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NEW SPECIES OF POROCRINIDAE AND BRIEF REMARKS UPON THESE UNUSUAL CRINOIDS

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Volume 22

NEW SPECIES OF POROCRINIDAE AND BRIEF REMARKS UPON THESE UNUSUAL CRINOIDS

ROBERT V. KESLING AND CHRISTOPHER R. C. PAUL

ABSTRACT—Four new species of Porocrinidae include two of *Porocrinus* and two of the new genus *Triboloporus*. Pore structures, exceptional in crinoids, seem to have been functional and used in respiration. Their development at plate corners was related to structural need in the calyx, whereby ridges between plate centers provided strength and rigidity and at the same time freed large intervening areas for the extremely thin, deeply folded goniospires.

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INTRODUCTION

UPON DISCOVERY of a new species of *Porocrinus* among some specimens on loan from the United States National Museum, we became intrigued with the taxonomic position, the functional morphology, and the specific characters of these crinoids. Their unusual combination of crinoid plate arrangement and cystoid-like pore structures was once the subject of speculation by such masters of paleontology as Elkanah Billings, F. A. Bather, and Otto Jaekel. But strangely, few modern echinoderm specialists have added to what was recorded a century ago.

The Middle and Upper Ordovician *Porocrinus* remains an enigma. Equipped with well-developed respiratory structures, crowned with a circlet of five oral plates, and bearing a hydropore, it closely resembles cystoids. Yet the peculiar placement and mode of growth of respiratory structures set *Porocrinus* apart from the rhombiferan cystoids. Its five infrabasal plates and its anal-X and radianal plates are more like those of crinoids than cystoids. The uniserial arms resemble those of crinoids, but they are unbranched. The stem is short, flared proximally, and appears to have been highly flexible with a large lumen, more like that of cystoids than crinoids. So the placement of the family Porocrinidae in the crinoids necessitates modification of the common definition of that class as having many plates in the ventral surface of the calyx and bearing branched arms. Perhaps the Porocrinidae and related echinoderms should be made into a distinct class.

While corresponding with the Geological Survey of Canada, we learned from Dr. G. Winston Sinclair that he and Miss Miriam Steele were actively and seriously investigating *Porocrinus*. And after requesting a loan of comparative material from the University of Iowa, we found that Mr. Harrell L. Strimple also had a continuing interest in the genus. Not wishing to infringe upon projects of long standing, we decided to confine our study to descriptions of some new species and a new genus, with a few pertinent comments on the morphology of Porocrinidae, leaving to others the opportunity to complete their research and reorganization of these echinoderms.

We are extremely grateful to Dr. Eugene S. Richardson, Jr., of the Chicago Natural History Museum for locating and loaning specimens in the collections of the Walker Museum (UCWM) and the Field Museum (FM); to Dr. Tom Bolton of the Canadian Geological Survey for the loan of types of *Porocrinus conicus* Billings from the Survey (CGS); to Mr. Frederick J. Collier of the U.S. National Museum for loan of specimens in the collection of that museum (USNM); and to Dr. Porter M.

Kier of the U.S. National Museum for his courtesy during the visit of the junior author to the Springer Collection in the Smithsonian Institution. Our thanks are extended also to others in our Museum of Paleontology: to Mr. Karoly Kutasi for his photographic assistance; to Mrs. Helen Mysyk for her typing; and to Prof. C. A. Arnold and Prof. E. C. Stumm for their review of the manuscript.

PREVIOUS WORK

More than a century and a decade ago, Elkanah Billings erected the genus *Porocrinus* with these words (1857, p. 279):

> Cup composed of three series of plates, with one or more small interradials on one side, and with a number of poriferous areas similar to the pectinated rhombs of the Cystidea. In this genus there are five pelvic plates [IBB], five sub-radials [BB], and five first primary radials [RR] alternating with each other as in *Poteriocrinus, Cyathocrinus,* and other allied genera.

He adequately described the type species, *P. conicus,* and again directed attention to the pore structures, which he said (1857, p. 279) resembled the "rhombs of the Cystidea in their structure, and probably adapted to performance of the same functions." Billings clearly understood the position of the organs at "the angles of three plates." All things into account, Billings did a clear and concise treatment of *Porocrinus*.

Two years later, Billings repeated his description of *Porocrinus* (1859, p. 33) and its type species *P. conicus* (1859, pl. 2, figs. 5a–5d). Some of his figures leave ample opportunity for improvement, as we discovered in comparing the type specimens against his plate.

Not long afterward, Meek & Worthen introduced two new species, *Porocrinus crassus* (1865, p. 145) and *P. pentagonius* (1865, p. 146). Just as Billings had done with *P. conicus,* they repeated their descriptions in a subsequent publication and published the first illustrations. In 1868 they dealt again with *P. crassus* (p. 330; pl. 4, figs. 2a, 2b) and *pentagonius* (p. 332; pl. 1, fig. 3) in the Geological Survey of Illinois. Meek & Worthen started the suggestion of *Porocrinus* as a missing link, going beyond the simple comparison of Billings; they said (1865, p. 145), "So it would seem this genus presents, as it were, a combination of the characters of the typical *Crinoidea* and *Cystoidea*."

Beyrich, variously known as Ernest, Heinrich Ernst, and Ernst Heinrich von, described *Porocrinus radiatus* from a crushed specimen found in Russia (1879, p. 60–63; text-fig.). His details of plates convince us that his crinoid was really a *Porocrinus*. Because, as discussed below, this specimen was awarded a special position of importance by Jaekel, we treat Beyrich's short article at length. He mentioned four RR (and said there was doubtless a fifth R), described the RA, and counted four BB, the position of a possible fifth B being crushed. His figure is clear, showing normal *Porocrinus*-type RR, BB, and IBB in the A, B, and E rays; in his sketch, the calyx plates are depicted as ridged and poriferous, much like those of *Porocrinus fayettensis* (our text-fig. 13). Beyrich reported on goniospires at the B-B-R and B-R-R plate corners, and did not rule out the possibility that they might also be present where the base of the calyx was missing.

It must be remembered that his specimen was incomplete and crushed, as Beyrich himself openly and explicitly acknowledged (1879, p. 61):

> Die Basis ist verdrückt und wird zugleich mit der Stelle, wo das fünfte Parabasalglied seinem Platz hätte, von einem unregelmässig gestalteten Körper eingenommen, welcher vielleicht der eingebrochenen Kelchdecke angehört.

Beyrich did introduce what we believe to be an error, one which was magnified by subsequent authors until it assumed generic significance. It concerns whether the corner pore areas are parts of the calyx plates or separated from them. Beyrich encountered some difficulty about the nature of the goniospires. His statements near the first and last parts of his article seem at variance. On page 61 Beyrich stated:

> . . . hätten die Porenfelder am *Porocrinus* die Form von sphärisches Dreicken, welche die Ecken, wo 3 Platten des Kelches aneinanderstossen, einnehmen, mit Schlitzen die senkrecht gegen die Seiten des Dreiecks und somit schief gegen die Verbindungsnähte der Kelchplatten gestellt sind.

This we translate in substance: the pore-areas of *Porocrinus* have the shape of spherical triangles, which occupy the corners where three calyx plates meet, with slits oriented perpendicular to the sides of the triangle and therefore oblique to the sutures of the calyx plates. In this Beyrich accurately described the arrangement of plates in *Porocrinus*. But on pages 62–63, Beyrich conceived of a suture across the corner of each plate, passing through the pore slits:

> Die einzelnen Porenfelder bestehen nicht blos aus Theilen der Kelchglieder, so dass einfach nur die Verbindungsnähte der umgebenden Kelchglieder in der Mitte je eines Porenfeldes zusammenstossen, sondern auch den Seiten der

> sphärischen Dreiecke entsprechen sehr deutlich zu sehende Nähte. Die senkrecht gegen die Seiten des Dreiecks gestellen Porenschlitze erreichen in diesen Nähten nicht ihr Ende, sondern greifen über dieselben fortsetzend noch in die Substanz der ungetheilten Kelchglieder ein.

In this, Beyrich possibly mistook the borders of the depression containing part of the goniospire for plate sutures. Beyrich failed to clarify whether the little segment within the spherical triangle and reaching to the middle of each goniospire should be considered part of the calyx plate (as indicated on his p. 61) or separated from the plate by a suture (as indicated on his p. 62–63).

Beyrich also gave the first of many repetitions of Meek & Worthen's linkage of cystoids and crinoids through *Porocrinus,* stating (1879, p. 63), "Die Gattung *Porocrinus* ist von hervorragendem Interesse als ein merkwürdiges Bindeglied zwischen Cystideen und normal Crinoideen."

In the same year, Karl A. von Zittel brought forth his great book on invertebrates. He was aware of Beyrich's work, for he reproduced the latter's text-figure. He interpreted Beyrich's description to mean (1879, p. 420) that each third of the pore structure lay half on a calyx plate and half on a little "Supplementtäfelchen" at the corner. With some misgivings about the taxonomic position of *Porocrinus,* Zittel included it with question in the family Encrinidae of the suborder Articulata in the crinoids (p. 384) and without question in the group Rhombiferi in the cystoids (p. 420), explaining that (p. 420): "Diese Gattung bildet ein Verbindungsglied der Cystoideen mit den Eucrinoideen."

In his Grundzüge (1895), Zittel gave about the same diagnosis of *Porocrinus* that he had in 1879; his analysis of plate distribution was correct and evidently adapted from Billings and from Meek & Worthen. The genus did not fare as well in later editions of this work. In the first edition of the Eastman translation and revision (known as the first Eastman-Zittel), Wachsmuth (1900, p. 184), misled by Beyrich's incomplete plate diagram (which Wachsmuth reproduced as fig. 304), stated, "Base composed of three plates. . . . Small supplementary pieces furnished with pore-rhombs intercalated in the re-entrant angles between the calyx plates." The second sentence may have influenced Jaekel two years later to create the genus *Perittocrinus*. Then in the second Eastman-Zittel, Springer (1913, p. 217) introduced: "Arms ten, unbranched. Calyx plates deeply folded at the engles, but folds do not cross the sutures or form true pore-rhombs." He placed *Porocrinus* in the subfamily Carabocrininae of the family Cyathocrinidae.

In 1894 Miller & Gurley (p. 24) created the family Porocrinidae thus:

> This family has five basals; five subradials; one by five radials; no regular interradials; small arms; and deep pits and pectinated rhombs, at the angles of the plates. It resembles, in its general structure, the *Cyathocrinidae,* and *Poteriocrinidae,* but the azygous area is not like that of any other known genus and the pectinated rhombs are like those belonging to *Cystideans.*

Miller & Gurley have been generally overlooked as the authors of the family.

Bather in Lankester's *Treatise* (1900, p. 172) wrote: "Deep folds lie at the angles of all thecal plates, directed towards the angle, . . . thus differing from hydrospires of Eublastoidea and from pectinirhombs." He placed *Porocrinus* in the family Palaeocrinidae, where it is retained by many paleontologists today. Grabau (1909, p. 473) thought the genus belonged in the cystoids.

In 1902 Jaekel introduced the genus *Perittocrinus* is a most informal manner (p. 1092–1099); he also (1902, fig. 27) presented a plate diagram of his new genus and sketches of hypothetical stages leading to the goniospires of *Porocrinus*. This figure has been copied many times and commented upon by other authors. His lack of systematic presentation makes it very difficult to separate what Jaekel saw from what he interpreted. Nowhere in the discussion did he mention how many specimens he had, where they were deposited, nor which was the type species. One can deduce that it was *Porocrinus radiatus* only because Jaekel contrasted his own representation with that of Beyrich (1902, p. 1095). Jaekel exalted *Perittocrinus* as the form through which camerate crinoids evolved into inadunates. For the embodiment of such a unique and significant taxon, it seems to us that *Perittocrinus* has rested upon a deficient and remiss basis from its inception. This is discussed further below under Jaekel's more widely known work on classification of crinoids.

Edwin Kirk studied numerous fossil pelmatozoans for their way of life. Noting the marked similarity of the proximally flared columns in *Porocrinus* and cystoids, he concluded (1912, p. 57): "In all probability we may consider that the members of this genus led the existence of vagile benthos and attached themselves at will by wrapping the distal portion of the stem about some object."

George H. Hudson was the first to look at details of *Porocrinus* respiratory structures from a functional viewpoint. He made some astute interpretations, both on the sequence of pore formation and on structural considerations of the calyx (1915, p. 163):

> In *Porocrinus* each hydrospire is situated at the junction of three plate corners, the folds meet the sutures at an acute angle (for they are parallel with radii running to the plate corners), the oldest folds lie nearest these corners and pressure on their elongated and therefore weakened walls is prevented by a heavy epithecal bar of stereom which crosses and strengthens the middle portion of each suture.

Hudson proposed that the unique structures in *Porocrinus* be given a special name (1915, p. 164):

> . . . the "triangular pectinirhombs" of *Porocrinus* might be called *goniohydrospires,* but as in all types of echinoderm respiration water is the medium through which oxygen is received, we might shorten the term, without loss, to *goniospires.* This name would be appropriate not only because of the position of these hydrospires at plate corners, but also because the folds themselves are bent abruptly through an angle of about 60 degrees as they cross the sutures.

Hudson then (p. 166) offered a classification of respiratory structures in echinoderms. All structures were called *endospires* (formed by invagination) or *exospires* (formed by evagination); endospires were divided into *simple hydrospires* (formed by regular thecal plates) and *flowing hydrospires* (formed by thecal plates associated with food grooves); simple hydrospires included *goniospires* (at plate corners as in *Porocrinus*) and *craspedospires* (at plate margins as in rhombiferan cystoids); and flowing hydrospires included *anaspires* (flowing orad as in eublastoids) and *cataspires* (flowing aborad as in parablastoids). His exospires were divided into *papulae* and *podia.* Hudson even considered circulation, for he stated (1915, p. 166) that "the simple hydrospires no doubt possessed ciliated fold-surfaces."

Hudson also reported a modification of the respiratory structures in *Porocrinus smithi* Grant (1915, explanation of his pl. 2):

> During growth the plate was strengthened by the spreading and thickening of the epistereom over the plate center and along the bar crossing the middle of each suture. This spreading epistereom formed and maintained linear series of small pores, about 0.1 mm in diameter, lying over and communicating with the external chambers in the covered and older portions of the hydrospires.

Hudson is the only person to observe such secondary deposits; we have looked for them in specimens described herein without success.

Because Jaekel introduced several novel concepts in the evolution of crinoids, we quote his remarks at some length (1918, p. 46; our translation and conversion of plate terms):

> The viscera, primarily depressed in the lowest part of the calyx, enter the rectum at the base; here the curvature of the rectum can be recognized by the oblique solar interposition of a few anal plates. Hence, at this place, in contrast to the anal field of the Cladocrinoidea, normally two anal plates are diagonally interpolated in the calyx, an X in the circlet of RR and an askew-lying RA to the left under the R of the C ray; occasionally, in the case of larger anal tubes, an X_2 (paranal) is added between X and the R of the C ray. In post-Paleozoic time these anals are pushed entirely out of the calyx and appear only in young forms.
>
> All things considered, it seems to me that the transition from Cladocrinoidea to Pentacrinoidea is negotiated through *Perittocrinus* from the Petersburg Lower Silurian [Ordovician]. This important form, which I described in 1901 and of which I later discovered a little species still more primitive, has not yet been adjudged worthy among the echinoderms, although in morphologic and systematic value alone it need not take second place to an *Archaeopteryx.* On the whole, it is perhaps the most interesting transition form because it not only binds two divergent classes, but also the course of its transformation is obvious with mathematical precision. In 1901 I precisely interpreted the nature of its evolution, so that I will here only mention that the iBrBr plates, which distinguish the calyx structure of the Cladocrinoidea, are here suppressed. They are crowded in the angle between the plates, which would then be the RR and BB of the Cladocrinoidea. That these little three-cornered platelets here are no new structures is demonstrated by their pore rhombs, which can be interpreted as an earlier system of tension rods that unite equal-valued plate centers like a sort of axle-iron. The same rod systems reappear at the same place in the somewhat younger *Porocrinus* and the dwarfing of the intervening plates is attained therein to the conclusion. At the same time the calyx is pentamerally regulated, the number of BB increased from 4 to 5 and the 8 groups of little upper stem elements of *Perittocrinus* are fused to form undivided IBB. These last are also here removed from the uppermost segment of the stem, which in lower forms was plated with many little platelets as a hollow tube. The RR of the Pentacrinoidea are probably derived from the PBrBr of the Cladocrinoidea, the OO from an upper or middle iBr, while the uniserial nature of the arms and their original isotomous bifurcation are thereby clear, inasmuch as these lower arm parts in the Cladocrinoidea were still simple R-PBr rows. The transformation process consists also in the reduction of the crown in its lower, ontogenetically older part, as we found

> already in *Lichenocrinus* [now interpreted as a plated holdfast and not a calyx] in the Cambrian and in *Parothocrinus* [now interpreted as a crinoid abnormality] in the Lower Silurian [Ordovician]. As *Porocrinus* was then the prototype of the younger Pentacrinoidea, and itself already entirely a member of the Cyathocrinoidea, so is manifested also the evolutionary significance of its ancestor *Perittocrinus* in the atavistic reversion of a group of aberrant Pentacrinoidea (*Heterocrinites* and others).

