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COMAROCYSTITES AND CARYOCRINITES

Cystids with pinnuliferous free arms.

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INDEX

I. Preliminary Remarks on the Arm Structure of Crinoids and Cystids.

1. *The origin of biserial arms.*—According to Dr. F. A. Bather (Caradocian Cystidea from Girvan, 1913, p. 385), "the brachioles of Blastoids and Cystids differ from the Crinoid brachium, not merely in more fundamental features, but also in the fact that they are invariably biserial and present no trace of an anterior uniserial stage." The crinoid arm, on the contrary, is regarded by Bather (Echinoderma, 1900, p. 116), to have

originated from a uniserial form, even in those cases in which the arm structure at present is biserial, and diagrams are given illustrating how a uniserial arm might develop into a biserial one. It is well known that biserial arms frequently are uniserial at the base, and the arrangement here is regarded as more primitive. (See also Wachsmuth and Springer, Revision of the Palaeocrinidea, II, 1881, pp. 22-25; III, sec. 1, 1885, p. 14; III, sec. 2, 1886, p. 230.)

According to Austin H. Clark (A Monoograph of the Existing Crinoids, 1915, pp. 184, 189, 350, 352, 354), however, the biserial arrangement is more primitive in crinoids; the biserial arrangement being the palaeozoic type, while the uniserial arrangement originated chiefly in post-palaeozoic times.

Clark's conception of the origin of the biserial arrangement of the ossicles of crinoid arms is so different fr m that commonly accepted that it is quoted here in full:

"The crinoid arms are primarily paired interradial structures which have become joined along their radial edges, forming a radial biserial appendage, the ossicles later slipping in between each other so that an elongate uniserial appendage results. The original arms were, therefore, primarily ten in number. . . Originally, before their union into five, the arms probably bore no ventral ambulacral structures, and had no function other than that of increasing the surface of the disk by increasing the distance between the points of attachment." (Loc. cit., p. 350.)

The following statement by Clark also is illuminating:

"In such fossil forms as have biserial arms it is to be remarked that at the arm bases the brachials become uniserial; this is not to be interpreted as indicating that the arms were originally uniserial, but quite otherwise; mechanical considerations have forced the amalgamation of the two primitive radials into one, and similarly have forced the uniserial arrangement of the first two, and partially of the third and fourth, brachials." (Loc. cit., p. 354.)

"It is probable that the pinnules represent the original type of crinoidal appendage, and that these appendages were arranged in five pairs, the two components of each pair being, so to speak, back to back; but the pinnules have become enormously reduplicated, while in addition (they) have come to lie along either side of long body processes (arms) of subsequent development." (Loc. cit., p. 274, but omitting all references to cirri.)

Since the pinnules of crinoids are uniserial, it is certain that Clark regarded the uniserial arrangement of ossicles as primitive among crinoid appendages. Even the primitive arms of crinoids were imagined to have been uniserial. However, in times preceding the advent of the actually known paleozoic crinoids, adjacent uniserial arms were supposed to have united laterally in pairs in such a manner as to give rise, first, to biserial arms, and, later, to pseudo-uniserial ones. According to this theory, the pinnules of the theoretical uniserial arms might be arranged in a single series along one side of the arm, while the pinnules of the pseudo-uniserial arms should occur in two series, successive pinnules being attached alternately to opposite sides of the series of arm ossicles. If the food-groove along the ventral surface of the crinoid arms be regarded as originating along the line of junction of the two imaginary primitive uniserial arms, this food-groove might be retained in pseudo-uniserial arms originating from biserial forms, but need not be present in the imaginary primitive uniserial arms.

The views favored by Clark, and the various possible deductions from them, are interesting. They would be more interesting if they found support in the probable phylogeny of fossil species. It must be conceded, however, that in the earliest known representatives of the crinoids, the primary radials and primibrachs of Clark already were united laterally so as to present an initial series of five, instead of ten arms, as demanded by Clark's theory, and all the arms bear food-grooves. Moreover, even the earliest known biserial arms are more or less uniserial at the base.

