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MORPHOLOGY AND RELATIONSHIPS OF *CYCLOCYSTOIDES*

BY

ROBERT V. KESLING

FROM THE

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CONTENTS

INTRODUCTION

THE GENUS *Cyclocystoides* contains an enigmatic assemblage of Paleozoic fossils, most of which are known primarily from the well-preserved ring of submarginal plates. Because these organisms are poorly understood, reliable separation into species cannot be made, and the family Cyclocystoididae includes only one distinct genus, the type genus. Cyclocystoids are small, subcircular, disk-shaped objects, apparently without columns and attached by the flat aboral side. The central parts, called disks, of both oral and aboral sides seem to have been weakly calcified, and the food-gathering structures are inadequately represented. Nevertheless, the association of features described in various cyclocystoids indicates that essential hard parts of these fossils have been discovered, that *Cyclocystoides* is an extinct pelmatozoan echinoderm, and that it is more closely related to the Cystoidea than to other taxa.

Although *Cyclocystoides* ranges from Middle Ordovician to Middle Devonian, relatively few specimens are known. This scanty record may be due in part to the small size and poor preservation, but mostly it may be attributed to lack of interest in fossils so imperfectly understood and to consequent perfunctory collecting.

The classification is deficient for two reasons. First, the paucity of the record does not reveal much of the diversity that probably existed in the group. Second, the essential systems of the animal cannot be discerned in sufficient detail for clear recognition of differences; very few specimens permit comparison of oral and aboral sides. Only one genus, *Cyclocystoides,* is accepted by all workers on the group, and this seems to be a matter of nomenclatoral necessity rather than a taxonomic conclusion.

Certain characteristics of cyclocystoids strongly invite comparison with other pelmatozoans. The disk-shaped theca and the marginal ring of tiny plates, imbricating and partly embedded in flexible integument to form a "shagreen," are remarkably like those in edrioasteroids. The facets, small tubercles with surrounding grooves lying in the submarginal ring, resemble the brachiole facets of cystoids. The sharp differentiation of oral and aboral surfaces and the ramification of the ambulacral system are more nearly like those in crinoids.

Differences, however, set the cyclocystoids apart as a class discrete from these other pelmatozoans. Multiple branching of the ambulacral system is unknown in the edrioasteroids; the flattened shape is foreign to the cystoids; and the flat aboral (dorsal) surface is unlike that in any crinoid. Other points of dissimilarity could be mentioned. Despite our ignorance of parts of their morphology, we can clearly separate the cyclocystoids from other echinoderms. Hence, they make up the class Cyclocystoidea.

In studying cyclocystoids, I selected *Cyclocystoides halli* Billings as the species for reconstruction. This is not only the type species of the genus, but it has more specimens showing characteristics of both sides than has any other species. For particulars on the junctures of certain parts, I have had to rely upon information from other species. Nevertheless, all features incorporated in my reconstruction are substantiated by fossil evidence.

In the course of this investigation, I examined specimens of *Cyclocystoides* from the Museum of Paleontology at the University of Cincinnati through the courtesy of Professor K. E. Caster. Most of the information, however, was assembled from published reports.

PREVIOUS WORK

Contributions to the knowledge of cyclocystoids are few. They are marked by tentative interpretations and confessions of doubt. Some are confused in orientation.

The first published account of one of these fossils by James Hall in *Report of the Geology of the Lake Superior Land District* by Foster and Whitney (1851, p. 209). Hall briefly described a specimen from the Escanaba region of Michigan and concluded that "This curious body is evidently

Crinoidean ... It is possible that it may be the elevated marginal ring of some one of the sessile Crinoids."

In 1858 (p. 86), J. W. Salter and Elkanah Billings named *Cyclocystoides* and presented a remarkably good analysis of its organization. They distinguished the "integument of the upper side" from the "integument of the under side," and accurately described the ring of submarginal plates (which they called "marginal plates") as bearing a channel with "marginal excavations" and "connected with the interior by small pores penetrating through the marginal plates." They erred in assuming that a dissociated tubelike fossil was part of *Cyclocystoides,* but on the whole their account is more lucid than several which appeared more than fifty years later. Salter and Billings (1858, p. 90) stated, "Regarding the affinities of the fossils, the choice seems to be between Star-fishes and Cystideae"; they also compared *Cyclocystoides* with *Amygdalocystites,* now regarded as a paracrinoid.

James Hall (1872, Pl. 6, Fig. 16) gave a figure showing an oval eccentric opening in the oral disk, which he interpreted as the mouth. In a modified version of the figure (1900, Fig. 8), F. A. Bather called this opening (p. 211) the "supposed region of the anus."

S. A. Miller and C. B. Dyer (1878, pp. 10–11) confirmed the presence of ducts or pores through the plates of the submarginal ring. In 1882 (p. 223), S. A. Miller set up the family Cyclocystoididae, without pertinent distinctions from other families. In 1895 (p. 61), Miller and W. F. E. Gurley erected the order Cyclocystoidea, more or less as a convenience in directing attention to the singular features of *Cyclocystoides.* F. A. Bather (1900, pp. 210–11) discussed the genus in his chapter on Edrioasteroidea, but he stated that it "probably belongs to this class, though not to any of the recognized families." This concept of diverse forms in the edrioasteroids reflects Bather's conviction that the "Edrioasteroidea are alone among Pelmatozoa in presenting a type of ambulacrum from which the holothurian, stellerid, and echinoid types may readily be derived."

P. E. Raymond (1913) believed that he could discern small plates covering the facet-bearing channel, or circular canal, in the distal part of the submarginal plates. He redescribed and refigured one of Salter and Billings' specimens. He paid special attention to the oral disk, and distinguished five main ridges that by successive bifurcations lead to the submarginal ring. Regarding the ambulacral system, he wrote (1913, pp. 27–28), "These ridges probably cover ducts which lead from the [submarginal] plate to the centre, and the inference might be that through them, food, in water, was carried from the series of collecting basins in the outer circular canal to the mouth, which would be central and beneath the plates of the disk." Raymond was uncertain, to say the least, about affinities of *Cyclocystoides;*

he thought the animal might be a "free Cystidean or Edrioasteroid," "highly specialized root of a free crinoid," or "it is even possible, if one is sufficiently imaginative, to think of this disk as a swimming organ, the method of propulsion being on the same principle as in some of the cephalopods."