For discussion of Jaekel's intriguing ideas, let us point out that for the most part his Cladocrinoidea = Moore & Laudon's (1943) Camerata, and his Pentacrinoidea = their Inadunata and Flexibilia.

As was his custom in classification of echinoderms, Jaekel proposed an ancestral "Vorform." For the inadunate crinoids, he selected *Perittocrinus* as the "Vorform," sacrosanct and not assigned to a particular taxon. His derivation of *Porocrinus* from his genus *Perittocrinus* was a grand effort to explain the unusual tripartite pore structures of the former as evolving from three pectinirhombs in the latter. Nevertheless, we raise doubts that the IBB of *Porocrinus* originated suddenly from fusion of columnal elements, that 16 small pore-bearing platelets and an accessory plate below X disappeared simultaneous with the appearance of an additional B, and that the result was the extremely regular plate arrangement which characterizes nearly all of the dicyclic inadunates.

Serious question concerns the reality of *Perittocrinus*. Jaekel's reasons for creating *Perittocrinus* for *Porocrinus radiatus* Beyrich are abstruse. From his publications, we have no evidence whether Jaekel had an opportunity to study the type specimen or whether he relied entirely on Beyrich's and other accounts. As we understand it, he regarded the goniospire areas in Beyrich's text-figure (1879, p. 62), each of which was enclosed by three arcs to represent supposed sutures, as separate tiny calyx plates without division into three parts by sutures meeting at the center. Jaekel did not believe that in each corner area the pore slits continued from one major calyx plate into another. Furthermore, he seems to have interpreted a dislocated B as a kind of RA and to have interpreted broken IBB as columnal elements, as indicated in his figures (1902, fig. 27; 1918, fig. 36) and his comments (1902, p. 1093–1097; 1918, p. 46–48) on *Perittocrinus*. As for Jaekel's second species of the genus, *Perittocrinus transitor,* he neglected to describe it except for brief remarks in the explanation of his figure (1918, fig. 37); his illustration shows, besides his reconstruction of a crown, seven isolated plates in which the poriferous corners seem to be broken or weathered away to produce an abnormal outline and to form false corners at the plate sides toward which the ridges are directed.

Without wishing to be inimical to Professor Jaekel's great work on pelmatozoan echinoderms or disparaging of his observations, we cannot avoid a conviction that his *Perittocrinus* is more illusory than real, a singular interpretation of Beyrich's description of a distorted specimen. Unquestionably, Jaekel was influenced by Beyrich's statement of a "sphärisches Dreieck" set off by sutures and by Zittel's remarks about "Supplementtäfelchen." Unfortunately, Beyrich's type and only specimen of *Porocrinus radiatus,* which could perhaps yield new information under microscopic examination, is not likely to be located for even as he wrote in 1879 it was in the private collection of Leopold von Buch.

For the sole genus *Porocrinus,* Jaekel (1918, p. 50) created the family Porocrinidae (evidently unaware of Miller & Gurely's earlier authorship), which he diagnosed as having unbranched arms, X and RA plates, no anal tube, and "Porenfalten" in the plate corners.

Otto Abel (1924, p. 277, fig. 412) presented a digest of Jaekel's 1918 conclusions regarding *Perittocrinus* as the direct ancestor of *Porocrinus*.

In the same year that Jaekel's work on classification of Pelmatozoa appeared, Yakovlev (1918, p. 26) stated:

> *Perittocrinus* Jaekel cannot be regarded as the representative of a special genus, but should be looked upon as an anomalous specimen of a crinoid belonging to the group of Monocyclica, and signifying the origin of these Feather-Stars from the *Cystoidea Rhombifera* by means of atrophy of *three* cycles of plates belonging to the dorsal theca.

We agree that *Perittocrinus* does not seem to warrant generic status, but ascribe a different reason. The holotype of the type species may not be "anomalous" but simply deformed by poor preservation. If, as we suspect, it is actually a *Porocrinus,* then Beyrich's partial plate diagram showing IBB plates is correct and the specimen is dicyclic and not a member of the "Monocyclica." Yakovlev (1918, p. 25) also supported the evolution of crinoids from cystoids by a "tendency to replace the pore-rhombs as respiratory organs by the development of arms."

For the most part, publications of *Porocrinus* in the last half century have concerned the placement of the genus in the family Palaeocrinidae, following Bather's 1900 classification. These include Bassler (1938, p. 156), Bassler

& Moodey (1943, p. 636), and Moore & Laudon (1943, p. 50).

In brief review, our knowledge of *Porocrinus* stems primarily from the efforts of Billings (1857), Bather (1900), and Hudson (1915).

PATTERN OF CALYX PLATES

The Porocrinidae show remarkable constancy in the pattern of their calyx plates, even though anomalous specimens are known. Each species has the same basic pattern: the flared proximal end of the column supports a circlet of small IBB, which is successively followed by circlets of larger BB, RR + X, and OO (text-figs. 11–13). The RA plate is diamond-shaped, as in many other dicyclic inadunates, and so small that it does not interrupt either the RR + X circlet above or the BB circlet below.

The IBB are pentagonal as viewed laterally; but in specimens from which the column is missing it can be seen that the sides converge toward the aboral pole on the stem facet and that each IB, therefore, is essentially four-sided. Proportions of IBB vary from species to species, and to a degree within a single species, some relatively high as in *P. conicus* (text-fig. 11) and some very low as in *P. shawi* (text-fig. 14). Generally, the IBB unite to form a plane surface for the stem cicatrix, but in some examples (text-fig. 12) the edges are serrate or fluted to fit closely against the similarly shaped proximal columnal.

The BB of the AB, AE, and DE interrays are similar and hexagonal, each plate bordered by two IBB, two BB, and two RR; the BB of the BC and CD interrays, however, are septagonal, the former bordered by two IBB, two BB, two RR, and RA, and the latter bordered similarly except that X is substituted for one R.

X is relatively small and pentagonal, inserted in the RR circlet and forming the lower edge of the periproct.

RR are hexagonal, all similar except that those of the C and D rays have corners indented to border the periproct. The arm facets are variously elevated in each species; they are small and low in *P. conicus* (text-fig. 11) and large and raised in *P. fayettensis* (text-fig. 13) and *P. elegans* (text-fig. 9).

The OO developed as plates equivalent in size and development with the RR, not set off as a tegmen. Posterior O larger than the others, with a conspicuous embayment along the upper side of the periproct. All OO definitely in contact around the mouth opening, with radial ambulacral grooves along their sutures. Posterior O with hydropore discernible in some specimens.

Four anomalies have come to our attention. First, the holotype of our *Porocrinus elegans* (text-fig. 9) has a supernumerary little quadrate plate inserted between X and R of the C ray; to accommodate the extra anal, the RA is pentagonal (pl. 3, figs. 5, 6). The extra plate has ridges to the bordering X, RA, and R plates, but it has a goniospire only at its junction with RA and R. Second, USNM 42196c, a specimen of *Porocrinus fayettensis,* has only four IBB; on the exterior of the calyx the fusion is difficult to detect because the large IB is developed completely as two normal IBB, but the stem facet reveals only four sutures. A small card accompanying the specimen bears the following in E. O. Ulrich's script: "*Porocrinus* ? (n. gen. ?) cf. *P. crassus* M & W. with 4 infrabasals—2 fused, also seems to have pentagonal stem. Richmond gr. Mill 1 mile NW of Ft. Atkinson, Iowa. This looks to me more like a cystid than a crinoid. E.O.U. 206R."

Third, a specimen in the U. S. National Museum, one of four catalogued as S2306, is questionably identified as *P. pentagonius;* the locality is given as "12 miles NW of Clermont, Iowa, Trenton." We suspect that it is *P. fayettensis*. Several features are unusual. The calyx is large, globular, and nearly free of ridges. The IBB of the A and E rays are pentagonal and normal; only two others are present, both large and hexagonal. Two supernumerary plates are intercalated in the BB circlet in the BC interray, one above the other: the smaller plate is pentagonal, its aboral apex inserted between the two abnormal IBB and its sides against two BB; the larger plate, approaching the size of a normal B, is hexagonal, bordered by the small supernumerary, two BB, 2 RR (B and C rays), and RA. By the insertion of the extra plates and the abnormal form of two IBB, the BB of the AE, CD, and DE interrays are scarecly affected; but the B of the AB interray is hexagonal, its horizontal base atop one of the enlarged IBB, one side adjacent to the B of the AE interray, the opposite side acuminate between the supernumeraries, and its top between RR of the A and B rays; and the B of the BC interray is displaced posteriorly to lie above the second hexagonal IB, reaching to X and RA, and bordered by B of the CD interray on one side and by the supernumeraries on the other, hence hexagonal in outline. The RA is nearly square but set somewhat askew from its normal orientation, bordered by X, R, B, and one of the spernumeraries. X is hexagonal, abnormal in having a junction with the displaced B of the BC interray. We find it difficult to determine the plate analysis in this calyx; perhaps the lower supernumerary is actually the fifth IB, displaced upward from its junction with the column and out of the circlet.

The fourth anomaly occurs in the holotype of *Triboloporus cryptoplicatus* n. sp. (text-fig. 7). One ambulacrum completely aborted, so that no arm grew from the R of the B ray (pl. 1, figs. 1, 4). Two OO appear to be fused in the AB and BC interrays, the one large plate bearing parts of two goniospires and extending from one interray into the other. The posterior interray, however, has two OO instead of one, with an apparent hydropore in the plate nearer the D ray (pl. 1, figs. 2, 8). Perhaps one O plate became displaced from the BC interray into the CD interray, whereupon the adjacent O grew to fill the available space and the ambulacrum of the B ray failed to develop because of the shift of the O-O suture into the posterior interray.

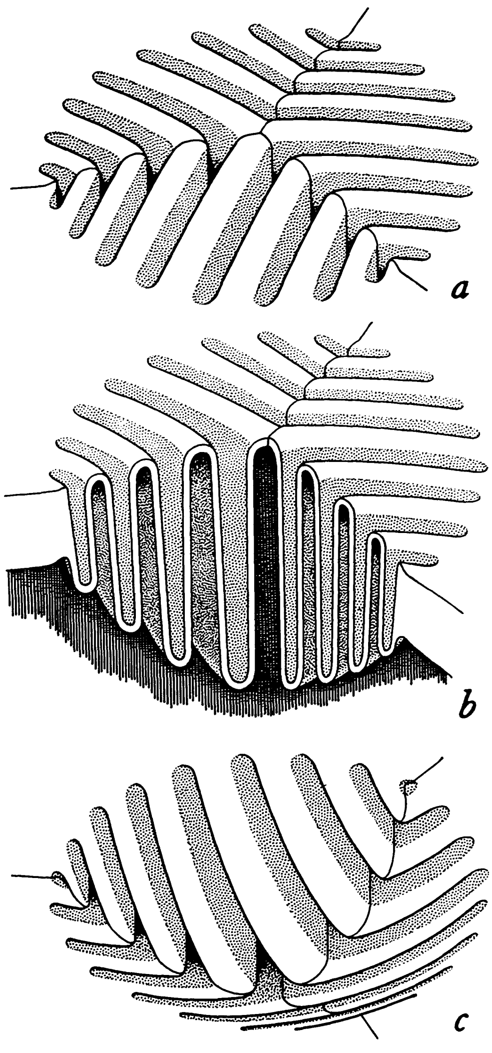
These departures from normality are similar to those known in other crinoids. Nevertheless, the same basic pattern of plates does occur in all species and in the majority of specimens.

GONIOSPIRES

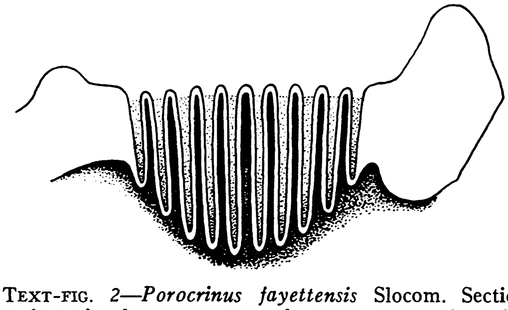
These unusual respiratory structures (text-figs. 1–3) have received much attention from a taxonomic standpoint and relatively little from a functional standpoint. Whether they are significant at the suprafamilial level remains to be decided, but at present they are disregarded. As succinctly summarized by Ubaghs (1953, p. 690–692; fig. 33), goniospires are only one type of calycinal respiratory structures which are found in several early crinoids and occur sporadically in later Paleozoic inadunates and camerates.

That these structures were respiratory seems a reasonable and warranted inference. This was suggested and supported by many students of *Porocrinus*. The clearest and strongest statements were those of Hudson (1915), who set up the classification of echinoderm respiratory structures and proposed the term goniospire.

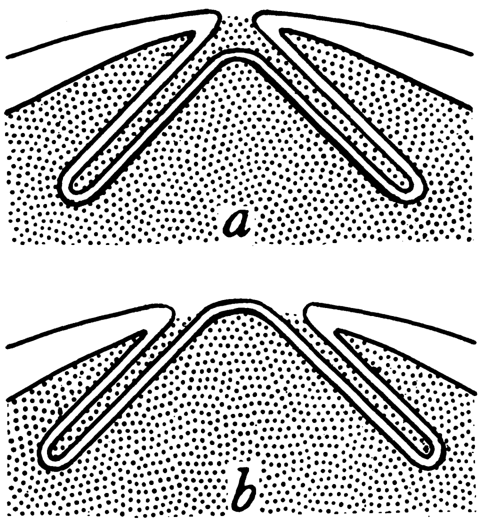
Each goniospire consists of three sets (six half-sets) of folds at adjacent corners of three calyx plates. These structures are endothecal, the folds extending into the calyx. The folds of the two half-sets on any one calyx plate are directly connected to those of one half-set each on the other two calyx plates (text-fig. 1a). Exposed parts of the folds are ridges, and the inner parts are troughs; each ridge and each trough is geniculate at the plate suture, bent at an angle of about 120°. In *Triboloporus* each half-set consists of one fold only (text-fig. 3), whereas in *Porocrinus* each half-set has several folds (text-figs. 1b, 2).



TEXT-FIG. *1*—Idealized goniospire of *Porocrinus*. *a*, as viewed obliquely from exterior. *b*, as viewed obliquely from exterior with one plate removed to expose deep folds; plate junctions are sites of confluence for three ridges. *c*, as viewed obliquely from interior of calyx; median elements expressed on interior as troughs.



TEXT-FIG. *2*—*Porocrinus fayettensis* Slocom. Section through plate corner to show structure of goniospire; section through R of C ray near R-X-RA corner in USNM 42196. High ridge at right borders periproct.



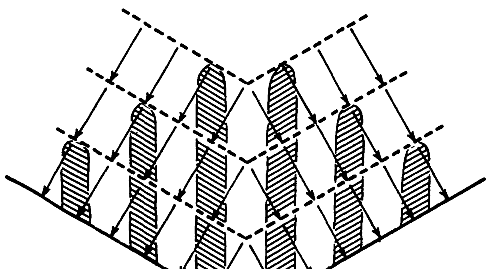
TEXT-FIG. 3—*Triboloporus* n. gen. Diagrammatic sections through plate corners to show structure of goniospires in *T. cryptoplicatus* n. sp. (*a*) and *T. xystrotus* n. sp. (*b*).

