a marginal framework and their complete lack of radial symmetry. They differ from all of them in the localization of their two main thecal orifices near one pole of the body and in having one or two epithecal grooves on the marginal frame leading to one of the orifices. In addition, they differ from the Stylophora in possessing a pedunculate appendage or stele and in lacking a brachial appendage comparable to the stylophoran aulacophore. They are separated from the Homoiostelea by the nature of the stele, primarily composed throughout its length of a double series of similar plates, and likewise by the absence of an arm.

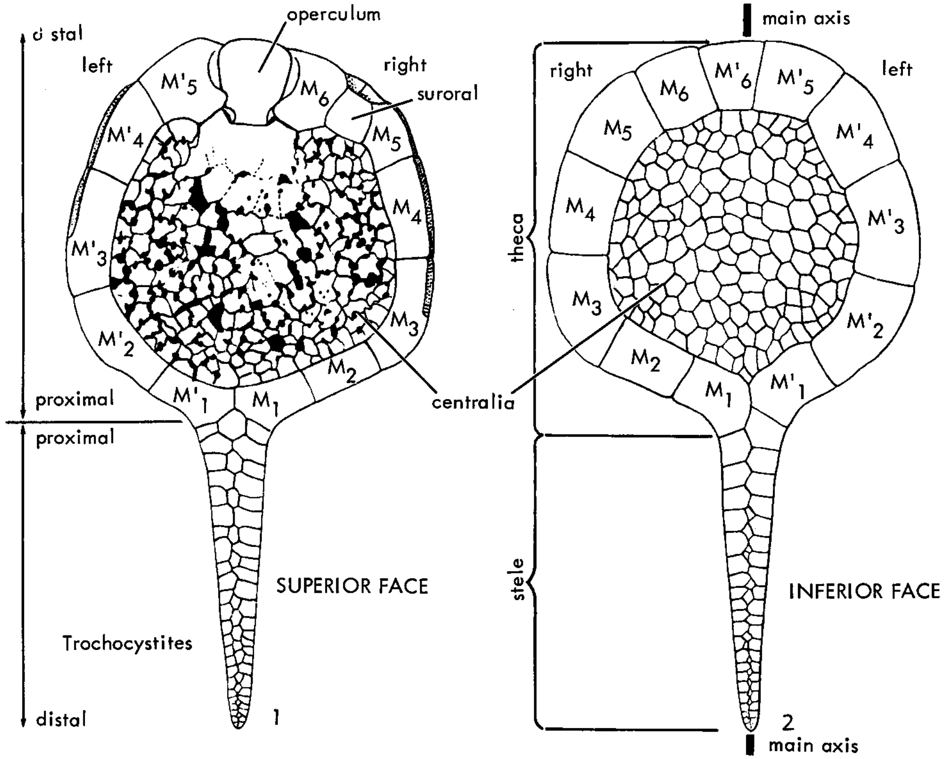
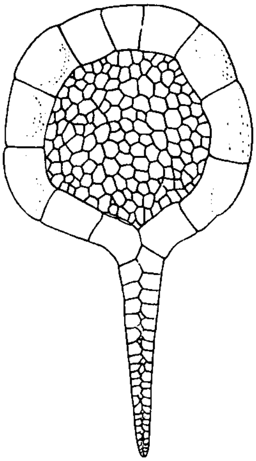


Fig. 363. Morphological features of Homostelea, based on **Trochocystites bohemicus* Barrande, M.Cam., Boh.; *1,2,* upper and lower faces, ×3 (Ubaghs, n).



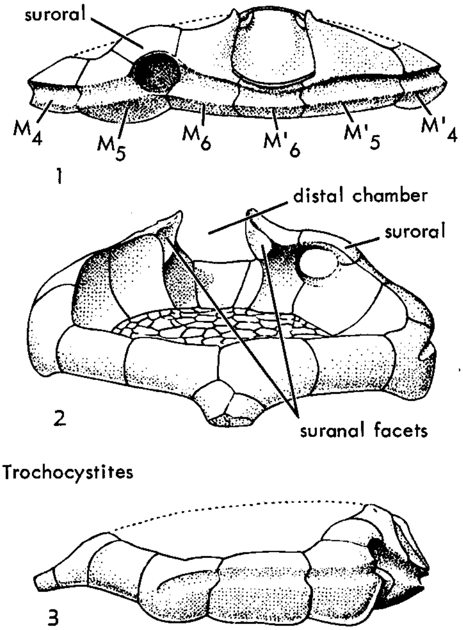


FIG. 364. Morphological features of Homostelea, based on **Trochocystites bohemicus* BARRANDE, M.Cam., Boh.; *1-3,* distal, proximal, and right lat. views, ×3 (Ubaghs, n).

MORPHOLOGY

GENERAL FEATURES

The skeletal parts of the Homostelea consist of a **theca** and a **stele,** the latter being essentially only a much-narrowed and tapering extension of the former. The theca is asymmetrical, although it may display some tendency toward bilateral symmetry (Fig. 363).

In outline the theca may be almost circular, oval, pyriform, or subtriangular. When pyriform, the stele emerges from the constricted part of the theca, and when subtriangular, from the apex of the triangle. Invariably, the theca grows thinner toward the stele.

The theca is flattened and shows two very dissimilar faces—a flat or concave one, on which the living animal presumably reposed, and an opposite convex one. The integuments covering a large median part of the two faces contain many small plates named **centralia** or **centrals.** Peripherally these meet the inner edges of thick plates that form the stout marginal framework of the theca and accordingly are named **marginalia** or **marginals.** On the convex upper face of the theca the marginal frame is pierced by two orifices which are located near to one another at the extremity opposite to the stele (Fig. 364,*1,2*). The smaller of the orifices is bounded laterally by a pair of marginals and above by a supplementary fixed plate named **suroral** (=eporal, JAEKEL, 1918[1]) resting on edges of the marginals (Fig. 364,*1,2*; 365,*3,4*). One or two epithecal grooves hollowed into the outer face of some of the marginals lead to this orifice. The neighboring relatively large orifice is bounded by three marginals, two laterally and one below, and is protected above by an apparently movable plate designated as **operculum** (Fig. 363,*1*; 364,*1*; 365,*3*).

The stele is flattened like the theca. It tapers distally away from the theca and shows the same organization throughout its length. It is composed of two series of opposed or alternating plates which meet along the mid-line of each face except

---

[1] Such terms as eporal, epanal, epicentral, and hypocentral, of combined Greek-Latin origin, here are replaced by terms with components derived from a single one of these languages.

where a varying number of tiny ossicles is intercalated between them. A narrow axial canal enclosed by the stele opens between two of the marginals into the thecal cavity.

ORIENTATION AND NOMENCLATURE

The plane in which the theca is flattened is termed the **extension plane** (Bather, 1913) or extensiplane (Gill & Caster, 1960). The two faces of the theca are differentiated with respect to this plane and the probable attitude of the living animal as **superior or upper face** (=obverse face, Bather, 1913) and **inferior or lower face** (=reverse face, Bather, 1913). The **main axis** of the theca and stele runs longitudinally midway between their lateral margins and marks the position of the **symmetry plane** (Bather, 1913) oriented at right angles to the extension plane. The body tends toward bilateral symmetry as defined by this plane.

Length is measured along the main axis and **width** normal to this axis in the extension plane. **Height or thickness** is defined as the distance between the two thecal faces normal to the extension plane.

For purposes of description, the junction of theca and stele is defined as marking the most **proximal or adsteleal** pole of the theca and the opposite extremity along the main axis of the **distal or absteleal** pole of the theca (Fig. 363). Similarly, the proximal part of the stele lies closest to the theca and the distal part nearest to its tip.

Right side and **left side** are purely conventional designations of halves of the

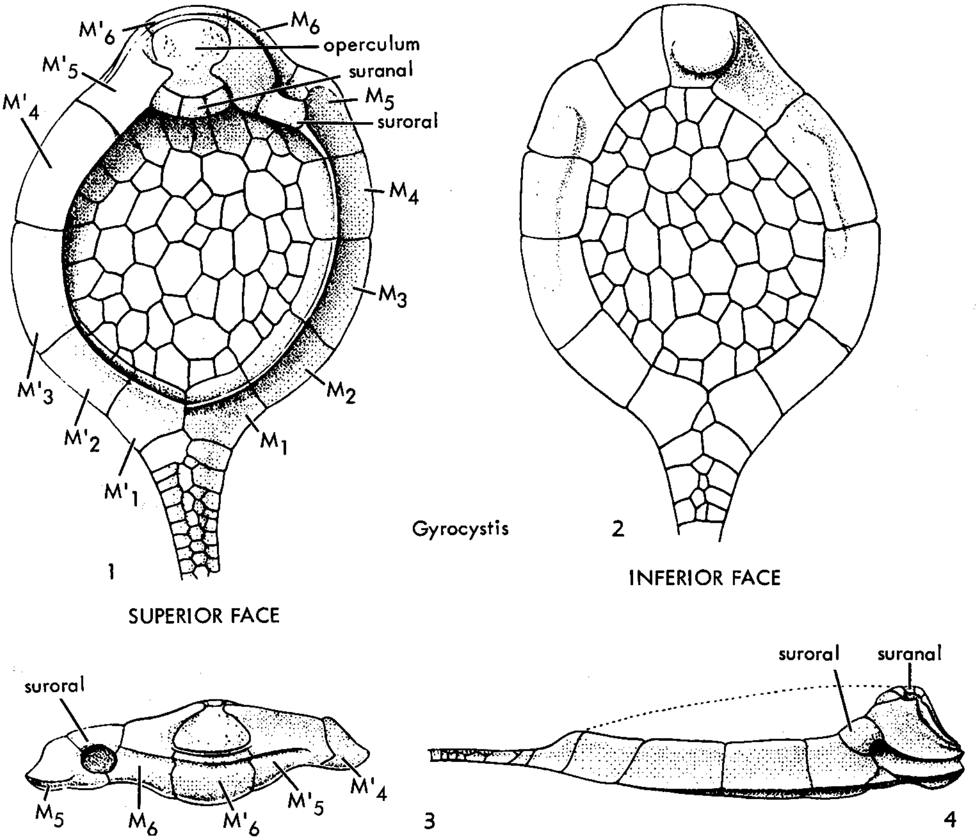


Fig. 365. Morphological features of Homostelea, based on **Gyrocystis barrandei* (Munier-Chalmas & Bergeron), M.Cam., Fr.; *1*, upper face, supracentrals lacking, ×3; *2-4*, lower, distal, and right lat. views, ×3 (Ubaghs, n).

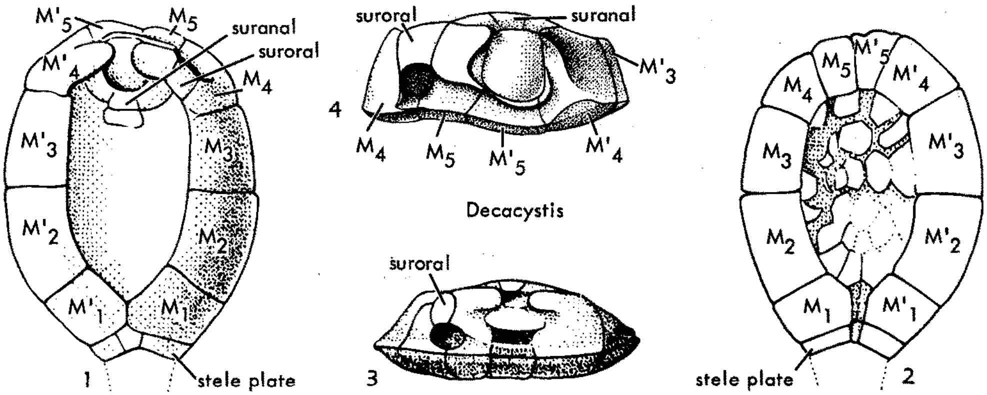


FIG. 366. Morphological features of Homostelea, based on *Decacystis*.——*1-3*. *_D. hispanica_ GISLÉN, M. Cam., Spain; upper, lower, and distal views, ×3 (10).——*4*. *D.* sp. cf. *_D. hispanica_ GISLÉN, M.Cam., Spain; distal view, ×5 (Ubaghs, n).

theca and stele on opposite sides of the symmetry plane when the fossil is oriented with the inferior thecal face directed downward and the stele toward the observer (downward in figures). According to convention, the marginal plates are designated by the symbols M_1, M_2, M_3 . . . on the right side of the theca beginning at the stele and by the symbols M'_1, M'_2, M'_3 . . . on the left side similarly (Fig. 363). It should be observed that identity in form of these symbols does not indicate homologies of the marginals in Homostelea and Stylophora.

MARGINALIA

The framework formed by the marginal plates comprises the strong peripheral part of the theca. The mode of designating individual marginal plates has just been explained. All are thick and they are joined firmly to one another. Both their positions and numbers (10 to 12 in different genera) are constant. The upper face of each plate may be distinctly convex (e.g., *Trochocystites*, Fig. 364,*2,3*), slightly convex to slightly concave (e.g., *Trochocystoides*), flat (e.g., *Decacystis*, Fig. 366,*3,4*), or almost flat to strongly concave (e.g., *Gyrocystis*, Fig. 365,*1*), whereas the lower face of each plate invariably is flat or convex and the inner (interior) face concave (Fig. 364,*2*). The external intersection of the upper and lower faces may be sharp-angled or regularly rounded and consequently its cross section varies from triangular (e.g., *Decacystis, Gyrocystis*) or inverted T-shaped (e.g., *Gyrocystis*) to more or less U-shaped (e.g., *Trochocystites*).

Prominent localized swellings or tumescences generally characterize the lower face of the marginals, but never in the proximal part of the theca. The swellings have lateral positions in *Trochocystites* and extend over several plates on both sides (Fig. 364,*2,3*). Opposite to the stele in *Gyrocystis* a large boss is seen beneath the main thecal orifice, generally flanked on both sides by less prominent elongate swellings (Fig. 365,*2*). The variations in shape and size of the prominences may reflect the microenvironments of individuals, though the precise nature of their function is unknown. Probably they helped to anchor the animals.

CENTRALIA

The superior and inferior plated integuments of the median part of the theca are affixed to the upper and lower inner edges of the marginal framework. Along the lines of attachment many small depressions observed in some specimens probably mark the sites of supple ligamentary bundles (see Fig. 370,*3*). Collectively, the plates of the central regions of the theca are designated as **centralia or centrals.**

The centrals of the superior thecal face are distinguished as **supracentralia or supracentrals** [=epicentralia, JAEKEL, 1918]. For the most part these small plates are discrete and in the living animal were probably united flexibly, thus accounting for their rare preservation. They are almost unknown in *Gyrocystis* and *Decacystis* except for isolated platelets, but in *Trochocystites bohemicus* they consist of small irregular and maladjusted ossicles with uneven integumentary spaces between them (Fig. 367,*1*). The spaces may have the aspect of generally distributed sutural pores with elliptical outlines. In places they are bordered internally by calcareous crests, and collectively they may form a transverse crescent (Fig. 367,*2-4*). As in eocrinoids and some other primitive echinoderms, these sutural

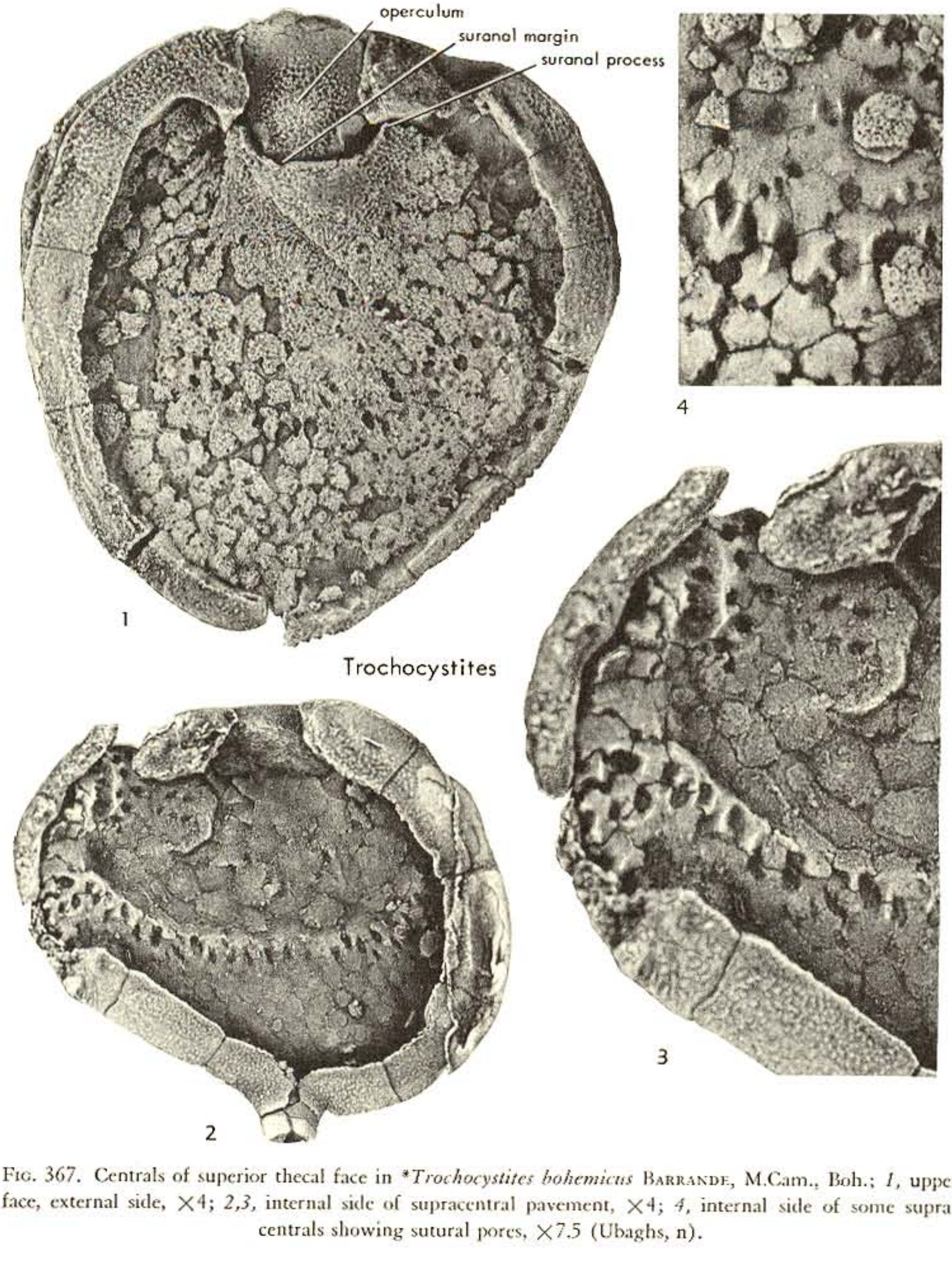


FIG. 367. Centrals of superior thecal face in **Trochocystites bohemicus* BARRANDE, M.Cam., Boh.; *1*, upper face, external side, ×4; *2,3*, internal side of supracentral pavement, ×4; *4*, internal side of some supracentrals showing sutural pores, ×7.5 (Ubaghs, n).

"pores" probably were not actual openings in the theca but merely small uncalcified parts of the integument or spaces occupied by papulae-like organs that served for gaseous exchange between coelomic fluids and sea water.

The integument of the lower thecal surface inside of the marginal frame was occupied completely by more or less numerous polygonal plates which formed a tessellated pavement (Fig. 363,*2*; 365,*2*). These plates are called **infracentralia or infracentrals** [=hypocentralia, JAEKEL, 1918].

A few special features of the superior face of the theca call for notice. In *Trochocystites* from near the middle, plates of the centralia become more tightly united in a distal direction toward the large thecal orifice so as to form a thick firm border around it, which is distinguished as the **suranal margin** (Fig. 367,*1*). Laterally and distally this margin is produced into two **suranal processes,** each of which rests against the **suranal facet** of a large apophysis borne by one of the pair of marginals that frame the orifice laterally (Fig. 364,*2*; 367,*1*). No

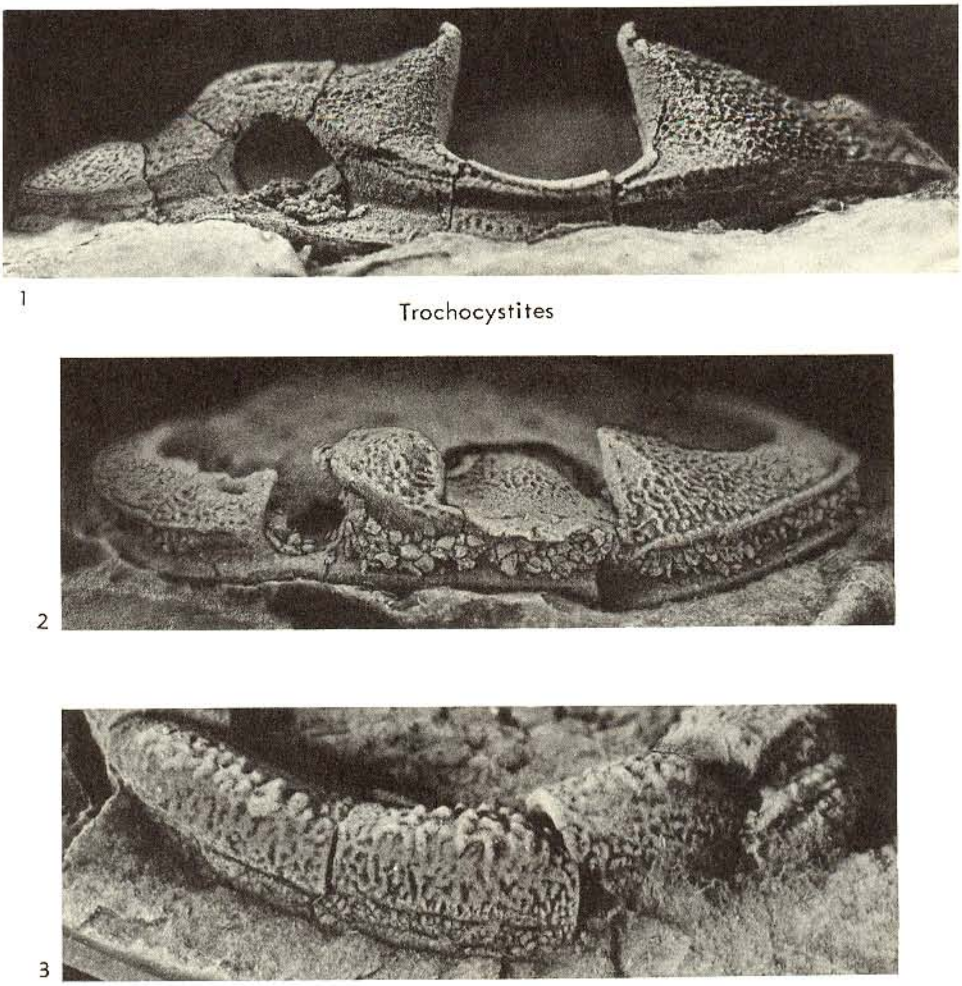


FIG. 368. Marginal grooves of **Trochocystites bohemicus* BARRANDE, M.Cam., Boh.; *1,* distal view showing empty grooves with tiny serial depressions which presumably served for attachment of cover plates along their margins, ×7.5; *2,* distal view of specimen showing grooves partially filled with cover plates, ×7.5; *3,* right lat. view showing grooves protected by cover plates, ×7.5 (Ubaghs, n).

continuous suranal margin is seen in *Decacystis* and *Gyrocystis,* but instead the larger orifice is bordered proximally by three or four thick **suranal plates** (=epanals, Jaekel, 1918) (Fig. 365,*1*; 366,*1*).

ORIFICES AND MARGINAL GROOVES

The marginal framework on the upper face of the theca is pierced by two openings—not three, as reported erroneously by Barrande (1887), Haeckel (1897), and Bather (1900). The orifices are unequal in size and shape and they differ constantly in location. The larger one is found near the absteleal pole of the theca and the smaller at a short distance from it to the right.

The small orifice is located between two marginal plates and is circular. Above it is an arched plate known as the **suroral** which laterally rests on edges of the marginals (Fig. 364,*1*; 365,*4*; 366,*3,4*). A groove leading to right from the orifice and another

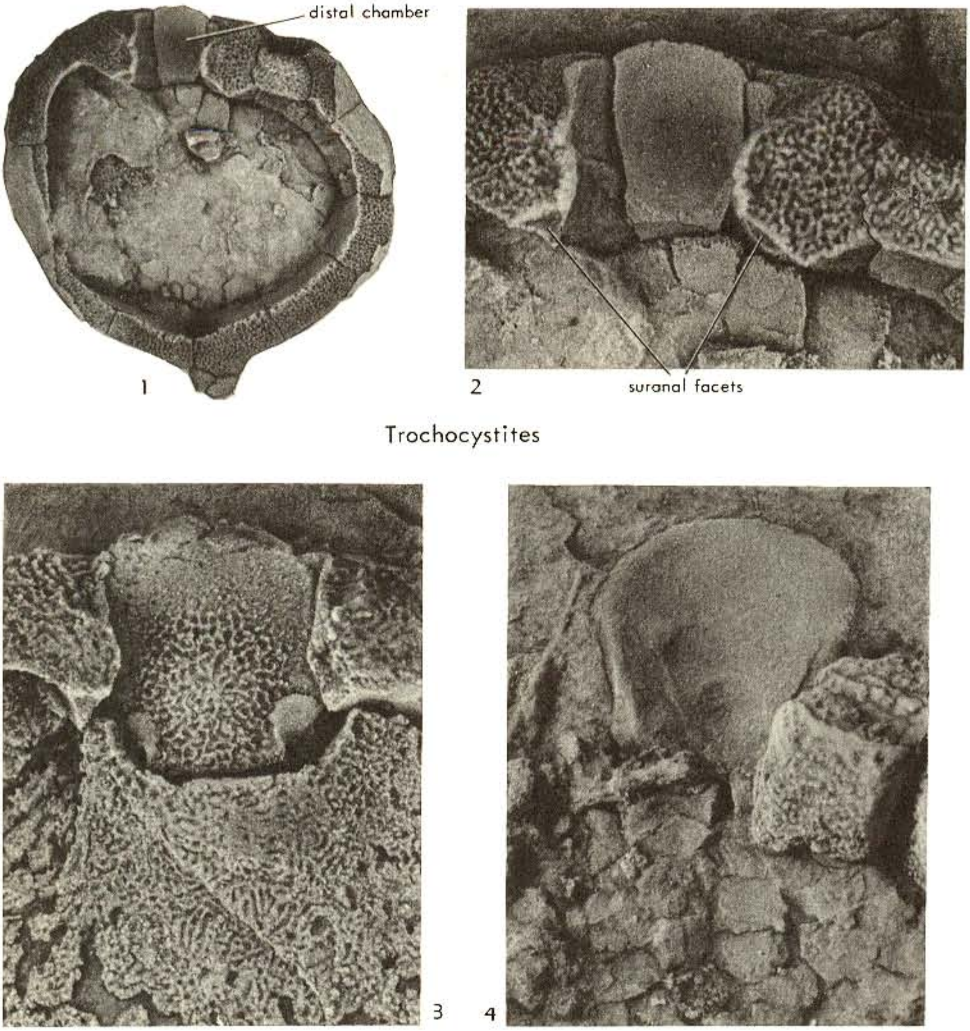


Fig. 369. Distal chamber and operculum of **Trochocystites bohemicus* Barrande, M.Cam., Boh.; *1,* upper face of theca with centrals not preserved, distal chamber open (without operculum), ×3; *2,* distal chamber, ×7.5; *3,4,* external and internal sides of operculum, ×7.5 (Ubaghs, n).

to the left are excavated in the outer face of adjacent marginals along the periphery of the theca just above the boundary between its superior and inferior faces. The grooves are long in *Trochocystites* and *Trochocystoides,* shorter in *Gyrocystis,* and still shorter in *Decacystis.* The right groove traverses marginals M_5 and M_4 in *Trochocystites* to a termination on M_3 (Fig. 363,*1*; 364,*1-3*), whereas in *Trochocystoides* it is confined to M_4 and M_3. The right-hand groove remains undeveloped in *Decacystis* or can barely be detected in a few specimens (Fig. 366,*4*). The left groove passes under the salient lower lip of the large orifice and is terminated on M'_3 in *Trochocystites* (Fig. 363,*1*; 364,*1*), and *Trochocystoides.* In *Gyrocystis* the left groove ends on M'_5 (Fig. 365,*1,3*) and in *Decacystis* on M'_4 (Fig. 366,*4*).

The marginal grooves of Homostelea range from shallow to deep. Those of *Trochocystites* and *Trochocystoides* are deep and in some specimens of the former marked by distinct borders (Fig. 368,*2*). The floor of the grooves is angular and smooth but each side bears a series of tiny depressions which seem to be attachment seats for cover plates (Fig. 368,*1*). The ends of the grooves away from the orifice are rounded and generally quite distinct.

The floor of the grooves in *Gyrocystis* rises rather abruptly near their distal extremity and their termination is not always clear. The right groove, in particular, leaves hardly any trace—at best only a very faint indication on the superior faces of M_5 and M_4 (Fig. 365,*1*). The corresponding groove of *Decacystis* is generally not differentiated at all, whereas the left one, deeply impressed proximally, vanishes on M_4 (Fig. 366,*4*). The grooves and the opening to which they lead are observed in many specimens to be filled with very tiny irregular ossicles, which may be so associated as to suggest that they are remnants of a pavement (Fig. 368,*2,3*). Morphologically and functionally the ossicles seem to be equivalent to the cover plates of the food grooves of many pelmatozoans.

The relatively large orifice of the theca opens into a sort of chamber—here called **distal chamber**—which is hollowed entirely into the thick framework of marginals at the absteleal pole of the theca. The chamber is truncate cone-shaped, expanding toward the interior of the theca, with which it is confluent (Fig. 364,*2*; 369,*1,2*). Its lower distal margin extends laterally outward as a lip which projects over the left marginal groove (Fig. 368,*1*). The walls of the chamber are smooth. Its concave floor, sloping toward the thecal interior, is formed by the upper surface of M'_6 in *Trochocystites* and *Gyrocystis* or of M'_5 in *Decacystis.* The side walls are cut into the two adjacent marginals and its ceiling is formed by a special plate termed the **operculum** (=*Analklappe,* JAEKEL, 1918; anal valve, GISLÉN, 1927; *clapet buccal,* CUÉNOT, 1953). The marginals which flank the orifice and partially overhang the operculum bear strong apophyses which extend more or less convergently inward and upward at the sides of the orifice (Fig. 364,*2*;368,*1*). A little below the summit of each apophysis is an articulatory fossette named the **suranal facet,** which receives a suranal process (e.g., *Trochocystites,* Fig. 364,*2*) or plate (e.g., *Decacystis, Gyrocystis,* Fig. 365,*1*; 366,*1*).

The operculum is a convex oval plate, wrinkled externally and smoothly concave internally (Fig. 369,*3,4*). It expands slightly in a distal direction with its lateral and distal edges adjusted to the walls of the chamber covered by it, but neither fused to these walls nor articulated with them. The proximal edge of the operculum is joined to the suranals (e.g., *Gyrocystis, Decacystis*) or suranal margin (e.g., *Trochocystites*) probably by a loose suture or ligamentary articulation and both extremities of this edge are more or less deeply notched. The notches are bordered in some specimens of *Trochocystites* by a smooth upbent lip which probably provided the attachment for muscles that served to open the operculum (Fig. 369,*3*). In closed position, the operculum sloped steeply downward distally, and when opened, probably an elliptical orifice was left between it and the lower margin of the distal chamber.

The structures just described have been subjects of diverse and often conflicting interpretations.

In view of SPENCER *(80),* CUÉNOT *(32),* NICHOLS *(68),* and GEKKER *(41),* the chamber of the large orifice (distal chamber) represents a stomodeal pouch or vestibule that was protected by the operculum and provided with protrusible tentacles for the capture of nutrients. It functioned then as a mouth and the small orifice was inferred to be the anus. Cuénot and Gekker supposed that the marginal grooves on either side of the "anus" served for transport of excreta away from the oral field, whereas Spencer and Nichols offered no guess concerning their function. If the grooves really carried excreta, in the case of *Decacystis* they would bring this waste into contact with the mouth.

Jaekel *(54,55)*, Bather *(13)*, and Gislén *(45)* adopted an opposite interpretation, concluding that the large orifice corresponds morphologically to the anus and the small one to the mouth. These suppositions are based mainly on the presence of the marginal grooves connected to the small orifice and the resemblance of these grooves to the food grooves of pelmatozoans—certainly a fact. Since the grooves are much shorter in *Gyrocystis* and especially *Decacystis* than in *Trochocystites*, Jaekel (1918) and Gislén (1930, 1934) judged that by evolution they tended to disappear, their reduction being correlated with change from buccal to anal feeding. They imagined that anal respiration analogous to that in crinoids and holothuroids existed in the Homostelea. If so, introduction of water into the digestive tube through the anus would have brought in small food particles and would have led eventually to reversal of the alimentary current, rendering the presence of nutritive grooves superfluous.

The interpretation just stated is opposed by the following observations: 1) though anal respiration does occur in crinoids and holothuroids, anal nutrition is entirely unknown in any echinoderm; 2) it is by no means established that the approximately contemporaneous genera *Trochocystites, Gyrocystis,* and *Decacystis* are progressive stages of a single lineage and consequently an inferred trend toward disappearance of their marginal prooves is quite unproved, for the contrary is possible or the three genera may belong to different lineages; 3) the alleged reduction of the grooves affects neither the dimensions of the small orifice nor the width of the left groove near it, and even in *Decacystis* the well-developed nature of the orifice and associated groove indicates that they must have been functional.

Differences between characters of the grooves in various genera and even in individuals belonging to the same genus (mainly *Gyrocystis* and *Decacystis*) suggest another explanation. In *Trochocystites,* which has long, deep, sharply terminated grooves, the food-capturing organs housed by them must have been totally affixed to the theca (epithecal) or nearly so. In *Gyrocystis* and above all in *Decacystis,* which have shorter and shallower grooves, difficult to perceive in some individuals and generally without clear terminations, the food-gathering organs must have projected more or less freely into the water (exothecal) away from their proximal attachments. This does not signify that the Homostelea possessed a pair of brachioles inserted on either side of the oral aperture, as imagined by Haeckel *(49)* and Meléndez *(62)*. Instead, the organization suggests the presence of a sort of two-branched lophophore which was epithecal in some genera and partly exothecal in others.

What then are the morphological implications of the large orifice, distal chamber, and operculum, and how did they probably function? The infundibular shape of the distal chamber and its protruding lower lip suggest the existence of a protrusive organ, which perhaps was a kind of tube designed for jet expulsion of excreta, or possibly a cloaca *(45)* into which not only the digestive tube but organs such as gonads could have emptied. The operculum doubtless would have protected these organs. Bather (1925) considered this cover to be "a movable shield to guide the excreta [away] from the inflowing food-stream." Certainly, the fact that the operculum is attached by its proximal border, with apophyses of the adjacent marginals overhanging it, proves that this plate could not turn its distal edge so as to extend in front of the theca to support food-catching organs of some sort, as supposed by Jaekel *(55)*, Cuénot *(32)*, Nichols *(68)*, and Müller (1963).

STELE

The stele tapers throughout its length and shows the same organization from one end to the other (Fig. 363, 370). Consequently, it is impossible to differentiate dissimilar parts, as in the Homoiostelea. The stele is depressed and like the theca shows a flattened inferior surface, which is slightly and regularly rounded, and a gabled superior surface with a median ridge above planate or slightly concave flanks. The two surfaces meet laterally in keels (Fig. 370,*1,2*).

Passage from the stele to the marginal framework of the theca is entirely gradational, for outlines of the stele comprise prolongation of the thecal contours. Also, the upper surface of the stele rises evenly to the superior face of the proximal marginals M_1 and M'_1 meeting it confluently. Its lower surface is at the level of the inferior face of these marginals and continuous with it. Above all, the form, size, and ornament of the first stele ossicles (most proximal ones) are transitional to plates of the thecal frame (Fig. 370,*1,2*). The passage is so gradual in *Decacystis* that GISLÉN *(44)* classed as marginals two plates that by analogy with other genera belong to the stele (Fig. 366,*1,2*).

The stele is composed basically of two series of opposed or alternating ossicles (called sphenoids by JAEKEL, 1918), with both conditions commonly present in the same stele. Along the mid-line of both faces a variable number of small supplementary plates (called intersphenoids by JAEKEL, 1918) generally are intercalated. They are polygonal or lozenge-shaped platelets inserted like wedges between the main plates and those on opposite surfaces of the stele do not correspond to each other.