Otto Jaekel (1918), in his monographic review and revision of the Pelmatozoa, ignored *Cyclocystoides*.

A. F. Foerste (1920, p. 34) assigned the Cyclocystoididae to the Edrioasteroidea, and distinguished, in addition to the type genus, two new genera, *Narrawayella* and *Savagella,* and an unnamed genus exemplified by *C. illinoisensis* Miller and Gurley. Foerste's new genera have not been generally accepted.

Foerste later (1924, p. 80) gave particular attention to *Cyclocystoides huronensis* Billings. He described "spout-like appendages" at the border of the submarginal and marginal rings, equal in number to the facets in the channel of the submarginal ring; such structures have not been confirmed by anyone else. Foerste also described an unnamed species from Tennessee as having marginal plates sloping outward, and went on to say (1924, p. 81): "This outward sloping of the marginal plates is so frequent in *Cyclocystoides* as to suggest that these plates could be moved at will, either so as to slope inward, thus covering the outer margin of the submarginal ring of plates, or so as to slope outward, exposing the margin." Thus, Foerste supported Salter and Billings' (1858) and Raymond's (1913) contention of plates covering the circular channel in which the facets are located. No author elaborated on such plates, and no convincing figures were offered to support this very important consideration. The "outward sloping" nature of the structures noted by Foerste leads me to the conclusion that they were not marginal plates but were broken distal, upturned edges of the spoon-shaped depressions in the submarginal plates. Inadvertently, Foerste seems also to have mistaken the collapsed oral disk for the aboral disk in his figure of *C. huronensis* (1924, Pl. 6, Fig. 3). Ten years later, this figure was copied by J. L. Begg (1934, Pl. 9, Fig. 7), who relied heavily on it for certain aspects of orientation; as a result, parts of Begg's descriptions are rather confused.

Begg (1934, pp. 220–24) compared *Cyclocystoides* with the carpoid *Cothurnocystis*. Although he referred to the oral disk as the "lower plate" and the aboral disk as the "upper plate," he described the submarginal ring as "beyond the spoon-shaped depressions [facets], and sloping downward and outward." At least part of the oral-aboral confusion was undoubtedly occasioned by the preservation of many of his specimens as external molds; yet some of Salter and Billings' original specimens were similarly preserved, and I am unable to follow some of Begg's comparisons.

Hertha Sieverts (later Sieverts-Doreck) in the same and the following year reviewed Begg's article. She further proposed (1934, p. 975; 1935, p. 46) that the facets were places for attachment of brachioles.

Gerhard Regnéll (1945, pp. 44–47, 215–23) reviewed the assignments of *Cyclocystoides* and described two species from Gotland in considerable detail. Concerning the facets, he stated (1945, p. 223), "The mamillary elevations cannot have been facets of brachioles, as supposed by H. Sieverts, 1934, nor is there anything to indicate that they were bases of spines. Both theories are made impossible by the fact that the canal, in which they are located, was evidently roofed over by small movable plates." Recently, however, Regnéll seems to have changed his position, for he wrote (1960, p. 78), "In the opinion of the present writer, *Cyclocystoides* differs so radically from the edrioasteroids that an attribution to that class is definitely not advisable .... The theca of the edrioasteroids is not differentiated into a dorsal and a ventral disk; the ambulacral cover-plates are invariably biserial; the ambulacral system is never tetra-radiate; brachioles do not occur in edrioasteroids." The implication is clear that *Cyclocystoides* does possess brachioles.

Hertha Sieverts-Doreck (1951) summarized previously described specimens and analyzed morphology; she revised ordinal, familial, and generic diagnoses; and she described a new Devonian species—all in excellent detail. Unquestionably, her work is the best substantiated, as well as the most concise, discussion of morphology.

MORPHOLOGY

General organization.—The cyclocystoid bears at least superficial resemblances to the edrioasteroid. Both of these pelmatozoans are disk-shaped and both acquire rigidity from peripheral rather than central elements.

The cyclocystoid theca was somewhat like a thin, inflated drum. The submarginal ring of stout plates formed the relatively rigid sides, the aboral disk extended across one side like a drumhead, and the oral disk arched across the opposite side (Fig. 1*b*). Although the two disks are collapsed and lie in close proximity in the fossil state, presumably space between them accommodated the soft organs in the living animal. The oral disk appears to have had greater flexibility or elasticity than the aboral disk, at least in some species. Possibly, it took on the shape of a blister, expanding in response to internal pressure.

The submarginal ring is made up of numerous thick, complex plates, which have surfaces exposed on both oral and aboral sides of the theca. Aborally (Fig. 2), the submarginal plates appear as truncated wedges; orally (Fig. 1*a*), they have distal beveled or concave surfaces that together