As seen in cross section through a plate corner (text-fig. 2), each third of a goniospire consists of thin folds of plate material. Presumably, gaseous exchange was possible through the organic tissue in the thin calcareous folds and the covering integument or skin, providing entry for oxygen and discharge for carbon dioxide and other wastes.

Growth and development of goniospires was a complicated process. Although the goniospires of the Porocrinidae and the pectinirhombs of the rhombiferan cystoids are both endothecal hydrospires, they were formed quite differently. As Hudson astutely pointed out many years ago (1915, p. 163–164), the first-formed fold in a goniospire was at the corner of the plate and folds were added in succession toward the middle of the plate side, whereas in pectinirhombs the first-formed fold was at the side of the plate and folds were added in both directions toward the plate corners. All echinoderm plates grow by extension of calcareous elements normal to the plate sides; to prevent the plate from becoming a set of radial bars from the center and to maintain the shape of the plate, new material is added in the corner areas as parallel calcareous elements. Growth lines and microstructures of echinoderm plates show this mode of growth to have been the same in crinoids, cystoids, and all other groups that have been investigated. In pectinirhombs (text-fig. 4b) the folds elongated by simple addition of calcareous material on each side of the suture. But in goniospires (text-fig. 4a), in which folds were not perpendicular to the sides of the plate, the folds elongated by extending into new calcareous elements. They required continuous adjustment relative to the growth direction of the plate. The first appearance of a goniospire, therefore, was a triad of thin spots at the meeting corners of three plates. This was the set of incipient median ridges. As each plate enlarged, the spot on the corner shifted into the new calcareous elements being formed. At the same time, the sides of the spot were turned inward to start the bordering troughs. The process was repeated periodically in the case of *Porocrinus,* with the result of evenly spaced and parallel folds.

To have been effective, the Porocrinidae must have developed some pattern of circulation whereby a fresh supply of water was introduced continuously into the goniospire to replace that from which the oxygen had been extracted. Circulation presents a problem in topology and graph theory, reminiscent of Euler's famous problem of the bridges across the river Preger at Königsberg.

If goniospires operated in the manner presumed for pectinirhombs in cystoids, one end of each complete trough would have been the adit for sea water and the opposite end would

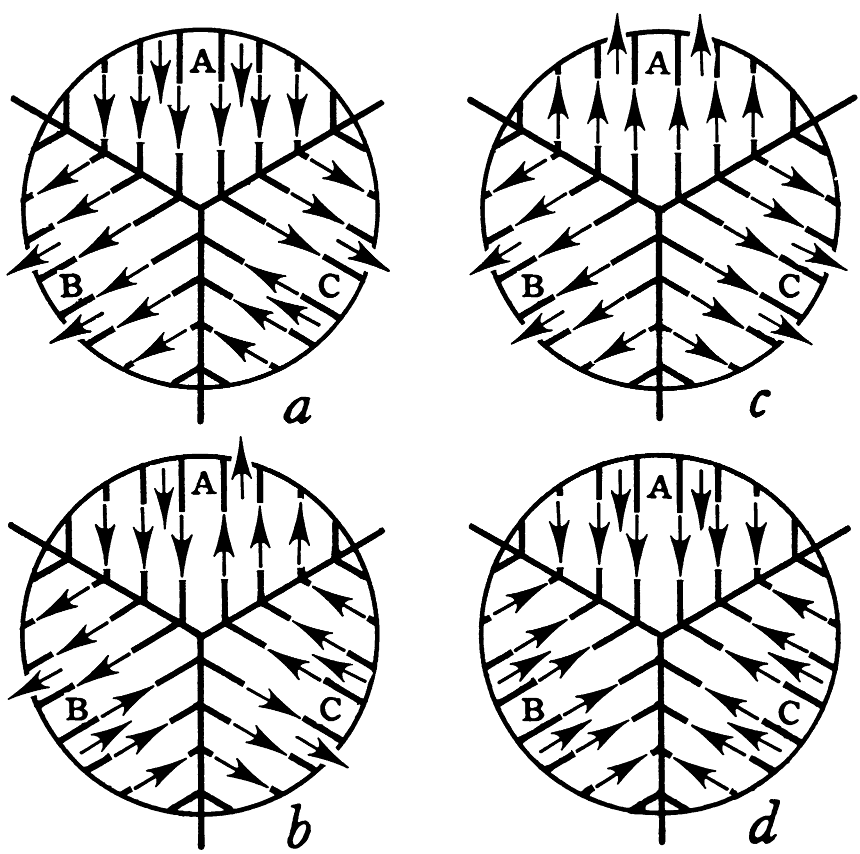


TEXT-FIG. 4—Contrast in growth and development between goniospire of porocrinoid (*a*) and pectinirhomb of cystoid (*b*). Heavy line represents plate edge, dotted lines represent growth lines, and arrows indicate directions of growth. First-formed fold in goniospire is nearest the corner, but in pectinirhomb is nearest middle of plate side. Folds in goniospires require continuous adjustment relative to growth directions, but those in pectinirhombs do not.

have been the exit. There are two possible flow patterns in such an arrangement. Either all three plates had both sets of adits and sets of exits (text-fig. 5b) or one plate had both sets (plate C in text-fig. 5a), with one of the other plates having only adits and the third plate having only exits. Recirculation of deoxygenated water could easily occur in either case because of the close proximity of adits and exits in at least one plate. Both flow patterns, therefore, would have been inefficient.

The circulation in goniospires may have differed from that in pectinirhombs. If, as we suppose, the two kinds of calycinal respiratory devices evolved independently, there is no reason to assume that their circulatory patterns were comparable. The only alternative flow patterns have all the water either entering or leaving around the periphery of the goniospire (text-figs. 5c, d). The former would seem to have imparted certain advantages (text-fig. 5d) since oxygenated water would be drawn in from a wide area and a strong united excurrent would force used sea water away from the calyx, reducing the chances for recirculation.

The thinness of the goniospire folds made them areas of weakness in the calyx. In *Porocrinus pyramidatus* (pl. 5, figs. 3, 5, 6) the centers of the goniospires were raised and ideally constructed for the suggested flow pattern, but the delicate folds were exposed and liable to mechanical damage. All other goniospires seem to fall into three groups exemplified by *Triboloporus, Porocrinus conicus,* and *P. shawi.* (1) The reduced goniospires of *Triboloporus* species probably did not weaken the calyx appreciably. Even so, the folds in *T. cryptoplicatus* were entirely internal and hence protected, leaving only three narrow clefts at the surface of each goniospire. (2) In *Porocrinus conicus* the weakness



TEXT-FIG. 5—Possible flow patterns in goniospires. Two major patterns involve flow through entire troughs (*a, b*) and through half-troughs only (*c, d*). *a,* all troughs of plate A admitting water, all troughs of plate B expelling water, and half of troughs of plate C admitting, half expelling water; reversal of flow direction on one plate only. *b,* half of troughs on each plate admitting water, half expelling water; reversal of flow direction on all plates. *c,* water admitted along plate sutures and expelled at periphery of goniospire. *d,* water admitted around perphery of goniospire and expelled along plate sutures; this pattern seems the most efficient to avoid recirculation of used water.

of the relatively small goniospires was probably compensated by the thickness of the calyx plates, and the spire areas were protected by being depressed into the plates. (3) In *Porocrinus shawi* and several related species the very large goniospires were separated by highly developed ridges which formed a rigid geodesic girder system. The strength of the calyx lay entirely in the girder system and the goniospires gained protection by the raised ridges. Depressed goniospires, which seem poorly adpated for the suggested flow pattern, may have evolved as a protection for the fragile goniospire folds.

No direct evidence is available on the distribution of oxygen internally by the body fluids. For increased interchange of oxygen and wastes, however, the body fluids may have been directed opposite to the flow of sea water outside; thus, if water entered the troughs at the ends and was expelled at the centers, the body fluids may have diverged from the plate junctions. It must be borne in mind that external goniospire ridges (text-fig. 1a) are the bases of internal goniospire troughs (text-fig. 1b, c).

The even distribution of goniospires over most of the surface of the calyx suggests that no definite circulation system was necessary internally. It appears likely that the inner surface of the folds bore cilia, whose agitation was adequate to oxygenate vital organs. The close spacing of the folds in *Porocrinus* probably necessitated some internal ciliary currents to change the body fluids in the same manner that external currents were required to replenish de-oxygenated sea water within the troughs.

Some differential development of goniospires indicates that they developed normally only when freely exposed to sea water. One specimen of *Porocrinus conicus* (CGS 22888) has one side of the calyx flattened; on this side the goniospires are represented by small depressed areas without folds (text-fig. 12; pl. 7, figs. 1, 4). The association of flattening and underdeveloped goniospires may well have resulted from the stem becoming detached at an early stage of growth, the calyx lying prostrate on the sea floor, and goniospires on the under side being "smothered" by sediment.

The holotype of *Porocrinus pyramidatus* (USNM Acc. 238630) has goniospires in the B and C rays underdeveloped or aborted (text-fig. 10; pl. 5, figs. 1, 2; pl. 6, fig. 7). At the B-B-R corner of the B ray and at the R-R-B corner of the BC interray, only raised median ridges represent the goniospires, which completely lack internal folds. The structure at the R-X-RA corner is small and similarly stunted except that small pores can be detected at the margins of the RA and adjacent plates. Only a shallow depression occurs at the R-B-RA corner. At one R-R-B corner, folds are present from the B of the AB interray onto the R of the A ray, but none can be found in the other two-thirds of the corner area.

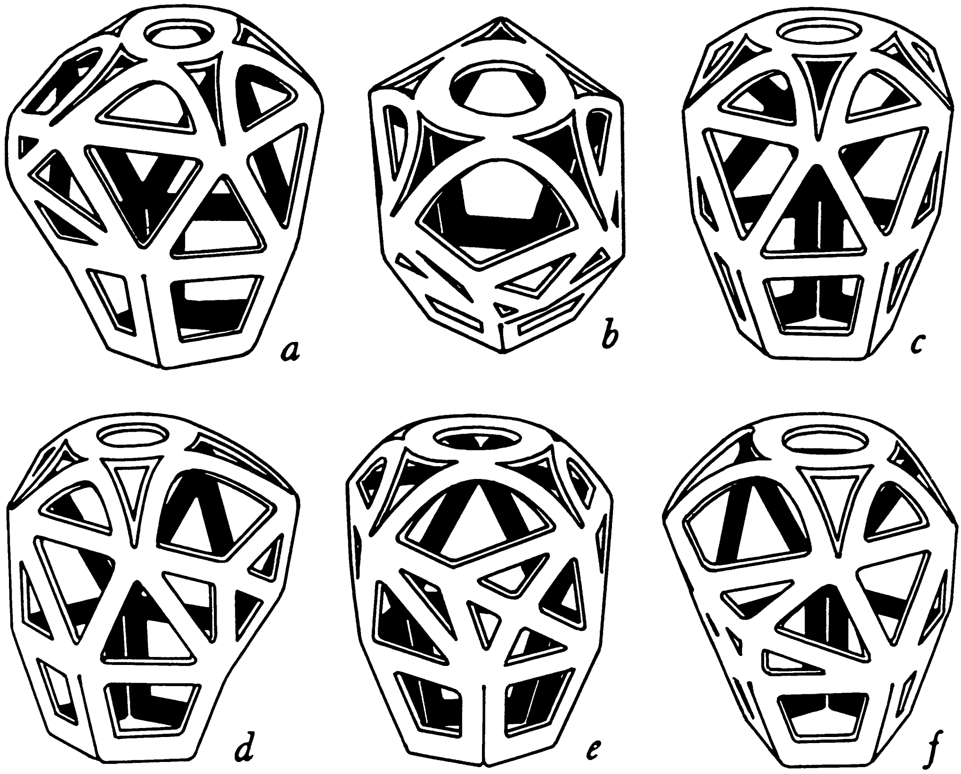
Thomas & Ladd (1926, p. 16; pl. 2, figs. 10–13; pl. 5, fig. 6) described and illustrated a similar specimen of *Porocrinus fayettensis* in which the median goniospires were characterized by prominent median folds and troughs "reduced to two, one or none," the reduction being strongest "especially on the right side."

Such anomalies make us wary of using details of individual goniospires as specific characters. Instead, it seems to us, the nature of goniospires in a species is expressed by the development of what could be termed "normal" structures, the largest and best developed observed at particular sites on the calyx. Unfavorable conditions appear to have dwarfed or aborted goniospires on areas of a specimen without serious impairment to the general physiology of the animal; the large number of unaffected goniospires adequately fulfilled respiratory needs and permitted continued growth of the calyx.

FRAMEWORK OF CALYX RIDGES

Those species of *Porocrinus* which have large goniospire areas (such as *P. fayettensis* Slocom, text-fig. 13, and *P. shawi* Schuchert, text-fig. 14) possess strong ridges linking the centers of BB, RR, RA, and X plates, rimming the IBB, and bordering the ambulacral grooves on the oral surface. Furthermore, the mouth opening is surrounded by a conspicuous collar or ring formed by thickened material on the proximal edges of the five OO plates. The strength and rigidity of the calyx appear to originate entirely with this framework and to be independent of the thin, deeply folded goniospires.

In simple structural terms, the frame consists of a ring supported by five inclined arches, a middle band of struts arranged in triangles, and a base of five U-shaped bars side-by-side and set upon the wide proximal columnal of the stem (text-fig. 6). Thus, the aboral half of the frame is nearly a mirror image of the oral half. Since the oral pole of the calyx lay directly above the stem facet, it would seem that the major stresses produced by the weight of the calyx and its contents were transmitted outward, tending to distend the calyx and to increase the equatorial diameter. It is in this central region, bounded above by an encircling hexagon through centers of RR and X and below by a pentagon through centers of BB (text-fig. 6), that the sides are provided with diagonal



TEXT-FIG. *6*—Strengthening ridges in Porocrinidae; plate sutures omitted. Figures variously inclined, centered on BC interray *(a)*, posterior interray *(b)*, anterior ray *(c)*, D ray *(d)*, posterior interray *(e)*, and C ray *(f)*. Note protuberance of posterior region below periproct in *a* and *d*.

struts. These struts, like braces in carpentry, utilize the basic strength of the triangle (pl. 8, fig. 5).

Of course, no element of the frame is undivided, since it links centers of contiguous plates and therefore must cross a suture. The oral collar is quinquepartite, composed of parts of the five OO plates (pl. 4, fig. 1). Each arch, alongside two adjacent ambulacra, is tripartite, its central part formed by an O plate and its ends by two RR (pl. 8, fig. 1). At each end, the arch is joined to the adjacent arch as well as to the middle band of struts at the arm facet (text-figs. 6, 7, 13). The U-shaped elements below are also tripartite, each arm of the U being shared by the IB and an overlying B (pl. 4, fig. 9). The two vertical elements in each B (text-figs. 9, 10) are side-by-side, so that U-shaped elements effectively unite arm-to-arm. All units in the middle band are straight and bipartite, crossing only one suture each (text-figs. 9, 10, 13, 14).

A degree of irregularity and weakness stems from the presence of X and RA. The X plate, set in the circlet of RR, makes the periproct particularly weak. The area is enclosed by the two arms of the arch (in the C and D rays respectively) and by the two X-R ridges; thus, the bounding frame forms a quadrangle, a geometric form lacking in rigidity (text-figs. 6b, 6c; pl. 8, fig. 2). Below, the problem of linking the RR-X hexagon to the BB pentagon is structurally solved by extra struts radiating from the two BB in the BC and CD interrays (text-fig. 6). Further strength is derived from the four ridges radiating from the RA, leading to the BB of the two posterior interrays, the R of the C ray, and the X plate, acting as cross braces in the posterior region (pl. 5, fig. 1; pl. 8, fig. 3). Such strength is needed in this region, because the presence of RA and X creates a bulge of the calyx (text-figs. 6a, 6d). Insofar as the Porocrinidae is concerned, RA fulfills two functions: reinforcement of the calyx in an overhanging part and creation of additional triangular areas for goniospires.

