

Text figure 54. *Lepidodiscus laudoni* (Bassler), 1936

- A. Central part of lower surface of SUIC 12546, (x 10), pl. 50, fig. 11.
 B. Central part of lower surface of SUIC 12545, (x 10), pl. 50, fig. 7.

central posterior part of the oral region. Plates immediately posterior to the center of the oral region appear to form an elevated connection between the hydropore protuberance and the central oral rise. This feature has not been found in most other specimens, and is apparently preservational.

USNM S-3886-A. Lectoparatype of *L. laudoni*. 29.5 mm axial by 28.4 mm transverse diameter.

Pl. 49, fig. 5, 6.

This specimen is more complete than the lectotype, missing only the distal part of ambulacrum III and many of the pedunculate zone and peripheral rim plates. However, the oral, hydropore, and oral frame structures, and the proximal parts of all five ambulacra are completely disrupted. The completely collapsed specimen is nearly free of matrix and exposes both the upper oral surface and parts of the pedunculate zone plates on the lower side of the specimen. Where lower surface plates are missing, the inner side of the upper oral surface is exposed, including: the floorplates of ambulacra I-II; interambulacrals in 1, and parts of 2 and 5; part of the anal structure; and the disrupted oral frame area. This individual complements the lectotype and preserves the distal curvature of ambulacra II-IV,

the ambulacral floorplates, and some of the lower surface pedunculate zone plates. Ambulacral coverplates are mostly well preserved in the central and distal parts. Interambulacrals are only slightly disrupted in 1 and 5. Preservationally formed striations are common on the smaller, nearly vertical, collapsed interambulacrals which flank the adradial sutures of the ambulacra. Ambulacrum II bifurcates as it approaches the ambitus and forms two equal distal branches. This is the only specimen of *L. laudoni* in which an extra or anomalous ambulacrum has been observed.

USNM S-3884. *L. laudoni* illustrated by Bassler (1936, pl. 3, fig. 6) as *Discocystis kaskaskiensis*. "Chester Group," Chesterian Series, Mississippian. Grayson County, Kentucky. 33.8 mm axial by 27.2 mm transverse diameter.

Pl. 49, fig. 7-12.

The specimen is preserved with the upper oral surface imbedded in matrix and exposes the lower side of the theca. As viewed from the lower side, the right half of the specimen preserves the exterior of the pedunculate zone plates, although the basal rim is missing. These pedunculate zone elements have been lost from the left side, which exposes the inner sides of the upper

oral surface plates, including the floorplates of ambulacra IV and V, and interambulacral plates of 4, and parts of 3 and 5. The central oral frame region is unfortunately obscured by tenacious matrix.

A small distal segment of ambulacrum IV, separated from the remainder of the theca by several missing plates, exposes the ambulacral coverplate pattern when viewed obliquely.

Bassler (1936) illustrated this individual as a *Discocystis kaskaskiensis*. However, the ambulacral coverplate pattern seen in the distal fragment of ambulacrum IV (pl. 49, fig. 9, 10) is that of *L. laudoni*. A five-plate cycle is preserved, comparable to the part of the ambulacrum seen in text fig. 53B, distal to the insertion zone of the final set of cycle plates. Moreover, the thin, imbricating plates of the pedunculate zone appear to be separated from the ambitus by only a few interambulacrals pertaining to the transition zone, as is the case in other *L. laudoni*.

SUIC 12545, 12546. *L. laudoni*. The type specimens of *Discocystis priesti* Strimple (1967). Pella beds, (St. Louis or Ste. Genevieve Limestone), Meramecian Series, Mississippian. Abandoned county quarry, NW $\frac{1}{4}$, NW $\frac{1}{4}$, sec. 9, T. 25 N., R. 18 W., Marian County, west of Harvey, Iowa.

SUIC 12545. Holotype of *Discocystis priesti* Strimple. 15.5 mm axial by 15 mm transverse diameter.

Text fig. 52A, B, 53B, 54B, pl. 50, fig. 1-7.

The specimen is a small adult *Lepidodiscus laudoni*. The clavate theca has collapsed and the upper oral surface is depressed against the lower, collapsed pedunculate part of the theca. Plate disruption is most pronounced in the medial parts of ambulacra I and II and the adjacent interambulacra. However, the oral-hydropore area and many of the ambulacral coverplates are only slightly disrupted and preserve the distribution patterns of the plates. Abrasion of the oral region has leveled off the upper ends of the plates. Text fig. 52A, B, 53B outline the plating of the oral-hydropore area and the ambulacral coverplate sequence. The complete six-plate cycles of coverplates are developed proximally.

This edrioasteroid has been separated from the brachiopod upon which it rested in life, and exposes the lower oral surface plates below the ambitus. The interambulacrals of the subambital transition zone form the outer, or proximal, part of the lower surface and are in two or three irregular "circlets." The transition plates are succeeded by the thin, subrectangular, imbricate plates of the pedunculate zone. Only the upper, or proximal, parts of the columns of plates of the pedunculate zone are visible when the specimen is whitened (pl. 50,

fig. 5), because the center of the lower surface is covered with secondary calcite. This externally preserves the impression of the brachiopod shell on which the specimen rested. However, when the specimen is under xylene (pl. 50, fig. 6), the secondary calcite becomes transparent and exposes the more distal, or lower, parts of the theca (text fig. 54B). Under the secondary calcite, the plates of the peripheral rim are preserved in life orientation, with the basal surfaces directed downward against the resting site (*i.e.*, the basal surface is exposed when viewed from the lower side of the specimen). During collapse the outer, or external, sides of the plates of the lower pedunculate zone were depressed against the outer surface of the peripheral rim plates. These lower pedunculate zone plates are thus hidden from view in the collapsed specimen and now lie directly above the peripheral rim plates (*i.e.*, under them when viewed from the lower surface of the specimen). As seen from the lower side of the specimen, the large plates of the proximal rim circlet are nearest the center of the specimen, surrounded by the more distal circlets of plates. The rim includes six or seven circlets, the plates decreasing in size outward, *i.e.*, distally. The large geniculate plates of the proximal circlet, located nearest the center of the lower side, bear large vertical ridges on their basal surfaces. These plates are tilted outward slightly, and thus the proximal ends of the ridges appear to extend toward the center of the specimen as acuminate projections. The plates of the surrounding, more distal rim circlets are also geniculate, but basal ridges were not observed. The smallest rim plates form the outermost, or distal, circlet of rim plates which lie furthest from the center of the lower surface. Surrounding these plates, the external sides of the central pedunculate zone plates are exposed.

The proximal circlet of rim plates surrounds a non-plated, central oral area, filled with secondary calcite. This zone is the center of the aboral surface and was probably covered by a soft membrane that was in contact with the adjacent brachiopod surface. The inner sides of a few of the plates of the upper oral surface can be seen through the secondary calcite that fills the collapsed thecal cavity.

SUIC 12546. Paratype of *Discocystis priesti* Strimple. 11.6 mm axial by 10.7 mm transverse diameter.

Text fig. 53A, 54A, pl. 50, fig. 8-12.

This specimen is another small adult *L. laudoni*. The clavate theca has collapsed, depressing the upper oral surface against the collapsed lower pedunculate zone. Freed from its resting site, the specimen exposes both the upper and lower parts of the theca. The oral and hydropore plates, interambulacrum 3 elements, and some of the pedunculate zone plates are disrupted.

The upper oral surface structures are comparable to those found in specimen SUIC 12545. Text fig. 53A shows the mode of cyclic coverplate insertion in the distal part of ambulacrum I. During collapse, the upper oral surface was depressed but it maintained some of its original upward convexity. The pedunculate zone and peripheral rim plates have been pressed against the inner surface of the convex-upward, upper oral surface; their external surfaces thereby are convex upward inside the upper surface plates (text fig. 54A). The distal pedunculate zone and adjacent rim plates now lie within the thecal cavity area, surrounding the oral frame. However, in contrast with the above specimen, the peripheral rim has not maintained its life orientation. Rather, the proximal rim circlets remain in life orientation, but the distal circlets of smaller plates have curled down and under the proximal rim plates. Thus, when viewed from the lower side of the specimen, the external surfaces of the distal rim plates are exposed. The larger plates of the proximal circlet are almost entirely hidden beneath the outer circlet plates. The basal surfaces of two large proximal rim plates, along with their large, vertical ridges, are seen projecting inward from the rim, adjacent to ambulacrum IV. Distorted during preservation, the rim follows an irregular course of nearly straight segments joined by abrupt angles. Moreover, a small section of the rim appears to be missing in the area of ambulacra I and II. Thus the segment of the rim lying on the inner surface of interambulacrum I appears to end, as does the segment lying adjacent to the proximal part of ambulacrum III. Many of the plates of the distal pedunculate zone are missing or hidden, thereby separating the rim from the pedunculate zone. Along the anterior margin of the rim, the inner sides of the upper oral surface plates are exposed between the rim and the pedunculate plates. The peculiar preservation of the rim in this specimen led Strimple (1968, p. 262) to describe it as a "long slender tube . . . presumed to be the stone canal."

In the center of the specimen's lower surface, the oral frame and central lumen are exposed (text fig. 54A, pl. 50, fig. 12). Abrasion and etching have obscured some plate boundaries, particularly in the area of ambulacra IV and V. The frame appears to include only the enlarged proximal ambulacral floorplates. The inner end of the stone canal passageway is exposed along the posterior margin of ambulacrum V, but plate boundaries are not distinct in this area.

The suture line between the proximal and second floorplates of ambulacrum II appears to be crenulate. This suggests a syzygial suture, locking the plates together. Similar suture development has not been observed in any other edrioasteroid specimen, and is only questionably preserved here.

