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THE EVOLUTION OF THE POROCRINIDAE**

BY

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# THE CRINOID *TRIBOLOPORUS CRYPTOPPLICATUS* AND THE EVOLUTION OF THE POROCRINIDAE

By

Robert V. Kesling

*Abstract.*—A previously undescribed specimen of *Triboloporus cryptoplicatus* Kesling & Paul adds to our knowledge of this oldest known porocrinid crinoid. It reveals, for the first time, the nature of the IBB circlet in the cup and the proximal section of the column. Only the arms remain unknown. This species is significant in showing conclusively that the goniospires, the pattern of calyx plates, the very large mouth and anal openings, the rapidly tapering column, and even the design and number of tegminal plates were firmly established for the family Porocrinidae at its appearance and changed remarkably little during its history.

Review of all porocrinids shows several evolutionary trends, the most dominant being enlargement of goniospire areas at the expense of the girder system of plate ridges. The various trends suggest that the external circulation in the goniospire folds was from periphery of the goniospire areas towards the plate edge, that the weak column was in many cases unable to continue support of the crown, that the animals which came to lie prostrate effectively eliminated the goniospire structures in contact with the sea bottom, and that calyx features were modified by resorption and re-secretion of plate material.

Several non-adaptive features of the porocrinids kept them at a disadvantage in the rapidly increasing competition during the last half of Ordovician time. The increased size of goniospires for respiration reduced the plate areas available for ridges to strengthen the calyx. The mouth and anal openings remained overly large for their function and were poorly protected. The column never achieved strength to keep these crinoids erect. Lying near or on the sea floor, they were practically at the end of food and oxygen supplies, their poorly protected ends of the digestive system made them likely victims of predation, and their calyces were increasingly vulnerable to crushing as goniospire areas enlarged.

Extinction of the family was foreshadowed by the features present in the ancestral *Triboloporus cryptoplicatus*.

## INTRODUCTION

Search for the oldest species of a taxon is important to the paleontologist. Extension of the range back in time is only one possible reward. More significantly for the taxonomist and the paleoecologist, the ancestral species reveals the nature of distinctive features of the taxon at their first appearance in the record. It may also provide clues as to the derivation of the taxon itself.

Whether the phylogenetic relationships under scrutiny are intergroup or intragroup, the characters of the oldest species have critical value greater than those of any of its descendants.

That is why, years ago, the German paleontologist Otto Jaekel (1918) placed great emphasis on the *Vorform*—the progenitor of each major taxon, the first animal having incipient morphological structures which in time were to become the chief and diagnostic characters of the group.

In seeking a logical basis for lineages within a taxon, many paleontologists turn to cladistics. The first significant application of cladistics to classification of organisms was proposed by Wagner in 1954. Most programs, however, were developed from a model which was not concerned with organisms at all (Prim, 1957) but with parsimonious investment in telephone wire; it had nothing to do with time, ancestors, descendants, radiation, or genetic relationships. Cladistics was not designed for paleontology. Not everyone will agree with Eldredge & Cracraft (1980, p. 11) that "a cladogram can be converted into a phylogenetic tree for species," and would prefer to regard the cladogram as a useful means for stressing the magnitude of differences (leading to hierarchical divergence) on the one hand and the closeness of similarities (leading to grouping) on the other. To recognize the temporal sequence of forms within a major taxon and the nature of phenetic modifications from the initial species, we must return to summarizing the changes or deviations from the "primitive state," as proposed by Wagner. In paleontology, however, the "primitive state" must be that of the oldest species, rather than that of the form incorporating the greatest number of characters common to the most species of the group, as used by Wagner and other zoologists. Granting that the fossil record is incomplete and that the oldest *known* species may not in fact be the oldest of the taxon, this is still the defensible approach to taxonomy. It is possible to apply Prim-type cladistics from one species to those of the immediately succeeding interval, but not to use parsimony for the whole assemblage; otherwise, the temporal sequence is ignored and the result has no evolutionary meaning.

The family Porocrinidae is well suited for evolutionary study. It contains few but distinct species, it was short-lived, it was apparently monophyletic, and it exhibits several trends in the modification of its peculiar and diagnostic features—goniospires. Insofar as known, the Porocrinidae appeared in the lower part of Middle Ordovician time and became extinct at about the end of that period. Its members are readily distinguished from other crinoids of the suborder Cyathocrinina—and indeed from other inadunates—by the development of goniospires at corner junctions of the calyx plates. Whereas the plate arrangement (including even the tegmen) remained remarkably constant throughout their brief history, the porocrinids are separable into two genera by the nature of their goniospires: *Triboloporus* with a simple trio of slits (which might be termed goniopores) at each junction, and *Porocrinus* with three sets of several slits each. Internally, the greater number of slits in *Porocrinus* required modification in the attitude of the infolds or goniospires.

The ancestral position of *Triboloporus cryptolicatus* in Porocrinidae was suggested at the time of its erection by Kesling & Paul (1968). However, the holotype and only known specimen had the infrabasal circlet broken off along with the column; it also lacked a facet on the radial of the B-ray and any corresponding ambulacral groove in the tegmen, apparently an anomalous development.