In an echinoderm made of hexagonal plates, rigidity can be imparted by radiating ridges in two ways: by ridges from plate centers to corners and by ridges from plate centers to sides. The two plans are very different from an engineering standpoint. If ridges radiate to plate corners, the overall pattern is a series of interlocking rhombs, the ends of ridges on each plate are acuminate, and three ridges meet at the common point of three plates. In contrast, if ridges radiate to plate sides, the overall pattern is a series of interlocking triangles, the ends of ridges on each plate are blunt, and each sutural junction involves only two ridges, which meet flush. The latter arrangement is stronger because (1) triangles are more rigid than rhombs and (2) the suture has more area between two ridges meeting at sides of contiguous plates than between any pair of ridges involved in a three-ridge junction at a corner. In addition, less material is involved in the shorter ridges. In the Porocrinidae, any junction of more than two ridges occurs at a plate center, so that the joining ridges are "cast" in one solid piece of plate material.

The material economy and the structural advantages of the center-to-side ridges as seen in the Porocrinidae are identical to those of similar ridges in other echinoderms. Glyptocystitid cystoids utilized the sides of some plates for pectinirhombs which strongly resemble goniospires in morphology and function. These cystoids rarely have ridges to the corners of plates. Instead, they have few pectinirhombs so that most plates were involved in the ridge framework. Some early glyptocystitid cystoids interrupted the pectinirhomb areas by ridges, thereby forming demirhombs, whereas later species developed specialized ridges to strengthen the pectinirhomb areas themselves.

In comparison of cystoids and the Porocrinidae, it appears to us that the former evolved simpler and more efficient pore structures but a more complex method of strengthening the theca, whereas the latter evolved more complex and less efficient pore strutcures and therewith retained the simpler and better framework of ridges.

Some Porocrinidae, such as *Porocrinus conicus,* have nearly smooth plates, lacking any appreciable ridges (text-figs. 11, 12; pl. 6, figs. 2–5; pl. 7, figs. 2–5). In many of these, the pore areas are sunk deep into the plates. The plate material above the level of the goniospire ridges is about as thick as the plate material composing the ridges in other species, such as *P. fayettensis* (text-fig. 13; pl. 8, figs. 3, 5–7). Hence, it is apparent that these species did not need ridges, for the whole of the plate (except for the pore areas) served the same purpose. In essence, the "ridges" of *Porocrinus conicus* are enclosed in other plate material. As compared with *P. fayettensis* or *P. shawi, P conicus* has the burden of considerable plate material in its plates which does not contribute effectively to strength of its calyx.

Family Porocrinidae Miller & Gurley

We prefer to resurrect Miller & Gurley's Porocrinidae rather than retain *Porocrinus* in the Palaeocrinidae. *Palaeocrinus* and *Porocrinus* differ in important respects. *Palaeocrinus* has exothecal pore structures, developed across plate sides, and branched arms. In contrast, *Porocrinus* and *Triboloporus* both have endothecal pore structures, developed at plate corners, and at least the former has unbranched arms (the arms of *Triboloporus* being unknown to date). Such drastic differences in the kind of respiratory structures and their location are good grounds, we feel, for familial separation.

The following key to species of Porocrinidae is artificial, for the most part, and not designed to suggest lineages. It includes the well-founded species of the genus:

- *Triboloporus cryptoplicatus* n. sp.—Lower M. Ord., Benbolt Ls., Va.
- *T. xystrotus* n. sp.—Black River, U. Chambersburg Ls., Pa.
- *Porocrinus pentagonius* Meek & Worthen—Black River, Platteville Ls., Ill.
- *P. conicus* Billings—Trenton, Hull Ls. Canada; Galena Dol., Wisc.
- *P. elegans* n. sp.—Trenton, Galena Dol., Minn.
- *P. smithi* Grant—Trenton, Hull Ls. Canada; also reported from Curdsville Ls., Ky.
- *P. shawi* Schuchert—Trenton, Baffinland.
- *P. crassus* Meek & Worthen—Richmond, Maquoketa Sh., Iowa.
- *P. fayettensis* Slocom—Richmond, Maquoketa Sh., Iowa.
- *P. pyramidatus* n. sp.—Richmond, Maquoketa Sh., Iowa.
- *P. scoticus* Ramsbottom—Ashgill, U. Drummuck Gr., Starfish Beds, Thraive Glen, Scotland.

The following were omitted because we consider them insufficiently known:

- *P. radiatus* Beyrich—M. Ord., Vaginaten Ls., Russia.
- *P. kentuckiensis* Miller & Gurley—Trenton, Curdsville Ls., Ky.

KEY TO SPECIES OF POROCRINIDAE

1. Goniospire with only one fold, set oblique to surface of plate, on each side of median ridge ....*Triboloporus* 2
Goniospire with several folds, nearly normal to surface of plate, on each side of median ridge ....*Porocrinus* 3
2. Median ridge of goniospire internal; calyx ornamented with inconspicuous narrow crests ....*T. cryptoplicatus*
Median ridge of goniospire external, exposed at plate level; calyx ornamented with broad, convex, low, striated ridges .... *T. xystrotus*
3. Calyx ridges weak or absent .... *P. conicus*
Calyx ridges definite, strong in many 4
4. Median ridge of goniospire expanded near plate junctions; pores on each plate not parallel .... *P. shawi*
Median ridges not expanded; pores parallel 5
5. Goniospire areas pyramidal, protuberant .... *P. pyramidatus*
Goniospire areas not protuberant 6
6. Goniospire areas decreasing from base to top of calyx, those of R-R-O corners small .... *P. elegans*
Goniospire areas nearly equal from base to top 7
7. Calyx tending to be conical; IBB relatively high, the circlet relatively small 8
Calyx subobovate to rotund; IBB relatively low, the circlet large, extending outward from stem facet 9
8. Goniospire areas very shallow, medium to large, subcircular .... *P. pentagonius*
Goniospire areas definitely depressed, small, triangular .... *P. scoticus*
9. Sutures in grooves; goniospire areas deeply depressed .... *P. crassus*
Sutures nearly flush; goniospire areas not deep **10**
10. Stem round; goniospire areas very large .... *P. smithi*
Stem pentagonal; goniospire areas medium to large but smaller than *P. smithi* .... *P. fayettensis*

Various measurements of Porocrinidae are listed in table 1. Maximum widths of all IBB, BB, and RR + X were combined to obtain the total widths of the respective circlets (a–c). Average width, height, and width/height ratios were determined for the IB, B, and R plates (d–1). The combined length of the two goniospire areas intercepted along each B-B suture was divided by the combined lengths of these sutures to yield an index to size of the pore areas (s). Expansion of the calyx (t) was found by subtracting the total width of the BB circlet from the total width of the RR + X circlet, and the expansion rate (u) was determined by dividing this figure by the average height of the B. The oral constriction (x) was found by subtracting the circumference of the oral area from the total width of the RR + X circlet, and the constriction rate (y) was determined by dividing this figure by the average height of the R. Of the various ratios, the average proportions of the B and R plates (i, 1) seem so nearly constant as to have little value for species differentiation. On the other hand, the average proportions of the IB (f) show some distinction between those species with relatively high IBB, such a *P. conicus,* and those with relatively low IBB, such as *P. shawi.* Another ratio which seems to be significant is the expansion rate (u), distinguishing to a degree between those that are subconical, such as *P. conicus,* and those that are obovate, such as *P. shawi* and *P. fayettensis.* Other ratios yielding indices of shape of calyx could be obtained by measuring the average diameters of the columnar facet, IBB circlet, BB circlet, RR + X circlet, and OO circlet and comparing the differences against average heights of each circlet of plates between levels at which the diameters were measured.

TRIBOLOPORUS n. gen.

Description.—Small crinoid. Calyx consisting of five nearly equal IBB, five well-developed BB, five RR, a subpentagonal X, a diamond-shaped RA, and five OO, as well as numerous little ambulacral covering plates. Arms facets horseshoe-shaped. Goniospires very simple; the element at each plate corner consisting of median ridge with one bordering deeply folded trough on each side.

Type species.—*Triboloporus cryptoplicatus* n. sp.

Remarks.—Calyx plates and their arrangement are identical in *Triboloporus* and *Porocrinus.* The new genus differs from *Porocrinus* only in the nature of its goniospires, but this character alone seems to us justification for setting it apart. One is tempted to regard *Triboloporus* as the ancestral form of the Porocrinidae and to consider its very simplified goniospire as the forerunner of the more complexly folded type in *Porocrinus.* This hypothesis can only be confirmed when the history of the family is established in greater detail.

The name is derived from the Greek *tribolos* (a caltrop; triradiate structure) and *porus* (a slit), referring to the form of each goniospire.

TRIBOLOPORUS CRYPTOPLICATUS n. sp.

Text-fig. 7; pl. 1, figs. 1–8

Description.—Calyx known only from holotype, very small, rotund. IBB not preserved; aboral sutures of BB with angular indentations to accommodate five IBB. BB large, each with goniospire at each corner except the aboral one

TABLE *1*—MEASUREMENT OF SELECTED SPECIMENS OF *POROCRINIDAE* (in mm.)

Character	*Triboloporus*		*Porocrinus*					
	crypto-plicatus	*xystro-tus*	*conicus*		*elegans*	*shawi*	*pyrami-datus*	*fayett-ensis*
Specimen	UMMP 56676	USNM 42196a	CGS 1423d	CGS 22888	USNM 42196b	USNM 28145	USNM 238630	UCWM 24700
a—Total width IBB circlet	9.4	12.9	15.8	12.5	12.0	13.6	14.6	12.2
b—Total width BB circlet	15.0	22.7	23.2	18.4	20.1	21.5	22.7	20.4
c—Total width RR+X circlet	18.0	24.9	25.6	20.5	23.8[1]	22.9[3]	25.2	23.2
d—IB ave. width	1.9	2.6	3.2	2.5	2.4	2.7	2.9	2.4
e—IB ave. height	......	2.0	3.1	1.8	1.8	1.4	1.7	1.5
f—IB w/h	......	1.3	1.0	1.3	1.3	1.9	1.7	1.6
g—B ave. width	3.2	4.5	4.6	3.7	4.0	4.3	4.5	4.1
h—B ave. height	3.1	4.5	5.3	3.8	4.0	4.3	4.7	3.9
i—B w/h	1.0	1.0	0.9	1.0	1.0	1.0	1.1	1.1
j—R ave. width	3.2	4.4	4.5	3.6	4.3	4.1	4.5	4.0
k—R ave. height	3.0	4.5	4.4	3.6	4.1	4.1	4.3	4.2
l—R w/h	1.1	1.0	1.0	1.0	1.1	1.0	1.0	1.0
m—X width	2.2	3.0	3.3	2.6	2.5[2]	2.5[3]	2.9	3.0
n—X height	1.5	2.1	2.9	2.3	2.0[2]	1.7[3]	2.2	1.8
o—RA diagonal	2.2	2.2	2.7	2.2	2.8[4]	2.3	2.3	2.6
p—Max. diam oral surface	4.4	5.9	6.5	6.7	5.9	6.5	6.0	6.4
q—Max. diam. mouth opening	......	......	......	......	2.4	2.3	2.3	2.1
r—Ave. distance between pores	......	......	0.18	0.19	0.18	0.20[5]	0.16	0.17
s—Length spire area / Length B-B suture	......	......	0.49	0.63	0.65	0.86	0.63	0.71
t—Expansion of calyx: c–a	8.6	12.0	9.8	8.0	11.81	9.3	10.6	11.0
u—Expansion rate t/h	2.8	2.7	1.8	2.1	3.01	2.2	2.8	2.6
v—Basal proportion: h/e	......	2.3	1.7	2.1	2.2	3.1	2.8	2.6
w—circumference of oral area[6]	12.7	18.1	19.6	18.8	17.8	20.0	19.2	18.8
x—Oral constriction: c–w	5.3	6.8	6.0	1.7	6.01	2.9	6.0	4.4
y—constriction rate: x/k	1.8	1.5	1.4	0.5	1.5	0.7	1.4	1.0

1. Includes both anal plates.
2. Supernumerary anal plate not included.
3. Measured from cavity left in calyx by missing X.
4. Abnormally pentagonal.
5. Median ridges expanded toward suture; measured through middle of plate corner area.
6. Measured between apices of adjacent 00, apices of 00 to periproct, and across oral edge of periproct.

EXPLANATION OF PLATE 1

All figures stereo pairs × 4 and coated with sublimate of ammonium chloride, except as noted

FIGS. *1–8*—***Triboloporus cryptoplicatus*** n. gen. n. sp. Holotype UMMP 56676; see text-fig. 7 for plate diagram; IBB circlet missing in specimen. *1,* oral view, showing the four ambulacra. *2,* inclined posterior view, showing plates around periproct. *3–6,* lateral views centered on C ray, B ray, A ray, and DE interray; ambulacrum missing on B ray. *7,* aboral view, × 10, specimen submersed in xylol, showing structure of the internal goniospires where IBB circlet is missing. *8,* posterior view, × 8, coated.