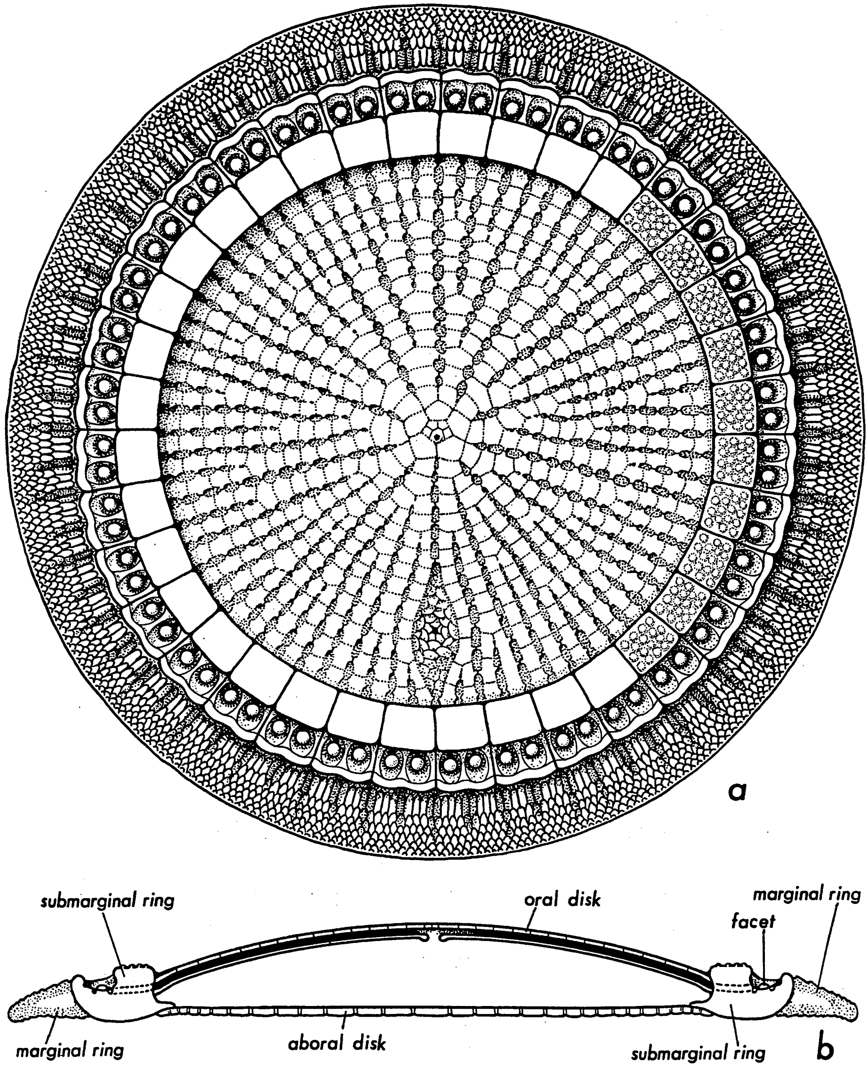

FIG. 1. *Cyclocystoides halli* Billings. *a*. Restoration of theca as viewed orally; ornamentation on proximal part of submarginal plates shown on only those at the right. *b*. Hypothetical cross section along ambulacra.

constitute a circular channel. In the channel, each plate bears one to four facets (Fig. 1*b*), presumably for attachment of brachioles. The proximal part of the submarginal plate is elevated, overhanging, and rather fiat-topped. Grooves lead from the facets to ducts or holes penetrating the proximal part of the plate, and these in turn connect with enclosed passageways just under the surface of the oral disk. These structures—facets, grooves, ducts, and passageways—are considered to be elements of the ambulacral system. The passageways proximally unite by pairs as they approach the center of the oral disk, and are properly regarded as ambulacral grooves (Fig. 3).

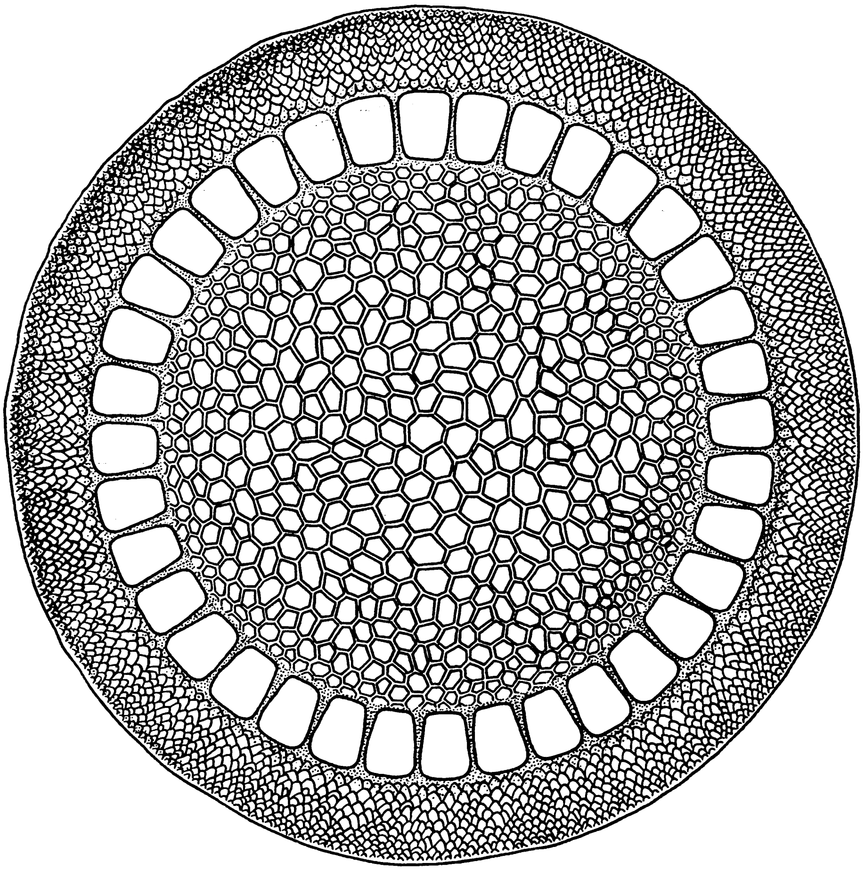

FIG. 2. *Cyclocystoides halli* Billings. Restoration of theca as viewed aborally. Compare with Figure 1*b* for identification of parts.

Surrounding the submarginal ring and forming the border of the cyclocystoid is the marginal ring (Fig. 1*b*), a band of small imbricating platelets that were probably embedded in flexible integument.

Orientation of the cyclocystoid is only inferred. It is believed by most paleontologists that the oral disk, which contains the hidden ambulacral grooves leading to the mouth, was uppermost, and that the more rigid, flat aboral disk, which possesses no essential openings, was lowermost in the living animal. Thus, the brachioles (or whatever kind of food-gathering structures were present at the ends of the ambulacral system) were on the upper side. The cyclocystoid probably remained attached to the sea bottom like a limpet, creating suction under the aboral disk by muscular contraction of the marginal ring.