The generous gift of a second specimen by Moya (Mrs. C.R.C.) Paul permits a more accurate assessment of the species. Whereas it is smaller than the holotype (and presumably immature) and has its posterior area crushed, it dispels the doubt about the B-ray being abnormal in the holotype and displays for the first time the infrabasal circlet and adjoining columnals. The two specimens thus complement each other in showing essential features of the species. Together, they provide the basis for this revised description and suggest the directions of evolutionary changes in Porocrinidae.

## OCCURRENCE

Lower Middle Ordovician (Mohawkian) Benbolt Limestone. Field exposures between Middle and South forks of Moccasin Creek, about 1/4 mile south of County Road 676, 1 1/2 miles due south of Hansonville, southern Russell County, Virginia. Site about 1 1/8 miles west of eastern edge of Hansonville Quadrangle (TVA 205-SW, N3645-W8207.5/.5), Lat. 36°48'05" N., Long. 82°08'44" W., elevation 2200 feet MSL.

Holotype, UMMP 56676, found by C.R.C. Paul in 1967. Hypotype, UMMP 57915 (described here for the first time), found by Moya (Mrs. C.R.C. Paul) in 1968.

## REVISED DESCRIPTION

Class CRINOIDEA Miller 1821

Subclass INADUNATA Wachsmuth & Springer 1885

Order CLADIDA Moore & Laudon 1943

Suborder CYATHOCRININA Bather 1899

Superfamily GASTEROCOMACEA Roemer 1854

Family POROCRINIDAE Miller & Gurley 1894

*Description.*—Cup simple, subconical to subovate with all parts of IBB circlet clearly visible in lateral view. Calyx plates consisting of five IBB, five BB, five RR, one RA, one X, and five OO (Text-fig. 1). IBB of about equal size and shape, all pentagonal. BB large, those of BC- and CD-interrays septagonal to fit against RA and X; all others hexagonal. RR hexagonal in lateral view, but the two upper sides of each fitting alongside the OO in nearly a straight line as seen from above (ventrally). RR of C- and D-rays separated by the subpentagonal X, bearing strong embayments to form the boundary of the very large anal opening or periproct.

RA small, square, bounded by R of C-ray, BB of BC- and CD-interrays, and X. OO large, disposed around large mouth opening or peristome; four of them pentagonal and equal, but the O of the posterior interray very wide, indented to accommodate both the large mouth and anal openings.

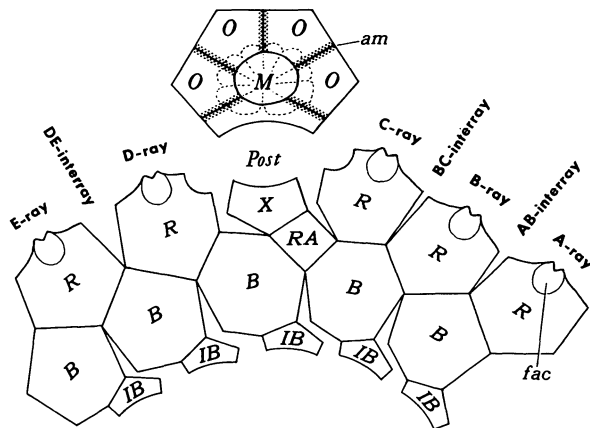
Goniospires at each triple junction of calyx plates in normally developed specimens except, in some species, the RA-R-X junction. Each goniospire with one or more slits in each of the plate corners involved.

Arms unbranched, long. Radial arm facets small, horseshoe-shaped; fulcra in arm facets weak or absent. Each of the ambulacral grooves shared by adjacent OO plates. Tegmen dominated by a rosette of ten radially arranged plates extending out beyond the mouth opening. A series of small biserial covering plates over the groove between the rosette and the arm facet.

Column tapering rapidly away from cup to very small diameter, probably relatively short.

*Remarks.*—The family is characterized by the goniospires. For further description and discussion of these unusual structures see Kesling & Paul (1968, p. 7-12).

The pattern of plates is identical in all species. Even the plate proportions vary only slightly.



TEXT-FIG. 1 — Generalized plate diagram of calyx in porocrinid crinoid. *M* = large mouth opening covered by rosette of tegminal plates (dotted); *fac* = small radial arm facet; *am* = ambulacral groove between adjacent OO plates; and *Post* = large anal opening in posterior position (CD-interray).

### Genus TRIBOLOPORUS Kesling & Paul 1968

*Type species.*—*Triboloporus cryptoplicatus* Kesling & Paul 1968, by original designation.

*Diagnosis.*—Porocrinids in which each plate corner in a goniospire area has but one slit or two close-set slits leading down into a pair of goniospire folds.

### TRIBOLOPORUS CRYPTOPLICATUS Kesling & Paul 1968

Pl. 1, Figs. 1–11; Text-fig.2

*Diagnosis.*—*Triboloporus* species with the ridge between each pair of goniospire folds situated below the level of calyx plate surfaces, so that only one slit is visible externally in each plate corner.

