Deltoblastus) reported from Sosio Limestone, Sicily.]

———, & Ivanov, A. P.

(190) 1956, *Morskie lilii i blastoidei kamennougolnykh i permskikh otlozheniy SSSR:* Vses. Nauchno Issledov. Geol. Inst., Trudy, v. 11, p. 1-142, text fig. 1-23, pl. 1-21. [*Crinoids and blastoids of the Carboniferous and Permian of the USSR.*] [Summarizes knowledge of blastoids of Russia.]

Yang, C. C., & Chu, M. T.

(191) 1965, *A Lower Carboniferous blastoid from Daoxian (Taohsien), Hunan:* Acta Palaeont. Sinica, v. 13, no. 2, p. 370-372, text fig. 1, pl. 1.

Zittel, K. A. von

(192) 1903, *Grundzüge der Paläontologie (Paläozoologie). 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,

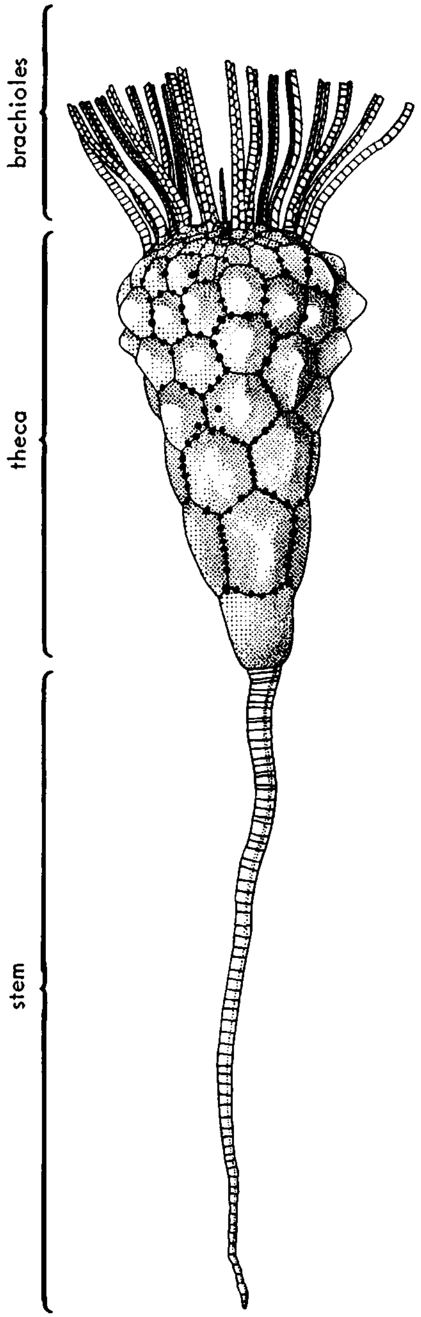


Fig. 292. Entire eocrinoid (reconstr.), showing threefold division of skeleton. *Rhopalocystis destombesi* Ubaghs (Rhopalocystidae), L.Ord., Morocco, ×1 (39).

---

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

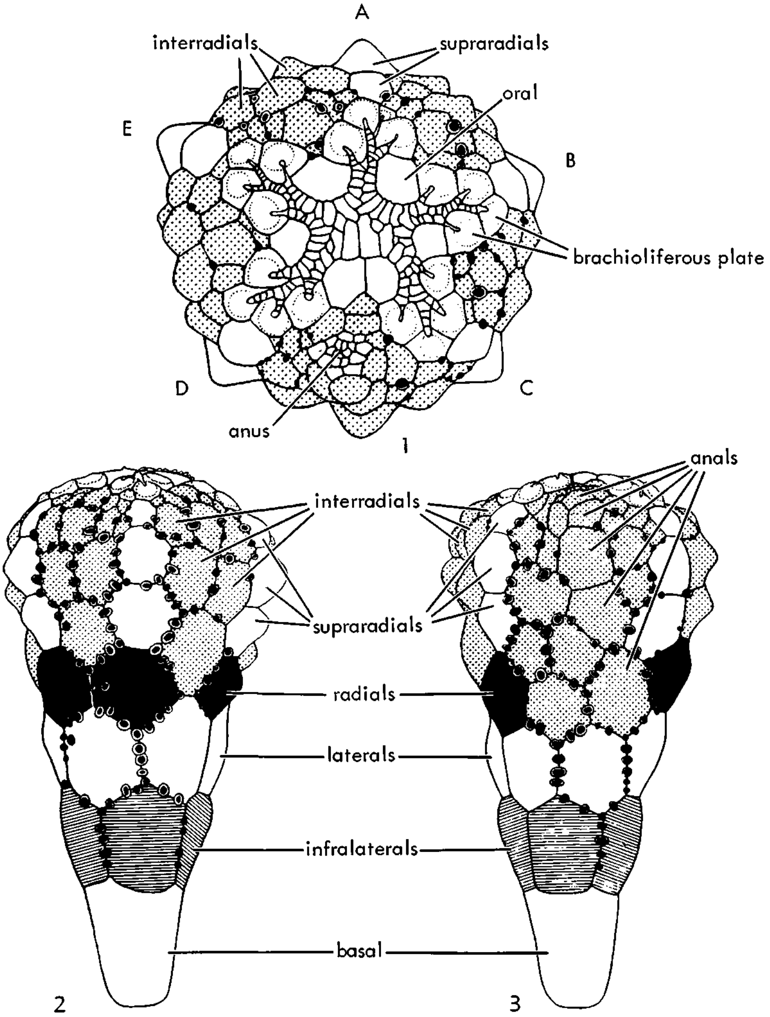


FIG. 293. Morphological features of eocrinoid theca (reconstr.). *Rhopalocystis destombesi* UBAGHS (Rhopalocystidae), L.Ord., Morocco; *1,* oral surface, brachioles lacking, ×2.75; *2,3,* side views of theca from *A*-ray and *CD*-interray sides, ×2 (all Ubaghs, n).

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-*

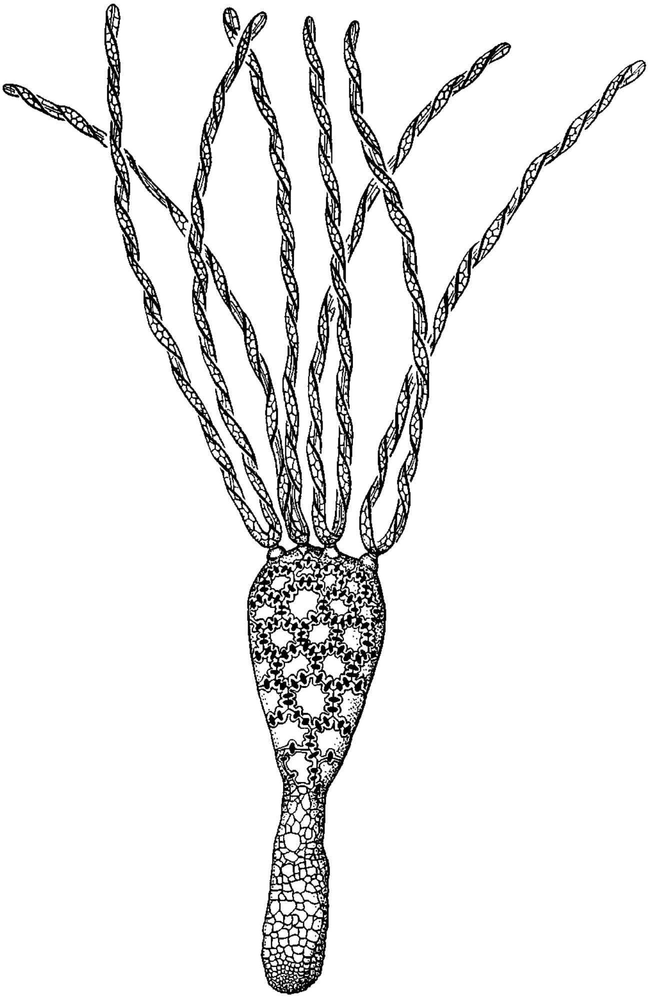


FIG. 294. Entire eocrinoid of rather primitive type (reconstr.), showing dissimilar proximal and distal parts of theca (latter with prominent sutural pores at borders of plates) and helicoidally twisted brachioles, side view. *Gogia spiralis* ROBISON (Eocrinidae), M.Cam., Can.(B.C.), ×2.3 (31).

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

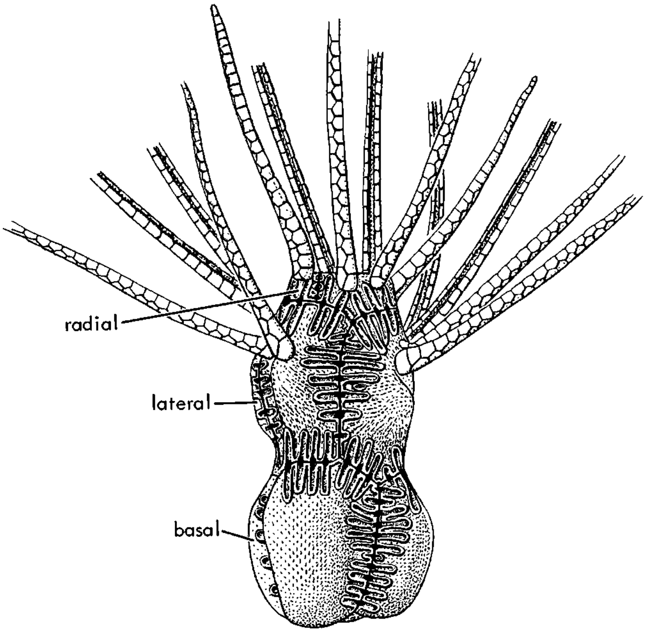


FIG. 295. Entire eocrinoid of type having three circlets of relatively large, regularly arranged thecal plates and well-developed biserial brachioles borne by lateral and radial plates, prominent epispires along sutures between plates (reconstr.). *Lichenoides priscus* BARRANDE (Lichenoididae), M.Cam.,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

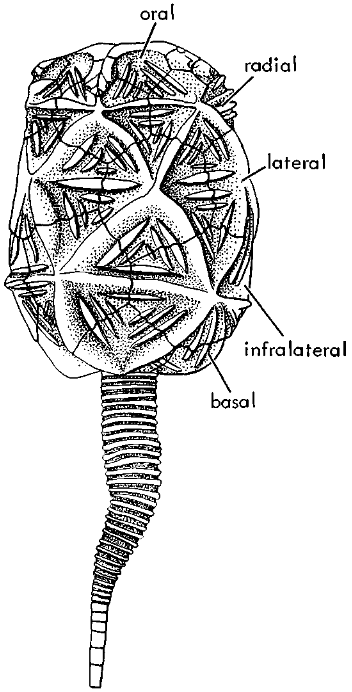


FIG. 296. Side view of theca showing five plate circlets and stem with dissimilar proximal and distal regions, brachioles omitted (reconstr.). *Mimocystites azaisi* THORAL (Macrocystellidae), L.Ord., France, ×2 (Ubaghs, n).

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

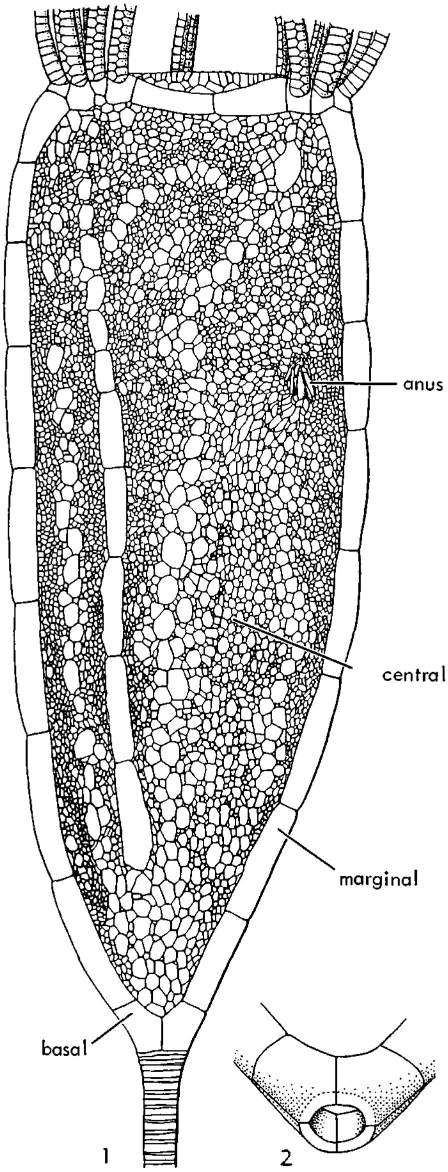


FIG. 297. Eocrinoid with strongly compressed elongate theca rimmed by stout marginal plates and extremely numerous, mostly very minute central plates (reconstr.). *Lingulocystis elongata* THORAL (Lingulocystidae), L.Ord., France; *1*, side view of theca with parts of stem and brachioles, ×4 (38); *2*,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

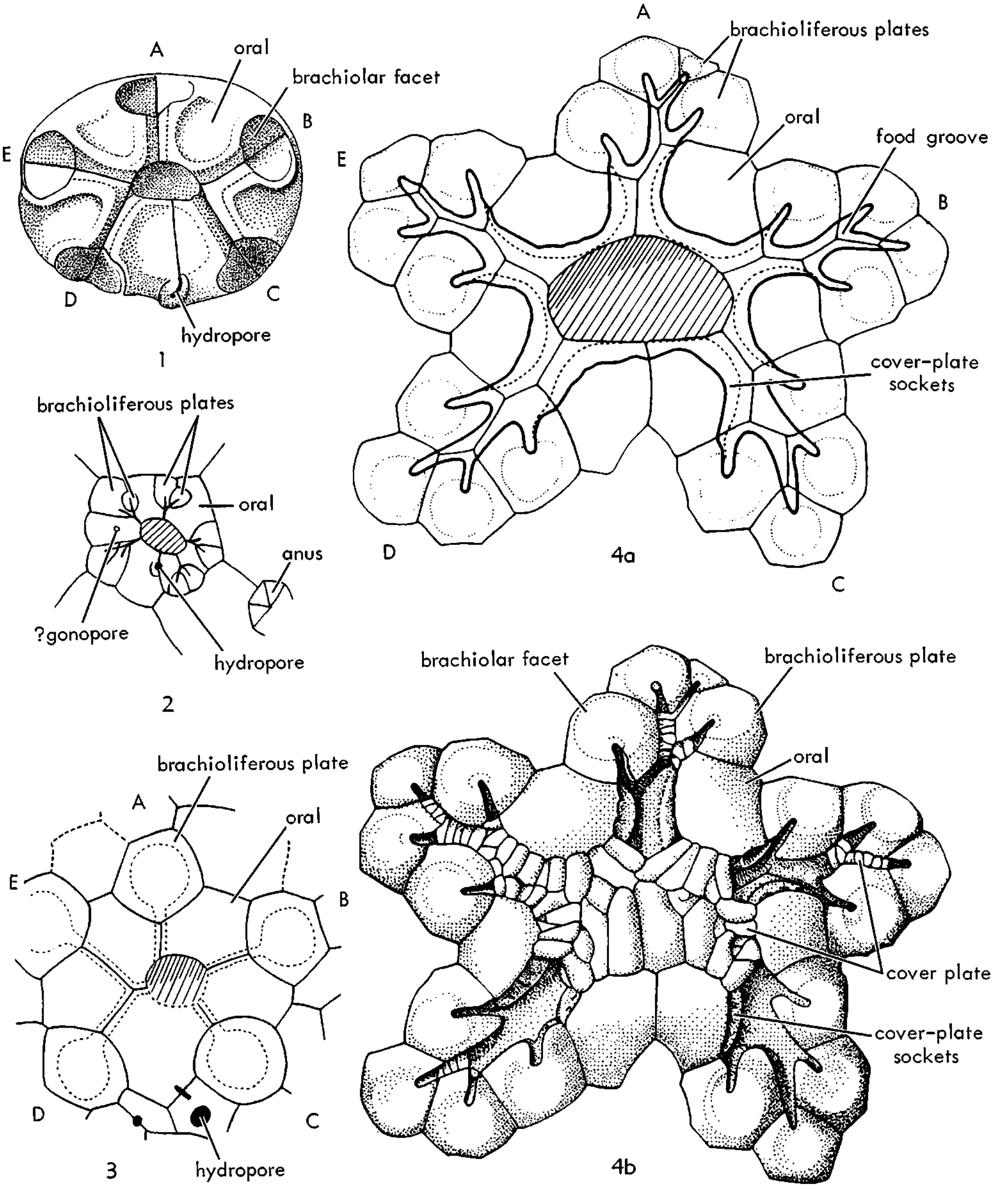


FIG. 298. Morphological features of oral surface of eocrinoid theca.

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).

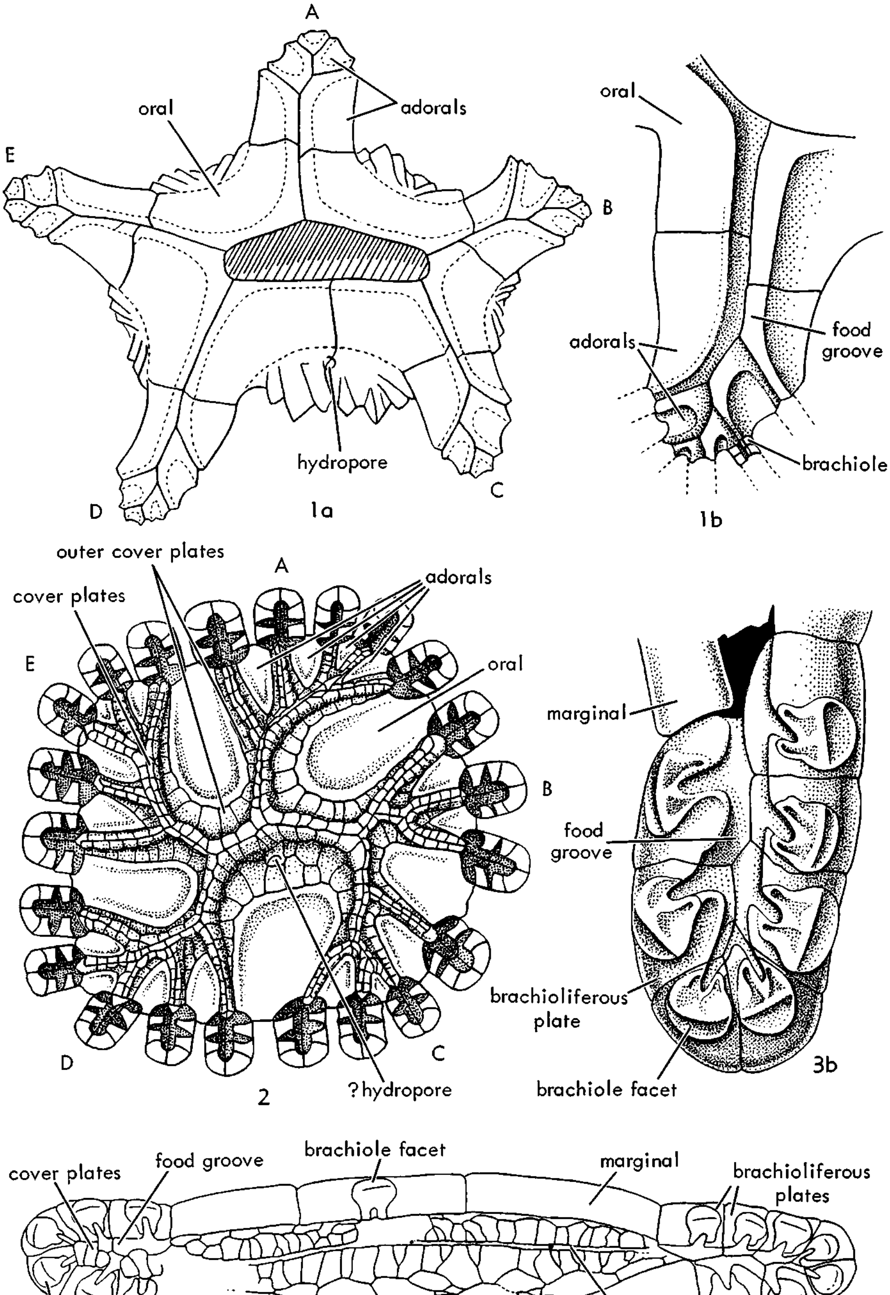


FIG. 299. Morphological features of oral surface of eocrinoid theca.

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).

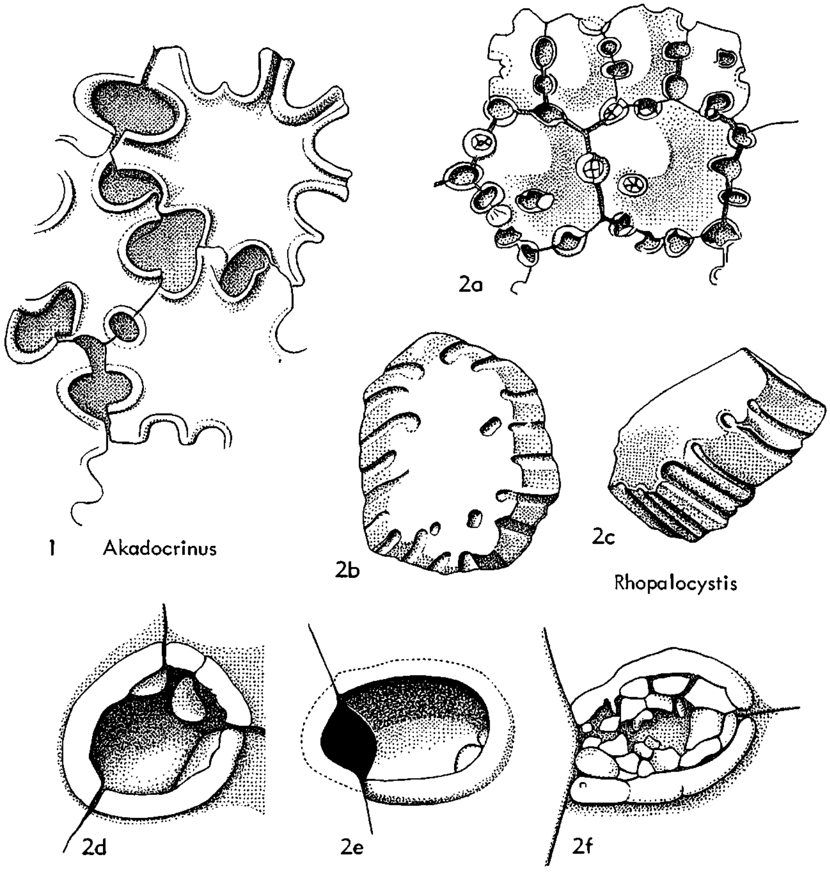


FIG. 300. Morphological features of eocrinoid sutural pores.

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-

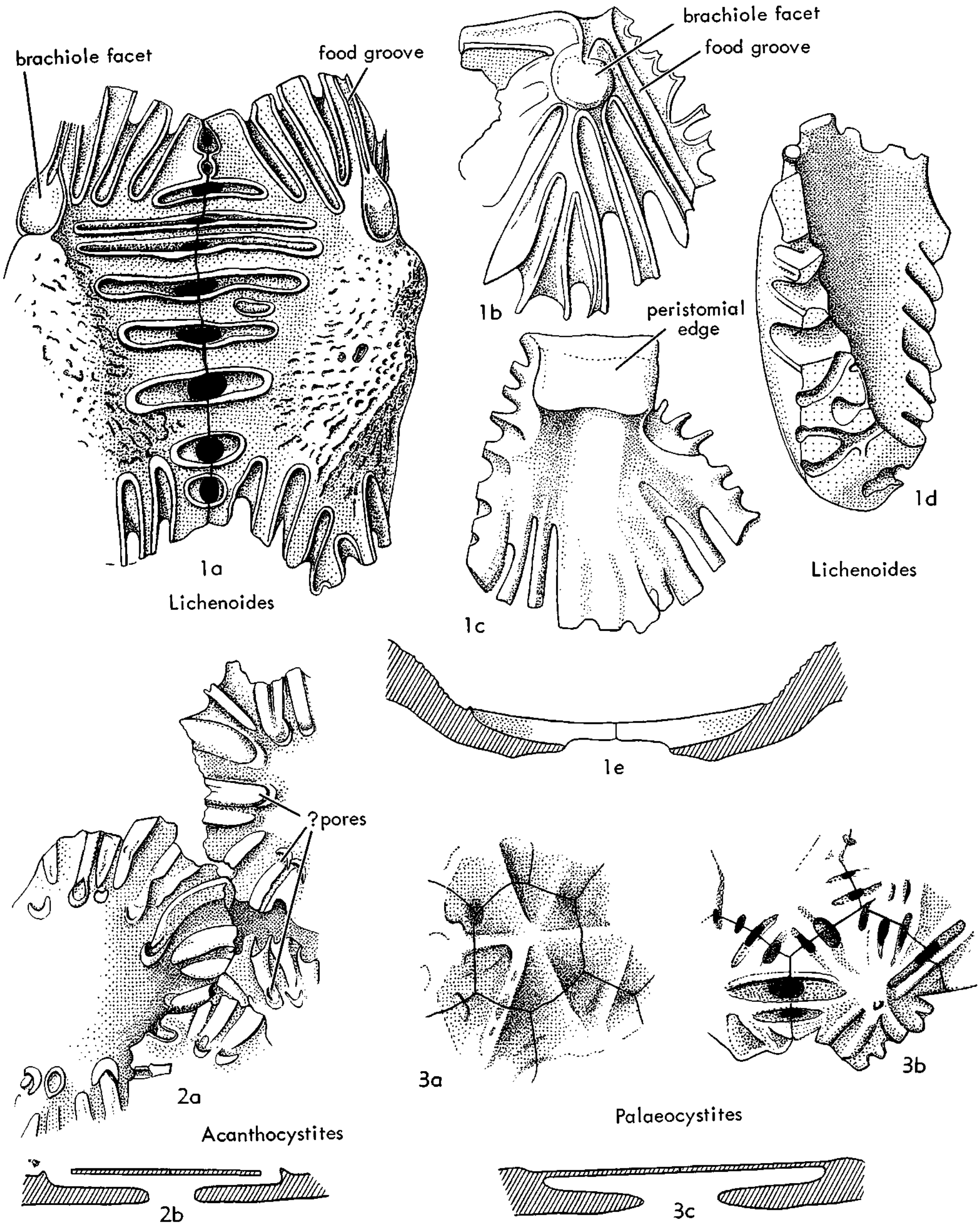


FIG. 301. Morphological features of epispires.