2. *Uniserial arms and pinnules in Comarocystites.*

In the absence of anything corresponding to the supposed primitive arm structure of crinoids, among known Crinoidea, it may be interesting to note that, among the Cystidea, the free arms of *Comarocystites* are uniserial (Plate III), do not bear a food-groove along the ventral side, and support pinnules arranged in a single row along the right side of the arm (the ventral surface being directed away from the observer, and the distal end of the arm being directed upward); moreover, the pinnules consist of a uniserial row of ossicles. In a similar manner the uniserial row of plates supporting the recumbent food-grooves of *Amygdalocystites* (Canadian Organic Remains, III, 1858, plate VI), also might be regarded as uniserial arms, bearing a single row of uniserial pinnules along the right side of each arm. It is probable that *Canadocystis* (Bulletin 80, N. Y. State Museum, 1905, pp. 273, 274),had an arm structure similar to that of *Amygdalocystites*. It must be admitted, however, that these forms are not normal cystids. The possession of uniserial pinnules in *Comarocystites* and *Amygdalocystites* is sufficient to indicate this. *Canadocystis* probably also had uniserial pinnules. However, none of these genera could have given rise to five biserial arms, in accordance with the theory favored by Clark. At best *Comarocystites* could have given rise to only two biserial arms.

3. *Biserial arms and brachiolar pinnules in Caryocrinites.*

Caryocrinites (Plate IV) is anomalous in presenting brachioliferous free arms in which the ossicles of both the brachioles and of the arms are biserial in arrangement. It is anomalous also in other respects. Successive ossicles on the same side of the arm usually alternate strongly in size, the lower ossicle of each successive pair being distinctly shorter, sometimes, in fact, being reduced to a small, transversely cuneate remnant along the inner half of the horizontal suture separating the larger ossicles. When both of these successive ossicles are more nearly of the same size, both are in contact with the base of the same brachiole, the lower, shorter ossicle of each pair being in contact with one of the series of ossicles forming the brachiole, and the upper, longer ossicle of the same pair being in contact with the other series of brachiolar ossicles. Hence, it is possible to regard not only the arm of *Caryocrinites* as made up by lateral junction of two uniserial arms, but, in a precisely similar manner, the brachiole of *Caryocrinites* might be regarded as built up by the lateral junction of two uniserial pinnules, the supporting brachial ossicles of each of these theoretical uniserial pinnules still remaining distinct.

As a matter of fact, the brachioles of *Caryocrinites* may be diagrammed also as uniserial forms, the ossicles alternating in position from right to left, across the brachiole, the lowest ossicle at the base being regarded as the first ossicle of the brachiole.

4. *Biserial brachiolar pinnules in Stephanocrinus.*

Biserial pinnules are so anomalous among crinoids that in the case of *Stephanocrinus*. the only crinoid known to possess them, Wachsmuth and Springer identified them as pinnules. (Revision of the Palaeocrinidea, III, sec. 2, 1886, pp. 283, 284, 292), stating: "that these appendages, although they are equally thin and short, are not pinnules, is proved by the fact that all are supported by a radial plate, instead of being distributed separately along the sides of an ambulacrum." More recently (Zittel, 1913, p. 207) Springer has described *Stephanocrinus* as possessing "arms with one short biserial trunk to the ray, giving off slender biserial, non-pinnulate side arms from the outer shoulder of each brachial."

Evidently, *Stephanocrinus* is as anomalous among crinoids as *Caryocrinites* is among cystids.