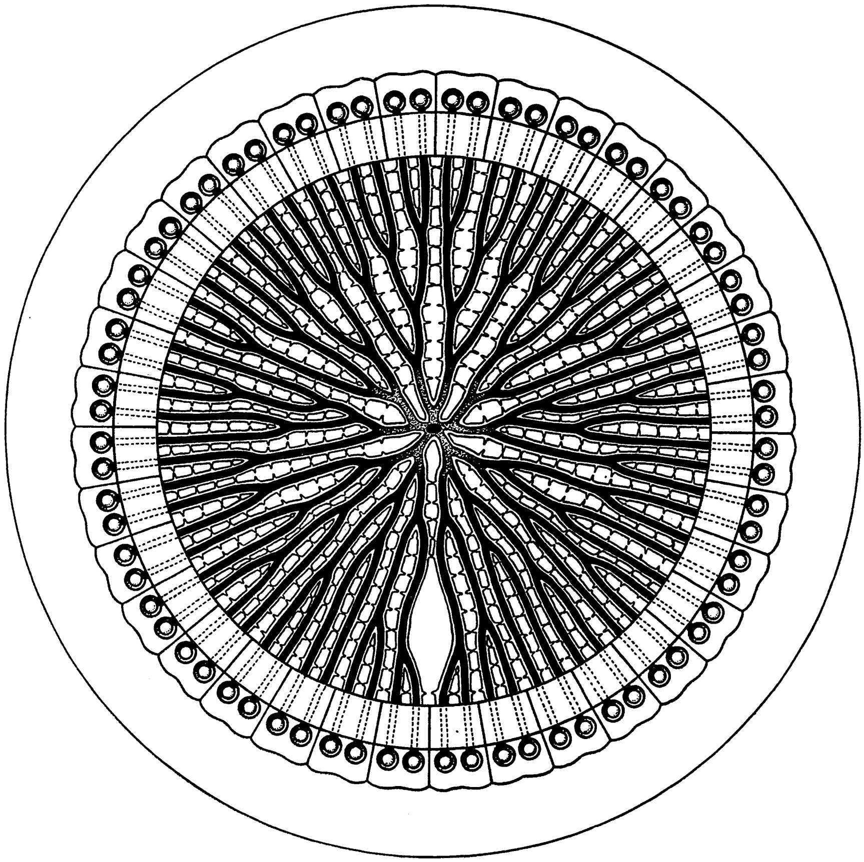

FIG. 3. *Cyclocystoides halli* Billings. Restoration of theca, with ambulacral covering plates removed to expose the ambulacral grooves (black) lying in the ambulacral flooring plates, as viewed orally. Compare with restoration of complete theca in Figure 1*a*.

Oral disk.—The oral disk has two significant characteristics—it contains a complicated ambulacral system and it undoubtedly possessed great elasticity. This is an unusual combination in pelmatozoans. Even the edrioasteroids, in which some degree of flexibility is indicated by the imbrication of interambulacral plates in many species, had limited expansion of the flooring and covering plates of the ambulacra.

On the oral surface, that which is exposed in a well-preserved specimen, the dominant feature of the disk is a set of low ridges which from the center bifurcate successively and radiate to the surrounding submarginal ring. This system of branching was well described by Raymond (1913, p. 27): "Upon analysis, it is seen that there are one or two ridges in front of each of the submarginal plates, and that each two adjacent ridges quickly unite to form a single ridge. Two of the ridges thus formed unite a little nearer the centre and are joined quite close to the centre by another long ridge formed from four shorter ones." Sieverts-Doreck (1951) was particularly concerned as to whether the branching was isotomous or heterotomous; unfortunately, so few specimens show the complete disk that the branching cannot be determined, nor can its taxonomic value be tested.

Some details of the plates are not clear, because the plates are thin and their edges are not sharply delineated, as emphasized by Sieverts-Doreck. This condition of plates is much like that in Recent holothurians, and supports the hypothesis that the plates of the oral disk lay embedded in an integument. At any rate, there is a sharp difference between plates of the oral disk and those of the submarginal ring. In his description of *Cyclocystoides halli,* Billings (*in* Salter and Billings, 1858, p. 87) early established that "the integument of the upper side, supposed to be the side on which the marginal plates are excavated, is connected to the inner edge of those plates [submarginal ring] and does not extend over them." This relationship of oral disk and submarginal ring has been confirmed in another species: in *C. lindstroemi,* Regnéll (1945, p. 217) reported that "the inner margin of the ossicles [submarginal plates] overlap slightly the adjacent rays of the central disk."

The number of ridges at the periphery of the oral disk was at first thought to equal the number of submarginal plates. In *Cyclocystoides davisii,* Salter (*in* Salter and Billings, 1858, pp. 89–90) said, "This species shews the complete surface, on which about as many radiations mark the margin as there are ossicles." In *C. decussatus,* Begg (1934, p. 221) stated, "The submarginal area is composed of thirty-two plates or ossicles, corresponding to an equal number of rays on the central disc." It seems plausible, however, to assume that all species were constructed similarly to *C. devonicus.* In that species, as described by Sieverts-Doreck (1951, pp. 14–15), each of the facets is aligned with a duct through the proximal, elevated part of the submarginal plate and each duct leads to an ambulacral groove. Thus, the peripheral number of ridges is the same as the number of facets, rather than the number of submarginal plates.

As Sieverts-Doreck (1951, pp. 23–24) pointed out, the plates composing the ridges are uniserial and serve to cover the ambulacral grooves or ducts. Thus, they are ambulacral covering plates, fulfilling the same protective function as the biserial covering plates in cystoids. The outer surface of the ambulacral covering plates may vary from one species to another. Those in *C. devonicus* were described as somewhat papillate or tuberculate. Regnéll (1945, p. 217) stated that "Each ray is divided medially by a faint groove . . . ." but added, "The rays seem to have been solid." Begg (1934, pp. 220–21) described *C. decussatus* as: "Each ray is probably divided medially, for the greater part of its length, by a thin narrow longitudinal ridge." From the sides of each ambulacral covering plate, one or possibly more lateral processes extend to meet similar processes on plates of the adjacent ridge or row, at least in *C. decussatus, C. lindstroemi,* and *C. devonicus*. These processes taper distally, so that they resemble spines. Those of most plates seem to be set directly opposite, but some variations have been reported. Together, the ridges and the lateral processes give the outer surface of the oral disk a reticulate appearance, the ridges being radial and the processes being more or less concentric.