UIPC Z6-B. *Lepidodiscus laudoni*. Gilmore City Limestone, Kinderhookian Series, Mississippian. University of Illinois locality Z6, one mile northwest of Gilmore City, Iowa. J. L. Carter, collector (1967). 30 mm axial by 22 mm transverse diameter.

Pl. 51, fig. 1-4.

The theca of this specimen has collapsed; the upper oral surface is nearly flat. The theca is slightly compressed and transversely shortened. The right side is disrupted and partially missing. Plating of the oral-hydropore area, ambulacra I-III, V, interambulacra 1, 2, and 5, and the anal structure are well preserved. The lower side of the specimen preserves the proximal plates of the pedunculate zone; these are pressed against the inner side of the plates of the upper oral surface. The remainder of the pedunculate zone and the basal peripheral rim are missing, which exposes the inner side of the upper oral surface plates. Proximal floorplates are seen in ambulacra I-II. The oral frame is exposed, but only the left side (the right, when viewed from the lower side of the specimen) is well preserved. The tessellate plates of interambulacra 1, 2, and 5 are also exposed. The inner side of the anal structure is largely covered with recalcitrant matrix, but the triangular shape of the plates that form the inner circlet can be seen.

NYSM 12778. *L. laudoni*. Glen Dean Limestone, Hamburg Group, Chesterian Series, Mississippian. Morrow County, Kentucky. W. H. White, Jr., collector (1968). 24 mm long by 13.2 mm wide.

Pl. 51, fig. 5-8.

This specimen is a fragment of a large adult which exposes the upper, ambulacral tunnel surfaces of ambulacral floorplates where the coverplates have been eroded away. The deep central trough and sloping lateral articulation zones are exposed. The lateral edges of the inner, or lower, surfaces of the floorplates appear to abut adjacent interambulacrals along irregular sutures, because complementary ridges and grooves are developed along the zone of contact. Coverplates are preserved proximal to the zone of exposed floorplates and form the typical six-plate cyclic sequence. The distal part of another ambulacrum is also preserved. Apparently located distal to the insertion zones of several of the coverplate sets, the cycles in this distal ambulacral segment include two plates distally, three plates in the more proximal part of the segment.

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A large suite of *L. laudoni* specimens from the Monteagle Formation, Ste. Genevieve, Mississippian, of Madison County, Alabama, has also been examined during this study. The specimens range in size from 10

to 40 mm in upper oral surface diameter. Thecal collapse is commonly vertical, depressing the specimens into nearly flat disks. However, some of the specimens apparently toppled sideways, and although laterally compressed, they preserve distended pedunculate zones and allow interpretation of thecal height. Specimens approximately 35 mm in upper oral surface diameter average 50 mm in height (see IUPG 10837-19, pl. 51, fig. 9, 10).

Discussion

Bassler (1936, p. 21) suggested that *Discocystis laudoni* is "distinguished by its narrow, well developed long ambulacra curving decidedly throughout their length," and thereby contrasted with other species of *Discocystis*, in which the "ambulacra are comparatively straight for the first third of their length and curve rather abruptly."

Ehlers and Kesling redescribed *Discocystis laudoni* (1958) and, like Bassler, they used only the two type specimens. Although primarily interested in the pattern of cyclic ambulacral coverplates, which had been overlooked by Bassler, their extensive description of the species included most taxonomically important thecal structures. The above redescription of the species follows Ehlers and Kesling in most aspects, although additional specimens have allowed more complete analysis in some areas. Ehlers and Kesling reported the possible occurrence of a genital pore in specimen USNM S-3886-B. "The posterior interambulacrum has a polygonal depressed area [to the right of the anal structure], apparently where one or more large interambulacral plates are missing from the specimen, which contains an elongate, narrow opening bordered by plates . . . much smaller than those in the adjacent area" (Ehlers and Kesling, 1958, p. 270). In other examples of *L. laudoni* this area is covered by large interambulacrals, and those specimens which expose the inner side of this area do not have small inner plates below the large, outer interambulacrals. Therefore, it appears that the "smaller" interambulacrals and supposed elongate opening in the lectotype results from breakage and depression of larger interambulacrals during preservation. They are not part of a genital pore structure as suggested by Ehlers and Kesling.

The holotype and one paratype of Strimple's *Discocystis priesti* (1968) are reillustrated here as small adult specimens of *Lepidodiscus laudoni* (text fig. 52A, B, 53A, B, 54A, B, pl. 50, fig. 1-12). Contrary to Strimple's interpretation, the ambulacral coverplates form six-plate cycles. This and other thecal features of these two specimens agree with those found in the type specimens of *L. laudoni*. Moreover, Strimple described the occurrence of a long, polyplated stone canal in

SUIC 12546. As seen in text fig. 54A, pl. 50, fig. 10-12, the supposed stone canal is the outer circlets of peripheral rim plates, curled under the larger, proximal rim plates. Thecal collapse has left the rim pressed against the inner side of the upper oral surface, distorting and breaking the rim. The position, the curling, and the irregular, broken path of the rim apparently misled Strimple as to the true identity of these plates.

Most clavate edriasteroids are depressed during thecal collapse associated with preservation. The plates of the pedunculate zone are usually telescoped together and pressed against the inner side of the upper oral surface. Fortunately, some specimens of *Lepidodiscus laudoni* from Alabama apparently toppled over sideways when buried. Although laterally compressed, these specimens preserve the original lateral outline of the inflated theca (pl. 51, fig. 9, 10). As suspected from depressed specimens, the ambulacra are limited to the convex-upward, upper oral surface. Below the ambitus of the upper gibbous part of the theca, the transition zone interambulacrals and the following thin, subrectangular, imbricate pedunculate zone plates form a downwardly tapering zone. Even in compressed specimens the numerous pedunculate zone plates are highly imbricate. The basal peripheral rim flares outward against the substrate, but the total diameter of the rim is only one-fourth or less the diameter of the upper gibbous part of the theca. Thus it must have been firmly attached to the substrate to prevent lateral toppling of the individual during life.

The large number of thin plates of the pedunculate zone, their high degree of imbrication, and the commonly depressed preservational state suggest that the theca was capable of great vertical extension and retraction. Specimens preserved in their extended state are often one and one-half times as high as the diameter of the upper gibbous head. The imbrication of the pedunculate plates suggests that the theca could easily have been further extended, perhaps reaching heights two or two and a half times the "head" diameter. Depressed specimens preserve the thin, imbricating pedunculate plates telescoped together, with the upper plates slipped inside the lower ones. The lower plates overlap the contiguous higher elements, so that complete collapse of the pedunculate zone requires lateral separation of adjacent lower plates because of the greater diameters of the upper circlets. Partially contracted specimens are also preserved; in these the total thecal height is only half the diameter of the upper gibbous area. These show no evidence of pedunculate zone disruption; therefore, at least this degree of contraction was possible in life.

Vertical extension of the theca would raise the food-gathering ambulacra above the sea floor, a condition found desirable in other sedentary, suspension-feeding

echinoderms. Retraction would lower the gibbous "head" and produce greater stability, both by reducing the total area exposed to currents, and by lowering the center of gravity. If the pedunculate zone were almost completely telescoped together, the ambitus of the upper convex oral surface would be pressed against the substrate. The theca would thereby assume a domal external shape and offer little resistance to turbulent waters, which would prevent lateral toppling of the theca.

Support for this proposed contractibility is found in the mode of thecal preservation. Most specimens are depressed. Only a few have toppled sideways and have been laterally compressed. Yet a highly extended, rigid, clavate theca with a small basal attachment disk would most likely topple sideways during burial, since precise vertical depression would be quite unlikely. Thus most specimens apparently contracted prior to burial, probably in response to the turbulent waters carrying the influx of sediment that buried them. Only a few were caught in the extended state and pushed over sideways.

RANGE AND OCCURRENCE: Mississippian of Iowa, Kentucky, and Alabama.

Lepidodiscus sampsoni (Miller), 1891

Text fig. 55; plate 51, fig. 11–13, plate 52

- 1891 *Echinodiscus sampsoni* Miller, S. A., Geol. Surv. Indiana, 17th Ann. Rept. (adv. pub.): 76, pl. 12, fig. 16.
- 1892a *Echinodiscus sampsoni* Miller, S. A., First Appendix to North American Geology and Palaeontology, Cincinnati: 678, fig. 1225.
- 1892b *Echinodiscus sampsoni* Miller, S. A., Geol. Surv. Indiana, 17th Ann. Rept.: 686, pl. 12, fig. 16.
- 1894 *Echinodiscus sampsoni* Miller, Keyes, C. R., Missouri Geol. Surv. 4 (1): 133.
- 1901 *Discocystis sampsoni* (Miller), Clarke, J. M., New York State Mus., Bull. 49 (2): 182-198.
- 1904 *Echinodiscus sampsoni* Miller, Klem, M. J., St. Louis Acad. Sci., Trans. 14: 73-74.
- 1943 *Discocystis sampsoni* (Miller), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 201.

Diagnosis

A *Lepidodiscus* with: clavate or subclavate theca, plates distal to ambulacra squamose, imbricate; cyclic ambulacral coverplates perradially raised, forming small, distinct perradial ridge; ambulacral floorplates abutting, each with four or more lateral projections on

lower side; interambulacra large, polygonal, tessellate.