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

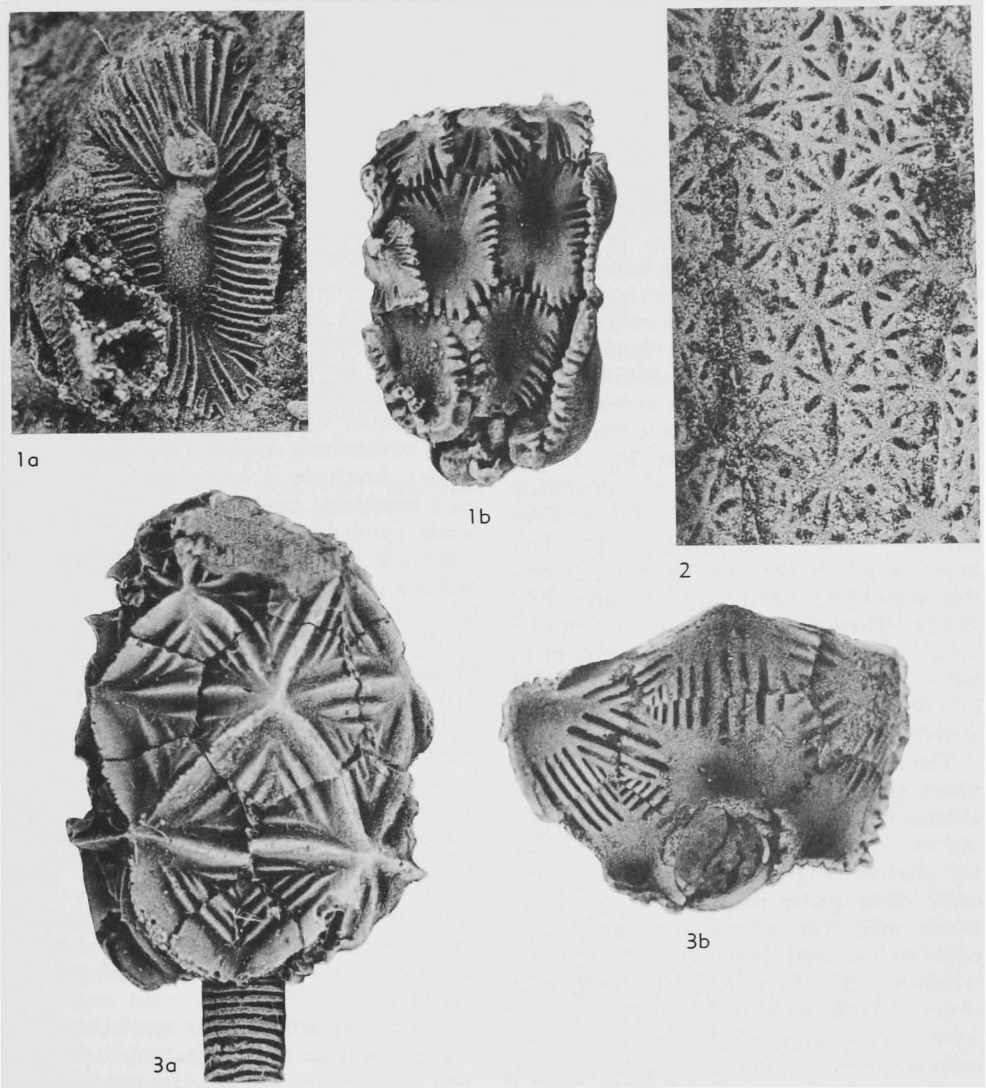


FIG. 302. Morphological features of epispires.

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

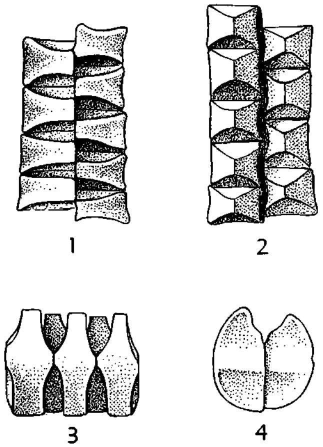


Fig. 303. Brachioles of *Ascocystites* Barrande (Ascocystitidae), M.Ord., Boh. (all Ubaghs, n).

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

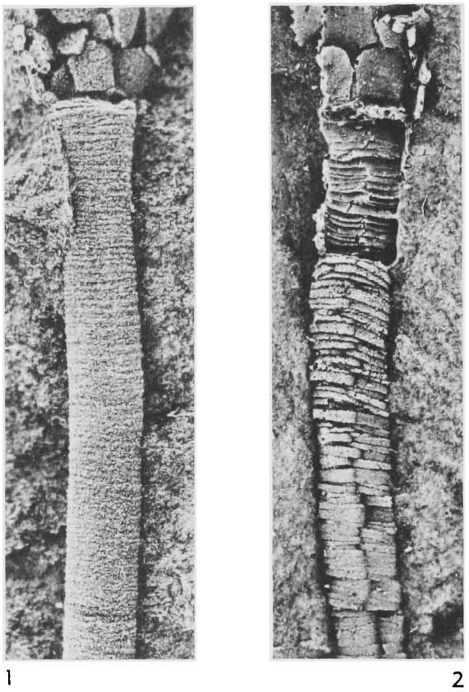


FIG. 304. Morphologic features of eocrinoid stem illustrated by *Akadocrinus nuntius* PROKOP (Eocrinidae), M.Cam., Boh. (Ubaghs, n).——*1.* Proximal part of theca and attached stem composed of wide, very short circular columnals, ×5.——*2.* Similar view of specimen showing large hollow interior of stem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

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

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

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

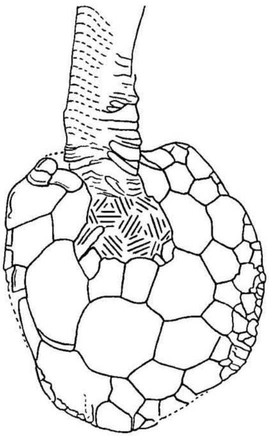


FIG. 305. Holdfast disc at distal extremity of stem of *Akadocrinus nuntius* PROKOP, M.Cam., Boh., ×9 (Ubaghs, n).

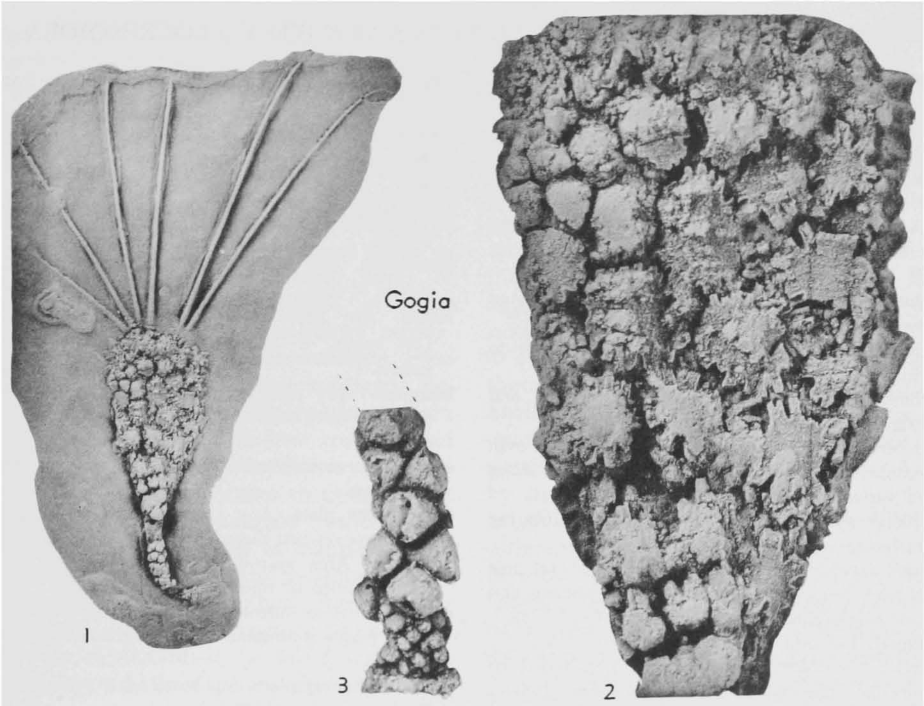


FIG. 306. Eocrinidae (p. S478).

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

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

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

GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO EOCRINOIDEA

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

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

anal. Supplementary plate in *CD* interray.

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

basal. Any plate of proximal circlet.

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

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

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

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

brachioliferous plate. Special thecal plate bearing brachiole.

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

columnal. Individual ossicle of column.

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

cover plate. Small plate covering part of food groove.

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

deltoid. See oral.

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

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

gonopore. Presumed outlet of genital products.

hydropore. Presumed orifice of water-vascular system.

infralateral. Any plate of circlet between basals and laterals.

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

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

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

oral. Any of interradially disposed plates around peristome.

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

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

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

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

radial. Any plate of circlet next distal to laterals.

stem. See column.

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

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

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

TAXONOMIC POSITION

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

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

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

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

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

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

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

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

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

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

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

CLASSIFICATION

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

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

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

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

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

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

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

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

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

SYSTEMATIC DESCRIPTIONS

Class EOCRINOIDEA Jaekel, 1918

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

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

Family EOCRINIDAE Jaekel, 1918

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

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

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

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

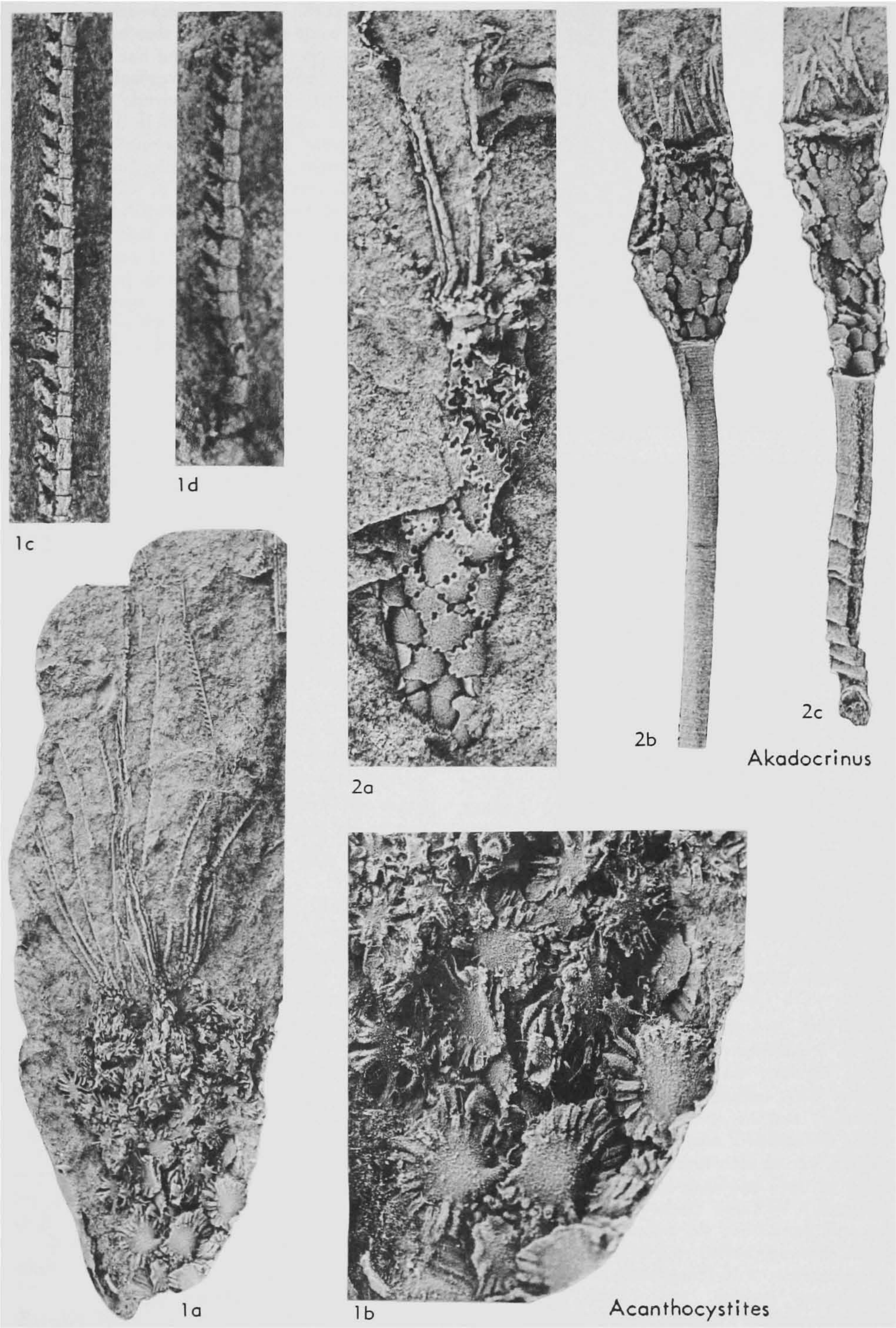


FIG. 307. Eocrinidae (p. *S*478, *S*480).

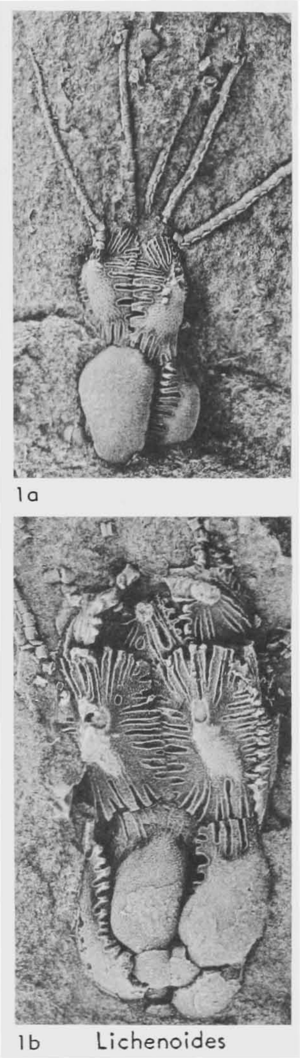


FIG. 308. Lichenoididae (p. S481).

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

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

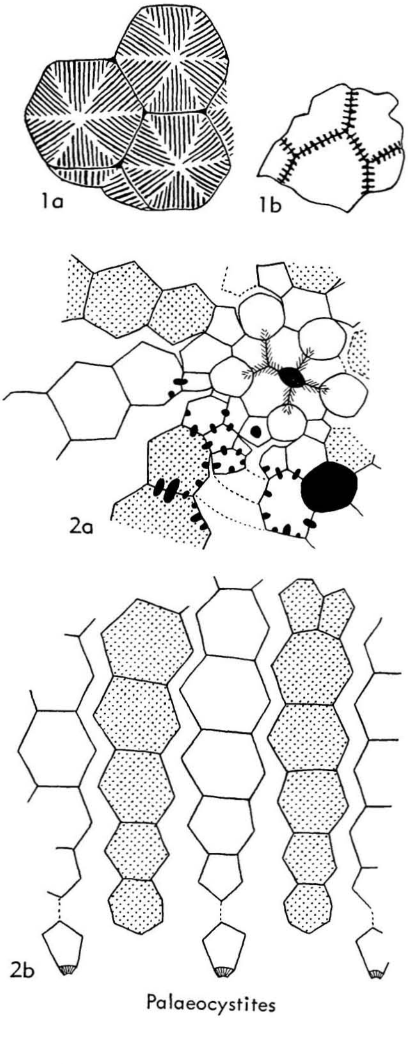


FIG. 309. Palaeocystitidae (p. S481-S482).

---

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

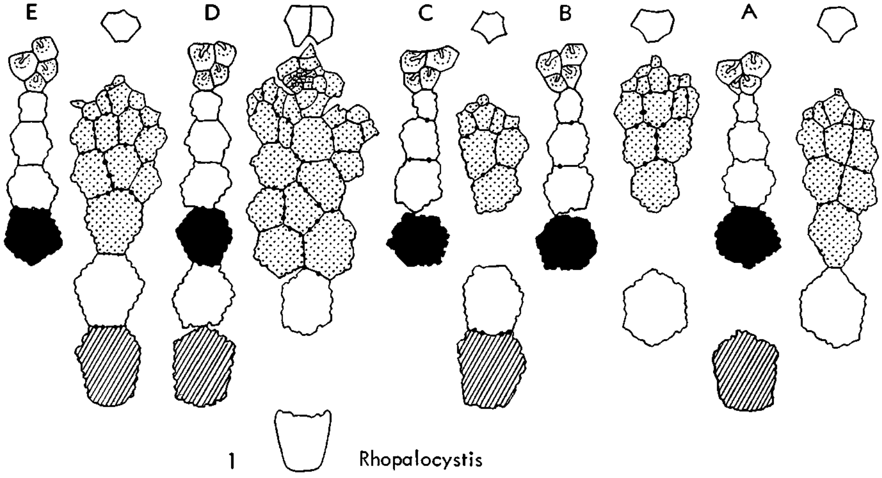


FIG. 310. Rhopalocystidae (p. S481-S482).

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)]

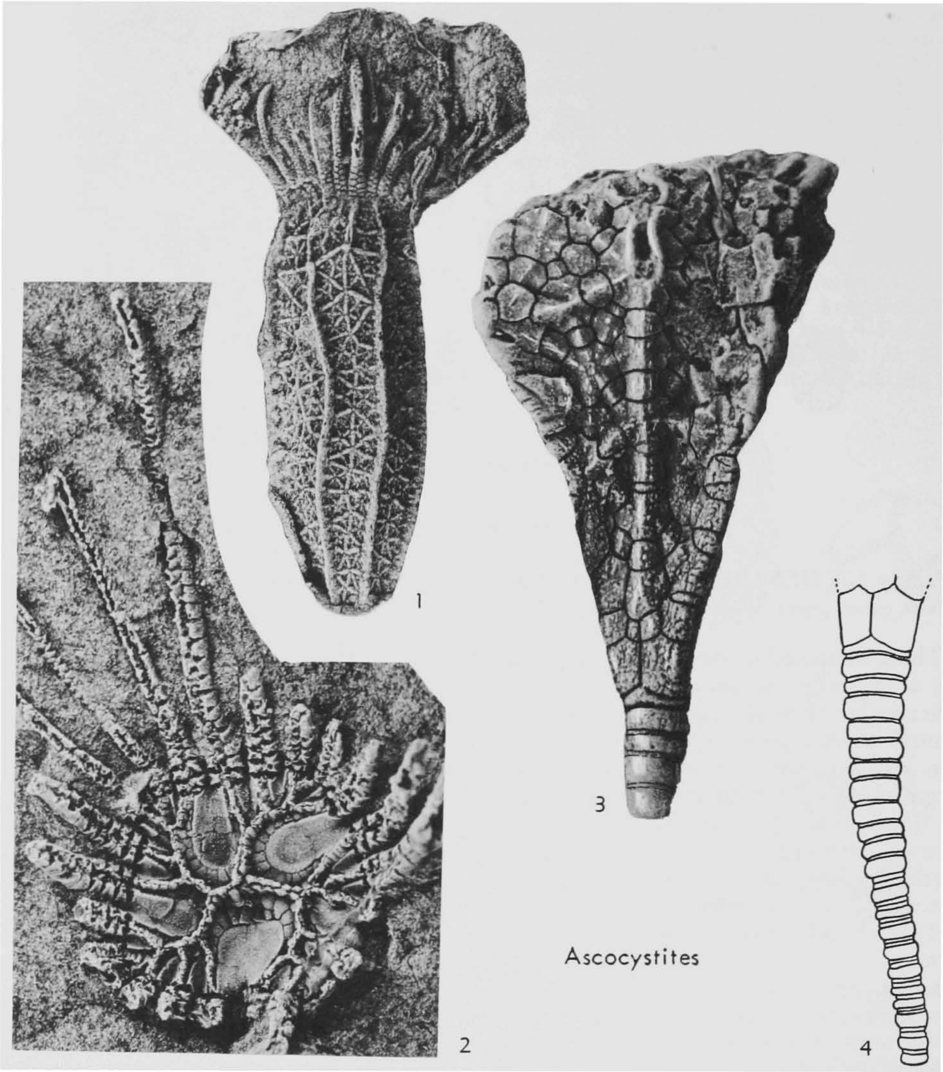


FIG. 311. Ascocystitidae (p. S483).

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)*.

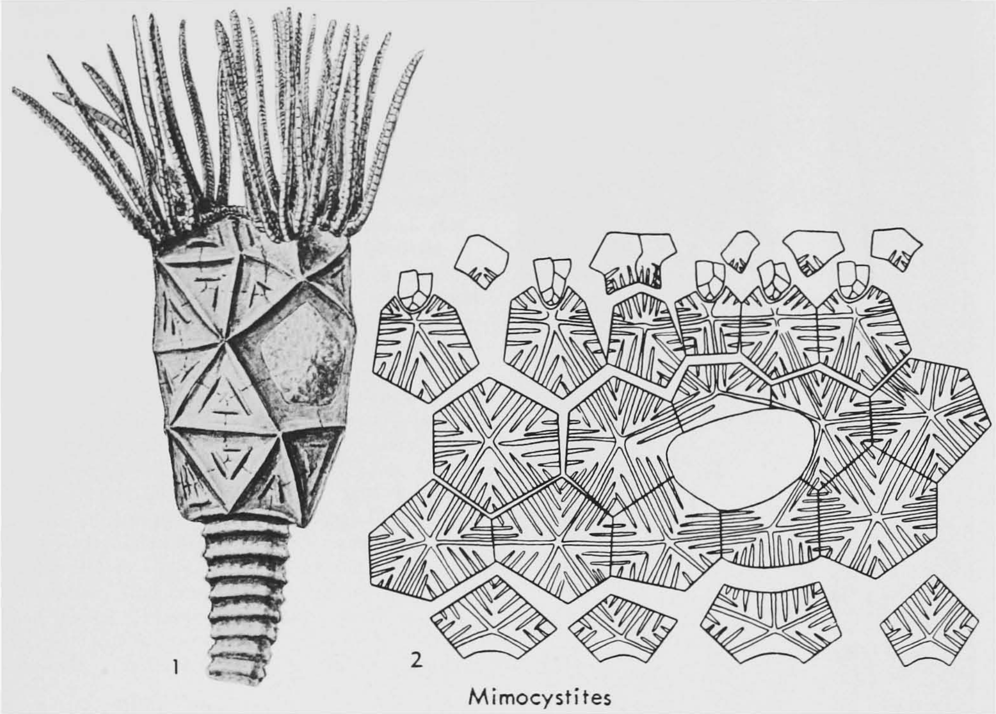


FIG. 312. Macrocystellidae (p. S484-S486).

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.*

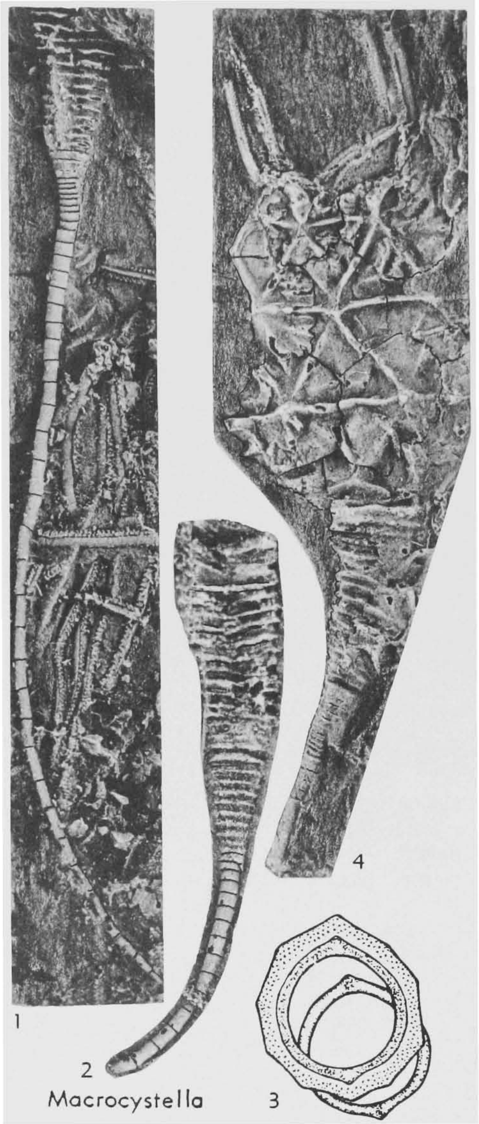


FIG. 313. Macrocystellidae (p. S484).

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

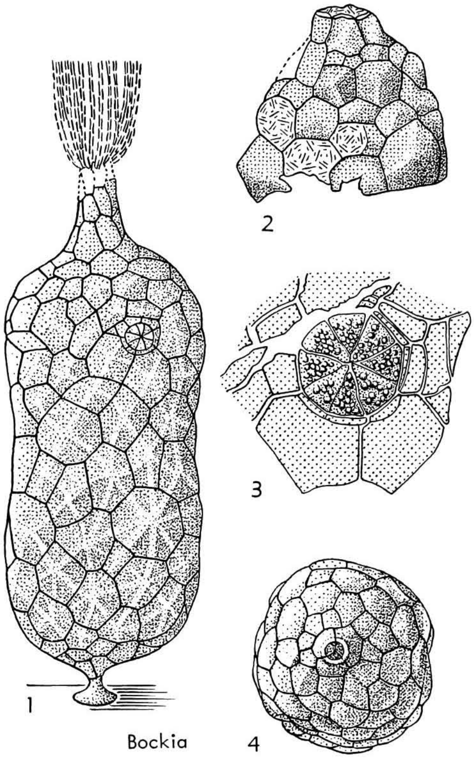


FIG. 314. Springerocystidae (p. S486-S487).

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.

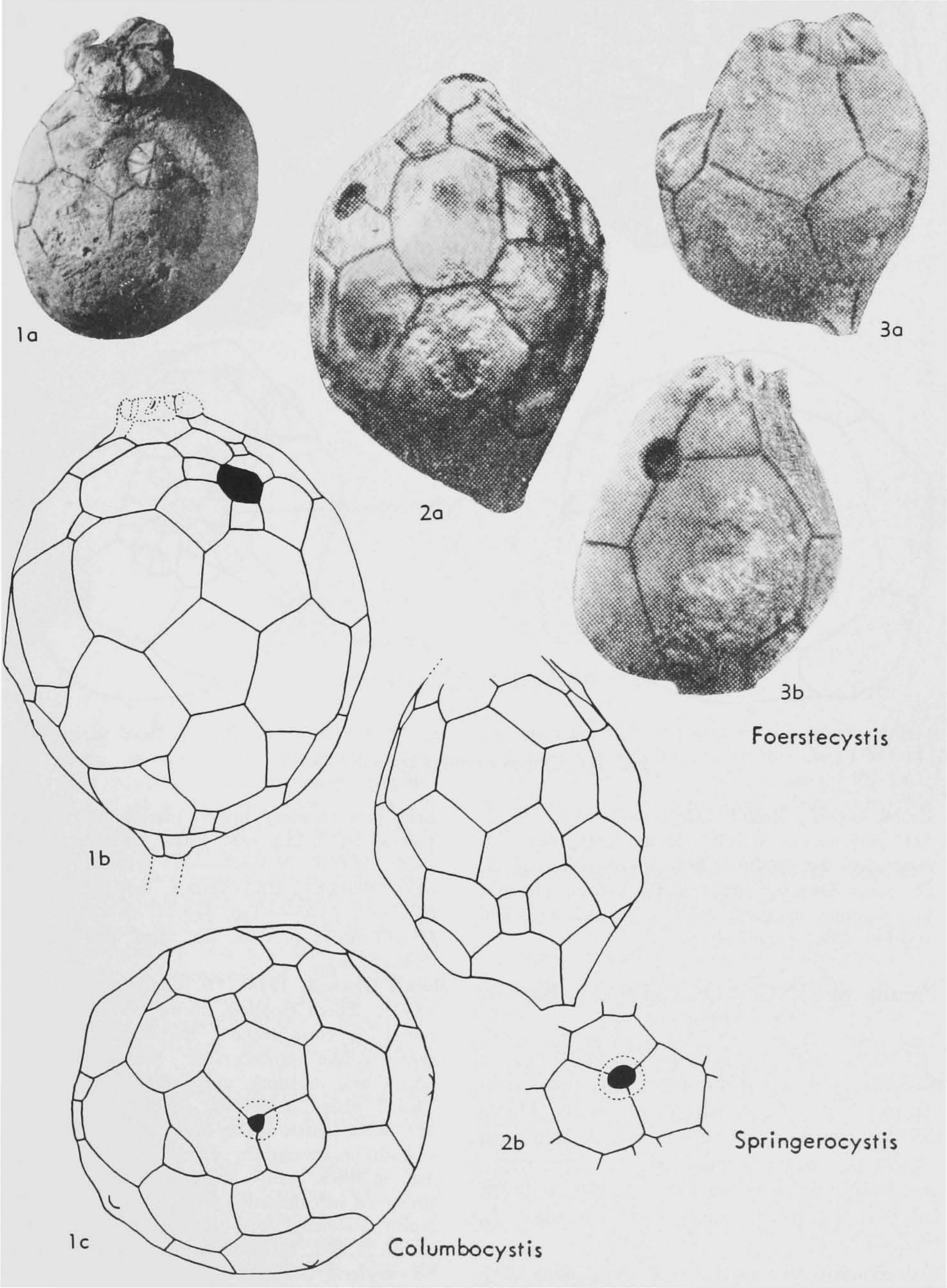


Fig. 315. Springerocystidae (p. *S*486-*S*487).