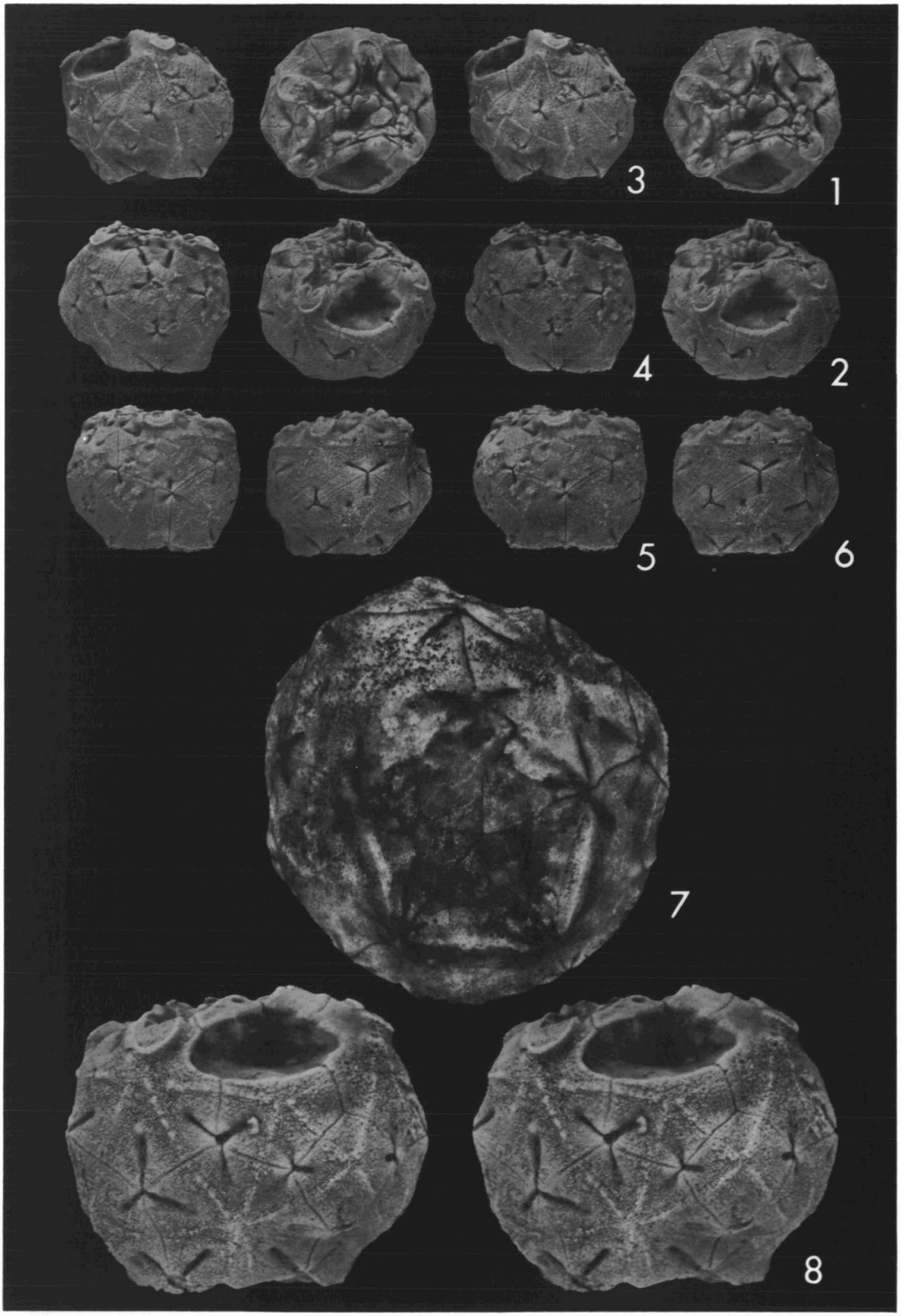


PLATE 1

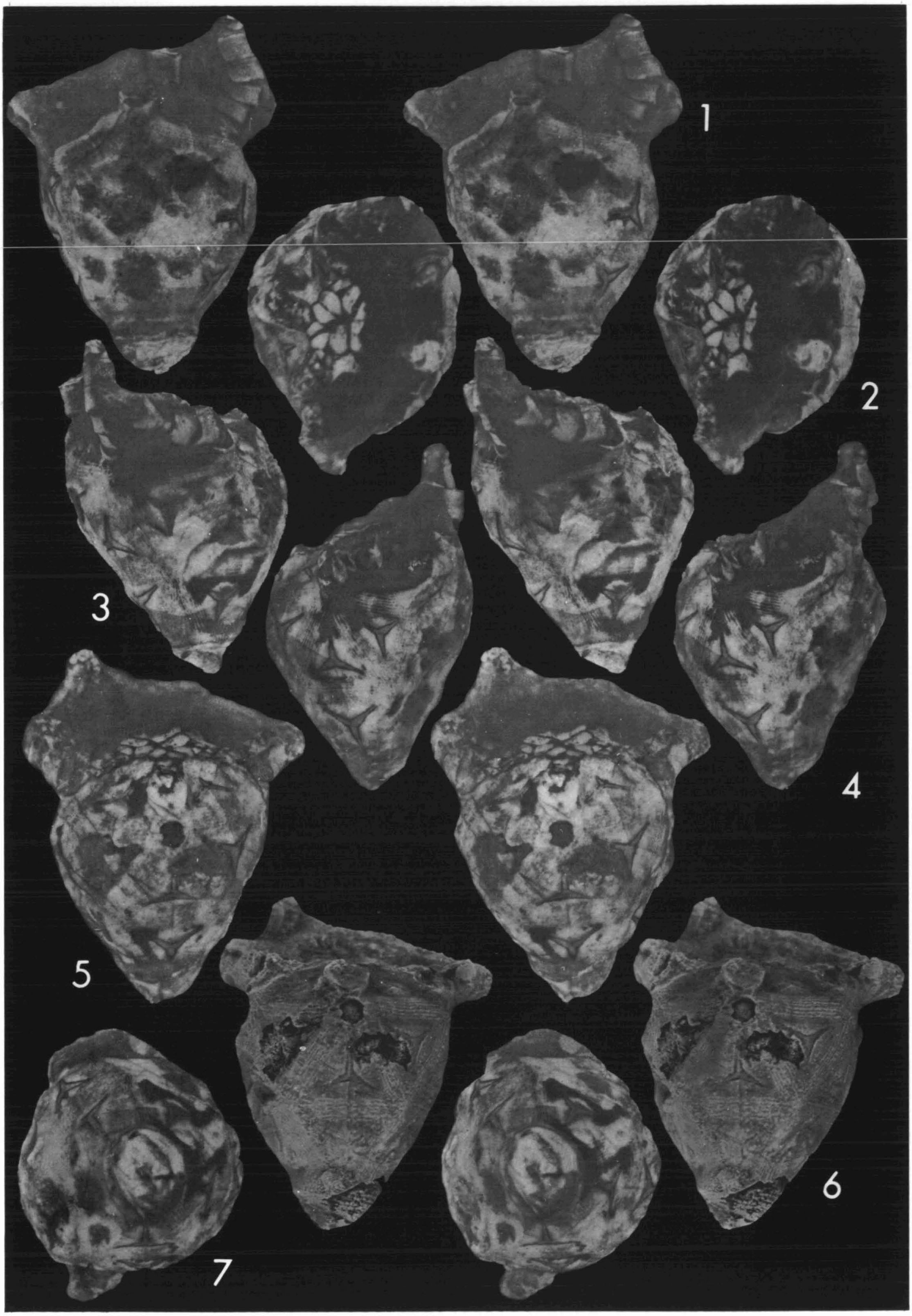
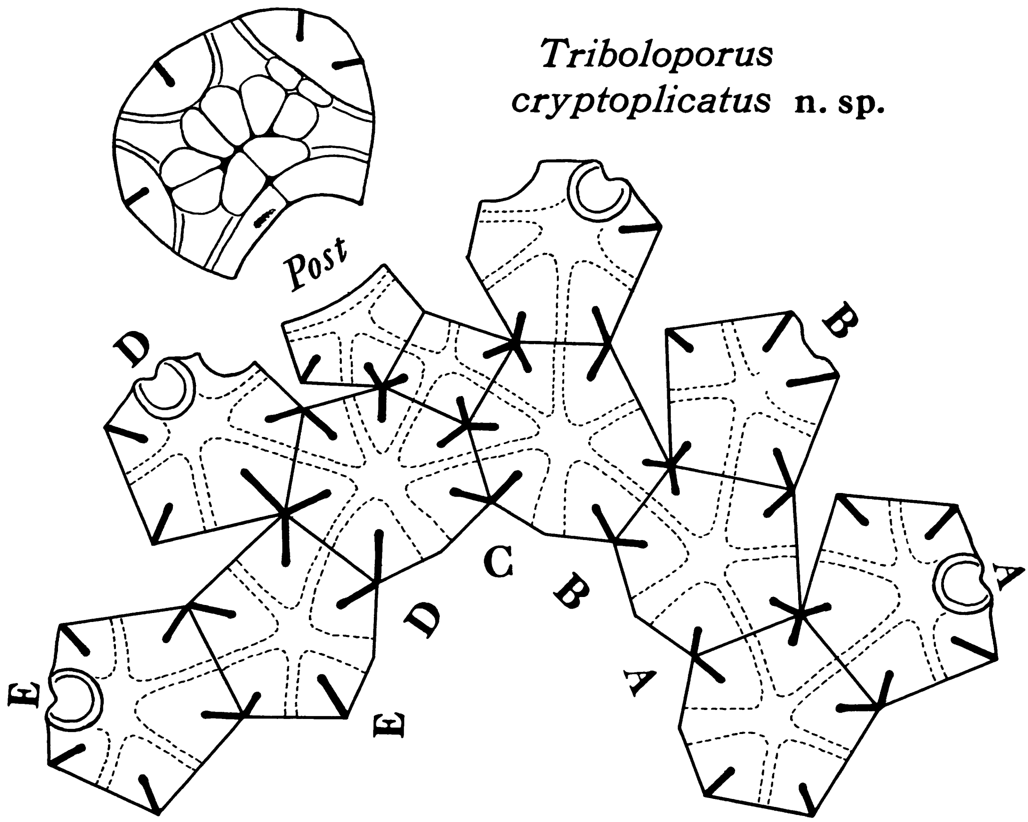


PLATE 2



TEXT-FIG. 7—*Triboloporus cryptoplicatus* n. gen. n. sp. Plate diagram based on holotype UMMP 56676; greatest width of diagram = 15 mm. Roman letters indicate rays according to Carpenter system; *Post* marks position of periproct. Plates in same arrangement as text-figure 11, which contains plate symbols. IBB plates missing in specimen.

(adjoining IB-IB suture); BB circlet forming a globular zone around calyx (pl. 1, figs. 3–6). RR about as large as BB. X large. RA large and protuberant (pl. 1, fig. 3). OO well developed.

Sutures nearly flush, difficult to discern without staining. Surface ornamented with narrow, delicate ridges between centers of plates (pl. 1, fig. 8); with specimen submersed in oil, ridges best viewed in silhouette along edges of calyx. Arm facets small, emphasized by a bordering ridge, moderately protuberant (pl. 1, fig. 8).

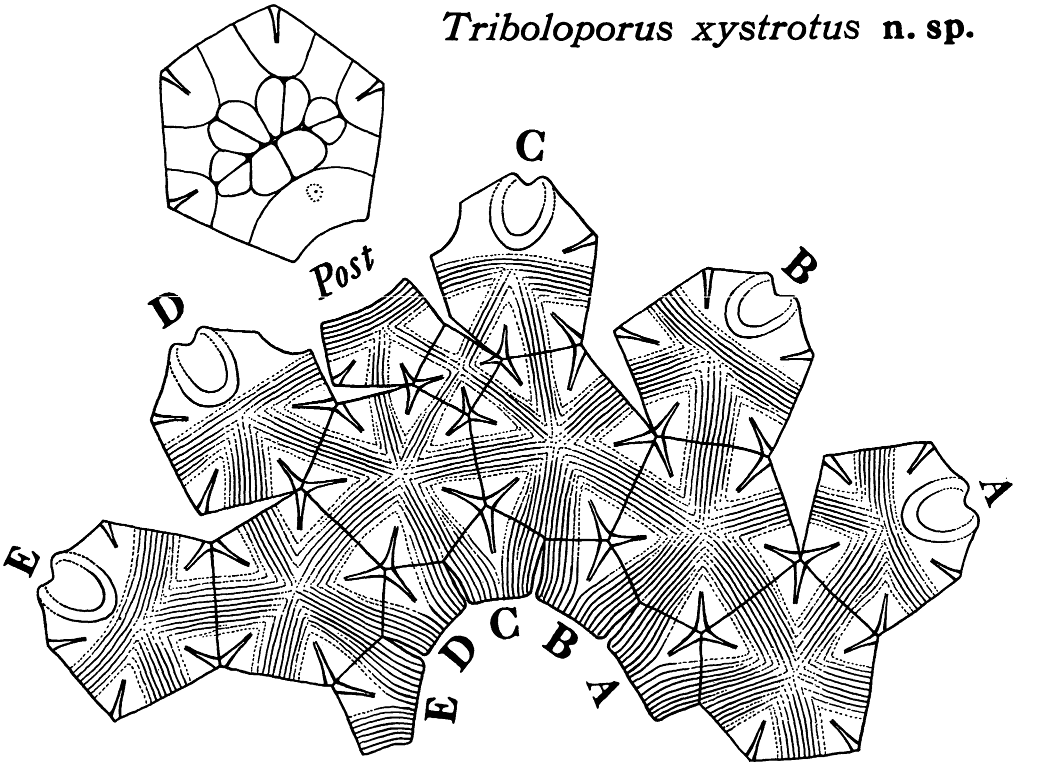
Oral surface large, confluent with RR as globose cap of calyx. Ambulacral grooves with recessed groove along borders to accommodate edges of covering plates. Peristome covered with large plates, two for each interray. In holotype, two OO plates in posterior interray; the one nearest the D ray bearing a short slit, perhaps the hydropore (pl. 1, figs. 1, 2, 8).

Goniospires expressed externally as triradiate

EXPLANATION OF PLATE 2

All figures stereo pairs × 4 and submersed in xylol, except as noted

FIGS. *1–7*—*Triboloporus xystrotus* n. sp. Holotype USNM 42196a; see text-fig. 8 for plate diagram. *2,* oral view, right half of specimen obscured by matrix. *1, 3, 4,* lateral views centered on C ray, BC interray, and CD (posterior) interray. *5, 6,* two views centered on A ray; *5,* slightly inclined in xylol; *6,* lightly coated with sublimate of ammonium chloride to show striated ridges. *7,* aboral view(C ray toward left side). Specimen in xylol printed especially light to show goniospires; actually, specimen very dark and matrix black.



TEXT-FIG. *8—Triboloporus xystrotus* n. gen. n. sp. Plate diagram based on holotype USNM 42196a; greatest width of diagram = 22 mm. Ambulacral covering plates not shown; light lines indicate their extent on oral surface.

slits or clefts. Median ridge of each third of goniospire internal, set in the cleft. Cleft apparently representing confluence of the two lateral troughs. One fold on each side of median ridge at about 45° (pl. 1, fig. 7).

Remarks.—In the holotype and only specimen, the R of the B ray lacks an arm facet (pl. 1, fig. 4) and the oral surface has no ambulacral groove leading to it (pl. 1, fig. 1). The AB and BC interrays on the oral surface are filled by one large O plate extending from the A to the C ray. This is undoubtedly an anomaly in the specimen. The two OO in the posterior interray are probably also anomalous. Possibly, one of the O plates was dislocated early in the ontogeny of the specimen, so that one arm was aborted by the lack of an ambulacral groove.

The name is derived from the Greek *cryptos* (hidden) and *plicatos* (fold), referring to the internal nature of the goniospire folds.

The form of the goniospire folds are clearly revealed where the IBB plates are missing (pl. 1, fig. 7).

Type.—UMMP 56676.

Age and locality.—Lower Middle Ordovi-

EXPLANATION OF PLATE 3

All figures stereo pairs × 4 and coated with sublimate of ammonium chloride or submersed in xylol

FIGS. *1–8—Porocrinus elegans* n. sp. Holotype USNM 42196b; see text-fig. 9 for plate diagram. *1, 2,* oral views, coated and submersed; note weak development of R-R-O goniospires and large hydropore structure. *3, 4,* lateral views centered on A (anterior) ray, coated and submersed. *5, 6,* lateral views centered on CD (posterior) interray, coated and submersed; note protuberant hydropore structure at apex and supernumerary anal plate. *7, 8,* lateral views centered on DE interray, coated and submersed. Other views of this specimen on pl. 4, figs. 7–9.