Description

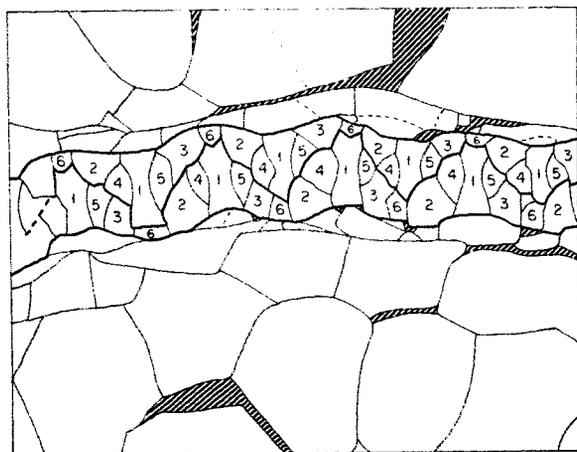
Lepidodiscus sampsoni (Miller) is represented by the incomplete holotype and eight fragmentary or partially disrupted topotypes. The theca appears to have been clavate, with the ambulacra extending down to the ambitus of the convex-upward oral surface. Below the ambitus a zone of squamose, imbricate plates apparently form a short pedunculate zone which is thought to constrict slightly in diameter downward. A basal peripheral rim flares outward and forms a wide zone of contact with the substrate.

Plate boundaries in the oral region are obscure in available specimens. Text fig. 55B tentatively identifies some oral plate boundaries in the oral and hydropore areas of the holotype. The oral plates are variable in shape and size and apparently mimic imperfectly the ambulacral coverplate pattern. Orals thus appear to grade into the coverplate sequence without apparent break. Around 30 lateral orals but only six or seven anterior orals are included in the region and thereby form a transverse elongation in the oral area outlined. Primary orals are not externally differentiated from other orals.

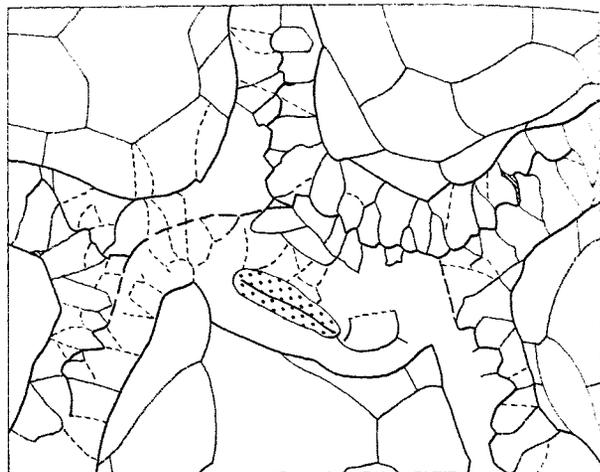
The hydropore structure (text fig. 55B, pl. 52, fig. 1, 2) extends in an oblique lateral direction from the right part of the left half of the posterior oral region toward the proximal posterior edge of ambulacrum V. The plates included in the structure are upturned and form the steep, nearly vertical sides of the protuberance. The elongate, slitlike hydropore extends along the summit of the prominence. Plate boundaries are obscure in the holotype, the only specimen which preserves the structure in nondisrupted state. Even in this specimen the summit has been leveled by abrasion, which also removed the upper ends of the plates.

Ambulacral curvature is commonly uneven, with the straight proximal segments followed by pronounced curvature near the ambitus of the upper oral surface. Distal to the zone of pronounced curvature, the ambulacra extend concentric with the upper oral surface margin. Distally, ambulacrum V may curve back toward the oral area into interambulacrum 5. Ambulacrum I and perhaps others may also exhibit distal curving back toward the oral region.

The ambulacral coverplates form six-plate cycles (text fig. 55A, pl. 52, fig. 3, 4). Those on opposite sides of the perradial line alternate, offset by half the length of a cycle. The alternating cycles form a broadly undulating, zigzag perradial line. Individual cycle plates occasionally form discrete perradial points which randomly superimpose small serrations onto the broader undulations. Plate sizes and shapes are similar to those found in



A



B

Text figure 55. *Lepidodiscus sampsoni* (Miller), 1891

Holotype, CFMUC 7000.

A. Proximal segment of ambulacrum V, (x 10), pl. 52, fig. 4.

1 through 6 are the first through sixth sets of ambulacral coverplates, respectively.

B. Oral area and adjacent structures, (x 10), pl. 52, fig. 2. Broken upper ends of the hydropore structure plates are marked by a dotted pattern.

other *Lepidodiscus* species. Thus the plate sets described below are considered homologous to those of *L. laudoni*, although the order of insertion has not been completely verified in specimens of *L. sampsoni*.

Primary set plates are the largest and longest, and form the center of each complete six-plate cycle. The adradial bases of the primary plates are broad. The lateral margins converge slowly from the adradial suture line, but near their perradial end they diverge for a short distance and form an expanded or swollen perradial end. The variable perradial margin may be pointed, nearly straight, or occasionally indented. This plate is opposed by the sixth set plate of the alternate cycle, which has a complementary perradial shape, *i.e.*, sloping, straight, or pointed, respectively.

The moderately large plates of the secondary set lie proximal to the primaries. Their left lateral edges abut the adradial part of the lateral edge of the adjacent primary. These secondaries are subtriangular to subrectangular with: wide adradial bases; nearly parallel, short, lateral margins which are approximately normal to the adradial suture line; and a broad perradial point. However, commonly only the right side of the angular perradial end extends along the perradial line; the left side is in contact with the adjacent fourth series plate. Occasionally the right side of the pointed perradial end does extend outward perradially, and thus the secondary forms a small, discrete perradial line angulation. The

third, or tertiary, set plates are mirror images of the secondaries, but lie distal to each primary cycle plate.

The quaternary set plates, smaller than plates of the first three sets, are subtriangular to rhomboidal. Commonly limited to the axial part of the ambulacrum, they lie between the perradial ends of the primary and secondary set plates. Perradially, the margin of the quaternaries may be straight and form the sloping central part of the cycle undulation; in others it is angular and forms a small serration along the perradial line. The quintary, or fifth, set coverplates are mirror images of the quaternaries and lie between the perradial ends of the primary and tertiary plates of each cycle.

The sixth and final element is the smallest plate in the cycle. It lies proximal to the secondary plate along the adradial suture line. It may be rectangular, or pentagonal and perradially pointed, or occasionally subtriangular. The proximal margin of this plate abuts the distal margin of the tertiary plate of the adjacent proximal cycle.

The margins of the coverplates which flank the perradial line are upturned and form a small, distinct perradial ridge along the undulating perradial line. Axially elongate interambulacrals overlap the adradial ends of the coverplates. The interambulacrals regularly extend further out over the central cycle plates and form a concave adradial suture line with the coverplates. The

adradial suture lines are thus sinuous, and each ambulacrum appears to have an undulating course.

The externally hidden adradial and ambulacral tunnel surfaces of the coverplates have not been observed in *L. sampsoni*.

Ambulacral floorplates are rectangular in plan view and elongate axially (pl. 52, fig. 9-11). Contiguous plates meet along vertical sutures. The inner, or lower, surface of each floorplate bears four large nodes which arise from the lateral parts of the convex-inward, lower surfaces. Two nodes are formed on each lateral margin, one directly above the other. The upper node appears to extend out under the adjacent interambulacrals, with the upper side of the node in contact with the inner surface of these interambulacrals. The lower, rounded node projects laterally and obliquely downward into the thecal cavity. On each plate the two lateral sets of nodes may lie directly across from one another, or may be offset with either set proximal to the other. Occasionally additional pairs of nodes may be formed on a floorplate. Although suggested by only two fragmentary specimens, every second suture between the uniserial floorplates appears to be more firmly united, perhaps even fused (pl. 52, fig. 9-11).

The central parts of the interambulacra are formed by large, thick, polygonal, tessellate plates. Along the adradial suture lines the interambulacrals are smaller, more elongate, and may imbricate slightly toward the adradial line. Distal to the ambulacra, apparently below the ambitus, the plates continuous with the interambulacral series are squamose and imbricate, and form a slightly downwardly constricting, short pedunculate zone.

The valvular anal structure is located near the center of interambulacrum 5. It includes perhaps 12 or more large, triangular plates, apparently alternating as inner and outer circlets. Outer circlet plates overlap the inner ones along a narrow zone of overlap which externally exposes most of the upper surfaces of the inner plates.

The basal peripheral rim is formed by six or seven circlets. The structure is poorly preserved in available specimens.

The external surface of the thecal plates is minutely pustulate, reflecting the microstructure of the plates.

Specimens

CFMUC 7000. Holotype of *Lepidodiscus sampsoni* (Miller), (1891, p. 76, pl. 12, fig. 16, as *Echinodiscus sampsoni*). Warsaw Formation, Keokuk Group, Osagean Series, Mississippian. Boonville, Cooper County, Missouri. 38.5 mm axial by 41 mm transverse diameter.

Text fig. 55A, B, pl. 52, fig. 1-6.

The holotype is incomplete and preserves only the center of the upper oral surface. Most of the distal parts of the ambulacra, which curve concentrically with the margin of the upper oral surface, are missing, along with the distal interambulacrals and the posterior half of the anal structure. If any of the squamose, imbricate, pedunculate zone plates or peripheral rim plates are preserved, they are hidden beneath the upper oral surface plates and matrix.

The upper oral surface of the specimen has collapsed against the substrate. The oral-ambulacral series, which is supported by the frame and ambulacral floorplates, remains elevated as prominent ridges above the collapsed interambulacrals. Oral-ambulacral series plates are only slightly disrupted, but suture lines commonly have been obscured. The hydropore protuberance also appears to be intact, but plate boundaries are not discernible and abrasion has leveled the summit of the structure. Interambulacrals are partially disrupted, especially along the ambulacral margins and the distal parts of the specimen. The ambulacral coverplate pattern is most clearly preserved in the remaining distal segments of ambulacra IV and V. The distal tip of ambulacrum V may be preserved to the left of the anal structure.

USNM S-3888 (A-H). Nine specimens, seven of which appear to be fragments or partially disrupted topotypes of *L. sampsoni*. Warsaw Formation, Keokuk Group, Osagean Series, Mississippian. Boonville, Cooper County, Missouri.

USNM S-3888-A. 37.3 mm axial by 36 mm transverse diameter.

Pl. 51, fig. 11.