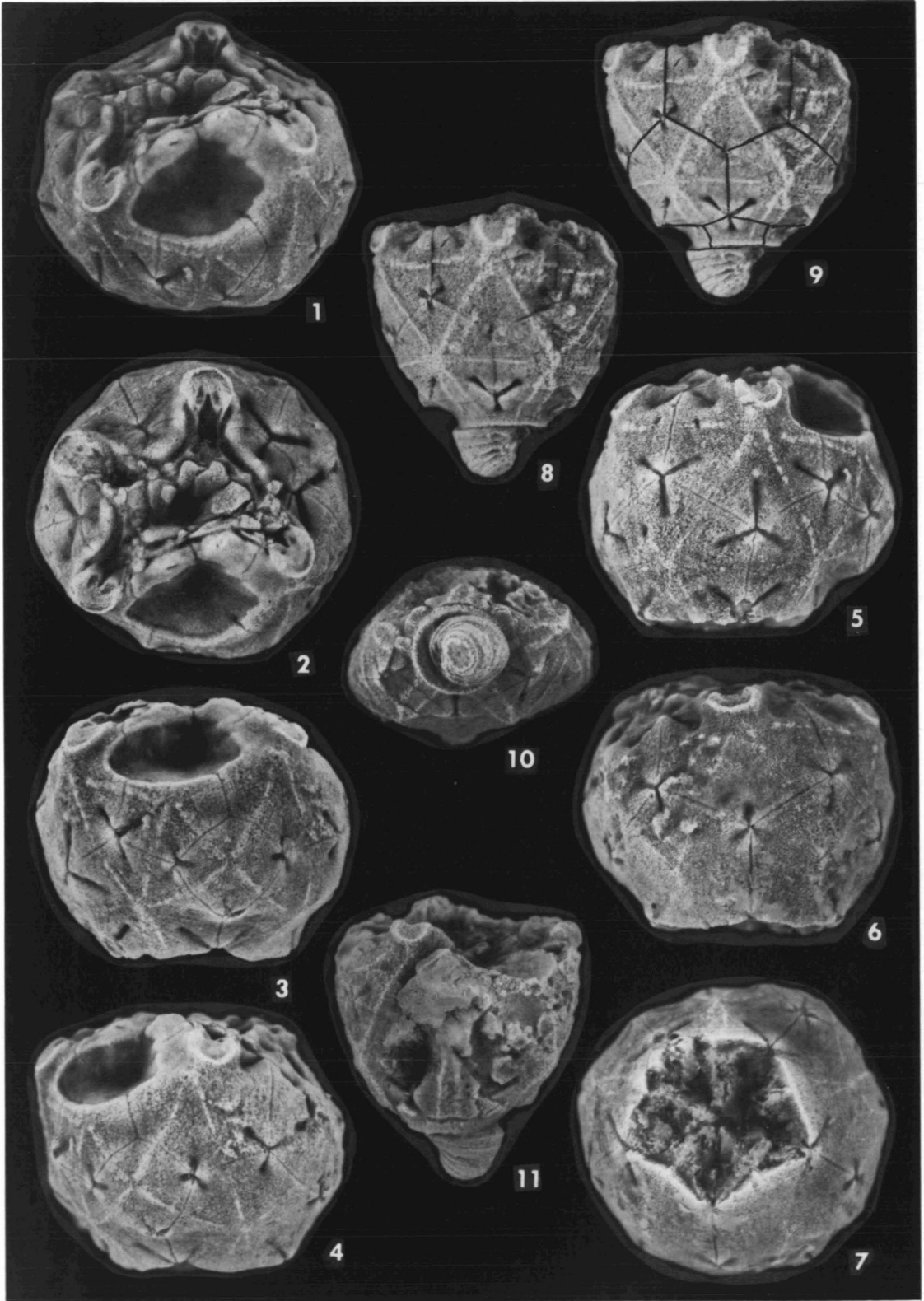
*Description.*—Calyx very small, about 7 mm in diameter in larger of the two known specimens, subovate, rotund in BB and RR-X circlets (Text-fig. 2). IBB low, about one-fourth the height of the RR (Pl. 1, Fig. 9). BB and RR nearly the same size, each plate about as wide as

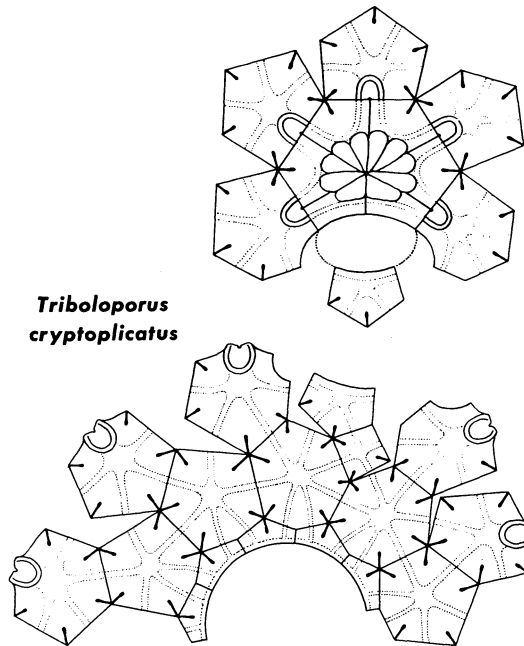
(Opposite page)

### EXPLANATION OF PLATE 1

(All figures x 7 1/4)

Figures 1–11 — *Triboloporus cryptoplicatus* Kesling & Paul. 1–7, holotype, UMMP 56676, lacking IBB circlet; 1, posteroventral view centered on large anal opening; 2, ventral (tegminal) view (note anomalous absence of radial facet and ambulacral groove on B-ray); 3, posterior view; 4, lateral view centered on C-ray; 5, lateral view centered on E-ray (note bulge associated with RA plate); 6, anterior view; 7, dorsal view, showing calcite filling calyx and (faintly) the infolds or goniospires. 8–11, hypotype, UMMP 57915, presumably immature specimen crushed in posterior area but preserving IBB circlet; 8,9, anterior views, with plate sutures inked on Fig. 9; 10, dorsal (basal) view showing small IBB circlet and rapidly tapering columnals; 11, posterior view, specimen badly crushed in area of X, RA, and R of C-ray.