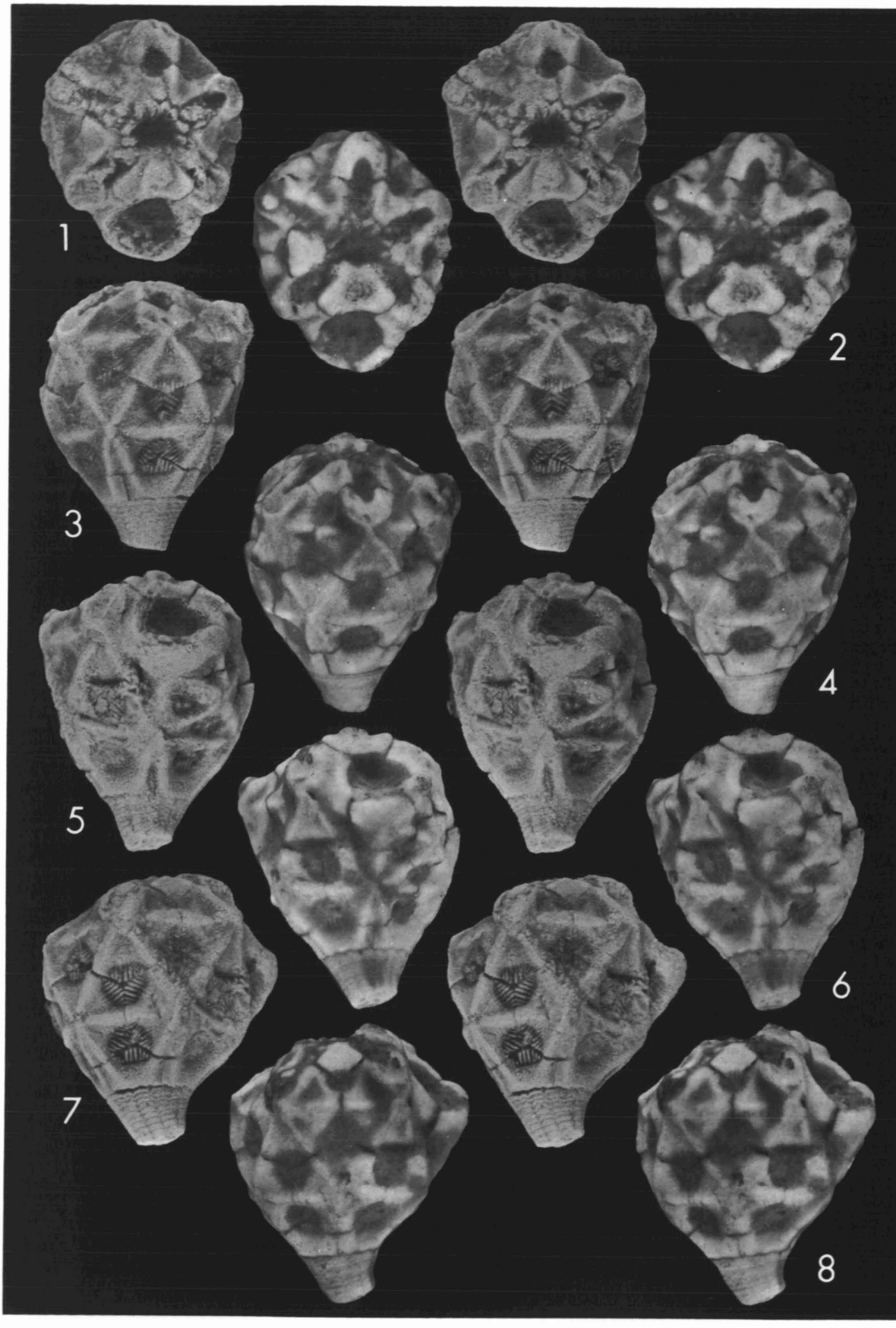


PLATE 3

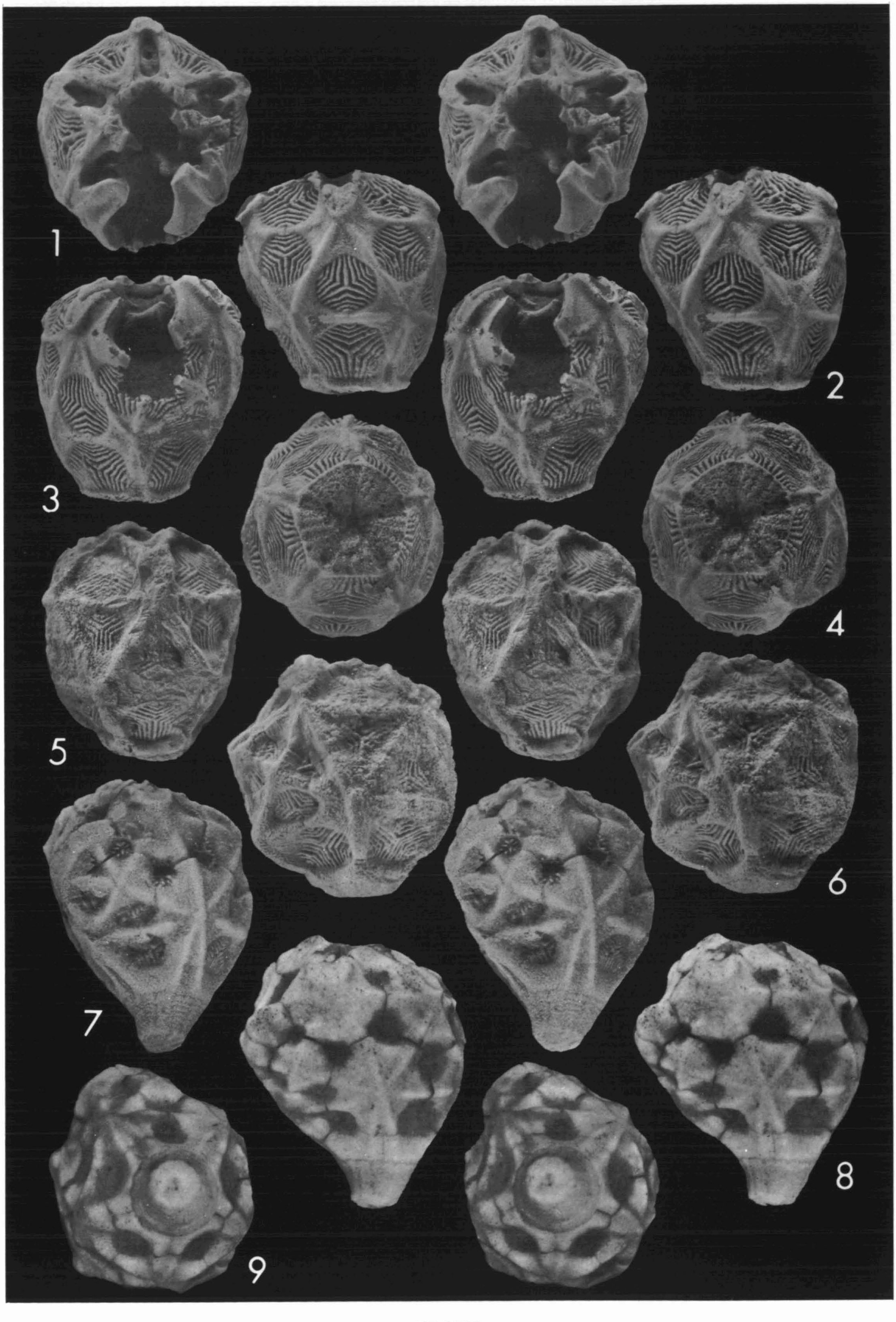


PLATE 4

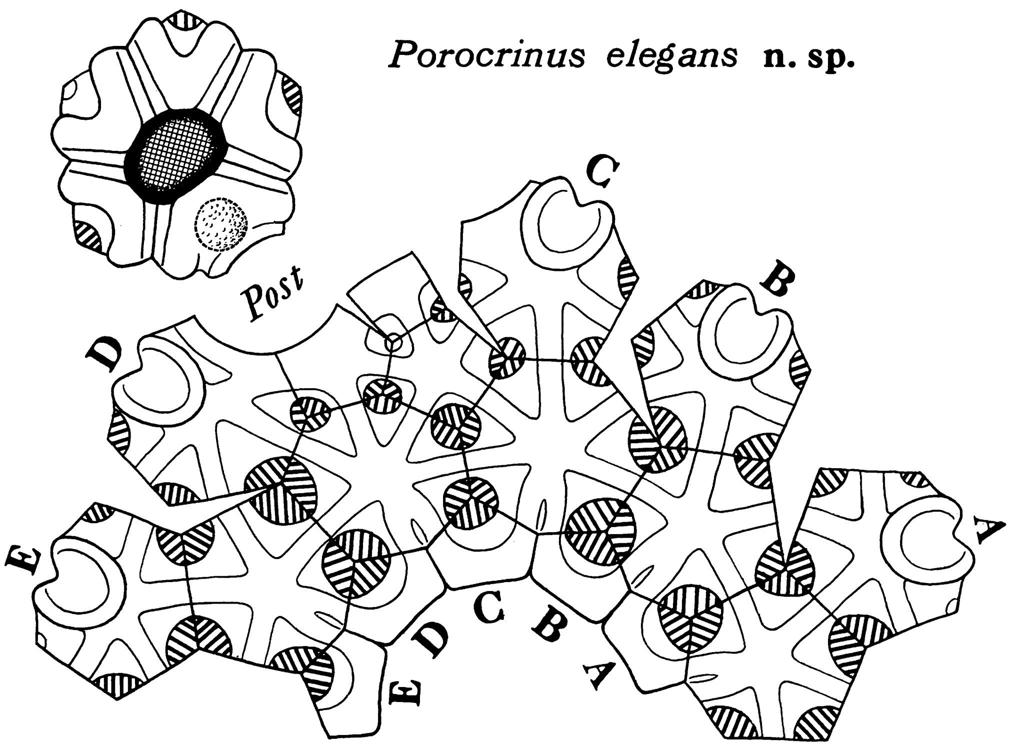
cian, Benbolt Limestone. Field exposure between Middle and South Forks of Moccasin Creek, about ¼ mile south of County road 676, 1½ miles due south of Hansonville and about 1⅛ miles west of eastern edge of Hansonville Quadrangle (TVA 205–SW, N3645–W8207.5/.5), elevation 2200 feet above MSL, Lat. 36°48′05″ N., Long. 82°8′44″ W., southern Russell County, Virginia.

Triboloporus xystrotus n. sp.

Text-fig. 8; pl. 2, figs. 1–7

Description.—Calyx plates as in genus. Cup obovate. IBB joining stem along a plane (pl. 2, figs. 1, 3); each IBB slightly constricted at about one-third the height, at which place each plate very gently concave and with very shallow indentations of the sides, above which the circlet flares to join the BB. BB about two and one-fourth times as high as the IBB (pl. 2, figs. 3, 4); as normal in the family, BB of AE, AB, and DE interrays hexagonal and those of the BC and CD interrays septagonal; each B at least as wide as high.

RR of A, B, and E rays about equal, the same size as the BB plates; RR of posterior rays slightly smaller. Arms facets large, horseshoe-shaped, elevated (pl. 2, figs. 5, 6). X ap-



Text-fig. 9—*Porocrinus elegans* n. sp. Plate diagram based on holotype USNM 42196b; greatest width of diagram = 21 mm. Extra anal plate is probably anomalous.

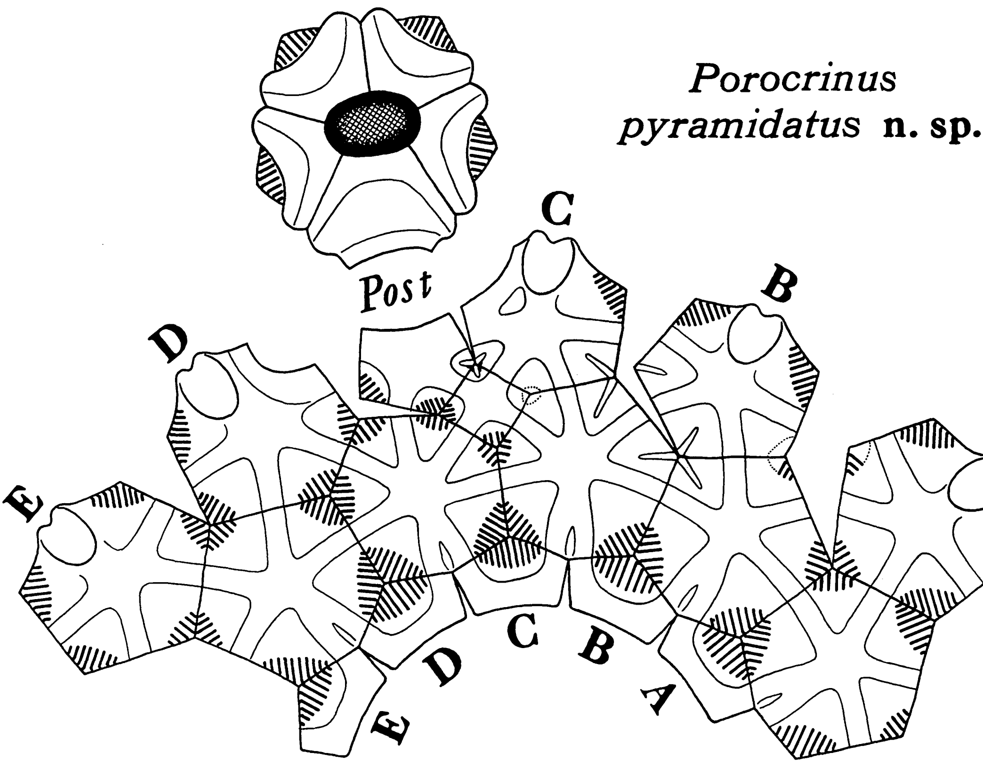
Explanation of Plate 4

All figures stereo pairs × 4 and coated with sublimate of ammonium chloride, except as noted

Figs. *1–4*—***Porocrinus shawi*** Schuchert. Holotype USNM 28145; see text-fig. 14 for plate diagram. *1,* oral view. *2, 3,* two lateral views centered on A (anterior) ray and CD (posterior) interray; note extreme size of goniospire areas and orientation of goniospire slits. *4,* aboral view; note large facet with radial crenulations.

5, 6—***Porocrinus fayettensis*** Slocom. Holotype UCWM 24700. *5, 6,* lateral views centered on A (anterior) ray and BC interrary. Other views of this specimen on pl. 8, figs. 1–5.

7–9—***Porocrinus elegans*** n. sp. Holotype USNM 42196b. *7,* lateral view centered on C ray. *8,* lateral view centered on BC interray, submersed in xylol. *9,* aboral view, submersed in xylol. Other views of this specimen on pl. 3, figs. 1–8.



TEXT-FIG. *10—Porocrinus pyramidatus* n. sp. Plate diagram based on holotype USNM Acc. 238630; greatest width of diagram = 25 mm. Heavy lines indicate actual pores in goniospires; light lines indicate median ridges of goniospires without bordering troughs.

proximately the same height as IBB but distinctly wider. RA small. Oral areas rather small, the posterior O large, the two anterior medium, and the two lateral OO quite small. Ambulacral covering plates small, but plates over the mouth (peristome) large and regular, a pair in each interray, their size proportional to that of underlying OO (pl. 2, fig. 2). Small protuberance on posterior O plate with apparent medial pore representing the hydrospire.

Goniospires developed at all B-B-IBB, B-B-R, B-B-RA, B-R-X, B-R-RA, B–X–RA, and R-R-O corners; in fact, only R-X-RA corner of C ray lacking goniospire of all possible positions (and this perhaps anomalous).

Ornamentation of cup distinctive, consisting of low, broad, striated ridges between adjacent BB, RR, X, and RA plates and from centers of BB to lateral margins of underlying IBB (pl. 2, fig. 6). Each ridge occupying about half of the suture. Striae rather sharp near center of each ridge, becoming faint and irregular near edge of triangular area containing goniospire.

Remarks.—Only one specimen is known. The name is from the Greek *xystrotos* (scraped, fluted) and refers to the distinctive surface of the ridges.

In the holotype and only specimen, part of the BC interray is chipped, showing that the

EXPLANATION OF PLATE 5

All figures stereo pairs × 4 and coated with sublimate of ammonium chloride, except as noted

FIGS. *1–6—Porocrinus pyramidatus* n. sp. Holotype USNM Acc. 238630; see text-fig. 10 for plate diagram. *1,* lateral view centered on C ray; compare with pl. 6, fig. 7 for view submersed in xylol. *2,* lateral view centered on A (anterior) ray. *3, 4,* two lateral views centered on DE interray; *3,* coated; *4,* submersed in xylol. *5,* lateral view centered on CD (posterior) interray; compare with pl. 6, fig. 6 for view submersed in xylol. *6,* aboral view, submersed in xylol; BC interray uppermost.