This specimen has collapsed obliquely; the anterior part of the upper oral surface has been folded under the remainder of the theca. Many of the thecal plates are disrupted, but outlines of the major structures are clear. The ambulacra curve, I-IV contrasolar, V solar. The distal tips of ambulacra I and V curve back proximally and extend into interambulacrum 5. The coverplate pattern appears to be like that of the holotype, but is mostly obscured.

USNM S-3888-B. 26.4 mm greatest length.

Pl. 51, fig. 13.

This specimen is obliquely compressed. Ambulacra I, II, III, and interambulacra 1 and 2 are exposed on the "upper" side of the specimen. The other half of the upper oral surface is folded under the upper side and is completely jumbled. Ambulacral curvature, coverplate pattern, and the large, polygonal, tessellate interambulacrals appear to be like those of other specimens of *L. sampsoni*.

USNM S-3888-C. 22.7 mm axial by 22.1 mm transverse diameter.

Pl. 52, fig. 7.

This specimen is partially collapsed. Only the upper oral surface is well preserved; it retains some of its original convexity. Although most plates appear to be only slightly disrupted, surficial etching has obscured most plate boundaries. The right side of the oral area and the hydropore structure appear to be only slightly disturbed. The ambulacra rise above the interambulacral areas as low, rounded ridges. Curvature agrees with the other specimens of this species. Distally, ambulacra I and V curve back proximally into interambulacrum 5. Other ambulacra may be similarly curved distally. The ambulacral coverplate pattern is obscure in all of the ambulacra. The anal structure is elevated into a low, subconical mound near the center of interambulacrum 5.

USNM S-3888-D. 18.3 mm axial by 20.4 mm transverse diameter.

Pl. 51, fig. 12.

This specimen has collapsed and most plates are disrupted. Depression was oblique, folding the posterior part of the upper oral surface onto the lower side of the specimen. The five curved ambulacra are recognizable, but disrupted. All of the interambulacrals are jumbled. The specimen does preserve one section of plates of the squamose, imbricate pedunculate zone, distal to ambulacra III and IV. A small anterior segment of the peripheral rim lies adjacent to these pedunculate zone plates.

USNM S-3888-F. 21 mm axial by 10.5 mm transverse diameter.

Pl. 52, fig. 8.

This specimen has collapsed and is laterally compressed. Plates are mostly jumbled. However, several of the large proximal rim plates are seen along the posterior margin of the theca. Small adjacent plates, now disrupted, probably represent the more distal plates of the rim.

USNM S-3888-G. 17.5 mm long by 10.9 mm wide.

Pl. 52, fig. 9, 10.

This specimen is a fragment of a large adult and exposes seven ambulacral floorplates and adjacent interambulacrals. The specimen suggests that every second floorplate suture is more tightly joined, perhaps even fused. The large, lateral, knoblike nodes are found on the floorplates, with four per plate.

USNM S-3888-H. 12.5 mm long.

Pl. 52, fig. 11.

Another fragment of an ambulacrum, this specimen also exposes the ambulacral floorplates. Each appears to

bear six or eight inner-surface lateral nodes, rather than four as in the above specimen. Every second floorplate suture again appears to be more tightly joined.

Discussion

S. A. Miller (1891, p. 76) briefly described *Echinodiscus sampsoni* as: "circular," interambulacra flat, depressed; ambulacra higher than wide; interambulacrals large, tessellate; "orals" [anals] partially preserved, located over half an inch from the central pole; ambulacra long, proximally straight, curved distally; ambulacral coverplates numerous, small, "thrown into a waving line on top." The accompanying illustration depicts the broken outline of the theca, the tessellate, polygonal interambulacrals, and the adradially undulating course of the ambulacra. Ambulacral plating is not shown.

The incomplete nature of the holotype, combined with the superficial original description, relegated *Lepidodiscus sampsoni* (Miller) to obscurity, for most subsequent authors have ignored it. Thought to be similar to *Discocystis kaskaskiensis*, *L. sampsoni* was listed by most authors under the genus *Discocystis* (the name substituted for the preoccupied *Echinodiscus*) without redefinition of the thecal features.

Lepidodiscus sampsoni (Miller) remains inadequately known. However, location of several topotypes in the United States National Museum has allowed confirmation of the ambulacral curvature direction. Moreover, these topotypes preserve the squamose, imbricating plates of the short pedunculate zone and parts of the basal peripheral rim. Two fragmentary specimens expose the only view of the ambulacral floorplates. Unfortunately, the topotypes are either poorly preserved or fragmentary, and do not preserve many thecal details that are also obscure on the fragmentary holotype.

L. sampsoni is differentiated from other clavate *Lepidodiscus* species by its pedunculate zone which is short, only slightly constricted, and composed of moderately thick, squamose, imbricate plates. Moreover, individual plate shapes in the six-plate cycles of ambulacral coverplates are distinctive. Most apparent is the unique shape of the elongate plates of the primary set, which perradially expand in width.

The hydropore protuberance may also be unique, for it apparently extends far into the left half of the posterior oral region. In most other species of *Lepidodiscus*, this structure ends at or near the axial midline. Unfortunately, the details of the hydropore plating are unknown. Oral and anal area plating are also inadequately represented in the available specimens.

RANGE AND OCCURRENCE: Osagean Series, Mississippian. Boonville, Missouri.

Genus *Ulrichidiscus* Bassler, 1935

- 1935 *Ulrichidiscus* Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 8, pl. 1, fig. 7.
- 1936 *Ulrichidiscus* Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 22.
- 1938 *Ulrichidiscus* Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 190.
- 1943 *Ulrichidiscus* Bassler, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 209.
- 1966 *Ulrichidiscus* Bassler, Regnéll, G., in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U171, text fig. 128-5.

TYPE SPECIES: *Agelacrinus pulaskiensis* Miller and Gurley, 1894.

Diagnosis

Agelacrinidae with: high domal or subclavate theca; numerous oral plates, primary orals undifferentiated; large hydropore structure separated from central oral rise; ambulacra curved, I-V contrasolar, coverplates forming seven-plate cyclic sequence; interambulacral polygonal or squamose, tessellate or slightly imbricate; valvular anal structure with two circlets of plates.

Description

Ulrichidiscus is monotypic. Therefore, separation of generic and specific taxobases is uncertain. Features outlined in the above diagnosis are inferred to be of generic rank from established taxobases of related Agelacrinidae genera.

Discussion

Diagnostic features of *Ulrichidiscus* noted by Bassler (1935, p. 8) were: "Body semiglobose with the oral side occupied by five narrow but well-defined, very long ambulacra all strongly curving to the left, with a well-defined anal pyramid of many long triangular plates in one circlet, and interambulacral areas composed of polygonal but slightly imbricating plates." Regnéll (1966) repeated Bassler's definition, adding thecal size of the type species and noting the large size of the interambulacral.

In addition to the characters noted by Bassler, the cyclic ambulacral coverplates in a seven-plate series separates *Ulrichidiscus* from other genera of Agelacrinidae.

RANGE AND OCCURRENCE: Chesterian Series, Mississippian of Kentucky.

Ulrichidiscus pulaskiensis
(Miller and Gurley), 1894

Text fig. 56-58; plate 53, plate 54, fig. 1-7

- 1894 *Agelacrinus pulaskiensis* Miller, S. A. and Gurley, F. E., Illinois State Mus. Bull. 5: 16, pl. 3, fig. 18.
- 1897 *Agelacrinus pulaskiensis* Miller and Gurley, Miller, S. A., Second Appendix to North American Geology and Palaeontology, Cincinnati: 733.
- 1935 *Ulrichidiscus pulaskiensis* (Miller and Gurley), Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 8, pl. 1, fig. 7.
- 1936 *Ulrichidiscus pulaskiensis* (Miller and Gurley), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 22.
- 1938 *Ulrichidiscus pulaskiensis* (Miller and Gurley), Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 190.
- 1943 *Ulrichidiscus pulaskiensis* (Miller and Gurley), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 209.
- 1966 *Ulrichidiscus pulaskiensis* (Miller and Gurley), Regnéll, G., in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U171, text fig. 128-5.

Diagnosis

An *Ulrichidiscus* with: distal oral plates reflecting ambulacral coverplate pattern and appearing to grade into proximal ambulacral; hydropore protuberance formed by many plates, anterior hydropore plates do not reach transverse oral midline per radially; ambulacra long, moderately narrow; valvular anal structure large.

Description

Ulrichidiscus pulaskiensis is represented by only four specimens: the moderately well preserved holotype, and three presumed topotypes. The theca appears to have been either a highly convex dome, or subclavate. The ambulacra curve distally concentric with the margin of the convex upper oral surface. Distal to the ambulacra, numerous irregular circlets of squamose imbricate plates form an elongate zone which was either nearly vertical or perhaps slightly constricting downward, thereby forming a subclavate theca. Distal to this zone, the peripheral rim flares outward in contact with the substrate. The diameter of the upper oral surface reached 30 mm. The diameter of the basal peripheral rim probably equaled or exceeded that of the upper oral surface.

The transversely elongate oral area includes numerous plates (text fig. 56A, 57, pl. 53, fig. 5, 12). Most orals are smaller than or equal in size to the proximal ambulacral coverplates. Those which form the anterior oral midline and the anterior side of the transverse oral midline partially mimic the cyclic ambulacral coverplate pattern. Thus, distally they appear to grade into the

ambulacrals without apparent separation between the two series. The posterior side of the area, posterior to the transverse oral midline, includes many more plates than the anterior side. A zone of small orals, one to two plates wide, flanks the adradial ends of those orals which perradially form the posterior margin of the transverse oral midline. The hydropore structure plates lie posterior to these elements, further widening the posterior side of the oral area. In contrast, only a single series of plates forms the anterior side of the transverse oral midline.