An axial canal of very small diameter extends throughout the stele but becomes enlarged toward its proximal end where it opens into the thecal cavity through a short

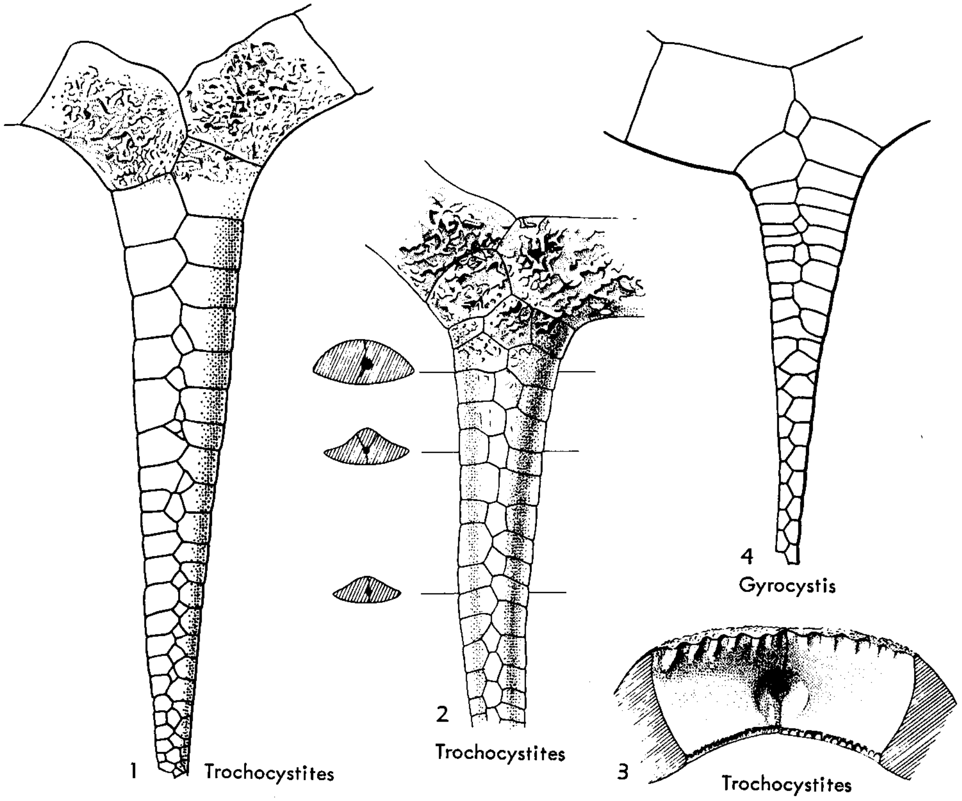


FIG. 370. Stele of Homostelea.——*1-3.* **Trochocystites bohemicus* BARRANDE, M.Cam., Boh.; *1,* lower face; *2,* upper face and transverse sections; *3,* thecal opening of axial canal of stele, all ×3.75 (Ubaghs, n).——*4.* **Gyrocystis barrandei* (MUNIER-CHALMAS & BERGERON), M.Cam., Fr.; lower face, × 3.75 (Ubaghs, n).

funnel excavated in the junction faces of marginals M_1 and M'_1. The floor of the funnel is at the level of the internal faces of the infracentrals, but its ceiling is well below the internal faces of the supracentrals (Fig. 370,*3*).

The stele of the Homostelea thus can be considered as a tubular extension of the theca having the morphologic nature of a peduncle. Nothing indicates that it is homologous to the stem of a Crinozoa, however, and in fact it may have been developed from quite a different body region. Further, nothing indicates that the stele served the same function as the crinozoan stem. Its depressed form, lack of flexible union with the theca, as well as union of its component ossicles, its rigid aspect, the lack of evidence that it served as means of fixation, seems to indicate that the stele never fulfilled the role of support, although it may have helped to stabilize the animal. Many fossils show the stele pointed obliquely downward from the plane of the lower thecal surface, suggesting that it was thrust into sea-bottom sediment during life.

THEORETICAL CONSIDERATIONS

According to WALTHER (1886) and HAECKEL (1896), the symmetry plane of the Homostelea should correspond to the plane of bilateral symmetry of the dipleurula and the theca interpreted as depressed dorsoventrally. This homology was challenged by NEUMAYR (1889) and rejected by BATHER *(11, 13, 21)*, of whom the latter judged that the extension plane of the homostelean theca should be considered as equivalent to the sagittal plane of the dipleurula, and its two surfaces then would be right and left. It may be noted that in 1900 BATHER identified the concave (inferior) thecal face as right and the opposite convex (superior) face as left, but in 1913 transposed these identifications. Subsequently (BATHER, *20, 21*) became convinced that the "carpoids" comprise a group of their own, distinct from all other echinoderms, and postulated that they were derived from a dipleurula fixed by its ventral surface and not by its preoral lobe. Thus attached, the ancestral organism would have reversed positions of its head and tail, acquiring a Y-shaped form with the tail pointed downward and the body upward with mouth and anus located at extremities of the divergent upper branches of the Y. No torsion of internal organs is postulated by this hypothesis. The Homostelea would have been derived from this archetype by shortening of the stem and branches and close approach of the two apertures to one another.

CHAUVEL *(30)* adopted another initial premise and consequences deduced from it, namely, a dipleurula attached by its preoral lobe rather than its ventral surface, thus having at the outset the imagined ancestral pelmatozoan condition with mouth at the body pole opposite to its point of fixation, with anus in lateral position, and with internal organs, particularly the digestive tube, subjected to a characteristic torsion. Then appearance of the two lobes bearing the mouth and anus would have led, as in the preceding hypothesis, to a Y-shaped ancestor which by convergence of the two apertures and development of ambulacral grooves could have yielded *Trochocystites* and genera allied to it. In sum, the Homostelea and other "carpoids" would have the same origin as the pelmatozoan echinoderms but because of their very early separation from the primitive stock would retain in common with others only the stem (stele), constructed on a very special plan, however.

Based on the postulate that the digestive tube of most primitive echinoderms had an arcuate shape with concavity on the ventral side, GISLÉN *(45)* concluded that the space between the mouth and anus represents an extremely shortened ventral surface. The approach of mouth and anus toward one another and their displacement to the superior face of the theca must constitute secondary phenomena, however, corresponding to the stage of asymmetry distinguished by HEIDER (1912) in the ontogenetic development of echinoderms generally. If the Homostelea belong to an equivalent phylogenetic stage, their left somatocoel should be found beneath the superior thecal face and the right one next to the inferior face. Also, the right axocoel should have been already much reduced and the left one well developed, located possibly beneath the anal operculum. The left hydrocoel should have extended beneath the ambulacral groove, thus being confined to the right anterior border of the body, whereas the right hydrocoel probably was much reduced.

Even if the concept of Gislén seems to accord with indications drawn from the study of early ontogenetic stages of living echinoderms, like other hypotheses it remains purely speculative. The interior of the homostelean theca has preserved such little trace of the organs and cavities enclosed by it that effort to reconstruct their true organization seems futile. No basis allows assertion that their stele is homologous to the pelmatozoan stem or that their digestive tube displayed the helicoidal torsion characteristically present in crinoids.

GLOSSARY OF MORPHOLOGICAL TERMS USED FOR HOMOSTELEA

[Terms considered as synonyms or terms of lesser importance are printed in italics].

absteleal. Directed away from stele.

adsteleal. Directed toward stele.

Analklappe. See operculum.

anal valve. See operculum.

axial canal. Longitudinal passageway through stele.

central(s) (pl., **centralia**). Plate(s) located inside marginal framework either on lower or upper face of theca *(see* infracentral and supracentral). theca *(see* infracentral and supracentral).

clapet buccal. See operculum.

dimere. Any ossicle of two main series which compose stele.

distal. Referring to direction away from junction of theca and stele.

distal chamber. Enclosed space hollowed into marginal framework between large orifice and thecal cavity.

epanal. See suranal plate.

epicentral(s) (epicentralia). See supracentral(s) (pl., supracentralia).

eporal. See suroral.

extension plane. Plane in which theca is depressed (syn., extensiplane).

extensiplane. See extension plane.

frame (framework). Series of plates which constitute margin of theca, i.e., marginals and suroral.

hypocentral(s) (hypocentralia). See infracentral(s) (pl., infracentralia).

inferior. Directed toward inferior face.

inferior face. Flattened or concave side of theca or stele, presumably toward sea bottom in life position *(syn.,* lower face, reverse face).

infracentral(s) (pl., **infracentralia**). Plate(s) located inside framework on inferior face of theca.

intersphenoid. Any supplementary small plate along mid-line of stele.

left side. Referring to side corresponding with left of observer, when theca is placed on its inferior face with aulacophore toward observer; opposite of right side.

lower. See inferior.

main axis. Imaginary longitudinal straight line through stele and prolonged across theca.

marginal(s) (pl., **marginalia**). Ossicle(s) of series framing theca.

marginal groove. Furrow running on outer side of marginals and leading to small orifice (mouth) (considered as ambulacral furrow).

obverse. See superior.

operculum. Seemingly movable plate covering distal chamber.

proximal. Referring to direction toward junction of theca and stele.

reverse. See inferior.

right side. Referring to side corresponding with right of observer, when theca is placed on its inferior face with aulacophore toward observer; opposite of left side.

sphenoid. See dimere.

stele. Relatively slender and tapering peduncular prolongation of body.

superior. Directed toward superior face.

superior face. Convex side of theca or stele presumably directed upward in life position; opposite of inferior face *(syn.,* upper face, obverse face).

supracentral(s) (pl., **supracentralia**). Plate(s) located inside marginal framework on superior face of theca.

suranal facet. Small slightly concave surface on framework serving for articulation of suranal process or suranal plate.

suranal margin. Thick firm proximal upper border of distal chamber; apparently composed of fused supracentrals.

suranal plate. Ossicle of series forming proximal upper margin of distal chamber.

suranal process. Lateral outgrowth uniting suranal margin with marginal framework.

suroral. Fixed thecal place above small orifice (mouth); included in marginal framework.

symmetry plane. Plane passing through main axis and perpendicular to extension plane.

theca. Body skeleton exclusive of stele.

upper. See superior.

MODE OF LIFE

That the Homostelea reposed on one of their thecal faces is proved beyond doubt by the depressed form of their body, by differentiation of the two surfaces of their theca and stele, and by the distal termination of the stele in a point, indicating that it was manifestly incapable of serving for vertical support. The surface of the theca that rested on the substrate can only be the one designated as inferior, as denoted by its flat or concave form, conformation of the marginal frame, and absence on this side of the body of orifices and associated structures having presumed respiratory function, which are concentrated on the opposite face.

Nonetheless, BATHER *(13)* considered it difficult to imagine such organisms as resting directly on a sea bottom occupied by the kind of sediments—muddy sands or marly limes—which is represented by the rocks commonly associated with the remains of these "carpoids," for in his view the sand grains and clay particles would have fouled the food grooves and filled the mouth much too easily. Accordingly, he supposed that the animals attached themselves like a cupping glass to the thallus of algae, no traces of which are preserved, of course. The protuberances and other inequalities of the underside of the marginal frame make a sucking action of the inferior thecal face quite impossible, however. It appears, then, that the Homostelea could not have lived in the manner imagined by BATHER.

We may recall that the nutritive grooves of the homostelean theca are protected by a cover of platelets. Possibly, as suggested by NICHOLS *(68)*, these animals led a semisessile existence on the sea bottom, exploring with their tentacles the area around them while fixed at a given place by their stele dug into the sediment—indicated, as previously mentioned, by the oblique downward attitude of the stele in many fossils. Perhaps they lived in still more fixed location, for the stele appears to have had almost no capacity for movement—indeed, they may have led a partial burrowing existence, limited to gathering food particles suspended in the sea water by their tentacular or mucociliary action and to producing vibratile respiratory currents on the surface of their body. Previously stated are reasons for support of the hypothesis that a sort of lophophore functioned in relation to the marginal grooves.

PHYLOGENY

The origin of the Homostelea and their descent—if such there may be—are equally mysterious. Confined within limits of the Middle Cambrian, these "carpoids" are tied to other echinoderms by no known intermediate links. They have long been regarded, it is true, as Pelmatozoa (Crinozoa), the modified ancestral characters of which must have been produced correlatively with acquisition of a recumbent and partially free mode of life. In support of this interpretation their possession of epithecal furrows analogous to the food grooves of pelmatozoans and close association of their mouth and anus near the thecal pole opposite to the stem have been cited. Accordingly, *Trochocystites* was said to be derived from a form resembling *Aristocystites* by lateral compression of the body *(11)*, or from a vermiform eocrinoid similar to *Cigara (55)*, or from a form *(Eikocystis)* supposedly related to *Stromatocystites (24)*.

These are only conjectures, at best. Detailed comparisons reveal no real resemblance of Homostelea to the pelmatozoan echinoderms and bring to light no certain homology with them. Quite unlike these echinoderms which display a fundamental radial symmetry from the moment of their appearance, the Homostelea exhibit not a trace of such symmetry. Their stele has a twofold structure that is unmatched by the stem of crinozoans. Their principal orifices of the theca possess entirely individual traits, and if the depressed form of their body, girdled by a massive frame, is not an exclusive attribute, at least these are constant characters which canont be explained—by lateral compression or play of secondary transformations—as derivatives of diagnostic pelmatozoan features.

When compared with other "carpoids," some of the Cornuta are not to be overlooked, for their theca, like that of the Homostelea, is framed by thick marginal plates and the integument of their superior and inferior faces is reinforced by small plates. KIRK *(56)* saw in *Trochocystites* the possible source of other "carpoids," Bather *(20)* viewed *Mitrocystites* and its allies as derivatives of a form close to *Trochocystites,* and Gislén *(45)* in agreement with Jaekel *(55)* delineated a morphological series beginning with *Trochocystites* and ending in the Mitrata which was thought to illustrate the progressive reduction and ultimate disappearance of ambulacral grooves in the course of evolution.

Nothing is less certain, however, than descent of the Mitrata from the Homostelea, or more broadly, any kinship whatever between the Homostelea and Stylophora. The former are distinguished from the latter by: 1) the presence of a stele, comprising a peduncular prolongation of the theca; 2) the absence of a brachial process possibly correlatable with the stylophoran aulacophore; 3) adjacent location of the two main thecal orifices near one pole of the body in contrast to their positions at opposite extremities of the theca in the Stylophora; 4) the peculiar nature of the homostelean orifices and their close association with the marginal frame; 5) the presence of one or two epithecal grooves excavated in the marginals and connected to one of the orifices; 6) the existence of a special plate termed operculum protecting the large orifice, quite without equivalent in the Stylophora; and 7) entire absence of such structures as the infundibulum, scutulae, septum, and internal marginal grooves which are found inside the theca of stylophorans.

Among the Homostelea and Stylophora, then, not a single morphological character can be considered to be homologous. The presence of a marginal framework in each group is not a significant phylogenetic link, since the same structure is seen in other classes (e.g., Eocrinoidea, Edrioasteroidea) with a high degree of resemblance.

A comparison of homosteleans with the Homoiostelea yields no more certain indication of affinities. To be sure, a peduncular prolongation of the theca is found in both groups, but in the Homostelea this displays the same organization throughout its length, whereas in the Homoiostelea it is clearly divided in characteristic manner into two quite distinct regions. Moreover, the relations of stele to theca and of the axial cavity of the stele, narrow in the one group and wide in the other, to the cavity of the theca show no similitude. Other features show still greater differences. For example, the Homostelea lack a brachial process such as occurs in the Homoiostelea. The mouth and anus lie close together in the former group but far apart in the latter. The two thecal faces generally are much less differentiated in the Homostelea than in the Homoiostelea, and the marginal frame, which is a constant attribute of the first, ordinarily is lacking in the second. Therefore, no justification seems to exist for placing the two groups in the same class, as hitherto done.

Concerning interrelationships of *Trochocystites, Gyrocystis,* and *Decacystis,* no significant facts allow elucidation. These genera are contemporaneous, or nearly so. Intermediate forms are lacking and the trends of their evolution are unknown.

SYSTEMATIC DESCRIPTIONS

Class HOMOSTELEA
Gill & Caster, 1960

[*nom. transl.* Ubaghs, herein (*ex* subclass Homostelea Gill & Caster, 1950)]

Homalozoa with skeleton composed of theca and stele; theca depressed in plane (extension plane) passing through main orifices and stele attachment, with convex surface (superior face) and opposite flat or slightly concave surface (inferior face) united in girdling frame of thick marginal plates; superior face formed within marginals by numerous loosely joined plates termed supracentrals except near pole opposed to stele where they fuse or are replaced by row of stout suranal plates; at absteleal pole and excavated in marginal frame is large thecal orifice inferred to mark location of anus; it is protected by apparently movable plate designated as operculum; adjacent is smaller circular orifice that probably represents mouth; periphery of theca adjacent to presumed mouth bearing one or generally two epithecal grooves hollowed in outer face of marginals, grooves connected to mouth and protected by multitude of minute cover plates; inferior thecal face formed within marginals of close-fitting polygonal infracentrals, without orifices. Stele tapered, depressed in same plane as theca, with convex superior

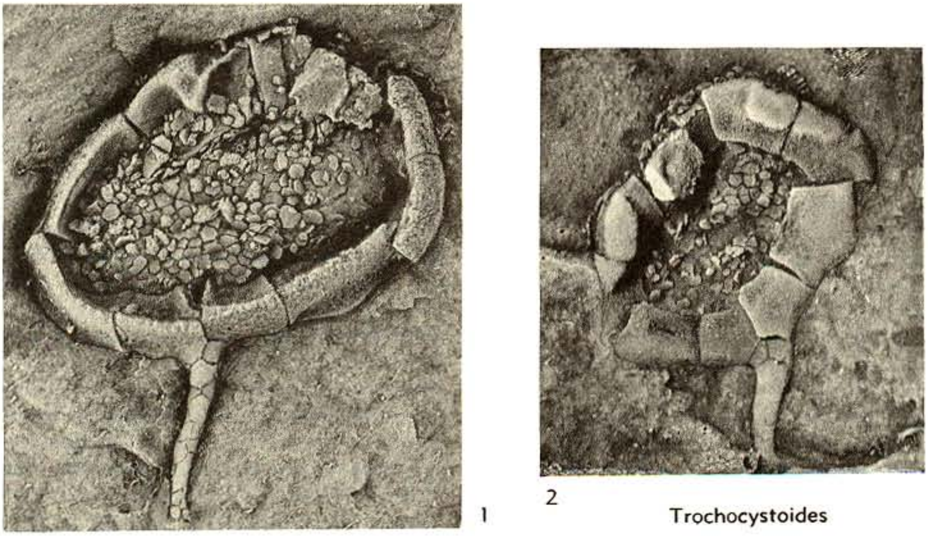


FIG. 371. *Trochocystitidae.*——*1. Trochocystoides* sp. cf. **T. parvus* JAEKEL, M.Cam., Boh.; upper face, ×5 (Ubaghs, n).——*2.* **T. parvus* JAEKEL, M.Cam., Boh.; lower face (?holotype), ×5 (Ubaghs, n).

face in form of ridge and flat or slightly convex inferior face which meet laterally as angled keels, constructed of two rows of opposed or alternating ossicles (dimeres) between which variable number of small irregular platelets commonly are intercalated on superior and inferior faces; narrow axial cavity of stele confluent with thecal cavity. *M.Cam.*

Order CINCTA Jaekel, 1918

[=suborder Marginata JAEKEL, 1901 *(partim)*]

Characters of class. *M.Cam.*

Family TROCHOCYSTITIDAE Jaekel, 1901

[=Trochocystidae BATHER, 1902 *(nom. van.)*]

Well-developed marginal groove on each side of small circular orifice (mouth), both of them long and deep; centrals of inferior thecal face small and numerous. *M.Cam.*

Trochocystites BARRANDE, 1887 [**T. bohemicus*; M] [=*Trochocystites* BARRANDE, 1859 *(nom. nud.)*; *Trochocystis* HAECKEL, 1896 *(nom. van.)* (obj.); *Trigonocystis* HAECKEL, 1896 (type, *T. trigona*)]. Marginals typically 12, with rounded upper external slope, knobs on lower face of M_2, M_4, M_5 and M'_2, M'_3, M'_4; marginal grooves generally ending on M_3 and M'_4; suranals indistinctly separable from adjoining centrals. *M.Cam.*, Boh.-?Ger.(Bavaria)-?Fr.——FIG. *364,1-3.* **T. bohemicus*, Boh.; *1-3,* distal, proximal, lat. views of theca, ×3 (Ubaghs, n). [See also Fig. 363, 367-370.]

Trochocystoides JAEKEL, 1918 [**T. parvus;* M]. Marginals typically 10, with slightly convex to concave upper external slope, knobs on lower face of M_3, M_4 and M'_3, M'_4; marginal grooves ending on M_3 and M'_3; stele relatively narrow, distinctly convex on upper face, slightly so on lower face. [A single specimen identified by JAEKEL as **T. parvus* which I have been able to study shows only the lower side (Fig. 371,*2*). It seems to belong to the same species as a small form that was confounded by BARRANDE with **Trochocystites bohemicus*. None of the specimens examined by me, however, exactly show features reported by JAEKEL to be diagnostic of this genus.] *M.Cam.*, Boh.——FIG. 371,*1,2.* **T. parvus*; *1,* upper side of specimen (cf. **T. parvus*) figured by BARRANDE (1887, pl. 3, fig. 6, 7), ×5 (Ubaghs, n); *2,* lower side of another specimen (?holotype), ×5 (Ubaghs, n).

Family GYROCYSTIDAE Jaekel, 1918

Marginal grooves relatively short, right one very much reduced or even wanting; centrals of inferior thecal face comparatively larger and fewer than in Trochocystitidae; suranals distinct, three or four. *M.Cam.*

Gyrocystis JAEKEL, 1918 [**G. platessa*; M (=**Trochocystites barrandei* MUNIER-CHALMAS & BERGERON, 1889; *?T. occidentalis* JAEKEL, 1901)] [=*Sucocystis* TERMIER & TERMIER, 1958 (type, *S. theronensis*)]. Marginals typically 12, with flat or concave upper external face, generally with prominent knob on marginal beneath large thecal orifice and less prominent swellings on either side; marginal grooves ending on M_5 and M'_6. *M.Cam.*, Fr.-Morocco.——FIG. 365,*1-4*. **G. barrandei* (MUNIER-CHALMAS & BERGERON), Fr.; *1-4*, upper, lower, distal, and right lat. views of theca, ×3 (Ubaghs, n).

Decacystis GISLÉN, 1927 [**D. hispanica*; M]. Marginals 10, with flat upper external face; right marginal groove wanting, left one ending on M'_4. *M.Cam.*, Spain-France.——FIG. 366,*1-3*. **D. hispanica*, Spain; *1-3*, upper, lower, and distal views of theca, ×3 (10).——FIG. 366,*4*. *D.* sp. cf. **D. hispanica*, Spain; distal view of theca, ×5 (Ubaghs, n).

[References for the chapter on Homostelea are included with those for Stylophora and Homoiostelea (*see* p. S624).]

HOMOIOSTELEA

By KENNETH E. CASTER

[University of Cincinnati]

[In the preparation of this section it has been necessary to re-examine much original type materials of BARRANDE, BATHER, JAEKEL, THORAL, and UBAGHS, and to study extensive supplementary material. To the officers and staff of the Narodni Museum, Prague; British Museum (Natural History), London; Museum of Humboldt University, East Berlin; Department of Geology, University of Lyon; Montpellier University, Lyon; University of Greifswald; Hunter Museum, Glasgow; United States National Museum, Washington; Geological Survey of Canada; Victoria National Museum, Melbourne; and to private collectors, R. COURTESSOLE and G. and G. GRIFFE, Carcassonne, FR. KRANTZ, Bonn, and many others, deepest thanks. Very special thanks go to GEORGES UBAGHS, RONALD PARSLEY, and EDMUND D. GILL.]

CONTENTS

INTRODUCTION

The Homoiostelea (U.Cam.-L.Dev.) form a part of the former class Carpoidea JAEKEL (1902) and are coextensive taxonomically, as herein revised, with JAEKEL's order Soluta. They share with other "carpoids" the possession of fundamental asymmetry of skeletal organization and show varying degrees of superimposed bilateralization; moreover, a tendency toward flatness (depression) is common to all. They possess an exothecal arm, plated theca and tail-like stele (heterostele).

THECAL APPENDAGES

The name Homoiostelea (similar stele) comes from GILL & CASTER (1960), who attempted to point up axial differentiation of the "tails" in the Soluta, and also in the Cornuta and Mitrata (Stylophora), into three zones, as against the condition in the Homostelea (=JAEKEL's Cincta) where zonation does not exist. It was the assumption of previous authors that all carpoid steles are homologous, both in origin and function. It now appears, as a result of work by UBAGHS (1961) on Cornuta and (elsewhere in this volume) on Mitrata (these two orders of JAEKEL comprising the new class Stylophora), that the functions of the solutan "tail" and arm were both performed by the single serial appendage of stylophorans, the aulacophore. Herein lies the basis for a difference of opinion as to the homologies and orientation of the whole organism as between the Soluta and Cincta on one hand and the Stylophora on the other.

UBAGHS (*Treatise,* p. S496) correlates the stylophoran aulacophore with the solutan arm because of their common subvective function. Consequently, he prefers to designate the base of the aulacophore, like the base of the arm, as anterior (see Fig. 325-326, 343-350, this volume), since both presumably lead to the mouth of the organisms. But, whereas mouths are always anterior in position in primordial bilaterians, "carpoids" appear to have undergone two stages of metamorphism beyond that condition: some degree of radial superimposition, perhaps associated with fixation; and secondary freedom and very advanced secondary superimposition of bilateralization, which is never complete. In most eleutherozoic echinoderms "anterior" is conventionally the direction of forward movement, and this seldom coincides with the position of the oral-anal axis or mouth.

It is my opinion that in this complex of convergently adapted eleutherozoans, which might be termed the "cladus Carpoidea," all exothecal tetramerous organs are modified biserial arms, and hence are all radial homologues. According to this view, all "carpoid" heterosteles are radially homologous. The stylophoran aulacophore has primitively retained the radiate subvective function, the while also serving the free-moving "tail" function of the heterostele in other "carpoid" classes. All seem best designated as heterosteles in accord with JAEKEL's original proposal (1901). The aulacophore is, then, a special kind of heterostele.

The convergent form of "carpoids" seems to have been selectively determined in accord with hydrodynamic principles and correlated with bottom-moving in a flatfish-like manner. A swollen anterior body (theca), usually rounded anteriorly, and depressed, more or less parallel-sided, and bearing a posterior caudal appendage (heterostele) for steering and locomotion, is the recurrent plan. The recurrent analogy of the heterostele to a fish tail in all three classes of "carpoids" seems to have orientational validity.

The steles ("tails") of Homostelea and Homoiostelea are apparently completely homologous both in origin (probably from a biserial arm) and in caudal, wholly locomotor, function. In the former, however, the mosaic plating and lack of axial zonation of the component meres bespeak much less motility of the stele than in the homoiosteles, where zonation and either marked imbrication or flexible integumentary suturing of the proximal stele meres is usual. In both classes the proximal steles (proxisteles) are tetramerous and the distal steles (dististeles) dimerous; this is achieved in both instances by the distal diminution of alternate series of tetrameres (see Fig. 378). In the Stylophora, the dististele (distal aulacophore) appears to be uniserial. In the homosteles the close proximity of mouth and anus on the anterior thecal margin localizes the oral-anal axis to a short line on the distal margin, whereas in the homoiosteles the axis is lateral (never in the axial plane) or diagonal, due to the wide separation of the two apertures. If mouth and anus determine anterior and posterior orientation of the organisms, in neither case is the caudal stele posterior. In no instance has the solutan mouth been observed to fall on the morphologic axial plane of the organism. In some stylophorans, where derived bilateral symmetry is most advanced among "carpoids," the oral-anal axis and axial or bisymmetry-plane do seem to coincide. However, in this last class, the anus lies on the leading, distal (anterior) margin of the theca and the mouth at the base of the aulacophore (subvective tail).

SYMMETRY AND ORIENTATION

Inasmuch as the homoiosteles are depressed (that is, flattened[1]) asymmetric

---

[1] Like all echinoderms, the homoiosteles were presumably bilaterians showing a fundamental asymmetry in their embryological development. However, the identification of their original bilaterian coordinates is highly speculative, as is also the degree to which their observed skeletal asymmetry correlates, if in any wise, with that of the dipleurulan

creatures which exhibit bilateral tendencies, they pose special problems in geometric nomenclature. It is quite impossible to employ the terms dorsum (dorsal), venter (ventral), and right and left sides in their true bilaterian morphologic sense. However, it now develops that the last two can be used pretty consistently in the Soluta in a purely descriptive conventional sense, thus rendering unnecessary the substitute and less clear terms which BATHER (1913) proposed. Synonymous names for morphology and symmetry components are indicated (Fig. 372).

Two planes of reference can be distinguished in the Homoiostelea: 1) the plane of flattening, which BATHER (1913) called the **extension plane,** and GILL & CASTER (1960) the **extensiplane;** and 2) the plane normal to this and passing through the axis, which BATHER termed the **symmetry plane,** with respect to which all forms show some degree of bilateralism, hence sometimes called the "bilateral plane" or bisymmetry plane. The main course of the organic axis is judged from the symmetry plane of the stele, which is then projected through the theca. Shortening normal to the extensiplane is **depression** (flattening), and in the extensiplane, normal to the symmetry plane, **compression** (shortening of the width).

Whereas in unmodified bilaterians the **oral-anal axis** coincides with the axial and bisymmetry planes, and hence determines the historic anterior and posterior orientation, in homoiosteles, like most other "carpoids," there is no such coincidence. In fact, the two axes usually meet at a high angle, or, exceptionally, cross one another. Hence the "anterior" and "posterior" labels on solutans are conventional and ecologic rather than historical and physiologic. Being, like all "carpoids," vagile benthos, the solutans (=homoiosteles) possessed a caudal organ that served a propulsive or steering function, or both. This organ was the tail, *"tige,"* or stele (heterostele), or, in the Stylophora, the aulacophore, a subvective stele. The caudal appendage was **functionally posterior.** Neither the position of the mouth or anus nor the trend of the oral-anal axis serves among homoiosteles (or in other "carpoids") to establish conventional, functional anterior and posterior.

The depression of the theca usually results in the existence of two thecal surfaces or **faces.** In the past, these, where recognized, have been variously denominated with respect to the correlation with arm-mouth or anus. Thus BATHER (1913) distinguished the "adbrachial" (="brachial" of authors) and "antibrachial," or "anal," and "antanal" faces. (In "carpoid" descriptions **ant-, anti-, counter** and **opposite** have been used synonymously.) BATHER (1913) also employed **obverse** and **reverse** for the thecal faces which he judged to have been respectively upper and lower in life. However, he was unable consistently to employ these terms, and did not attempt to use them in describing homoiosteles. With exception of the seemingly almost fusiform (data for this conclusion doubtful) *Heckericystis,* the seemingly truly globular *Dehmicystis,* and the nummuloid *Rutroclypeus,* the two faces can be identified consistently and homologized. Therefore, the denominations obverse (upper, carapace) and reverse (lower, plastron) are quite acceptable. Since the position of the anus is highly variable, both as to the side and face on which it occurs—and to some degree the same is true of the solutan arm—face denominations with respect to these organs are misleading. BATHER (1913) also identified the **sides** (flanks) in terms of the anus and arm position. Since top and bottom faces are now pretty generally recognizable in homoiosteles, there seems to be no good reason for not using the simple terms right and left for the sides.

The distance between the two faces of the theca is the **height** or **thickness;** it is usually measured in the symmetry plane. The distance between the sides is **width; length** is an axial dimension. The plane of contact of the stele and theca is conventionally known as the **proximal plane.** However, it is notable that this is apparently not the same plane of reference commonly employed among Crinozoa. Directions toward the proximal plane are **proximal** and away from it **distal.**

---

larva. It now seems quite probable that more than one mode of flattening of the bilaterian body has occurred among "carpoids" and that to characterize them all as pleuronect creatures (lying on one side, like flounders) is too comprehensive a generalization, and possibly quite a wrong one. This is a certainty: every "carpoid" is a multiple palimpsest of superimposed symmetries.

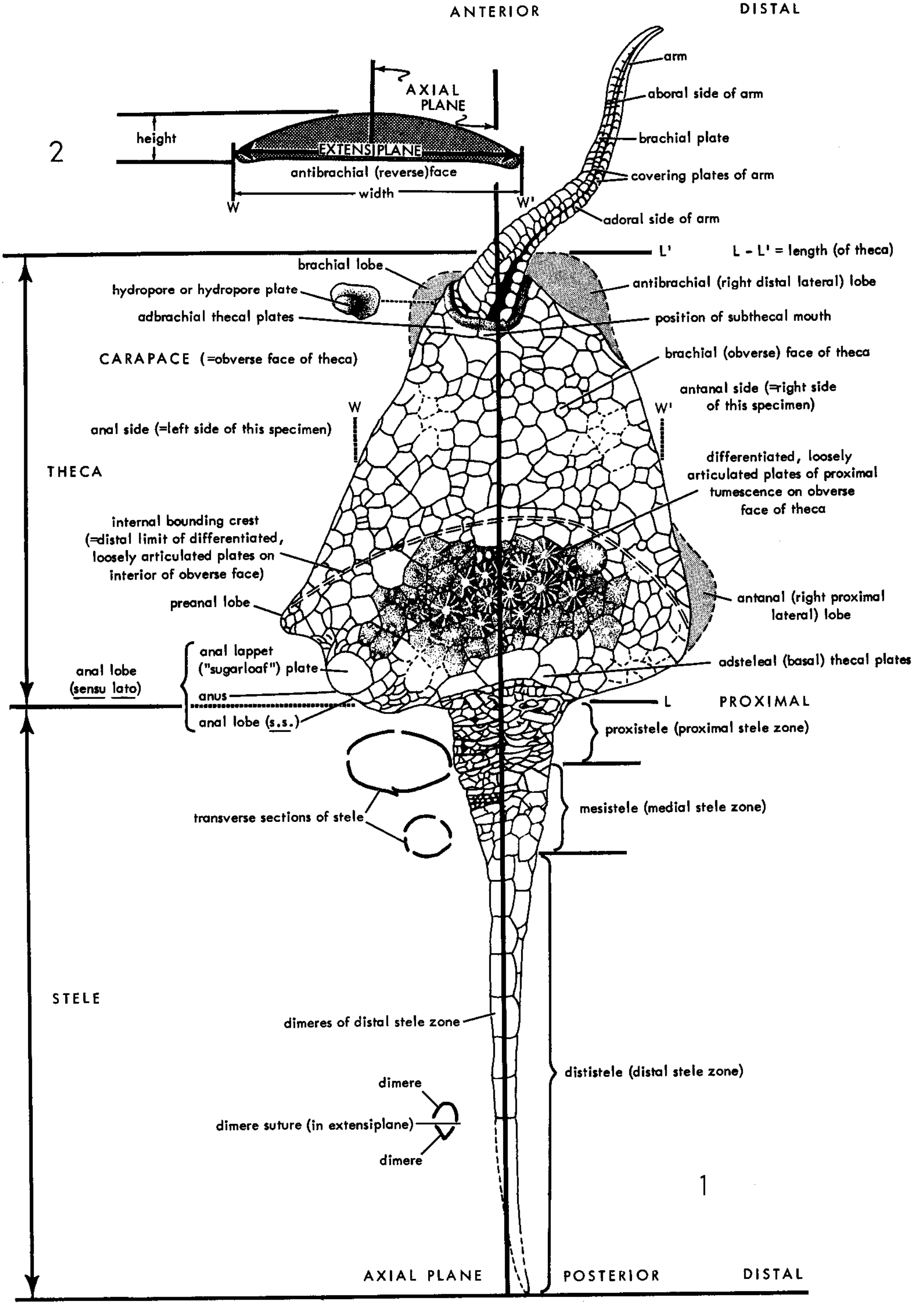


FIG. 372. Homoiostele morphology and orientation (based on **Dendrocystites sedgwicki* (BARRANDE), a generalized solutan "carpoid"). *1*, extensiplane view obverse side, ×1.7; *2*, generalized cross section of theca, ×1.7 (Caster, n; drawn by Elizabeth A. Dalvé from photos and sketches of Barrande specimens from Praha).