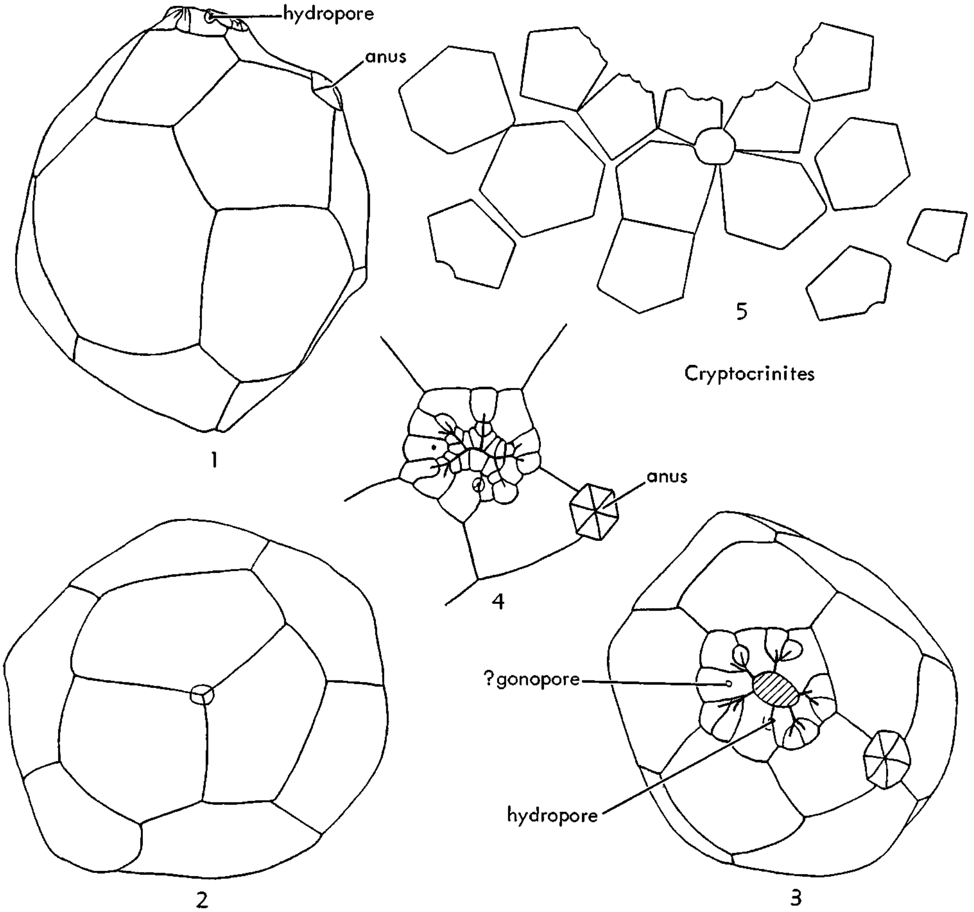


FIG. 316. Cryptocrinitidae (p. S487-S488).

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)*.

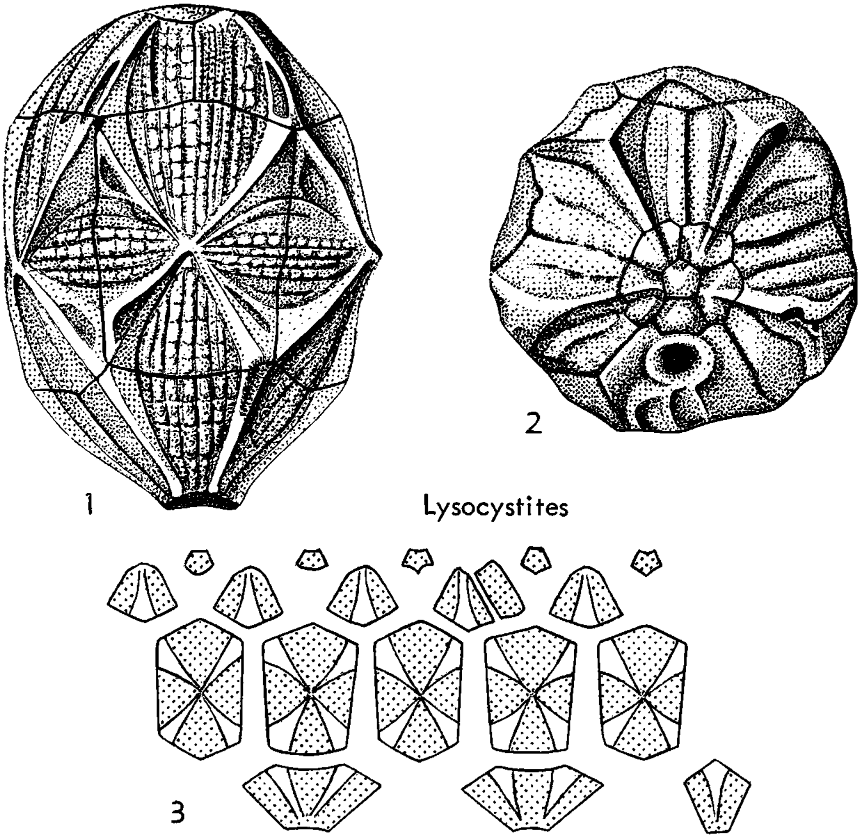


FIG. 317. Cryptocrinitidae (p. S488-S489).

?**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*

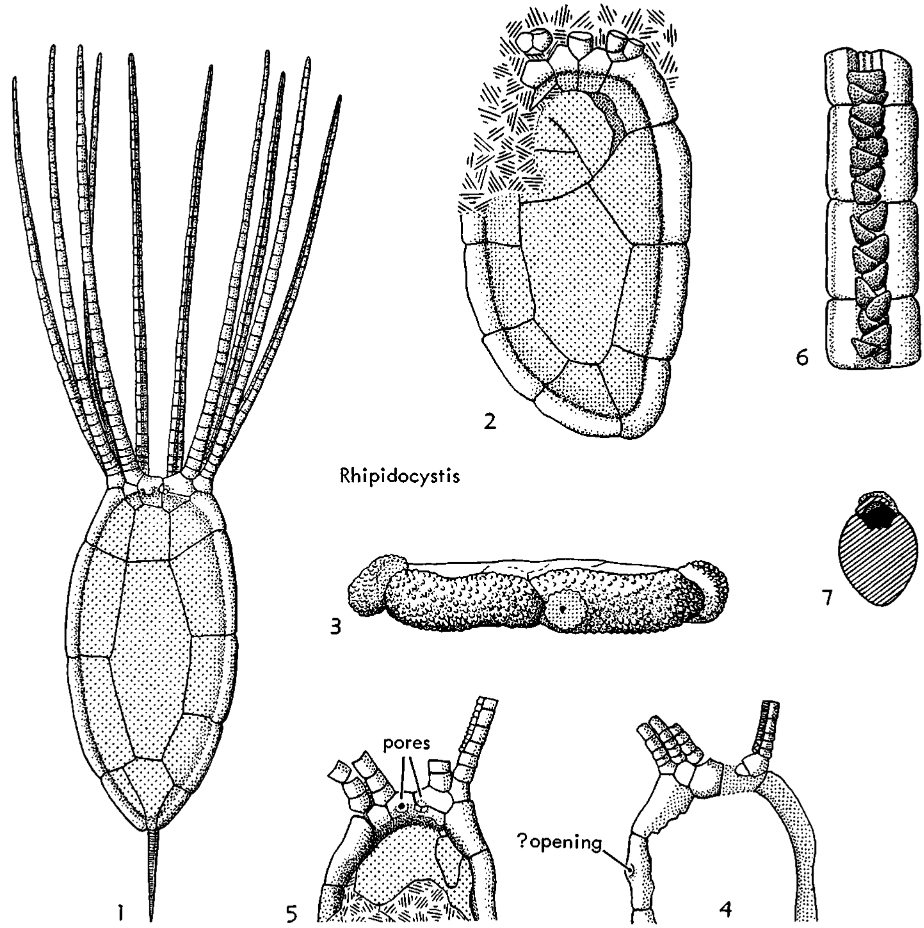


FIG. 318. Rhipidocystidae (p. S489).

(=*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-

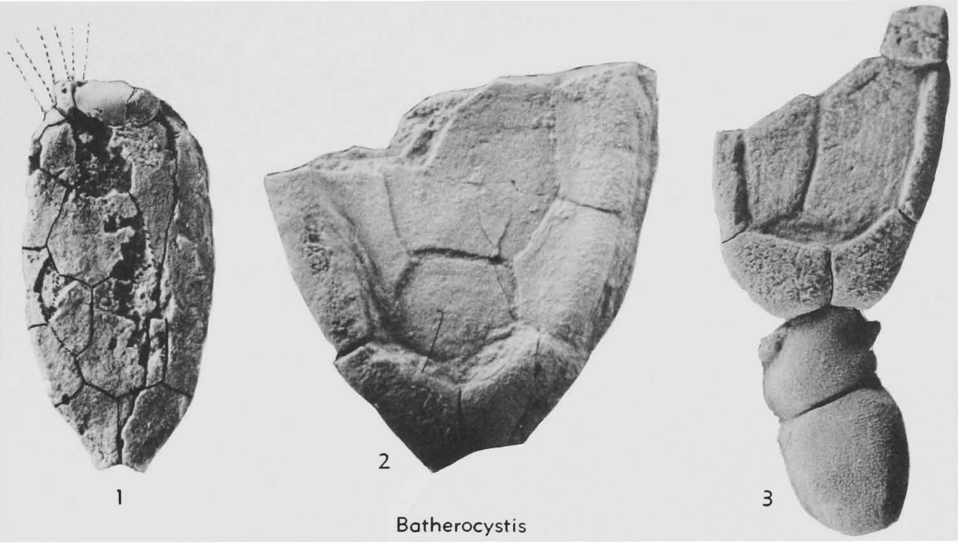


FIG. 319. Rhipidocystidae (p. S489-S490).

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

Family RHIPIDOCYSTIDAE Jaekel, 1901

[=Batherocystidae Bassler, 1950]

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

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

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

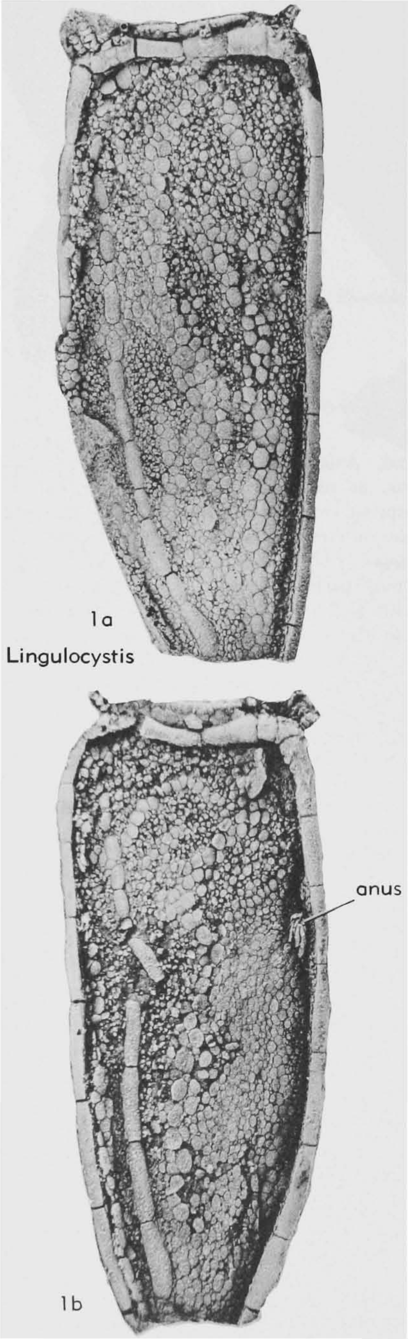


FIG. 320. Lingulocystidae (p. S490-S491).

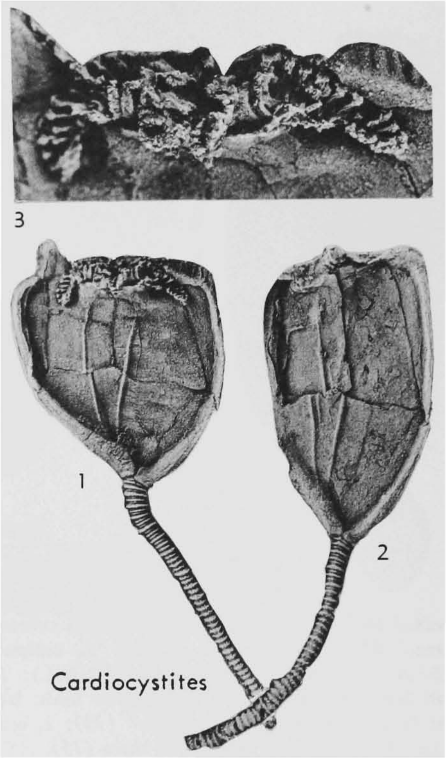


FIG. 321. Unclassified genera (*Cardiocystites*) (p. S491-S492).

Family LINGULOCYSTIDAE Ubaghs, 1960

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

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

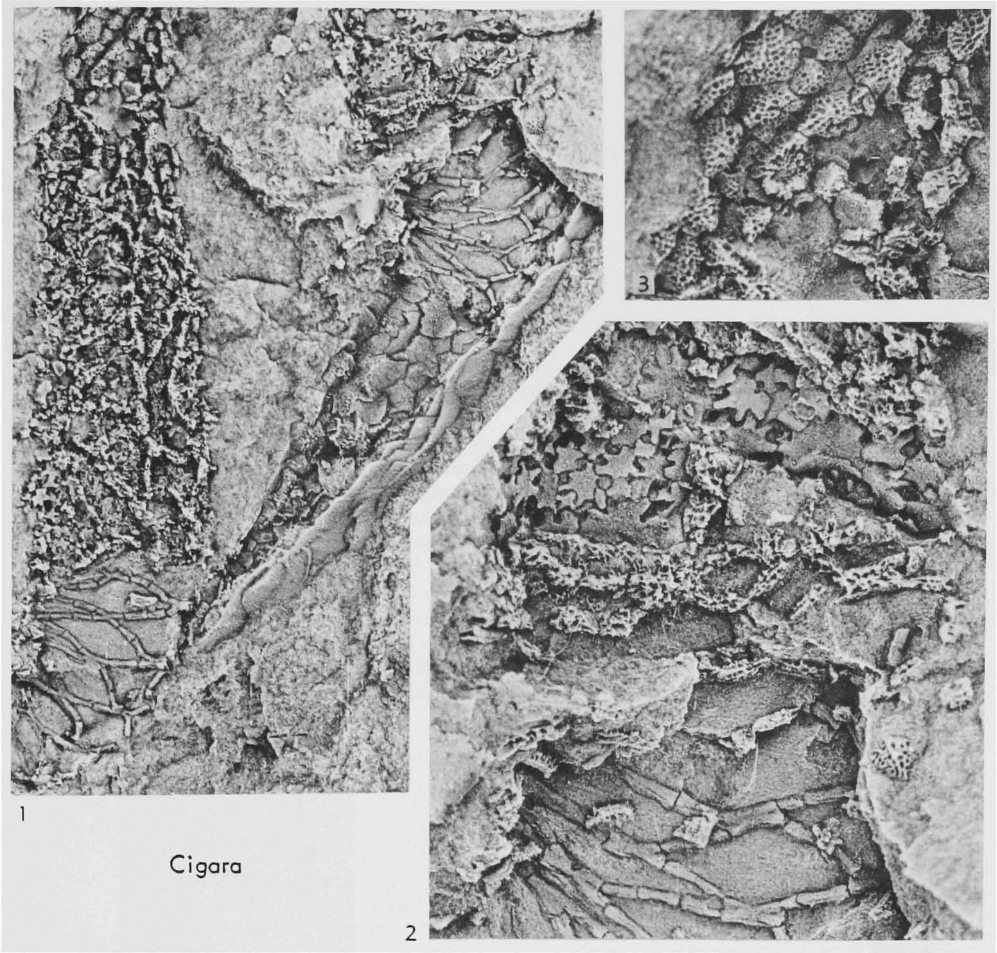


Fig. 322. Unclassified genera *(Cigara)* (p. *S*492-*S*493).

and oral surface. Flattened faces apparently pliant, each unequally divided by longitudinal series of relatively large, elongate, slightly convex plates. Anus protected by pyramid of numerous needle-like 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.,*

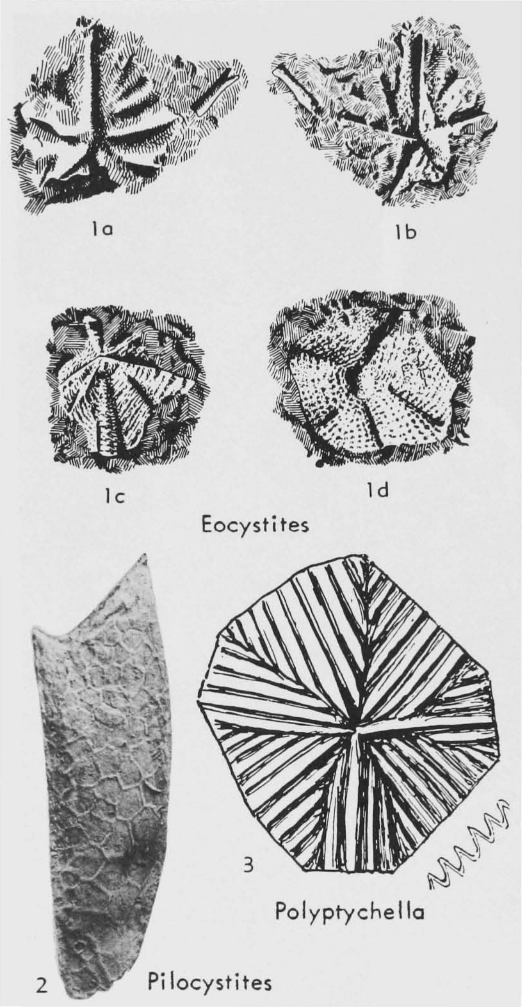


FIG. 323. Unclassified genera *(Eocystites, Pilocystites, Polyptychella)* (p. S492-S493).

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 tisistoideyami:* 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

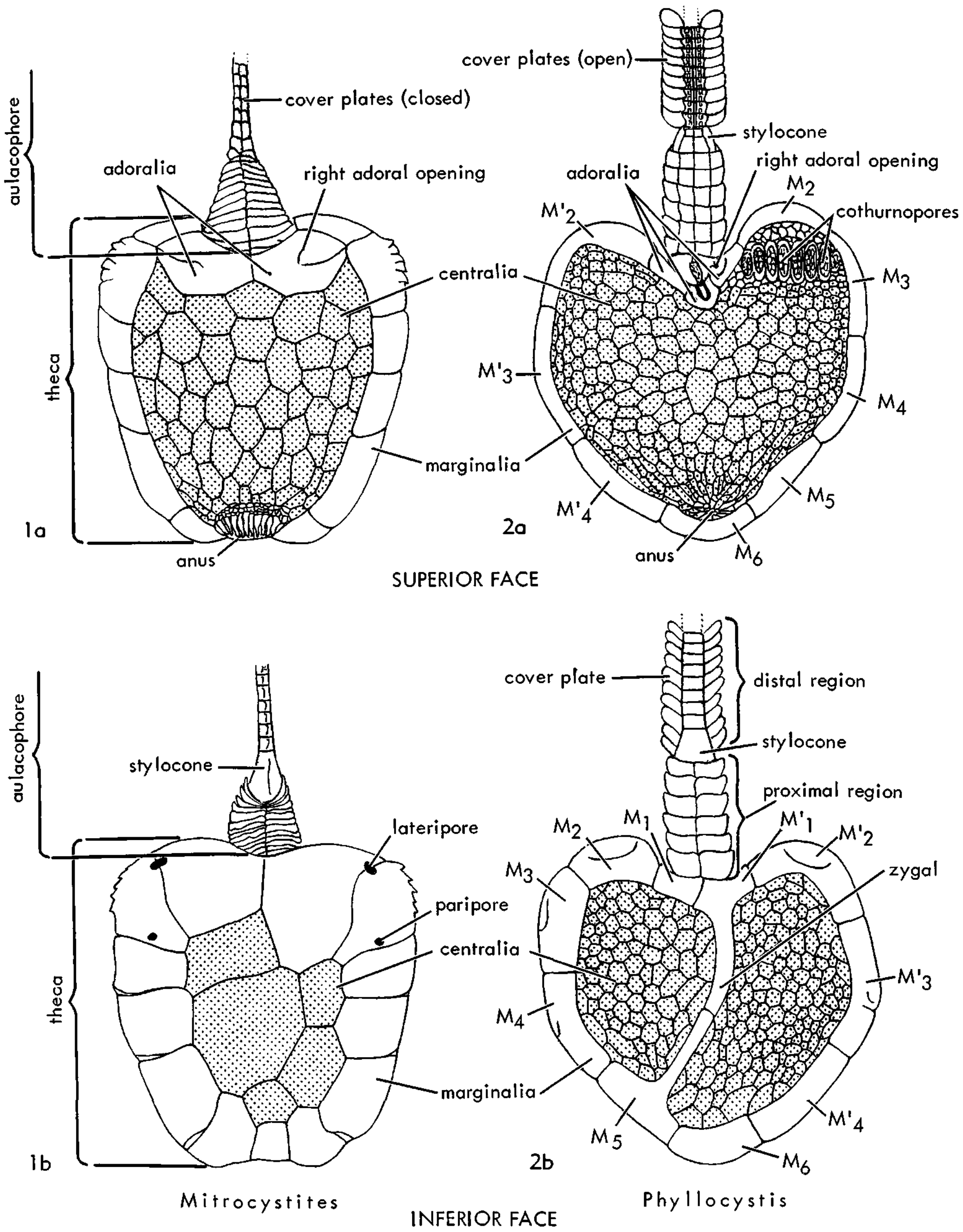


FIG. 325. General features of Stylophora.——*1. Mitrocystites mitra* BARRANDE, M.Ord., Boh; *1a,b,* superior and inferior faces, ×2.2 (Ubaghs, n).——*2. Phyllocystis blayaci* THORAL, L.Ord., Fr.; *2a,b,* superior and inferior faces, ×1.5 (Ubaghs, n) (M_1-M_6, right marginalia; M'_1-M'_4, left marginalia;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

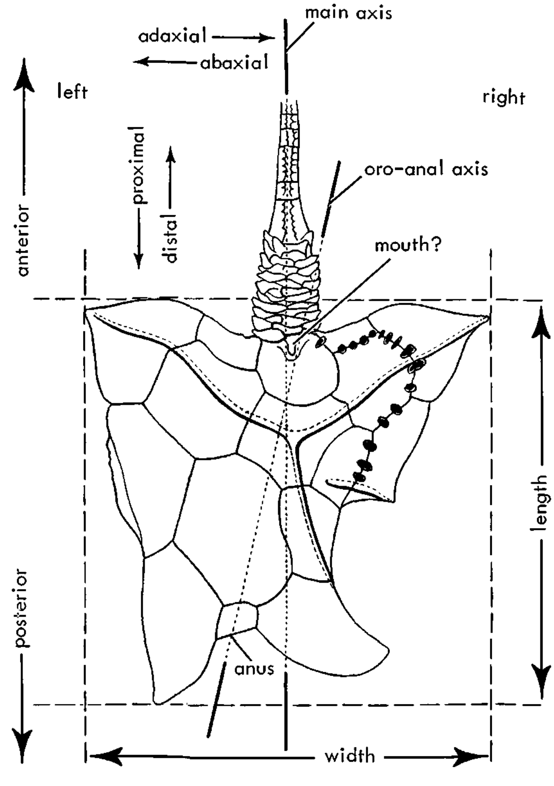


FIG. 326. Orientation of Stylophora. *Ceratocystis perneri* JAEKEL, M.Cam., Boh.; superior face, ×1.8 (Ubaghs, n).

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

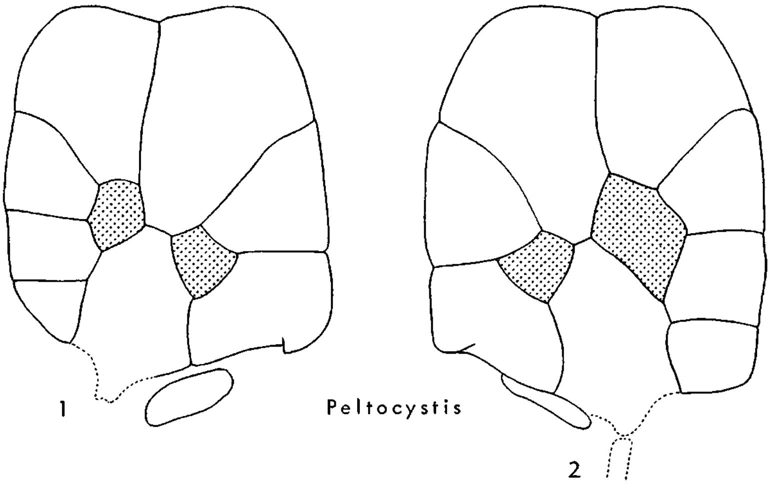


FIG. 327. Reversed asymmetry. *Peltocystis cornuta* THORAL, L.Ord., Fr.; *1,2,* inferior face, of normal and abnormal specimens, ×4.1 (Ubaghs, n).

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

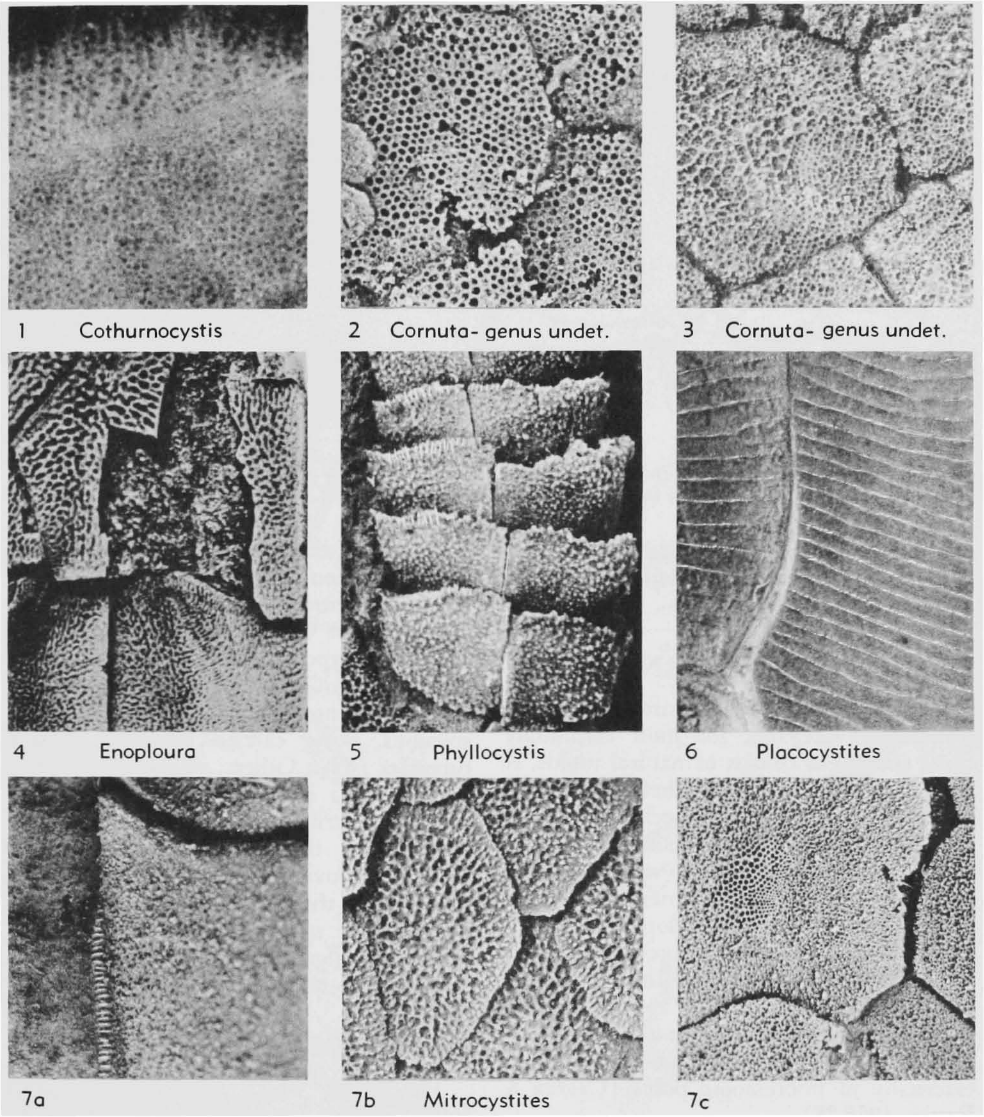


FIG. 328. Stereom and ornament among Stylophora.——*1. Cothurnocystis elizae* BATHER, U.Ord., Scot.; longitudinal section through a marginal, ×35 (Ubaghs, n).——*2.* Cornuta, genus and species indet., M. Ord., Boh.; external surface of supracentralia, ×15 (Ubaghs, n).——*3.* Cornuta, genus and species indet., 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).