The anterior oral midline extends directly outward along the axial midline of the theca. In contrast, the transverse oral midline is V-shaped with the anteriorly directed central point meeting the anterior oral midline. The perradial tips of those oral plates which flank the oral midlines are flexed upward and form a small, distinct central ridge.

The large, transversely elongate hydropore protuberance (text fig. 56A, 57, pl. 53, fig. 5, 12) extends along two-thirds of the posterior side of the oral area, from the proximal posterior edge of ambulacrum V over to the left half of the oral region. The structure is formed by many elongate plates, including approximately 12 wide and 20 narrow ones, all sloping upward to form the steep sides of the prominencè. The wide plates reach the summit of the elevation where they are laterally in contact. One or two narrow plates are wedged between the basal ends of every two contiguous large plates and appear to end externally just below the summit of the structure. The large outer plates may overlap the narrower ones. The hydropore opens along the summit of the transversely elongate protuberance.

The long, moderately narrow ambulacra curve contrasolarly. Commonly, curvature is gradual and is initiated near the oral region. The distal parts gradually become concentric with the margin of the upper oral surface. Occasionally curvature is more abrupt, with a straight proximal zone followed by a pronounced, curved area as the ambulacrum approaches the upper oral surface margin. The distal part of each long ambulacrum is concentric with the margin of the adjacent ambulacrum, but they remain separated by several interambulacrals.

The ambulacral coverplates form seven-plate cyclic sets. Cycles on opposite sides of the perradial line alternate, offset by half the length of a cycle, and form a broadly undulating, zigzag perradial line. Individual plates of the cycles are perradially pointed, superimposing small serrations along the large undulations. Homologous plates in adjacent cycles vary somewhat in shape, but maintain a constant relationship to the other plates of the cycle.

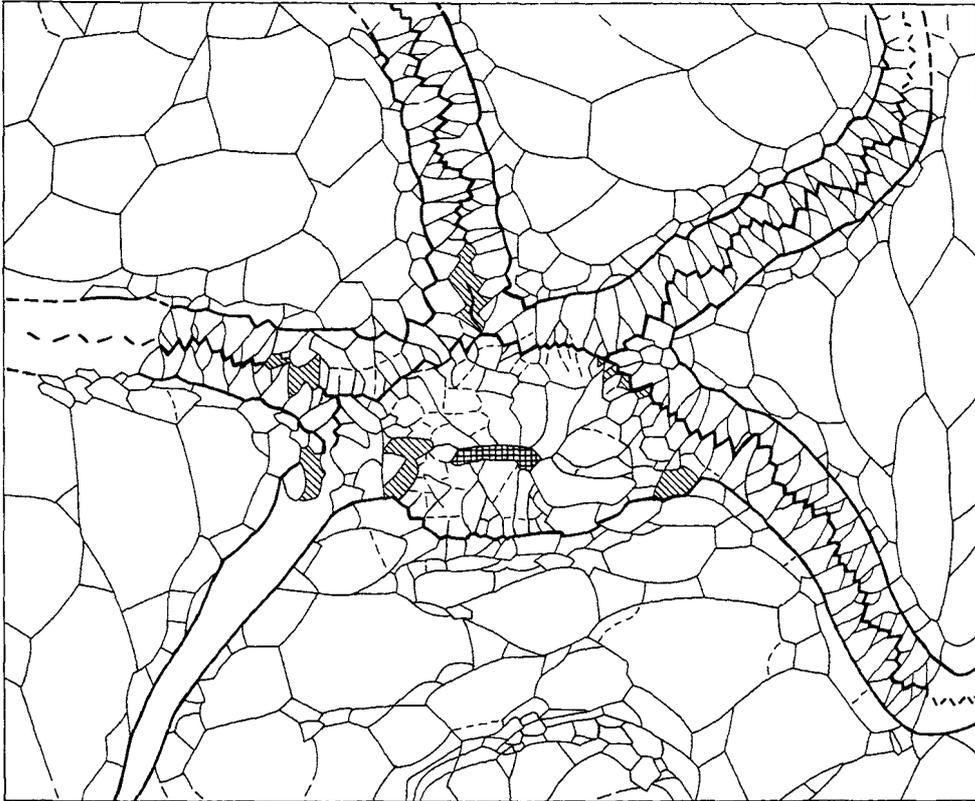
Actual plate shapes are shown in text fig. 56A and 56B. These are somewhat regularized in text fig. 58A, which tentatively identifies the plates by their order of

insertion. Plates of sets one, two, and three are generally subtriangular with broad adradial bases and pointed perradial ends. Plates of set one are the largest and longest; plates of sets two and three are nearly equal in shape and are intermediate in size. Plates of sets four and five are often similar in size, but smaller than the plates of sets two and three. Plates of sets six and seven are commonly very small. Modifications of those plate shapes shown in the text figures occur when a single plate forms two perradial points and the angular perradial tip of an opposing cycle plate fits between the double points.

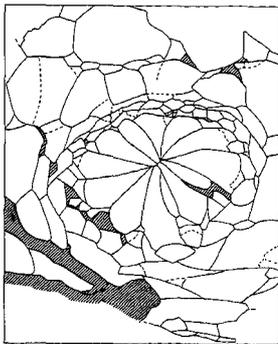
The order and position of insertion of the coverplate sets is tentatively reconstructed in text fig. 58A, a schematic regularization of the distal part of an ambulacrum. In the drawing, one new set is included in each successive cycle, except for the most distal plates. Specimens suggest that the plates of the first set (primaries) are added singly at the distal tip and move alternately left and right. Plates of the second set (secondaries) are added about three primary plates from the tip of the ambulacrum. They are inserted along the proximal sides of the primaries. Third set plates (tertiaries) are added three or four two-plate cycles proximal to the insertion zone of the secondary set, and are inserted along the distal sides of the primaries. After four to seven three-plate cycles, the plates of the fourth (quaternary) and fifth (quintary) sets are added in adjacent cycles: the quaternaries are inserted between the perradial tips of primary and secondary plates; the quintaries between the perradial tips of primary and tertiary set plates. In a few instances, the elements identified as plates of the fifth set appear to be added before those of the fourth set. Plates of the sixth set are inserted one or two five-plate cycles proximal to the zone of insertion of the plates of the fifth set. These sixth set plates are formed between the perradial tips of the primaries and the quintaries. The seventh, and final, set of plates is inserted two six-plate cycles proximal to the insertion zone of the sixth set. These plates of the seventh set are added proximal to the tip of the secondaries, thus distal to the tips of the plates of the third set of the adjacent proximal cycle.

Interpretation of the coverplate insertion zones is based on isolated segments of ambulacra in three specimens. It thus remains tentative, particularly for the fourth and fifth sets, and perhaps also for the sixth and seventh sets. Fracturing of larger plates may be responsible for some of the apparent irregularity in the insertion sequence. In the proximal part of the ambulacra, anomalous plates occasionally appear to be present. These may also be a result of fractures rather than sutures.

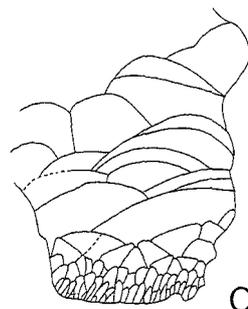
Sutures between contiguous plates of the cycles appear to be vertical, without suggestion of lateral overlap.



A



B



C

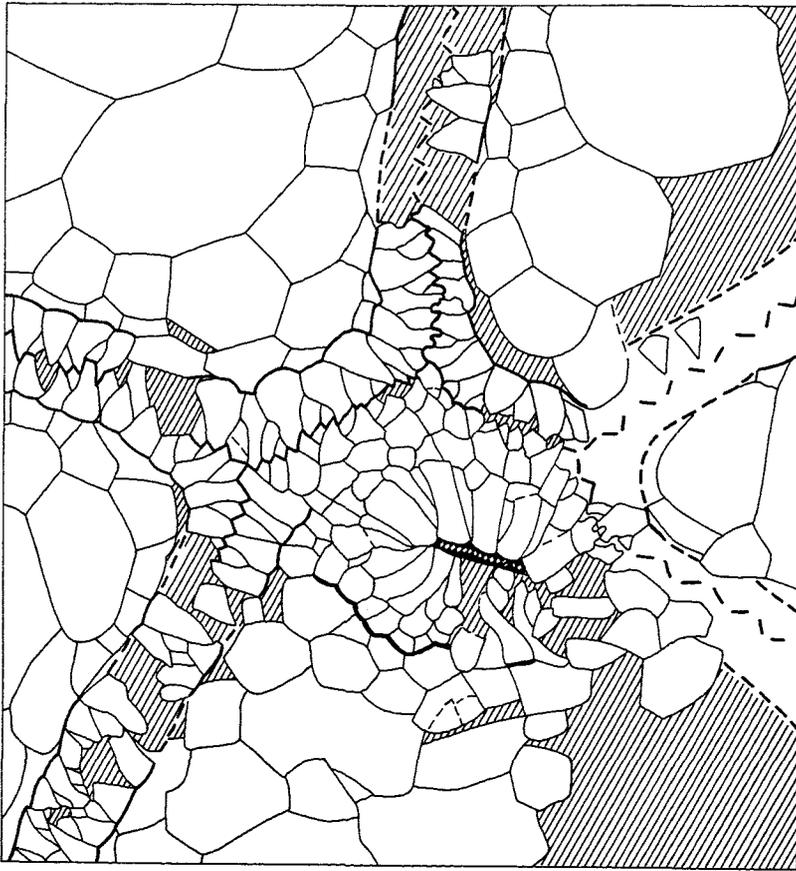
Text figure 56. *Ulrichidiscus pulaskiensis* (Miller and Gurley), 1894

Holotype, CFMUC 6419.