MORPHOLOGY

GENERALITIES

The morphologic nomenclature of the Homoiostelea is given in Figure 372. However, this figure hardly conveys the aspect of more advanced members of the class which are commonly strongly homeomorphic with the stylophorans. The body is composed of three regions: 1) the anterior (really anterolateral) biserial **arm,** which commonly has been called a "brachiole" *(13, 43)*; 2) the main body, which was invested with a **theca** of calcareous plates; and 3) the **stele** or **heterostele,** as JAEKEL *(54)* preferred in order to counter the common mistake of referring to the posterior appendage as a "column" or "stem" under the misapprehension that it is homologous with the pelmatozoan column. It is also commonly called a tail or *"tige,"* which best describes its apparent function in life. Undoubtedly, there was in life the usual echinodermal mesodermal fleshy investiture of all calcareous parts. The labyrinthine canals in the skeleton (stereom), occupied in life by fleshy strands (stroma), are commonly preserved (e.g., CASTER & EATON, 1956, described similar histology in Mitrata). Most of the fleshy anatomy of the organism was housed in the theca, but significant extensions undoubtedly reached into the large lumens of the arm and proxistele. The plates of both arm and stele are **bilaterally** arranged; those of the theca quite imperfectly so (*Syringocrinus,* see Fig. 393; *Iowacystis,* see Fig. 394) or not at all (*Dendrocystites,* Fig. 372; *Dehmicystis,* see Fig. 388; *Rutroclypeus,* see Fig. 391, 392; *Girvanicystis,* Fig. 373, 374, see Fig. 389, 390). Plates adjacent to arm, anus, and stele are to some degree regularized, and consistently identifiable in certain genera and to some degree homologous. In some forms, the plate size, number, arrangement, and ornament differ on the two faces, sometimes markedly so; this is termed **facial differentiation.** There may also be **regional differentiation** of plates within a face or organ.

ARM AND RELATED STRUCTURES

Although the exothecal subvective organ

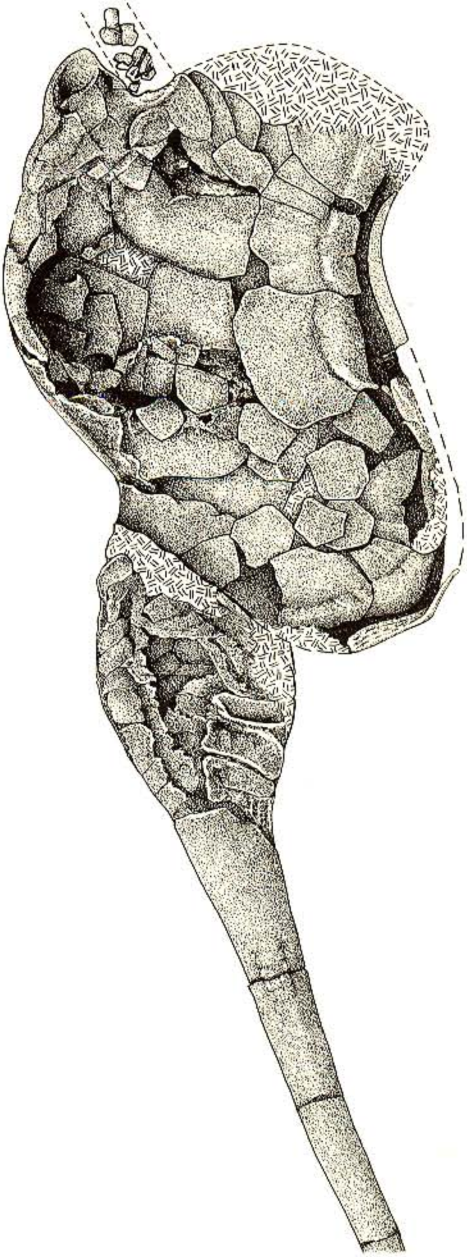


FIG. 373. Morphological features of **Girvanicystis batheri* CASTER, n. gen., n. sp., U.Ord., Scot. (Girvan), showing obverse face of somewhat deformed paratype having well-defined marginal groove for reception of thickened margin of reverse face, ×2.4 (Caster, n; drawn by E. A. Dalvé from photo of BMNH, Begg Coll. no. E5830).

in homoiosteles has been commonly called a brachiole, it is technically an **arm** since it is a skeletized extension of the body cavity (as is the stele) and not a solid serial skeleton such as are true brachioles. It has been termed a "proboscis," under the mistaken impression that it bore a terminal mouth; it also has been erroneously identified as an anal structure. The arm is usually a long, tapering, broadly based organ (e.g., *Dendrocystites*), subterete or somewhat compressed, and covered by two matching but unequal biseries of plates (i.e., it is essentially tetramerously invested) arranged bilaterally. The larger biseries, termed **brachial plates,** usually cover about two-thirds of the arm flanks and meet tightly or flexibly on the **aboral** side; the aboral suture is usually zigzag, reflecting the alternation of the brachial biseries; no aboral suture has been found in *Minervaecystis* (See Fig. 381). There may be slight distal imbrication of the brachial plates. Each plate is about twice as wide as long, and bowed. The adoral gape between the bowed brachials is covered by the matching lesser biseries of plates, the **cover plates,** which articulated with the brachials and met ad-

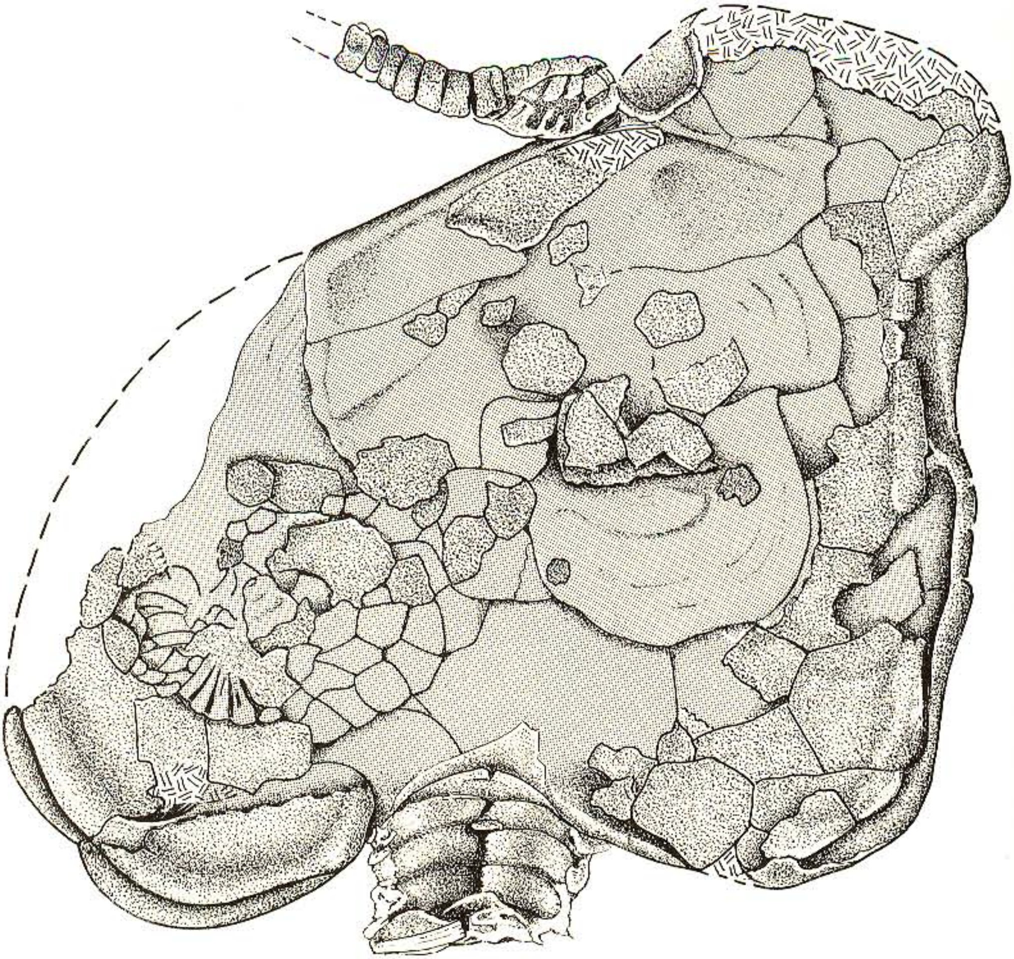


FIG. 374. Morphological features of **Girvanicystis batheri* CASTER, n. gen., n. sp., U.Ord., Scot. (Girvan); obverse face of paratype with pillbox articulation of two faces along extensiplane, ×3.7 (tone pattern on exterior of obverse plates, interior surface of reverse plates stippled) (Caster, n; drawing by E. A. Dalvé from photo of BMNH, Begg Coll. no.E5824).

orally along a zigzag line. The relative width of brachials and cover plates is variable within taxa; they may form a confluent arm surface, or the cover plates may rise in a gable on the adoral side and their articulation with the brachials be a depressed line. Internally both brachials and cover plates bear articulatory muscle scars. The adoral gape of the brachial plates presumably defines the ciliated food groove (ambulacrum) of the living animal. This leads to the concealed mouth, which presumably was situated near the end of the groove, within the theca. As in all other echinoderms, the normal feeding position of the arm was undoubtedly with the adoral side of the arm and the associated ambulacral groove upwardly exposed when the cover plates were open. Thus, the life position of the arm determines the orientation of the whole organism. This is the ultimate recourse in the sometimes perplexing problem of thecal orientation and face determination of the fossil. The adoral features of the arm correspond in position to the obverse side of the theca.

The mouth and gut being unknown, the intestinal course is speculative between the base of the arm and the anus. Of a certainty, it does not follow the oral-anal axis, and the asymmetrical form of the homoiostele theca suggests that it has an arcuate, or perhaps even looped course, and that it probably does not lie wholly in the extensiplane.

The transition from arm to theca is abrupt; nothing has been observed which would support BATHER's (1913) contention that the solutan arm skeleton passes gradationally into thecal skeleton (Fig. 375). The arms, so far as known, are consistently tetrameral (except possibly in *Minervaecystis,* see Fig. 381, where quite probably the lack of an aboral suture reflects ankylosis of a biseries). Adbrachial thecal plating is rarely four-part, and the junction between the theca and arm is consistently integumentary, in keeping with the manifest motility of the arm as a whole. In *Dendrocystites sedgwicki* (Fig. 372, see Fig. 383) adults many small polygonal plates occupy the contact zone. These may be sclerites of the integument, or more likely represent the breakup of larger adbrachial plates in the same man-

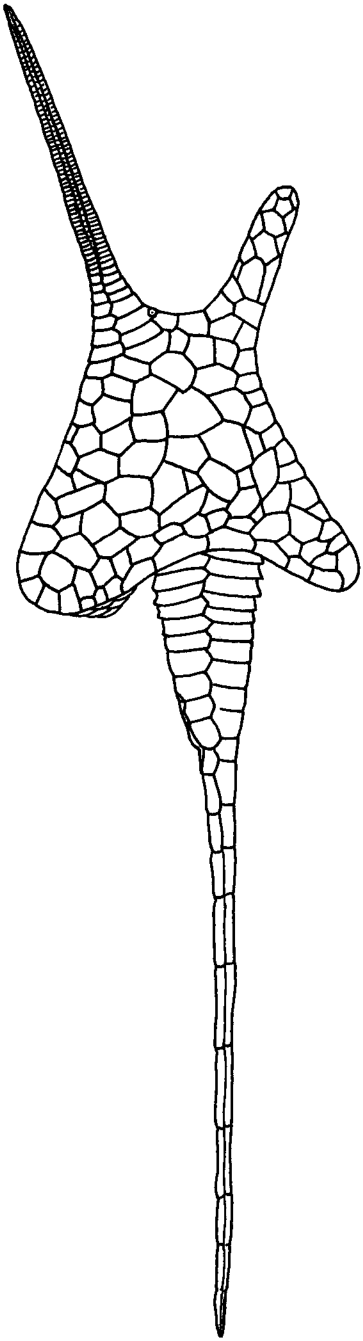


FIG. 375. Complete skeleton of **Dendrocystoides scoticus* (BATHER) viewed from obverse side (reconstr.), U.Ord., Scot. (Girvan), ×1.3 (Bather, 1913).

ner as observed in the proxistele of this species. These small plates may have been the basis for much of Bather's speculation about the relation of arm plating to thecal.

The large adbrachial plates of the theca are always distinctive. They are generically consistent in number and form. They may be a more or less rigid circlet of strongly fused plates, as in *D. sedgwicki* adults; a thickened rim may be developed on them around the arm orifice, as in *Girvanicystis;* this becomes a prominent bordering flange in *Iowacystis* (see Fig. 394). In *D. barrandei* (see Fig. 384, 385), and the Scottish *Dendrocystoides* (Fig. 375, 387), and the French *Minervaecystis* (see Fig. 381), adbrachials strongly geniculate to encircle the arm base and laterally imbricate to form a scalelike sheath. The number of adbrachials in the circlet varies from perhaps six in *Dendrocystites* to four (or fewer) in *Iowacystis.* In In *Girvanicystis* (see Fig. 389, 390) there are apparently four adbrachials, two obverse and two reverse, which are deeply excavated to form the brachial foramen. The size and shape of this foramen depends on the configuration of the proximal arm. Certainly within genera, and possibly more widely, the various adbrachial plates can be homologized.

One adbrachial, lying on the left side of the arm base and usually extending well onto the adoral surface, consistently bears an organ which probably represents a hydropore. In *Dendrocystites* and *Dendrocystoides* this takes the form of a single (see Fig. 386) or multiple (Fig. 376) warty tumescence on the plate. In *Minervaecystis* (see Fig. 381) two distinct prominences, one of which may be gonadal, appear on this plate. In *Girvanicystis* (see Fig. 390) a rimmed pore is developed in the same position, and two produced phialine pores in *Iowacystis* (see Fig. 394); here again, the lesser pore tube may be gonadal. Some of the illustrations of *Rutroclypeus* (see Fig. 391, 392) suggest the presence of a similarly located warty prominence, although it was not originally observed. Since the hydropore structures in most solutans are usually in a slightly inferior position on the adoral side of the arm aperture, they are best seen on specimens revealing the reverse face of the theca.

The arm generally emerges from the left distal area of the theca and from the marginal zone of the obverse face. In *Girvanicystis* (Fig. 373, 374) the arm position is normal, but the foramen is excavated on the peculiar bounding suture between the two faces; also, more of its excavation lies in the two reverse adbrachials than in the obverse ones. Correlating with a recurrent tendency among homoiosteles for the distal theca to become narrow, the arm becomes nearly axial in position (e.g., *Heckericystis,* see Fig. 384,*1*; *Dendrocystites barrandei,* see Fig. 384,*2*; *Dendrocystoides*), or crosses the axis to lie consistently on the right distal side of the theca, as in the deltoidal *Iowacystis* (see Fig. 394). Probably the arm commonly lies in the plane of balance of these usually highly irregular organisms; this seems very much the case in the anomalous girvanicystids.

In *Dendrocystites* and *Dendrocystoides* (and no doubt elsewhere) occur what might be termed mirror anomalies in the position of the arm. Thus, right-armed individuals may occur in a dominantly left-armed assemblage. Only the locus of the arm shifts, however, without any reversal of orientation of correlated structures (i.e., in right-armed forms, the adbrachial hydropore plate is still consistently on the left side of the brachial foramen).

The arm and anus commonly occur on the left side of the theca, as seen in *Dendrocystites, Dendrocystoides,* and *Girvanicystis.* When the arm shifts to an axial or near-axial position this may be hard to prove, and in *Iowacystis* (see Fig. 394) the oral-anal axis crosses the symmetry plane. In forms exhibiting the mirror anomaly, the arm and anus are on opposite sides. But in quite another category is *Minervaecystis* (see Fig. 381), the oldest well-documented homoiostele, where the anus lies on the left proximal lobe and the arm in the exceptional right distal position. This is the best example of the "opposite" condition of mouth and anus. In this inadequately known genus we may be observing a mirror anomaly with respect to the anus. No transitional stages in either the brachial "mirrors" or in attaining the reversed anal position are known.

THECA

The homoiostele theca is depressed, asymmetrical, and multiplated, and recurrently it exhibits a tendency toward bilateralism. The differential flattening in the extensiplane results in a wide variety of depressed thecae. The degree of flattening has usually been exaggerated during fossilization and thecal topography commonly is masked thereby. Moreover, what were tight sutures between thecal plates have been opened in the process and an illusion of thecal flexibility created, whereas in life the form was fixed and relatively rigid. However, since the inferior thecal face, usually the reverse face (*Girvanicystis* is resupinated in this respect), is commonly planate or nearly so, it is less deformed and usually gives a fair clue to the living thecal outline.

But since all homoiosteles are essentially asymmetrical, the form of the thecal perimeter in the extensiplane is difficult to describe. *Dendrocystites* is subcordiform; *D. barrandei* and *Heckericystis* subvasiform?; *Dendrocystoides* irregularly shrubby or tunicate; *Girvanicystis* obliquely subcordiform; *Minervaecystis* and *Syringocrinus* ovoid; *Iowacystis* triangular; *Rutroclypeus* circular; *Dehmicystis* probably globular. In addition, hourglass-shaped, subquadrate, and subtrapezoidal forms are known.

Lateral lobation is especially characteristic of the dendrocystitid solutans, but is seldom seen elsewhere in the class. There are two broad unequal **proximal lobes,** the left being usually the larger. In most specimens the left lobe would correlate with Bather's (1913) "anal" lobe and the right with his "antanal" lobe. In *Minervaecystis* the larger proximal lobe and "anal" lobe is on the right. Both lobes are usually broadly, but asymmetrically, curved and the left one especially may have considerable posterior development *(Dendrocystites).* In some *Dendrocystoides* either proximal lobe may be produced posterolaterally as an attenuate process. In *Dendrocystoides,* and in *Girvanicystis* especially, a broad, rounded, right **distal lateral lobe** (Bather's "antibrachial" lobe) is developed. In right-armed variants a corresponding lobation may occur on the left side, but never to the same degree as on the right. The distal lateral lobe may grade into or be distinct from a **distal lobe,** which is rarely developed on the thecal asymmetry axis; the distal lobe, when developed, extends forward from the base of the arm. In *Dendrocystites sedgwicki* the distal lobe is commonly well developed, but distal lateral lobation is inconspicuous. Both a distal and a distal lateral lobe occur in *Girvanicystis* (see Fig. 390) and are broadly confluent. In addition to these broad and usually depressed extensions of the thecal faces, long, hollow, hornlike plated processes occur in *Dendrocystoides* (Fig. 376, see 386, 387). The most frequently encountered of these lies in an "antibrachial" position, usually right distolateral. However, these processes can develop almost anywhere on the theca, reverse or obverse face. The "antibrachial" horn may arise from either face, or on the flank, or may arise in common with the arm from a distal thecal tumescence. Several such horns have been observed on a single specimen. In a few specimens what appears to be a terminal perforation of a horn has been seen.

The left proximal lobe (usually the "anal" lobe) shows secondary lobation in several genera, especially where the anus is marginal or nearly so. The anus itself is in these specimens associated with the larger, rounded, posterior lobe, the true anal lobe, usually bearing Bather's "sugarloaf" plate, the anal plate, or anal lappet; this is the **anal lobe,** *s.s. (Dendrocystites, Dendrocystoides)* (see discussion of anus, below). Distally from the true anal lobe and usually marking the widest part of the theca, is a subangular **preanal lobe,** best seen in the above two genera. In *Dendrocystites* this lobe is swollen and possibly bears a marginal aperture. Internally the inside surface of the obverse thecal plates bears an undulatory imprint of a soft-part structure which leads to the apex of this lobe; this may be an organ or conduit.

Heckericystis, as restored by Gekker [Hecker] (1940), was inflated and not facially differentiated; however, it does show a proximal lateral bulge on the anal side. At the present time it is impossible to assess the accuracy of the restoration of this form.

Although the thecal plates of homoiosteles are commonly imbricated when encountered, this seems to be due to deformation. The plating appears to have been mosaic, with either firm sutures or integumentary junctures. Even among the supposedly wholly flexible dendrocystitids, there is good evidence that the thecal configuration was quite constant in life and that many of the plates were firmly joined (e.g., Fig. 382,*1*).

Restudy of the types of the Bohemian *Dendrocystites sedgwicki* and of considerable new material indicates that young specimens bore fewer and relatively larger

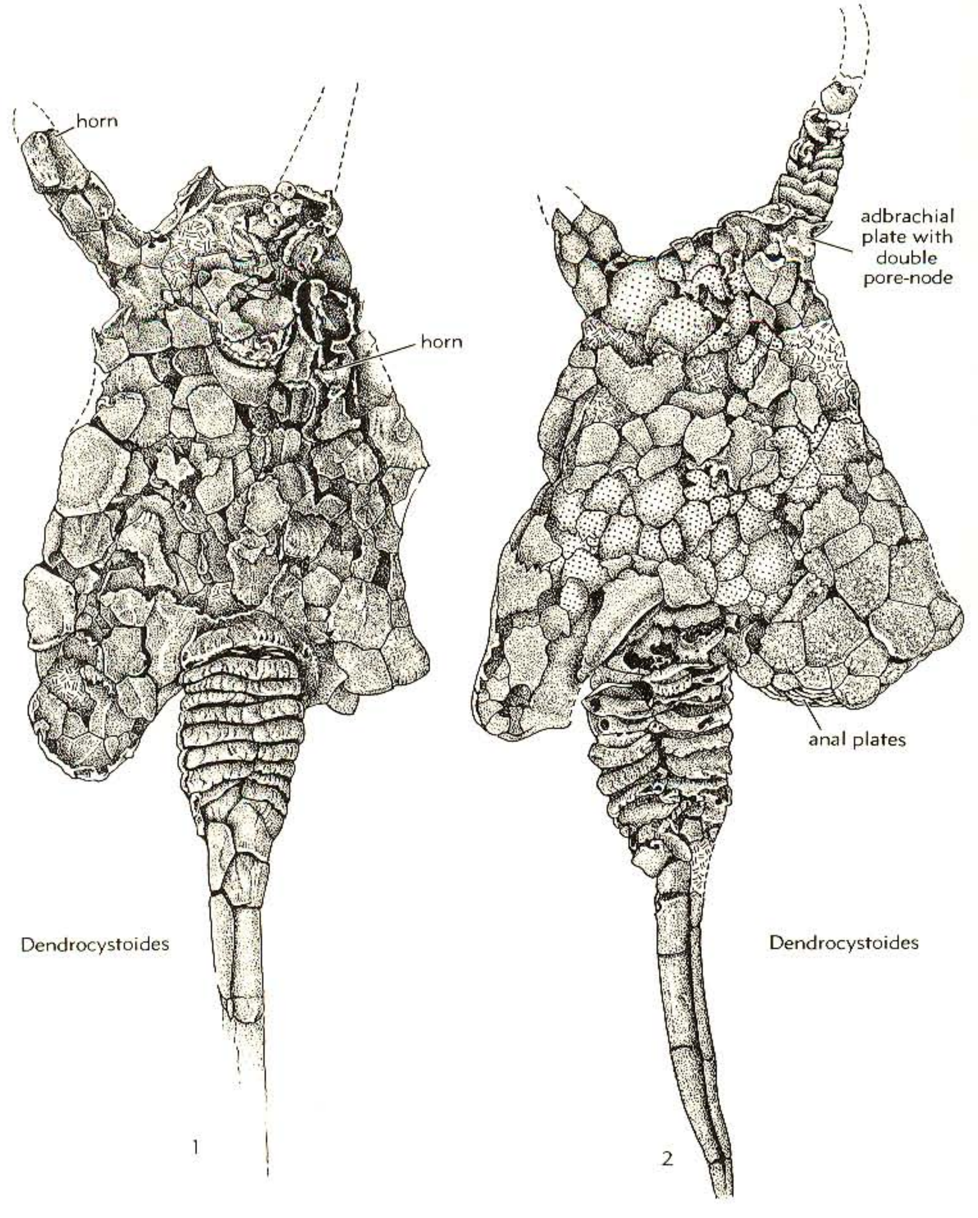


FIG. 376. Morphological features of **Dendrocystoides scoticus* (BATHER), U.Ord., Scot. (Girvan); *1*, reverse face of theca with thecal spine arising from deep in face, stele well preserved, ×2.3; *2*, reverse face of another specimen with double pore node on adbrachial plate, coarse dot pattern indicating interior of obverse plates, ×2.2 (Caster, n; drawings by E. A. Dalvé from photos from BMNH specimens H5A and H103A).

plates than adults (see Fig. 383). New plates seem to have been added in rosettes around previously introduced plates. A very similar mode of plate increment was noted by GILL & CASTER (1961) in the Australian rutroclypeids.

Around the arm, anus, and stele foramina considerable regularization of plate number and form is seen; there is also considerable plate differentiation on the two faces of convexi-planate forms, such as *Dendrocystites, Dendrocystoides, Iowacystis, Syringocrinus,* and *Girvanicystis.* The only known exceptions to the rule of facial differentiation among homoiosteles are the apparently vasiform *Heckericystis,* globular *Dehmicystis,* and biplanate, nummuloidal *Rutroclypeus* (see Fig. 391, 392). The planate face bears fewer and larger plates than the convex one, as a rule, although the reverse is true in *Minervaecystis* and *Iowacystis.* Moreover, the plates of the planate face (usually the reverse) commonly are tightly sutured, whereas those of the convex face (usually obverse) are generally wholly or in part joined integumentally. In *Girvanicystis* (Fig. 373, 374) the convexities are reversed, and both faces are covered by tightly joined plates.

In the dendrocystitids the obverse topography is complex. Both a proximal and a distal plated swelling is present. A **distal tumescence** lies just proximal to the arm insertion and most probably correlates with the forward part of the gut. This prominence was firmly plated. *Dendrocystites barrandei* shows a localized distention adjacent to the arm; this, when flattened in preservation, is probably what BATHER had before him when he described an "antibrachial hump." This may correlate with the common antibrachial process or horn in *Dendrocystoides,* although other plated protuberances, horns, spines, etc., occur on other regions of the theca in this genus.

The **proximal tumescence** (Fig. 372) is a far larger and presumably more important elevation of the theca. This is a transversely oval zone, occupying the widest part of the obverse theca. The plates covering this area have usually collapsed and become imbricated during fossilization, reflecting their integumentary union in life. The proximal border of the zone is the firmly sutured adsteleal circlet of plates; the distal border is a bounding arc of thecal plates, firmly sutured and usually medially upbent proximally, to which the plates of the tumescence were flexibly united. Internally, along the transplate line of geniculation of the bounding arc, there is a sulcar ridge. This extends from the apex of the "antanal" right proximal lobe to the apex of the preanal lobe of the left proximal lobe. Both the bending of the plates of the bounding arc and the internal sulcus serve as indices of the obverse face of the theca, a matter that is often not easy to determine in fragmental material. In *Dendrocystites sedgwicki* the loosely joined plates of the proximal tumescence are somewhat larger than those over the rest of the theca, also thicker and umbonate, with marginal bosses at the plate angles (and in some specimens between them) or with prominent radial ridges (not plicae as usually described), which are not visible on the interior surface. In *D. barrandei* the plates of this tumescence are unornamented. In *Syringocrinus* (see Fig. 393) and *Iowacystis* (see Fig. 394) much of the obverse face seems to be occupied by the homologue of this tumescence, likewise covered by flexibly united plates. In some specimens of *D. sedgwicki* there is a secondary out-pouching of the theca on the adanal side of the proximal tumescence, which may have accommodated a large cloaca, perhaps bearing respiratory trees.

In the convexi-planate forms, where, to employ turtle nomenclature, the obverse face was carapace-like and the reverse, plastron-like, the latter was possibly flexibly conformable to the substrate surface, although seemingly generally more or less rigid and somewhat concave. In the resupinate *Girvanicystis* (Fig. 373, 374) the reverse face is very convex, and bears striking prominences which involve the flexuring of plates; the obverse face was apparently concave and essentially "opercular" in relation to the reverse. The juncture of the two faces, except possibly at the distal margin, was like that of a pillbox (Fig. 374) and conspicuously integumental on the extensiplane; both faces seem to have been composed of rigidly united plates.

Clearly in most, if not all homoiosteles, there is provision in the thecal organization for expansion and contraction of the soft anatomy, or pumping action of the cloaca.

This seems clearly to be the meaning of the proximal tumescence in dendrocystitids, of the many and loosely united plates of the obverse faces in *Iowacystis* and *Syringocrinus,* and of the extensiplane peripheral suture in *Girvanicystis.*

In *Syringocrinus* and *Iowacystis,* and to some degree in *Minervaecystis,* the thecae are homeomorphic with the Stylophora. This entails the development of a turtle-like (testudinate) investiture wherein the obverse face is very like a carapace and the reverse like a plastron. Some thecal plates become definitely lateral in position. In *Minervaecystis* and *Syringocrinus* a loaf-like thecal form is invested with thin plates which form a curved mosaic on the flanks. In *Iowacystis* the lateral plates are constant in number and position, very thick, and geniculate onto both faces to form a **marginal frame** within which are the **somatic plates;** obverse somatics are **supracentrals;** reverse, **infracentrals.** *Rutroclypeus* has the aspect of having been pressed in a die, the polyplating being but little, if to any degree, correlated with the nummuloidal thecal form that results.

The thecal plates adjacent to orifices have been to some extent regularized so that some of them can be consistently identified and homologized. This is especially true of adbrachials and adsteleals, but less so of adanals. Adsteleal plates are commonly larger, thicker, and more firmly united than most thecal plates; thus they form an **adsteleal girdle** about the steleal foramen. In *Dendrocystites* the girdle is well developed, but the number of plates in it is variable. However, a single axial one on the obverse and two adaxial ones on the reverse face are constant. *Girvanicystis* and *Iowacystis* have single axial adsteleal plates on each face. Four symmetrically disposed adsteleals encircle the steleal aperture in *Syringocrinus.* In *Girvanicystis* the extensiplane peripheral suture passes through both the arm and stele apertures. In *Dendrocystites sedgwicki,* and probably elsewhere, the median adsteleal plates bear internal, elevated muscle ridges or platforms, some with apophyses, for attachment of the strong proxistele muscles. Around the inner margin of the adsteleal girdle there is commonly a shallow, narrow groove, presumably for the attachment of integument.

ORNAMENT

The thecal plates are commonly granular (*Dendrocystites, Girvanicystis*), but *Minervaecystis* seems to be smooth. *Iowacystis* is extremely granular and papillose with a prominent labyrinthine ornament on the marginal plates. Central plate bosses (*Heckericystis*), umbones (*D. sedgwicki*), and long spines (*Rutroclypeus*), marginal bosses and radial ribs are external ornament. In *Girvanicystis* certain thecal plates are warped into spines and comblike excrescences which affect the entire plate, as do radial plicae of certain large plates in this genus. The supracentrals of *Iowacystis* are radially plicated. The plated spines and excrescences of *Dendrocystoides* are unique.

ANUS

The homoiostele anus is usually very large, although it has not been discovered in *Rutroclypeus* despite an abundance of fossil materials. It commonly lies in the left proximal lobe; however, in *Minervaecystis* it is right proximal. The aperture is usually near or at the thecal margin, but may invade either the obverse or reverse face. *Girvanicystis* is unusual in that it deeply invades the reverse face of the left proximal lobe. When the anus is at or near the margin its presence is usually indicated by the development of the anal lobe (*s.s.*) on the proximal lobe.

Usually special anal plates effect the anal closure; **adanal plates** surround the anal orifice; between them there may be many flexibly united platelets constituting a periproctal zone. In *Minervaecystis* the anus is closed by a low pyramid of long trigonal plates which radially imbricate over the aperture. In *Dendrocystoides* many small platelets are puckered around the anus, and the closure seems to have been sphincteral, as Bather (1913) supposed. Here the anus is in a posterior inframarginal position. The adanal plates of the obverse face form a trigonal lappet over the anal area and extend posteriorly to form a projecting anal lobe. The lappet plates are coarsely grained and ridged externally. In *Dendrocystites sedgwicki* the anal lappet bears a swollen median plate of subtrigonal outline. This is Bather's "sugarloaf" or epianal **(suranal)**

plate. Laterally and subjacent to the lappet there were on either side of the anus itself groups of long platelets which may represent relics of an anal pyramid or specialized periproct.

In *Dendrocystites barrandei* (see Fig. 384,*2*) the anal orifice lies on the posterior left flank or slightly on the reverse face of the rounded flank. Although an ovate anal lobe exists on the flattened specimens, indicating an anal bulge of the theca, no lappet has been observed, despite Bather's (1913) drawing of both lappet and "epi-anal" plate. A large, truncated oval adanal plate is present and usually stands at a high angle in the fossils. This may be the antecedent homologue of the suranal in *D. sedgwicki*. But in *D. barrandei,* the older species, its position is *beneath* the anus (subanal), rather than above it (suranal). The broad base of this plate seems to bear articulatory apophyses and is notched as though a sutural pore of some kind were present.

Iowacystis bears the most specialized of homoiostele anal apparatuses. The marginal anus, located at the left posterior angle of the triangular theca, is closed by a pair of calcareous quarter-spheres which serve as opposable valves, opening on the extensiplane and making, when closed, a large hemispherical boss. The valves are probably modified subanal and suranal plates. Surrounding the anal boss is a rosette of quadrangular adanal plates.

The anuses of *Minervaecystis* and *Girvanicystis* (see Fig. 389) lie well within the proximal lateral thecal face. It is left and obverse in the former, and left, reverse in the latter. In *Girvanicystis* the suranal plate is seen to be large and near the center of a large proctal area which is otherwise occupied by tessellated, or perhaps slightly imbricating, periproct plates. Although previous studies of the Rhenish Devonian solute *Dehmicystis globulus* (Dehm) had not revealed the anal apparatus, it is now quite clear (see Fig. 388,*2*). The theca is here reevaluated as having been essentially globular in life, rather than flattened in the rutroclypeid manner, as Gill & Caster (1960) supposed. The anal zone is large and circular and, although postlateral and marginal on the flattened specimen, does not appear to be associated with thecal lobation. Narrow trigonal plates form a low pyramid over the anal aperture; additional periproctal or adanal plates surround the pyramid, and a large suranal plate seems to be poorly preserved. The anus of *Syringocrinus* remains problematic despite rather full knowledge of the thecal anatomy (Parsley & Caster, 1965). The many small, flexibly united, supracentral plates are probably the homologue of the proximal tumescence of *Dendrocystites,* developed as the pumping apparatus; still the appearance is very much like a periproct zone in other echinoderms. However, there is no aperture within this supracentral area.

STELE

The very name of the class signifies that the stele is a primary taxobasis thereof. It is also an organ of fundamental import in the economy of homoiosteles. Like the arm, the demarcation between stele and theca is sharp, rather than gradational; the juncture is always muscular and integumental, the skeletal plating on the two sides of this juncture, of distinct organization (Fig. 377, 378). Like the arm, the stele (heterostele) or tail is bilaterally tetramerous, i.e., is composed of four series of plates, and possesses, at least proximally, a large central lumen. Among homoiosteles, in contrast to the Stylophora, where the stele (aulacophore) is quite similar in plane and caudal function, the homoiostele organ had no subvective function, although it may well have evolved from an arm.

Three axial zones of the heterostele are differentiable: the proximal zone or **proxistele,** mesial or **mesistele,** and distal or **dististele** (Fig. 372, 375; see Fig. 381, 384). The proxistele is fundamentally tetraserial, i.e., tetramerous, four plates completing a circle; and the dististele biserial, i.e., dimerous. The transition from four-part to two-part symmetry occurs in the mesistele (see Fig. 384). This is achieved through distal suppression of alternate series of tetrameres and concomitant rotation of the resulting biseries, so that the dimere suture lies for most of its length in the projected extensiplane of the theca, and the dimeres thus take on a corresponding obverse and reverse orientation.