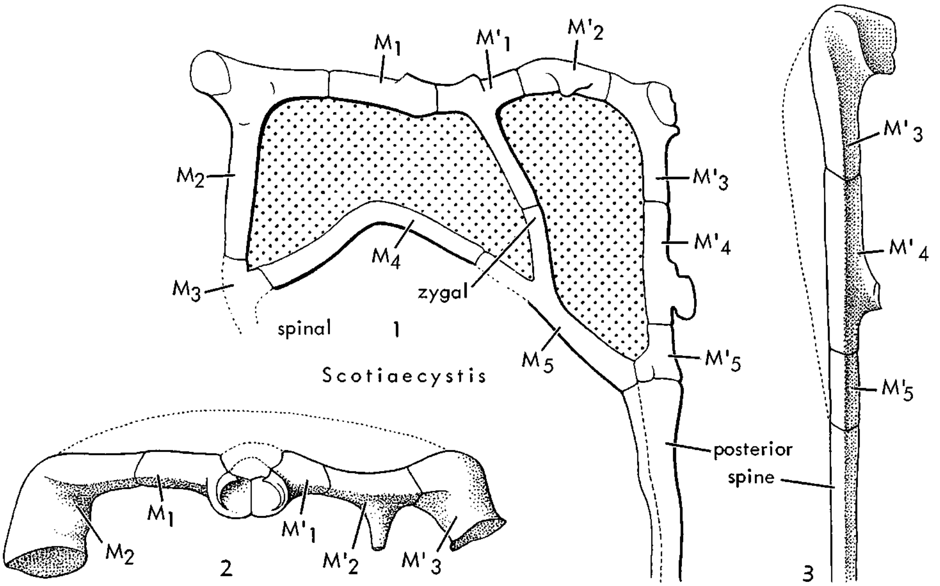


FIG. 329. Marginal frame of a cornute Stylophora.——*1-3, Scotiaecystis curvata* (BATHER), U.Ord., Scot.; inferior, anterior, and right lateral faces, ×3 (*M_1-M_5,* right marginalia; *M'_1-M'_5,* left marginalia) (Ubaghs, n).

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-

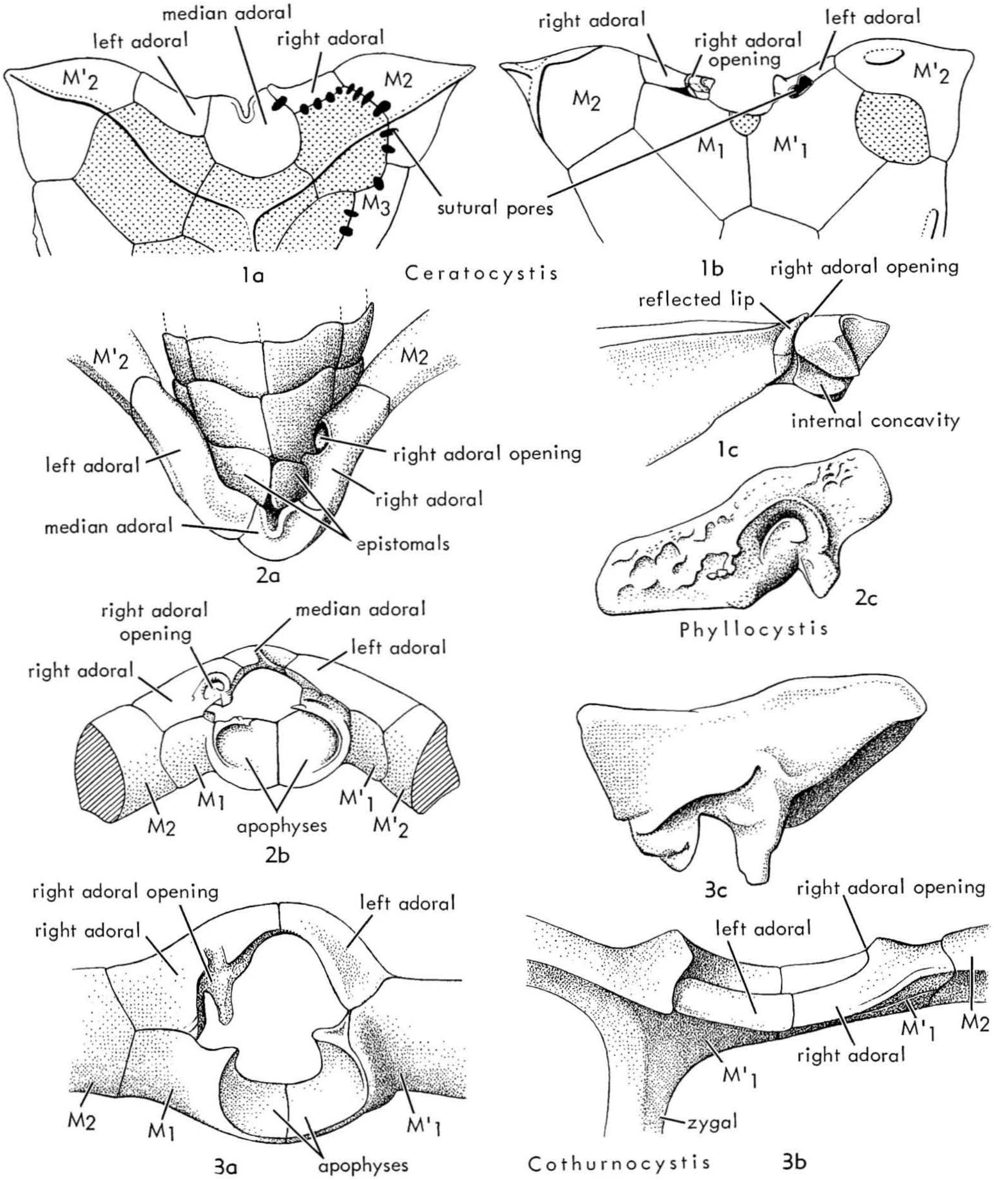


FIG. 330. Adoralia among cornute Stylophora.——*1. Ceratocystis perneri* JAEKEL, M.Cam., Boh.; *1a,b,* superior and inferior faces, ×2.2; *1c,* adaxial part of right adoral, inferior face, ×8.3 (Ubaghs, n).——*2. Phyllocystis crassimarginata* THORAL, L.Ord., Fr.; *2a,b,* superior and anterior faces, ×5; *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).

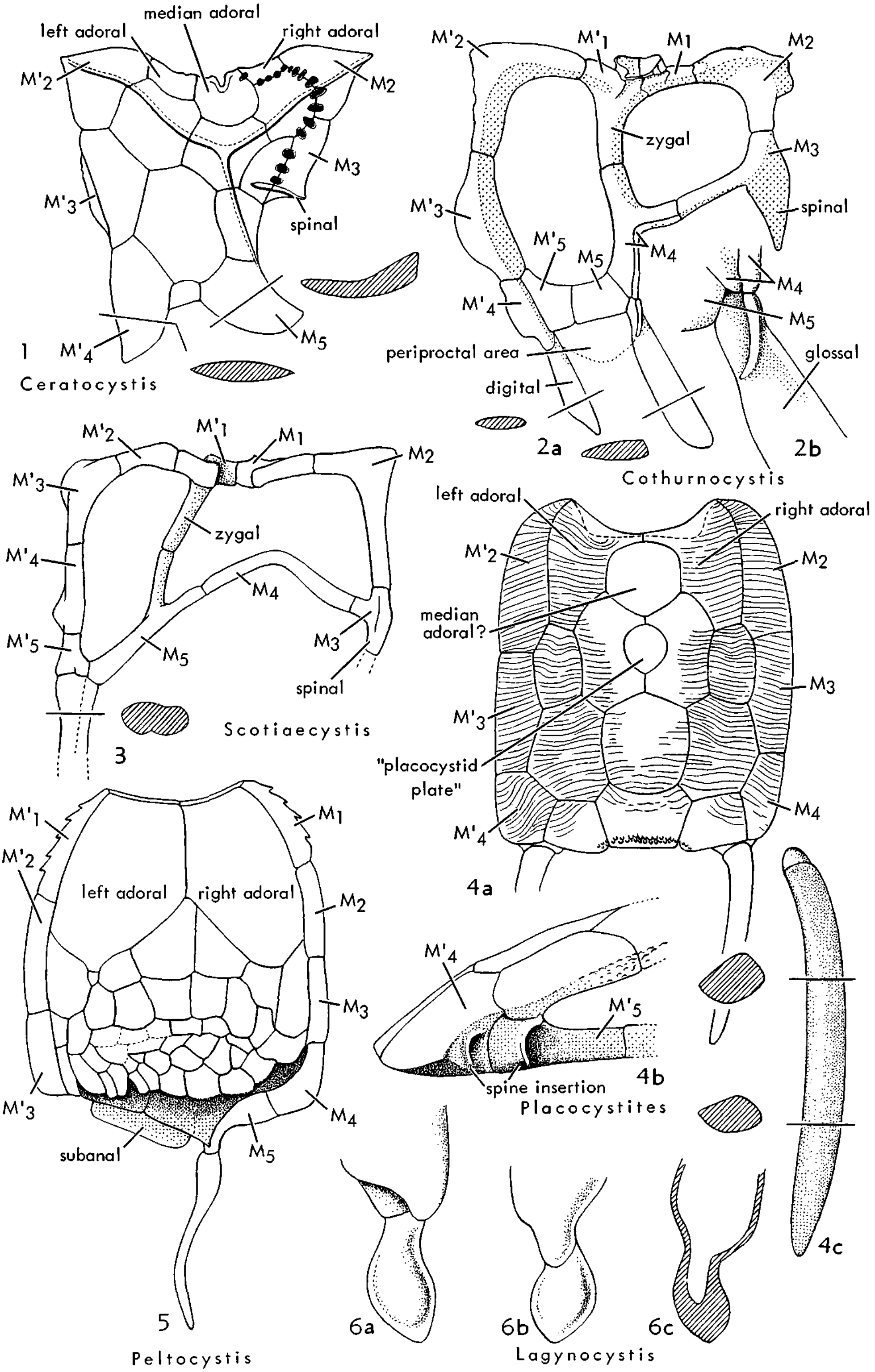


FIG. 331. [*Explanation on facing page.*]

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)*.

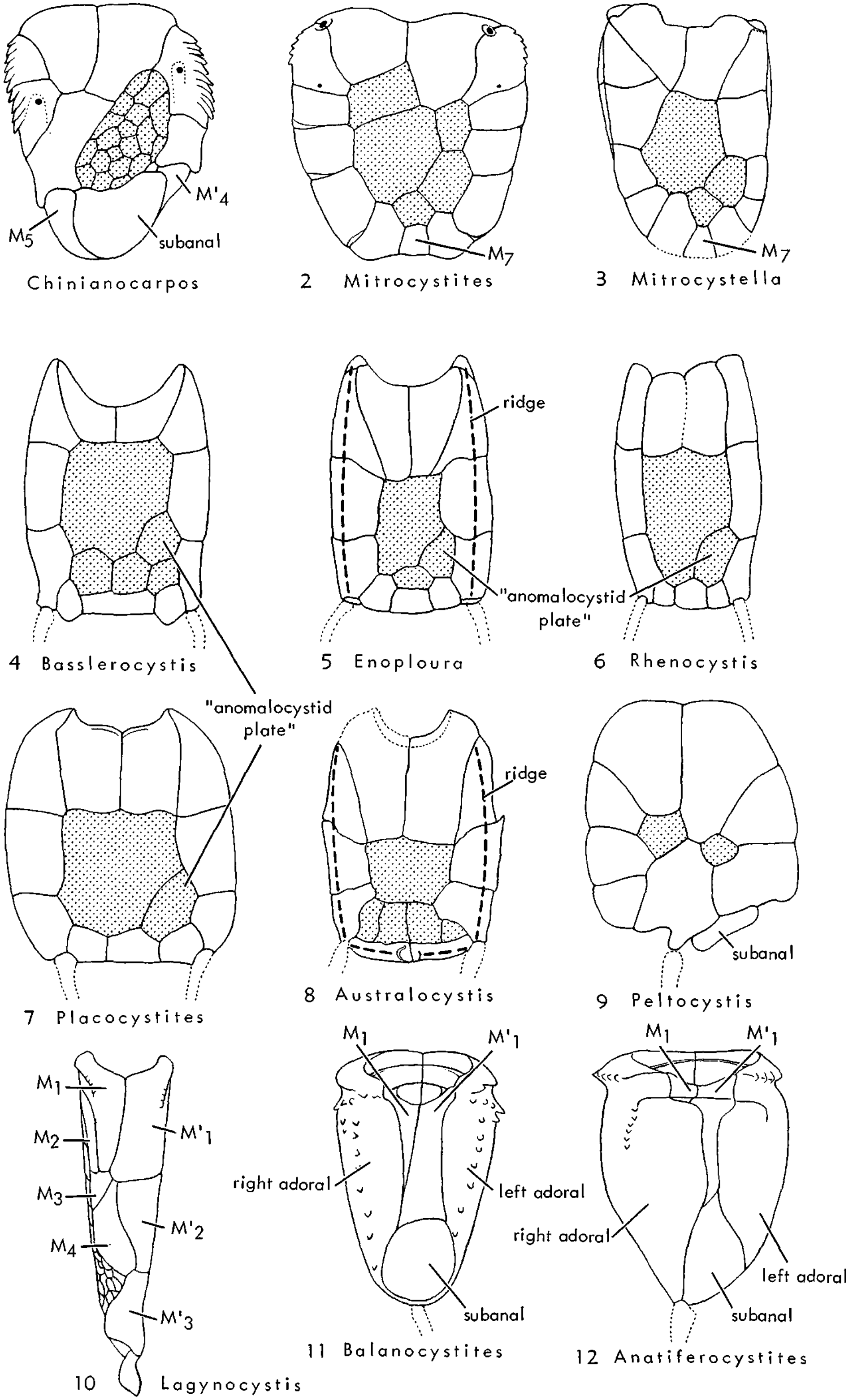
The two median anterior marginals of the Cornuta *(M_1, M'_1)* call for special notice in that (1) they form part of the thecal frame only on the inferior face (Fig. 325,*2b*), being covered by adorals on the superior face (Fig. 325,*2a*); (2) the inner side of each bears a powerful apophysis on which 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).



1 Chinianocarpos 2 Mitrocystites 3 Mitrocystella 4 Basslerocystis 5 Enoploura 6 Rhenocystis 7 Placocystites 8 Australocystis 9 Peltocystis 10 Lagynocystis 11 Balanocystites 12 Anatiferocystites

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

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

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

MARGINAL APPENDAGES

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

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

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

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

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

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

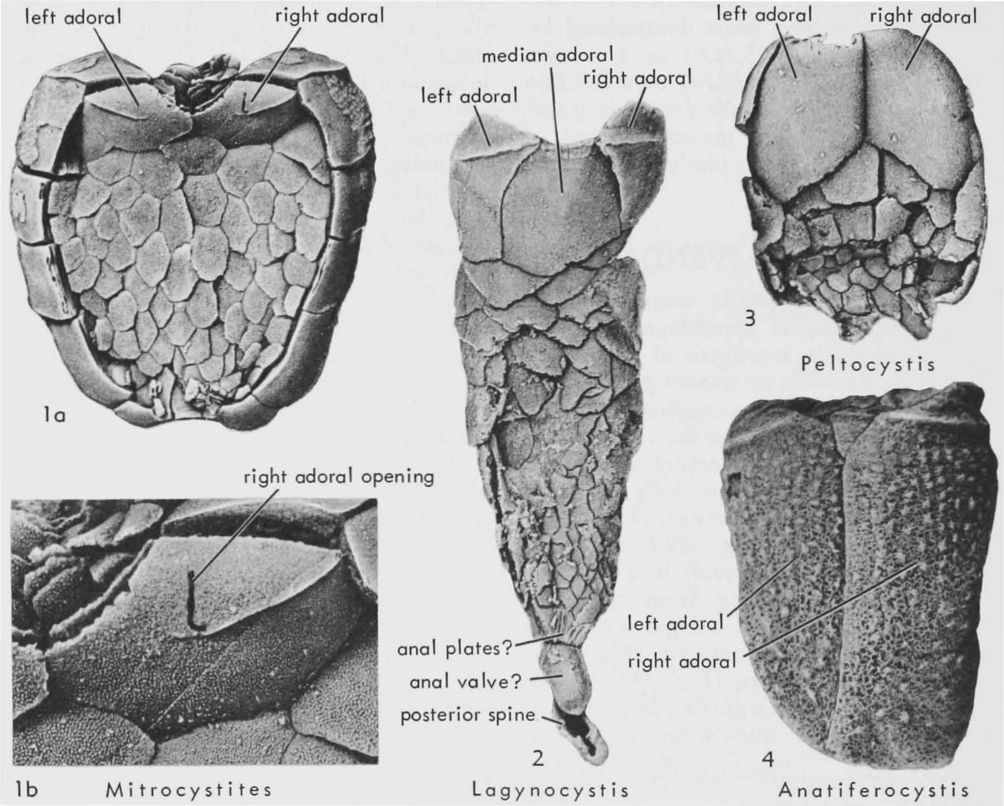


Fig. 333. Adoralia among mitrate Stylophora.——*1. Mitrocystites mitra* Barrande, M.Ord., Boh.; *1a,* superior face of theca, ×2.2; *1b,* right adoral, ×6 (Ubaghs, n).——*2. Lagynocystis pyramidalis* (Barrande), M.Ord., Boh.; superior face of theca, ×3 (Ubaghs, n).——*3. Peltocystis cornuta* Thoral, L.Ord.,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

ADORALIA

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

At first glance, adorals of the Mitrata seem quite unlike the similarly designated plates in the Cornuta (Fig. 333). Invariably they are much more developed and either partly or completely cover the superior face. Even so, they are held to be homologous to the adorals of Cornuta, since they have the same relationship to the M_1 and M'_1 plates and the aulacophore and since the right adoral (e.g., in *Mitrocystites*) may be pierced by an unpaired orifice, as in the Cornuta (Fig. 333,*1a,b*). They are two or three in number (Fig. 333,*1,2*). The median plate does not attain the anterior upper margin in some genera (e.g., *Placocystites,* Fig. 331,*4a*), and in others it ceases 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_9, M'_9*) may form part of this anterior ring, bringing to six the number of plates around the base of the aulacophore. Also, the presence of two deltoid "interbasal" plates between the marginals and adorals has been recorded in *Mitrocystella* by CHAUVEL (30) and in *Enoploura* by CASTER (25). Carefully made latex casts of *Mitrocystella*, however, demonstrate that the presumed extra plates are merely reflected downward margins of adorals separated from other adorals by a ridge (see Fig. 340,*3*). The so-called interbasals of *Enoploura,* which admittedly are very small, may be sutural wrinkles. In any case, the "hexabasal" pattern of the anterior ring of plates is no more significant than the "tetrabasal" scheme postulated by JAEKEL (55) as a diagnostic feature of his class Carpoidea.

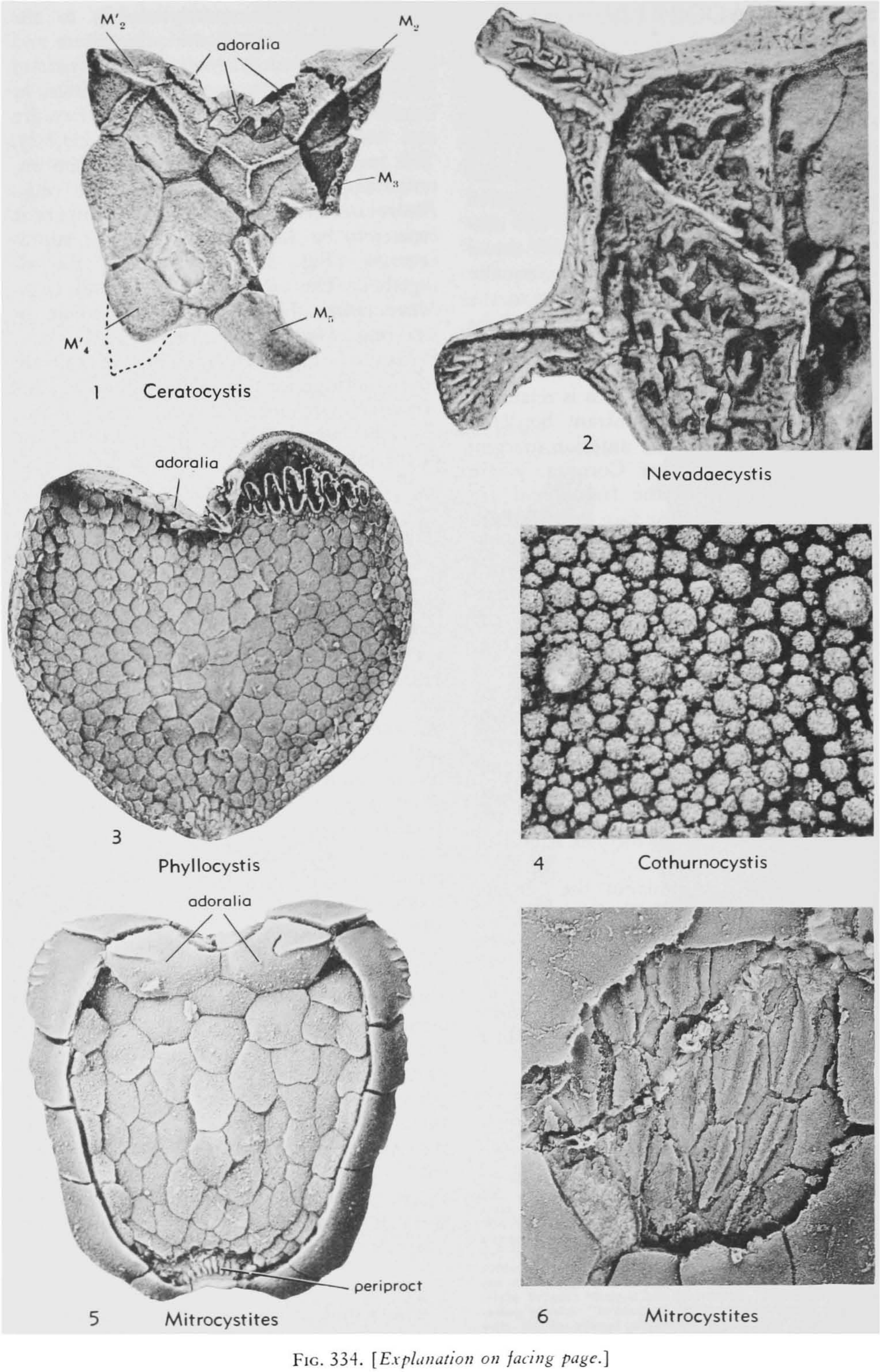


FIG. 334. [*Explanation on facing page.*]

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

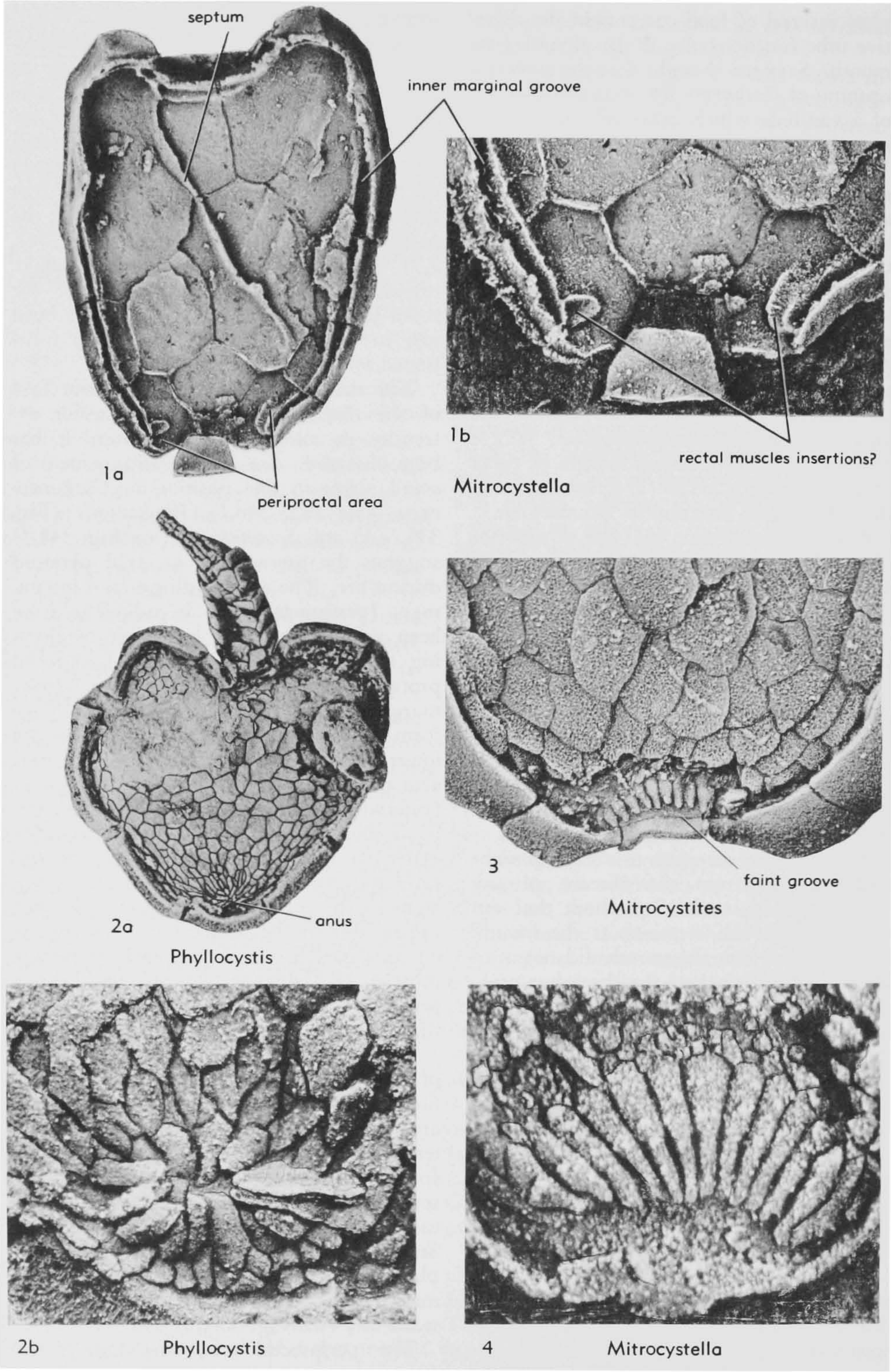


FIG. 335. [*Explanation on facing page.*]

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).