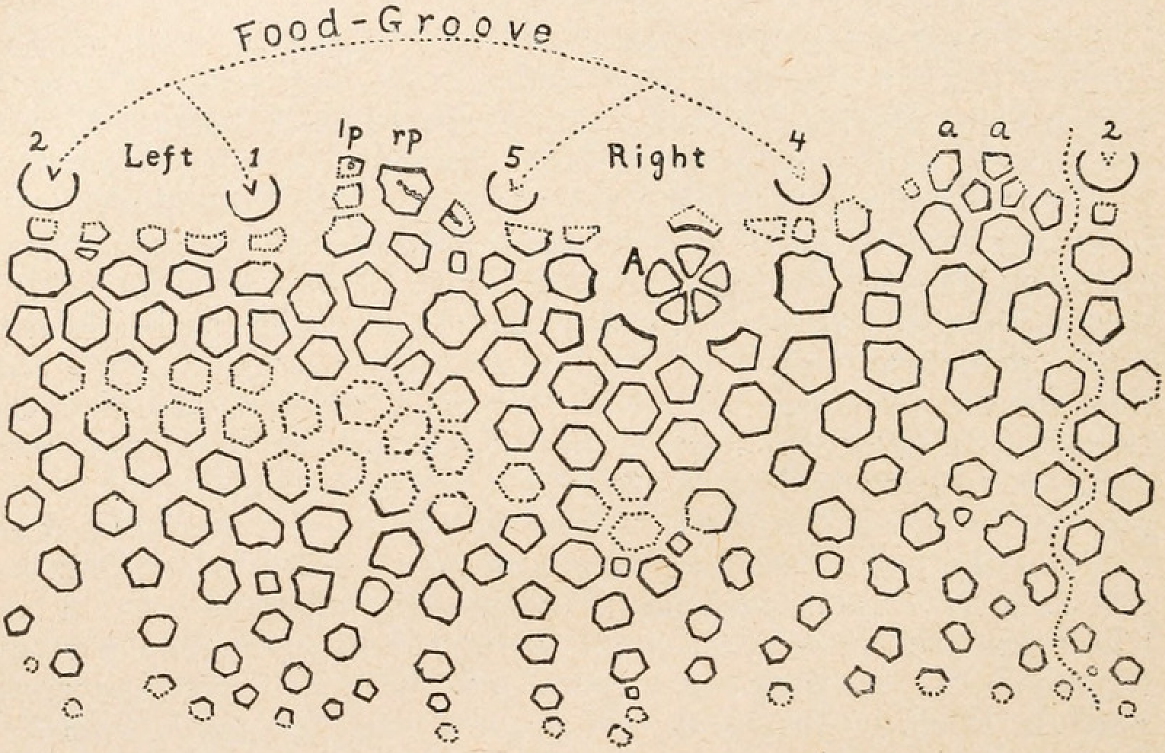
In presenting the preceding lines, there is no desire to favor the view that the biserial arms of crinoids have originated by the lateral junction of pairs of uniserial arms, but rather to call attention to the fact that the arms of certain cystids apparently present similar problems. Since these cystids are not as fully known as desirable, a more detailed description of *Comarocystites* is given here, and a few notes on *Caryocrinites* are appended. Moreover, these are the only cystids known at present in which the arms are free and pinnuliferous, and, as such, possess special interest. Both genera are American, occuring both in Canada and in the United States.

II. DETAILED DESCRIPTION OF COMAROCYSTITES PUNCTATUS BILLINGS.

5. *Chief characteristics of the theca.* Theca obovate, sometimes attaining a length of 75 millimeters, composed of about 150 plates, most of which are hexagonal in outline. Theca moderately compressed from front to rear. The two primary food-grooves diverge toward the right and left from the mouth in such a manner as to present the appearance of a single transverse, slightly curved, food-groove (Plate II, figs. 1A, 1B). The mouth does not present the appearance of a slit, as in *Aristocystis bohemicus* Barrande, and apparently also in *Caryocystis angelini* Haeckel, but takes the form of a more or less circular or elliptical aperture located in the bottom of the transverse apical food-groove already described. At each end of this food-groove the latter branches dichotomously on the proximal side of a nodular protuberance of stereom about 10 or 11 millimeters in diameter. Each nodular protuberance supports two arms. There are, therefore, four arms, arranged in pairs, one pair at each end of the transverse apical food-groove. These correspond in position to the lateral arms of the five-rayed cystids, there being no arm corresponding to the anterior arm of other cystids. The anal pyramid (Plate II, figs. 1A, 1B, 2; also Plate III) is situated a short distance below the protuberance supporting the pair of arms on the right side of the specimen. In larger specimens the transverse apical food-groove, between the points of dichotomous branching, has a length of about 13 millimeters, thus giving to each of the two lateral primary rays a length of 6 millimeters. Throughout its length the transverse apical food-groove follows the suture line between the anterior and posterior peristomial thecal plates. Along the basal margin of the nodular stereom protuberance, the exterior surface of the adjoining thecal plates of some specimens presents the appearance of being crowded back by the growth of the protuberance, and consequenlty of being reduced in size. The upper margin of these thecal plates appears to rest against the lower half of the protuberance, but cross-sections of other specimens indicate that the upper inner margin of these thecal

plates extends sufficiently beneath the base of the protuberance to suggest the origin of the latter as an accessory stereom deposit upon the surface of the theca, necessitated by the demands for support made by the growing arms.