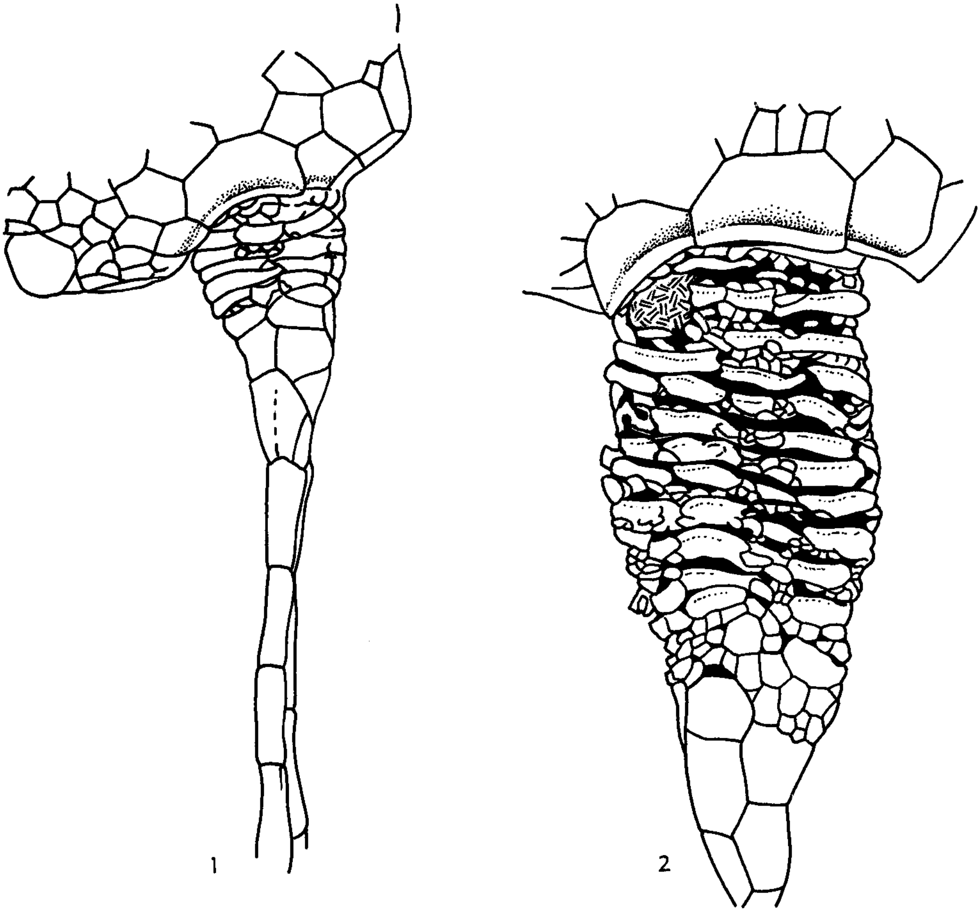


FIG. 377. Morphological features of homoiostelean steles illustrated by obverse views of immature specimens showing two stages in stele development, both identified as **Dendrocystites sedgwicki* (BARRANDE), M.Ord., Eu.(Boh.); *1*, tetramerous proxistele with few platelets both between annuli and between tetrameres of same ring but distal transition from proxistele to mesistele unobscured by platelets, ×3.8; *2*, specimen showing later stage of stele ontogeny in which each annulus is composed of at least 8 meres with many platelets between them in ring, as well as between adjacent rings, transition from proxistele to mesistele obscured by rosetting around major plates, ×3.3 (Caster, n; drawings by E. A. Dalvé based on specimens from Narodni Museum, Praha, Frič and Barrande Colls.).

PROXISTELE

The proximal stele, or proxistele, was the main zone of mobility in the homoiostele. It is strongly plated, usually in the form of telescopically imbricating tetramere rings. Internally the large lumen presumably contained a complex of muscle fibers which served as attachment of the heterostele to the theca and performed as the main locomotor organ of the creature. Movements of extension and contraction of the ring-covered area, right and left, up and down and, by differential contraction of the muscles, somewhat rotatory, are implied. Prominent ridges or platforms inside the stele aperture of the theca were the concentrated zone of proximal muscle fixation; the inside surface of the bourrelets of the rings were distal fixation sites; the conical lumen of the mesistele probably served as the main seat of distal attachment of lengthening and shortening muscles. Probably the main locomotor function of the dististele was controlled in the proxistele.

The archetypical proxistele plan would seem to be that of the single unnamed Upper Cambrian homoiostele described (1963) by UBAGHS from Nevada, and the Lower Ordovician *Minervaecystis* from France. In both, well-developed, axially imbricating, tetramere rings are present. This organization, which is the dominant one in the Homoiostelea, is shared with the mitrate Stylophora (anomalocystitids), where the aulacophore shows an identical organization, which is here assumed to be homologous. This proxistele condition is termed **anomalocystitoid** (Fig. 379, see Fig. 381,*6*). The archetypic proxistele was essentially terete (possibly slightly compressed), the tetrameres of each ring flexibly meeting end-to-end on the obverse symmetry-plane, on the extensiplane laterally, and slightly imbricating on the reverse symmetry plane. The combined telescoping of rings and sagittal imbrication of the tetrameres on the reverse face creates a characteristic zigzag shingling on the reverse mid-line; all of which is "anomalocystitoid," although in most homoiosteles and Stylophora the proxistele (proximal aulacophore) tends to be somewhat depressed.

In *Minervaecystis* (see Fig. 381) the proxistele is exceptionally long, distally tapering, and comprising some 25 to 30 long, thin, imbricating rings. Since both in this genus and in the Nevada form the proxisteles are preserved in an inflated condition, it seems that the constituent tetrameres of the telescoping rings were relatively firmly joined obversely and laterally; reversely they show a slight zigzag imbrication.

Each tetramere is thickened proximally into a **bourrelet** which curves outward as a thickened rim; distally the rings thin to a feather edge. Because of axial imbrication, the bourrelet is normally deeply concealed beneath the thin margin of the proximally adjacent ring.

Several solutans show a marked tendency for the distal stele to twist to the right, thus bringing what are proximally and serially (and probably historically) obverse skeletal elements to a lateral position, and concomitantly lateral ones to the reverse position (see Fig. 384). Correlated with this torsion, the tetramerous condition of the proxistele passes within the mesistele zone into the dimerous condition of the dististele. In this process the distal dimere suture, which is continuous with the sagittal sutures of the proxistele, comes to lie in the extensiplane. In *Minervaecystis* this dextral torsion (Fig. 378,*2d*) of the mid-stele zone is uniquely recorded by a crest which passes across the mesistele diagonally onto the distal proxistele plates: the left reverse tetrameres (to the right of the observer when the reverse surface is viewed) each bear subangular longitudinal median folds which continue as a low keel onto the mesistele where the fold axis crosses the symmetry plane. It appears that in life the organism lay with the left half proxistele distally twisted toward the right, so that the keel came to lie in a position normal to the sea floor. It was functionally a proximal continuation of the pectinate keel or rudder on the proximal reverse dimeres.

In *Syringocrinus* (see Fig. 393) of the Middle Ordovician of Canada the slightly compressed proxistele comprises 11 or 12 smooth, imbricating rings, of which the tetrameres imbricate both obversely and reversely on the symmetry plane. In *Iowacystis*, of the Upper Ordovician, the proxistele is very short, comprising 5 or 6 rings, each of which bears an encircling railroad rail-like flange at its mid-length. The ring margins are smooth and apparently without a bourrelet; they imbricate telescopically. The lateral tetramere sutures are tight, but those on the symmetry plane imbricate slightly on both faces. The whole proxistele is slightly depressed. *Rutroclypeus* of the Australian Lower Devonian has a remarkably depressed theca and a correspondingly much-depressed proxistele of unusual trigonal outline, which first led to its identification as the buckler of a xiphosuran. All of the tetrameres were loosely joined and the two faces in close proximity. The tetrameres strongly imbricate on the symmetry plane of both faces. In keeping with the spinose theca, most specimens show a prominent spine on each tetramere. This is perhaps the most anomalocystitoid of solutan proxisteles.

Heckericystis, of the Baltic Middle Ordovician, is shown by Gekker [Hecker] as possessing a terete proxistele, recalling the swollen proximal columnals of the cystoid *Pleurocystites,* of 12 or 13 narrow rings. Although it is supposed that the rings are tetramerous, no sutures have been reported. Both Gekker (1940) and Gill & Caster (1961) assumed that the rings were nonimbricating and united by integument only. This may be a misconception.

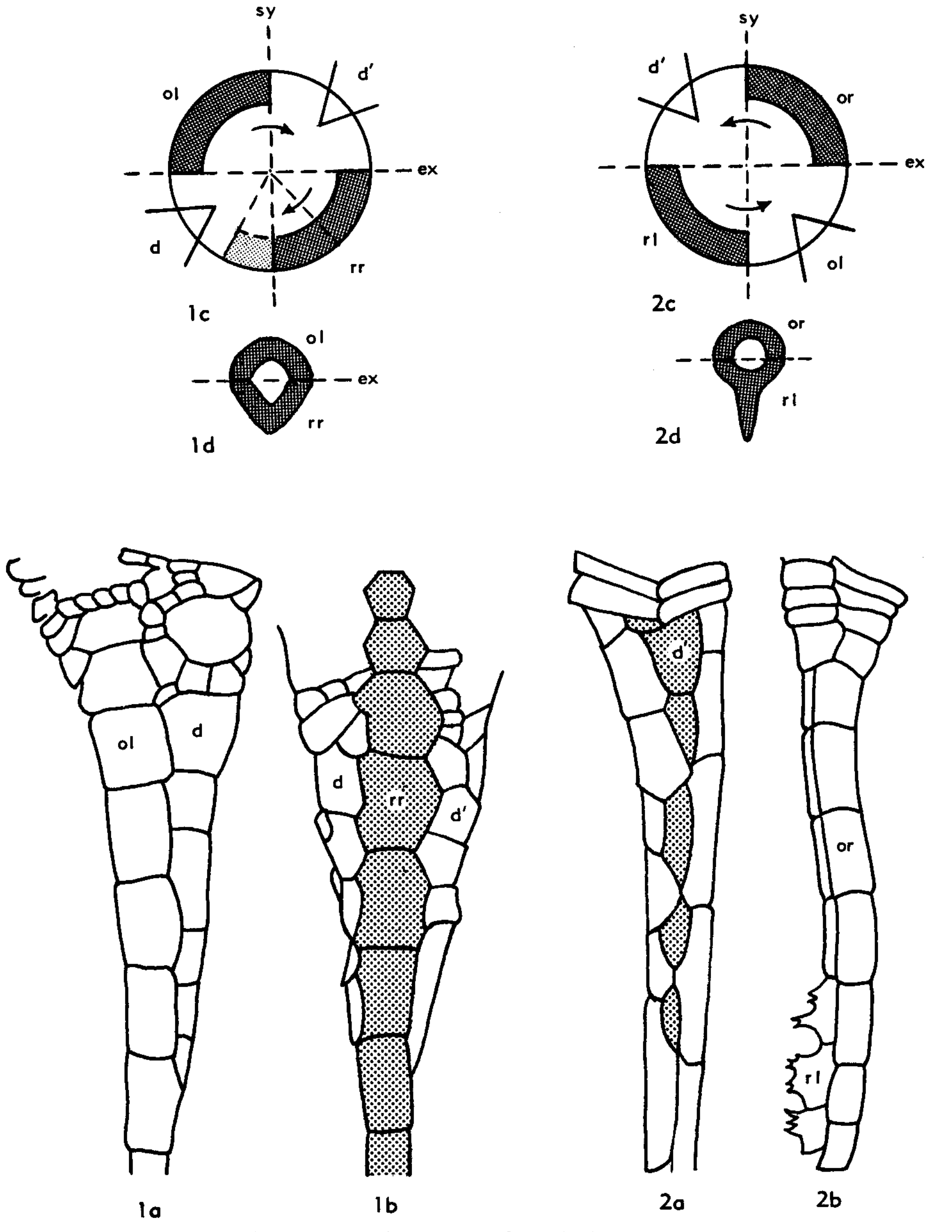


FIG 378. Mesistele transition from tetrameral condition of proxistele to dimeral condition of dististele in Homoiostelea.

1. **Dendrocystites sedgwicki* (BARRANDE), M.Ord., *1a,b,* obverse and reverse faces of stele (reverse tetramere series stippled); *1c,* schematic cross section of proxistele in which those tetramere series which persist through mesistele and into dististele are stippled, and those which become evanescent in this passage are indicated by chevrons; *1d,* dimere disposition in dististele (Caster, n; based on materials in Narodni Museum, Praha).

2. *Minervaecystis* UBAGHS & CASTER, n. gen., L.Ord.; *2a,* left view of mesistele (left obverse tetramere series dotted; *2b,* obverse face of same stele (keeled reverse dimeres turned sideward during fossilization); *2c,d,* same analysis of this genus as shown in *1c,d* (Caster, n; based on holotype of **M. vidali,* courtesy G. Ubaghs).

[Explanation: Arrows indicate direction of rotation of persisting tetramere series when traced through

The Bohemian Middle Ordovician *Dendrocystites sedgwicki* and the Scottish Upper Ordovician *Dendrocystoides* and *Girvanicystis* show many small platelets in association with the proxistele tetrameres, or, in the first instance, seemingly in lieu of them (Fig. 372, see Fig. 382). Every stage from complete tetrameres to rudimentary remnants submerged in a melange of platelets can be seen. *Dendrocystites barrandei* (BATHER), of the Lower Middle Ordovician of Bohemia, and related undescribed forms, commonly preserve distinct tetrameres, or identifiable remnants thereof, the while adding platelets in the annulus series with them so as to create penta-, hexa- or polymere annuli. Between the flanged rings of the tetramere plates many very small platelets occupy the zone of integumentary junction. In what appear to be young individuals of *D. sedgwicki*, the *D. barrandei* plan is closely approximated and the tetramere elements readily identified. In adult and typical *D. sedgwicki* most evidence of the tetramerous proxistele is eradicated by the multiplicity of platelet development and the reduction in size of the tetramere elements. This proliferation occurs both within the annuli and between them, all sclerites being flexibly joined. This is the most inflated of homoiostele proxisteles and certainly the most flexible one. However, close scrutiny does reveal among the platelets a few which exhibit the characteristic flange and bourrelet of the tetrameres. These are found in the circles of larger platelets. The wider zones of small plates seem to have been folded into rugae between the more prominent rings. The whole proxistele lumen of the fossils is commonly choked with discrete platelets.

In some specimens of *Dendrocystites sedgwicki* the disposition of the platelets in the prominent rings suggests that they may derive from the splitting of tetrameres. It is also clear that in *Dendrocystites* the process of rosetting, by which small plates develop in the sutures around large plates, operates both in the theca and the proxistele-mesistele.

Dendrocystoides (Fig. 376; see Fig. 386) of the Upper Ordovician consistently shows many small polygonal plates in the proxistele lumen, but little or no evidence of them externally; they probably were embedded in the integument which connected the telescoping rings. Here, too, there is a remarkable range in surface nature of the tetrameres, and apparently all at the same growth stages of the type species. Thin, smooth, squamose tetrameres are found along with thick, rugose, pitted or radiately ribbed ones, with frayed or spinose distal margins (Fig. 379). *Girvanicystis,* from the same beds, has a depressed anomalocystitoid proxistele with rugosely flanged and carinate tetrameres (Fig. 374, see Fig. 390). Adjacent to the flange both distally and proximally there are many external adherent subpolygonal platelets which seem to pertain to tissues originally covering the stele. Here no platelets have been observed inside the lumen.

BATHER (1913 and elsewhere) apparently largely employed the proxistele morphology of *Dendrocystites sedgwicki* in formulating his idea that the solutan stele derived from thecal plates by regularization. He imagined the regularized stele to grade into the essentially chaotic theca. In the process, perhaps by fusion of platelets or by differential growth and reduction, tetrameres would emerge. However, in this species no gradation from stele to theca occurs, and instead of being a primitive solutan, it now appears to be one of the most advanced, at any rate in stele development. The multiplating is derived from the anomalocystitoid condition, from tetrameres (plus supplements), rather than being antecedent to them. What are judged to be young forms of the species, in association with adults, show tetrameres along with a few platelets. The antecedent *D. barrandei* BATHER of Bohemia, which was still recognizably anomalocystitoid in adulthood, closely parallels the young forms

---

[*Continued from facing page*]

mesistele; plate sutures or margins which were on symmetry-plane in proxistele come to lie on extensiplane of dististele; *d,d'*, tetrameres of series which distally disappear; *d*, reverse; *d'*, obverse; *ex*, extensiplane of theca projected through stele; *ol*, obverse left tetramere; *or*, obverse right tetramere; *rl*, reverse left tetramere; *rr*, reverse right tetramere; *sy*, bisymmetry-plane.]

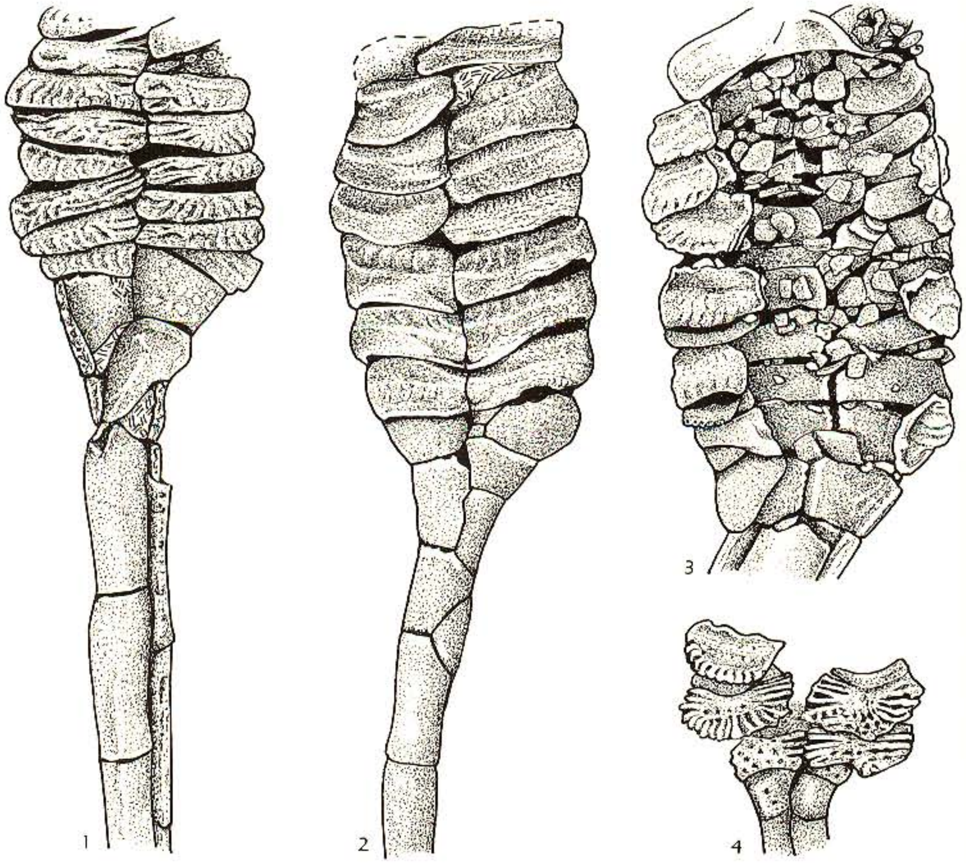


FIG. 379. Reverse views of four anomalocystitoid steles of **Dendrocystoides scoticus* (BATHER), U.Ord., Scot. (Girvan), showing variations within the species, in specimens of essentially same stage of growth, in nature of ornament and presence of internal integumental platelets. *1,2,4,* exterior reverse faces, torsion of mesistele well shown in *1* and aspects of radial ribbing in *2,4*; *3,* internal view of obverse face showing many small platelets concentrated mainly in integumental zone between annuli. (Caster, n; drawings by E. A. Dalvé based on specimens in Hunterian Museum, University of Glasgow: *1,* no. E5803, ×4; *2,* no. E5718, ×3.5; *3,* no. E5827, ×3.8; *4,* no. E5719, ×4.3).

of *D. sedgwicki,* and was at about the same stage of platelet development as the Scottish *Dendrocystoides* and *Girvanicystis.*

PROXISTELE INSERTION

The proxistele is inserted well within the stele foramen, which is usually recessed into the proximal thecal margin. The aperture conforms in shape to the proxistele, from circular to very depressedly ovate. The adsteleal plates of both thecal faces are to some degree regularized and can be homologized within limits. They were commonly rigidly fused to form an adsteleal girdle, a marginal flange of which extended over the proximal proxistele. Just inside the flange there is usually a shallow groove, probably for integument attachment; deeper within the aperture, and mainly developed on or adjacent to the symmetry plane, each genus shows characteristic scars, calluses, or paired apophyses which were places of attachment of the powerful proxistele muscles. In *Dendrocystites sedgwicki* strong bilateral apophyses are present both reversely and obversely, so tilted as to suggest that obverse tetrameres were connected by muscles to the reverse apophyses, and reverse to the obverse.

MESISTELE

The mesistele is a relatively rigidly plated conical coupling between the proxistele and the dististele. It served mainly as the distal termination of proximal muscle strands responsible for the main movements of the dististele "tail." Within the mesistele the transition from the proximal tetramerous condition to distal dimerous was made. It is usually possible, especially in anomalocystitoid forms, to trace across the mesistele (Fig. 378) the serial homologies between tetrameres and dimeres, or biseries. (Biseries, biserial, is employed for **alternate** positioning of plates, with a resultant zigzag suture; dimeres, dimerous, for **opposite,** semicylindrical plates having a rectilinear suture.) In these the distal tracing of tetramere series reveals that alternate ones persist and diminish in the passage of the mesistele zone. Alternate series commonly become evanescent in the distal mesistele. However, in *Iowacystis* (see Fig. 394) and *Syringocrinus* remnants of the diminishing series persist as discontinuous intercalates on the zigzag sutures of the distal biseries. The correlation between tetramere quadrants and dimeres or biseries have taxonomic import (Fig. 376).

In *Minervaecystis* (Fig. 378), the oldest well-known solutan, the mesistele is relatively simple. The obverse right series of tetrameres passes directly into the tightly sutured right series of the mesistele, which in turn is serially continuous with the right dimere series of the proximal dististele; the left obverse tetrameres align with two or three plates which appear as intercalates on the mesistele equivalent of the proximally zigzag and distally dimerous suture of the dististele. Tracing the left obverse tetramere series distally, it is seen to diminish serially in size and finally to disappear in transit of the mesistele. On the reverse face the left tetramere series continues the length of the mesistele and aligns with the left series of the proximal dististele; the right reverse tetramere series, similarly traced, peters out in two or three distally diminishing plates.

This general plan, alternate tetrameres aligned serially with dimeres and their alternates disappearing distally within the mesistele, seems usual among homoiosteles. In *Dendrocystites* (Fig. 378,*1*) wherein the general structural scheme is common to all other anomalocystitoid solutes, quadrants antipodal to those in *Minervaecystis* persist and diminish distally; however, the basic relationships are the same, and the dimere series is thus to be identified and serially homologized with proxistele tetrameres.

In *Dendrocystites sedgwicki* (Fig. 372, 377), where auxiliary platelets and rosetting obscure serial relationships, the juveniles suggest that the prevailing homologies pertain.

Throughout the class the same modifications of the meres take place in the transition from a tetraseries to a biseries. Those tetramere quadrants which are serially vacated by the distally diminishing alternate series are serially invaded by the persisting series as their configuration changes from quarter circles to semicircles. On both faces the proportional serial enlargement is across the symmetry plane; the original extensiplane (lateral) sutures remain constant in position. The effect of this opposing proportional enlargement of the serially persisting plates is that of distal rotation of the stele. When the dimere condition is fully attained, the two half cylinders meet on the extensiplane and in obverse and reverse position, each astride the symmetry plane, rather than being half-right and half-left, as in the proxistele. Customary representations of the dimeres meeting on the symmetry plane seem to be in all cases 90 degrees out of life orientation. The diagonal carina of the reverse face of the *Minervaecystis* proximal stele, mentioned above, which crosses the symmetry plane, conforms to this principle of distal stele rotation. Apparently the rotation is one of the oldest of homoiostele traits, and seems to correlate with the development of an obverse keel or "caudal" fin in free-moving animals. In *Iowacystis,* where no such modification is known, the rotation seems to be suppressed, and for that matter, mesistele plate organization persists through much, if not all, of the distal stele.

The nature of serial transitions of *Minervaecystis* suggests that historically the whole stele was covered by a tetraseries of alternating plates. In this respect *Iowacystis* is the most generalized solute yet encountered; however, the rest of the highly specialized anatomy of this genus suggests that this is a derived simplicity. Unfortunately, there are as yet no ontogenetic data available on stele development, and neither the mode of, nor focus of, stele plate origination is known.

The mesistele of *Syringocrinus,* M.Ord., Canada, is both anomalous and instructive. It has been called a dendrostyloid by PARSLEY & CASTER (1965) because of its homeomorphic resemblance to the styloid of the Stylophora. It is unusually long, petiolate, and covered by rigidly sutured asymmetrical plates (see Fig. 393). It is lachrymal in cross section, i.e., rounded on the obverse face (in life) and keeled on the reverse (see Fig. 393,*1a*). Prominent nodes occur on the left side of the keel; none on the right. The plating is triserial, the right side being invested by a biseries, while the left has a continuous axial row of long plates separating the plates of the biseries. These axials are serial homologies of discontinuous left intercalates which extend through most of the dististele. In the mesistele the axial plates cover most of the rounded surface. The suture between the biseries on the right side of the mesistele is rectilinear and continues as a straight suture to the end of the dististele.

The main mesistele plating in this genus is a disparate biseries, three long plates on the obverse face occupying exactly the same distance as five nodose ones on the keel side. The five plates bear the nodes or bosses at mid-length and marginally on the left side of the keel; these continue onto the first two dististele keeled plates. The distal keel margins are subspinously produced as imbricating caps which give the keel a characteristic serrate appearance; this continues essentially for the length of the tail. These serrations and nodes on the rigid mesistele are the basis for comparing this organ with the mitrate stylocone.

The presence of a narrow, apparently unsutured, annulus between the proxistele and mesistele makes direct correlation between the serial plating of the two zones difficult. The annulus may bespeak unusual rotational activity in this zone in the living organism. It is also no doubt correlated with the usual sinistral rotation of plate series in the mesistele. It is assumed that the keeled edge of the distal mesistele and dististele was, in the main, downwardly directed in life, and that the lanceolate expansion of the dististele served mainly as a laterally moving caudal fin. However, the nodes on the left side of the keel-forming plates of the middle stele zone, and the markedly different plating on the two sides of the postproxistele tail, pose problems of symmetry, balance, and serial homology. It is no doubt significant that the asymmetrical ornament and the direction of the distal serial rotation are both sinistral. The nodes may have served as a counterbalance to inherent muscular forces tending to return the tail to a primordial orientation, such that the dimere suture would lie in the sagittal plane. The extra plating on the left side of the tail may have a similar correlation. As for the serial homologies between the proxistele and the rest of the tail, this is most speculative. Probably, as in other sinistrally rotating homoiosteles, the axial plates of the mesistele, and their discontinuous correlates along the zigzag suture of the left dististele, are serial homologues of the right obverse quadrants of the proxistele. If this is so, then what is the meaning of a single small plate (see Fig. 393,*1a*) on the suture between the first axial and an adjacent nodose plate? It may be adventitious; in other solutes one would tend to correlate it with a tetramere series, it being the only tetramerous element in the mesistele. If this is elected, then *Syringocrinus* is unique in having distally diminished both obverse tetramere series, and in having the resultant biseries wholly of reverse derivation. On the other hand, the compelling evidence of sinistral rotation argues for disregarding this platelet, and correlating the nodose keel plates of the biseries as left obverse in origin, as in *Dendrocystites.* In this genus the left reverse tetrameres diminish distally in the mesistele, but in *Syringocrinus,* if the right plates of the biseries are to be correlated, as is conventional, with the right reverse series, they do not appear in the mesistele. The left reverse series would seem to have no postannulus correlates. This reasoning is supported by the rectilinear suture on the right side of the tail. Intercalated plates, representing a distally diminishing tetramere series, are generally associated with the biserial zigzag relationship of plates; straight sutures derive from zigzag, just as opposite plates derive from alternate. In these terms the right side of the *Syringocrinus* tail is considerably more specialized than the left. The annulus of this genus might be likened to a temporal hiatus, in the crossing of which much that transpired has been eliminated from the record.

In *Dendrocystites sedgwicki* (Fig. 372, 377) the mesistele is a tessellated, multiplated, conical connection between the very flexible and profusely plated proxistele and the dimerous dististele. The adult mesisteles usually show an advanced condition of rosetting by which earlier-formed plates become isolated among many platelets which form in circles around them. However, on both larger steles and especially so on immature ones, it is possible to trace through five or six large plates the continuous serial course of dimeres into the tetramere series (Fig. 377). On the obverse mesistele the left half of the face is occupied by a continuation of the distal dimere series; the right side, by a distally diminishing series of six or seven plates which alternate with the left series. Laterally and at the junction with the dimere series, small plates may be intercalated; proximally the initial large plate of the diminishing series is commonly rosetted. This series disappears at a shoulder on the first obverse dimere. On the reverse face of the mesistele the inferiorly oriented dististele dimeres pass without interruption through a series of six or seven median plates. This median series of mesistele plates seems to correspond to a right proxistele series. A low axial keel is present on these median plates, and continues onto the corresponding dististele plates. On the right side of the median series the distally diminishing series of the obverse face covers about one-third of the reverse face; on the left there is another distally diminishing series of plates bounding the reverse medians; this series disappears on a left shoulder of the first dististele dimere on this side. Obviously, the mesistele bears tetramerous elements, just as in the much older *Minervaecystis,* but with this basic difference: the apparent rotation in the mesistele zone is in an opposite direction in the two genera (Fig. 378,*1c,2c*), and antipodal quadrants distally continue and diminish. *Dendrocystoides* show the basic mesistele gradation from four-part to two-part symmetry, accompanied by lateral rotation of keeled dimeres to a reverse position, the dististele being largely biserial. In *Iowacystis* the mesistele is undifferentiated from the dististele. In the mesistele zone there are no axial intercalates on the obverse face; on the reverse, one series of axial inserts is preserved. Both mesistele and dististele are somewhat depressed, and no rotation is in evidence.

DISTISTELE

Ordinarily the dististele is a long, rather firmly plated "tail," subequal in length to the remainder of the stele and in some specimens as long as the rest of the organism (some specimens of *Dendrocystoides*). Its plating is dominantly biserial or dimerous, usually passing from the first condition to the second distally. The basic orientation of the biseries, as described in morphology of the mesistele, is bilateral, one element deriving from the right or left obverse face, and the other from the left or right reverse, and consistently in a antipodal manner. Distal rotation either to right or left usually brings the biseries-dimeres to a fully obverse-reverse orientation with the sutures between the semicylinders lying in the projection of the thecal extensiplane. In *Dendrocystites sedgwicki* the dististele is attenuated and nearly terete, only a low keel occurring on the reverse dimere. In *Dendrocystites* and *Rutroclypeus* some specimens suggest a slight degree of prehensileness in the distal "tail." In *Heckericystis* a terete and highly attenuate dististele has been illustrated by GEKKER [HECKER] (1940). Usually the dististele is markedly flattened, and commonly asymmetrically. Whereas this flattening is always morphologic *depression,* the accompanying distal rotation creates the appearance of compression. The obverse members of the biseries are usually somewhat horseshoe-shaped in section; the reverse ones angular or keeled, some extending downward in a blade or comb. This asymmetry creates a caudal fin. This is lanceolate in profile in *Syringocrinus,* with serrations along the reverse edge created by distal imbrications of reverse dimeres; in *Minervaecystis* the pectinate comb of the keel might be likened to a "heterocercal" fish tail. In *Iowacystis* the biserial elements are essentially symmetrical and bilaterally disposed. They are depressed, being somewhat flattened in the extensiplane. Either no rotation occurs here, or in terms of the conditions illustrated in Figure 378 the two distally persisting homologues of the proxistele tetrameres rotate in opposite directions to occupy the vacated quadrants.

Because of the asymmetry and flattening of the dististele in most homoiosteles, the organ is usually preserved with the plane of depression parallel to the bedding; hence the usual restorations show the zigzag or rectilinear suture in the sagittal plane rather than the extensiplane. *Iowacystis* is the only form known so far in which the fossil dististele is actually preserved wholly in life position, and in this unique genus the suture was sagittal. *Girvanicystis* (Fig. 373) appears to have a very long dististele, composed of unequal but very long dimeres, but the suture lies in the extensiplane.

OCCURRENCE

DISTRIBUTION

Homoiostelea range in time from the Cambrian of Nevada and Upper Tremadocian (Lower Ordovician) of France well into the Lower Devonian of Victoria, Australia, and Germany. The maximum expansion came in the Middle and Upper Ordovician of Europe and North America. No Silurian representatives are yet known, and none from Asia, Africa, South America, or Antarctica.

PRESERVATION

Although homoiosteles, like other "carpoids," are among the rarest fossils, under exceptional circumstances they are abundant (see Fig. 385). In the Girvan Upper Ordovician of Scotland, the Middle Ordovician of Drabov and Zahorãny, Bohemia, and the Kingland district of Victoria, Australia, extraordinary concentrations have been encountered. Such deposits are clastic polymict sediments, and the fossil concentrations are commonly on single bedding planes. This probably represents the death setting under conditions of roily flow. The carcasses seem to be hydrodynamically oriented (see Fig. 385). Presumably roiliness was especially injurious to microphages such as these. The occurrences usually preserve the fossils as collapsed thecae, quite probably attesting to their rapid burial. Moreover, they are now encountered as ochre-stained molds comprising the residue from solution of the stereom lime and reduction of a pyrite filling of the stroma canals of the skeleton. Rapid burial of the living animal would probably create a reducing environment inside the labyrinth of canals of the skeleton; this setting is commonly one propitious for pyrite deposition. The resultant sediment, being relatively porous, permits ready circulation of water during weathering, and resultant solution of lime and oxidation of the pyrite. The sulphuric acid released in the transition from pyrite to limonite abetted solution of the calcium carbonate. In less porous clastics, like the fine-grained micaceous shales such as cover some specimens (see Fig. 383), the stereom is still intact. Lime ooze was especially fine for the preservation of dead skeletal parts in essentially living articulation. No concentrations of remains have yet been found in such deposits. Probably homoiosteles, like other "carpoids," were far more abundant in Paleozoic seas than fossils indicate; their delicate and commonly inflated thecae, whether tightly or loosely plated, were prone to destruction. Dissociated plates have never been reported. However, this is more artifactual than real. Commonly, beds which contain homoiosteles also contain many other echinoderms, starfishes, other "carpoids," cystoids, machaerids, and eocrinoids. Other organisms are usually rare in this echinoderm facies.

PHYLOGENY AND EVOLUTION

"Carpoids" as a whole have proved enigmatic as to broader phylogenetic relationship.

Homoiostelea share with other "carpoids" indubitable echinoderm relationships. They appear, however, to lie completely outside

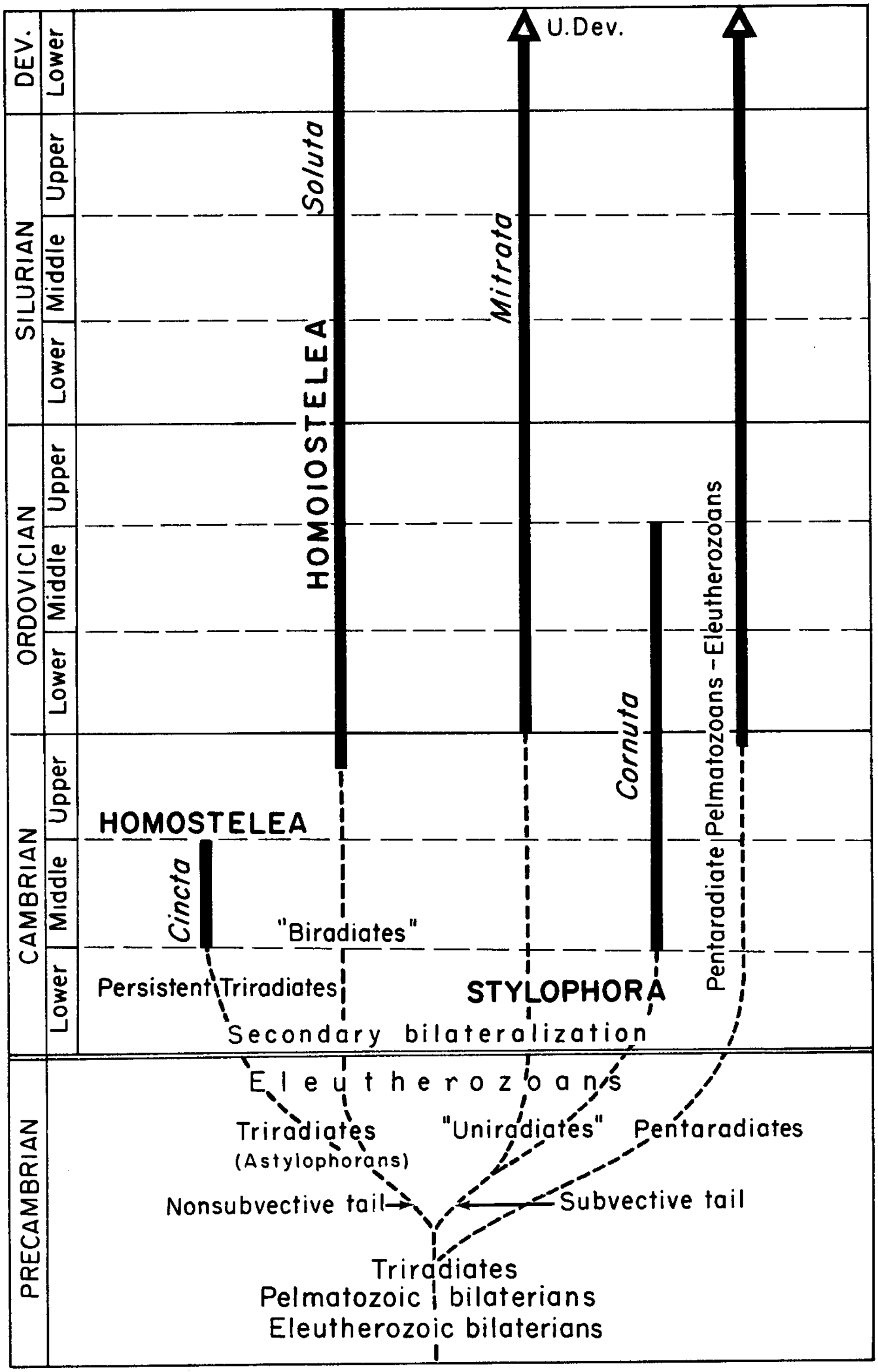


FIG. 380. Speculative phylogeny of "carpoid" classes (Caster, n).

any other echinoderm evolution. This is so fundamental that it presumably denotes a separate course, or courses, since pre-Phanerozoic times. It is my opinion that comparative "carpoid" morphology bespeaks a common ancestry of the three classes (Fig. 380). The still quite unknown triradial archetype would lie not only in the "carpoid" ancestry, but presumably also in that of all pentaradial pelmatozoans or pelmatozoan-derived classes.