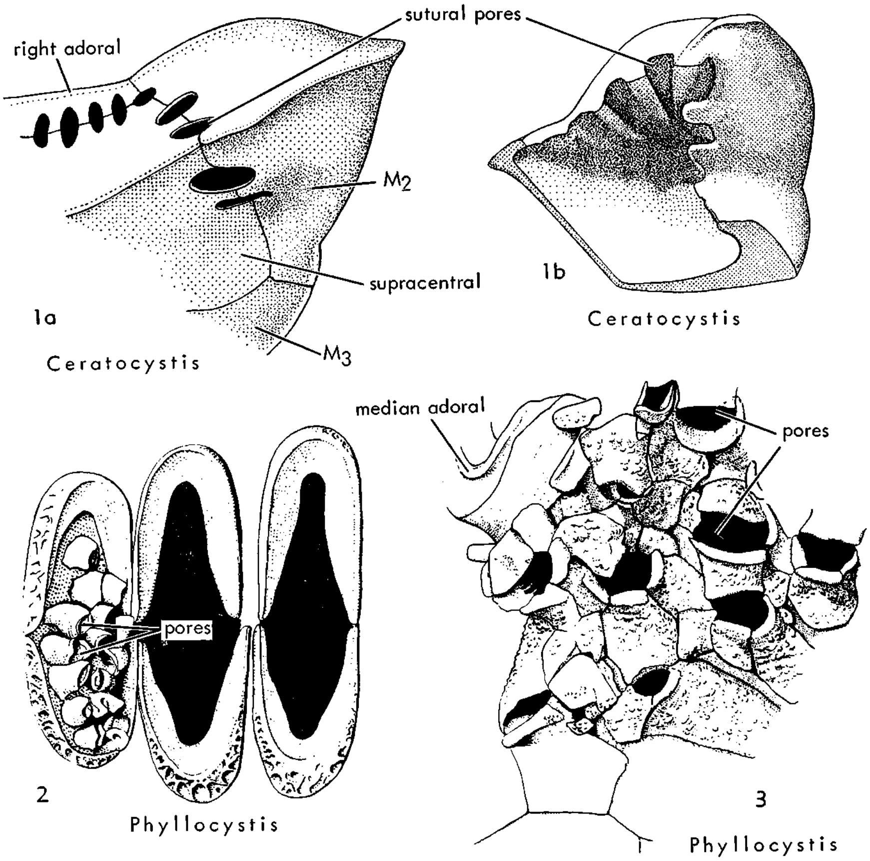


FIG. 336. Sutural pores and cothurnopores among cornute Stylophora.——*1. Ceratocystis perneri* JAEKEL, M.Cam., Boh.; *1a,* right anterior corner of theca, details, ×5 (Ubaghs, n); *1b,* right anterior marginal, oblique view showing internal grooves leading to sutural pores, ×5 (Ubaghs, n).——*2. Phyllocystis blayaci* THORAL, L.Ord., Fr.; cothurnopores, the left one with platelets preserved, ×15 (Ubaghs, n).——*3. Phyllocystis crassimarginata* THORAL, L.Ord., Fr.; sutural pores; ×15 (Ubaghs, n) (M_2, M_3, right marginalia).

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

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

FIG. 337. Sutural pores and cothurnopores in Cothurnocystidae.——*1. Phyllocystis crassimarginata* THORAL, L.Ord., Fr.; *1a,* theca, superior face; *1b,* upper right anterior area, details, ×10 (Ubaghs, n); *1c,* sutural pores, internal aspect, ×10 (Ubaghs, n).——*2. Phyllocystis blayaci* THORAL, L.Ord., Fr.; *2a,* theca, superior face, ×2 (Ubaghs, n); *2b,* cothurnopores, details, ×15 (Ubaghs, n); *2c,* a few cothurnopores, internal aspect, ×7.5 (Ubaghs, n).

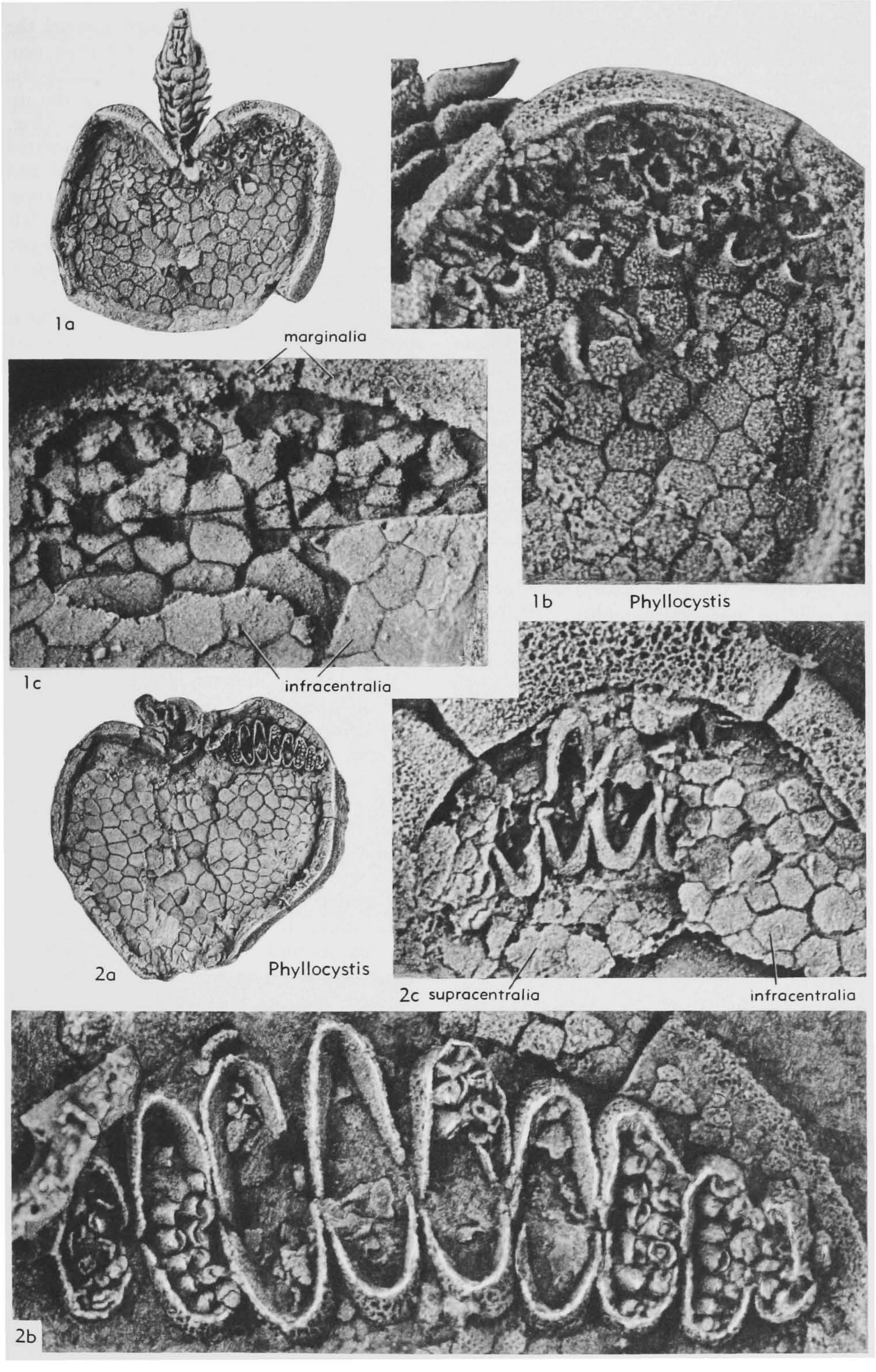


FIG. 337. [*Explanation on facing page.*]

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

SUTURAL PORES

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

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

COTHURNOPORES

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

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

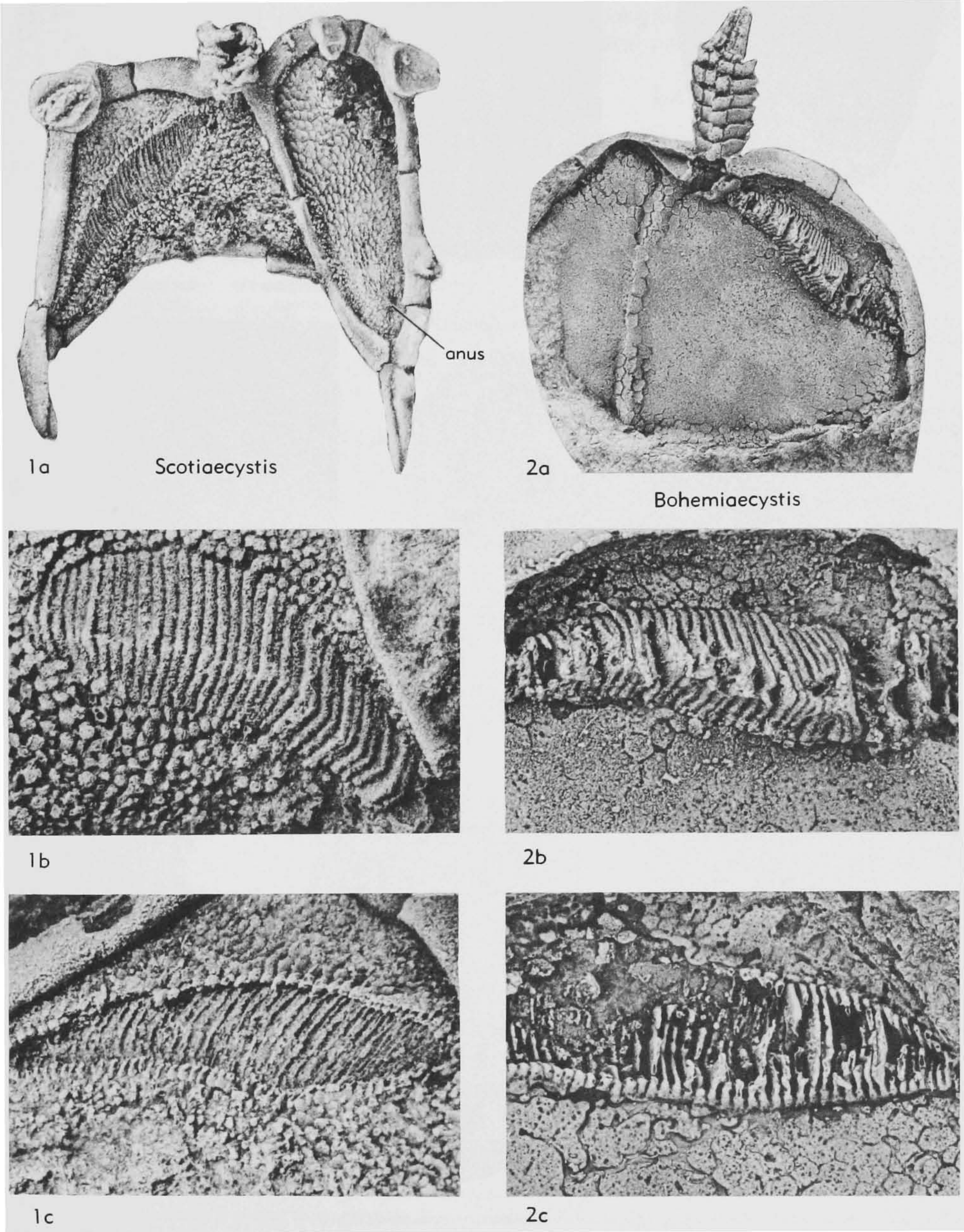


FIG. 338. Lamellipores in Scotiaecystidae.——*1. Scotiaecystis curvata* (BATHER), U.Ord., Scot.; *1a,* theca, superior face, ×2.5 (Ubaghs, n); *1b,c,* lamellate organ, external and internal aspects, ×5 (Ubaghs, n).——*2. Bohemiaecystis bouceki* CASTER, n. genus, n. species, M.Ord., Boh.; *2a,* theca, superior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

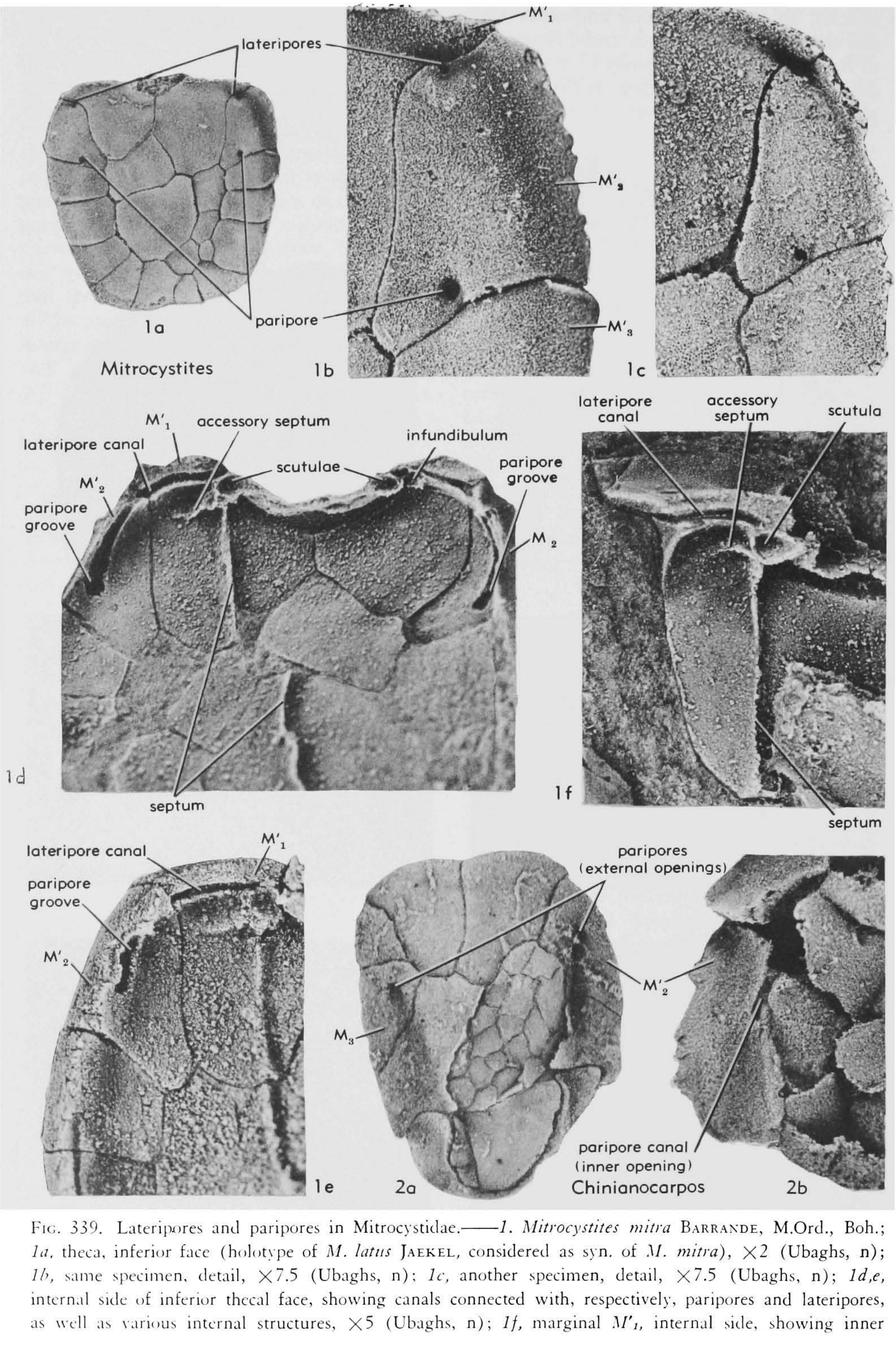


FIG. 339. Lateripores and paripores in Mitrocystidae.——*1. Mitrocystites mitra* BARRANDE, M.Ord., Boh.; *1a*, theca, inferior face (holotype of *M. latus* JAEKEL, considered as syn. of *M. mitra*), ×2 (Ubaghs, n); *1b*, same specimen, detail, ×7.5 (Ubaghs, n); *1c*, another specimen, detail, ×7.5 (Ubaghs,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

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

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

LAMELLIPORES

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

LATERIPORES

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

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

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

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

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

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

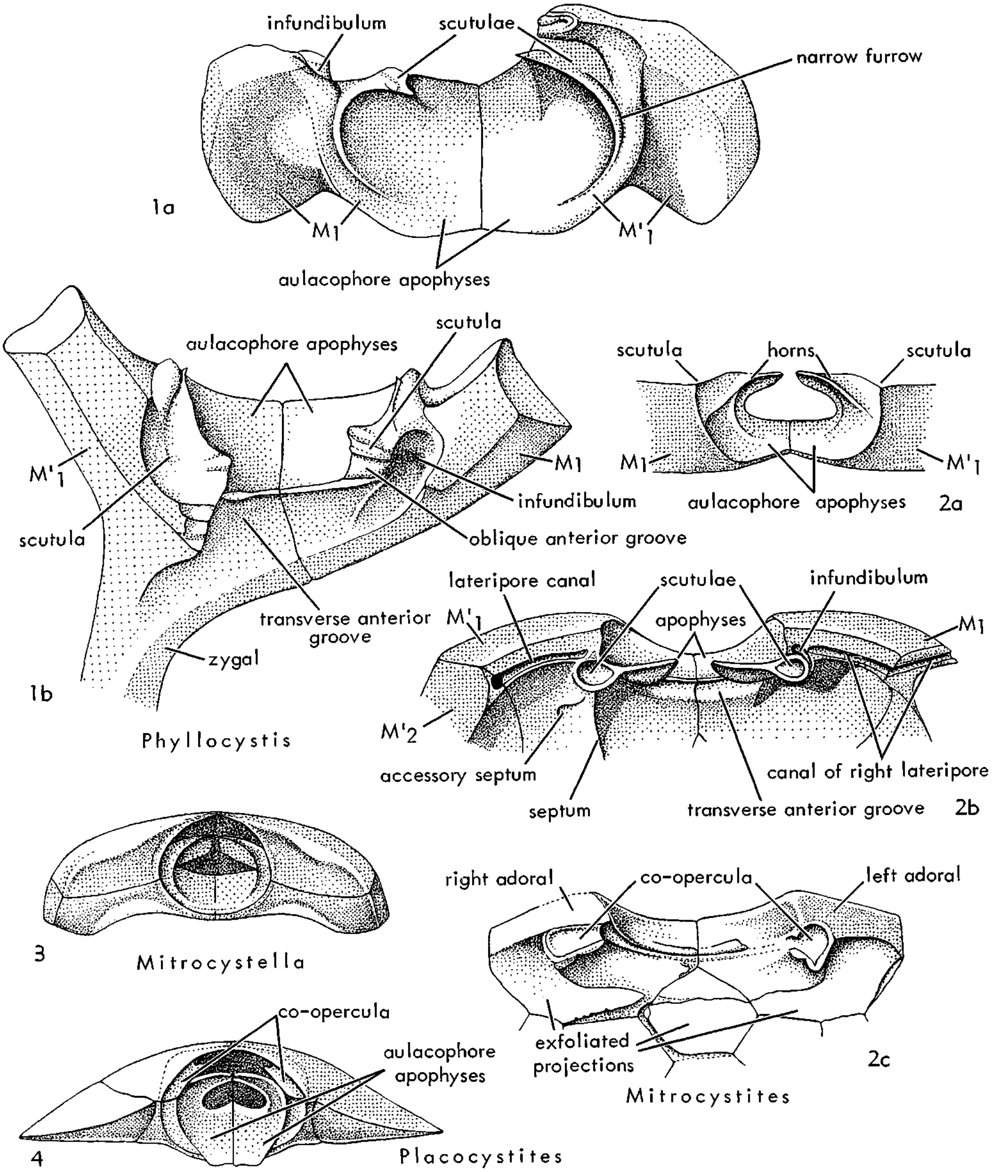


Fig. 340. Internal thecal structures among Stylophora.——*1. Phyllocystis blayaci* Thoral, L.Ord., Fr.; *1a,b,* aulacophore insertion and adjacent structures, in anterior and superior aspects, ×16 (Ubaghs, n).——*2. Mitrocystites mitra* Barrande, M.Ord., Boh.; *2a,b,* aulacophore insertion and adjacent structures, in anterior and superior aspects, ×4.4 (Ubaghs, n); *2c,* adoralia, internal side, ×4.4 (Ubaghs, n).——*3. Mitrocystella barrandei* Jaekel, M.Ord., Boh.; anterior face of theca, ×2.5 (Ubaghs, n).——*4. Placocystites forbesianus* de Koninck, Sil. (Wenlock Ser.), Eng.; anterior face of theca, ×1.6 (Ubaghs, n) (M_1, M'_1, median anterior marginals).

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

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

PARIPORES

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

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

FUNCTION OF ACCESSORY ORIFICES IN STYLOPHORA

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

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

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

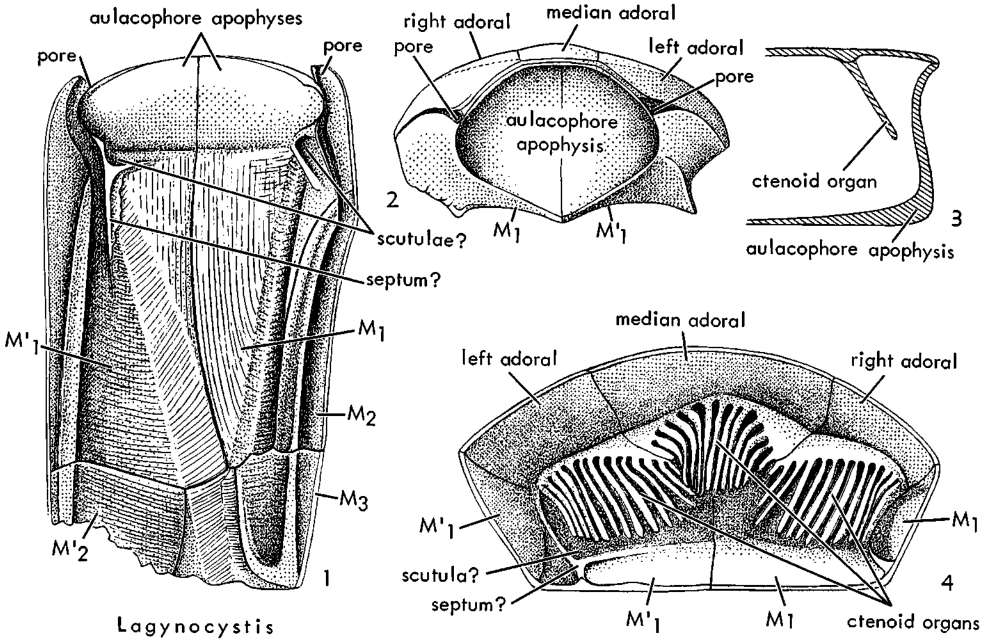


FIG. 341. Morphology of *Lagynocystis pyramidalis* (BARRANDE), M.Ord., Boh.——*1.* Internal anterior thecal structures of inferior face, ×5 (Ubaghs, n).——*2.* Anterior face of theca, ×5.3 (Ubaghs, n).——*3.* Schematic longitudinal median section through anterior part of theca, ×5.3 (Ubaghs, n).——*4.* Ctenoid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

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

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

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

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

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

INTERNAL CHARACTERS OF THECA

INSERTION OF AULACOPHORE

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

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

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

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

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

SCUTULAE

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

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

CO-OPERCULA

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

The role of co-opercula and scutulae is uncertain. CHAUVEL *(30)* postulated that they marked the placement of ganglionic masses from which nerves extended in thickened thecal elements, such as the wrinkles mentioned in *Microcystella incipiens miloni* and *Paranacystis*. The presence of nerve concentrations in this region of the theca seems reasonable in view of the large development and apparently considerable importance of the proximal musculature of the aulacophore. Thus, one is tempted to consider scutulae as possible sites of nerve centers.

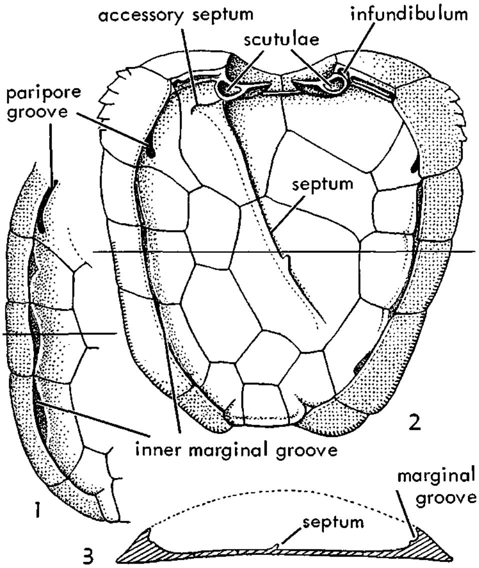


FIG. 342. Internal thecal structures of *Mitrocystites mitra* BARRANDE, M.Ord., Boh.——*1*. Left lateral side of inferior face of theca, slightly oblique view to show inner marginal groove, ×2.2 (Ubaghs, n).——*2*. Inner side of same, ×2.2 (Ubaghs, n).——*3*. Cross section of theca, ×2.2 (Ubaghs, n).

INFUNDIBULUM

A depression excavated between the right scutula and upper edge of the inner side of marginal M_1 is here termed the **infundibulum** (Latin, funnel). Its topographic relationships to the right adoral orifice have been noted previously. In *Ceratocystis* the infundibulum is shallow and rounded, but in other Cornuta (e.g., *Cothurnocystis, Phyllocystis*) and the Mitrata (e.g., *Mitrocystites, Mitrocystella*) wherever observable it is deeply impressed in the substance of the plate (Fig. 340,*1b,2b*). A generally well-marked furrow **(transverse anterior groove)** hollowed on inner surfaces of M_1 and M'_1 runs from its base along the posterior face of the aulacophore apophyses, passes beneath the scutulae, and becomes lost either on the inner surface of the zygal (in Cornuta) or at the origin of the septum (in Mitrata), described subsequently. Another furrow **(oblique anterior groove),** which is much narrower and weaker than the transverse groove, may be seen in some specimens of *Cothurnocystis* and *Phyllocystis*. This leaves the bottom of the infundibulum, rises obliquely, and ends at the summit of the adjacent apophysis just beneath the adaxial angle of the right scutula (Fig. 340, *1b*). Seemingly, it connects the infundibulum with the aulacophore. Finally, in *Ceratocystis* and some specimens of *Phyllocystis* and *Mitrocystella,* a third groove, which generally is very weak, runs from the infundibulum toward the right and disappears on the inner face of the anterior marginals on this side of the theca. Thus it appears that the infundibulum is a sort of center toward which a group of structures converge, and this supports the inference that it exercised a complex role.

If, as previously supposed, the orifice by which the infundibulum communicated with the exterior (right adoral orifice) represents a hydropore, possibly combined with a gonopore, the infundibulum should be the seat of a part of what presently constitutes the axial complex of echinoderms. At any rate, it must have inclosed the hydroporic canal, perhaps accompanied by the small ampulla (remnant of the left axocoel) which in modern echinoderms is placed at its junction with the stone canal.

The anterior oblique groove of stylophorans probably inclosed the hydrocoel branch which penetrated into the aulacophore, and the anterior transverse groove may have contained another hydrocoel diverticle passing beneath the esophagus and possibly corresponding to the stone canal and the periesophageal ring of radially symmetrical echinoderms. The transverse groove may also have contained part of the axial sinus. The faint groove on the inner surface of the right anterior marginals perhaps marks the course of the genital rhachis.

SEPTUM

A low wall or ridge observed on the floor of the thecal cavity of most Mitrata is termed the **septum** (Fig. 335,*1a*; 342,*2,3*). It originates on the M'_1 marginal slightly below the level of the left scutula and runs obliquely toward the right posterior corner of the theca without reaching it. The course of the septum is slightly irregular and its height is steadily reduced toward the rear. It leans toward the left in its anterior part so as to have an asymmetrical transverse section but straightens up in the posterior part, providing a more symmetrical section. Presence of the septum is marked on internal molds by a very characteristic strong incision, which was clearly illustrated by BARRANDE *(2)* and was called *sillon transversal* by CHAUVEL *(30)*, who was the first to draw attention to its existence.

A small **accessory septum** diverges in a general leftward direction near the anterior extremity of the septum (Fig. 340,*2b*; 342,*2*). Also, a diminutive spur is seen on the right side of the septum in the posterior third of its length in some specimens (Fig. 335,*1a*; 342,*2*).