Little is known about the junctions of the ambulacral covering plates in each row. Foerste (1924, p. 81) stated that in a specimen of *C. illinoisensis* Miller and Gurley, "the ventral or upper disk consists of numerous scutellate plates imbricating toward the centre of the disk." No other author has suggested imbrication in these plates, and one may question whether Foerste's specimen was normally preserved.

Between the distal parts of adjacent ridges and extending proximally until the ridges join (Fig. 1*a*) is a narrow band of small plates, the interambulacrals. Although the edges of these plates, like those of the adjoining ambulacral covering plates, are poorly defined, it appears that the interambulacrals are uniserial. They are set somewhat below the general level of the ambulacral plates and their sutures may be hidden by the spinose processes of the latter.

Neither ambulacral covering plates nor the intervening interambulacrals have any pores through them, insofar as known. They seem to have provided a plated cover, ribbed like an umbrella, over the soft parts of the animal.

As Regnéll (1945) and Sieverts-Doreck (1951) have stressed, the oral disk is composed of more than one layer of plates. To enclose the ambulacral grooves, troughlike ambulacral flooring plates are attached under the ambulacral covering plates (Fig. 3). In *C. devonicus,* no divisions of these flooring plates have been discerned, perhaps because they were composed of continuous, weakly calcified sections of integument. In this species, Sieverts-Doreck (1951, p. 23) reported that the flooring plates were supplied with lateral processes like those of the overlying covering plates.

The actual number of ambulacra in the circumoral region may not have been the same in all cyclocystoids. In *C. davisii,* Salter (in Salter and Billings, 1858, p. 90) said, "The center of the flat disk is occupied by a star of about eight narrow rays." In *C. decussatus,* Begg (1934, p. 221) described the central area as having "four rays in the form of a St. Andrew's Cross." In *C. huronensis,* Raymond (1913, p. 29) stated that "only 5 branches reach the centre."

The oral region is poorly known, primarily because the plates there are small, thin, and fragile. An eccentric space between two ambulacral ridges, figured by Hall (1872, Pl. 6, Fig. 16) and supposed by him to be the mouth, can scarcely be interpreted as such, inasmuch as it is removed from the place where the ambulacra converge. Instead, as Bather (1900, p. 211) suggested, it is probably the periproct. No anal pyramid has been discovered in cyclocystoids, and the anus may have been covered by tiny plates no larger or thicker than the ambulacral covering plates and interambulacrals.

Aboral disk.—Underlying the body of the animal, on the aboral or dorsal side of the theca, the aboral disk is a circular layer of plates filling the space within the submarginal ring. In *Cyclocystoides lindstroemi,* Regnéll (1945) determined that the aboral inner edge of each submarginal plate extends as two lappets on the oral side of the aboral disk, so that on the aboral surface (bottom) of the theca, the aboral disk overlaps the border of the submarginal ring.

Most writers who have commented upon the matter agree that the aboral disk had greater strength and rigidity than the oral disk. In some cyclocystoids, the plates of this disk are definitely thicker and have better defined edges than those of the oral disk above.

Plates in the aboral disk are of two kinds. Some cyclocystoids (*e.g., Cyclocystoides wrighti* Begg, *C. halli* Billings) have plates in a mosaic; others (*e.g., C. devonicus* Sieverts-Doreck) have them imbricating in a radial arrangement. As Sieverts-Doreck (1951, p. 10) believed, the mosaic plates probably made a stronger, less flexible layer than did the imbricating plates. In both kinds the size of the plates decreases away from the center.

The imbricating plates are interpreted to have an arrangement corresponding to the branching of the ambulacra in the oral disk. They seem to have been at least partly embedded in integument, so that the structure is indistinct. Nevertheless, Sieverts-Doreck (1951, p. 24) discerned certain features in *C. devonicus;* she reported that the aboral disk is marked by strong radial ridges, which in places are not in contact but are separated by radial grooves. Around a small central area that cannot be deciphered, there are five plates in the shape of a pentagon. One row of plates that could be traced without interruption to the margin of the disk contained 11 to 13 plates. Sieverts-Doreck distinguished two kinds of plates in the aboral disk (1) those in elevated rows, each subquadrate or elongate oval to rounded pentagonal or hexagonal in outline, its surface nodose or tuberculate, many of the corners of such plates depressed, numerous plates broader distally than proximally, lateral processes extending to processes of adjacent rows like those of the oral disk, at many places the plates imbricating toward the margin, and (2) elongate oval, rather flat plates corresponding to the interambulacrals of the oral disk. A small structure near the center in an interambulacral position she called questionably a hydropore, but this location would indeed seem impossible for intake of water.

Some kind of central structure was previously indicated by Raymond (1913, p. 28), who said that in *C. halli* the center of the aboral disk contained "a minute opening, surrounded by an elevated ring of 5 plates. . . ." He added:

> The remainder of the disk is covered by small plates which seem to be arranged in a somewhat radial fashion, with larger plates towards the centre and very small ones at the outer margin. Adjoining the sub-marginal ring, there seem to be two very small plates in front of each sub-marginal plate. These small plates do not make a solid covering, but have large pores between them. Around the small mound which resembles an anal pyramid, there are five small, deep depressions, which may indicate the main trunks of the sinuses which extend beneath the integument.

It is possible, of course, that the minute central opening and the pores near the submarginal ring were features of preservation in the specimen studied by Raymond. It is equally possible that the aboral surface contains more complicated structures than most authors have believed.

In an unnamed species from Tennessee, the aboral disk was described by Foerste (1924, p. 81) in somewhat different terms. He stated: "The dorsal [aboral] disk within the submarginal circle consists of numerous erect plates, like fence-palings in form, which incline inward sufficiently to be said to imbricate in the direction. The height of the more central plates is such as to have produced a strong support though still permitting a certain amount of flexibility." If authors prepared high quality photographs or accurate drawings to show how plates fit together in such a complex, several points of structure would be clarified.

The mosaic type of aboral plates is best exemplified by the specimen of *Cyclocystoides wrighti* illustrated by Begg (1940, Pl. I, Fig. 5), in which the rather close-fitting plates constitute a pavement. The arrangement in *C. halli* has been similarly depicted.