This hypothesis entails the radial homologizing of arm and stele in the homoiosteles; according to this theory both were originally biserial subvective organs. Hence, the homoiosteles are termed "biradiates" (Fig. 380), the third radius having been suppressed prior to our encounter with the class. The aulacophore "tail-arm" of the Stylophora was the sole radial survivor there, and this group is labeled "uniradiates."

Within the class Homoiostelea there are too many hiatuses in the record and too much morphologic differentiation between the forms so far encountered to make phylogenetic speculation very meaningful. However, a few generalities are in order. Much has been discovered since the speculations of BATHER (1900, 1913, 1930) and JAEKEL (1899, 1901, 1921), which have largely colored all subsequent thinking about "carpoid" relations. In that phase of echinodermology the "Amphoridea" concept played a prominent role; since the "carpoids" were thought of as Pelmatozoa, and all fixed forms were supposed to derive from a loosely plated saclike form fixed at one extremity, regularization of plates was postulated as focusing on the point of fixation and at the arm base; both arms and peduncle were thought of as regularized extensions of the theca. Thus, when BARRANDE's *Dendrocystites sedgwicki* of the Bohemian Middle Ordovician was supposed to be one of the oldest "carpoids" (although the Cincta: Homostelea were then and still are oldest of all), its theca composed of many, apparently loosely articulated and little-if-at-all-regularized plates, its polyplated proxistele, and many small plates in the zone between first plates of the arm biseries and large thecal plates, all seemed —especially to BATHER—to support the "Amphoridea" hypothesis. Now, with better knowledge of the organization of BATHER's *D. barrandei,* from somewhat lower in the Bohemian Ordovician, of the juvenile stages of *D. sedgwicki* itself, and especially with the discovery of the Tremadocian *Minervaecystis* and a comparable stele from the Nevada Cambrian, the *Dendrocystites* support of the "Amphoridea" hypothesis fails. Instead of polyplating of the stele and gradational plating from theca to arm being archetypical, both are now seen to be specializations. In both the oldest forms and in juveniles of the specialized ones, tetramerous proxisteles and adbrachial regularized plates are the rule. *D. sedgwicki,* in the new light, is a highly specialized form, in which interstitial platelets and fractionation of antecedent large plates both occur.

Minervaecystis is far from a primitive homoiostele, and in many respects (e.g., its pectinate dististele keel) is very specialized. In its stele anatomy, however, it probably is the most primitive form yet known. Thus, far, no data are available which might indicate what organization of the proxistele may have antedated the tetramerous one. If the appendage is a modified arm, as here urged, its biserial nature and cover-plate series may be very ancient indeed (e.g., eocrinoids). Certainly this genus possesses the largest number of tetramere annuli known. Even so, its mesistele and dististele represent advanced locomotor specialization.

Until it is known how stele plates proliferated, any biogenetic interpretation of the axial differentiation of the stele is risky. When the stele was thought of as "another kind of stele," (i.e., column, hence "heterostele"), small attention was paid it. Its growth would be presumed to be mainly by intercalation of new skeletal elements at the proximal plane as in "other Pelmatozoa." Thus, if any biogenetic significance were to be attached to axial differentiation, the more distal elements would reflect an older phylogenetic state. If, on the other hand, the stele is a modified arm, it presumably grew like arms, with distal increments of parts. Thus it might be, and here is urged, that the distal succession from tetrameres to biseries to dimeres is quite possibly palingenetic[1] and Jacksonian,[2] hence of considerable phylogenetic importance. The very long series of tetrameres in *Minervaecystis* would seem to support this concept; likewise the well-documented transition from four-part to two-part symmetry of the oldest mesisteles, and distal transition from biseries to dimeres in many dististeles. (However, in *Minervaecystis* and *Dendrocysittes sedgwicki* the distal sequence is from dimeres to biseries. Thus the latter may well correlate with the prehensile flexibility of the tip of the tail.) In general, the older solutes have more armlike steles, solutan arms being basically tetramerous.

Within the Homoiostelea too many geologic and morphologic gaps separate the known genera to make lineage speculation worthwhile. Except at the species level, relationships are obscure. Although Gill & Caster (1960) indulged in a bit of speculation in this field, further information does not especially enhance their surmises. As the classification brings out, the generic differentia are, for the most part, comparable to family taxobases used elsewhere in the phylum.

---

[1] Palingenesis, a succession of ontogenetic events which appear in the same order as the phylogenetic events which they supposedly recapitulate; this would be documentation of biogenesis.

[2] Robert Tracy Jackson attempted to apply the "biogenetic law" (biogenesis) to serially developing organs such as an ambulacral series of plates. It was his contention that the ontogeny of such a series tends to rehearse the evolutionary history of the organ.

SYSTEMATIC DESCRIPTIONS

Class HOMOIOSTELEA
Gill & Caster, 1960

[*nom. transl.* Caster, herein (*ex* subclass Homoiostelea Gill & Caster, 1960) (of the class Carpoidea Jaekel)] [=order Amphoridea Haeckel, 1896 (of class Cystidea) *(partim)*; Dendrocystidae Bather, 1899 (of order Amphoridea); order Soluta Jaekel, 1901 (of class Carpoidea, subclass Heterostelea); suborder Heterostelea Bather, 1913 (of order Amphoridea); class Carpoidea Bather, 1929 *(partim)*; superorder Astylophora Gill & Caster, 1960 (of subclass Homoiostelea)]

Ancient, eleutherozoic, asymmetrical echinoderms without obvious radial symmetry elements; usually depressed, and tending toward bisymmetry; theca of fixed form, multiplated; plates usually both facially and regionally differentiated (adsteleal, abbrachial, adanal); some regional provision for visceral expansion and contraction usual in thecal plating; single biserial, usually distal-lateral, arm bearing biserial cover plates; mouth subthecal; anus posterolateral in most forms; heterostele ("tail") posterior, long and composed of axially differentiated plates: proxistele flexible and fundamentally tetramerous; mesistele transitional from four-part to two-part plate symmetry: dististele usually biserial proximally and dimerous distally; adbrachial plate bearing hydropore and gonopore, where known. *U.Cam.-L.Dev.*

Order SOLUTA Jaekel, 1901

[=suborder Soluta Jaekel, 1901 (of class Carpoidea, order Heterostelea, *partim*); suborder Soluta Jaekel, 1918; order Soluta, Gill & Caster, 1960]

Characters of class. *U.Cam.-L.Dev.*

Seven families and ten genera of Soluta are recognized as follows:

1) Minervaecystidae Ubaghs & Caster, n.fam., *?U. Cam.,L.Ord.*, Eu.(France)-N.Am.(USA).
    Minervaecystis Ubaghs & Caster, n.gen., *U. Cam.*, N.Am.(Nev.) ("unnamed solutan," Ubaghs, 1963); *L.Ord.*, Eu.(France). (**Dendrocystis vidali* Thoral).
2) Dendrocystitidae Bassler, *M.Ord.-L.Dev.*, Eu.-N.Am.
    Dendrocystites Barrande, *M.Ord.*, Eu.(Boh.). (**Cystidea sedgwicki* Barrande); *D. barrandei* Bather.
    Dendrocystoides Jaekel, *U.Ord.*, Eu.(Scot.). (**Dendrocystis scotica* Bather).
    Heckericystis Gill & Caster, *M.Ord.*, Eu. (Est.). (**Dendrocystites kuckersianus* Hecker).
    Dehmicystis Caster, n.gen., *L.Dev.*, Eu.(Ger.). (**Dendrocystites (Dendrocystoides?) globulus* Dehm).
3) Girvanicystidae Caster, n.fam., *U.Ord.*, Eu. (Scot.).
    Girvanicystis Caster, n.gen., *U.Ord.*, Eu. (Scot.). (**G. batheri* Caster, n.sp.).
4) Rutroclypeidae Gill & Caster, *L.Dev.*, Australia.
    Rutroclypeus Withers, *L.Dev.*, Australia (Victoria). (**R. junori* Withers); *R. withersi* Gill & Caster.
5) Syringocrinidae Parsley & Caster, *M.Ord.*, N. Am.(Can.).
    Syringocrinus Billings, *M.Ord.*, Can.(Ont.). (**S. paradoxicus* Billings); *S. sinclairi* Parsley & Caster.
6) Iowacystidae Gill & Caster, *U.Ord.*, N.Am. (USA).

Iowacystis Thomas & Ladd, *U.Ord.*, USA (Iowa). (**I. sagittaria* Thomas & Ladd).

7) Belemnocystitidae Parsley, n.fam.[1] *M.Ord.*, USA.

Belemnocystites Miller & Gurley, *M.Ord.*, USA(Ky.). (**B. wetherbyi* Miller & Gurley).

Family MINERVAECYSTIDAE
Ubaghs and Caster, new family

Characters of *Minervaecystis*. *?U.Cam.*, *L. Ord.*

Minervaecystis Ubaghs & Caster, **new genus** [**Dendrocystites vidali* Thoral, 1935; M] [=*Dendrocystis* sp., Bather, 1913]. Large solutans with inflated, somewhat depressed theca, unequally biconvex, or possibly convexisubplanate; ovoid in profile, without lobation; thecal plates large, thin, nonimbricate, unornamented except near anus where they are granular; obverse plates somewhat smaller than reverse ones; flanks covered by regularly curving tessellation; facial differentiation gradual over the flanks. Arm and anus opposite; arm emerging abruptly, without plate gradation, from distal right margin of obverse face or slightly on flank; anus on proximal left in obverse face near posterior margin; arm long, narrow and very flexible in life, compressed, slightly angular aborally, presumably biserial and composed of opposite brachial plates, however, no aboral suture in evidence; confluent brachiole pairs imbricate distally; cover plates large, subequal in width to brachial flank, meeting in low arch over ambulacral groove, apparently not quite in series with brachials. Adbrachial circlet of plates forms imbricating collar or sheath about arm base; left, obverse, lateral sheath plate bearing 2 hemispherical prominences which presumably represent hydropore and gonopore. Anus covered by low circular "pyramid" of elongate subtrigonal plates. Stele very long and complexly zoned; proxistele inflated, slightly compressed, nearly terete, tetramerous and anomalocystitoid, comprising some 25 to 30 annular, telescopically imbricating rings, last 6 or 7 progressively diminishing in diameter toward mesistele and last tetrameres about twice as long as others, each tetramere bearing proximal external bourrelet or thickened lip which deeply imbricates beneath proximal adjacent tetramere, distal margins of tetrameres scalelike and feather-edged, also with low angular fold crossing each left reverse tetramere at mid-width in alignment with carina which diagonally crosses mesistele and becomes prominent keel on proximal dististele; mesistele short, mainly covered by 2 series of plates, one of which aligns with right obverse tetrameres and other, with left reverse, distally continuing as dististele dimeres-biseries (Fig. 378); alternate tetrameres aligned with 2 series of 2 or 3 distally diminishing plates which lie between dominant series of mesistele; mesistele zone short, and making distal transition from 4-part to 2-part symmetry; almost no mesistele in some specimens; dististele very long, narrow tail showing compression of double series of plates, and rotation (Fig. 378); proximal dististele composed of 2 or 3 long dimeres, suturing on extensiplane, reverse dimeres being carinate; mesial zone of long plates which show distal transition from dimerous to biserial, each of 3 proximal plates in this zone reversely bearing very high, comblike blade at about midlength of postproxistele tail; distal dististele forms narrowly lanceolate, caudal fin composed of biserial plates, flattened in extensiplane (plane of zigzag suture); obverse fin plates asymmetrically rounded, reverse ones angular; stele elements all flexibly joined *?U.Cam.*, N.Am.(Nev.); *L.Ord.(Tremadoc.)*, Eu.(France).——Fig. 381. **M. vidali* (Thoral), Tremadoc., France; *1*, reverse face of holotype, ×2; *2*, oral detail of holotype arm and adbrachial pore plate, ×6; *3*, aboral view of holotype arm (note lack of aboral suture), ×6; *4*, anal pyramid of holotype, ×6; *5*, lateral view of mesistele and proximal dististele, ×4; *6*, obverse aspect of complete stele with cross sections at indicated places, ×3.5; *7*, detail of distal 2 pectinate dimeres of dististele, ×12 (Ubaghs, n). [See Fig. 378,*2*.]

Family DENDROCYSTITIDAE
Bassler, 1938

[=Dendrocystidae Bather, 1899]

Theca widely variable, but always asymmetrical; usually depressedly inflated; faces poorly or well differentiated; most plates tessellated and firmly joined; always some provision for expansion and contraction of viscera by flexible union of some thecal plates; arm and anus commonly on left side, but variable in position; proxistele fundamentally tetramerous and anomalocystitoid, but commonly modified by the addition of secondary platelets and possibly modified by tetramere fusing into narrow annuli; mesistele showing distal transition from four-part to two-part symmetry of plate series; obverse left and reverse right tetramere series distally continuous with biseries-dimeres of dististele. *M.Ord.-L.Dev.*

Dendrocystites Barrande, 1887, p. 142[2] [**Cystidea*

---

[1] While this section of the *Treatise* was in preparation, *Belemnocystites* was discovered by Ronald L. Parsley of the University of Cincinnati to be a solutan and in Parsley's opinion a new family is essential for its inclusion. His more detailed analysis will appear elsewhere.

[2] Several authors have attributed new taxa published in *Système Silurien . . . de la Bohême: Classe de Echinodermes, Ordre des Cystidées* (v. 7, pt. 1) to Waagen, who served as Barrande's posthumous editor. In the introduction to the volume, Waagen took pains to deny any share in authorship; thus the new taxa presented therein belong to Barrande.

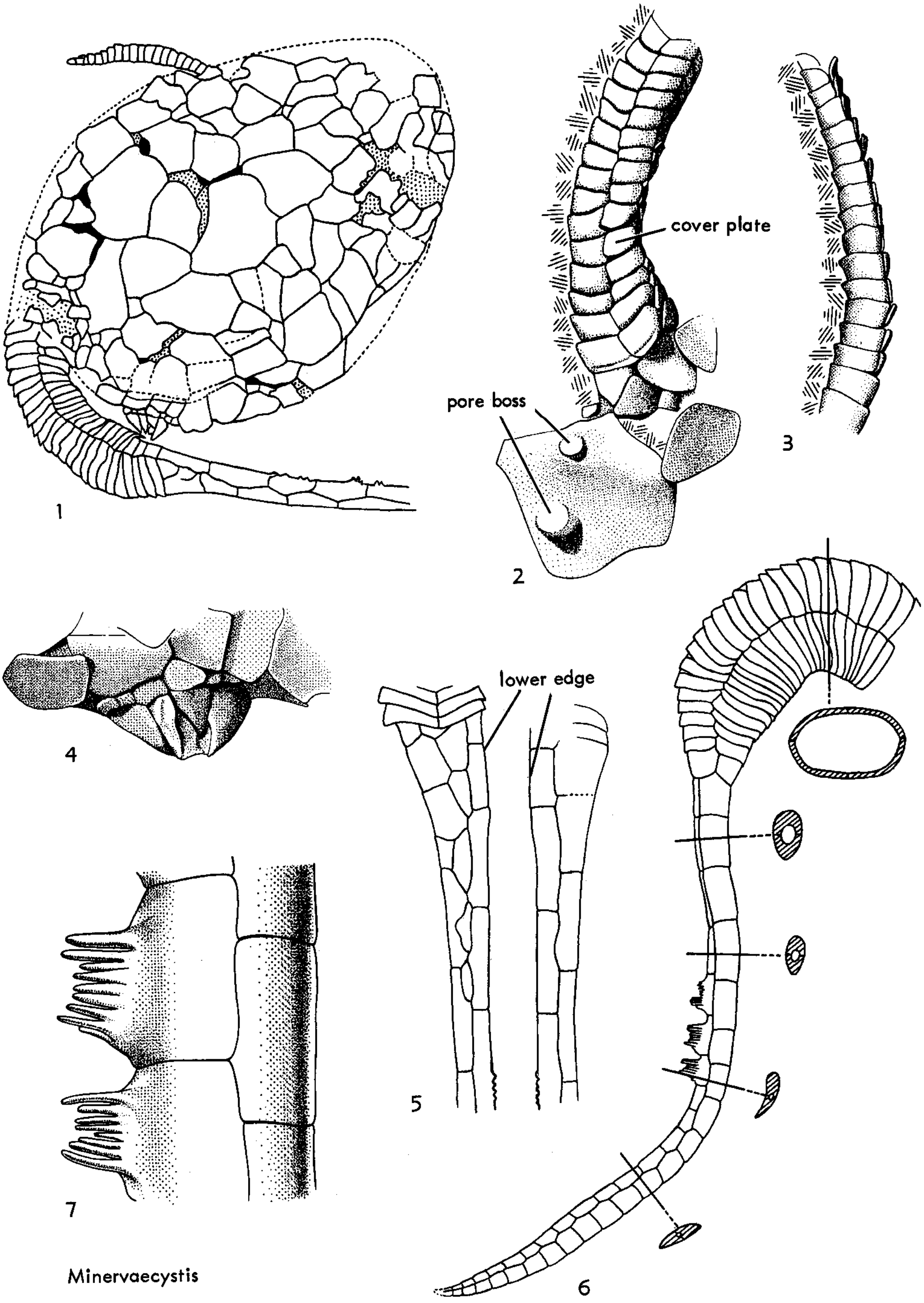


Fig. 381. Minervaecystidae (p. *S606*).

Sedgwicki Barrande, 1867, p. 179; OD] [=*Dendrocystis* Bather, 1889, p. 268 (obj.) *(nom. van.)*]. (Diagnosis based on type species.) Large dendrocystitids with lobately triangular thecal outline, especially in usual flattened state; theca depressedly inflated, obverse and reverse faces differentiated both in configuration and in plate details, obverse face usually convex and topographically complex, reverse flat to concave and simple; thecal margins usually rounded, may be subangular or sutural; position of arm, anus and thecal lobation asymmetrical; prominent, angular left proximal lobe, but only very faint lobate rounding on right side; left lobe composite, with large angular preanal lobe and rounded anal lobe *(s.s.)*; distal margin moderately lobate. Arm commonly distal and sinistral, emerging from obverse thecal face; may be nearly axial and in some individuals dextral. Anus marginal and usually on posterior lateral face of left proximal lobe, rarely on right side, when large proximal lobe is also dextral. Thecal plates many, tessellated, firmly united in life (not imbricated as in usual crushed specimen), except for localized flexible junction, these plates about equal in size and number on both faces, relatively large and few in juveniles but abundant and smaller in adults; plate increment mainly by sutural intercalates (rosetting). Obverse face somewhat swollen in distal third, with broad oval tumescence of flexibly joined, large, ornamented, polygonal plates in widest proximal part of theca (apparently to accommodate expansion and contraction of viscera); larger movable plates bearing central boss and radiating costae; ribs increase in width and elevation toward plate margins, smaller (younger) plates bearing low central umbo and peripheral nodes, latter increasing in prominence and extending toward center of plate with increase in plate size. Mobile tumescence proximally bordered by tightly fused girdle of adsteleal plates and distally by bounding arc of unornamented, firmly united thecal plates, each of which upwardly geniculates at low angle toward tumescent area, and on inner surface bears low bounding ridge on line of geniculation. This ridge can be traced across plates of internal obverse face from preanal lobe to widest part of right proximal lobation. [The bounding ridge and geniculated plates serve in complexly preserved and incomplete specimens as an excellent key to the obverse face.] Brachial orifice nearly circular and surrounded by constant number of adbrachial plates, one on left side bearing wartlike node which is apparently madrepore-hydropore. Adbrachials, like entire distal thecal plates, firmly joined in life, with low flange developed adjacent to orifice; between adbrachials and tetramerous arm, several circlets of small platelets intervene in largest specimens and are inconspicuous in juveniles. Marginal anus covered above by rounded lappet which makes outline of anal lobe *(s.s.)*; center of lappet occupied by ovate-subtrigonal, convex suranal plate (Bather's "sugarloaf plate"); this is distally margined by arc of small, polygonal plates, and laterally-reversely by radiating narrow plates (probably periproctal); preanal lobe very prominent and angular. Arm slightly compressed and longer than theca; aboral suture between brachial biseries apparently open; brachials about twice as wide as cover plates, with which they are essentially in annular series; cover plates meeting in zigzag adorally. Stele long and axially differentiated into 3 zones: proxistele basically anomalocystitoid, but in adulthood many small platelets are developed so as to conceal juvenile 4-part symmetry. [This is especially true of *Dendrocystites* where young forms show tetrameres (or octameres) between which platelets form on all sides.] The ephebic proxistele is an alternating series of 6 to 8 larger and smaller rings of platelets, the first being composed of larger firmly united elements, and the second of many plates loosely joined. Despite rosetting, the mesistele bears evidence of tetramere series, 2 of which persist distally into the dimerous series; 2 alternates diminish in size and disappear in length of the mesistele. Here, as in *Minervaecystis,* the dististele is proximally dimerous and distally biserial; plates of distal extremity loosely joined, and faceted so as to permit some prehension; dististele may be somewhat compressed, and reversely keeled. *M.Ord.,* En.(Boh.), questionable elsewhere.——Fig. 382, 383. **D. sedgwicki* (Barrande), M.Ord., Boh.; 382, rubber molds of type and topotype specimens in National Museum, Praha (all photos Caster, n); 382,*1,* oblique view into undeformed proximal interior of obverse thecal face (proxistele insertion as in life, anal lappet at right) showing tessellation of plates and rigidity of test (Barrande type), ×2; 382,*2,* obverse view of immature form in which proxistele tetrameres are in process of fractionation (note rosetting of proximal mesistele), ×2; 382,*3,* reverse view of interior surface of obverse plates showing usual imbrication of plates due to compression during fossilization (note hydropore pustule on adbrachial plate, multiple platelets of proxistele, and carination of axial series of mesistele) (Barrande type), ×1.5; 382,*4,* obverse view of topotype with complete stele which lacks evident keeling and shows distal dimere sutures beveled as for some degree of prehension (Barrandium, Praha), ×1; 382,*5,* obverse view of young individual with short tetramerous proxistele and tessellated thecal plates which are relatively few and very large (topotype, Barrandium, Praha), ×2; 383,*1-3,* obverse views of new material (Narodni Museum, Praha) showing calcareous plates intact, ×1 (Caster, n.).——Fig. 384,*2;* 385. *D. barrandei* Bather, Low.M.Ord., Boh.; 384,*2,* specimen figured by Bather (1913), ×1.7; 385, rubber mold of part of slab covered by oriented specimens in usual state of preservation of homoio-

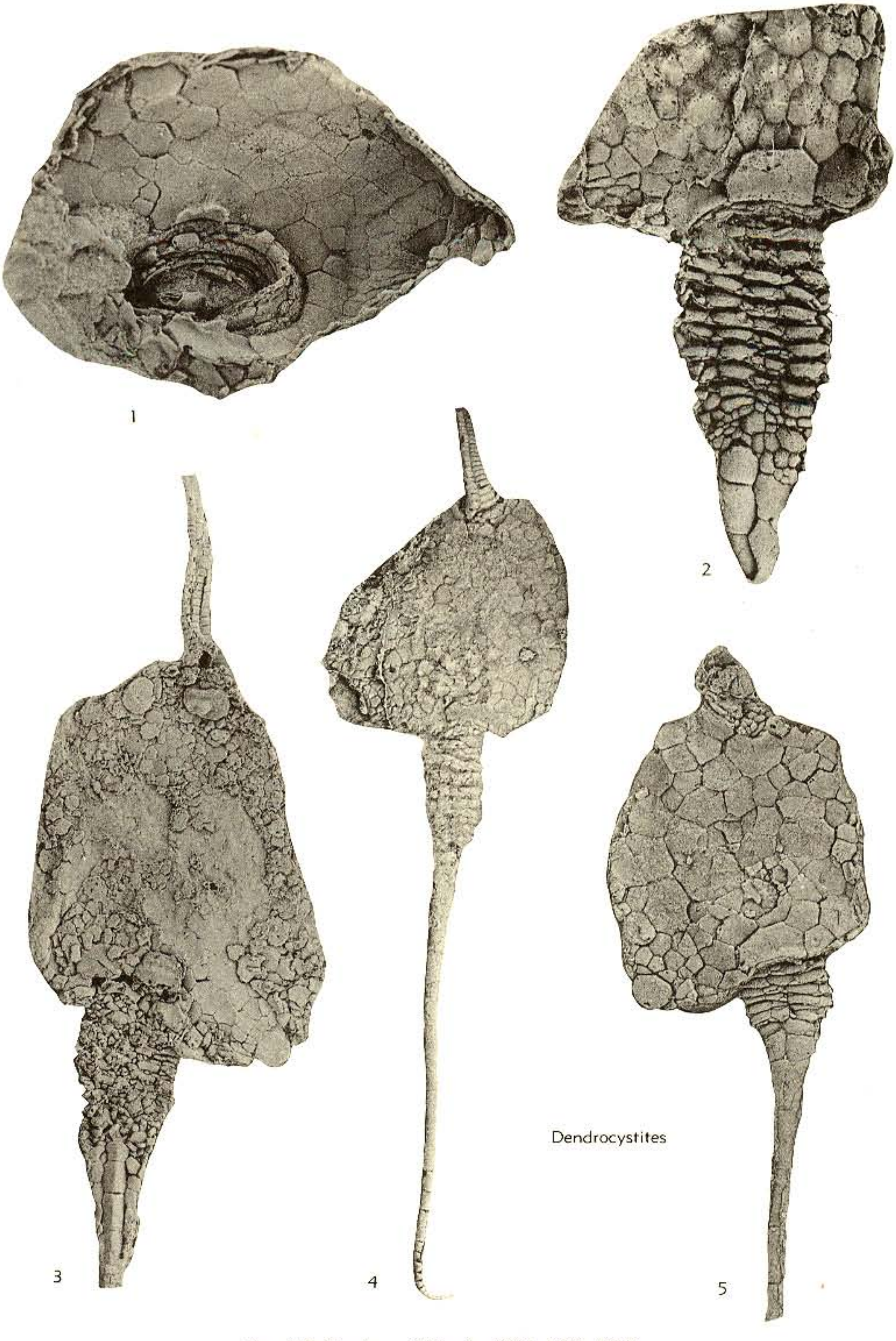


FIG. 382. Dendrocystitidae (p. S606, S608, S610).

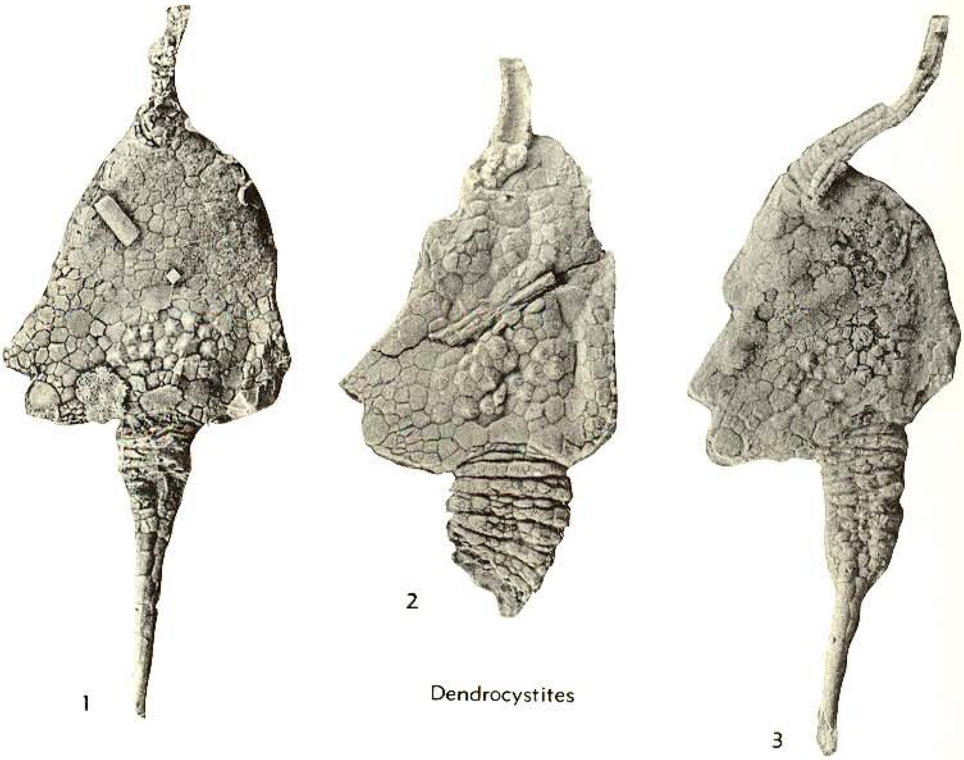


FIG. 383. Dendrocystitidae (p. S606, S608, S610).

steles (note tetramerous proxisteles), ×2.7 (Caster, n). [See Fig. 387.]

[Although it shares several traits with *Dendrocystites sedgwicki*, the form designated as *D. barrandei* is more pyriform, less lobate, and more symmetrical. Also, its faces are less well differentiated and more of its thecal plates are loosely articulated, a maximal tumescent zone not being distinguished. Probably the species named by BATHER is generically distinct from *Dendrocystites*. The thecal plates of *D. barrandei* are relatively fewer and larger than those of *D. sedgwicki*, with rosetting unimportant and platelets few. The arm of *D. barrandei* is nearly axial in position, with large geniculating adbrachials which imbricate laterally to form an adbrachial sheath. No obvious anal lobe or lappet is seen and a single subanal plate occurs beneath the anus on the reverse side or rounded posterior wall of the theca. The preanal lobe is equally angular and prominent in both species. The proxistele of *D. barrandei* is tetramerous and anomalocystitoid, with a few platelets in some individuals between the tetramere sutures and annuli. The mesistele bears clear indication of distal transition from tetrameres to dimeres.]

Dendrocystoides JAEKEL, 1918, p. 123 [**Dendrocystis scotica* BATHER, 1913, p. 391; M]. Large dendrocystitids with hornlike processes and large, unequal, proximal lobes. Outline very irregular, but main theca generally trapezoidal; some hourglass-shaped; arm and anus on left side, marginal; arm emerges from obverse distal margin; anus from posterior reverse margin of left proximal lobe; subangular and protuberant preanal lobe; rounded inconspicuous anal one. Obverse face irregularly convex; reverse face nearly flat. Theca commonly much constricted just proximal of emergence of arm and antibrachial process. Usually with large antibrachial horn arising from right distal corner, its dimensions highly variable, but commonly subequal to arm; it may arise from obverse surface or distally; commonly very broad-based and almost lobelike; supplementary processes of similar dimensions may occur on distal left or laterally; antianal lobe may be extended in a process. All processes plated like theca, and containing extension of thecal cavity. Thecal plates large, angularly polygonal and nonimbricating in life; no striking differentiation in size or configuration of two faces; surface finely granular except on reverse face near anus, where plates are coarsely granular or pitted. Adbrachial plates rise as imbricating sheath about base of arm; left lateral adbrachial bearing complex tumescence which probably represents hydropore. Arm long, compressed and flexible; aboral suture ligamental; cover plates about half as wide as brachials; ambulacral groove narrow, cover plates standing at high angle over it and meeting adorally in zigzag, but in series with brachials to which they articulate; cover plate-brachial suture line sharply depressed; internally each cover plate grooved for its whole width. Anus may have been sphincterally closed and slitlike; its region on posterior surface crowded with very long and narrow periproct plates; anus floored by broad reverse lappet in which ovate subanal plate lies to one side of concentration of periproct plates. Stele long and differentiated. Proxistele tetramerous and anomalocystitoid, with many small polygonal integumentary plates in zone of flexible tissue between tetramere rings; best

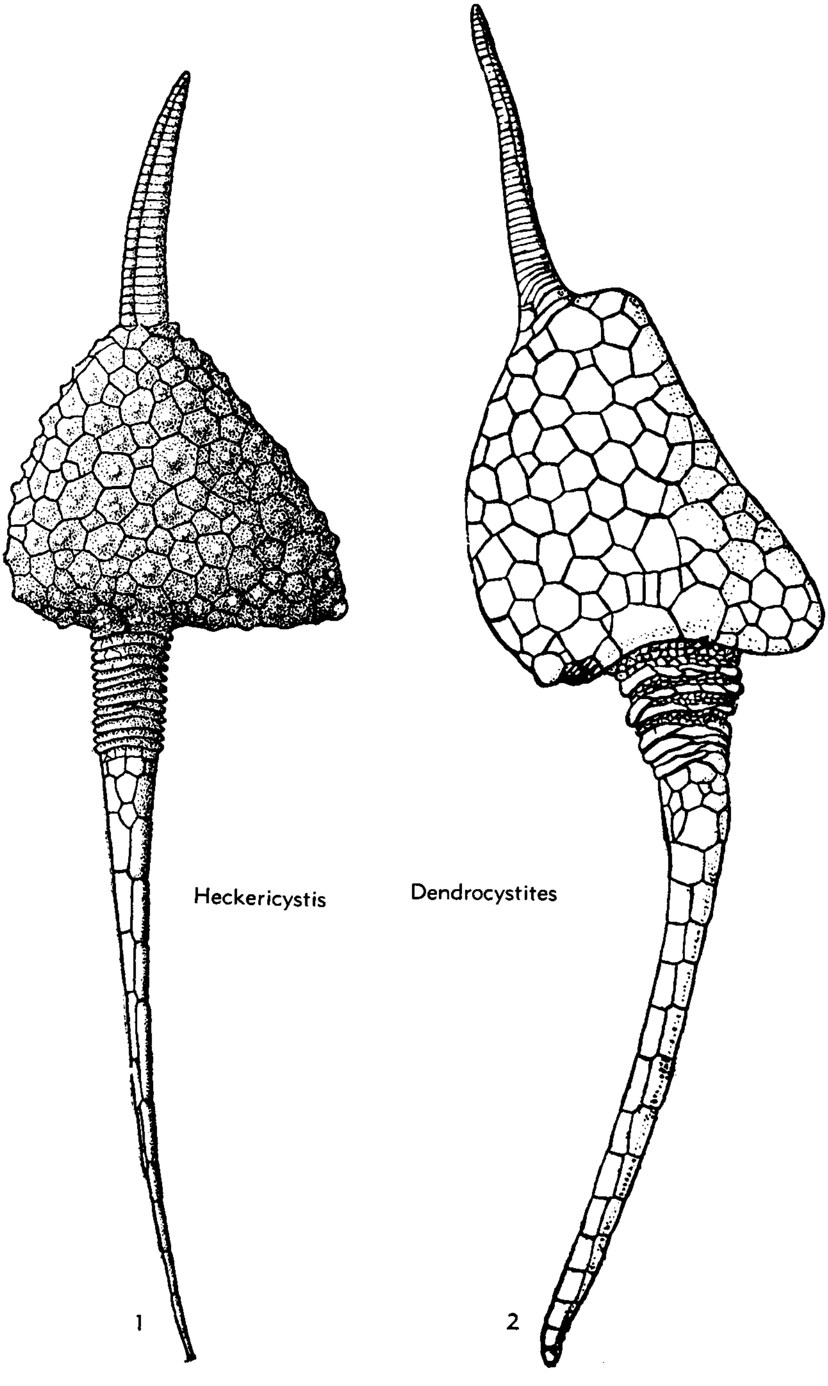


Fig. 384. Dendrocystitidae (p. *S*606, *S*608, *S*610, *S*613).

seen in specimens preserving inside view of tetrameres. Externally proxistele meres may be smooth, thin and almost scalelike, or very much thickened and complexly, radially rugose in completely unique manner. Mesistele reminiscent of *Minervaecystis,* with biseries of dististele correlating across mesistele with tetrameres in same manner as in that genus. Dististele very long and narrow, terete and composed of long dimeres proximally; these shift to alternating position distally; actual end of stele not seen. Dimere orientation obverse and reverse; suture in extensiplane. *U.Ord.,* Eu.(Scot.).