ZYGAL

Among the Cornuta a septum is lacking, but this structure appears to be replaced by a skeletal bar extending from M_1 to the right posterior margin of the lower thecal face. This bar, named the **zygal** *(89)*, is probably equivalent in function to the septum and perhaps also in morphology. The two structures are closely similar in position and connection with other parts of the theca—for example, with the marginal M_1, the anterior transverse groove, and the left scutula—and they show a like oblique placement with respect to the main axis of the body. A median crest runs on the inner surface of the zygal, serving possibly for attachment of organs or mesenteries, as likewise in the case of the septum. The marginal M'_1 of the mitrate *Anatiferocystis,* which is almost identical in form with that of the equivalent marginal of *Cothurnocystis,* is a thin narrow plate that forms a ridge on the floor of the thecal cavity. This is curiously similar to the zygal of the Cornuta.

Ceratocystis and *Nevadaecystis* seem to have neither a zygal nor a septum. *Lagynocystis* also lacks a septum but has a much shorter ridge parallel to the left border of the theca, and possibly this is homologous to the septum seen in other Mitrata (Fig. 341,*1*). According to CASTER *(26)*, the superior face of the theca of *Paranacystis* has an internal groove that externally is marked by a rounded ridge, and this structure may correspond to the normally developed septum.

FUNCTIONS OF SEPTUM AND ZYGAL

CHAUVEL *(30)* viewed the septum of Mitrata as the place of attachment for a mesenteric membrane that supported one of the loops of the digestive tube. He thought to have discovered traces of two other mesenteries, at right and left, running along the marginals, and assigned to them a comparable role in fixation of the digestive canal. Thus he judged that he could determine the approximate course of this organ, concluding that it turned around like that of crinoids and holothuroids. This interpretation lacks the anatomical foundation inferred by CHAUVEL, for what he

FIG. 343. Morphology of aulacophore in cornute Stylophora.——*1-5. Phyllocystis crassimarginata* THORAL, L.Ord., Fr.; *1,* proximal region, stylocone, and proximal part of distal region, aboral face *(1a)*, oral face *(1b)*, ×7 (Ubaghs, n); *2,* stylocone, oral face *(2a)*, left lateral face *(2b)*, longitudinal median section *(2c)*, ×30 (Ubaghs, n); *3,* ossicles of distal region, oral face *(3a)*, left lateral face *(3b)*, proximal face *(3c)*, distal face *(3d)*, ×30 (Ubaghs, n); *4,* two cover plates, inner or oral face, ×30 (Ubaghs, n); *5,* diagrammatic reconstruction of a portion of distal region, with cover plates widely open and water-vascular organs (in black) (M_1, M_2, right marginalia 1, 2; M'_1, M'_2, left marginalia 1, 2).

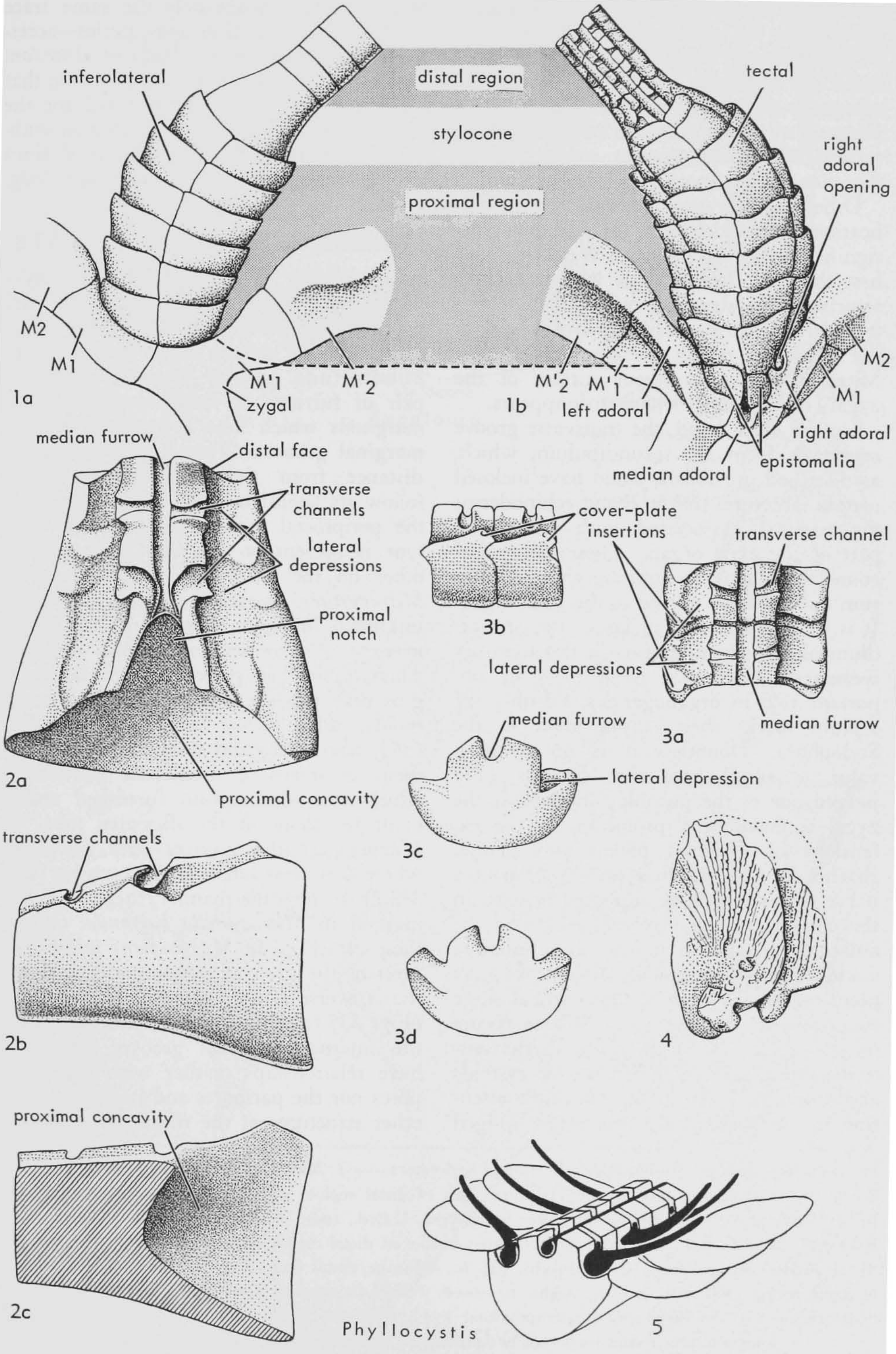


FIG. 343. [*Explanation on facing page.*]

considered to be emplacements of lateral mesenteries in reality represents the projecting adaxial borders of grooves excavated on the inner surface of the lateral marginals (Fig. 335,*1a*). CASTER *(26)*, who inferred a similar function of the septum, arrived at a much simpler course for the digestive tube, almost in a straight line.

Other considerations perhaps allow clarification in some degree of the morphological significance of the septum. We may recall first the close relationships which seem to associate this structure with the anterior transverse groove. This groove leads to the point of origin of the septum (in Mitrata) or to the upper surface of the zygal (in Cornuta), where it disappears.

On the other hand, the transverse groove originates from the infundibulum, which, as discussed previously, could have inclosed certain structures that in living echinoderms are narrowly associated with the aboral part of the axial organ. These anatomical connections seem to indicate that the septum also could be related to the axial organ. It is well known that in larvae the primordium of this organ appears in the accessory mesenteries and that these play an important role in organogenesis. Possibly the septum marks their emplacement in the Stylophora. Doubtless it is not without value to recall here that BATHER *(13)* judged one of the possible functions of the zygal to have been protection of the extensions of a blood plexus and genital rhachis, in addition to a prolongation of a nerve center which he supposed to exist in the opening of the proximal region of the aulacophore—that is to say in summation, a kind of axial complex. Finally, we may point out that a more or less vertical ridge suggestive of the septum in Mitrata occurs on the inner side of the theca in the posterior interray of certain Paleozoic cystoids and crinoids. JAEKEL *(55)*, who drew attention to the presence of this ridge, judged that it had approximately the same trace as that of the vertical mesenteries—accessory mesenteries—in the larva of *Antedon.* For all these reasons we may postulate that the septum of stylophorans served for the attachment of mesenteric membranes, within the thickness of which the axial sinus and axial organ possibly could find lodgment.

INTERNAL MARGINAL GROOVES

In addition to already described stylophoran grooves or canals, such as the paripore grooves, lateripore canals, and transverse anterior groove, some genera of the Mitrata (and possibly Cornuta) possess a pair of furrows on the inner side of the marginals which here are named **internal marginal grooves.** They begin at variable distance from the front of the theca, follow its lateral borders, and disappear in the periproctal region (Fig. 335,*1a*; 342). One is present on the right side and the other on the left. They are constant in *Mitrocystites,* sporadic in *Mitrocystella,* and unknown in other mitrates. [They appear to exist also in an undescribed cornute.] Their somewhat projecting adaxial margins may produce narrow slits on internal molds, called *sillons latéraux* by CHAUVEL *(30)*, who discovered them and interpreted them as traces of mesenteric membranes which with the septum furnished attachment for loops of the digestive tube. In *Mitrocystites* the grooves tend to vanish where they cross intermarginal sutures (Fig. 342,*1*). In opposite manner, they are clearly marked in *Mitrocystella barrandei* only at these crossings. In *M. incipiens miloni* features of the grooves are unmodified where they traverse sutures between the marginals (Fig. 335,*1a*). At their anterior extremity the internal marginal grooves appear to have relationships neither with the lateripores nor the paripores and indeed with no other structures of the theca. They cannot

FIG. 344. Morphology of aulacophore in mitrate Stylophora.——*1. Mitrocystella barrandei* JAEKEL, M.Ord., Boh.; proximal region, stylocone and proximal part of distal region; *1a,* oral face; *1b,* left lateral face, ×7.5 (Ubaghs, n).——*2. Enoploura wetherbyi* CASTER, U.Ord., Ind.; ×1 (90).——*3. Mitrocystites mitra* BARRANDE, M.Ord., Boh.; *3a,* stylocone and three ossicles of distal region, left lateral face, ×15 (Ubaghs, n); *3b,* stylocone, oral face, ×10 (Ubaghs, n); *3c,* stylocone, distal face, ×15 (Ubaghs, n); *3d,* ossicles of distal region, oral face, ×15 (Ubaghs, n).——*4. Peltocystis cornuta* THORAL, L.Ord., Fr.; ossicle of distal region in laterodistal *(4a),* lateroproximal *(4b),* and oral *(4c)* views, ×30 (Ubaghs, n); *4d,* diagrammatic reconstruction of two articulated ossicles to show how they can move.

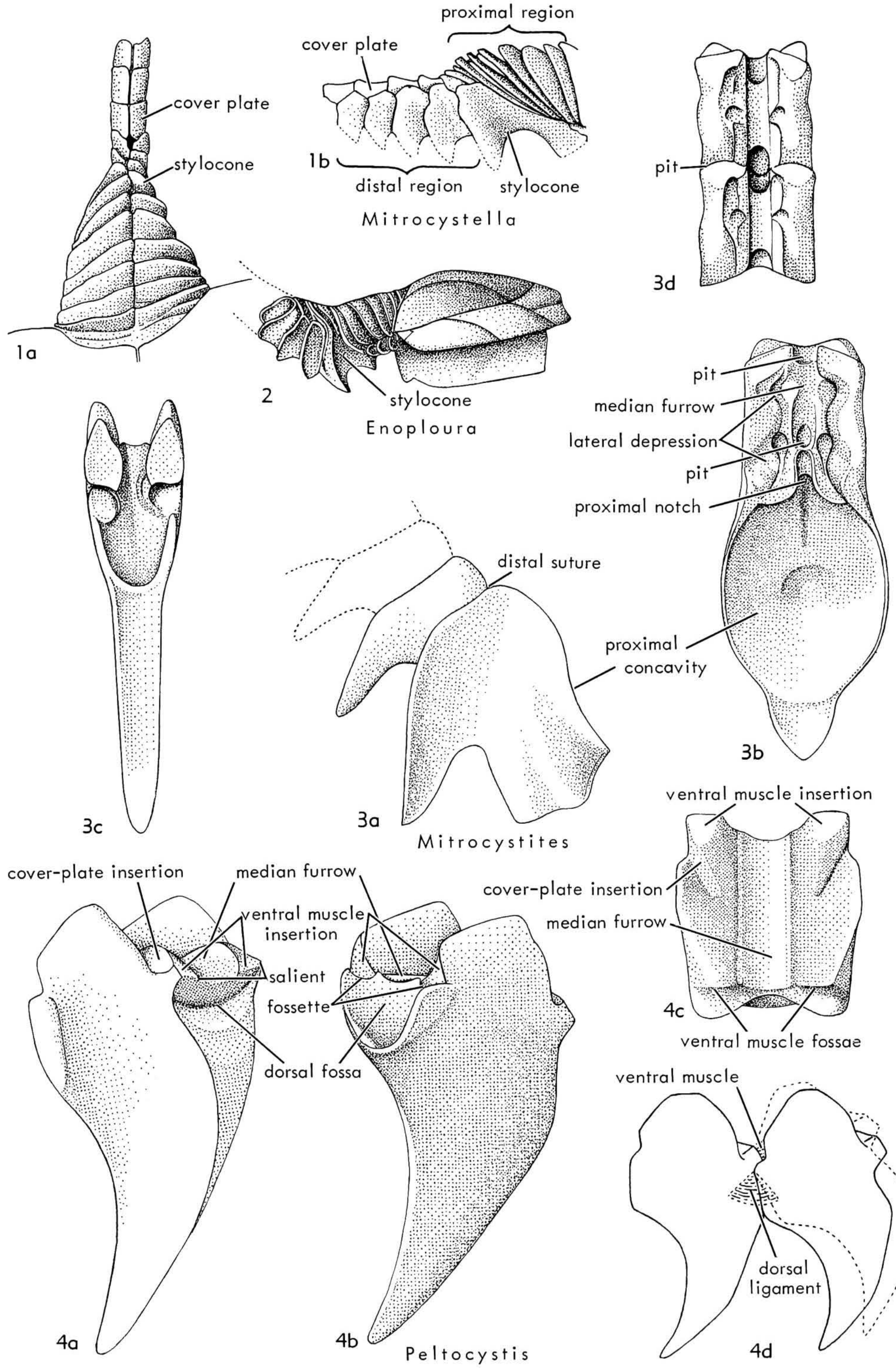


FIG. 344. [*Explanation on facing page.*]

be interpreted reasonably as these invaginated subvective grooves which BATHER *(14)* supposed to exist in *Mitrocystites.* Perhaps they are the passageways of nerves leading to the rectum or some other posterior organ. Their actual function is unknown.

CTENOID ORGANS

Structures composed of lamellae in arrangements that resemble the teeth of a comb are here named **ctenoid organs.** They were discovered by CHAUVEL *(30)* in *Lagynocystis pyramidalis* and as yet are unknown in other stylophoran genera. They occur in three groups, one median and the other two placed laterally (Fig. 341,*4*). Each ctenoid organ is supported by a ridge on the inner surface of an adoral and end to end the three ridges together form an arc which is thin at its center and extremities but thickened at crossings of sutures between the adorals. The lamellae of the organs converge at the same time in three directions—downward, forward, and toward the median axis of the body. Thus they form a sort of grill or filter in the anterior part of the theca. Previously evoked is the possible existence of an atrium in front of the thecal cavity in which a water current charged with food particles must have been induced by the aulacophore, perhaps emerging through exhalant orifices at right and left. The function of the ctenoid organs then would have been to catch food particles suspended in the water, agglutinate them with mucus, and conduct them toward the mouth. The possibility that the organs exercised a respiratory function also is not to be excluded, for they may have served as support for gill structures.

AULACOPHORE

The name **aulacophore** has been introduced by UBAGHS *(88)* for the appendage of Stylophora that formerly was thought to be the same as the stele in Homostelea and Homoiostelea. The designation is morphologically descriptive in indicating that the appendage bears a groove (Greek, *aulacos,* furrow or groove, +*phoros,* bearer). It is in no sense a peduncular process or stem, but is here interpreted as a brachial appendage provided with an ambulacrum. Its unique nature warrants the adoption of a special morphological term.

The aulacophore comprises three parts—(1) a proximal hollow region which is inflated, relatively large, and protected by imbricated plates or by quadripartite rings generally one inserted within another, (2) a massive intermediate piece named the **stylocone,** and (3) a distal region composed of a single series of massive ossicles placed end to end and each provided with a pair of cover plates (Fig. 325; 343,*1a,b*; 344, *1a,b*).

PROXIMAL REGION

Next to the theca is part of the aulacophore defined as the **proximal region.** It encloses a wide hollow space which communicates with the thecal cavity. A covering composed of numerous imbricated scale-like plates is seen in *Ceratocystis* and *Lagynocystis* (see Fig. 345, 354), but in other genera, where known, of a fixed number of four-piece rings which generally are telescoped together, but not invariably so. The ring elements are subequal in the Mitrata, with sutures between them located in mid-superior, mid-inferior, and two mid-lateral positions. The pieces are unequal in size in the Cornuta but symmetrically disposed with respect to the aulacophore plane of symmetry, which coincides with the sutures between plates on the upper and lower sides. Each lateral half ring contains a small plate, above, here called **tectal,** and a large one, below, here termed **inferolateral,** the tectal covering less than half of the mid-part of the upper surface, whereas the inferolateral not only covers an entire half of the lower surface but much of a side as well (Fig. 343,*1a,b*). Each ring was joined to its contiguous neighbor or neighbors by muscles and probably also by ligaments. In addition, powerful muscles attached them in a proximal direction to the inner apophyses of marginals M_1 and M'_1 and in a distal direction to the stylocone. Without doubt, the proximal region of the aulacophore enjoyed great freedom of movement both vertically and laterally and probably it controlled general movements of the whole appendage.

STYLOCONE

The intermediate part of the aulacophore, interposed between its proximal and distal regions, is the unique ossicle named *stylocone*[1] (*Styloconus* or *Styloid* of JAEKEL, *55*). Lengthwise, it is a minor portion of the appendage, though important in reducing within a very short distance the broad width of the proximal region to the narrow diameter of the distal region. Its constant presence and complex nature prove that it must have had considerable functional significance. Its structure is essentially the same in cornute and mitrate Stylophora, thus denying a morphological basis for JAEKEL's *(55)* usage of stylocone for Cornuta and styloid for Mitrata. Nevertheless, the stylocones of the two groups are readily distinguished by external characters, whether viewed from the inferior face or in profile. It appears smooth and regularly rounded in the Cornuta (Fig. 343,*1a,b, 2a-c*), whereas in the Mitrata it bears diverse excrescences—1) a narrow crest in the plane of symmetry, 2) a single long spine incurved toward the theca (e.g., *Mitrocystites, Chinianocarpos*), 3) a series of points (e.g., to six in *Lagynocystis*), or 4) transverse blades resembling plowshares (e.g., *Enoploura*) (Fig. 344,*1-3*). The excrescences just mentioned doubtless served as fulcra for lifting the distal region, which normally was raised at an angle (Fig. 344,*2,3a*). According to CASTER *(43)*, the stylocone blades of *Enoploura* contain coarse radial canals of unknown function and morphological significance.

The stylocone has the general form of a funnel with excavated relatively wide proximal part and narrower semicylindrical distal part. The obliquely chiseled proximal face (more so in Mitrata than Cornuta) is occupied entirely by a deep concavity directed upward and toward the theca (Fig. 343, *2a,c*; 344,*3b*). It served for insertion of the distal extremities of muscles occupying a part of the cavity of aulacophoral proximal region. The distal face of the stylocone in Cornuta is perpendicular to the longitudinal axis of the ossicle, serving for a little or not at all differentiated sort of ligamentary articulation with the proximal plate of the distal region (Fig. 343,*2b*). In the Mitrata this distal stylocone face is oblique and directed upward (Fig. 343,*3a*) and is joined to the first ossicle of the distal region by a very highly differentiated articulation, like those uniting the distal ossicles with one another (Fig. 344,*3c*).

In Mitrata the rather short upper face of the stylocone is framed by steep elevated walls which give it the appearance of a rather narrow throat (Fig. 344,*3b*). The walls are much lower in the Cornuta, being less elevated even than the axial structures which they border on each side (Fig. 343, *2a*). In both Cornuta and Mitrata a deep notch, bordered by raised lips, occurs on the proximal border of the upper face at its middle. This notch leads to a groove **(median furrow)** which extends to the distal extremity of the stylocone, passing there onto ossicles of the distal region. The groove is somewhat raised in the Cornuta and limited by relatively wide rims (Fig. 343,*2a*). It is flanked from place to place by **lateral depressions** and at two points both margins of the groove are generally interrupted by a short **transverse channel** leading to lateral depressions on either side. In Mitrata the median furrow lies in the middle of the throat, which occupies the entire width of the upper face (Fig. 344,*3b*). It is not elevated noticeably and is bordered on each side by a very narrow ridge. The ridges are continuous in some genera (e.g., *Peltocystis*) but interrupted at two points on each side in others (e.g., *Mitrocystites*). Where interrupted, the furrow communicates with small lateral depressions, two on each side, which lie slightly lower than the furrow, but they are not observed in *Peltocystis*. It may be noted also that in some Mitrata (e.g., *Mitrocystites, Mitrocystella*) a small pit or fossa occurs in the floor of the groove at each end, the distal one being divided by the suture between stylocone and first ossicle of the distal region (Fig. 344,*3b*).

The upper face of the stylocone was protected by plates, four pairs of them having been counted in Cornuta. The two proximal pairs closely resemble the median upper plates in rings of the adjacent aula-

---

[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.*

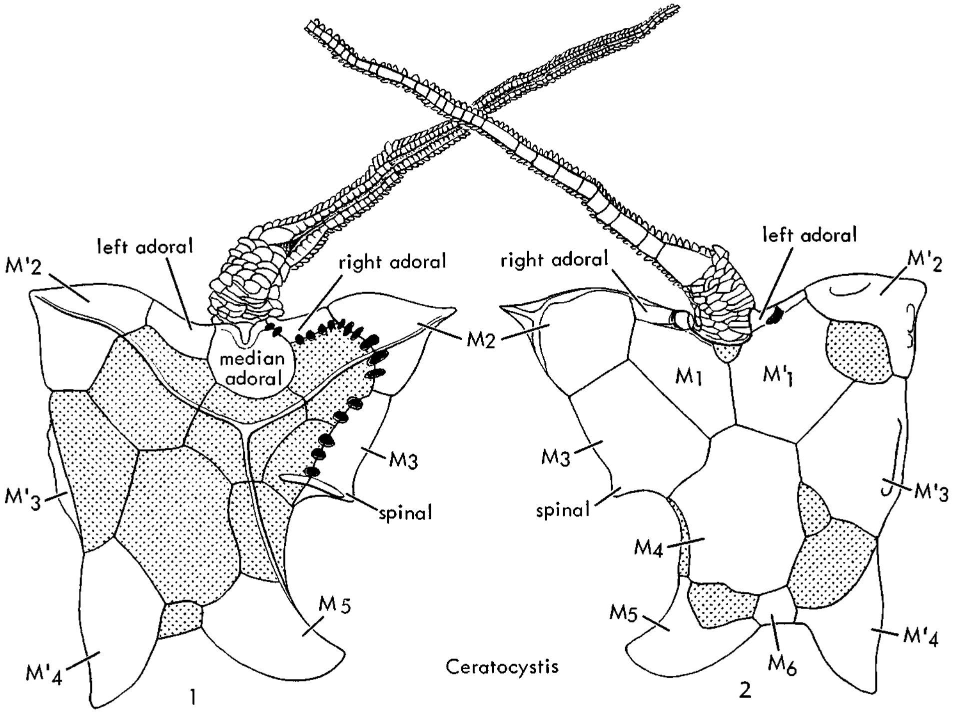


FIG. 345. Ceratocystidae (p. S548).

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

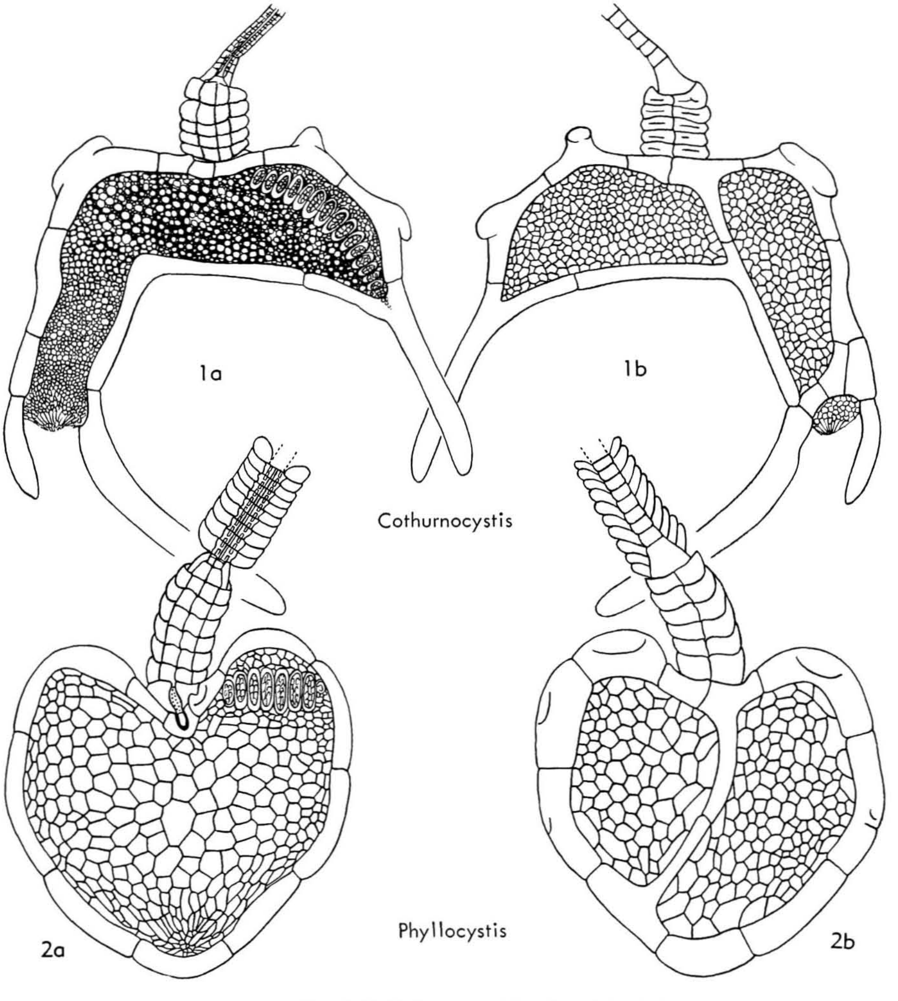


Fig. 346. Cothurnocystidae (p. S549-S550).

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).

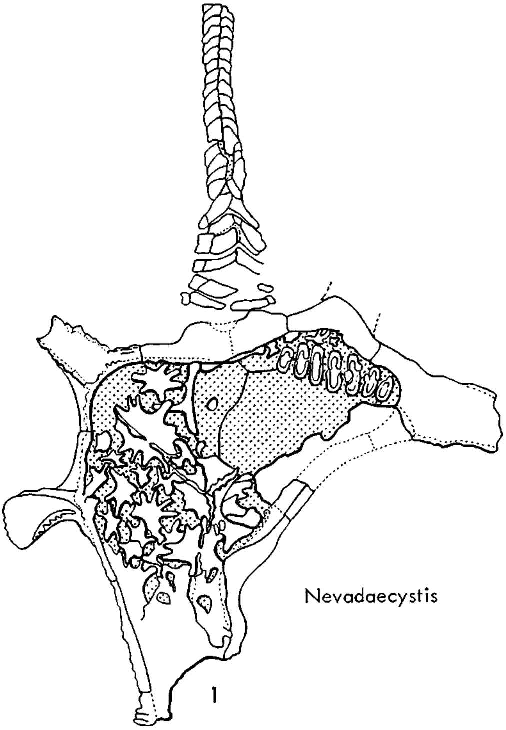


FIG. 347. Cothurnocystidae (p. S549).