TEXT-FIG. 2 — *Triboloporus cryptoplicatus* Kesling & Paul. Plate diagrams of ventral region (above) and calyx region (below). The division of the posterior O plate is probably anomalous.

high. RR of C- and D-rays with arcuate indentations to form boundary of large anal opening (Pl. 1, Fig. 1).

RA small, each of its sides less than half the diameter of adjacent BB (Pl. 1, Fig. 4). X about half as high and three-fourths as wide as adjacent RR, its upper (ventral) edge gently concave to form boundary of large anal opening (Pl. 1, Fig. 3). OO large (Pl. 1, Fig. 2), adjacent pairs sharing ambulacral groove; posterior O rather narrow between mouth and anal openings, wider than other OO.

Arms unknown. Radial arm facets small, each only slightly more than one-fourth the width of the R plate; ambulacral notch forming a deep cleft (Pl. 1, Fig. 2). Rosette of ten radially disposed plates in center of tegmen, extending out beyond edge of large mouth opening (Pl. 1, Fig. 2; Text-fig. 2), with a pair of matched plates in each interray. Only proximal section of column known, tapering rapidly away from calyx (Pl. 1, Fig. 10).

The three slits in each goniospire area of about equal length, but considerable variation between those of different goniospire areas (Pl. 1, Figs. 2-8; Text-fig. 2); the longest nearly one-third the dimension of the plate. Distal end of each slit clearly defined. Goniospire folds concealed below surface of plates (Pl. 1, Fig. 7).

Plates ornamented with low, narrow (in part faint or interrupted) ridges more or less radiating from plate center to each adjacent plates and thus bisecting the sides of the plate (Text-fig. 2); those from each B to the pair of IBB plates below becoming subparallel (Pl. 1, Fig. 10).

*Remarks.*—The apparent absence of goniospire development in the RA-R-X junction in both the known specimens may be anomalous. Such a goniospire is developed in most porocrinid specimens, although it is typically small. In the holotype, the R of the B-ray lacks an arm facet and the oral surface has no ambulacrum leading to it (Pl. 1, Fig. 2); the arm facet is present in the corresponding R in the hypotype (Pl. 1, Fig. 8), and I conclude that the holotype is anomalous in this feature.



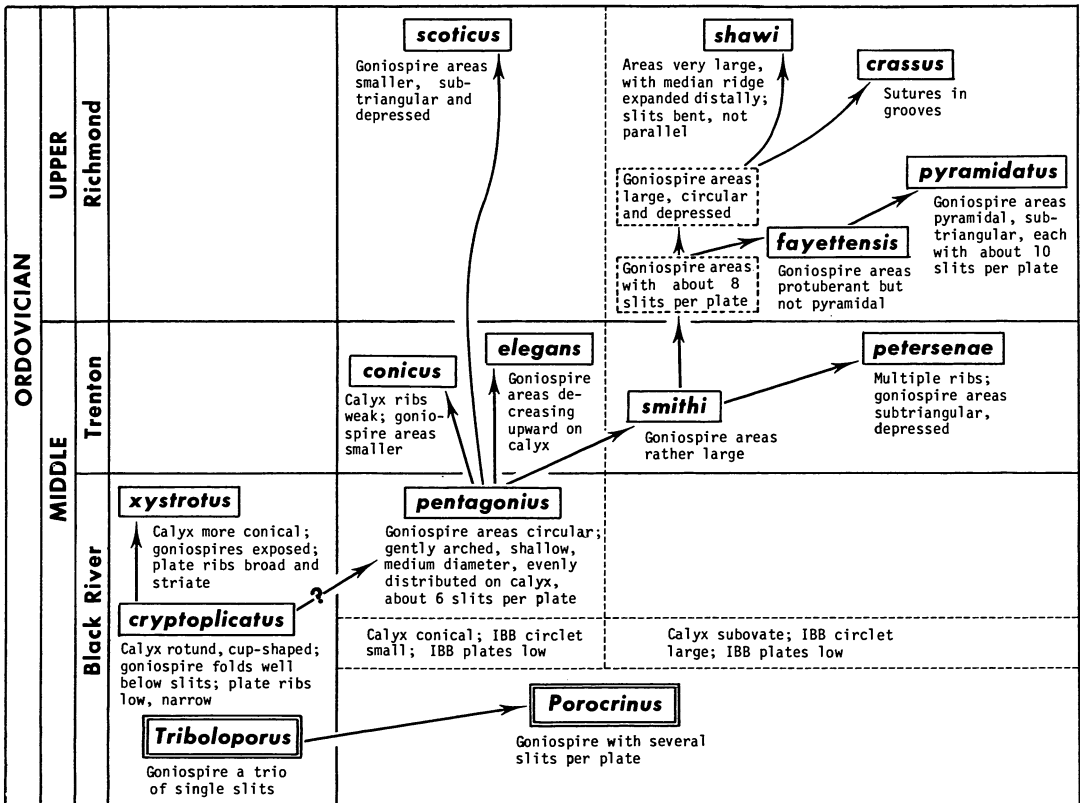
The column is probably incomplete in the hypotype (Pl. 1, Figs. 8–11); however, in the 1.2mm preserved, it has tapered from 1.7 mm to only 0.7 mm in diameter. I consider it unlikely that the column was ever much longer. The specimen has little or no development of a goniospire at the R-B-B junction in the A-ray (Pl. 1, Fig. 8) and possibly the crinoid lay with this side on the sea floor.