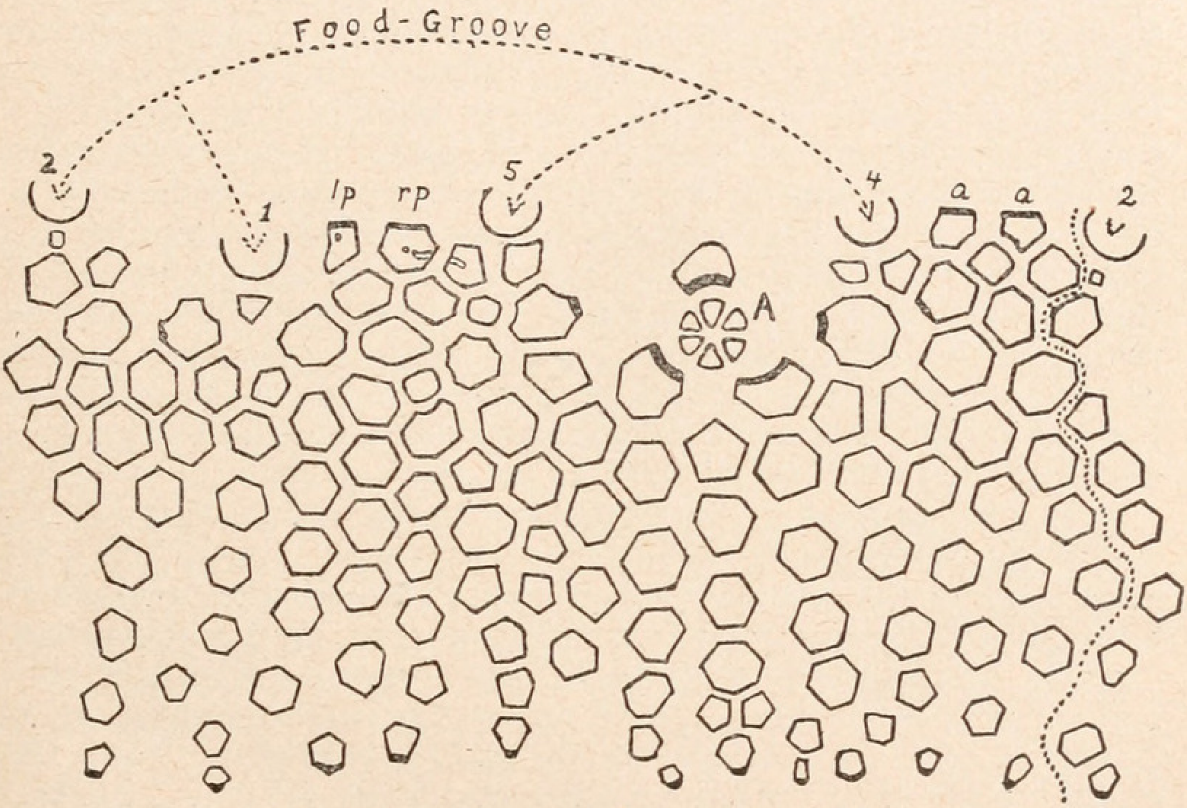
The degree of compression of the undistorted theca is moderate, the horizontal diameter from front to rear equalling about .80 to .84 of the lateral diameter. Specimens preserved in soft clay frequently present a much greater degree of compression, due to distortion after death. The length of the theca equals about ten-sevenths of the greatest transverse diameter.



Text figure No. 1. Diagram of the thecal plates of the specimen represented by figure 1 on plate II. The plates on the right of the vertical sinuous line on the right side of the figure duplicate those at the left margin of the diagram. The anterior peristomial plates are lettered *a*, *a*; the right and left posterior peristomial plates are lettered *rp* and *lp* respectively. The relative position of the different arm facets is indicated by the numbers *2*, *1*, *5* and *4*, explained in the text. The dotted line indicates diagrammatically the transverse apical food-groove which forks at each end, each branch leading to the base of one of the arms, the latter being arranged in pairs. The anal pyramid is indicated at A. The linear hydropore extends from the middle of plate *rp*, diagonally downward and toward the right, as far as the middle of the adjoining plate.

Viewed from a direction at right angles to the plane of symmetry passing vertically through the theca, and parallel to the transverse apical food-groove, the sides of the theca differ slightly in outline. On the anal side the outline is more angularly convex, the maximum convexity being near midlength. On the opposite side the maximum convexity tends to be distinctly less curved. This difference in outline evidently is due to the location of the anus which has been dragged sufficiently by the gut to reduce the convexity of the upper part of the theca along its outline on the right, thus lowering the point of maximum convexity on this side.