It might be well to direct attention to the state of our understanding of oral and aboral disk relationships. Of the approximately 21 valid scientific names for cyclocystoids, only six have been applied to fossils for which both oral and aboral sides are known.

Submarginal ring.—Because the submarginal ring of plates is the best-preserved part of the cyclocystoid, it has received exceptional attention in the definition of species, undue attention in my opinion. According to the summary by Sieverts-Doreck (1951, p. 18), three species are each known from one specimen showing only the oral side of the submarginal ring, and five species are each known from one specimen showing only the aboral side of the submarginal ring; all other structures are missing. Such species are highly questionable.

Since plates of the submarginal ring are exceptionally thick and fit one against another, they have been referred to as "ossicles" by several authors. They extend from one side of the theca to the other, being exposed on both oral and aboral surfaces. Although not absolutely rigid, they were evidently firmly attached to one another and provided the frame for maintaining the shape of the theca.

The outline of each submarginal plate in radial cross section is not the same in all species. Foerste (1920, p. 59–61) attached considerable importance to this feature in erecting *Narrawayella* and *Savagella*. According to his classification, *Cyclocystoides s.s.* (exemplified by *C. Anteceptus, C. halli,* and *C. bellulus*) has submarginal plates with the proximal half strongly elevated above the distal half, *Narrawayella* (exemplified by *C. cincinnatiensis, C. nitidus,* and *C. mundulus*) lacks depressions in the distal halves of the plates, *Savagella* (exemplified by *C. ornatus*) shows subtriangular cross sections with a steep inner face on the submarginal ring, and an unnamed genus represented by *C. illinoisensis* has submarginal plates with a "flattened elliptical form" in cross section. Sieverts-Doreck (1951, p. 15) described *C. devonicus* as lacking deep depressions in the distal parts of the plates.

The oral side of the submarginal plates is more complex than the aboral side. The lateral surfaces of each plate converge slightly toward the center of the theca, so that adjacent plates have nearly parallel facing surfaces. On external molds, the spaces between plates are filled with matrix, which takes the form of radial partitions; this is the preservation in many specimens, the whole of the plates having been dissolved away. The oral part of the submarginal plates is divided into two parts: (1) proximal elevated part, forming a prominent ring, and (2) distal part bearing facets. The division between the two parts is sharp, tending to be emphasized by the overhanging edge of the proximal part, so that Hall (1872, p. 218) concluded that two circles of plates were present. However, as convincingly shown by Regnéll (1945, Fig. 28*b*) in cross sections, only one circle or ring of plates exists.

The proximal part of each submarginal plate has the general form of a subquadrate block. Its oral surface is variously ornamented. Most species bear numerous low tubercles or papillae (*e.g., Cyclocystoides salteri* Hall, *C. halli* Billings, *C. magnus* Miller and Dyer, *C. decussatus* Begg, *C. lindstroemi* Regnéll, and *C. devonicus* Sieverts-Doreck); one has radial grooves dividing the surface into four or five low ribs (*C. ornatus* Savage); another was described by Begg (1940, p. 23) as having little round punctae (*C. wrighti* Begg); and still another was said by Foerste (1920, p. 60) to be "coarsely pitted" (*C. cincinnatiensis* Miller and Faber). The ornamented part overhangs both the outer plates of the oral disk on the proximal side and the edge of the rest of the submarginal plate on the distal side in *C. lindstroemi* and probably in some other species, but not in *C. devonicus* Sieverts-Doreck and in some of the species referred to by Foerste (1920).

The distal part of the oral side of submarginal plates bears facets, small circular to elliptical elevations. No plate is known which lacks a facet, some plates have only one facet, some as many as four, and in certain species each submarginal plate has just two. Whether such constancy of facet/plate ratio is a character of species or of maturity has not been proved. In *C. halli* and *C. lindstroemi,* the facets lie in a circular trough called the channel. In *C. devonicus,* however, they are on the beveled edge of the plate in very shallow concavities, called by Sieverts-Doreck (1951, p. 15) the platform. Those facets within a channel are surrounded by some kind of depression. *C. halli* was described by Billings (*in* Salter and Billings, 1858, p. 87) as having the outer half of each submarginal plate "deeply excavate, smooth, divided by a radiating ridge into two shovel-shaped portions, which at their inner base are each deepened into a circular pit with a tubercle in it." Other authors have referred to similar areas around facets as "spoon-shaped depressions." Even in *C. devonicus,* external molds show that the facets are in shallow excavations.

The lack of a well-incised channel in *C. devonicus* led Sieverts-Doreck (1951, p. 15) to postulate that the parts of submarginal plates under the facets were hollow and that a channel was a secondary feature caused by collapse of the facet-bearing section during fossilization. She concluded that the channel was not connected with the ambulacral system. The regularity of the channel in specimens of *C. halli* illustrated by Salter and Billings (1858, Pl. 10 *bis,* Figs. 2, 8, 9) and by Raymond (1913, Pl. 3, Figs. 1, 3) and the lack of any cavities shown in the cross sections of *C. lindstroemi* illustrated by Regnéll (1945, Fig. 28*b*) raise considerable doubt about her analysis. Sieverts-Doreck stated (1951, p. 15, my translation), however, "Should my interpretation not prove correct, then there exists a conspicuous contrast between those species of *Cyclocystoides* which possess a peripheral ring-canal and those which lack it."

Insofar as known, facets are invariably aligned with radial ducts perforating the proximal part of the submarginal plate. These ducts appear to connect with the ambulacral grooves. Authors agree that food entered the ambulacral system through the channel or platform area. The presence of "small pores" leading from the channel to the interior of the theca and perforating the submarginal plates was made part of the definition of *Cyclocystoides* originally (Salter and Billings, 1858, p. 86).

One of the critical and unsolved problems of cyclocystoids concerns the function of covering plates over the channel, if indeed they exist. The supposition that the channel was covered by movable plates originated with Salter and Billings (1858, p. 86), who based their interpretation on small isolated plates in the channel of one or two submarginal plates. From his study of the same specimen, Raymond (1913, p. 26) also concluded that the channel was roofed over. The curious structures called "spout-like appendages" by Foerste (1924, p. 80) and supposed by him to be moved by the animal at will to expose or enclose the depressions containing the facets, have not been confirmed by other workers; possibly, these are fractured outer edges of the spoon-shaped depressions. A similar explanation could be offered for the "outward sloping of the marginal plates" noted by Foerste in another cyclocystoid (1924, p. 81).