If, as seems logical from their size differential, the hypotype is immature and the holotype is adult, then the ornamentation of ridges seems to have become less pronounced with age. This and the diminution of certain goniospires (which are presumed to have been in contact with the sea floor) indicate that the animal had the ability to resorb and re-secrete calcium carbonate to modify its skeleton.

EVOLUTIONARY TRENDS IN THE POROCRINIDAE

At least nine trends become apparent in the simple cladogram shown as Text-fig. 3. Two involve the generic change from *Triboloporus* to *Porocrinus*, another the change from *T. cryptoclasticus* to *T. xystrotus*, and the others changes observed within the genus *Porocrinus*.

(1) *Goniospire areas with one slit per plate to those with several slits per plate.*—The increase in slits per plate has been emphasized by Paul (1975, p. 17, Fig. 1). *Triboloporus* has but one slit or pair of slits per plate in each goniospire area, with the three slits or close-set pairs confluent at



TEXT-FIG. 3 — Simple cladogram outlining evolutionary trends in the family Porocrinidae.

the plate triple junction. *Porocrinus*, on the other hand, has at least six slits in each well-developed goniospire area in all species. No intermediate numbers of slits have been found. The generic change, therefore, seems to have been a quantum jump in development of slits, at least insofar as the record of the family is known.

(2) *Goniospire folds becoming parallel*.—In addition to the increased number of slits and corresponding infolds, the change from *Triboloporus* to *Porocrinus* is marked by the attitude of the goniospire folds. Those in *Triboloporus* are arranged in divergent pairs, each about 45 degrees to the surface of the plate; those in *Porocrinus* are nearly vertical and parallel. Again, no intermediate stages are known in which the folds have slight divergence.

(3) *Goniospire folds emergent to the surface*.—In *Triboloporus cryptoplicatus*, the fold between the two pleats or pockets of the goniospire is well below the surface of the plate, visible only deep within the slit. In *Triboloporus xystrotus* and in all species of *Porocrinus*, the fold or folds project to the surface of the goniospire area. Whether one classifies *T. xystrotus* as having in each plate a single slit divided by an emergent fold or, as Paul (1979, p. 424) suggests, two close-set slits, is a matter of terminology.

(4) *Cup becoming more subovate*.—The oldest known species of *Porocrinus* (*P. pentagonius*) has a subconical cup. This shape persisted in *P. conicus*, *P. elegans*, and the British Upper Ordovician *P. scoticus*. *Porocrinus smithi* and its Trenton and Richmond descendants, on the other hand, are more nearly subovate. The conical shape is largely the product of a small IBB circler combined with high IBB plates, whereas the subovate shape results from a large IBB circler and low plates. Once established, the subovate shape permitted larger goniopore areas and more slits.

(5) *Goniopore areas becoming pyramidal*.—This trend is shown only in the lineage from *Porocrinus smithi* to *P. pyramidatus*. In *P. smithi* the goniopore areas are only very gently arched; in *P. fayettensis* they are slightly protuberant but not yet pyramidal; and in *P. pyramidatus* the three facets form a low pyramid in each area (Text-fig. 4).