6. *The numbering of the rays of the food-groove system.*— There is no trace of an anterior ray of the food-groove system in *Comarocystites.* However,it is possible to number the arms present in such a manner as to make comparisons with the rays of cystids whose food-groove system shows evidence of pentameral symmetry readily possible. (Plate II; figs. 1A, 1B; also text diagrams 1 and 2).



Text figure No. 2. Diagram of the thecal plates of the specimen represented by figure 2 on plate II. All letters and numbers as in text figure No. 1. That edge of the thecal plates which is in contact with the anal pyramid is heavily blackened. That edge of the basal plates which is in contact with the column is blackened in a similar manner.

In that case the left posterior arm is numbered 1, the left anterior arm, 2; the right anterior arm, 4; and the right posterior arm, 5. The absence of an anterior ray is indicated by the omission of the number 3.

7. *The thecal plates bordering on the transverse apical food-groove.*– If the thecal plates bordering on the transverse apical food-groove be termed peristomial plates, then the anterior side of this food-groove (Plate II, fig. 1A) may be described as bordered by two peristomial plates sufficiently similar in width to place the intermediate suture-line about half-way

between the ends of the transverse food-groove. It is evident that if an anterior ray ever was present in any of the ancestral forms leading to *Comarocystites*, this ray may have rested on the suture between the two anterior plates (between plates a, a, of the text diagrams) here under discussion. The outline of the right anterior peristomial plate is more or less obliquely hexagonal, while that of the left anterior peristomial plate is pentagonal.

The posterior side of the transverse apical food-groove also is bordered by two peristomial plates (Plate II, fig. 1B; also thecal plates lp and rp in text diagrams), of which the right is so much larger that it forms about two-thirds of this posterior border. The general outline of this plate is hexagonal, but the apex of the angle on the left side is broadly truncated by a concave curvature, as though three plates were in contact with the left margin of this plate:—a large, more or less hexagonal plate along its lower left margin, and two more or less quadrangular plates in contact respectively with the middle and upper parts of this left margin. The line of contact between these two quadrangular plates is not defined distinctly in any of the specimens examined, but the upper one of these plates borders on the left third of the transverse apical food-groove, and may be described as the left peristomial plate.

8. *The location of the hydropore.*—The orientation of the cystids is determined, not by the location of the mouth and anus but by the vertical plane passing through the mouth and hydropore. The hydropore is regarded as occupying a position directly posterior to the mouth. In *Comarocystites* the only surface structure suggestive of an entrance to a hydropore is a narrow, sinuous, almost linear ridge, extending from the middle of the right posterior peristomial plate (Plate II, fig. 1B; also thecal plate rp in text diagrams), across the suture on its lower right-hand margin, to the middle of the adjoining plate. The upper margin of the latter plate is in contact with the posterior margin of that nodular stereom protuberance which supports the right pair of arms. Along the top of the narrow, linear ridge there is a very narrow, faint groove, suggesting the presence of a narrow slit-like opening. Whatever the homology of this ridge, it evidently locates the posterior side of the theca. In several specimens there is a minute pit just beyond the upper left-hand termination of this hydropore ridge; however, since it was not observed in the majority of specimens, it cannot be determined definitely as a gonopore.

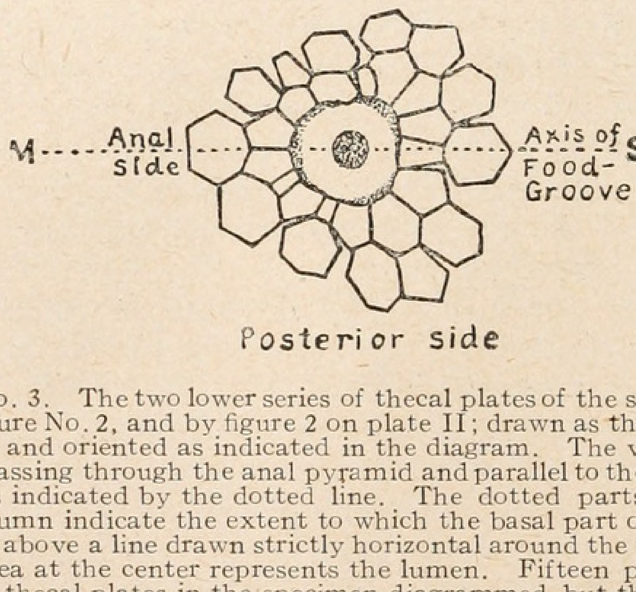
Nothing suggesting a hydropore is known at present in *Amygdalocystites*. In *Canadocystis emmonsi*, however, G. H. Hudson (N.Y. State Museum Bulletin 80, 1905, pp. 273, 274) has figured a possible madreporite at the posterior end of the suture between the two posterior peristomial plates making it possible to orient this species in the same manner as *Comarocystites* with the anal pyramid on the right side of the theca.