A. Oral area and adjacent structures, (x 10), pl. 53, fig. 5.

B. Anal area and adjacent interambulacral plates, (x 5), pl. 53, fig. 7.

C. Segment of the basal peripheral rim and adjacent pedunculate zone plates, (x 5), pl. 53, fig. 3.



Text figure 57. *Ulrichidiscus pulaskiensis* (Miller and Gurley), 1894

Oral area and adjacent structures, USNM S-3193-A, (x 6), pl. 53, fig. 12.

Thus smaller coverplates are apparently limited to the axial part of the ambulacra both externally and internally. Inner surfaces of the coverplates have not been observed.

Isolated ambulacral floorplates are exposed on the jumbled lower surface of one specimen (pl. 53, fig. 10). Apparently the floorplates are extremely thick. The upper surface is centrally concave downward and forms a deep central trough that is flanked by narrow, upper lateral margins that slope slightly toward the trough. The lower, or inner, surfaces of the floorplates expand laterally and have a broad base. Below the laterally expanded zone, the inner surface may be evenly convex inward. Sutures between contiguous floorplates are vertical.

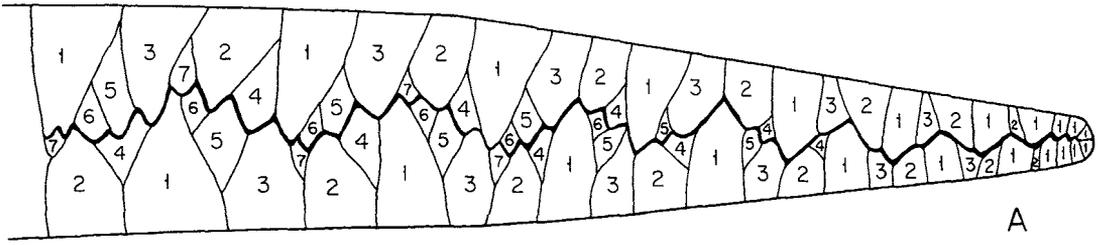
The interambulacral plates are large and polygonal in the central parts of the interambulacra, and smaller and more squamose where they flank the adradial sutures. Interambulacrals abut one another, or are slightly imbricate. Distal to the ambulacra, the plates of the marginal

or pedunculate zone are large, thick, squamose, and imbricate.

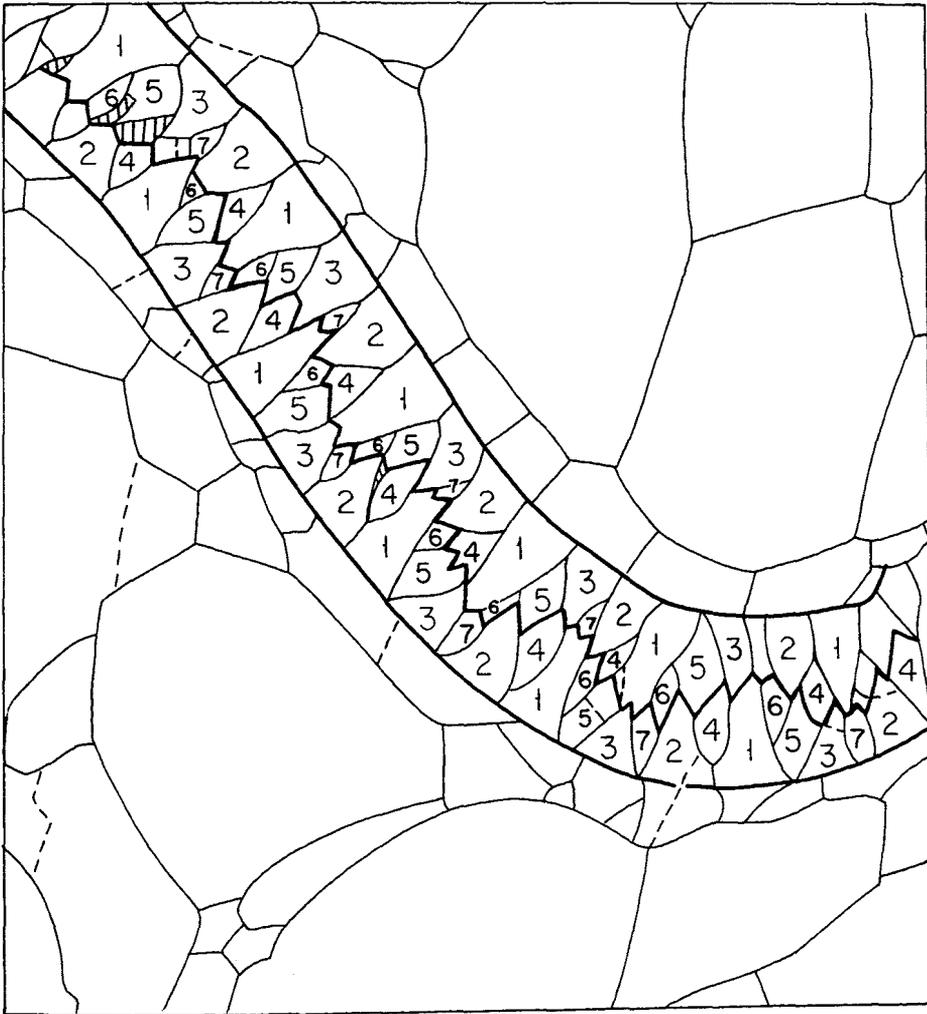
The valvular anal structure is unusually large, and fills the entire central part of interambulacrum 5. Well preserved only in the holotype (text fig. 56B), it includes approximately 14 large, triangular plates which alternate as inner, and overlapping outer, circlelet members. Some of the inner ones may have been hidden during preservation.

Text figure 58. *Ulrichidiscus pulaskiensis* (Miller and Gurley).
1894

- A. Model of ambulacral coverplate development showing the mode of formation of the seven-plate cycles.
- B. Proximal segment of ambulacrum V and adjacent interambulacrals, holotype, CFMUC 6419, (x 25), pl. 53, fig. 6.
1 through 7 are the first through seventh sets of ambulacral coverplates, respectively.



A



B

The peripheral rim forms the base of the theca; it includes five or six circlets. The very large plates of the proximal circlet are surrounded by small, externally triangular plates; the apices of adjacent ones are alternately directed proximally and distally. The outer three or four circlets include small plates that are either radially elongate (text fig. 56C, pl. 53, fig. 3) or similar to the second circlet plates, *i.e.*, externally triangular with adjacent plates pointing alternately proximally and distally (pl. 54, fig. 1). A few isolated large plates, exposed on the jumbled lower side of specimen USNM S-3193-A, are tentatively identified as proximal rim plates. They are geniculate and appear to bear small, vertical basal ridges, perhaps five per plate.

Thecal plate exteriors are smooth, except for minute pustulation which reflects the microstructure of the plates.

Specimens

CFMUC 6419. Holotype of *Ulrichidiscus pulaskiensis* (Miller and Gurley) (1894, p. 16, pl. 3, fig. 18, as *Agelacrinus pulaskiensis*). "Kaskaskia Group," Chesterian Series, Mississippian. Pulaski County, Kentucky. 23.8 mm axial by 24.3 mm transverse diameter.

Text fig. 56A-C, 58B, pl. 53, fig. 1-7.

The holotype is moderately well preserved. The upper oral surface retains much of its original convexity. However, plates distal to the ambulacra have been folded under and pressed against the inner sides of the upper plates. Many of these lower plates are missing. The oral region and entire lower side of the specimen was covered with resistant matrix prior to this study.

Fracturing of the oral and some hydropore structure plates obscures the relationship of some of the plates in this area (text fig. 56A). The outline of all five ambulacra is distinct, but coverplates are well preserved only in the proximal parts of ambulacra III-V. Interambulacral and anal plates are only slightly disrupted (text fig. 56B). One complete section of the plates distal to the ambulacra, including the basal peripheral rim, is preserved on the lower side of the specimen (pl. 53, fig. 2, 3). The total length of this series is approximately 15 mm. When this is added to the convex upper oral surface height, approximately 13 mm, the total noncollapsed thecal height appears to have been at least 25-30 mm.

USNM S-3193 (A-C). Three specimens of *U. pulaskiensis*, believed to be topotypes. Chesterian Series, Mississippian. Pulaski County, Kentucky.

USNM S-3193-A. 30.6 mm axial by 22.5 mm transverse diameter.

Text fig. 57, pl. 53, fig. 8-13.

This specimen is separated from its resting site. The left two-thirds of the upper oral surface is well preserved, but most of the right third is disrupted and in part folded under the remainder of the specimen. The lower surface of the specimen is a mass of jumbled thecal plates which exposes several isolated ambulacral floorplates and some of the geniculate rim plates. On the upper surface, most of the oral area and hydropore structure plates are in place. The ambulacral coverplate sequence is preserved in parts of ambulacra I-IV. Interambulacra 1 and 2 are also well preserved. The anal structure is completely disrupted.

USNM S-3193-B. 28.6 mm long by 16.8 mm wide.

Pl. 54, fig. 1-6.

The specimen is a fragment of a large individual resting on a small rugose coral. It includes parts of three ambulacra, adjacent interambulacrals, the squamose, imbricate marginal plates, and an adjacent section of the peripheral rim. Distal sectors of the ambulacra preserve the insertion zones of several ambulacral coverplate sets. The marginal zone of squamose, imbricate plates, proximal to the peripheral rim, appears to be much shorter in this specimen than in the holotype, and suggests that the theca may have been domal.

USNM S-3193-C. Upper oral surface: 27.4 mm greatest diameter by 22.5 mm. Peripheral rim: 24.9 mm greatest diameter by 18.3 mm.

Pl. 54, fig. 7.

This individual, also resting on a rugose coral, is poorly preserved. The upper oral surface is almost totally disrupted. Partially disrupted distal sections of two ambulacra are retained. Below the ambitus of the upper oral surface, the squamose, imbricate marginal plates and the basal peripheral rim plates are preserved in part. This individual also appears to have been less highly elevated than the holotype, but the marginal zone does constrict downward to form a short pedunculate zone.