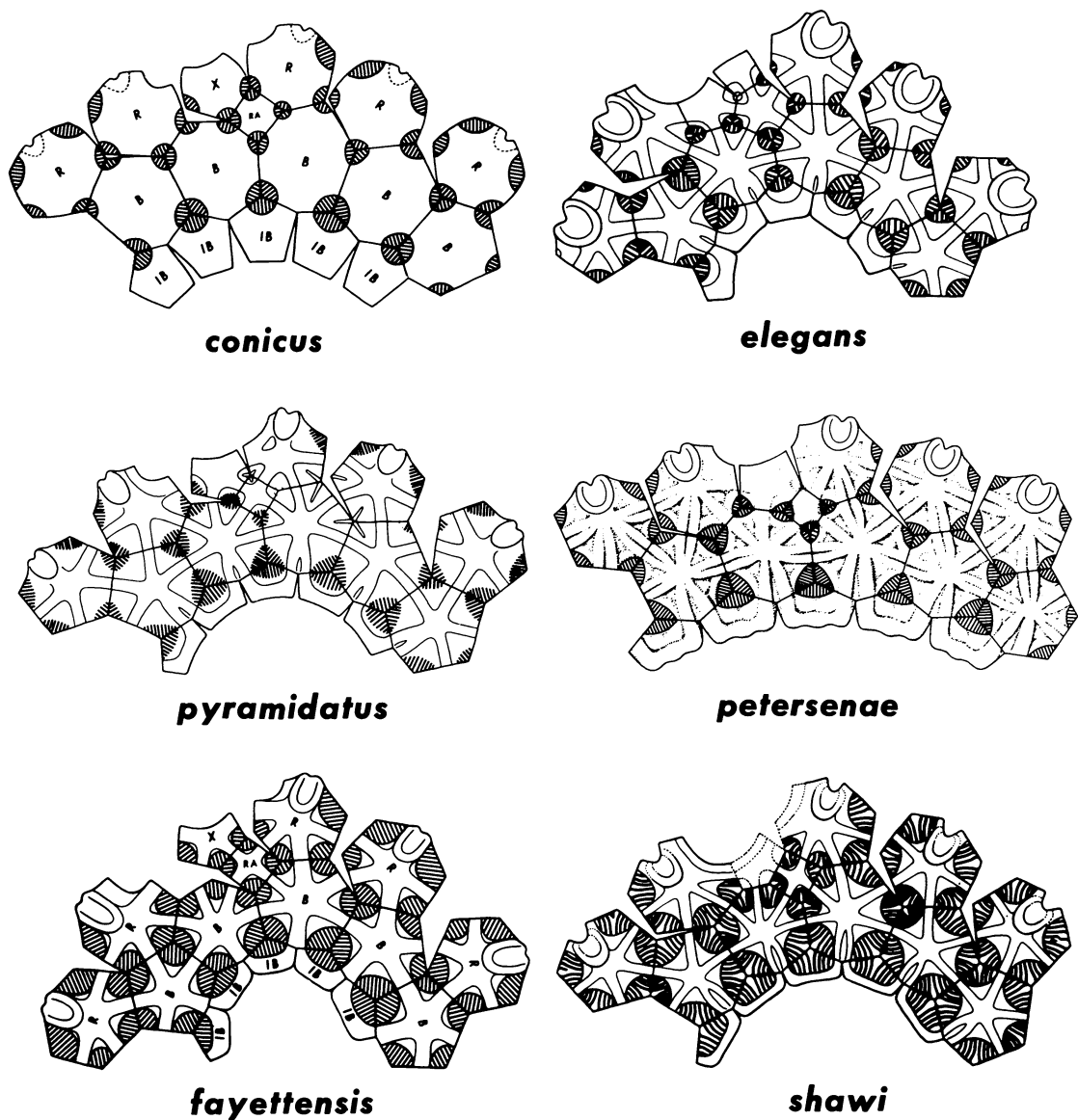
(6) *Goniospire areas becoming subtriangular*.—This tendency appears sporadically; it does not seem to denote a lineage, and may well be a case of convergence. It occurs in the Trenton *P. petersenae*, the North American Richmond *P. pyramidatus*, and the British Upper Ordovician *P. scoticus*, species which have no relationships in calyx shape, number of slits per plate, or shape of goniospire areas.

(7) *Depression of goniospire areas*.—This feature is simply an expression of increased thickness of the portion of the plates not involved in goniospire areas. It is pronounced in *Porocrinus petersenae*, *P. crassus*, *P. shawi*, and *P. scoticus*. These species differ in other respects, even in the relative size of the goniospire areas. The thickening of plates seems to have been an attempt to produce a stronger framework of the calyx, a critical problem for all members of the Porocrinidae brought on by the triple junctions being weakened by the thin goniospires.

(8) *Enlargement of goniospire areas*.—This general trend in North American porocrinids is well shown by comparison of the B plate of the AE-interray in three species:

	<i>conicus</i>	<i>fayettensis</i>	<i>shawi</i>
Goniospire area/remainder of plate	23%	54%	92%
Goniospire intercepts/total perimeter	50%	71%	85%

The area of this B plate can be divided into the goniospire areas (for respiration) and the non-goniospire areas (for strengthening the calyx). In *Porocrinus conicus*, the oldest of the three



TEXT-FIG. 4 — Cup plate diagrams of six representative species of *Porocrinus*.

species, the ratio of goniospire/non-goniospire areas averages only 23% in two specimens measured (GSC 22888 and GSC 1423d); in *P. fayettensis* the ratio is 54%; and in the Richmond *P. shawi*, with extremely large goniospire areas, the ratio reaches a remarkable 92% (Text-fig. 4). The extent of goniospire enlargement is further emphasized by comparing the amount of the perimeter occupied by goniospires to that occupied by strengthening non-goniospire areas (in most species developed as ridges). In *Porocrinus conicus* (based on specimen GSC 1423d), 50% of the perimeter is devoted to goniospire areas in *P. fayettensis* (holotype UCWM 24700), 71% is used for goniospire areas; and in *P. shawi* (holotype USNM 28145), 85% is occupied by goniospire areas and only 15% by the intervening ridges.

Obviously, enlargement of the goniospire areas for respiration is necessarily achieved by reduction in the strength of the calyx framework or girder system of ridges and thick plate material. Conversely, as Paul points out (1975, p. 16), the enlargement of goniospires was only possible with a more efficient "triangulated" girder system.

(9) *Addition of ribbing to strengthen the calyx.*—Two species of Porocrinidae substituted belts of ribbing from the single ridges connecting adjacent plates in other species. *Triboloporus xystratus* developed low, arched, striate structures in place of the narrow ridges of *T. cryptoplicatus*, and *Porocrinus petersenae* (Text-fig. 4) developed multiple ribs. Both appear to have been attempts to obtain additional calyx strength without additional weight by corrugation.

### FUNCTIONAL INFERENCES

The whole history of the Porocrinidae involves varying solutions to the conflict between respiration through goniospires and calyx strength through reinforcement of the girder system of ribs. The trends outlined above suggest the method of operation of the diagnostic goniospires in the Porocrinidae.