The general resemblance of the ambulacral system in cyclocystoids to that in cystoids supports their assignment to the Pelmatozoa. In cystoids and blastoids, food was collected by brachioles; in crinoids and paracrinoids, the ambulacral system was further branched outside the calyx or theca and food was gathered by pinnules on the arms. Only in edrioasteroids was food gathered directly into ambulacral grooves. The enclosed ambulacral grooves of cyclocystoids seem irrefutable evidence that food entered from the channel, specifically at the facets. The form of the facets is strikingly like that in cystoids. It is difficult to conceive of brachioles sufficiently developed to gather adequate food for the cyclocystoid and yet so small as to be retractable beneath covering plates of the channel.

Perhaps an alternative suggestion will explain both the small plates and the facets. In some species the facets are not in contact with the ducts, but set a short distance away from the openings. Possibly, small plates served as covering plates over this part of the ambulacral system. There is no reason to doubt that small plates may also have covered parts of the channel between facets. As will be pointed out below, the complexity of each submarginal plate may be regarded as an indication of its having evolved by fusion of several plates.

On the sides of the submarginal plates—the surfaces facing adjacent submarginals—the oral margin is marked by striae normal to the edge. Such striae have been interpreted as scars of ligaments which bound plates of the submarginal ring together and still allowed appreciable flexibility. These markings are prominent in some cyclocystoids, but have not been found in others.

On the aboral side of the theca, the exposed part of the submarginal ring has less radial extent than that on the oral side. Each submarginal plate is slightly convex and trapezoidal in outline. Plates are in contact or nearly in contact only at their distal corners; sides of adjacent plates diverge toward the center of the theca (Fig. 2). As illustrated by Regnéll (1945, Fig. 28*b,c*), each submarginal plate in *C. lindstroemi* has two lappets along its proximal edge, which are overlapped and concealed by the aboral disk; probably, this arrangement prevailed in other species.

Although practically nothing is known of the ontogeny of cyclocystoids, Regnéll (1945) and Sieverts-Doreck (1951) have suspected that the number of submarginal plates increased with size and age in each species, and that several of the "species" based solely on the number of submarginal plates may represent growth stages of one species. The latter author also directed attention to a specimen with one submarginal plate having the shape of a thin wedge, as though it were being intercalated into the ring. If plates were added in the ring during ontogeny, the process was intimately correlated with branching of the ambulacra, so that the ambulacral grooves joined to the ducts through the submarginal plates.

Marginal ring.—Around the periphery of the theca, the cyclocystoid has a ring of imbricating plates remarkably similar to that present in several edrioasteroids. On both oral and aboral sides, the plates decrease in size toward the outside edge. Apparently, they were embedded in a thick integument which formed a seal against the bottom and enabled the cyclocystoid to hold fast by suction. No evidence has been presented to show whether the marginal ring was composed of two layers or one, but from differing accounts of the oral and aboral surfaces of the same species, one is led to believe that the little plates of the two sides were in separate layers that joined at the periphery. For the ring to have functioned in attachment, much of the center must have been filled with muscles.

Unsubstantiated and unknown structures.—In this category must be listed the hydropore, gonopore, periproct, peristome, and brachioles, structures which might be expected in such a pelmatozoan. The space between ambulacra noted by Hall (1872, Pl. 6, Fig. 16) and interpreted by Bather

(1900, p. 211) as the anus, very likely was occupied by small, rather undifferentiated plates of the periproct. In comparison with other pelmatozoans, one would suppose the hydropore and gonopore to have been on the oral side of the theca, probably in the circumoral region.

RELATIONSHIPS

Several students of cyclocystoids have been puzzled by the circular rather than radial terminus of the ambulacral system and by the great thickness of the submarginal plates, extending from oral to aboral sides of the theca. These have been regarded as unique among pelmatozoans.

Even though certain diplopore-bearing cystoids do not duplicate these unusual features, they show exceptional similarities. The genus most closely reflecting cyclocystoid organization is *Tholocystis* (Fig. 4), of the order

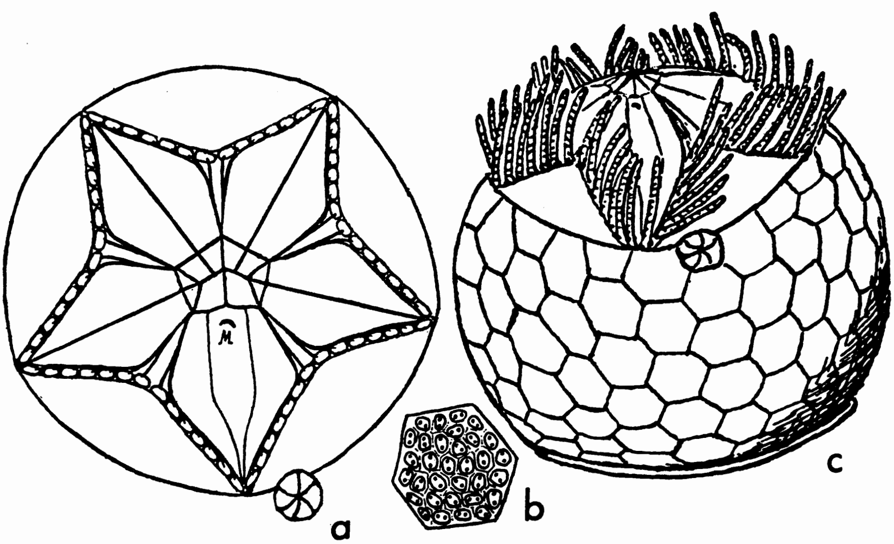

FIG. 4. *Tholocystis kolihai* Chauvel. *a*. Oral region, showing regular arrangement of plates, distribution of brachiole facets, and location of anal pyramid, enlarged; *M,* hydropore. *b*. Plate from side of theca, enlarged to show diplopores. *c*. Restoration of theca as seen laterally, about x6. All from Chauvel, 1941.