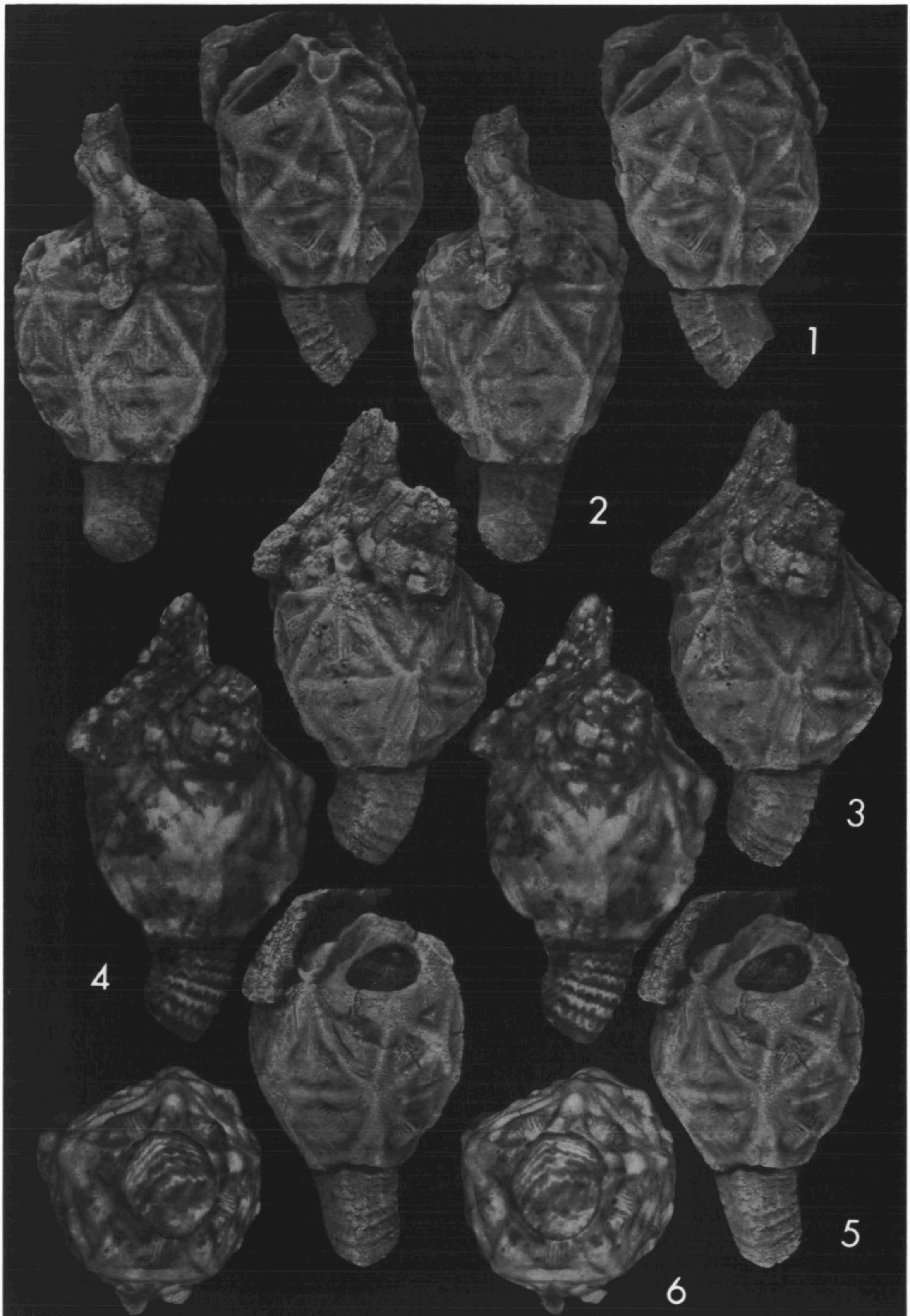


PLATE 5

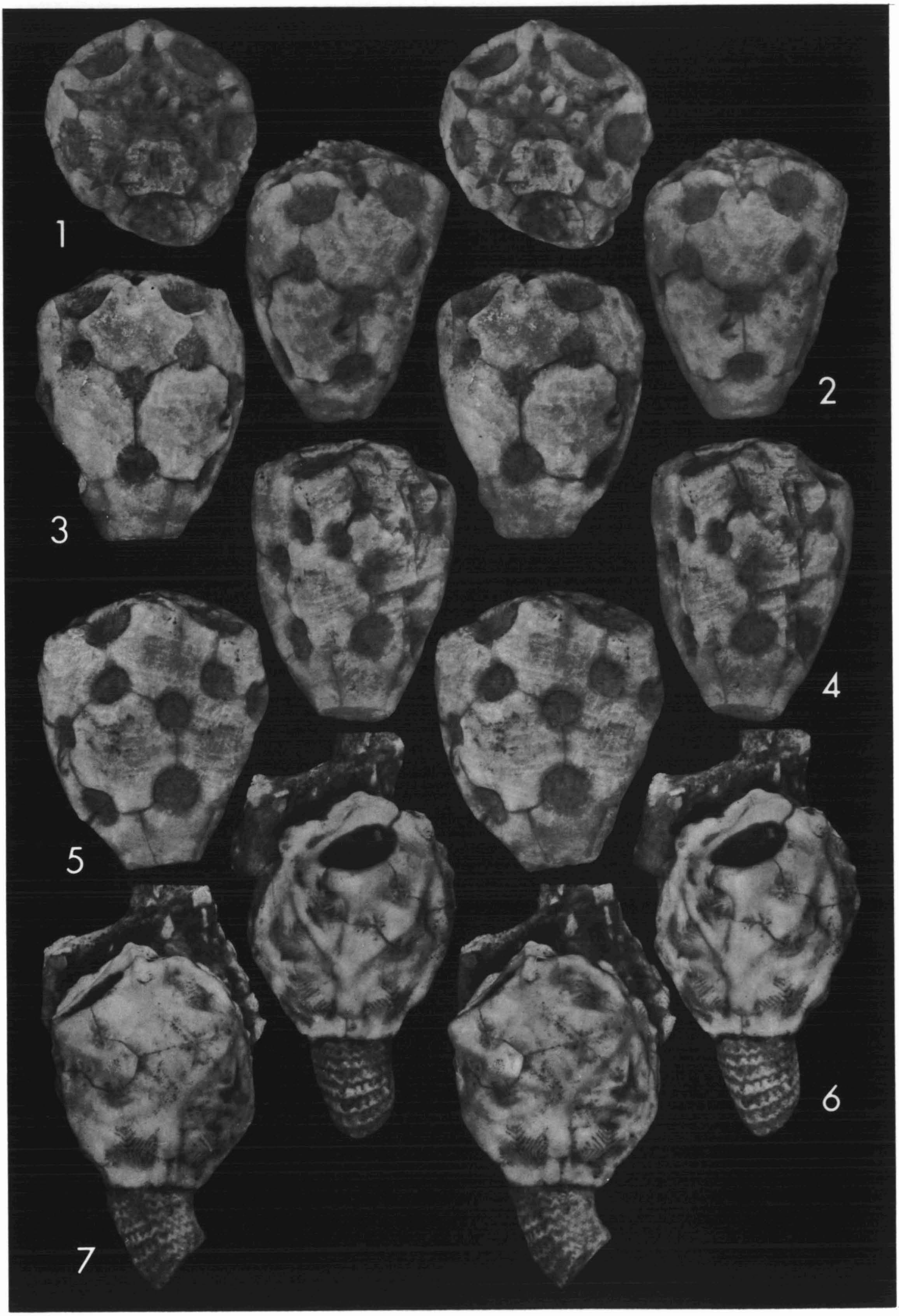


PLATE 6

folds of the goniospires on each plate corner diverge downward and that the central ridge is the apex of an inverted V. As in *Porocrinus,* plate walls are extremely thin in the goniospire structure. In contrast to most species of *Porocrinus,* the pores on each plate corner are not parallel, but diverge toward the plate junctions (pl. 2, figs. 4–6).

Type.—USNM 42196a.

Age and locality.—With the specimen is a card in E. O. Ulrich's script:

> Porocrinus n. sp. D. Upper Chambersburg ls. about 50 ft. + above the *Amecystis* bed (Bed 10a Ulrich's 1905 section), west end RR cut 2 mi. west of Kauffman, Pa. (Loc. 293i).

Porocrinus elegans n. sp.

Text-fig. 9; pl. 3, figs. 1–8; pl. 4, figs. 7–9

Description.—Calyx obovate. IBB wider than high (pl. 3, figs. 3, 7). BB as wide as high, more than twice as high as IBB (pl. 4, figs. 7, 8). RR slightly larger than BB. X and RA well developed (pl. 3, figs. 5, 6). OO circlet much smaller than RR circlet. Mouth opening large, subelliptical. Ambulacral grooves rather strongly entrenched along O-O sutures, crossed by low ridge near mouth margin (pl. 3, figs. 1, 2). Hydropore a large globose structure, the opening or openings indistinct (pl. 3, figs. 1, 5, 6).

Goniospires decreasing in size upward on calyx, medium on IBB plates (pl. 4, fig. 9) and small on OO plates (pl. 3, figs. 1, 2). Each goniospire depressed in corner area. Ridges definite but not as strong as in later species.

Remarks.—The decrease in size of goniospires from base to top of calyx sets this species apart from the younger *Porocrinus fayettensis* (pl. 8, figs. 5–7). The ridges are less strongly developed than in *P. fayettensis* (pl. 8, figs. 3, 5–7), *P. shawi* (pl. 4, figs. 2, 3), and *P. smithi.*

The holotype has an extra little quadrate plate between the X and the R of the C ray, inserted in the RR + X circlet (pl. 3, figs. 5, 6). To accommodate the extra plate, the RA is pentagonal (pl. 4, figs. 7, 8). At the four R-R-O corners, three goniospires are small and one is absent (text-fig. 9).

This specimen was selected by E. O. Ulrich to be the type of a species bearing this name, as indicated by an accompanying note in his handwriting. Ulrich never published on it.

In many respects this species resembles *P. fayettensis* and it may have been the ancestor of that species.

Type.—USNM 42196b.

Age and locality.—From a label with the specimen: "Mid. 3rd Trenton shales. South St. Paul, Minn."

Porocrinus pyramidatus n. sp.

Text-fig. 10; pl. 5, figs. 1–6; pl. 6, figs. 6, 7

Description.—Calyx small, as in other species of the genus, obovate. IBB broad, their width/height ratio about 1.7 (pl. 5, figs. 1, 5). BB more than twice as high as IBB, nearly as wide as high (pl. 6, figs. 6, 7). RR in the three anterior rays about as large as BB, those in the two posterior rays somewhat smaller. Arms facets elevated, with narrow bordering rim (pl. 5, fig. 1). X relatively large (pl. 5, fig. 5). RA small (pl. 6, figs. 6, 7). Oral surface rather small; OO and mouth opening normal for genus, ambulacral covering plates and hydropore not seen.

Goniospires well developed in B-B-IB and R-R-O corners, less so in middle part of calyx; each goniospire area pyramidal, protuberant, its apex extending beyond ridges on calyx (pl. 5, figs. 2, 6). Framework of ridges between plate centers distinct, well developed (pl. 5, figs. 1–3).

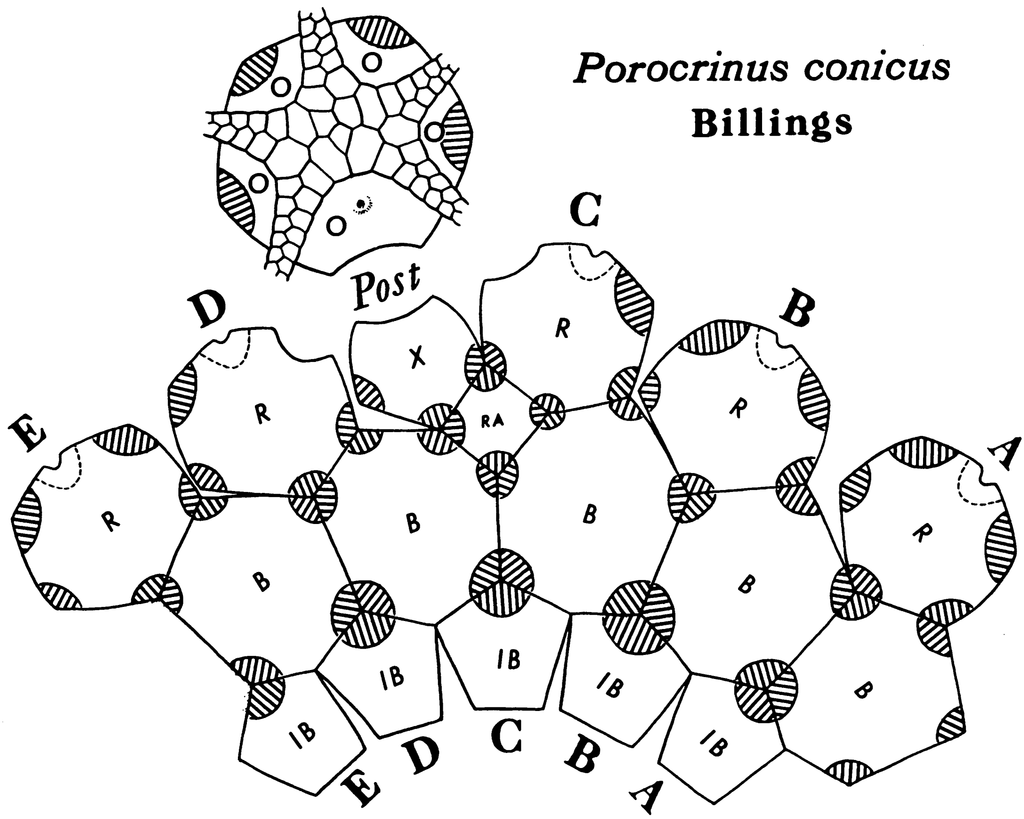
Remarks.—In the holotype and only specimen, goniospire absent at R-B-RA corner, its position marked by a shallow depression (pl. 6, fig. 7); those at R-R-B corner of B and C rays and at B-B-R corner of B ray are developed only as raised median ridges (pl. 5, figs.

Explanation of Plate 6

All figures stereo pairs × 4 and submersed in xylol

Figs. *1–5*—*Porocrinus conicus* Billings. Syntype CGS 1423d; see text-fig. 11 for plate diagram. *1,* oral view. *2, 3,* lateral views centered on E and D (anterior) rays. *4,* slightly inclined posterior view; parts of RA, R of C ray, and B of BC interray damaged. *5,* lateral view centered on D ray.

6, 7—*Porocrinus pyramidatus* n. sp. Holotype USNM Acc. 238630. *6,* lateral view centered on CD (posterior) interray; compare with pl. 5, fig. 5 for view coated with ammonium chloride. *7,* lateral view centered on C ray; compare with pl. 5, fig. 1 for view coated with ammonium chloride.



TEXT-FIG. *11*—*Porocrinus conicus* Billings. Plate diagram based on type specimen GSC 1423d; greatest width of diagram = 25 mm. Italic letters are conventional crinoid plate symbols.

1, 2; pl. 6, fig. 7); that at R-R-B corner of A and B rays developed as pores from B to R of A ray only; that at R-X-RA corner present as small median ridges with single pores from R to RA and from X to R plates, no pores from R to X. We are unable to determine, without additional specimens, if the aborted or underdeveloped areas are normal for these positions, were stunted by some malady, or perhaps were smothered by sediment during growth as a result of the stem being broken or uprooted. A pentagonal column is now attached to this specimen, but it does not match the calyx in color or shape; it is simply glued on.

In shape, *Porocrinus pyramidatus* resembles *P. shawi,* but it has smaller and protuberant goniospires. It is also readily distinguished from *P. fayettensis* of the same age and locality by its goniospire development.

Type.—USNM Acc. 238630.

Age and locality.—Clermont Shale Member, Maquoketa Formation. Road cut at Eldorado, Iowa. Specimen purchased from Geological Enterprises and labeled *Porocrinus fayettensis.*

POROCRINUS CONICUS Billings

Text-figs. 11–12; pl. 6, figs. 1–5; pl. 7, figs. 1–5

EXPLANATION OF PLATE 7

All figures stereo pairs × 4 and submersed in xylol, except as noted

FIG. *1–5*—*Porocrinus conicus* Billings. CGS 22888; see text-fig. 12 for plate diagram. *1,* lateral view centered on C ray; note poor development of goniospires on this flattened side. *2,* lateral view centered on D ray. *3,* lateral view centered on E ray. *4,* lateral view centered on AB interray. *5,* lateral view of specimen only partly exhumed from matrix, centered on E ray, coated with sublimate of ammonium chloride.