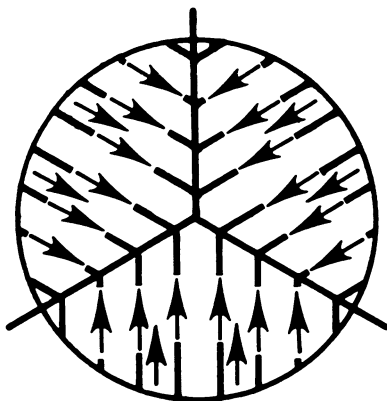
(1) *Direction of flow in goniospires.*—That the goniospires were respiratory structures is not questioned. The endothelial folds, divergent in *Triboloporus* and isoclinal in *Porocrinus*, are composed of calcium carbonate sufficiently thin to have served for gas exchange between the oxygen derived from sea water and the carbon dioxide excluded from the body. To have been efficient, the directions of internal body fluids and the external sea water flow were most likely opposite.

The direction of flow in the pectinirhombs is readily inferred in some cystoids by the taper of the slits (to avoid entrapment of foreign particles) and in certain other cystoids by the development of separate inhalent and exhalent openings of different widths. In a few cystoids, the latter are combined into a spoutlike structure to further aid in directing the oxygen-depleted water away from the calyx.

The direction of flow in goniospires is more difficult to decipher, inasmuch as three sets of folds are involved in each. With six half-sets of slits in each goniospire area, 68 ways of circulation are possible, involving 16 different patterns. Goniospire slits are equally wide throughout their length, showing no taper; nor are the slits modified as inhalent and exhalent openings. Hence, their operation differed from that of the pectinirhombs by nature of their geometry.

Two recurrent features of goniospire areas, however, may offer an indication of the external flow direction. First, the areas in *Porocrinus fayettensis* and, especially, *P. pyramidatus* (Text-fig. 4) are protuberant at the center, with each plate providing a triangular facet. If these species had circulation comparable in any manner to that in certain advanced cystoids, in which the exhalent spouts protrude, then it would appear that the exhalent ends of the goniospires lay along the plate junctions. Second, several species of *Porocrinus*, including *P. petersenae*, *P. pyramidatus*, and *P. scoticus*, developed subtriangular goniospire areas (Text-fig. 4). Presumably, this shape did not adversely affect the efficiency of circulation. If so, the distal ends of the slits would seem to have functioned equally well whatever their distance from the plate edge; this would be the case if the periphery of the goniospire area acted as the intake area.

From these considerations, I agree with Kesling & Paul (1968) that the logical circulation pattern included entry of oxygen-bearing sea water at the outer ends of the slits (rim of the goniospire area), conduction through the goniospire channels toward the plate junctions, and



TEXT-FIG. 5 — Inferred external circulation (current directions) in goniospire slits and folds of porocrinid.

expulsion of the oxygen-depleted, carbon-dioxide-enriched water in a narrow triradiate area along the plate edges (Text-fig. 5). In this pattern, the “used” water would have been forcefully directed away from the calyx by the convergence of currents.

(2) *Attitude of the animal.*—Very few porocrinids have much of the column preserved and I know of none with an unequivocal distal termination. In the new specimen of *Triboloporus cryptoplicatus* (Pl. 01, Figs. 9-11), the preserved section of the column tapers rapidly away from the crown. In a specimen of *Porocrinus conicus* illustrated by Kesling & Paul (1968, Pl. 7, Fig. 5), the proxistele is strongly tapered and the mesistele is very thin; it is doubtful that this column could have kept the animal upright against currents of any appreciable strength.

Still another line of evidence on the attitude of the animal should be noted here. The calyx of specimen CGS 22888 of *Porocrinus conicus* is noticeably flattened on the C-ray side (see Kesling & Paul, 1968, Pl. 7, Fig. 1). In this area, the junctions of B-B-RA, B-R-RA, and R-RA-X in the C-ray and of R-R-B in the BC-interray are depressed but have no goniospires whatever, although these positions have normally developed goniospires in other specimens of the genus. In addition, the calyx of the holotype of *Porocrinus pyramidatus*, USNM 238630, also lacks goniospires in the area covered by the B-R-RA and R-RA-X junctions in the C-ray, the R-R-B in the BC-interray, and the B-B-R junction in the B-ray (see Kesling & Paul, 1968, Pl. 5, Figs. 1,2,5); these junctions are marked by depressions and three of them bear a triradiate structure formed by the meeting of three small ridges, each bisecting a plate corner.

My conclusion is that some, perhaps many, individuals of porocrinids were unable to maintain an erect position by their feeble columns, but continued to survive prostrate on the sea floor. The plate junctions in contact with the bottom either failed to develop goniospires, or the goniospires there “smothered” and were filled in with secondary secretions of calcium carbonate.

(3) *Tegminal protection of the oral opening.*—Re-examination of specimens of *Triboloporus* and *Porocrinus* indicates that plates of the tegmen, as well as those of the cup, were essentially fixed in a pattern at the first appearance of the family and remained unchanged throughout its history. This tegminal protection of the vital mouth area was structurally very weak.