Discussion

The original description of *Agelacrinus pulaskiensis* Miller and Gurley (1894, p. 16) was very generalized; they recorded: the high convexity of the theca; the pedunculate or marginal zone plates squamose and imbricate (thought by them to be the peripheral rim plates); interambulacrals large, imbricate; five long, narrow ambulacra, "four sinistral and one dextral," with a single biseries of coverplates; numerous small orals; 12 anal plates; and plate surfaces "finely granular." In contrast with the written description, an accompanying line drawing of the holotype correctly shows ambulacrum V curving contrasolarly.

Bassler (1935) noted the contrasolar curvature of all five ambulacra in this species. For this reason he designated a new genus, *Ulrichidiscus*, for the species.

The expanded description of *U. pulaskiensis* presented here is based on restudy of the holotype after removal of matrix which had obscured the oral area and the entire lower surface of the specimen. Three new specimens, believed to be topotypes, are also included. Thecal shape is still uncertain, for the specimens suggest either a highly convex-upward domal form or a

subclavate theca with a short, slightly constricting pedunculate zone. Taxonomically distinctive features include the shape of the transverse oral midline, the large number of posterior oral plates, the plating of the hydropore structure, the ambulacral coverplate sequence, and the large size of the anal structure. Internal thecal features are mostly unknown.

RANGE AND OCCURRENCE: Chesterian Series, Mississippian of Pulaski County, Kentucky.

Genus *Cooperidiscus* Bassler, 1935

- 1935 *Cooperidiscus* Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 8, pl. 1, fig. 9.
 1936 *Cooperidiscus* Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 22.
 1938 *Cooperidiscus* Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 72.
 1943 *Cooperidiscus* Bassler, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 199.
 1944 *Cooperidiscus* Bassler, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, pl. 49, fig. 16.
 1966 *Cooperidiscus* Bassler, Regnéll, G., in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U169, text fig. 128-2.

TYPE SPECIES: *Lepidodiscus alleganius* Clarke, 1901.

Diagnosis

Agelacrinitidae with: transversely elongate oral area, probably formed by numerous small plates; large hydropore protuberance posterior to central oral rise; five long, extremely narrow ambulacra, curved I-V solar; two or more sets of ambulacral coverplates; interambulacra numerous, squamose, imbricate; valvular anal structure with two circlets of plates.

Description

Cooperidiscus Bassler (1945) is monotypic. Therefore, separation of generic and specific taxobases is uncertain. Features cited in the above diagnosis are in part inferred to be of generic rank from established generic taxobases for related genera of Agelacrinitidae. *Cooperidiscus* is the only Agelacrinitidae in which all of the ambulacra curve solarly.

Cooperidiscus alleganius (Clarke), 1901

Text fig. 59; plate 54, fig. 8-11, plate 55, fig. 1-6

- 1901 *Lepidodiscus alleganius* Clarke, J. M., New York State Mus., Bull. 49 (2): 194-195, pl. 10, fig. 1-5.
 1910 *Agelacrinitus (Lepidodiscus) alleganius* Clarke, Grabau, A. W. and Shimer, H. W., North American Index Fossils, Invertebrates, New York, 2: 472.
 1914 *Lepidodiscus alleganius* Clarke, Foerste, A. F., Denison Univ., Sci. Lab. Bull. 17 (art. 14): 399-456, pl. 6, fig. 2a-b.
 1935 *Cooperidiscus alleganius* (Clarke), Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 8, pl. 1, fig. 9.
 1936 *Cooperidiscus alleganius* (Clarke), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 22.
 1938 *Cooperidiscus alleganius* (Clarke), Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 72.
 1943 *Cooperidiscus alleganius* (Clarke), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 199.
 1944 *Cooperidiscus alleganius* (Clarke), Shimer, H. W. and Shrock, R. R., Index Fossils of North American, New York: 131, pl. 49, fig. 16.
 1966 *Cooperidiscus alleganius* (Clarke), Regnéll, G., in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U169, text fig. 128-2.

Diagnosis

A *Cooperidiscus* with: convex-upward, upper oral surface; large hydropore structure arising from the posterior margin of the central oral rise, apparently formed by numerous plates; ambulacra distally becoming concentric with margin of upper oral surface but remaining widely separated from each other; interambulacra wide.

Description

Cooperidiscus alleganius (Clarke) is known only from external molds preserved in coarse sandstone. The critical plates of the oral-ambulacral series are poorly preserved in all known specimens.

The upper oral surface of the theca is known to be convex upward. It includes the oral-ambulacral structures, hydropore, anal area, and interambulacral plates. The lower part of the theca, below the ambitus, was described by Clarke (1901) as being concave upward and entirely covered by squamose, imbricate plates that overlap proximally. Greatest observed upper surface diameter is 44.5 mm.

The transversely elongate oral region forms the central oral rise. It apparently comprises numerous small plates, but none of the specimens preserves the details. The faint impressions of finely serrate oral midlines are seen on two specimens (pl. 55, fig. 4, 6). The course of the transverse oral midline, beginning at the lateral bifurcation plates, appears to be angled anteriorly (almost V-shaped); the central point intersects the proximal end of the short, straight anterior oral midline.

The large, transversely elongate hydropore structure arises from the posterior margin of the central oral rise. It appears to extend from the proximal posterior margin of ambulacrum V across most of the posterior side of the oral region. The structure probably includes many plates, oriented oblique to the thecal surface, that form the steep sides of the protuberance. The hydropore opening may be an elongate, anteriorly arched, arcuate slit that extends along the summit of the protuberance.

The ambulacra are long and extremely narrow. In proportion to thecal diameter they appear to be less than half as wide as the ambulacra of any other known edrioasteroid. All five ambulacra curve solarly. Proximal parts are nearly straight, followed by a rapidly curving zone. Distally they become concentric with the margin of the upper oral surface, but each ambulacrum remains widely separated from adjacent ambulacra by a broad zone of interambulacrals. Irregular, minor sinuations are not uncommon along the course of the ambulacra in some specimens, particularly in the distal parts.

The ambulacral coverplate sequence appears to include at least two sets of plates which perhaps form either an alternating double biseries, or more likely, a two-plate cyclic series. Text fig. 59A attempts to outline the coverplate sutures in the medial part of ambulacrum IV of the holotype. The drawing is regarded as highly tentative because of the poor preservation, although this is the best preserved material available. The coverplates are preserved steeply inclined to the thecal surface and form sharply defined, narrow ridges. This orientation further obscures the plate pattern. The coverplate series may be much more complex than suggested in text fig. 59A.

The wide interambulacra are covered with numerous, squamose, imbricate plates. These extend between the distal parts of the ambulacra, and apparently continue onto the lower side of the theca.

The valvular anal structure includes 10 large, triangular plates in the lectotype (text fig. 59B, pl. 54, fig. 10). There are suggestions of alternate overlapping outer circlets and overlapped inner ones.

Plate surfaces appear to have been smooth.

Specimens

NYSM 4962. Lectotype of *Cooperidiscus alleganius* (Clarke) (1901, pl. 10, fig. 4, as *Lepidodiscus alleganius*). "Chemung SS," probably Canadaway or Conneaut Group, Chautauquan Series, Upper Devonian. Loose at Alfred, New York. 33.6 mm axial by 38.5 mm transverse diameter.

Text fig. 59A, B, pl. 54, fig. 8-11.

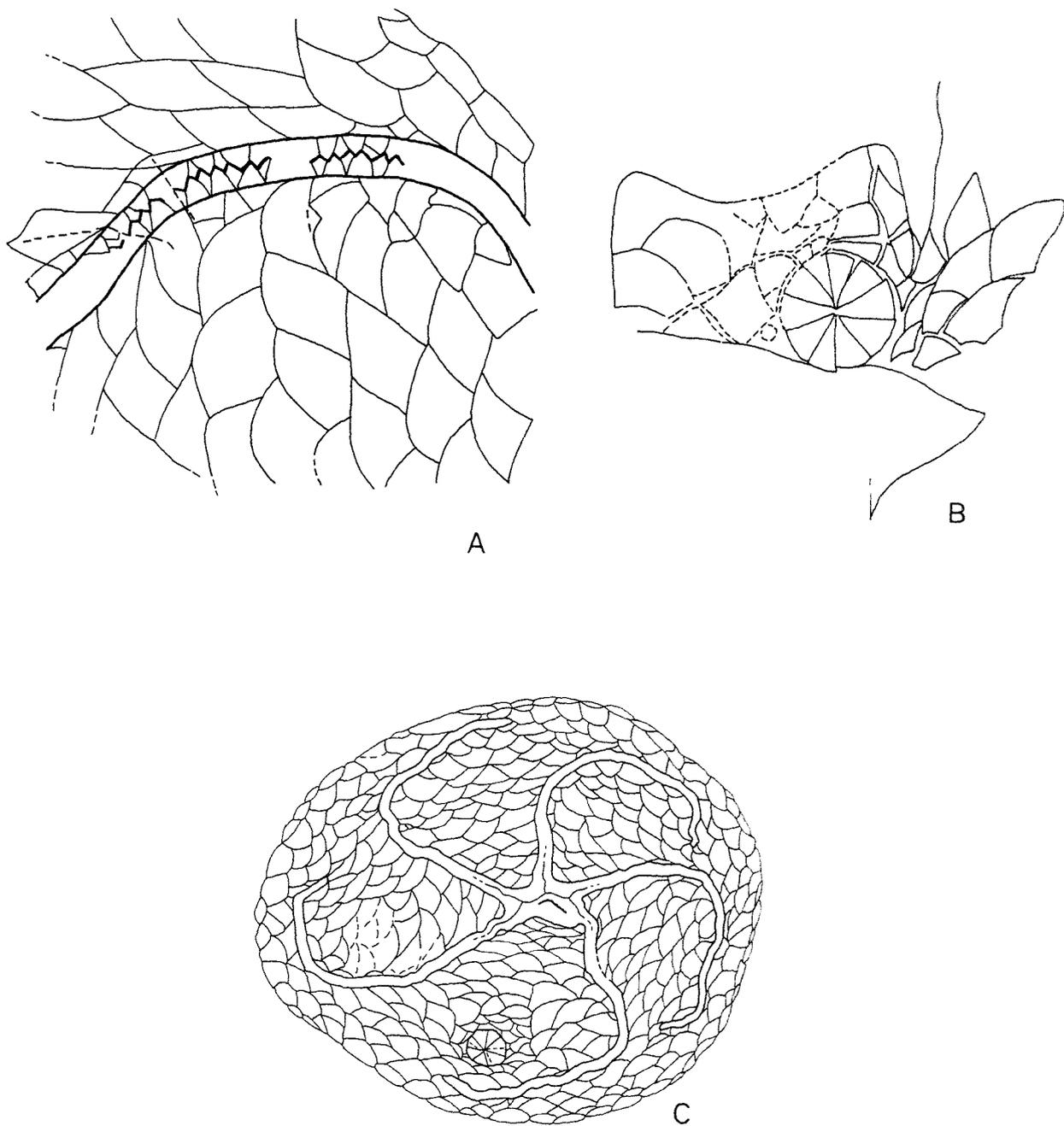
This specimen, one of five in Clarke's type series, is here designated the lectotype. It and all following specimens are external molds, preserved in coarse sandstone. The lectotype preserves the upper oral surface. Ambulacra I and II are poorly preserved, as is the oral area and the proximal part of the other three ambulacra. The coverplate pattern has been tentatively interpreted from the curved medial part of ambulacrum IV. The serrate perradial line is also seen in the distal part of ambulacrum V, but individual coverplate boundaries are not clear. The anal structure is preserved in the posterior interambulacrum. The squamose, imbricate interambulacrals distally appear to extend past the ambitus, onto the lower surface of the specimen.