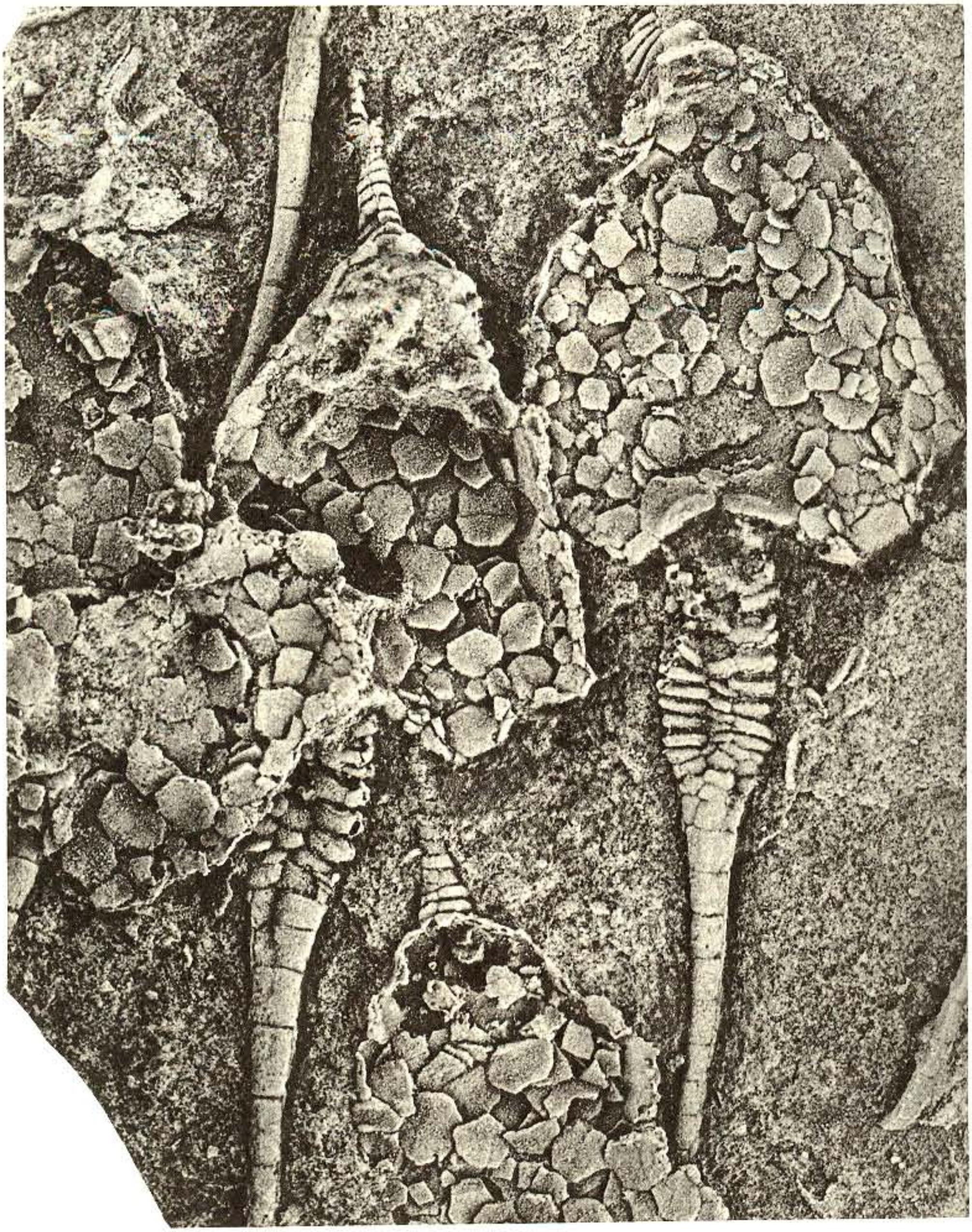


FIG. 385. *Dendrocystites barrandei* BATHER (Dendrocystitidae) (p. S606, S608, S610).

——FIG. 386, 387. **D. scoticus* (BATHER); 386, reverse face of BMNH E23700, fairly complete but with somewhat disarranged thecal plates, ×2.1 (Caster, n; drawing by E. A. Dalvé); 387, *1-6,* rubber molds of topotypes, all from BMNH; 387,*1,* reverse face showing usual imbrication of plates induced by compression during fossilization, with complete "antibrachial" horn, large hydropore pustule on right side of figure; arm slightly twisted so as to conceal aboral suture of brachial biseries (E23700), ×2.2; 387,*2,* reverse view showing proximal plates in tessellated life position (note granular ornament on these plates) imbricate periproct plates on posterior margin of anal lobe at right, hydropore pustule apparently with 2 pores, proximal stele unornamented (E5732), ×2.2; 387,*3,* arm detail, obverse view with adbrachials in place, hydropore pustule prominent (E5823), ×2; 387,*4,* reverse view of highly ornamented proxistele (note also many platelets inside lumen) (E5827), ×2.5; 387,*5,* reverse view of ornamented proxistele and interior surface of obverse tetrameres showing bourrelets (note axial rotation of keel in mesistele) (E5719), ×2.2; 387,*6,* reverse view of distal theca and arm (note biserial meeting of cover plates) (E5822), ×2 (all Caster, n). [See Fig. 376, 379.]

Heckericystis GILL & CASTER, 1960, p. 16 [**Dendrocystites kuckersiana* GEKKER [HECKER], 1940, p. 23; M]. Theca inflated, asymmetrically trigonal in profile; probably somewhat depressed, proximal subangular anal lobe; arm distal; anus at apex of anal lobe and apparently closed by or beneath prominent mammelon (or "sugarloaf plate"); thecal plates small and polygonal, each with central prominence; nothing known of facial or regional thecal differentiation. Arm biserial and moderately long; stele long and terete throughout, differentiated into 3 zones. Proxistele sheathed in many narrow elevated rings, probably tetramerous, but no sutures reported; intervening zones apparently integumentary; mesistele shown as composed of 3 circlets of polygonal platelets decreasing in number in each ring distally and suggesting transition from tetramerous to dimerous; dististele attenuate, sheathed in dimeres which are laterally opposed proximally, and obversely-reversely in distal region. *M.Ord. (Kuckers),* Est.——FIG. 384, *1. *H. kuckersiana* (GEKKER) [HECKER], ×1.7 *(43).*

Dehmicystis CASTER, **new genus** [**Dendrocystites (Dendrocystoides?) globulus* DEHM, 1934, p. 20; M]. Spherically inflated (or moderately depressed), appearing circular when crushed; thinly plated, unornamented; anus large, circular and proximal, covered by large pyramid of elongate trigonal imbricating plates; some periproctal plates between anal pyramid and adanal thecal plates. Proxistele anomalocystitoid, very flexible; dististele long and dimerous. [GILL & CASTER (1960) tentatively assigned this species to *Rutroclypeus,* but further examination of the holotype reveals a large circular anal area, and strongly supports DEHM's original idea that the theca was inflated in life; hence the new assignment.] Only incomplete holotype known. *L.Dev. (Bundenbach),* Eu. (Ger.).——FIG. 388,*1,2. *D. globulus* (DEHM); *1,* original figure, ×1.1 *(34)*; *2,* drawing from

FIG. 386. Dendrocystitidae (p. S610-S613).

photograph of holotype and only known specimen (note anal pyramid), ×1.4 (Caster, n).

Family GIRVANICYSTIDAE Caster, new family

Solutans covered by relatively few large plates rigidly fused into two opposable faces united by flexible peripheral suture on extensiplane; prominent crest and spines on reverse face; proxistele anomalocystitoid, with many small platelets on proximal exterior of tetrameres. *U.Ord.*

Girvanicystis Caster, **new genus** [**G. batheri* Caster, **new species**; M]. Large, obliquely cordiform

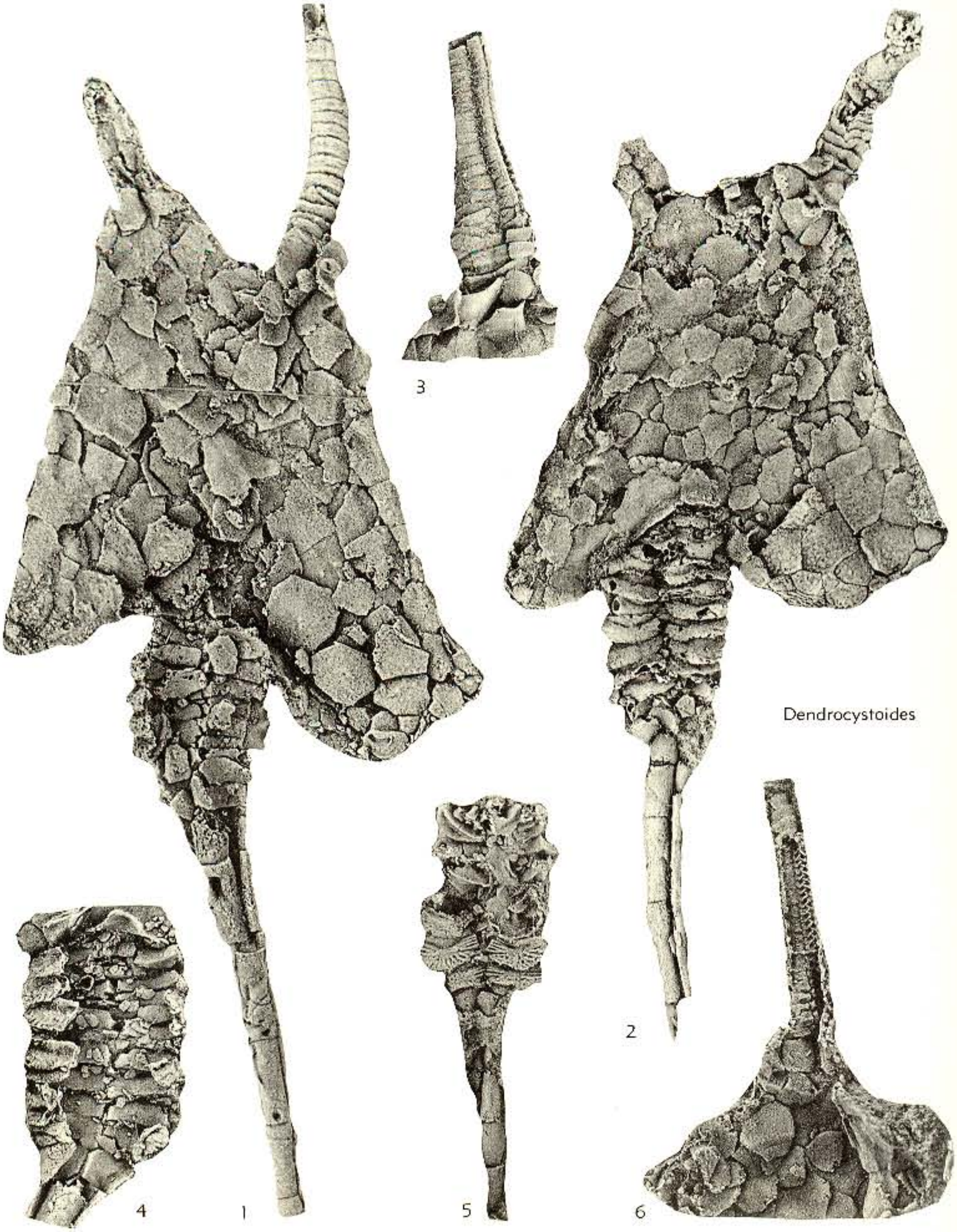


Fig. 387. Dendrocystitidae (p. S610-S613).

dendrocystitid, prominently and asymmetrically trilobate, with very large, unequal, rounded proximal lobes, anal one being larger; right anterolateral rounded lobe which extends well on distal side of level of arm insertion. Arm and anus on left side; anus well within reverse face of anal lobe; arm inserted on perimeteral suture between 2 thecal faces and essentially on thecal axis of balance. Deep rounded proximal re-entrant for insertion of stele. Thecal profile complex, but in general subplano-convex, obverse face being far less inflated than reverse one; marginally, except in immediate vicinity of arm base, both faces subplanate (perhaps slightly concavo-convex), in broad zone and apparently nearly in contact in life; obverse face apparently rose in broad axial arch, whereas reverse one shows distinct zones of tumescence: central area of anal lobe distended and bearing periproct with very high, asymmetric tumescence on distal side of this on left of thecal axis and extended to distal margin where it formed vertical distal wall of theca; beneath arm

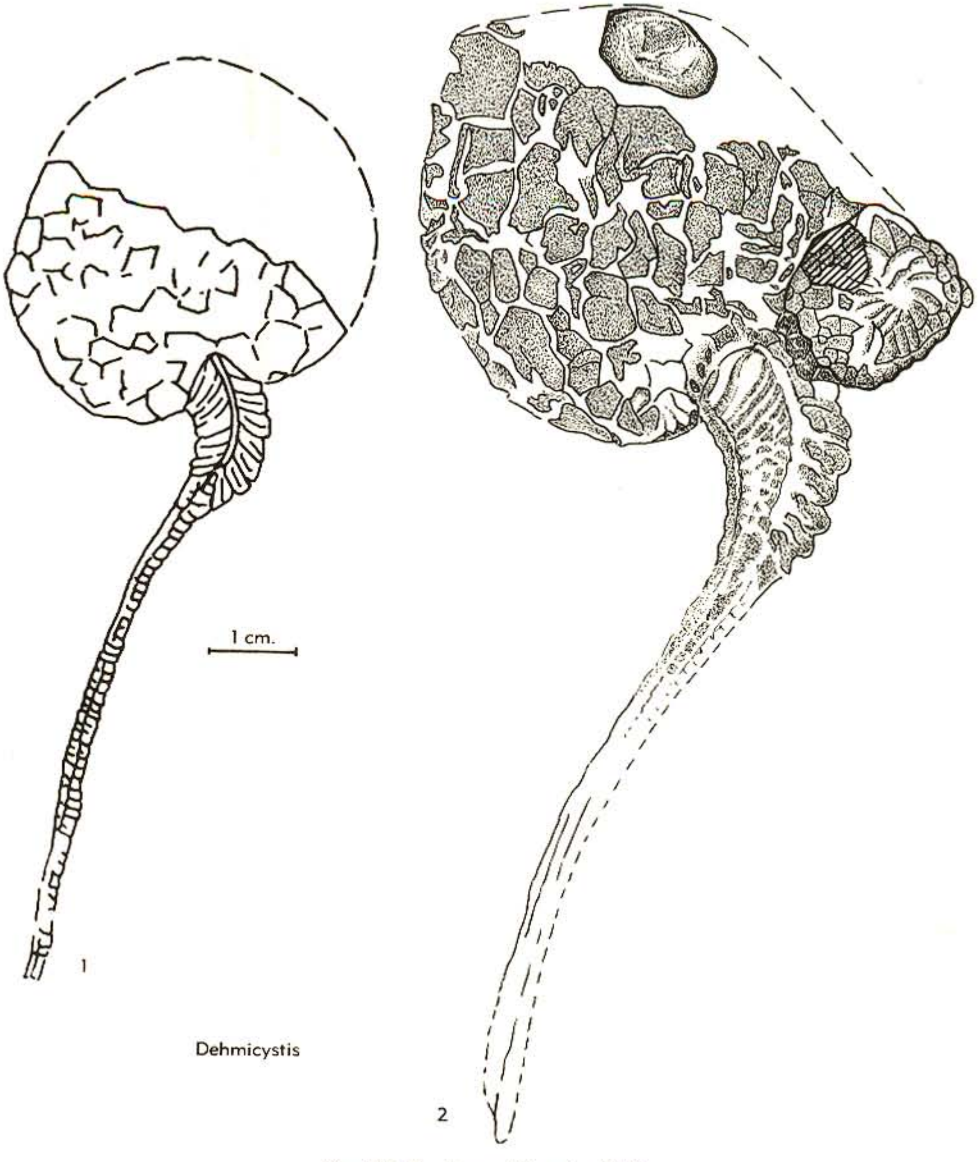


FIG. 388. Dendrocystitidae (p. S613).

insertion reverse theca was bowed angularly and sharply. [Thecal surfaces appear to have been largely rigid in life, their contact sutural and integumentary; with obverse face narrower and shorter than reverse one, and with something of an opercular nature; both perimeters are thickened considerably and in such way that they articulated in pillbox manner with obverse margin lying within the reverse one and fitting into a smooth deep groove just inside the thickened margin of the reverse face.] Thecal plates extraordinarily large, those of reverse side being larger and (discounting periproct area) fewer than obverse. Tight fusion of plates of both faces manifest and breakage does not always seem to follow old suture lines. On right distal lateral side of reverse theca, just proximal of anterior lobe, several large plates fuse to form radially broadly pleated stellate plate of very large size; single large axial adsteleal plate present in both faces. Aside from the marginal thickenings of the 2 faces and surface granulation, scattered hollow excrescences are the only other "ornament"; several plates in the distal and right distal area of the obverse face each bear a high sharp or blunt broad-based spine; on the obverse proximal region the adsteleal and several other plates bear groups of small warts or tubercles. Anus in central area of reverse face of anal lobe, covered by broad, low circlet ("pyramid") of elongate, lunate, imbricating plates; this in turn is surrounded by circle of many relatively small polygonal plates, probably loosely articulated also in life, a periproct zone; the whole is set within a subcircular foramen through the large plates which firmly invest this part of the theca. Arm emerging on extensiplane and from facial suture, but with brachial orifice more excavated in vertical wall of obverse plates in distal region than in obverse "opercular" surface; apparently 4 large plates complete adbrachial series, those of obverse side sutured (not imbricated) and showing transverse marginal excavation to accommodate oral surface of arm; adbrachial margin flanged; near flange on left obverse adbrachial, tiny perforation with collared neck may represent hydropore. Proxistele tetramerous, anomalocystitoid, with imbrication of ring pairs on both obverse and reverse axial sutures; imbricate telescoping of rings sharply defined, each ring bearing circular median crest or flange and showing on distal postflange margin many small polygonal platelets, apparently originally embedded in investing integument (but no platelets have been observed inside proxistele). Mesistele showing usual dendrocystitoid transition from tetramerous to dimerous condition, exhibits slight median reverse keel and passes into dististele within short distance; dimeres are opposite there for most of length and are sutured in extensiplane; disistele relatively stout and long. *U.Ord.*, Scot.——FIG. 389, 390. **G. batheri*; 389, reverse face of holotype, presumably upwardly oriented in life (note adbrachial spinous hydropore) (BMNH, Gray Coll., 28473), ×3.4; 390, obverse face of paratype (obverse plates coarsely stippled, interior of reverse plates finely so) (note flanged hydropore with radii on interior of adbrachial plate which bears spine in surface) (BMNH, Begg. Coll., E5791), ×3.1 (all Caster, n). [See Fig. 373, 374.]

Family RUTROCLYPEIDAE Gill & Caster, 1960

[Rutroclypeidae GILL & CASTER, 1960, p. 22]

Solutans with nummuloidally depressed thecae, with or without prominent lobation, covered by many small polygonal plates which may be smooth, centrally umbonate, or prominently spinose; arm nearly axial, emerging from obverse face, no other facial differentiation; proxistele anomalocystitoid, dististele dimerous, with suture in symmetry plane. *L.Dev.*

Rutroclypeus WITHER, 1933, p. 18[1] [*emend.* GILL & CASTER, 1960, p. 30] [**R. junori*; M]. Thecal outline circular, nummuloidally depressed, giving impressions of polyplated (commonly hexagonally) sphere which has been pressed into nummuloidal mold; lobation may develop *(R. withersi)*; thecal margins vertical, coinlike, with plates and sutures falling as they may without any evident adjustment to form, plates small and usually bearing umbo, boss, or elongate solid spine in type species (although holotype is sparsely spinose). Juveniles show relatively fewer, larger, and less spiny plates than adults and they are more fusiform in outline, as well as possibly less depressed. Plate increment in *R. withersi* (possibly mainly on its lobations) is by exaggerated rosetting (see *Dendrocystites sedgwicki*) and hundreds of tiny platelets appear around larger primary plates, each with miniscule spine, thus creating appearance recalling miliary spines about bosses of echinoids. [These zones of small plates seem to have been flexibly joined and may be a form of facial differentiation. The spines may extend onto the proxistele, one to a plate, and apparently only on the obverse face; a single median proximal one on the mesistele has been noted.] Adult arm short and inserted distally to left of axis and within obverse disc; no adbrachial thecal plate differentiation noted, but some evidence indicates that at least one adoral plate bears swollen hydropore tumescence like that of Dendrocystitidae. Juvenile arm proportionately shorter and broader than in adults and axially inserted or nearly so. Anus unknown but must be marginal (slight marginal swelling adjacent to stele may mark spot). Stele long and differentiated; proxistele tetramerous, triangular

---

[1] Originally described as a xiphosuran arthropod.

in outline, and flatly anomalocystitoid (more inflated in juveniles); mesistele very short and conical, its plating recording transition from proximal tetramerous to distal dimerous arrangement (see *Minervaecystis*); dististele long and narrow, becoming spatulate distally in some specimens, with dimeres opposite apparently throughout its length and somewhat depressed, suture is in symmetry plane. *L.Dev.*, Australia (Victoria).——FIG. 391,*1*. **R. junori;* diagrammatic sketch of holotype,

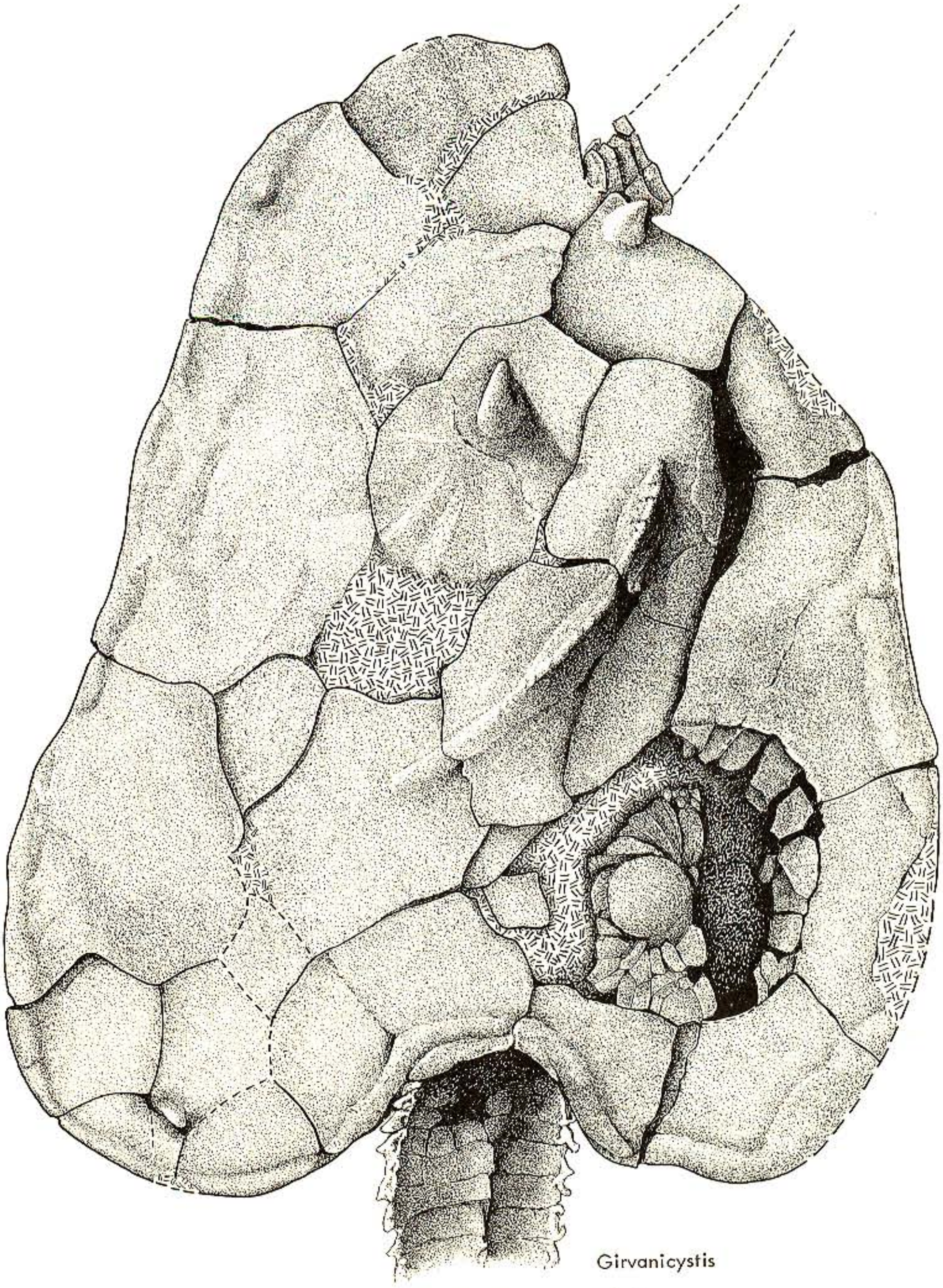


FIG. 389. Girvanicystidae (p. *S*614-*S*616).

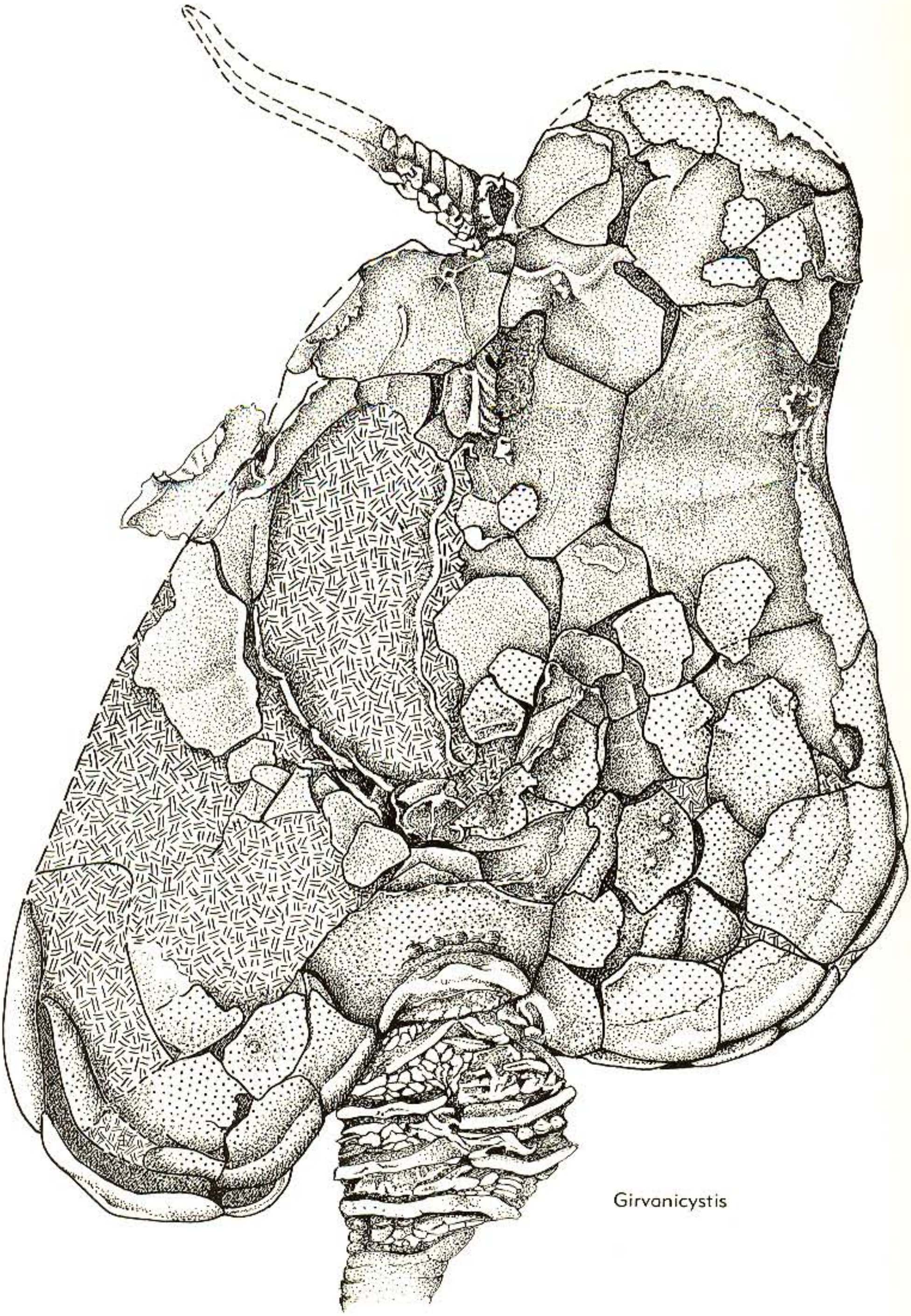


FIG. 390. Girvanicystidae (p. S614-S616).

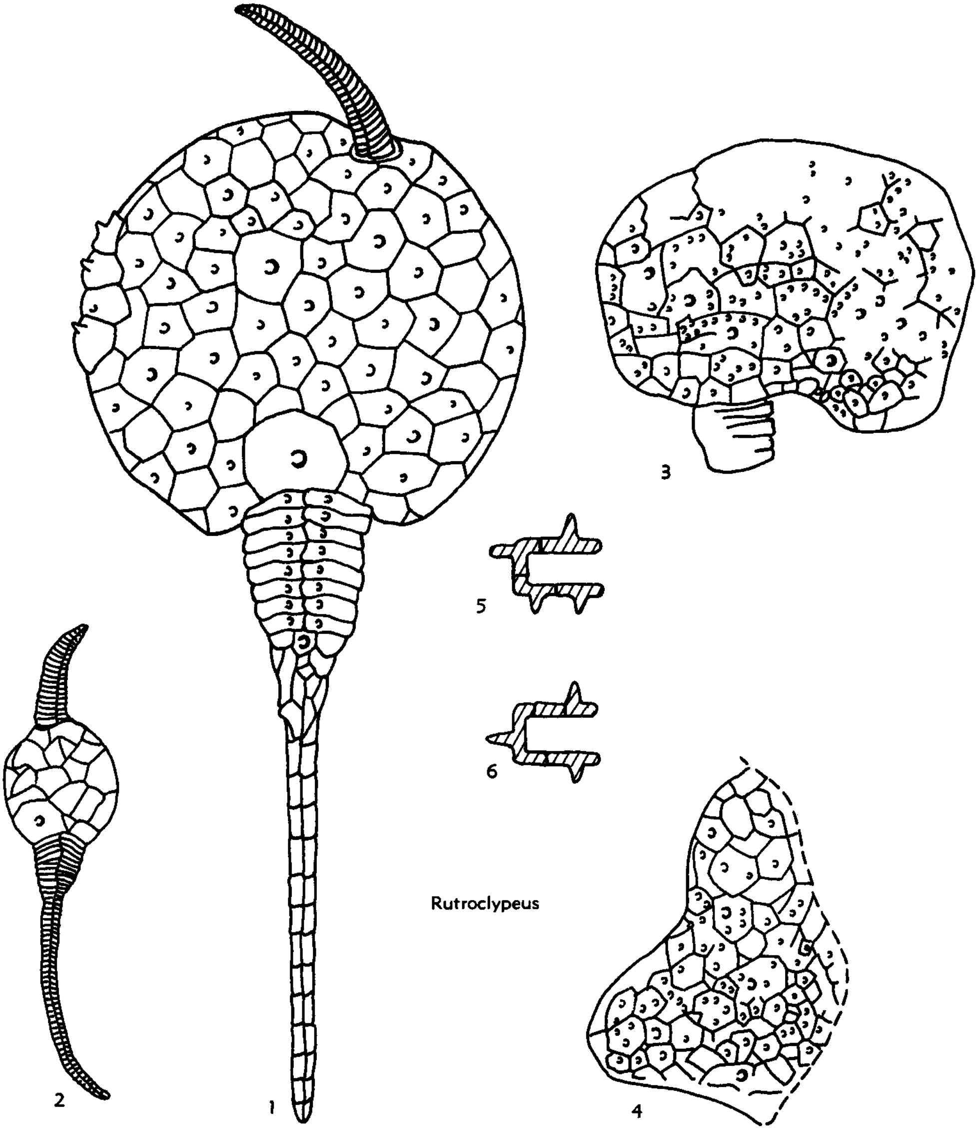


FIG. 391. Rutroclypeidae (p. *S616-S617*, *S619*).

×1.7 (Caster, n).——FIG. 391,*2*. *R. victoriae* GILL & CASTER, somewhat crushed juvenile specimen showing its relatively few larger plates and large arm, ×1.7 (Caster, n).——FIG. 391,*3-6*. *R. withersi* GILL & CASTER; *3*, specimen showing thecal lobation (?anal) and miliary granules, ×1.7; *4*, partial theca (holotype) with pronounced (?anal) lobe, ×1.7; *5,6*, diagrammatic cross sections of thecal periphery showing nummuloidal geniculation of plates, enl. (all Caster, n).——FIG. 392. *R. wilkinsi* GILL & CASTER; stereoscopic views of antanal side of theca showing spines on all of its plates but none on proxistele, ×1.8 *(43)*.

Family SYRINGOCRINIDAE
Parsley & Caster, 1965

[Syringocrinidae PARSLEY & CASTER, 1965, p. 115]

Elongate, ovoid, rigid and inflated theca; facially differentiated, convexi-planate (or inferiorly concave), covered mainly by few

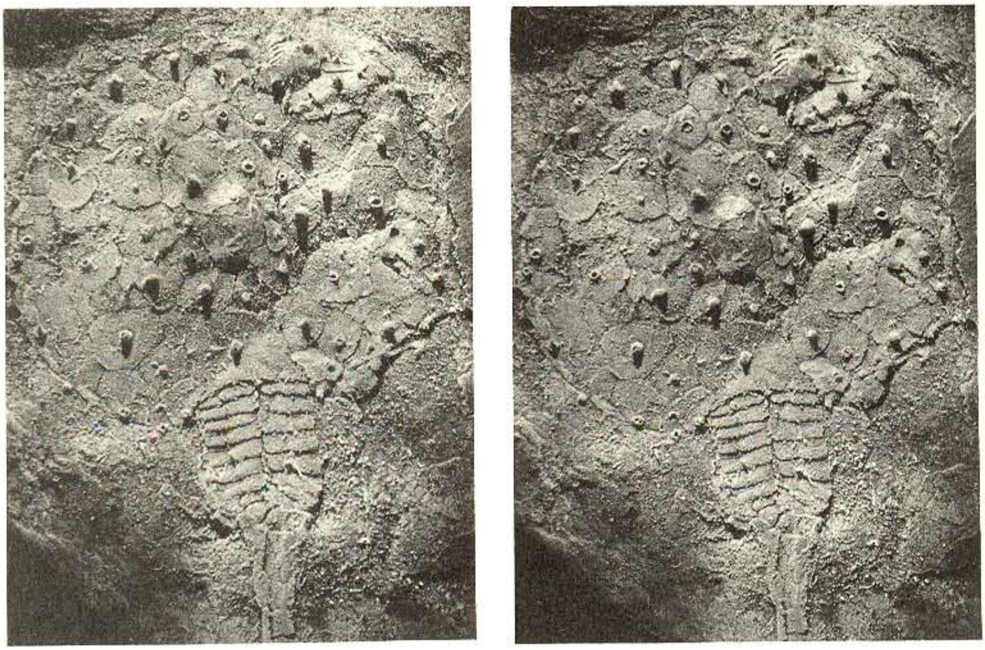


FIG. 392. **Rutroclypeus wilkinsi* GILL & CASTER (Rutroclypeidae) (p. S616-S617, S619).

large plates, few large infracentrals, many small, flexibly joined supracentrals in ovoid area, and possibly partially surrounded by larger supracentrals; anus unknown. Arm long, terete, emerging from distal left margin of theca. Stele axially differentiated; proxistele anomalocystitoid, inflated; mesistele long, petiolate to lanceolate dististele; proximal mesistele unit an annulus; remaining surface with three series of plates, two of which are in series with dististele biseries and third in median position, composed of distally diminishing series of long plates; dististele biserial, becoming nearly dimerous at end with suture in extensiplane, along which considerable compression forms finlike structure, reverse dististele plates keeled and spinose. *M.Ord.*

Syringocrinus BILLINGS, 1859, p. 65 [**S. paradoxicus*; M]. Characters of family. [The pseudostylocone of the mesistele and proximal dististele is an especially typical feature. Restorations (Fig. 393) depict all available information on this genus.] *M.Ord.*, Can.(Ont.).——FIG. 393,*1*. *S. sinclairi* PARSLEY & CASTER; restorations based on type specimens; *1a*, obverse face with cross sections of stele indicated in life orientation, ×3.8; *1b*, reverse face, ×3.8 *(69)*.——FIG. 393,2. **S. paradoxicus*; views of holotype; *2a*, BATHER's (1913) drawing of stele as known to him, ×1.9; *2b*, present condition after bit of preparation, ×1.9 *(43)*.