9. *The covering-plates of the transverse apical food-groove.*—The transverse apical food-groove is covered by two series of quadrangular covering-plates (Plate II, figs. 1A, 1B, also C), one on each side of the food-groove. These plates meet along the middle line of the food-groove so as to form an acute ridge. They are ornamented by minute granules similar to those of the adjacent thecal plates and there also is a tendency toward a low elevation along the median line of each covering plate. About five covering-plates occupy a length of 3 millimeters along the food-groove. In one specimen 8 or 9 covering-plates occupy the entire distance along the unbranched part of the food-groove, and 3 or 4 covering-plates line each side of that short branch of the food-groove which leads from the left end of the food-groove to the base of the left posterior arm. In another specimen about 15 or 16 covering-plates occur on each side of the unbranched part of the transverse apical food-groove, and 3 or 4 covering-plates line each side of the branches leading from the left end of the food-groove to the bases of the left anterior and left posterior arms.

10. *The anal pyramid.*—The number of plates exposed in the anal pyramid (Plate II, fig. 2; also A in the text diagrams) varies in different specimens from 5 to 6. The general form of the pyramid is semi-globose, but the apical part is more or less flattened. In all of the specimens examined, the anal pyramid is bordered by 5 thecal plates. Of these, two plates form the lower border, one plate occurs on each side, and the fifth plate forms the upper part of the border. The plate on the right side of the pyramid always is larger than the rest. The upper margin of the plate forming the upper border of the anal pyramid is overlapped on each side by a narrow plate separating the latter from direct contact with the base of the nodular stereom protuberance supporting the right pair of arms. The sutures of these overlapping plates often are indistinctly defined. That part of the thecal plates which borders directly on the anal pyramid is smooth, and moderately elevated.

11. *Fixity in arrangement of thecal plates limited to the immediate vicinity of the transverse apical food-groove and of the anal pyramid.*—Evidently there is a considerable degree of fixit in the number of thecal plates bordering on the transverse apical food-groove and in the number of those surrounding the anal pyramid, and there also is an approximation toward fixity in the general outline of these plates; but this fixity in number,

position, and outline usually is absent among those thecal plates not bordering on the transverse apical food-groove or on the anal pyramid. However, certain tendencies may be observed even among these other thecal plates. For instance, the plate directly below the middle of the anal pyramid (Plate II, fig. 2; also text diagrams), but not in contact with the latter, is pentagonal in form, and has its upper angle inserted between the two plates forming the lower border of the pyramid. Directly beneath this pentagonal plate is a series of hexagonal plates which, instead of forming a strictly vertical row, are arranged along a line which curves moderately toward the front on approaching the base of the theca. Parallel to this series of plates, on its anterior side, are similar series of hexa-



Text figure No. 3. The two lower series of thecal plates of the specimen represented by text figure No. 2, and by figure 2 on plate II; drawn as though viewed from the lower side and oriented as indicated in the diagram. The vertical projection of the plane passing through the anal pyramid and parallel to the transverse apical food-groove is indicated by the dotted line. The dotted parts surrounding the top of the column indicate the extent to which the basal part of the lowest series of plates rises above a line drawn strictly horizontal around the top of the column. The dotted area at the center represents the lumen. Fifteen plates occur in the basal series of thecal plates in the specimen diagrammed, but the number varies greatly in different specimens.

gonal plates, causing the anterior side of the theca to present the appearance of diagonally intersecting rows, with the angles of the thecal plates directed toward the top of the specimen. On the posterior side of the theca, a similar tendency toward the arrangement of plates in rows causes one of the sides of the hexagonal plates, rather than one of its angles, to face the top of the specimen.