The dominant feature in the ventral region of the calyx is a circlet of five large OO around the large mouth opening or peristome, of which the posterior (CD-interray) O is much wider than the others. Ambulacral grooves, clearly exposed in most specimens, lead from the arm facets to the mouth along junctions of the OO. In the center of the tegmen and extending out beyond the perimeter of the mouth opening is a rosette of ten wedge-shaped plates, with a matched pair in

each interray. These radially arranged plates probably formed a low dome above the opening; as preserved in all specimens examined, however, the plates have collapsed into the mouth opening. Very few specimens have been found showing the series of small plates covering the ambulacra between the rosette and the arm facets, but they appear to have been disposed in biserial fashion and more or less a continuation of the ambulacral covering plates of the arms.

The identical pattern of central rosette plates apparent in *Triboloporus cryptoplicatus* and *T. xystrotus* can be seen at least partly preserved in several specimens of *Porocrinus*. Thus, the restoration of *Porocrinus conicus* by Kesling & Paul (1968, Text-figs. 11, 12), showing irregular plates in the middle of the tegmen, is in error. From an engineering standpoint, the rosette of plates was particularly weak; it was simply one more of the structural shortcomings of this short-lived family.

(4) *Protection of the anal opening*.—No trace of plates associated with the very large anal opening or periproct has been found. Possibly, the anus lay within this area surrounded simply by puckered skin. If this dermal layer were provided with ossicles of appreciable size, one might expect that some would have been preserved; none has. The anus seems to have been even more vulnerable than the mouth.

(5) *Resorption and re-secretion of plate material*.—All plates which have goniospires increased their extent by peripheral growth. The complexity of maintaining essentially straight goniospire folds and slits at an angle to plate edges and growth direction has been discussed by Kesling & Paul (1968, p. 8).

In the same porocrinid specimen, some goniospire slits are long, others short, and occasionally they are absent in calyx locations where slits occur in other specimens. The diminution or absence of a goniospire can be explained only as: (1) the incipience of certain goniospire areas at a later than normal ontogenetic time (if ever), or (2) the filling in of unnecessary or non-functional goniospire structures by additional plate material. The first suggestion seems highly unlikely; I cannot envisage conditions within the animal or in its environment which delay goniospire formation. On the other hand, it is reasonable to assume that goniospires in certain areas were retarded in their respiratory function by the animal losing its upright position and coming to lie on its side on the sea bottom.

Every slit adjoins that of another plate; no slit has ever been discovered which is separated from the plate edge by a band of calcium carbonate. Hence, whenever a goniospire was altered, the whole structure was re-modeled or replaced. This must of necessity have involved resorption of the goniospire folds within the plate as well as filling of the slits. The process was accomplished by the porocrinid so precisely that no scar of the former slit or its proximal extension can be detected.

The weaker (even interrupted or eliminated) ridges in the immediate areas which lack normal goniospires also indicate resorption of carbonate. It may be proposed that this material was converted by the porocrinid to a more efficient use or urgent need, such as plugging the smothered goniospire slits.

## CONCLUSIONS

The wonder is not that the porocrinids became extinct, but that they managed to survive for as long as they did. Paul stated (1979, p. 415):

The different evolutionary patterns at class and generic level probably result from colonization of the marine biosphere initially under conditions of low competition

which allowed relatively inefficient "designs" to survive, followed by later elimination of less efficient groups as competition increased. This colonization-radiation/competition-retrenchment model implies that early, small, short-lived groups were less efficient than larger, extant classes.

This certainly applies to the porocrinids at the family level.

The Porocrinidae evolved no innovations in plates of the crown. The same arrangement of IBB, BB, RR, RA, X, OO, and tegminal plates is present in all members of the family. Both mouth and anal openings remained large, presumably over-size for their function. In both early and late forms, the column tapered rapidly away from the calyx.

The whole evolutionary history of the family is dominated by a dilemma: increasing the size of the goniospire areas for greater respiration while still retaining enough plate area for a girder system of ridges to keep the calyx intact. The trend toward enlarged goniospire areas points to an increased need for oxygen. Situated low above the sea floor or upon it, the porocrinid may well have been at an increasing disadvantage in the battle for oxygen as well as food as new competitors evolved.

Its basic form was scarcely a match for that of some of its contemporaries. I agree with Paul (1979, p. 424) that "clearly the three-pronged goniospires can never develop an efficient respiratory current system." Likely, goniospires were less well suited for respiration than were the pectinirhombs of rhombiferan cystoids; further, being situated at plate corners, their mode of growth was much more complex than that of pectinirhombs, which were along plate sides, and involved continuous compensation and adjustment to maintain the direction of the slits. An ultimately more successful solution to respiration was achieved by those crinoids which performed that function in the arms, and thereby avoided the conflict between special structures and strength of the calyx.

The body of the porocrinid was poorly protected. For an animal fixed near or on the sea floor, its calyx, weakened by goniospire areas, was particularly vulnerable to crushing. The digestive tract was inadequately shielded at its ends; the large mouth was covered by a weak rosette of plates and the large anal area by skin (whether or not reinforced by ossicles).

Surprisingly, no porocrinid is known to have experimented in ways by which (1) respiration could be accomplished better than by enlargement of goniospire areas, (2) the column could be strengthened to provide better and higher support of the crown, (3) the mouth and anal openings could be reduced to a size in keeping with their functions, (4) the anal opening could be protected by a plated chimney and shifted into the tegminal area, or (5) the arms could be made stronger by larger facet areas, more movable by increased fulcra, and more efficient by branching.

Briefly stated, crinoids of the porocrinids were non-adaptive in a time of rapidly increasing competition—with predictable results.

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