Family IOWACYSTIDAE
Gill & Caster, 1960

[Iowacystidae GILL & CASTER, 1960, p. 20]

Trigonal, much-depressed solutes with advanced differentiation of thecal plates, including rigid frame of marginal plates and characteristic supracentral and infracentral plates; arm on distal right side of obverse face; anus marginal at proximal left corner, closed by bivalved boss. Stele somewhat depressed, with short tetramerous proxistele which is narrowly annular, inconspicuous mesistele, and dominantly biserial (not dimerous) disistele with suture in symmetry plane. *U.Ord.*

Iowacystis THOMAS & LADD, 1926, p. 6 [**I. sagittaria*; M]. (Diagnosis based on restudy of type materials by PARSLEY & CASTER, 1965.) Thecal outline in form of isosceles triangle, with rigid marginal framework and high facial differentiation; facial surfaces parallel, one with few rigidly united large infracentrals, highly ornamented, and other with many large supracentrals which are flexibly joined together and also highly ornamented; single large median adsteleal plate on

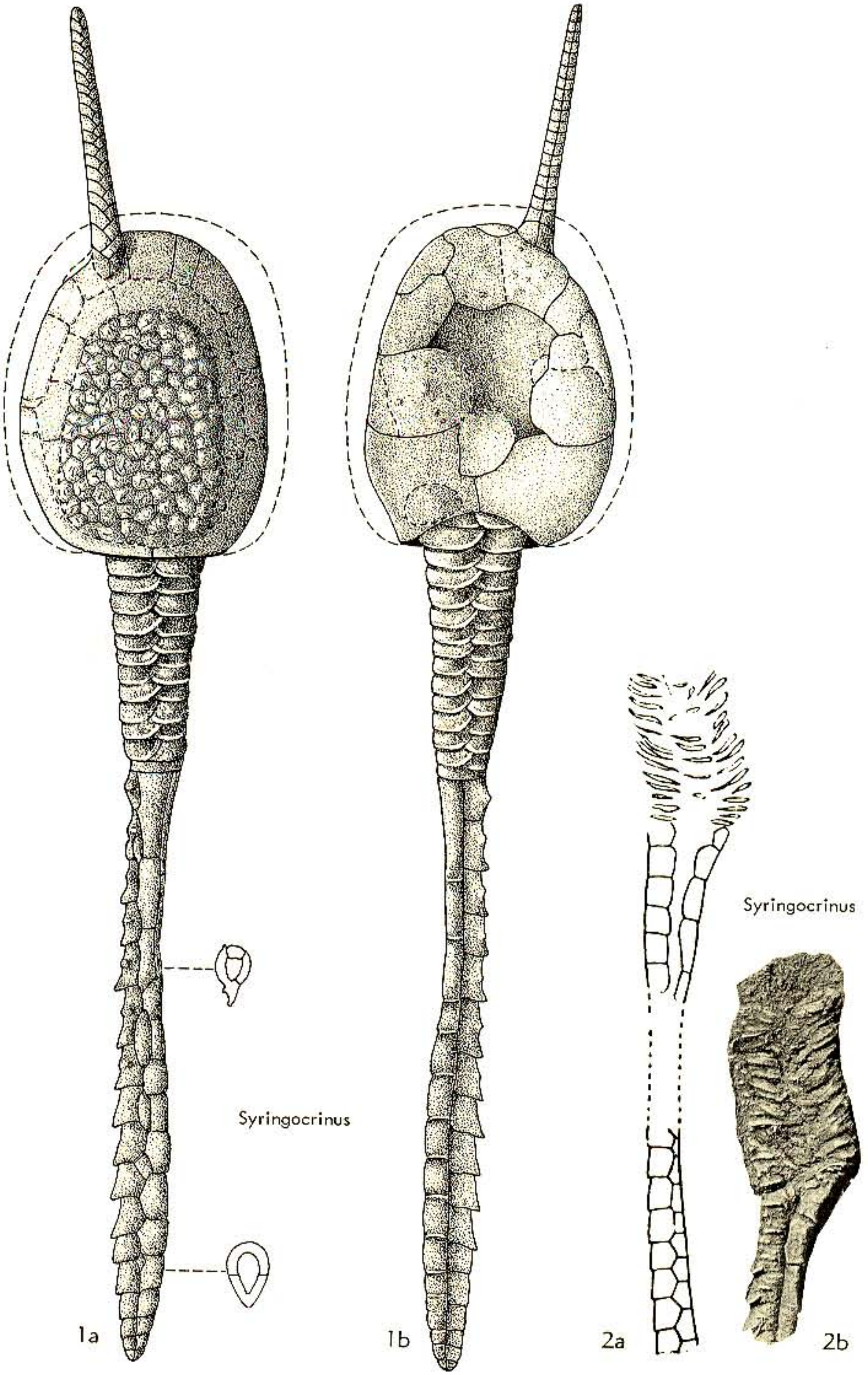


FIG. 393. Syringocrinidae (p. S620).

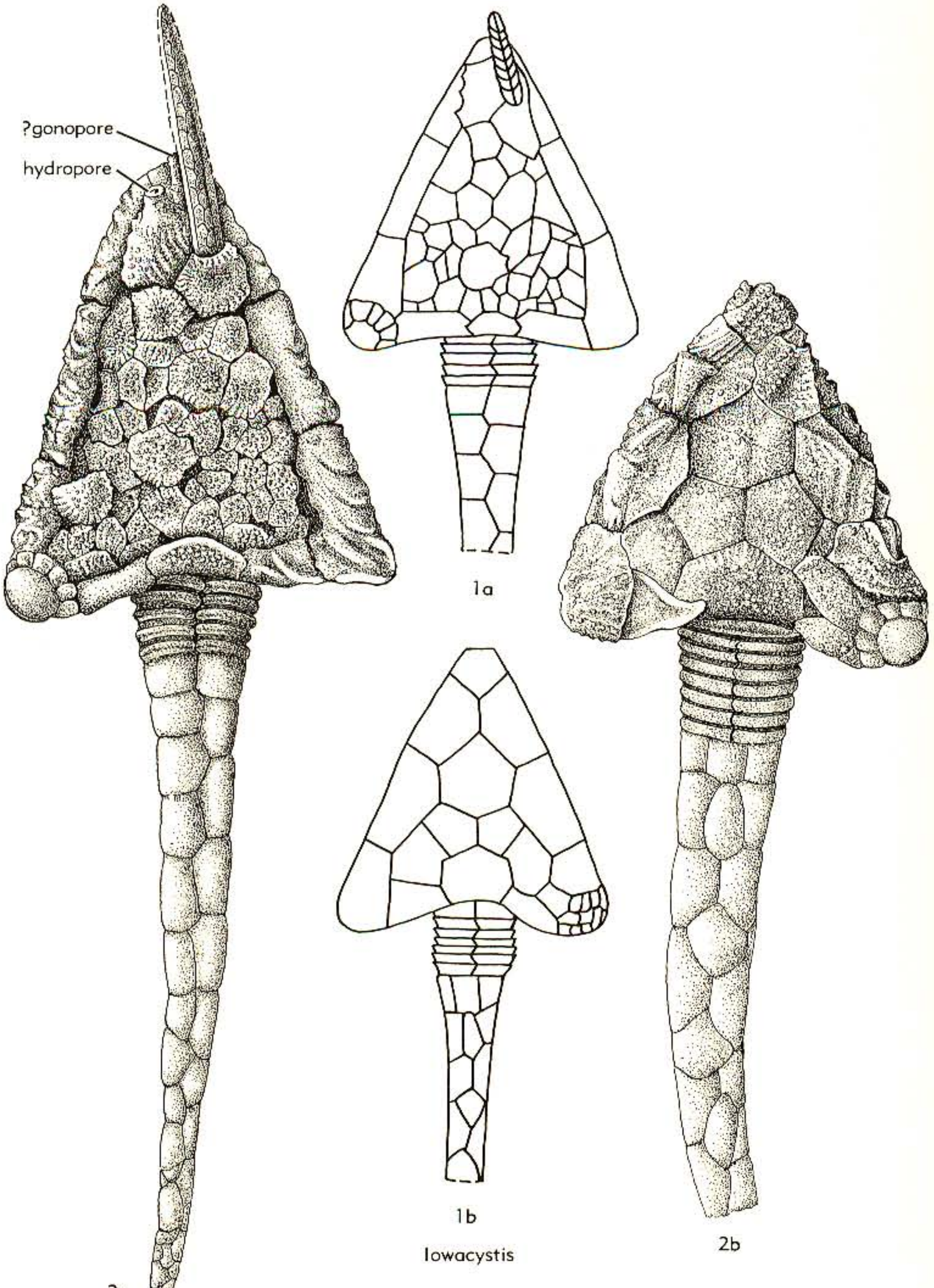


FIG. 394. Iowacystidae (p. S620, S623).

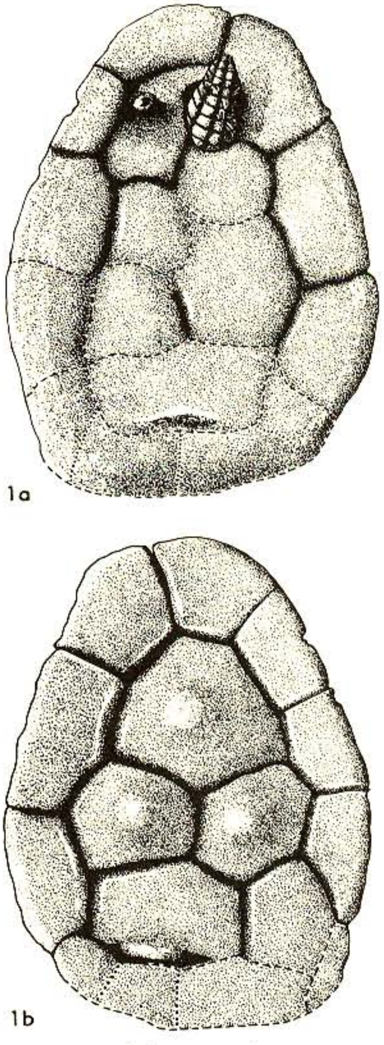
each face, also with adanal and adbrachial differentiation; anus closed by bivalved boss of 2 quarter-spheres parting in extensiplane, surrounded by circlet of small quadrilateral plates and on reverse side with 3 large adanal plates, creating lobelike aspect; left adoral plate bearing phialine hydropore aperture, with smaller phialine pore distally from it (?gonopore). Arm emerging from right distal supracentrals and located on sutural complex between 4 plates excavated to form brachial orifice; arm terete, relatively short and narrow. Stele somewhat depressed, thick and stubby, axially differentiated but less so than in most homoiosteles, with 5 or 6 carinate tetrameres; mesistele visible only on reverse side, where 1st 2 pairs of biseries of distal plates are separated by large median plates; dististele with several more such inserts discontinuous along reverse surface; mesistele and dististele merging on obverse side, dististele biserial (not dimeral) with suture in symmetry plane. *U.Ord.*, USA(Iowa).——Fig. 394. **I. sagittaria*; *1a,b*, obverse and reverse faces, ×1.7 *(84)*; *2a,b*, same, based on restudy of types, ×2.5, ×2.25 *(69)*.

Family BELEMNOCYSTITIDAE
Parsley, new family

[Family diagnosis and revised diagnosis of *Belemnocystites* furnished by Ronald L. Parsley, University of Cincinnati]

Solutes with regularized marginal and somatic plates; single nonterminal biserial arm with adjacent coniform pore plate. Stele holomerous or apparently so. Characters essentially those of type genus. *M.Ord.*

Belemnocystites Miller & Gurley, 1894, p. 6 [**B. wetherbyi*; M] [=*Belemnocystis* Bather, 1900, p. 51 (obj.) *(nom. van.)*]. Theca suboval, depressedly biconvex in cross section; depression especially marked in somatic areas, with 11 regularized marginals, 5 ventral somatic plates, and *ca.* 6 dorsal somatic plates, marginals extending equally over both faces. Single biserial arm appears to be very short, extending anteriorly from dorsal distal somatic area; left adbrachial plate bearing coniform aperture, presumably hydropore. Stele deeply inserted into theca, not extensively anchored to proximal adsteleals, but mainly to adjacent large somatic plates; proxistele undifferentiated and apparently holomerous (*ca.* 15 ?annular) segments with very large lumen; distal stele structure unknown. Granular prosopon, poorly preserved, plates apparently with fairly prominent concentric growth rings. Anus not identified, probably lateral, in proximal left corner of theca. [This genus bears a number of common traits with *Iowacystis* (e.g., configuration, location and interrelationship of the arm and pore plate, unusual somatic biconvexity of the theca, and similar nature and symmetry of the ventral somatic plates, including what appears to be an azygous adanal plate).] *M.Ord.*, USA(Ky.).——Fig. 395,*1*. **B. wetherbyi*; *1a,b*, obverse and reverse faces, based on holotype, ×3 (Parsley, n). [?=*Myeinocystites* Strimple, 1953.]



Belemnocystites

Fig. 395. Belemnocystitidae (p. S623).

REFERENCES

[FOR STYLOPHORA, HOMOSTELEA, AND HOMOIOSTELEA]

Barrande, Joachim

(1) 1859, *État actuel des connaissances acquises sur la faune primordiale:* Soc. Géol. France, Bull., v. (2) 16, p. 543.

(2) 1887, *Classe des Échinodermes. Ordre des cystidées:* in Systême silurien du centre de la Bohême, Pt. I, v. 7, 233 p., 39 pl., Řivnáč (Prague), Gerhard (Leipzig).

Bassler, R. S.

(3) 1932, *The stratigraphy of the Central Basin of Tennessee:* Tennessee Div. Geology, Bull. 38, 268 p., 4 text fig., 49 pl.

(4) 1935, *Description of Paleozoic fossils from the Central Basin of Tennessee:* Washington Acad. Sci., Jour., v. 25, p. 403-409.

(5) 1938, *Pelmatozoa Palaeozoica:* Fossilium Catalogus, pt. I. Animalia, W. Quenstedt (ed.), pars 83, p. 1-194, W. Junk('s-Gravenhage).

(6) 1943, *New Ordovician cystidean echinoderms from Oklahoma:* Am. Jour. Sci., v. 241, p. 694-703, pl. 1.

(7) 1950, *New genera of American Middle Ordovician "Cystoidea":* Washington Acad. Sci. Jour., v. 40, p. 273-277, text fig. 1-19.

———, & Moodey, M. W.

(8) 1943, *Bibliographic and faunal index of Paleozoic pelmatozoan echinoderms:* Geol. Soc. America, Spec. Papers no. 45, 733 p.

Bather, F. A.

(9) 1889, *The Cystoidea of Bohemia:* Nature, v. 40, p. 267-270.

(10) 1899, *A phylogenetic classification of the Pelmatozoa:* Brit. Assoc. Adv. Sci., Rept., sec. D (1898), p. 816-923.

(11) 1900, *The Pelmatozoa-Cystoidea:* in A treatise on zoology, E. Ray Lankester (ed.), v. 3, p. 38-77, text fig. 1-48, Adam & Charles Black (London).

(12) 1906, *Ordovician Cystidea from Burma:* in F. R. C. Reed, The Lower Paleozoic fossils of the Northern Shan States, Burma, Geol. Survey India, Mem., new ser., v. 2, no. 3, p. 6-40.

(13) 1913, *Caradocian Cystidea from Girvan:* Royal Soc. Edinburgh, Trans., v. 49, pt. 2, no. 6, p. 359-529, 79 text fig., pl. 1-6.

(14) 1925, *Cothurnocystis: a study in adaptation:* Paläont. Zeitschr., v. 7, p. 1-15, text fig. 1-12.

(15) 1926, *Preface:* in T. H. Withers, Catalogue of the Machaeridia (*Turrilepas* and its allies) in the Department of Geology: Brit. Museum (Nat. History), p. 6-11.

(16) 1926, *Review* (A. O. Thomas, and H. S. Ladd): Zentralbl. Geol., v. 34, p. 233-234.

(17) 1928, *The fossil and its environment:* Geol. Soc. London, Quart. Jour., v. 84, p. 61-98.

(18) 1928, *Dendrocystis in North America:* Geol. Survey Canada, Dept. Mines, Bull 49 (Geol. ser. 48, Contrib. Canadian Paleont.), p. 5-8, text fig. 1.

(19) 1929, *Echinoderms:* in Encyclopaedia Britannica, edit. 14, p. 895-904.

(20) 1929, *Une classe d'échinodermes sans trace de symétrie rayonnée:* Assoc. Franç. Avanc. Sci., p. 435-438.

(21) 1930, *A class of Echinoderma without trace of radiate symmetry:* Arch. Zool. Ital., v. 14, p. 431-439, text fig. 1-6.

Billings, Elkanah

(22) 1859, *On the Crinoideae of the Lower Silurian rocks of Canada:* Canadian Organic Remains, dec. 4, p. v-vi+7-66.

Breder, C. M.

(23) 1955, *Observations on the occurrence and attributes of pentagonal symmetry:* Am. Museum Nat. History, Bull., v. 105, p. 177-219.

Cabibel, J., Termier, Henri, & Termier, Geneviève

(24) 1958, *Les échinodermes mésocambriens de la Montagne Noire (Sud de la France):* Ann. Paléontologie, v. 44, p. 281-293, text fig. 1-10, pl. 1-2.

Caster, K. E.

(25) 1952, *Concerning Enoploura of the Upper Ordovician and its relation to other carpoid Echinodermata:* Bull. Am. Paleontology, v. 34, no. 141, p. 1-47, text fig. 1-2, pl. 1-4.

(26) 1954, *A new carpoid echinoderm from the Paraná Devonian:* Acad. Brasil. Ciências, An., v. 26, p. 123-147, text fig. 1-8, pl. 1-2.

(27) 1954[1956], *A Devonian placocystoid echinoderm from Paraná, Brazil:* Paleont. do Paraná (Centennial volume), p. 137-148, text fig. 1-4, pl. 8.

———, & Eaton, T. H., Jr.

(28) 1956, *Microstructure of the plates in the carpoid echinoderm Paranacystis:* Jour. Paleontology, v. 30, p. 611-614, text fig. 1-2, pl. 74.

Chauvel, Jean

(29) 1937, *Les hétérostélées armoricaines:* Soc. Géol. Mineral. Bretagne, Comptes Rendus somm., v. 2, p. 1-3.

(30) 1941, *Recherches sur les cystoïdes et les carpoïdes armoricains:* Thèses présentées à la Faculté des Sciences de l'Université de Rennes, no. d'ord. 3, sér. C, 286 p., 7 pl.

Cuénot, Lucien

(31) 1948, *Anatomie, éthologie et systématique des échinodermes:* in Traité de zoologie, P.-P. Grassé (ed.), v. 11, p. 3-272, text fig. 1-312, Masson (Paris).

(32) 1953, *Classe des hétérostélés:* in Traité de paléontologie, Jean Piveteau (ed.), v. 3, p. 599-606, text fig. 1-12, Masson (Paris).

Dehm, Richard

(33) 1932, *Cystoideen aus dem rheinischen Unterdevon:* Neues Jahrb. Mineralogie, v. 69, Abt. B, p. 63-93, text fig. 1-13, pl. 1.

(34) 1934, *Untersuchungen an Cystoideen des rheinischen Unterdevons:* Akad. Wiss. München, Sitzungsber., Math.-Naturwiss., Abt. 1934, p. 19-43, text fig. 1-6, pl. 1-2.

Delpey, Geneviève

(35) 1941, *Mode particulier de nutrition de certains échinodermes: l'ouverture interne de la bouche:* Soc. Géol. France, Bull., v. 11, p. 87-95, text fig. 1-3.

(36) 1943, *Histoire des échinodermes jusqu'au Dévonien inférieur:* Same, Bull., v. 14, p. 247-278, text fig. 1-17.

Durham, J. W., & Caster, K. E.

(37) 1963, *Helicoplacoidea: a new class of echinoderms:* Science, v. 140, no. 3568, p. 820-822.

Foerste, A. F.

(38) 1917, *Notes on Silurian fossils from Ohio and other central states:* Ohio Jour. Sci., v. 17, p. 187-204, 233-266, pl. 8-12.

Gekker [Hecker], R. F.

(39) 1938, *Novye dannye o rode Rhipidocystis Jkl (otryad Digitata n. o., klass Carpoidea Jkl) i novyy rod Bockia n. g. (podklass Eocrinoidea Jkl, klass Crinoidea Mill.) iz nizhnego silura Leningradskoy oblasti SSSR i Estonii:* Acad. Sci. URSS, Comptes Rendus, new ser., v. 19, no. 5, p. 421-424, 2 text fig. [*New data on Rhipidocystis Jkl (Order Digitata n. o., class Carpoidea Jkl) and on a new genus Bockia (subclass Eocrinoidea Jkl, class Crinoidea Mill.) from the Ordovician of Leningrad Province, U.S.S.R., and Estonia.*]

(40) 1940, *Carpoidea, Eocrinoidea, i Ophiocistia nizhnego silura Leningradskoy oblasti i Estonii:* Acad. Sci. URSS, Travaux (Trudy), Inst. Paleont., v. 9, no. 4, p. 5-82, text fig. 1-43, pl. 1-10. [*Carpoidea, Eocrinoidea and Ophiocistia from the Ordovician of the Leningrad region and Estonia.*] (Russian with German summary.)

(41) 1964, *Klass Carpoidea, Karpoidei:* in Osnovy Paleontologii, Yu. A. Orlov (ed.), Iglokozhie, gemikhordovye, pogonofory, i shchetinkochelyustnye, p. 23-28, pl. 1, text fig. 5-10 (Moskva). [*Class Carpoidea,* in Fundamentals of paleontology, echinoderms, hemichordates, pogonophores, and chaetognaths.]

Gigout, Marcel

(42) 1954, *Sur un hétérostélé de l'Ordovicien marocain:* Soc. Sci. Nat. Phys. Maroc, Bull., v. 34, p. 3-7, text fig. 1-2.

Gill, E. D., & Caster, K. E.

(43) 1960, *Carpoid echinoderms from the Silurian and Devonian of Australia:* Bull. Am. Paleontology, v. 41, p. 1-71, text fig. 1-12, pl. 1-10.

Gislén, Torsten

(44) 1927, *A new Spanish carpoid:* Arkiv Zoologi, v. 19 B, no. 2, p. 1-3, text fig. 1-4.

(45) 1930, *Affinities between the Echinodermata, Enteropneusta, and Chordonia:* Zool. Bidrag Uppsala, v. 12, p. 199-304, text fig. 1-46.

(46) 1934, *Evolutional series toward death and renewal:* Arkiv Zoologi, v. 26 A, no. 16, p. 1-19, text fig. 1-22.

Gregory, W. K.

(47) 1935, *Reduplication in evolution:* Quart. Review Biology, v. for 1935, p. 272.

(48) 1951, *Evolution emerging:* Chapt. 5, p. 84-100, Macmillan Co. (New York).

Haeckel, Ernst

(49) 1896, *Die Amphorideen und Cystoideen: Beiträge zur Morphologie und Phylogenie der Echinodermen:* Festschr. siebenzigsten Geburtstage v Carl Gegenbaur, v. 1, p. 1-179, text fig. 1-25, pl. 1-5, W. Engelmann (Leipzig).

(50) 1896, *Die cambrische Stammgruppe der Echinodermen:* Jenaische Zeitschr., v. 30, p. 393-404.

Hall, James

(51) 1861, *Crinoideae and Cystoideae of the lower Helderberg limestones and Oriskany sandstone:* Nat. History N.Y. (Geol. Survey N.Y.), Paleontology, v. 3, pt. 1 (1858), p. 99-152; pt. 2, pls.

Hyman, L. H.

(52) 1955, *The invertebrates: Echinodermata. The coelomate Bilateralia:* v. 4, 763 p., 280 text fig., McGraw-Hill (New York, Toronto, London).

Jaekel, Otto

(53) 1899, *Stammesgeschichte der Pelmatozoen: Pt. 1, Thecoidea und Cystoidea:* x+442 p., 18 pl., 88 text fig., Julius Springer (Berlin).

(54) 1901, *Über Carpoideen, eine neue Klasse von Pelmatozoen:* Deutsch. Geol. Gesell., Zeitschr., Jahrg. 1900, v. 52, p. 661-677, text fig. 1-11.

(55) 1918, *Phylogenie und System der Pelmatozoen:* Paläont. Zeitschr., v. 3, p. 1-128, text fig. 1-114.

Kirk, Edwin

(56) 1911, *The structure and relationships of certain eleutherozoic Pelmatozoa:* U.S. Natl. Museum, Proc., v. 41, 137 p., 11 pl.

Kobayashi, Teiichi

(57) 1934, *The Cambro-Ordovician formations and faunas of South Chosen, Pt. 2: Lower Ordovician faunas:* Imperial Univ. Tokyo, Jour. Fac. Sci., sec. 2, v. 3, pt. 9, p. 525, pl. 1.

Koninck, L. G. de

(58) 1869, *Sur quelques échinodermes remarquables des terrains paléozoïques:* Acad. Royal Sci. Belgique, Bull., sér. 2, v. 28, p. 544-552, pl. 5.

(59) 1870, *On some new and remarkable echinoderms from the British Palaeozoic rocks:* Geol. Mag., v. 7, p. 258-263, pl. 7.

Meek, F. B.

(60) 1872, *Descriptions of new species of fossils from the Cincinnati group of Ohio:* Am. Jour. Sci. & Arts, v. 3, p. 423-425.

(61) 1873, *Description of invertebrate fossils of the Silurian and Devonian systems:* Ohio Geol. Survey, Rept. Paleont. Ohio, v. 1, pt. 2, p. 1-243.

Meléndez, Bermudo

(62) 1952, *Los carpoideos de España:* Las Ciencias, v. 17, no. 3, p. 497-516, text fig. 1-8, pl. 1-2.

(63) 1954, *Los Trochocystites del Pirineo:* R. Soc. Española Historia Nat., Bol., v. 51, p. 97-105, text fig. 1-2, pl. 10.

Miller, S. A.

(64) 1877, *The American Paleozoic fossils: a catalogue of the genera and species:* 253 p. (Cincinnati).

(65) 1889, *North American geology and paleontology:* 664 p.,Western Methodist Book Concern (Cincinnati).

———, & Gurley, W. F. E.

(66) 1894, *New genera and species of Echinodermata:* Illinois State Museum, Nat. History Bull., v. 5, p. 5-53, pl. 1-5.

Müller, A. H.

(67) 1963, *Lehrbuch der Paläozoologie, v. 2, pt. 3, Arthropoda 2-Stomochorda:* 698 p., 854 text fig., Gustav Fischer (Jena).

Nichols, David

(68) 1962, *Echinoderms:* 200 p., 26 text fig., Hutchinson Univ. Library (London).

Parsley, R. L., & Caster, K. E.

(69) 1965, *North American Soluta (Carpoidea, Echinodermata):* Bull. Am. Paleontology, v. 49, no. 221, p. 109-174, pl. 16-18.

Pope, J. K.

(70) 1962, *Zoological affinity of the Lepidocoleidae, a family of the Machaeridia:* Geol. Soc. America, Spec. Paper, v. 68, p. 248-249 (abstr.), Cincinnati meeting, 1961.

Prokop, R. J.

(71) 1963, *Dalejocystis, n.gen.; the first representative of the Carpoidea in the Devonian of Bohemia:* Jour. Paleontology, v. 37, p. 648-650, text fig. 1, pl. 83-84.

Reed, F. R. C.

(72) 1925, *Revision of the fauna of the Bokkeveld beds:* South African Museum, Ann., v. 22, p. 27-226.

Regnéll, Gerhard

(73) 1945, *Non-crinoid Pelmatozoa from the Paleozoic of Sweden:* Medd. Lunds Geol.-Mineral. Inst., no. 108, 255 p., 30 text fig., 15 pl.

(74) 1960, *"Intermediate" forms in early Palaeozoic echinoderms:* Internatl. Geol. Cong., Rept. 21st Session, pt. 22, p. 71-80 (Copenhagen).

(75) 1960, *The Lower Palaeozoic echinoderm faunas of the British Isles and Balto-Scandia:* Palaeontology, v. 2, pt. 2, p. 161-179.

(76) 1960, *Données concernant le développement ontogénétique des pelmatozoaires du Paléozoïque (Echinodermes):* Soc. Géol. France, Bull., sér. 7, v. 1, p. 773-783, text fig. 1-6.

Rennie, J. V. L.

(77) 1936, *On Placocystella, a new genus of cystids from the Lower Devonian of South Africa:* S. Afr. Museum, Ann., v. 31, p. 269-275, pl. 36.

Schuchert, Charles

(78) 1904, *On Siluric and Devonic Cystidea and Camarocrinus:* Smithsonian Misc. Coll., v. 47, p. 201-272, pl. 34-44.

(79) 1913, *Anomalocystidae:* Maryland Geol. Survey, Lower Devonian Vol., p. 228-229.

Spencer, W. K.

(80) 1938, *Some aspects of evolution in Echinodermata:* in Evolution, Essays on aspects of evolutionary biology presented to Professor E. S. Goodrich on his seventieth birthday, G. R. de Beer (ed.), p. 287-302, pl. 1-2, Clarendon Press (Oxford).

Springer, Frank

(81) 1913, *Cystoidea:* in K. A. Zittel, transl. & ed. by C. R. Eastman, Textbook of Palaeontology, v. 1, p. 145-158, Macmillan (New York).

Strimple, H. L.

(81a) 1953, *A new carpoid from Oklahoma:* Washington Acad. Sci., v. 43, p. 105-106, 2 text fig.

Termier, Henri & Termier, Geneviève

(82) 1948, *Les échinodermes du Paléozoïque inférieur:* La Revue Scientifique, Année 86, pt. 10, p. 613-626, text fig. 1-41.

(83) 1950, *Paléontologie marocaine II. Invertébrés de l'ère Primaire. IV. Annélides, arthropodes, échinodermes, conularides et graptolithes:* Serv. Carte Géol. Maroc, Notes & Mém., 1950, p. 1-279, pl. 184-241.

Thomas, A. O., & Ladd, H. S.

(84) 1926, *Additional cystoids and crinoids from the Maquoketa Shale of Iowa:* Iowa Univ. Studies Nat. History, v. 11, no. 8, p. 5-18, pl. 1-6.

Thoral, Marcel

(85) 1935, *Contribution à l'étude paléontologique de l'Ordovicien inférieur de la Montagne Noire et revision sommaire de la faune cambrienne de la Montagne Noire:* 363 p., 35 pl. (Montpellier).

Ubaghs, Georges

(86) 1960, *Le genre Lingulocystis Thoral (Echinodermata, Eocrinoidea) avec des remarques critiques sur la position systématique du genre Rhipidocystis Jaekel:* Ann. Paléontologie, v. 46, p. 81-116, text fig. 1-9, pl. 1-3.

(87) 1961, *Un échinoderme nouveau de la classe des carpoïdes dans l'Ordovicien inférieur du département de l'Hérault (France):* Acad. Sci. Paris, Comptes Rendus séances, v. 253, p. 2565-2567, text fig. 1.

(88) 1961, *Sur la nature de l'organe appelé tige ou pédoncule chez les carpoïdes Cornuta et Mitrata:* Same, v. 253, p. 2738-2740, text fig. 1.

(89) 1963, *Cothurnocystis Bather, Phyllocystis Thoral and an undetermined member of the order Soluta (Echinodermata, Carpoidea) in the uppermost Cambrian of Nevada:* Jour. Paleontology, v. 37, p. 1133-1142, pl. 151-152.

Wetherby, A. G.

(90) 1879, *Description of a new family and genus of Lower Silurian Crustacea:* Cincinnati Soc. Nat. History, Jour., v. 1, no. 4, p. 162-166.

(91) 1879, *Description of a new family and genus of Lower Silurian Crustacea:* Same, v. 2, pl. 7, text fig. 1-1g.

Whitehouse, F. W.

(92) 1941, *Early Cambrian echinoderms similar to larval stages of Recent forms:* Queensland Museum, Mem. 11, pt. 1, p. 1-28, 4 pl.

Wilson, A. E.

(93) 1946, *Echinodermata of the Ottawa Formation of the Ottawa-St. Lawrence Lowland:* Canada Geol. Survey, Dept. Mines Res., Bull. no. 4, p. 1-46, text fig. 1-2, pl. 1-6.

Withers, R. B.

(94) 1933, *A new genus of fossil king-crabs:* Royal Soc. Victoria, Proc., v. 45, p. 18-22.

Woodward, Henry

(95) 1880, *Notes on the Anomalocystidae, a remarkable family of Cystoidea, found in the Silurian rocks of North America and Britain:* Geol. Mag., new ser., dec. 2, v. 7, p. 193-201, pl. 6.