12. *The arrangement of the basal thecal plates.*—The outline and arrangement of the basal thecal plates, where in contact with the stem or column, varies from 11 to 15 (Text diagram No. 3) in different specimens. The line of contact between the basal thecal plates and the top of the column is not strictly horizontal, but rises and falls in an irregular manner, varying

in different specimens. All efforts to diagram the basal thecal plates of *Comarocystites punctatus* in such a manner as to secure a primary series of 3, 4 or 5 plates has failed, nor is it possible to demonstrate the presence of any radial plan of arrangement of the lower thecal plates, extending outward from a supposed primary basal series.

If any increase in the number of plates forming the theca takes place in any except the earliest stages of growth, this increase in number can take place only at the base of the theca, where in contact with the column. Elsewhere the plates of the theca are almost uniform in size. The series of plates in contact with the column, however, frequently are unequal in size, smaller plates not infrequently being wedged in between larger ones, and the line of contact between the margin of the lowest plates and the top of the column is more or less irregular.

EXPLANATION OF PLATE II.

Fig. 1. Comarocystites punctatus Billings. Specimen belonging to James E. Narraway. A, anterior side, photographed so as to show the thecal plates nearest the transverse apical food-groove, and coverplates on the anterior side of the food-groove; also the position of the anus and of the masses of stereom supporting the two pairs of arms. Several of the plates give distinct indications of the pairs of lunate pores which occur directly beneath the epistereom. B, posterior side, photographed so as to show the thecal plates along the upper half of the specimen, the cover plates on the posterior side of the food-groove, and the linear hydropore passing from the right posterior plate diagonally backward and to the right toward the middle of the adjoining plate. The facet for the support of the left posterior arm and the branch of the food-groove leading to the margin of this facet are well preserved; only a short part of the adjoining branch of the food-groove is seen. The upper part of the mass of stereom on the right of the food-groove has broken off beneath the level of the facets supporting the right pairs of arms. In both figures the anal pyramid is located on the right. C, five of the cover-plates of the food-groove enlarged. D, one the thecal plates enlarged so as to show the indications of the presence of pairs of lunar pores presented by the epistereom in unweathered specimens. A, B, enlarged 3 diameters; C, enlarged 13 diameters; D, enlarged 8 diameters. The form and relative location of the thecal plates of this specimen are indicated in text diagram 1.

Fig. 2. Comarocystites punctatus Billings. Specimen belonging to Walter R. Billings; view of right side, magnified 2.4 diameters. Photographed so as to show the anal pyramid, the thecal plates immediately surrounding the anal pyramid, and the diagonal arrangement of the thecal plates on this side of the specimen. Indications of the transverse apical food-groove terminating at the two masses of stereom supporting the pairs of arms are seen along the upper part of the figure.

Figs. 3, 4. Comarocystites punctatus Billings. One of the brachials and one of the pinnulars of the type illustrated on plate III, magnified. 3, three views of a brachial, magnified 3 diameters; A, cross-section with indication of facet for attachment for the pinnule on the right; B, side opposite the facet; C, side showing the facet. 4, three views of a pinnular, magnified 6 diameters; A, cross-section; B, side opposite the cover-plates; C, side showing three cover-plates along one edge.

(*To be continued*)