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.*

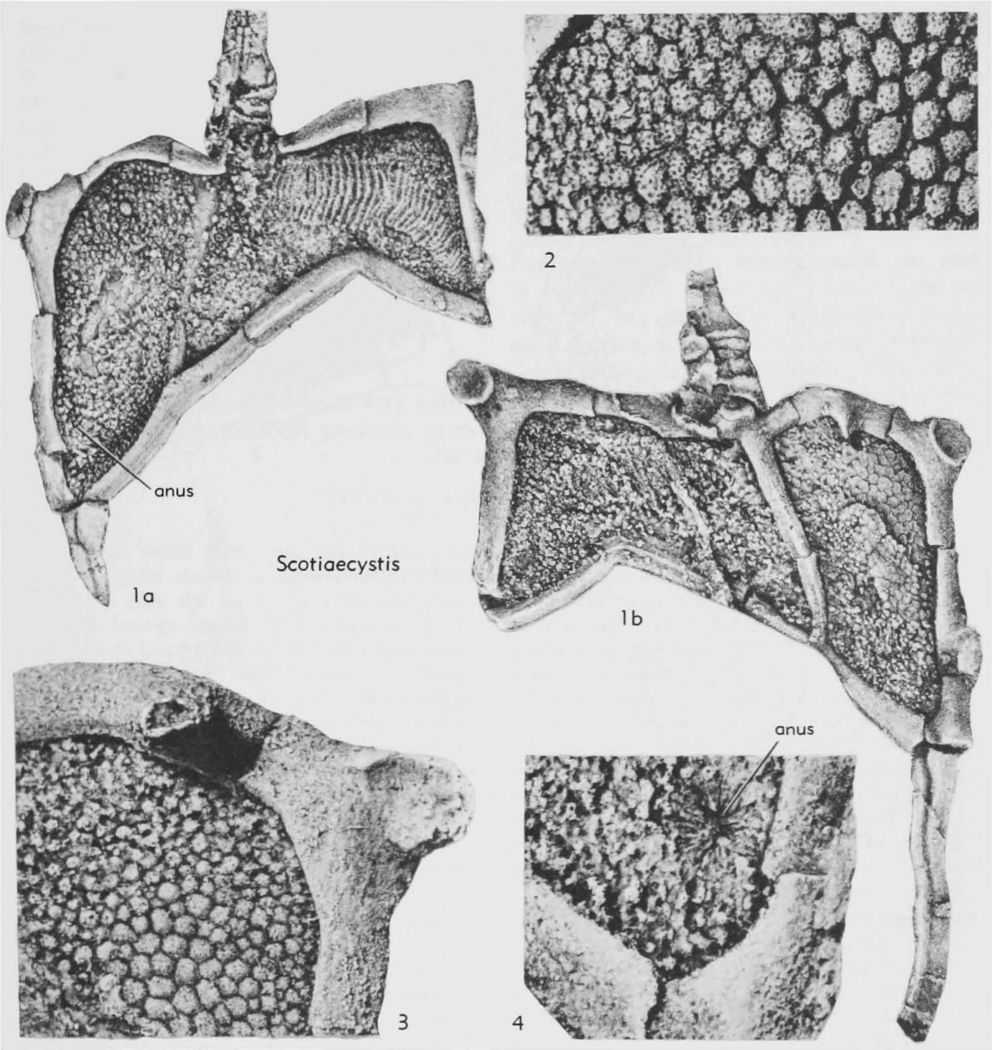


Fig. 348. Scotiaecystidae (p. S550).

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,e)]

Posterior margin evenly arcuate or slightly notched; infracentrals numerous, either small and nearly equal in size, or few and very unequal; adorals moderately developed; supracentrals rather small and more or less numerous; proximal region of aulacophore covered by imbricating quadripartite rings; aboral face of stylocone and following distal ossicles each with strong median curved spine. *L.Ord.-U.Ord.*

Mitrocystites Barrande, 1887 [**M. mitra*; OD] [=*Mitrocystis* Bather, 1889]. Thecal outlines subtrapezoidal or subrectangular, somewhat asymmetrical, slightly notched at both ends; marginals 12 or more, generally 13 (5 or 6 on left side, 7 on right side), relatively thick and folded upward at an acute angle; M'_1 distinctly larger than M_1; lower outer edge of M_2 and M'_2 denticulate;

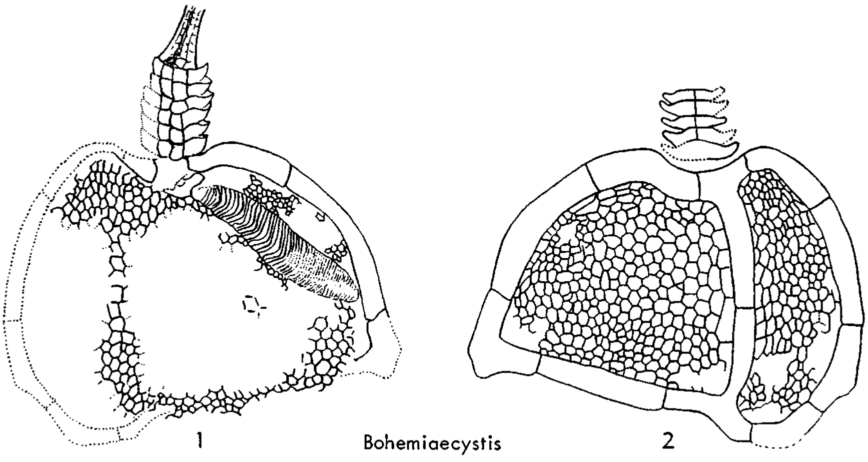


FIG. 349. Scotiaecystidae (p. S550).

infracentrals 4 to 6, largest one subcentral and separated from M_1 by median-sized plate; adorals bearing transverse fold, right one pierced by slitlike opening; supracentrals not imbricate or only slightly so, if at all; periproct semicircular, on upper side, covered by granular integument surrounding perianal row of elongate toothlike platelets; paripores on M_2 and M'_2; lateripores near outer extremity of sutures M_1, M_2 and M'_1, M'_2. *M.Ord.-U.Ord.*, Boh.-Fr. [A very doubtful species has been recorded by Dehm (1934) in the Lower Devonian (Hunsrück Sh.) of Germany].——FIG. 350,*1*. *M. mitra M.Ord. (Šárka Shale), Boh.; *1a-c,* lower, upper, lat. faces; *1d,* cross section of theca, ×2 (Ubaghs, n).

Chinianocarpos Ubaghs, 1961 [*C. thorali; OD]. Thecal outlines asymmetrical; posterior margin evenly arcuate, anterior margin hardly notched on lower side, moderately so on upper side; no anterolateral lobes; marginals 9 (4 on left side, 5 on right side), relatively thick, folded upward at acute angle, all of them more extended on lower than on upper side, except M'_4 and M_5 which cover whole upper posterior area; lower external border of M_2, M_3 and M'_2 denticulate; M'_1 larger than M_1; M_4 separating M_1, M_2, and M_3 from infracentrals, which are numerous, small, polygonal, subequal, and tessellate, occupying median elliptical area; one large subanal between infracentral area and marginals M_4, M_5, and M'_4; adorals without transverse fold and opening; supracentrals moderately numerous, tessellate; paripores on M_3 and M'_2; periproct unknown. *L.Ord.*, Fr.——FIG. 351,*1-4*. *C. thorali; *1,2,4,* upper, lower, and lat. faces; *3,* cross section of theca, ×4 (Ubaghs, n).

Mitrocystella Jaekel, 1901 [*Anomalocystites incipiens Barrande, 1887; OD]. Similar to *Mitrocystites,* but theca relatively more elongate and more asymmetrical, rounded or barely notched at posterior end, and with rather deep median embayment between 2 distinct lobes at anterior end; marginals 13 (6 on left side, 7 on right side), relatively thin, folded upward almost at right angle; M_1 and M'_1 about equal in size; infracentrals 2, one of them very large, always in contact with M'_1, and generally also with M_1; adorals without transverse fold and opening, transversely striated in some species; supracentrals apparently imbricate; paripores and lateripores unknown. *M.Ord.*, Boh.-Fr.——FIG. 350,*2*. *M. barrandei* Jaekel, 1901, Šárka Sh., Boh.; *2a-c,* lower, upper and lat. faces; *2d,* cross section of theca, ×2 (Ubaghs, n).

Family PARANACYSTIDAE Caster, 1954

Posterior margin acute and prominent; infracentrals few, about equal in size, elongate and roughly hexagonal; adorals very large, covering half or more of upper surface; infracentrals few and rather large. *L.Dev.*

For this monotypic family alone, Caster (1954) proposed the new suborder Paranacystida. It does not seem that our present knowledge is sufficient to justify recognition of a higher category than family for this rather admittedly aberrant assemblage of Mitrata.

Paranacystis Caster, 1954 [*P. petrii; OD]. Theca lancet-shaped to ovate, with nearly vertical lateral surfaces; anterior corners of upper side moderately inflated, produced subangularly; anterior margin more excavated for aulacophore insertion on lower than on upper face; posterior thecal plates seemingly imbricated and prolonged into beak-shaped structure; 2 (possibly 3) marginals on each lateral surface, taking no part in covering of upper side; infracentrals 2 (possibly 3); supracentrals 3 or 4, rather large; anteromedian supracentral quadrangular; aulacophore considerably longer than theca; stylocone 2-bladed, ossicles of aulacophoral distal region with strong median aboral spines. *L.Dev.*, S.Am.(Paraná, Brazil).——Fig. 352,*1-3*. **P. petrii*; *1,* paratype, external mold, upper side, ×10; *2a,b,* holotype, external molds, upper and lower faces, ×5.3; *3,* paratype, external mold, lower face, ×5 *(26)*.

Suborder LAGYNOCYSTIDA Caster, 1952

Thecal outlines moderately to very asymmetrical; a single exothecal posterior process. *M.Ord.*

Family PELTOCYSTIDAE Ubaghs, new family

Thecal outlines moderately asymmetrical, irregularly pentagonal, slightly excavated for aulacophore insertion on both sides; posterior margin unequally divided by marginal protuberance bearing elongate sigmoid spine; marginals eight (three on left side, five on right side), taking almost no part in covering of upper face; lower external edge of M_1 and M'_1 denticulate; infracentrals two, small, not in contact; subanal subquadrangular, outside marginal frame; adorals two, large, extending to mid-length of theca; supracentrals numerous and small, seemingly tessellate; proximal region of

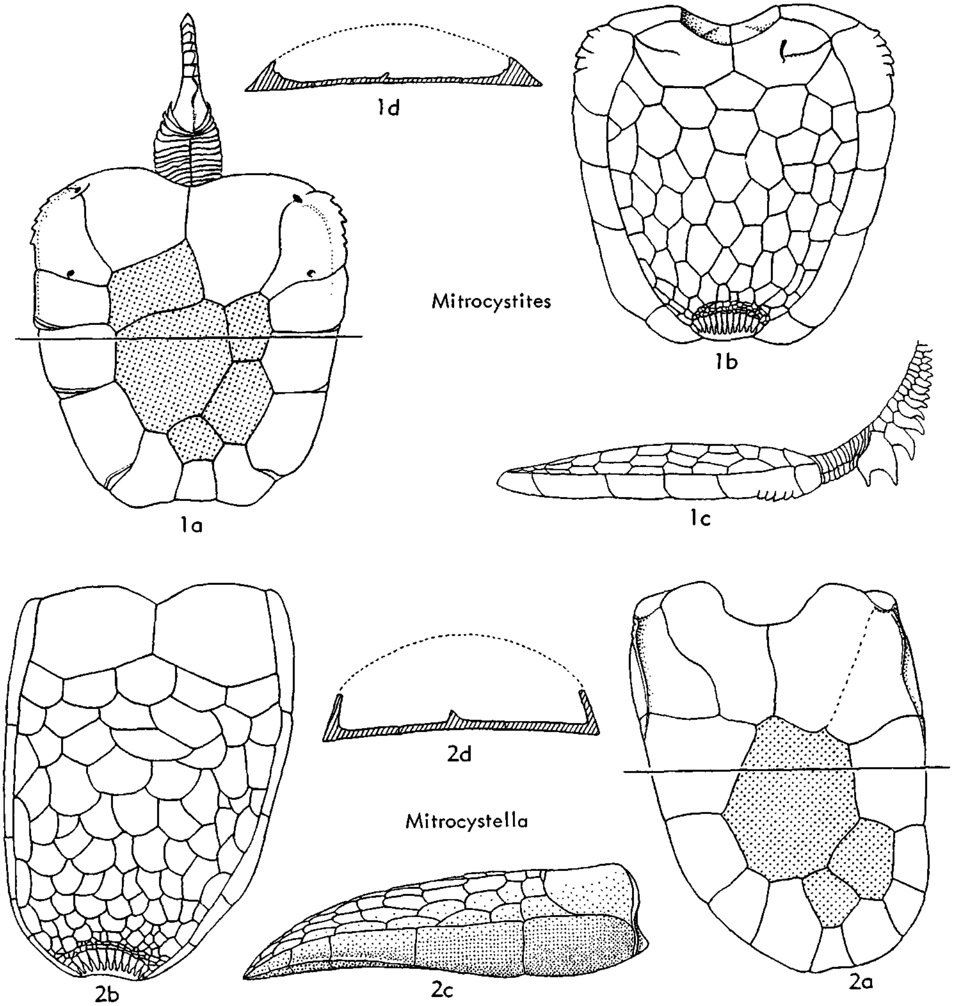


Fig. 350. Mitrocystitidae (p. S551-S552).

aulacophore covered by imbricating tetramerous ring; stylocone and following distal ossicles with strong curved aboral spines. *L.Ord.*

Peltocystis THORAL, 1935 [**P. cornuta*; OD]. Characters of family. *L.Ord.*, Fr.——FIG. 353,*1-4*. **P. cornuta*; *1,3,* interior and exterior of lower face; *2,* upper face; *4,* anterior face; ×3 (Ubaghs, n).

Family LAGYNOCYSTIDAE Jaekel, 1918

Theca elongate, pyramidal, subquadrate in cross section, very asymmetrical; posterior end obliquely truncated, with short hollow calcareous process attached to left posterior corner; left lateral surface higher than right one; lower left lateral edge sharper than right one; no infracentrals, whole inferior face being covered by seven marginals (three on left side, four on right side) and few scalelike platelets in lateral connection with supracentrals; adorals three, moderately large; supracentrals numerous, imbricating; posterior hollow conical piece (?anal valve) terminating upper face; sutural pore on each side of aulacophore insertion; proximal part of aulacophore protected by spinous scalelike imbricated platelets; stylocone elongate, very shallow, with median aboral row of four or five spines; distal region of aulacophore composed of elongate ossicles, each with short distal triangular aboral projection. *M.Ord.*

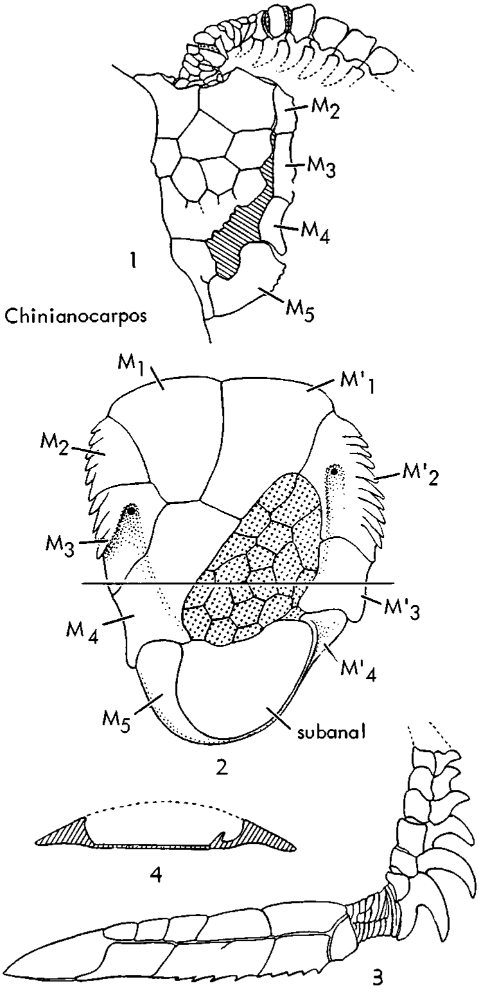


FIG. 351. Mitrocystitidae (p. S552).

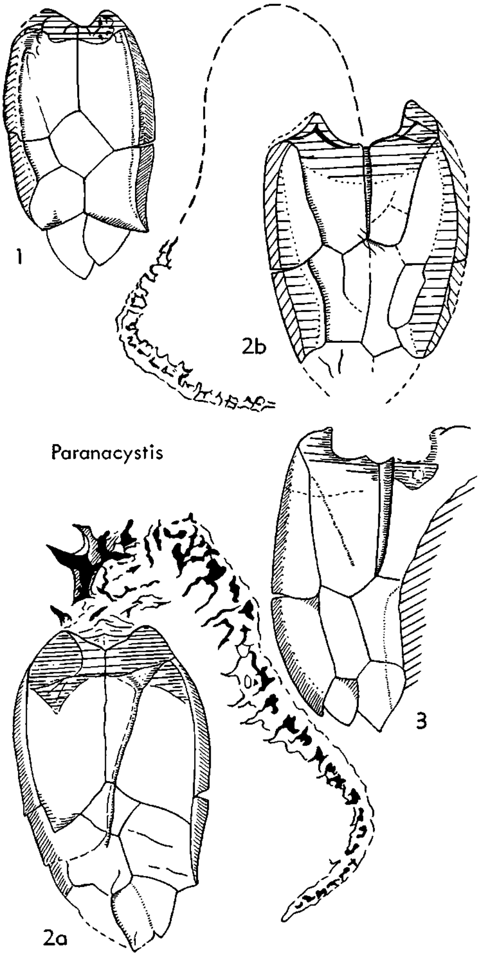


FIG. 352. Paranacystidae (p. S552-S553).

Lagynocystis Jaekel, 1918 [**Anomalocystites pyramidalis* Barrande, 1887; OD]. Characters of family. *M.Ord.*, Boh.——354,*1-5*. **L. pyramidalis* (Barrande), Šárka Sh.; *1-4*, lower, upper, right lateral and ant. faces; *5*, cross section of theca, ×3 (Ubaghs, n).

Family KIRKOCYSTIDAE Caster, 1952

[*nom. transl.* Ubaghs, herein (*ex* Kirkocystinae Caster, 1952)]

Theca plano-convex, asymmetrical, composed of only two adorals, two marginals (M_1, M'_1) and one subanal, and with calcareous posterior process; adorals convex, elongate, subequal, very large, covering entire upper face and large part of lower face as well; M_1 and M'_1 more or less reduced, M_1 smaller than M'_1, which touches large subanal inserted between posterior and adaxial lower margins of adorals; proximal region of aulacophore protected by quadripartite rings; stylocone and following distal ossicles each with aboral spine. *M.Ord.*

Balanocystites Barrande, 1887 [**B. lagenula;* OD]. M'_1 relatively large, widening in posterior direction and broadly in contact with subanal; M_1 triangular, extending for some distance along side of M'_1; subanal suparallel to extension plane. *M.Ord.*, Boh.-?Fr.——Fig. 355,*1*. **B. lagenula,* Šárka Sh.; *1a-c,* lower, anterior, upper faces of theca, ×3 (Ubaghs, n).

Anatiferocystis Chauvel, 1941 [**A. barrandei*; OD] [=*Kirkocystis* Bassler, 1950 (type, *Enoploura? papillata* Bassler, 1943)]. M'_1 narrow, in contact with subanal by short suture; M_1 subquadrate, not extending along side of M'_1; subanal oblique to extension plane. *M.Ord.*, Boh.-Fr.-USA (Okla.).——Fig. 355,*2*. **A. barrandei,* Šárka Sh., Boh.; *2a,b,* lower, upper faces, ×3 (Ubaghs, n).——Fig. 355,*3*. *A. papillata* (Bassler), Blackriv., USA(Okla.); *3a-e,* lower, posterior, upper, right and left lateral faces of theca, ×6 (Ubaghs, n).

Suborder ANOMALOCYSTITIDA Caster, 1952

[*nom. correct.* Ubaghs, herein (*pro* Anomalocystida Caster, 1952)] [=suborder Placocystida Caster, 1952]

Thecal outlines nearly bilaterally symmetrical, with two exothecal posterior spinous processes articulated at base. *M. Ord.-L.Dev.*

The genera classified herein under this suborder were placed by Caster (1952) under two new monotypic suborders—Anomalocystida and Placocystida—under the erroneous assumption that the Anomalocystitida are provided with segmented brachia and the Placocystida with unsegmented rodlike processes. In fact, as demonstrated by Caster (see under *Anomalocystites*), the Anomalocystitida have no jointed brachia at the posterior end of the body. Therefore they do not differ in any essential way from the placocystid genera.

Family ANOMALOCYSTITIDAE Bassler, 1938

[=Anomalocystidae Meek, 1872 (invalid family-group name based on *nom. van.*, Code, Art. 11,e); fam. Anomocystida Haeckel, 1896 (invalid) (*partim*); subfam. Placocystida Haeckel, 1896 (invalid) (*partim*); fam. Atelocystida Haeckel, 1896 (invalid) (*partim*); Placocystidae Caster, 1952 (invalid); Placocystinae Caster, 1952 (invalid); Enoplourinae Caster, 1952; Basslerocystinae Caster, 1952; Placocystitidae Gill & Caster, 1960]

Theca achieving high degree of bilateral symmetry in general outlines, as well as in

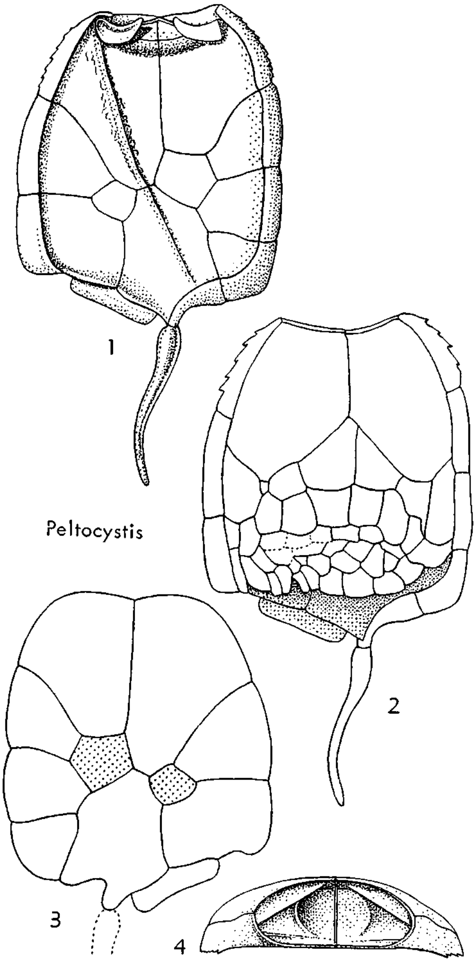


Fig. 353. Peltocystidae (p. S554).

shape and arrangement of plates, particularly on upper face; marginals 11 (two on anterior face, three on each lateral face, and three on posterior face; infracentrals few, including one large plate usually in median position accompanied by small "anomalocystid" plate at its left posterior corner and possibly by one to four additional posteriorly placed small plates; supracentrals tessellate, forming apparently solid pavement; thecal ornament typically consisting of transverse wavy lines. *M.Ord.-L.Dev.*

Partition of the anomalocystitid genera into subfamilies, seems inadvisable to me, at least until better understanding of phyletic relationships has been obtained.

Anomalocystites Hall, 1859 [**A. cornutus*; SD S. A. Miller, 1889] [=*Anomalocystis* Bather, 1889 *(nom. van.)*; *Anomocystis* Haeckel, 1896 *(nom. van.)*] [Diagnosis furnished by K. E. Caster after study by him of Hall's types.]. Theca subovoid in outline, upper face convex and lower one concave, with lateral rim; lateral faces longitudinally arcuate, posterior and anterior upper margins transversely arcuate, inferior face deeply arcuate for reception of aulacophore. Upper thecal surface composed of 12 laterals, 3 large adorals (median one touching margin), 3 large adprocteals, and 14 supracentrals arranged in 4 transverse rows (3 in proximal row, 5 in 2nd, 4 in 3rd, 2 in 4th). Lower thecal face composed of 6 marginals, 2 large adaulacophorals deeply excavated proximally, 3 adprocteals, and 2 infracentrals. Theca partially ornamented by transverse wavy lines, at distal lateral extremities bearing 2 articulated spines. Aulacophore broad proximally, formed of 8 or 9 telescoping rings which imbricate axially on lower side; styloid with 3 axial elements, short blades; distal part of aulacophore long and narrow, apparently biserial. [According to Schuchert (1904), 2 segmented brachia bearing exothecal ambulacra were inserted on the posterior thecal margin. This conclusion is er-

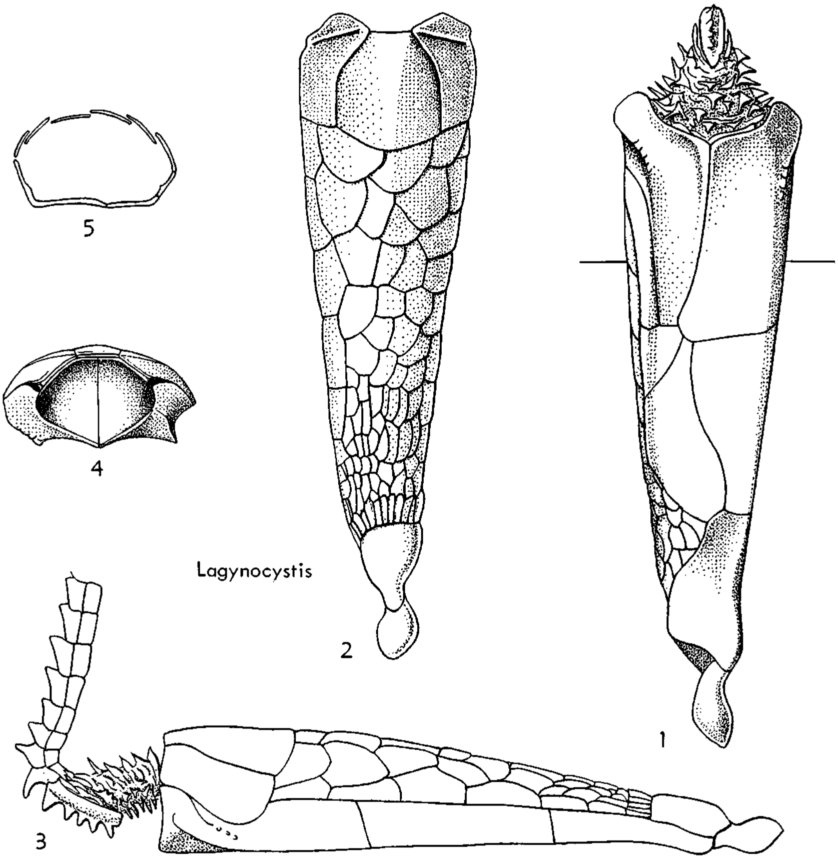


Fig. 354. Lagynocystidae (p. S555).

roneous, for it was based on the distal stele of an adjacent specimen on the same slab (USNM no. 35078). Hall's types preserve the bases of articulated spines in the position of Schuchert's inferred ambulacra.] *L.Dev.*, USA(N.Y.).——Fig. 356,*1*; 357,*1*. **A. cornutus*; 356,*1a-d,* four of Hall's type specimens (AMNH no. 2288); 356, *1a* (holotype), *1b* (previously unfigured paratype), showing superior face; 356,*1c,d,* paratypes showing inferior face (356,*1c*, figured by Hall, 356,*1d,* previously unfigured); all ×3 (Caster, n); 357,*1a,b,* plate arrangements of superior face (holotype) and inferior face (paratype, ×4.5 (Caster, n).