PLATE 7

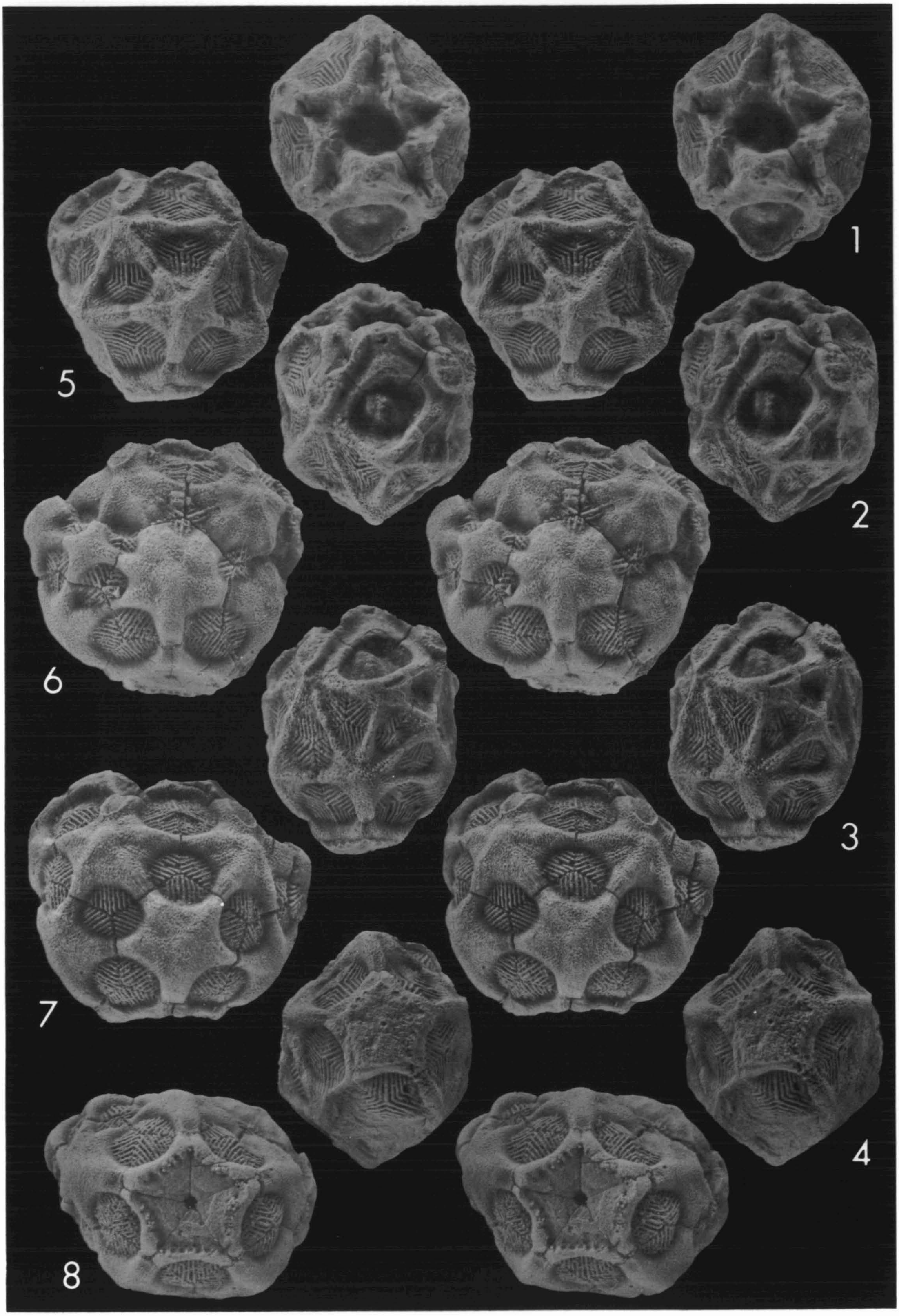


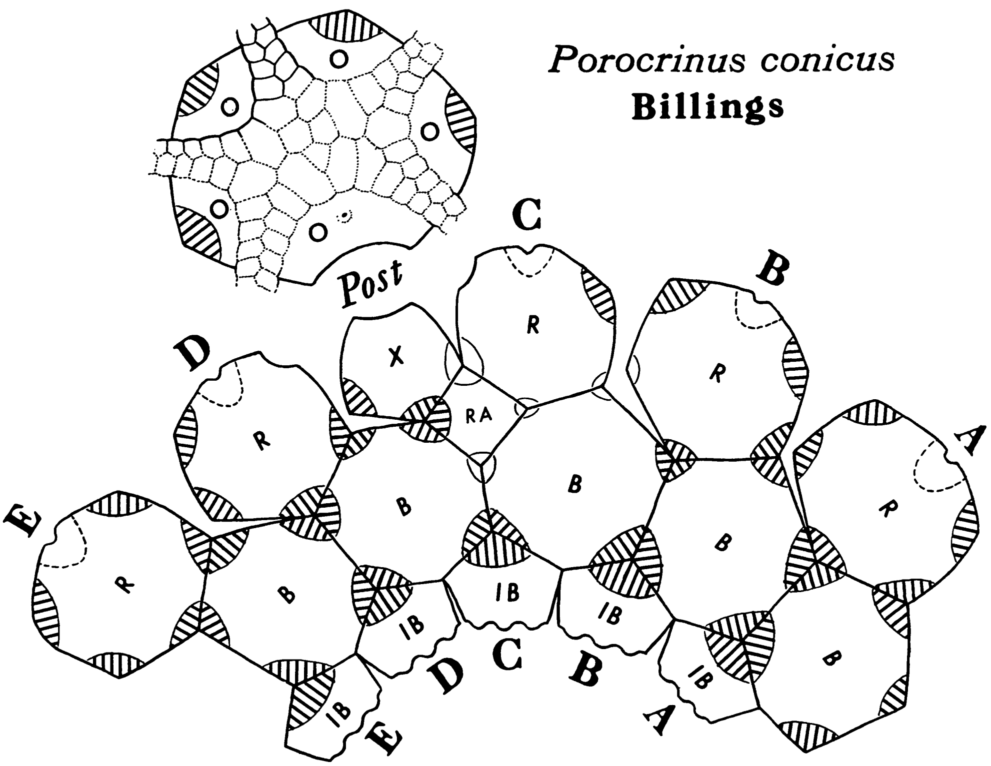
PLATE 8

Of the several specimens of this species we have studied, some are like the type specimens described by Billings, some have distinctly shallower and more triangular goniospires, and some are intermediate. Because the differences between specimens are gradational, we include all under one species. Two extremes are described below, one of the type specimens and a recently identified specimen from Wisconsin.

Description of type, GSC 1423d.—Calyx subconical. IBB as high as wide, the highest observed in any *Porocrinus* specimen (pl. 6, figs. 3–5). Junction of IBB circlet with column apparently a plane surface. BB less than twice as high as IBB (table 1), each B higher than wide (pl. 6, figs. 2–5). RR nearly the same size as BB, those of posterior rays somewhat smaller. Arm facets very slightly elevated (pl. 6, figs. 1–3). X slightly wider than high, about as wide as IB plate (pl. 6, fig. 4). RA well developed. OO circlet relatively small, rather strongly constricted from RR circlet (pl. 6, fig. 1). Numerous small ambulacral and peristomial covering plates, not sharply differentiated. Hydropore apparently a small pore in posterior O (pl. 6, fig. 1).

Goniospires small and circular, deeply recessed in thick calyx plates. No ridges discernible. Sutures flush.

Remarks.—This specimen displays no evi-

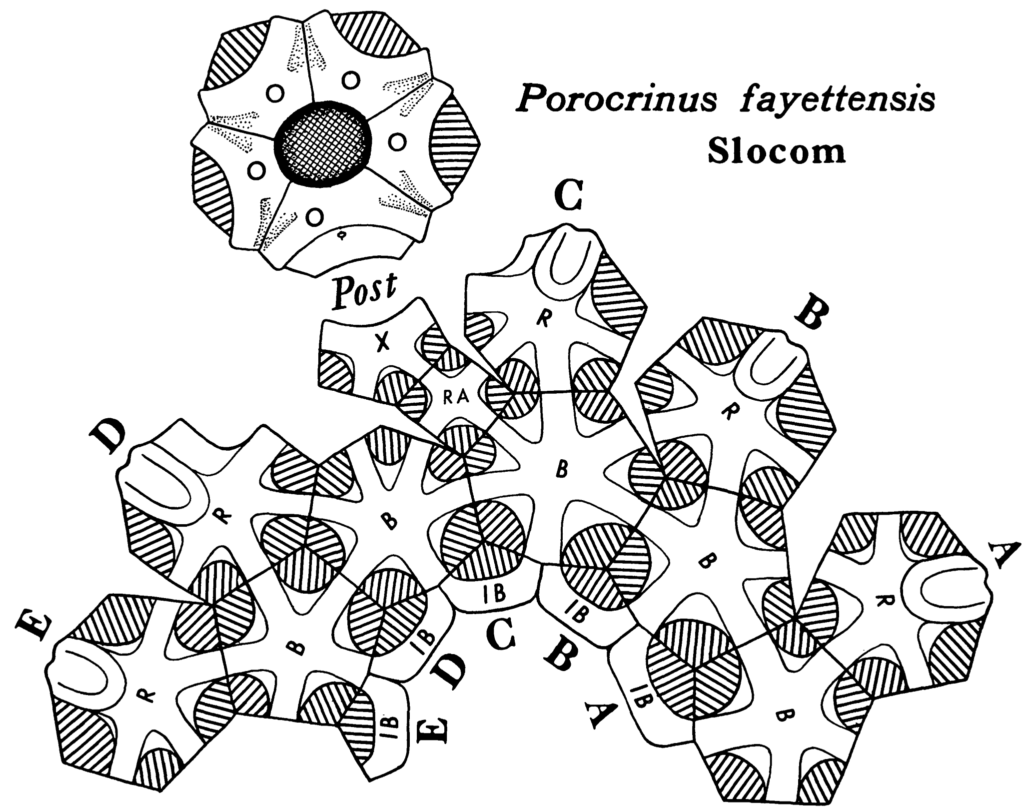


TEXT-FIG. 12—*Porocrinus conicus* Billings. Plate diagram based on CGS 22888, an example of specimen with shallower and more triangular goniospire areas than those in the type specimens (cf. text-fig. 11); greatest width of diagram = 20 mm. In this specimen base of IBB is fluted or crenulate at junction with column. Dotted lines indicate interpreted form of ambulacral covering plates hidden by arms in the specimen.

EXPLANATION OF PLATE 8

All figures stereo pairs × 4 and coated with sublimate of ammonium cloride

FIGS. *1–8*—*Porocrinus fayettensis* Slocom. *1–5,* holotype UCWM 24700; see text-fig. 13 for plate diagram. *1–3,* oral, inclined poterior, and posterior views. *4,* aboral view. *5,* lateral view centered on DE interray. other views of this specimen on pl. 4, figs. 5, 6. *6–8,* paratype FM P11262; large, laterally compressed specimen. *6, 7,* two lateral views centered on BC and DE interrays. *8,* aboral view.



TEXT-FIG. 13—*Porocrinus fayettensis* Slocom. Plate diagram based on holotype UCWM 24700; greatest width of diagram = 21 mm. Symbols same as in text-figure 5.

dence of extensive wear, so the smooth surface is regarded as the original character of plates.

Age and locality.—Trenton Group, Hull Limestone. Ottawa, Ontario.

Description of GSC 22888.—Calyx subconical. IBB definitely wider than high (table 1). Junction of IBB circlet with column fluted or serrate, matching contours of scalloped column, with three lobes on each IB plate (pl. 7, fig. 2). BB slightly more than twice as high as IBB, about as wide as high (pl. 7, figs. 2–5). RR almost as large as BB, those of posterior rays smaller. Arm facets low (pl. 7, figs. 1–3) but more elevated than those in the type. X a little wider than high. RA well developed. OO circlet relatively large, only slightly constricted from RR circlet. Ambulacral covering plates small (pl. 7, fig. 3).

Goniospires medium in size, subtriangular, shallowly depressed. Ridges very faint (pl. 7, fig. 5). Sutures not depressed. Column round, tapering sharply from junction with cup, edges scalloped in the proximal part of column (pl. 7, fig. 5). Arms long, uniserial, brachials much higher than wide; covering plates small and biserial, less than half as high as brachials.

Remarks.—One side of the specimen is flattened and the goniospires on that side are poorly developed or absent (text-fig. 12; pl. 7, fig. 1). As mentioned in the discussion of goniospires above, we suggest that this crinoid lived much of its life prostrate on the sea floor, its under side becoming flattened and the goniospires in that area being "smothered" by contact with the sediment during growth and development of the calyx.

This specimen was found in a collection of cystoids loaned to our Museum of Paleontology by the Geological Survey of Canada. Only a small part of the calyx was exposed on a small slab. By careful application of Airdent abrasion, one side was exposed (pl. 7, fig. 5). Hardness of the matrix prevented complete exhuming of the specimen by this method, so slots were cut with a diamond wheel close to the two sides of the calyx and additional cleaning performed with vibrotool and air abrasive. The whole of the calyx was finally laid bare except for the top of the tegmen, which lies protected within the circlet of upturned arms (pl. 7, fig. 3).

Age and locality.—Trenton Group, Galena Dolomite. Duck Creek, Wisconsin.

POROCRINUS FAYETTENSIS Slocum
Text-fig. 13; pl. 4, figs. 5, 6; pl. 8, figs. 1–8

As already reported by Thomas & Ladd (1926, p. 15) this species is variable, having a range of calyx shapes. Two of the types are here illustrated for comparison with *Porocrinus pyramidatus* n. sp.

POROCRINUS SHAWI Schuchert
Text-fig. 14; pl. 4, figs. 1–4

The holotype and only specimen of this species is illustrated here to show the extreme development of goniospires.

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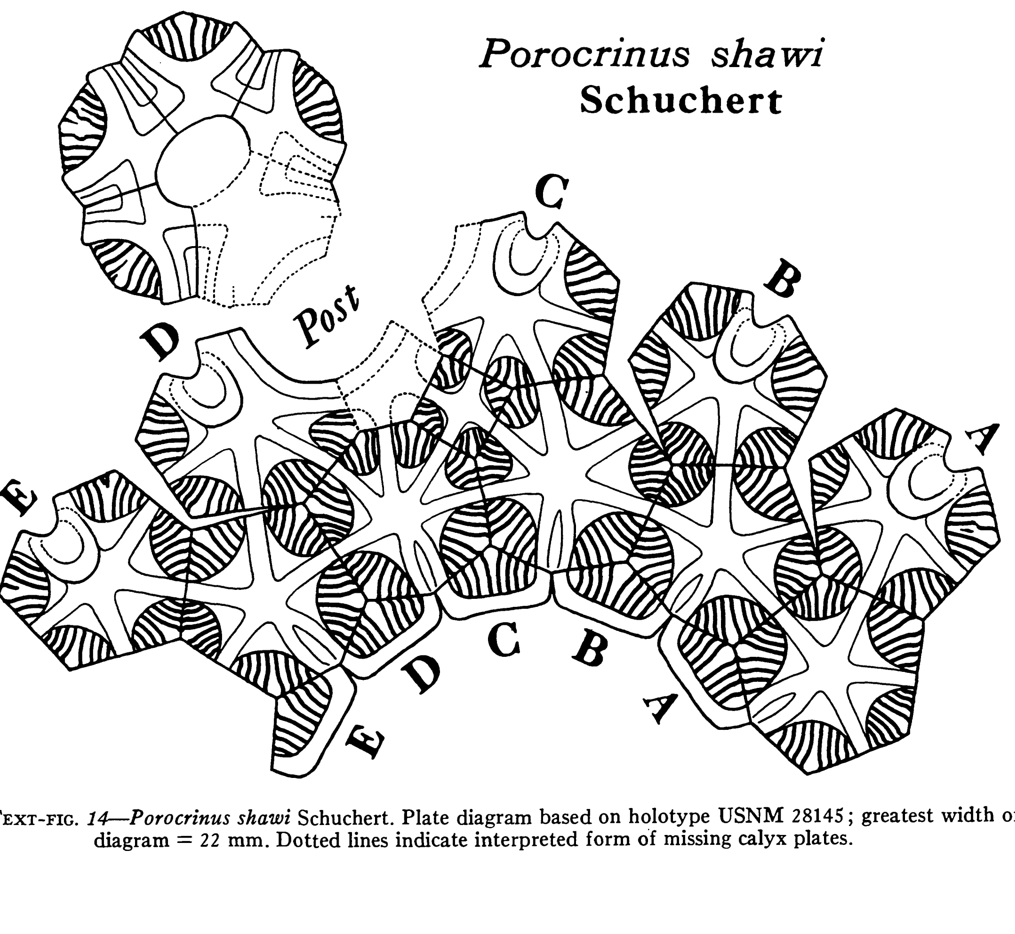

TEXT-FIG. *14*—*Porocrinus shawi* Schuchert. Plate diagram based on holotype USNM 28145; greatest width of diagram = 22 mm. Dotted lines indicate interpreted form of missing calyx plates.

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