Diploporita, superfamily Sphaeronitida, and family Sphaeronitidae. This cystoid was described by Chauvel (1941, p. 88) as shaped like a kettle, with large, orderly disposed radials, orals, and peristomial covering plates corresponding to the lid of the kettle (Fig. 4*a*). The globose sides of the theca (Fig. 4*c*) are made of thick hexagonal plates with typical diplopores

(Fig. 4*b*). The broad base of *Tholocystis,* known only from its impression, was probably composed mostly of integument, inasmuch as it shows no outlines of plates, and was called by Chauvel the "sole." It is of special interest that *Tholocystis* has (1) branched ambulacra leading to brachioles arranged in a broad-angled pentagram, more or less a circle except for the re-entrants that accommodate the radial plates, (2) brachiole facets borne on quadrangular plates or "adambulacrals" which are thicker than other plates, and (3) a large circular base that is flexible. Presumably, the ambulacral grooves across the oral region were covered by small plates which left no record.

Cyclocystoides may have descended from a pelmatozoan not very different from *Tholocystis* (Fig. 5). The aboral disk and marginal ring of cyclo-

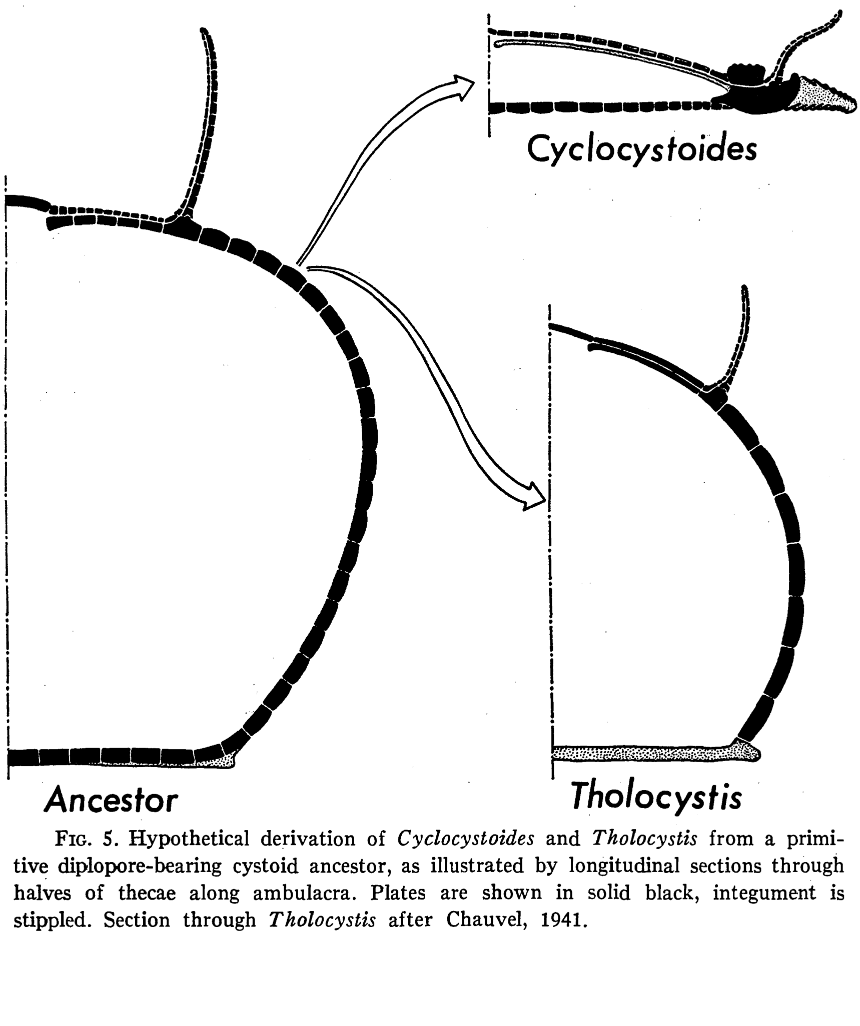

FIG. 5. Hypothetical derivation of *Cyclocystoides* and *Tholocystis* from a primitive diplopore-bearing cystoid ancestor, as illustrated by longitudinal sections through halves of thecae along ambulacra. Plates are shown in solid black, integument is stippled. Section through *Tholocystis* after Chauvel, 1941.

cystoids seem analogous with the base or "sole" of *Tholocystis* and the facet-bearing part of the submarginal ring with the thick quadrangular plates. Ambulacral ducts through plates are novel features in pelmatozoans; yet those in cyclocystoids may have originated by fusion of surrounding plates. The function of protection and enclosure of the ambulacral conduit suggests that the part of the submarginal plate oral to the ducts may have been derived from ambulacral covering plates and that the part aboral to the ducts may have been modified from ambulacral flooring plates. Obviously, *Cyclocystoides* did not attain the exceptional symmetry of *Tholocystis,* but the outer part of its base became more differentiated.

Both *Tholocystis* and *Cyclocystoides* appeared in Middle Ordovician time. The oldest known relative of *Tholocystis* is *Sphaeronites,* from Lower Ordovician strata. Even this genus, however, shows specialization of structures in the circumoral region; its theca is more or less round and attached by the basal surface, which in many specimens retains the imprint of objects to which it was fastened. The Cambrian ancestor of both *Sphaeronites* and *Tholocystis* probably had a theca composed of numerous plates, none of which was highly specialized; such a primitive diploporitan cystoid is conjectured as the possible ancestor of both *Tholocystis* and *Cyclocystoides* (Fig. 5). Whereas no diplopores have been observed in plates of *Cyclocystoides,* the integument in which plates of the oral disk are embedded may have fulfilled the same function as diplopores. At any rate, the strongest similarities to cyclocystoids occur in this group of sphaeronitid cystoids.

According to this hypothesis, the cyclocystoid is a derivative of the Diploporita in which the theca has undergone extreme oral-aboral compression, the oral region has greatly expanded without plate specialization, submarginal plates have resulted from fusion of "adambulacrals" with proximally adjacent ambulacral flooring and covering plates, the aboral side of the theca has been greatly extended, diplopores have degenerated or have been replaced, and the brachioles have migrated outward to form a circle.

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