ADDENDUM

CAMPTOSTROMATOIDS

By J. Wyatt Durham

[University of California (Berkeley)]

Class CAMPTOSTROMATOIDEA Durham, 1966

[*nom. correct.* Durham, herein (*pro* Camptostromoidea Durham, 1966, p. 1219)]

Free-living, apparently medusaeform radially symmetrical echinoderms; body wall heavily plated and containing several different types of ossicles; mouth and anus at opposite poles, with no elongation along this axis; sutural pores abundant on oral and external lateral surfaces but absent from region of aboral pole; detailed organization uncertain but presumably radial; arms radail, plated, attached to periphery of test; seemingly no calcareous ring. *L.Cam.(Olenellus Zone).*

The genus *Camptostroma,* for which this class has been established, was originally (ref. *1*) described by Ruedemann *(4)* as a probable floating "tubularian hydrozoan." Subsequently Kieslinger *(3)* included it in the Scyphozoa, an assignment that was followed by Harrington & Moore *(2)* in part F of the *Treatise on Invertebrate Paleontology.* Careful examination of the type and other original material (all external molds) suggested that *C. roddyi* was an echinoderm (a possibility recognized by Ruedemann). Fortunately, a recently discovered specimen retains the original calcite plates, the cleavage and reticulate microstructure of which confirm assignment to

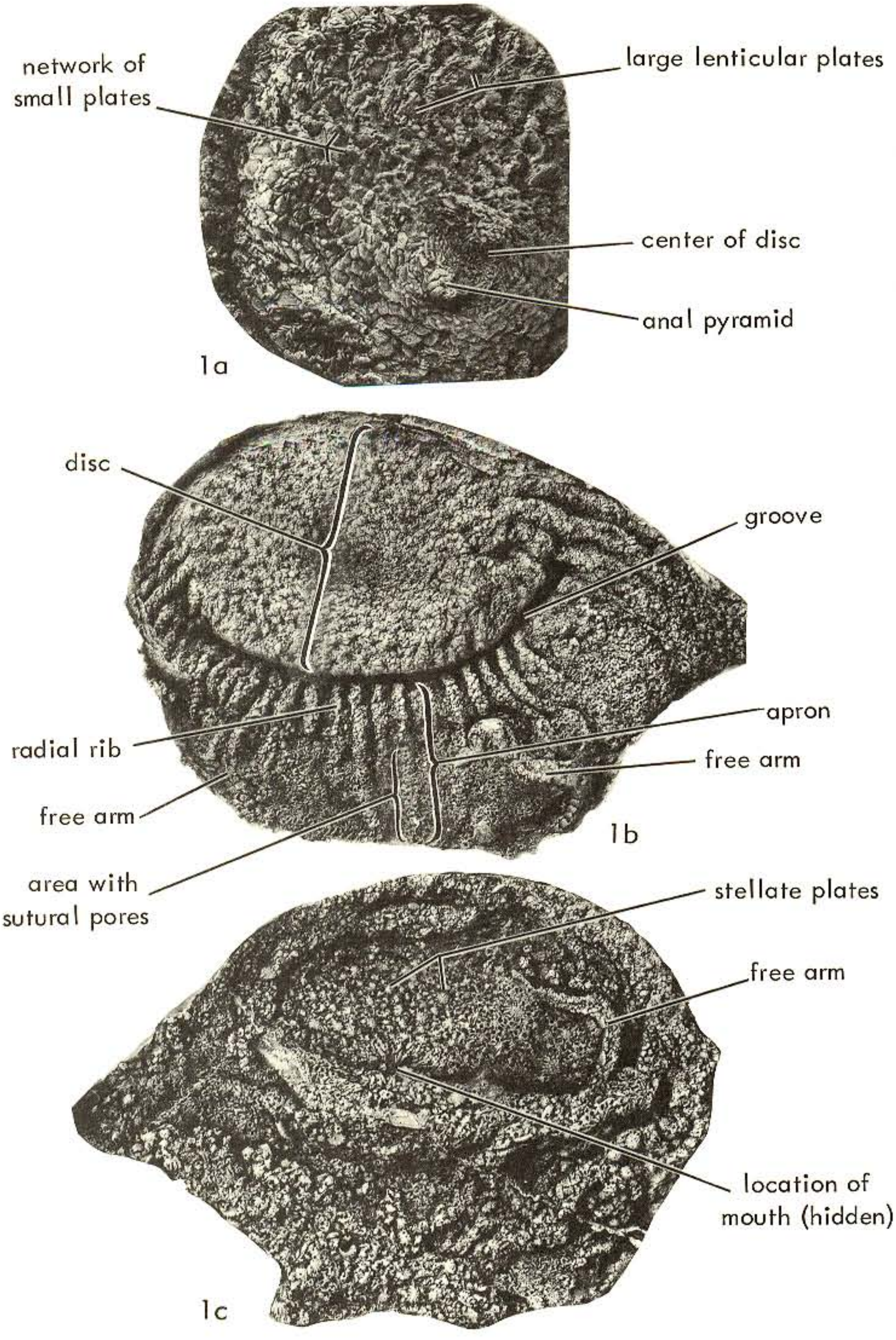


FIG. 396. Camptostromatidae (p. S630).

the echinoderms. *C. roddyi,* the type species (other species referred to *Camptostroma* do not appear to be congeneric), occurs in shales of the Lower Cambrian Kinzers Formation of Pennsylvania, in the same strata that contain lepidocystoids. About 15 specimens of *C. roddyi* have been found, but none are as complete as the type and some are very poor. Disassociated plates apparently referable to *Camptostroma* are abundant in some limestones associated with the shales.

Some details of the organization and structure of the test of *Camptostroma roddyi* have not been resolved, but it appears to have been medusaeform in shape, with a centrally domed aboral surface and a peripheral radially ridged apron with a few marginal free arms, and with the oral surface concave. Except immediately around the peristome, sutural pores are abundant on the oral surface and extend onto the upper margin of the peripheral apron. On the oral surface (but not on the peripheral apron) the small plates with sutural pores are arranged around larger stellately ridged plates. On the upper surface of the distal margin of the peripheral apron is an area of uniformly small plates, deeply incised for sutural pores. Proximally the poriferous area merges into a nonporiferous, strongly ribbed area built of small plates. Centrally the aboral domed disc is built of large flat lenticular plates imbedded in a network of numerous small plates. When the surface is contracted the flat plates are more or less overlapped by the meshwork of small plates, but when expanded these plates are the most conspicuous elements of this surface. A conspicuous raised structure considered to be an anal pyramid is present, slightly off center, on the aboral surface of some specimens. It appears to be composed of about seven elongate plates. The peripheral free arms are incompletely preserved on the available specimens but were relatively slender and had large plates on the aboral surface. Their length appears to have been sufficient to reach to the mouth. The number of arms is uncertain but seems to have been between four and eight. The central domed area is set off from the peripheral apron by a well-marked groove on the type and some other individuals, but there is a possibility that this groove may be an artifact of burial. The peristomial area, although surrounded by plates of several types, in contrast to other areas of the test, seems to be composed largely of flattened lenticular plates without sutural pores.

None of the plates of the test are firmly sutured to one another, and away from the peristomial region the plates seem to have been distributed through a thick body wall much as in many holothurians. Presumably the tissues would have decayed rapidly after death, the plates becoming disassociated and scattered easily. No evidence of a pentaradiate symmetry is recognizable, but the numerous radial ridges surrounding the aboral disc indicate a well-defined radial symmetry. On a nonleached specimen more than 40 of these ridges were observed, but on the holotype (although marginally incomplete) there appear to have been about 60. Another specimen seems to have had at least 50 ridges.

It is suggested that the sutural pores contained tube feet more or less similar to those of modern echinoderms and that they were connected by an internal radial plexus of the water-vascular system. Presumably the tube feet served primarily for respiration, but they probably also were utilized in food gathering or transport of food toward the mouth. The few slender arms do not suggest that they were used for locomotion—probably they were primarily food-gathering organs. The mouth seems to have been relatively small, so that food was probably of small particle size. No madreporite or genital aperture has been recognized, but the plates are so numerous and often so disarranged in detail that it would be easy to overlook these features.

The mode of life of *Camptostroma* is somewhat uncertain, but in view of the apparent medusaeform body it is suggested that it was probably pelagic or bathypelagic. It may have been comparable to the pelagic holothurian *Pelagothuria* or bathypelagic types such as *Benthodytes* and *Galatheathuria.* A comparison might also be made with the free-living comatulid crinoids, but the body structure is not at all comparable to that of the crinoids. The camptostromoid test, built of several different types of ossicles in intimate relationship, is suggestive of that of some holothurians, especially

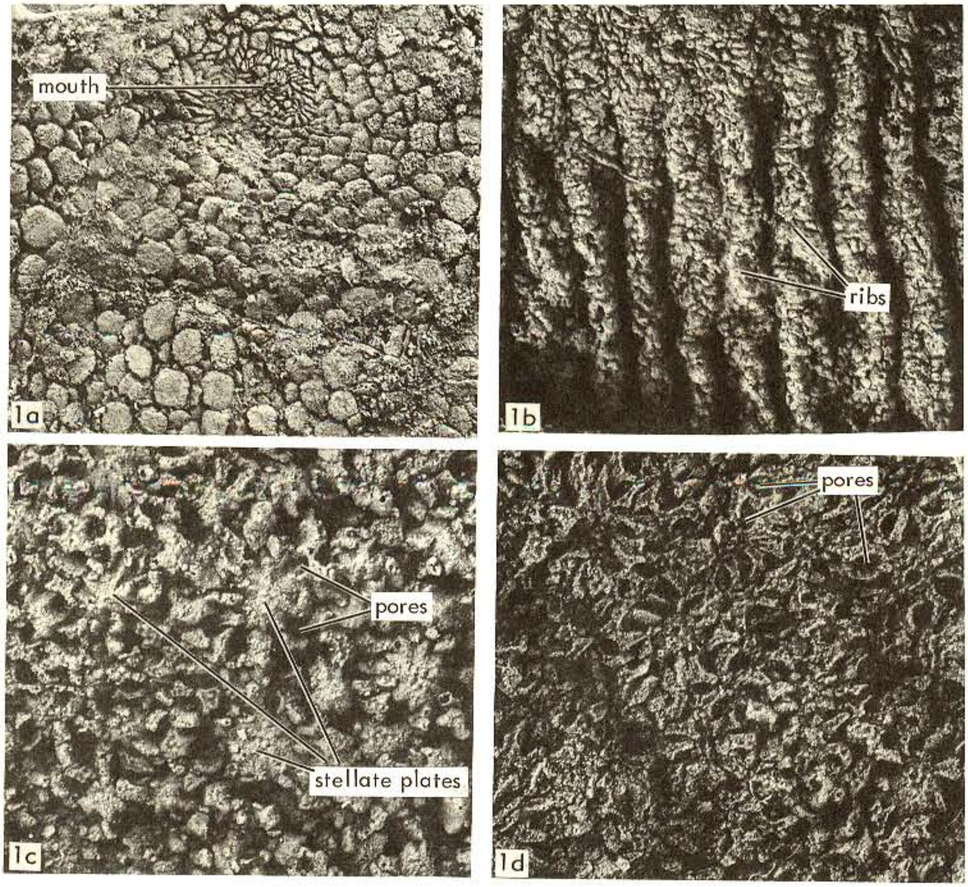


FIG. 397. Camptostromatidae (p. S630).

members of the Dactylochirotida and Dendrochirotida. However, the presence of peripheral arms that are heavily plated (adoral plated arms known in the Devonian holothurian *Palaeocucumaria*, 5) instead of adoral nonplated arms, the apparent lack of pentaradiate or bilateral symmetry, and the absence of elongation along the oral-aboral axis distinguish camptostromatoids from holothurians. Further, although the densely plated test of *Camptostroma* makes recognition of a calcareous ring difficult, no evidence of one was observed and it is assumed that it was absent. Grossly, the camptostromatoids might be compared with the ophiocistioids, but the lack of firmly sutured plates and the multiple types of ossicles in the wall of the test readily differentiate the camptostromatoids.

Family CAMPTOSTROMATIDAE
Durham, new family

Characters of class. *L.Cam.(Olenellus Zone)*.

Camptostroma RUEDEMANN, 1933, p. 5 [**C. roddyi*; OD]. Test medusaeform, with few heavily plated peripheral arms; anus on aboral surface near center, with well-developed pyramid; most areas of wall composed of several types of ossicles; sutural pores on oral surface and upper distal margin of peripheral apron. *L.Cam.(Olenellus Zone)*, USA (Pa.).——FIG. 396-397. **C. roddyi*; 396,*1a*, part of aboral disc, ×2.5; 396,*1b-c*, aboral, oral views of same individual, ×1.4; 397,*1a*, adoral region, ×5; 397,*1b*, ribbed area of apron, ×5; 397,*1c*, detail of mid-oral surface, ×10; 397,*1d*, detail of aboral surface of distal portion of apron, ×10 (P. M. Kier, n).

REFERENCES

Durham, J. W.

(1) 1966, *Camptostroma, an Early Cambrian supposed scyphozoan, referable to Echinodermata:* Jour. Paleontology, v. 40, p. 1216-1220, text fig. 1-2.

Harrington, H. J., & Moore, R. C.

(2) 1956, *Scyphomedusae:* in R. C. Moore (ed.), Treatise on Invertebrate Paleontology, Part F, p. *F*38-*F*53.

Kieslinger, A.

(3) 1939, *Scyphozoa:* in O. H. Schindewolf (ed.), Handbuch der Paläozoologie, v. 2A, p. A67-A109.

Ruedemann, Rudolf

(4) 1933, *Camptostroma, a Lower Cambrian floating hydrozoan:* U.S. Natl. Museum, Proc., v. 82, art. 13, p. 1-8, pl.1-4.

Seilacher, Adolf

(5) 1961, *Holothurien im Hunsrückschiefer:* Hess. Landesamt Bodenforsch., Notizbl. v. 89, p. 66-72, pl. 10-11.

LEPIDOCYSTOIDS

By J. Wyatt Durham

[University of California (Berkeley)]

Class LEPIDOCYSTOIDEA Durham, new class

Free-living, placoid echinoderms with differentiated oral and aboral surfaces; oral surface with numerous small plates with sutural pores, free biserial arms, and anal aperture; character of oral aperture unknown; aboral surface with numerous imbricating plates originating at apex of surface; anus marginal on oral surface, with well-developed anal pyramid; arms grooved, with cover plates, arranged in concentric circlets on oral surface, oldest outermost, resting on flat basal plates; arms presumably for feeding; organs in sutural pores presumably respiratory. *L.Cam.(Olenellus Zone).*

This group of echinoderms is known from a few more or less crushed specimens from the Kinzers Formation of Pennsylvania, where they occur in the same strata as medusaeform camptostromatoids. Most individuals seem referable to the single described species, *Lepidocystis wanneri* Foerste (1). Two specimens have three circlets of arms, probably with five arms to a circlet (no specimen has a complete circlet of arms; it is possible that there might be only four). Arms of each circlet are aligned along radii from the presumed central location of the mouth. One smaller specimen (Fig. 398,*1b*), preserved partly in the round (either immature or else representing another species), seems to have only a single circlet of free arms (but draped along the side of the test during burial). The basal plates of the outermost arms are adjacent to the margin of the aboral imbricating plates, but the bases of the inner arms are set in the midst of the small, marginally incised plates of the oral surface. There is one cover plate to each segment of the arm, with the distal margin of the cover plate serrate and slightly overlapping the proximal margin of the next. The oral surface is covered with small, relatively thick plates, with three or four deep marginal grooves for sutural pores (one to each face). These pores are very numerous and the oral surface must have been densely covered with the organs that extended through them. It is assumed that these organs were respiratory in function and connected by an internal plexus of the water-vascular system.

No feature recognizable as a mouth has been observed, but it seems probable that this was centrally located on the oral surface. It is uncertain how food was transported from the arms: food particles may have been transferred to the mouth by the arms themselves; they may have been moved from the base of the arms to a central mouth by ciliary action; or there may have been subvective channels from the arms. A well-developed anal pyramid built of numerous plates is situated marginally on the oral surface midway between two of the outermost arms. Two specimens indicate that the elongated portion of the test covered with imbricating plates was more or less conical and that the oral surface was arched. The presence of presumed respiratory organs in the sutural pores on the oral surface suggests that *Lepidocystis* lived up-

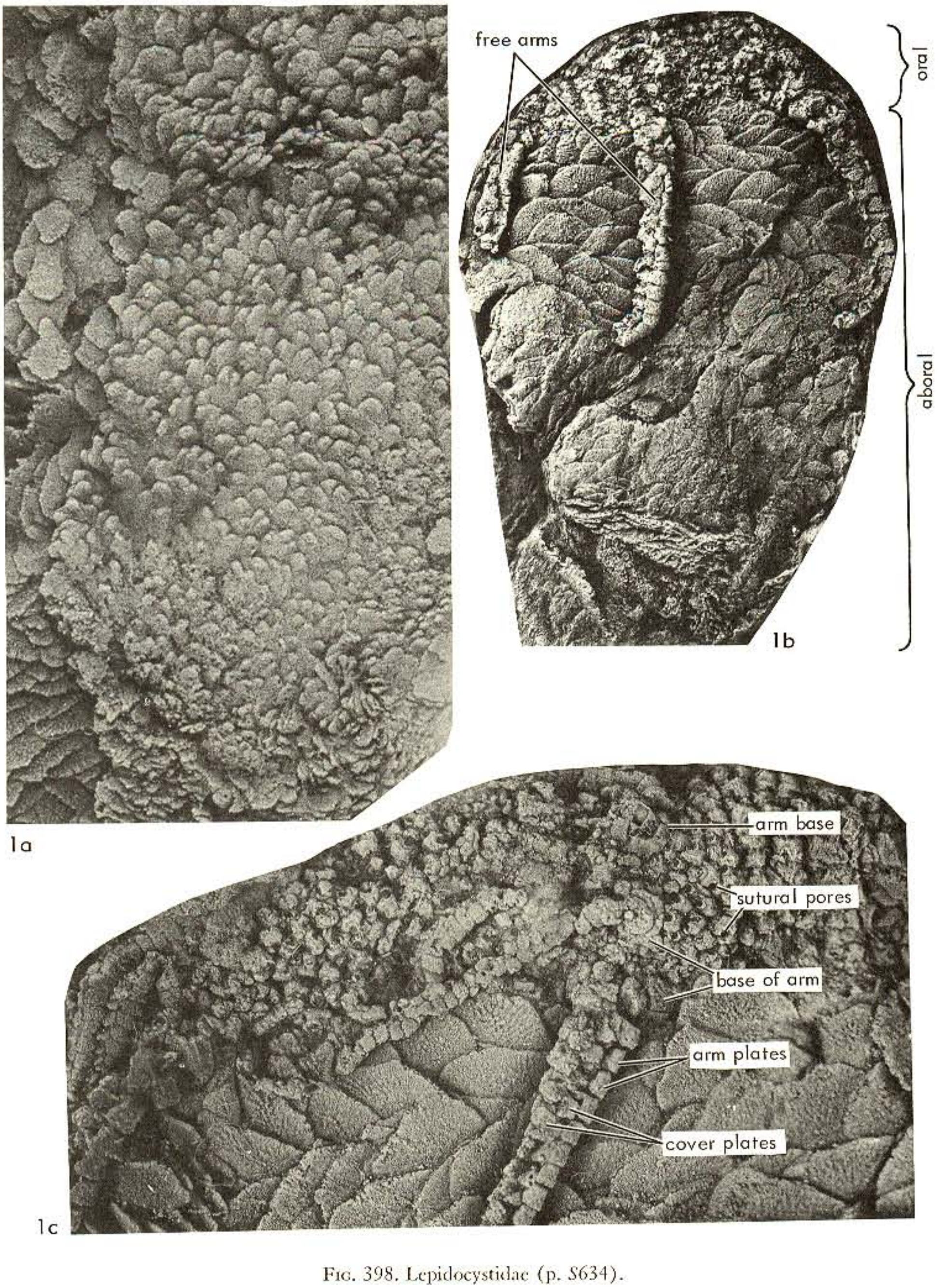


FIG. 398. Lepidocystidae (p. S634).

right on the sea floor with the apical portion of the aboral surface imbedded in sediment (Fig. 399).

The lepidocystoids differ from eocrinoids by restriction of the sutural pore-bearing area to the interbrachial oral surface, the presence of imbricating plates on the aboral surface, the circlets of arms on the oral surface, and the mode of attachment of the arms. They differ from most edrioasteroids, cystoids, and helicoplacoids by the presence of sutural pores, and from camptostromatoids by the possession of only a single type of plate in any area, as well as the position of the anus on the oral surface. They differ from the edrioasteroid *Stromatocystites,* which has sutural pores on the oral surface, by the presence of free arms.

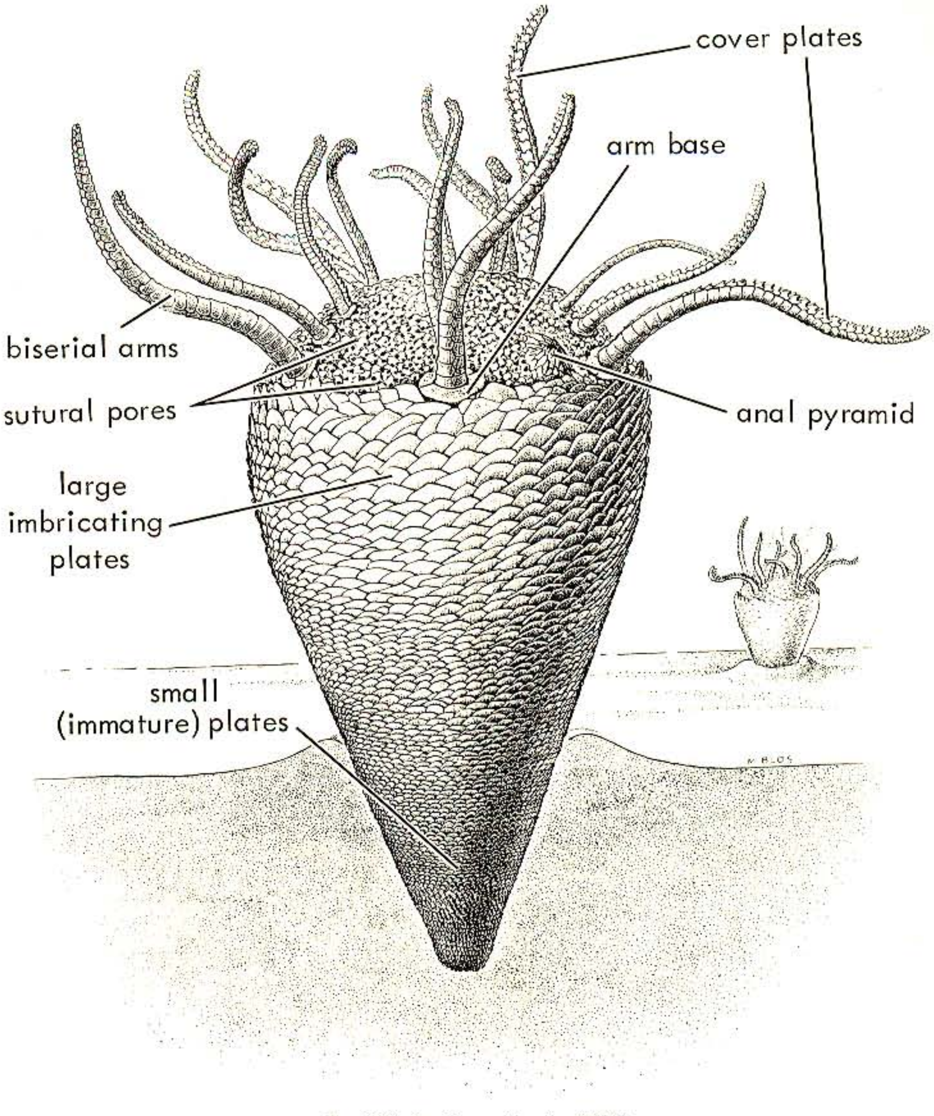


FIG. 399. Lepidocystidae (p. S634).

Family LEPIDOCYSTIDAE Durham, new family

Characters of class. *L.Cam.(Olenellus Zone).*

Lepidocystis Foerste, 1938, p. 212 [**L. wanneri*; M]. Aboral surface of test conical, built of numerous scalelike imbricating plates, those of oral surface small, heavy, deeply incised by single large sutural pore on each side; anus at margin of oral surface, with well-developed anal pyramid. *L.Cam.(Olenellus Zone),* USA(Pa.).——Fig. 398-399. **L. wanneri*; 398,*1a,* detail of small adapical plates, ×8.5; 398,*1b*, small individual with free arms draped along side of test, ×3.1; 398,*1c,* part of oral surface of specimen with 3 circlets of arms, ×4; 399, restoration showing probable mode of life, approx. ×1.5 (Durham, n).

REFERENCE

Foerste, A. F.

(1) 1938, *"Echinodermata":* in C. E. Resser & B. F. Howell, Lower Cambrian *Olenellus* zone of the Appalachians, Geol. Soc. America, Bull., v. 49, p. 212-213, pl. 2.

CYMBIONITES AND PERIDIONITES—UNCLASSIFIED MIDDLE CAMBRIAN ECHINODERMS

By Georges Ubaghs

[Université de Liège, Belgium] [Typescript translated by R. C. Moore]

INTRODUCTION

Cymbionites and *Peridionites* are nominal genera proposed in 1941 by Whitehouse (ref. *11*) on the basis of fossils found in lowermost Middle Cambrian strata (Zone of *Xystridura*) of Queensland, Australia. Specimens of the first-mentioned form were obtained in abundance from the basal 40 feet of the zone and less numerous representatives of the second in a bed of limestone approximately 24 feet higher in the section.

For the purpose of classifying these two genera, both of which are monotypic, Whitehouse introduced new families named Cymbionitidae and Peridionitidae, which respectively were assigned to the new classes Cycloidea and Cyamoidea, and both were placed in a new subphylum of the Echinodermata named Haplozoa.

DESCRIPTION

Each of the two fossil forms displays a thick calcareous skeleton comprised of a few plates disposed around a median crateriform depression. The animals are judged to have been free-living on the sea bottom, for no trace of fixed attachment has been observed.

The remains of *Cymbionites* consist of a hemispherical or thimble-shaped body with average diameter of 12 mm. (Fig. 400,*1a*). Less commonly the fossils are barrel- or saucer-like. Typically they are composed of five tightly joined massive plates of wedge-shaped form, with sutures discernible only on weathered specimens. The median depression, variable in depth, possesses fluted sides. A transverse section through the bottom of the depression commonly shows the presence of a tiny central plate additional to the five main ones and surrounded by them in manner that entirely conceals the small central plate in view of the exterior. The festooned edge of the calyx bears a minute peripheral groove.

The skeleton of *Peridionites* resembles a biconvex half-lens having almost perfect semicircular outline in side view and an elliptical shape in apical view (Fig. 400, *2a-e*). The fossils are diminutive in size, with maximum diameter mostly less than 10 mm. Biradial in form, they are composed of five massive calcareous plates—a median apical one adjoined by two large terminal plates and two smaller mediolateral plates located on opposite sides of a moderately deep central cavity which is

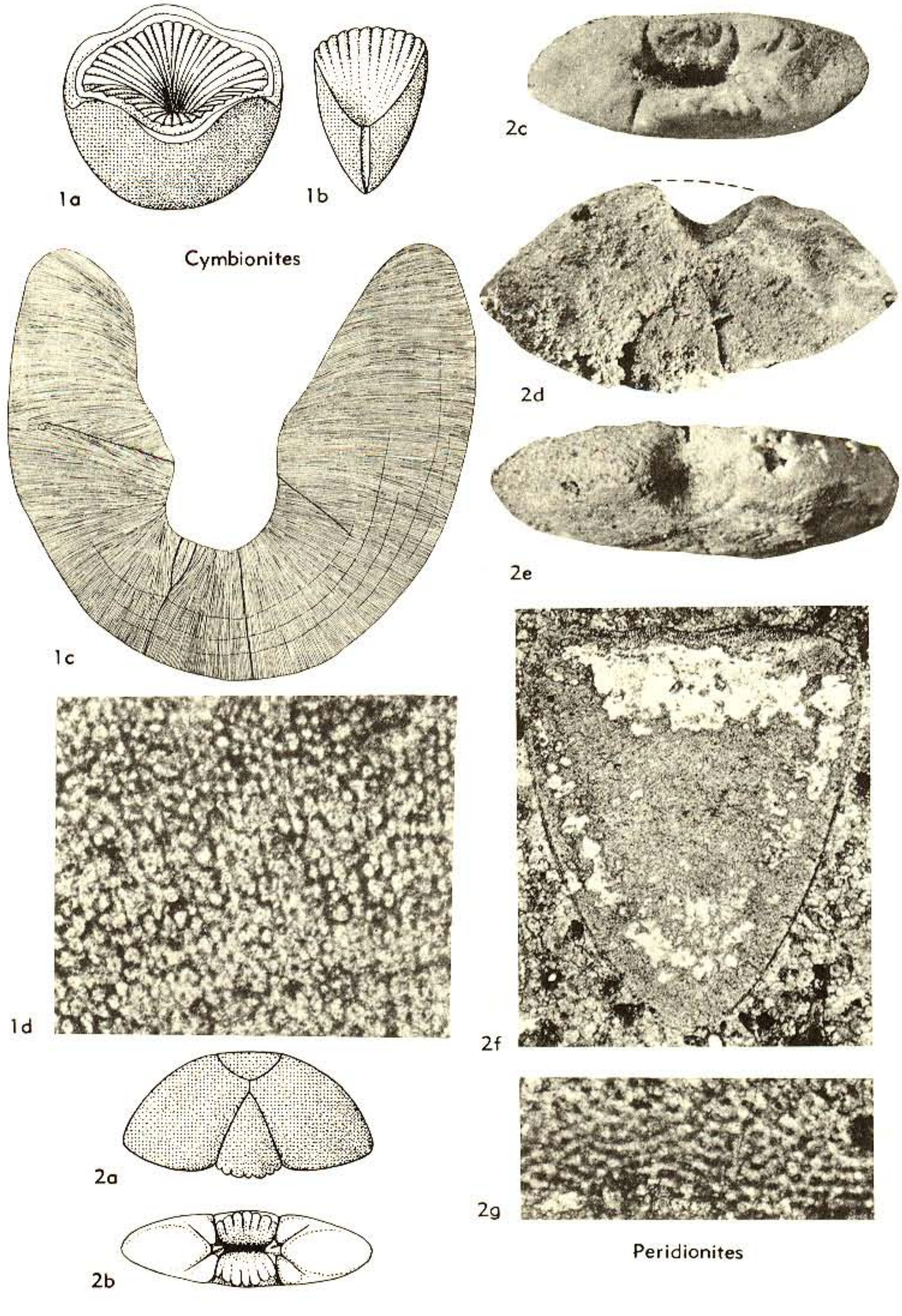


FIG. 400. **Cymbionites craticula* WHITEHOUSE *(1)*; **Peridionites navicula* WHITEHOUSE *(2)* (unclassified M.Cam. echinoderms) (p. S637).

radially fluted internally. The truncate abapical face of each terminal plate is marked by three shallow depressions set off from one another by diverging narrow furrows.

Each plate in both of these genera consists of a single calcite crystal showing optical continuity. In specimens of *Peridionites* subjected to dolomitization or silicification, the original stereomic reticulation of the plates generally cannot be observed, although it may be visible locally in small patches of the surface (Fig. 605,*2f,g*). On the other hand, the reticular microstructure of plates belonging to *Cymbionites* commonly is very evident. They are composed of close-packed "but intermittently impinging" prismatic fibers with a calcite network optically continuous with the fibers between them (Fig. 400,*1c,d*).

INTERPRETATIONS

These two genera of fossils have been interpreted in extraordinarily different ways.

1) In the view of WHITEHOUSE *(11)* both forms are echinoderms. *Peridionites* is considered to be the dorsal skeleton of a bilaterally symmetrical five-segmented organism which corresponds morphologically to the dipleurula stage in larval development of echinoderms. *Cymbionites* is judged to be the aboral skeleton of an essentially radiate organism equivalent to the pentactula stage in ontogeny of eleutherozoic echinoderms. Asteroids, ophiuroids, and echinoids are thought to be derivatives of the Cycloidea (class represented solely by the genus *Cymbionites* as now known), and those in their turn are supposed to come from the Cyamoidea (class represented only by *Peridionites* among yet discovered fossils). The Cyamoidea are interpreted as ancestral also to the Homalozoa ("Carpoidea" and Machaeridia) in one line and to the Pelmatozoa [Crinozoa] (Cystoidea, Blastoidea, Edrioasteroidea, Crinoidea) in another line. These concepts have been accepted by some *(7)* but rejected by most workers *(1-3, 5, 6, 8, 9)*.

2) According to GISLÉN *(2)* (as well as TERMIER & TERMIER, *9*), *Cymbionites* is an echinoderm provisionally interpretable as a cystoid with only the basal part of the theca calcified. *Peridionites,* however, is not an echinoderm but possibly a ctenophore modified for benthonic existence like the modern *Platyctenida* and distinguished by having a calcareous skeleton.

3) Neither of the two discussed fossils is an echinoderm, in the opinion of CUÉNOT & TÉTRY *(1)*. Instead, both are considered to be representatives of phyla which vanished without producing known descendants. In the phylogeny of the animal kingdom they may belong in the great gap separating the cnidarians and ctenophores from the beginning of deuterostomians marked by the echinoderms.

4) Finally, SCHMIDT *(6)*, who accepted both genera as echinoderms, interpreted them as eocrinoids having greatly reduced thecae that functioned merely as stabilizing structures.

The temerity of some of these hypotheses contrasts with the weakness of evidence in support of them. That *Cymbionites* and *Peridionites* are truly echinoderms can hardly be doubted, for not only are their plates composed of single crystals but reasonably well-preserved specimens exhibit unequivocal traces of honeycomb microstructure of the stereom which is characteristic of the phylum. Although this much is established, nothing more is certain. Do the fossils constitute complete skeletons, as their morphology and manner of preservation (including lack of associated fragments) seem to indicate, or, oppositely, are they incomplete remains? What was the nature of soft parts originally associated with the skeletons? How may the remains be oriented correctly in relation to morphology of the organisms? Such questions presently are unanswerable. *Cymbionites*—but not *Peridionites*—suggests the basal part of the theca of such crinozoans as *Parorthocrinus* and *Rhopalocystis,* but the resemblance is quite superficial in that it relates only to external form of a small part of the body *(10)*, thus meriting no serious consideration of possible relationships. Inasmuch as these fossils fail to provide information necessary for understanding of the organization of animals represented by them, it seems improper to assign them either to extant or extinct classes of echinoderms, and in my opinion not even to recognize them as distinct families. Beyond statement of what can be observed, all is speculation.

SYSTEMATIC DESCRIPTIONS

Cymbionites Whitehouse, 1941, p. 9 [**C. craticula*; M]. Echinodermal remains consisting of calcareous dome-shaped bodies composed typically of 5 equal curved plates of thick wedge-shaped form, firmly joined together laterally and apically as cuplike structure with fluted wall surrounding more or less deep central depression; stereom composed of closely packed prismatic fibers with calcite meshwork in optical continuity with fibers occurring between them; each plate consisting of single crystal. *M.Cam.(Xystridura Zone),* Australia(Queensl.).——Fig. 400,*1*. **C. craticulata*; *1a,b,* oblique lat. view of complete specimen and single isolated plate, ×3 *(11)*; *1c,* long. (vertical) sec. showing sutures and growth lines, ×7 *(11)*; *1d,* tang. sec. showing honeycomb structure of stereom, ×120 (Ubaghs, n).

Peridionites Whitehouse, 1941, p. 5 [**P. navicula*; M]. Echinodermal remains comprising calcareous dome-shaped bodies which are laterally compressed and biradial in form, composed of 5 plates including single apical plate, 2 large end plates, and 2 somewhat smaller mediolateral plates bordering narrow deep central fossa; each plate comprising single crystal with originally reticulate stereom. *M.Cam.(Xystridura Zone),* Australia (Queensl.).——Fig. 400,*2*. **P. navicula; 2a,b,* lat. and truncate faces, ×5 *(11)*; *2c-e,* truncate, lat., and apical faces (*2d,e,* holotype, with apical plate lacking), ×5.6 (Queensland Univ. photographs, n); *2f,* long. (vertical) sec. of end plate showing preserved remnant of honeycomb stereom structure on upper edge, ×15 (Ubaghs, n); *2g,* tang. thin sec. showing stereom reticulation, ×120 (Ubaghs, n).

REFERENCES

Cuénot, Lucien, & Tétry, Andrée

(1) 1949, *Deux prétendus echinodermes du Cambrien d'Australie:* 13e Congr. Internatl. Zoologie (1948), Comptes Rendus, p. 568 (Paris).

Gislén, Torsten

(2) 1947, *On the Haplozoa and the interpretation of Peridionites:* Zool. Bidrag Uppsala, v. 25, p. 402-408, fig. 1-3.

Hyman, L. H.

(3) 1955, *The invertebrates: Echinodermata, the coelomate Bilateralia:* v. 4, 763 p., 280 fig., McGraw-Hill (New York, Toronto, London).

Müller, A. H.

(4) 1963, *Lehrbuch der Paläozoologie, v. 2, Invertebraten, pt. 3, Arthropoda 2, Stomochorda:* 698 p., 1854 fig., Gustav Fischer (Jena).

Nichols, David

(5) 1962, *Echinoderms:* 200 p., 26 fig., Hutchinson (London).

Schmidt, Hermann

(6) 1951, *Whitehouse's Ur-Echinodermen aus dem Cambrium Australiens:* Paläont. Zeitschr., v. 24, p. 142-145, fig. 1-2.

Shrock, R. R., & Twenhofel, W. H.

(7) 1953, *Principles of invertebrate paleontology:* edit. 2, 816 p., McGraw-Hill (New York, Toronto, London).

Tarlo, L. B.

(8) 1960, *The invertebrate origins of the vertebrates:* Internatl. Geol. Congress Norden, Rept. 2i, pt. 22, p. 113-123, 7 fig. (Copenhagen).

Termier, Henri, & Termier, Geneviève

(9) 1948, *Les échinodermes du Paléozoïque inférieur:* Revue Scientifique, Année 86, p. 613-626, 41 fig.

Ubaghs, Georges

(10) 1963, *Rhopalocystis destombesi n.g., n.sp., Eocrinoïde de l'Ordovicien inférieur (Trémadocien supérieur) du Sud Marocain:* Service Géol. Maroc, Notes, v. 23, no. 172, p. 25-40, 9 text fig., 3 pl.

Whitehouse, F. W.

(11) 1941, *Early Cambrian echinoderms similar to the larval stages of Recent forms:* Queensland Museum, Mem., v. 12, pt. 1, 28 p., 9 text fig., 4 pl.

INDEX

Italicized names in the following index are considered to be invalid; those printed in roman type, including morphological terms, are accepted as valid. Suprafamilial names are distinguished by the use of full capitals and authors' names are set in small capitals with an initial large capital. Page references having chief importance are in boldface type (as **S332**).