Ateleocystites Billings, 1838 [**A. huxleyi*; OD] [=*Ateleocystis* Lindström, 1888 *(nom. van.)*; *Atelecystis* Bather, 1889 *(nom. van.)*; *Atelocystis* Haeckel, 1896 *(nom. van.)*] [Diagnosis furnished by K. E. Caster after study by him of Billings' types]. Small anomalocystitid mitrates

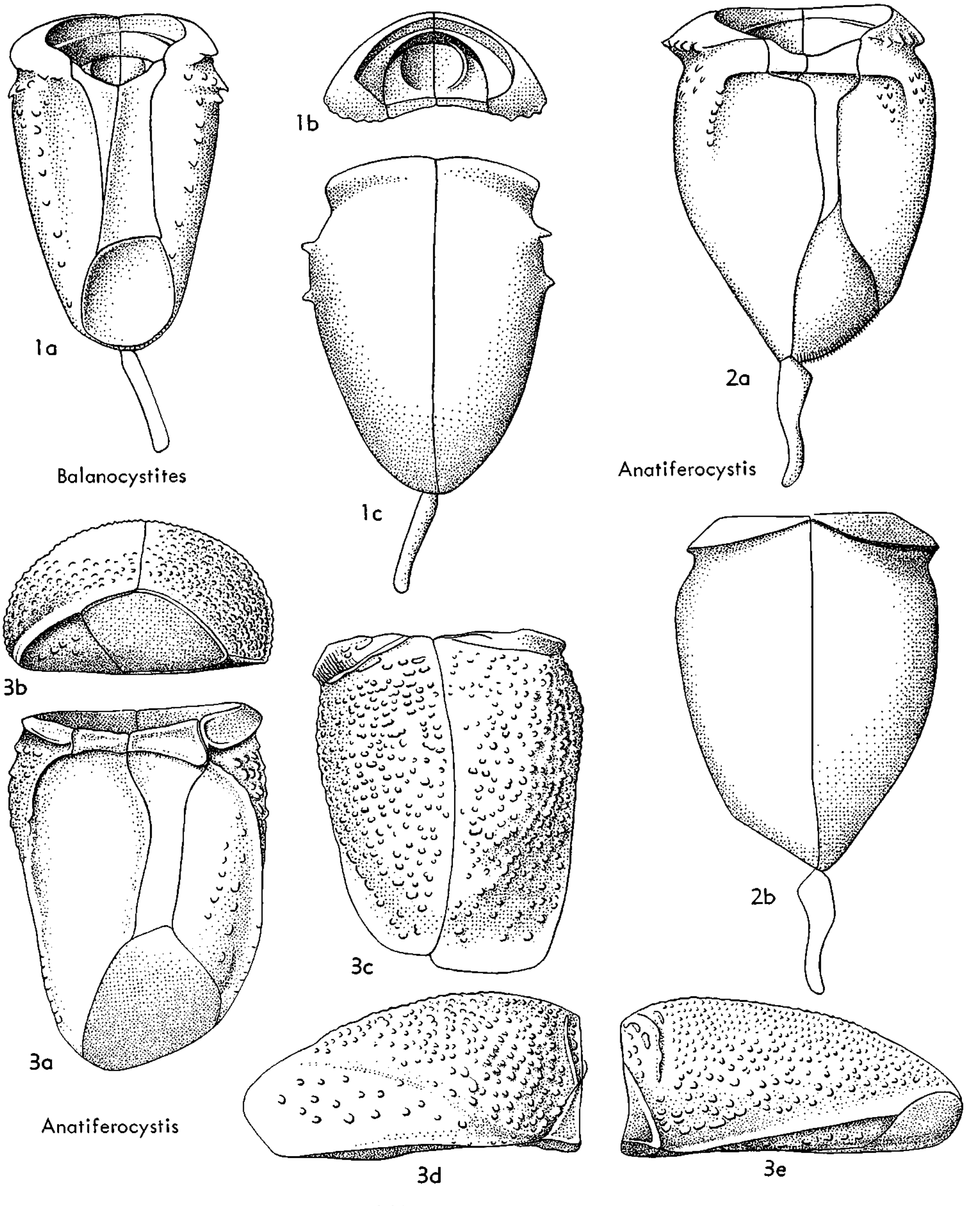
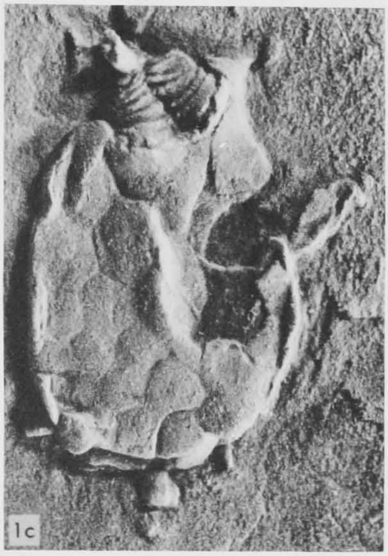
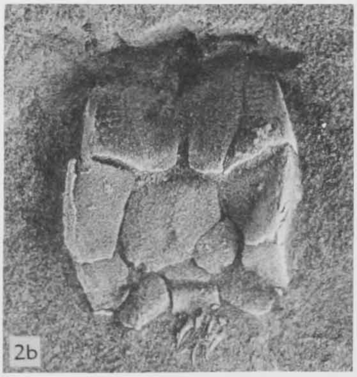


Fig. 355. Kirkocystidae (p. S555).

Anomalocystites





Ateleocystites

with inferior (plastron) surface composed of 14 plates, of which 3 are somatic and others marginal, as in *Enoploura*; superior (carapace) surface poorly known, but with more numerous somatic plates and considerably narrower adaulacophore axial plate than in *Enoploura,* superior

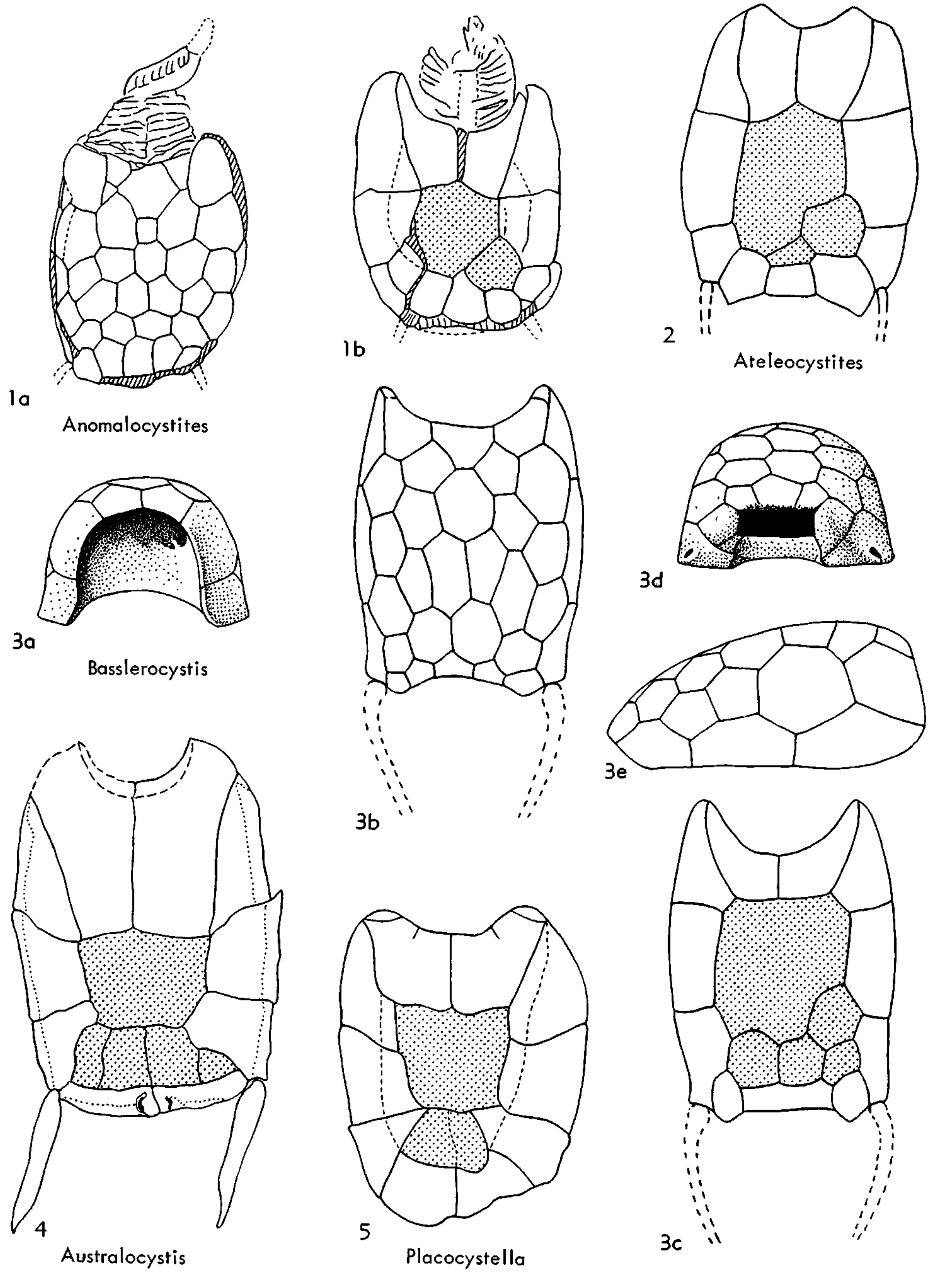
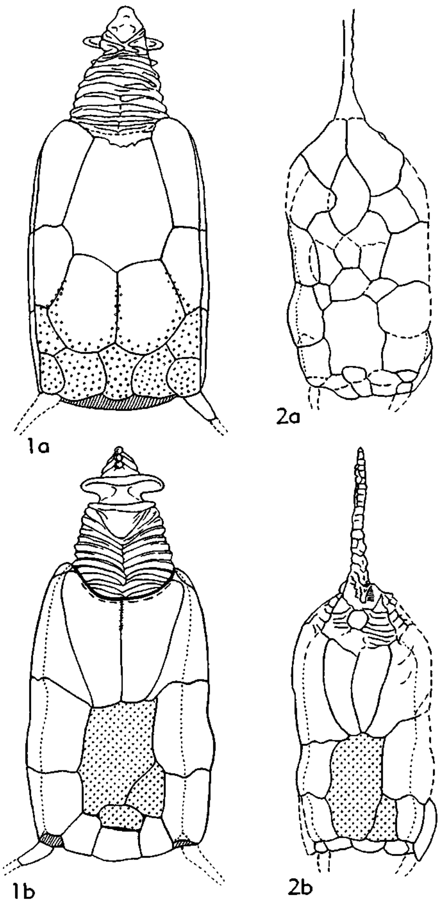


FIG. 357. Anomalocystitidae *(1-3)*; Australocystidae *(4-5)* (p. S556-S557, S559-S560).

FIG. 356. Anomalocystitidae (p. S556-S557, S559-S560) [*On facing page*].



Enoploura Victoriacystis

FIG. 358. Anomalocystitidae (p. *S*560-*S*561).

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 (Übaghs, n).

Victoriacystis Gill & Caster, 1960 [**V. wilkinsi*; OD]. Theca elongate, with subpentagonal outline; lower face flat or slightly concave; upper face strongly convex; lateral margins nearly vertical; upper anterior border overarching proximal region of aulacophore, lower anterior margin arcuately excavated by wide aulacophore insertion; four most anterior marginals occupying nearly half of lower thecal face; infracentrals 2, moderately large median plate and small one at its left posterior corner ("anomalocystid plate"); adorals 2, small, posteriorly separated by lozenge-shaped plate (?third adoral); supracentrals numerous and rather small, except relatively large one in median posterior position; anterior upper plates ornamented with transverse wavy lines. *U.Sil.,* Australia.——Fig. 358,*2*. **V. wilkinsi,* Victoria; *2a,b,* upper and lower faces, ×1.5 *(43).*

Family AUSTRALOCYSTIDAE Caster, 1954 [1956]

[*nom. transl.* Ubaghs, herein (*ex* Australocystinae Caster, 1954 [1956])]

Theca achieving high degree of bilateral symmetry in general outlines, as well as in shape and arrangement of plates on both thecal faces; marginals 10, two on anterior face, three on each lateral face, and two on posterior face; infracentrals few, comprising one large subcentral plate and generally some additional smaller ones. *L.Dev.*

Australocystis Caster, 1954 [1956] [**A. langei;* OD]. Theca subrectangular in outline arcuately excavated for reception of aulacophore on lower face (only one known); lateral and posterior inferior margins raised in prominent rounded flanges; marginals 10 (12 according to Caster) and infracentrals 5 (3 according to Caster) almost symmetrically arranged; no "anomalocystid plate"; transverse row of 4 small infracentrals immediately behind large central plate; posterior margin entirely occupied by only 2 massive transversely elongate marginals. *L.Dev.,* S.Am.(Paraná, Brazil).——Fig. 357,*4*. **A. langei*; lower face, ×3.6 (27).

Placocystella Rennie, 1936 [**P. capensis*; OD]. Theca apparently cordiform in outline; lower face made of ?12 plates (10 marginals, 2 infracentrals), more or less symmetrically arranged. *L.Dev.,* S.Afr. ——Fig. 357,*5*. **P. capensis,* Bokkeveld Ser.; lower face, ×2.5 (27, modified).

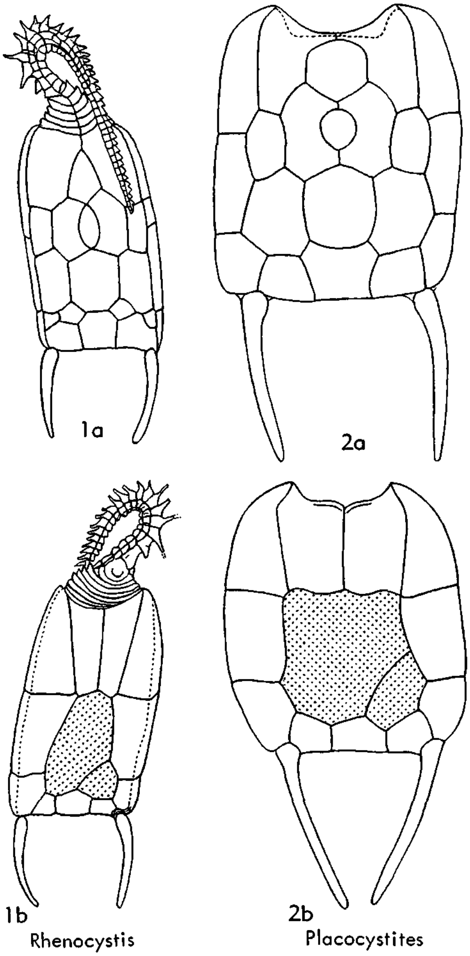


Fig. 359. Anomalocystitidae (p. *S*560-*S*561).

Family ALLANICYTIDIIDAE Caster & Gill, new family

Mitrate, anomalocystid Stylophora of nearly perfect bilateral symmetry both in outline and thecal plate arrangement; with pair of articulated distal lateral spines, articulatory bases for which are seen on thecal corners; one large somatic plate in superior (carapace) face, and two subequal, paired somatics in inferior (plastron) face; aulacophore large, three-zoned, one styloid blade of quite exceptional width. *L.Dev.*

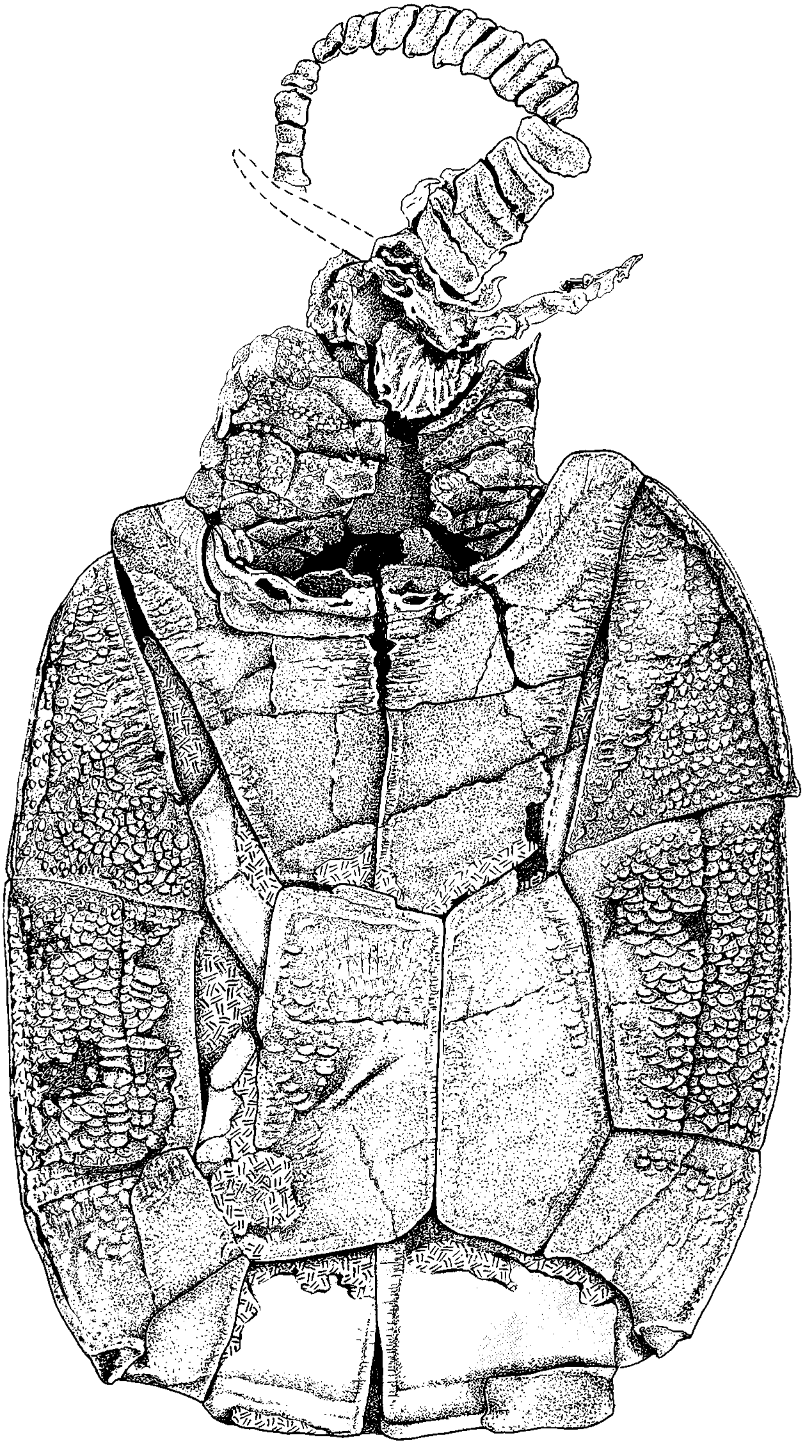


FIG. 360. *Allanicytidium flemingi* CASTER & GILL (Allanicytidiidae) (p. S564).

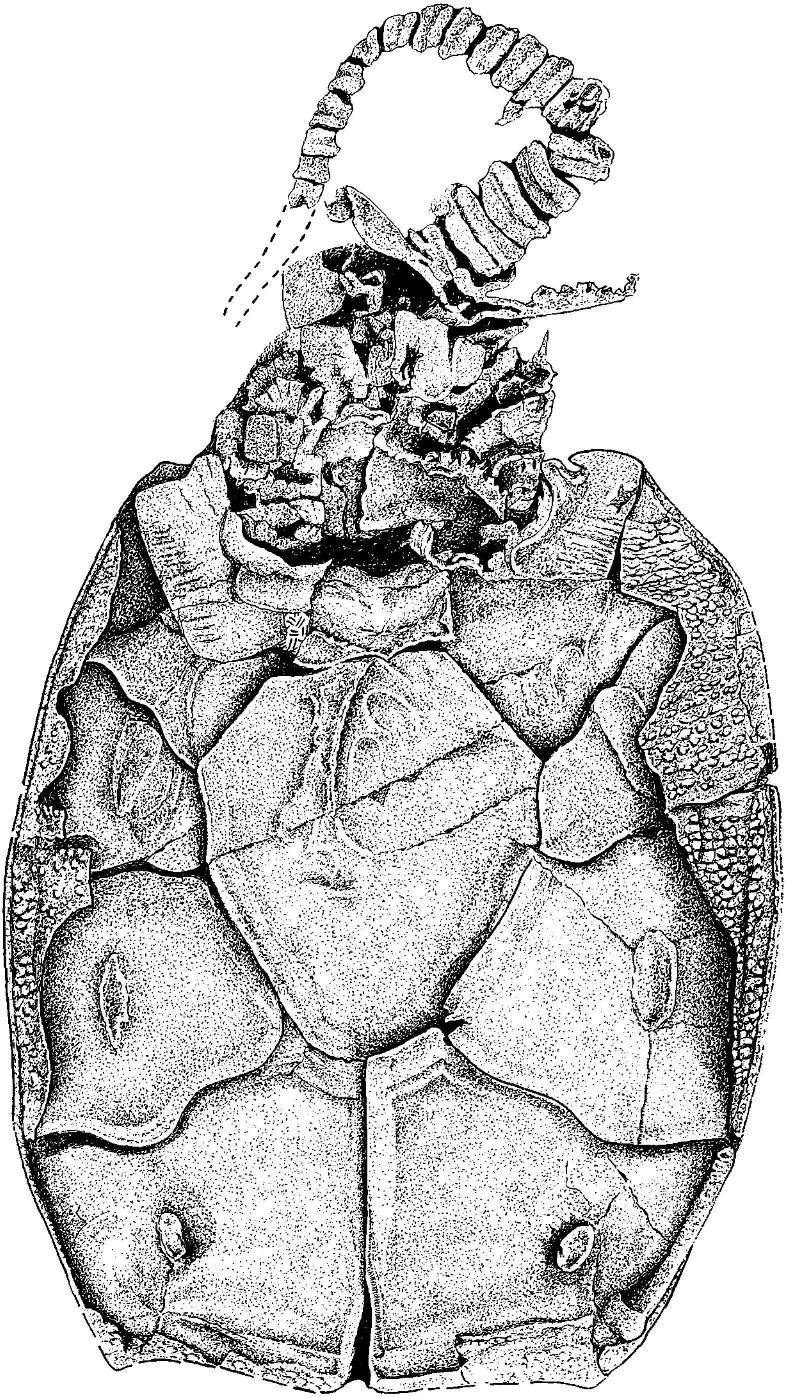


FIG. 361. *Allanicytidium flemingi* CASTER & GILL (Allanicytidiidae) (p. S564).

Allanicytidium Caster & Gill, **new genus,** herein (named for Robin S. Allan; *cytidium,* little box) [**A. flemingi* Caster & Gill, n.sp.; OD]. Large placocystoid, with boxlike theca, tripartite aulacophore and paired, basally articulating distal-lateral spines. Theca quadrately ovoid in plan; broadly convexi-concave in cross section; length to width as 13:11; broad-margined re-entrant of both thecal faces for aulacophore insertion. Surface of thecal plates prominently scaly in appearance, with pseudo-overlap away from aulacophore; imbrice scale aspect merging into typically mitrate transverse ridging on the adaulacophore plates (surface ornament seen so far only on inferior thecal face). Coarse granular ornament on proximal aulacophore tetrameres. Inferior (concave, plastron) thecal surface covered by probably 13 large nonimbricating plates, only 2 of which are somatic. Plates seemingly flexibly united in life (holoperipheral growth lines prominent on interior of plates), except possibly at margins of theca, where either there was fusion of plates of both thecal surfaces, or more likely marginal plates bend laterally so as to form lateral surface and extend onto both thecal surfaces. [For purposes of description here, the marginal plates seen on each surface are treated as though separate plates.] Lateral thecal margin bears narrow, downwardly directed keel; remainder of inferior surface forming broad vault. Holotype has 9 marginal plates but 2 more are reasonably inferred at distal margin; somatic pair are elongate, subequal in size and shape, meeting on axial plane. Right somatic (as seen with theca inverted and aulacophore directed away from viewer) is slightly smaller in area and pentagonal, rather than quadrate. Superior (convex, carapace) thecal surface covered by 9 large plates, only one of which has appearance of being somatic, but in reality is large adaulacophore basal axial plate. (Only the interior surface on the carapace plates is known.) The disposition of the plates and the circumperipheral lines of growth indicate that the plate sutures were flexible and integumentary. Most of the superior plates bear prominent, cuplike calcareous myophores. *L.Dev.,* N.Z.——Fig. 360, 361. **A. flemingi*; Reefton Beds, South Island, N.Z. (Rain Creek, Waitahn); views of holotype (N.Z. Geol. Survey no. 38/370203), 360, 361, inferior (plastron) and superior (carapace) surfaces, ×8 (Gill & Caster, n).

[These new taxa differ markedly from any other Stylophora in nature of the plate arrangement; they are mainly covered by the homologues of marginal plates in other forms; the somatic elements are as a correlate much reduced in number and highly modified. The right somatic of the plastron appears to be the homologue of the small asymmetric "anomalocystid" plate in other mitrates (e.g., *Placocystites, Enoploura*). The central "somatic" of the carapace is a distally migrated and enlarged central basal plate of other forms; in this genus it no longer makes contact with the aulacophore. Only the Australocystidae (*Australocystis,* L.Dev., Brazil; *Placocystella,* L.Dev., S. Afr.) approach the Allanicytidiidae in bilaterality; however, the plate arrangements of the two families are quite different. The new genus, being monotypic, is characterized by large size, pseudosquamose ornament, and extraordinary large styloid blade.]

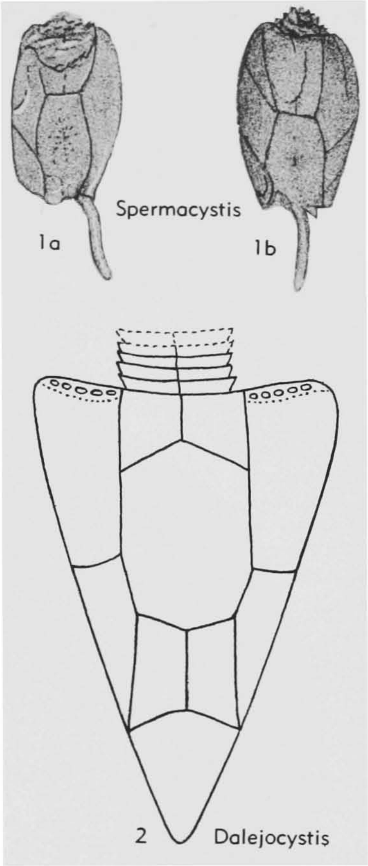


Fig. 362. Stylophora, Suborder and Family uncertain (p. S564-S565).

Suborder and Family UNCERTAIN

Dalejocystis Prokop, 1963 [**D. casteri*; OD]. Theca symmetrical, showing form of rounded isosceles triangle; upper face composed of fairly large symmetrically arranged plates and ending in rounded massive triangular plate; anterior margin bearing row of conical tubercles on both sides of aulacophore insertion; lower face unknown. *M.Dev.,* Boh.——Fig. 362,2. **D. casteri,* Daleje Sh. (Couvinian); upper face, schematic reconstruction, ×6 (71).

Spermacystis Ubaghs, herein [*nom. subst. pro Anomocystis* Jaekel, 1918, p. 122 (*non* Haeckel, 1896)] [**Anomalocystites ensifer* Barrande, 1887; OD]. Thecal outline nearly symmetrical; anterior border emarginated for aulacophore insertion, lateral margins longitudinally arcuate, posterior margin straight; one (possibly 2 according to Barrande) posterior exothecal rodlike process;

number and arrangement of plates, as well as aulacophore, unknown. [This nominal genus, based on scanty and poorly preserved material, was placed among Anomalocystidae by Jaekel (1918) and Chauvel (1941). Possibly it belongs in the Lagynocystida.] *M.Ord.*, Boh.——Fig. 362, *1*. **S. ensifer* (Barrande); *1a,b*, different specimens, orientation unknown, ×1.5 (2).

[References for the chapter on Stylophora are included with those for Homostelea and Homoiostelea (*see* p. *S*624).]

HOMOSTELEA

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, Národní Museum, Prague, Czechoslovakia; Dr. Gerta Wehrli-Olbertz, Ernst-Moritz-Arndt-Universität, Greifswald, Germany. Photographs, drawings and assemblage of figures have been prepared by Mrs. Marie Masson. To all these people I express deep thanks.

[2] Numbers enclosed by parentheses, other than years, indicate serially numbered publications in the list of referenecs at end of this chapter.