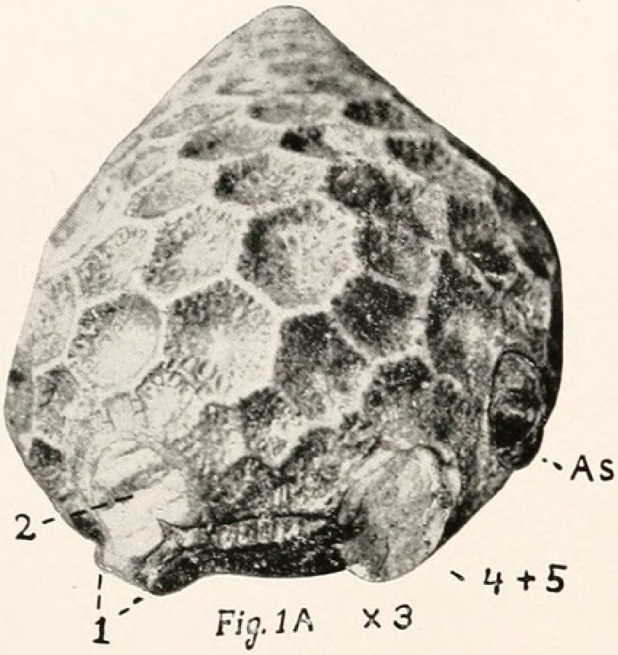


Fig. 1A ×3

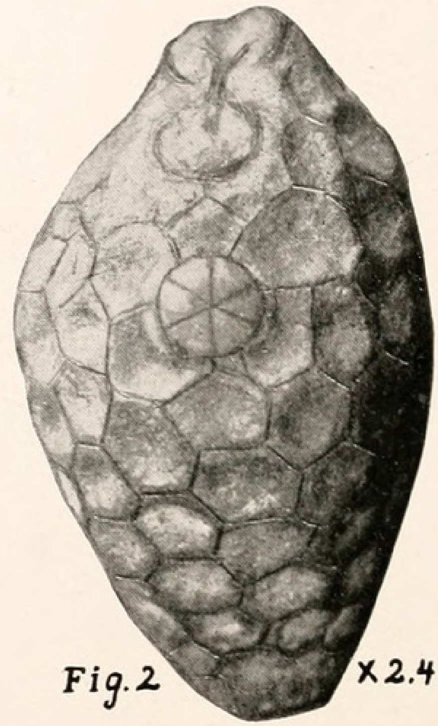
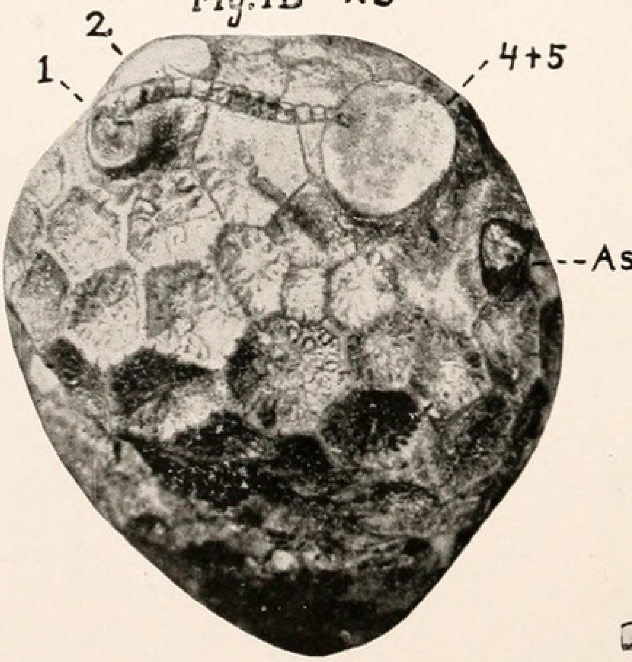


Fig. 2 ×2.4

Fig. 1B ×3



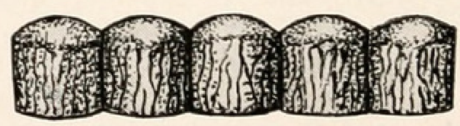


Fig 1C ×13

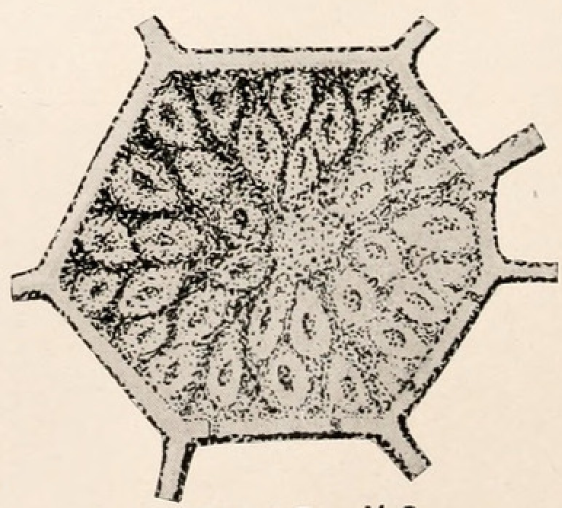


Fig. 1D ×8

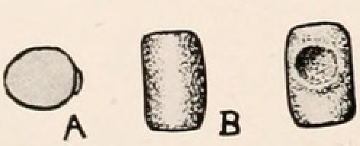


Fig. 3 ×3

Fig. 4 ×6