NYSM 4959. Lectoparatype of *C. alleganius* (Clarke) (1901, pl. 10, fig. 1). "Chemung SS," probably Canadaway or Conneaut Group, Chautauquan Series, Upper Devonian. Loose at Alfred, New York. 27.4 mm axial by 25.3 mm transverse diameter.

Pl. 55, fig. 1, 2.

This specimen was described by Clarke (1901) as a juvenile with straight ambulacra that extend to the margin of the upper oral surface. The specimen appears to be only the central sector of the upper oral surface of a large adult, since the distal curved parts of the ambulacra and the adjacent interambulacrals are missing. The specimen preserves the shape of the oral-hydropore region and the proximal parts of the ambulacra, but all plate boundaries within these areas are obscure. Only the proximal interambulacral plates are distinct. The anterior half of the anal structure is preserved along the posterior margin of the preserved portion of interambulacrum 5.

USNM 34131 (A, B). "Upper Chemung SS," probably Chautauquan Series, Upper Devonian. West Beech Woods Creek, 1½ miles south of Sabinsville, Clymer Township, Tioga County, Pennsylvania.



Text figure 59. *Cooperidiscus alleganius* (Clarke), 1901

A-B. Lectotype, NYSM 4962.

A. Central segment of ambulacrum IV and adjacent interambulacra, (x 7), pl. 54, fig. 11.

B. Anal structure and adjacent plates, (x 7), pl. 54, fig. 10.

C. Lectoparatype, USNM 34131-A, (x 2), pl. 55, fig. 3.

USNM 34131-A. Lectoparatype of *C. alleganius* (Clarke) (1901, pl. 10, fig. 3). 33.6 mm axial by 40.7 mm transverse diameter.

Text fig. 59C, pl. 55, fig. 3, 4.

This large adult preserves only the collapsed, axially compressed upper oral surface. The outline and elevated form of the oral area and hydropore structure are preserved, but plate boundaries are indistinct. The oral midlines and the hydropore opening are preserved as faint impressions. The ambulacra show minor sinuations along their course, distally in particular. The anal structure is elevated into a small, conical mound. Suggestions of inner circlet plates are exposed.

USNM 34131-B. Specimen of *C. alleganius* on slab adjacent to USNM 34131-A. 44.5 mm axial by 41 mm transverse diameter.

Pl. 55, fig. 5, 6.

This large individual also preserves only the collapsed and laterally compressed upper oral surface. The oral area and hydropore structure are distinct, but suture lines are obscure. The anterior and transverse oral midlines and the hydropore opening are preserved as faint impressions. The ambulacral coverplate pattern is not recognizable. The anal area and some adjacent interambulacra are missing.

Discussion

Clarke's (1901) original description of *Lepidodiscus alleganius* reported: the transversely elongate oral area; the long, narrow, solarly curved ambulacra with sinuous perradial lines; squamose, imbricate interambulacra; and 10 triangular anal plates. Moreover, he included two specimens, now missing, purported to be molds of the lower side of the theca. Clarke suggested that the lower surface was slightly concave upward, and entirely covered with squamose, proximally imbricate plates.

Reinvestigation of the available type specimens and latex pulls of these has added little to Clarke's description, except for the identification of the hydropore protuberance. Plating of the oral area, hydropore structure, and ambulacra is poorly preserved in all of the specimens.

Clarke's statement that in two specimens (now missing) a plated aboral thecal surface was seen, is enigmatic. If correct, this is the only species of Agelacrinitidae, indeed, the only Isorophida, in which the aboral surface has been shown to be fully plated. Clarke's drawings of these specimens suggest that the center of the lower side was poorly preserved in both. Thus it seems likely that the theca was clavate, and that a small, basal peripheral rim was overlooked.

RANGE AND OCCURRENCE: Upper Devonian of northwestern Pennsylvania and southwestern New York.

Genus and Species Indeterminate

Plate 56

Two fragments of an extraordinarily large edrioasteroid species were collected by N. Gary Lane from the Madera Formation, Magdalena Group, Upper Pennsylvanian of New Mexico.

Although probably a new species, the specimens are considered too incomplete to designate a new taxon. They are described here because only one other Pennsylvanian edrioasteroid species has been reported. *Agelacrinites hybolopus* Fraunfelter and Utgaard (1970), from the Conant Limestone member of the Jamestown Cyclothem, Carbondale Formation, Middle Pennsylvanian of southern Illinois.

Specimens

UCLAPC 48166, 48167. Two fragmentary specimens. Roadcut on east side of dirt lumber truck road in Guadalupe Canyon, 9.5 miles north of junction of Guadalupe Canyon Road with New Mexico Route 4, Guadalupe Canyon, New Mexico. Madera Formation, upper part, Magdalena Group, Virgilian Series, Pennsylvanian.

UCLAPC 48166. 39.3 mm long by 22.8 mm wide.

Pl. 56, fig. 1-8.

The upper surface of the specimen includes segments of three ambulacra and the adjacent large, polygonal interambulacra. These interambulacra continue around the marginal ambitus of the theca onto the lower surface. Distal to the large, polygonal, lower interambulacra a few thin, elongate, imbricate, pedunculate zone plates are preserved. The inner sides of the upper and lower surface plates have been pressed together during thecal collapse.

UCLAPC 48167. 17.1 mm long by 14 mm wide.

Pl. 56, fig. 9-11.

This fragment preserves two ambulacral segments and adjacent interambulacra. The lower surface of the fragment includes only the large polygonal plates adjacent to the ambital region. The upper and lower surface plates have been pressed together during collapse.

The two fragments, probably from different individuals, demonstrate that the theca was clavate. The upper oral surface included the oral-ambulacral structures, large, thick, polygonal, tessellate interambulacrals, and presumably the anal structure. Similar interambulacrals form the ambitus and the proximal part of the lower surface. Distal to these elements, elongate, thin, rectangular, imbricate plates apparently formed a pedunculate zone, probably similar to that of *Discocystis kaskaskiensis*. If the arc formed by the ambitus of the larger specimen is used to define the circumference of the complete theca, the diameter obtained is over 70 mm, one of the largest for any edrioasteroid.

The ambulacral coverplates are disrupted in all but two small parts of one ambulacrum in the larger specimen. These two areas demonstrate that the coverplates are cyclic, with three or four plates per cycle in this part of the ambulacrum. However, the variability in shape, size, and arrangement seen in the two small segments suggests preservational distortion of the coverplate series. Therefore, confident description of the cyclic elements is impossible.

The ambulacral floorplates are uniserial, axially elongate, and unusually thick. A deep, steep-sided trough is incised into the upper surface of each floorplate. The uppermost lateral margins that flank the trough are somewhat less steeply inclined and thereby form a very narrow zone of articulation with the bases of the overlying coverplates. The lateral sides of the floorplates abut the thick interambulacrals. These adradial sutures are oblique planes, slanting downward and away from the ambulacral axis, with the floorplates widening downward. The lower, basal surfaces of the floorplates appear to be nearly flat, parallel with the inner flat surfaces of adjacent interambulacrals.

This Pennsylvanian form shows similarity to the Mississippian *Discocystis kaskaskiensis*. Both have clavate thecae, thin, elongate, imbricate plates of the pedunculate zone, and perhaps also a three- or four-plate cyclic series of ambulacral coverplates. However, only the distal ambulacral coverplates are preserved in the Pennsylvanian species, and thus the cycles may be incomplete. The shape of the ambulacral floorplates appears to be unique in the Pennsylvanian species.

Family Uncertain

Genus *Hadrochthus* Bell, gen. nov.

Diagnosis

Isorophina with: domal theca; oral area formed by few plates, primary orals differentiated externally; small hydropore structure semi-integrated with central oral rise; broad ambulacra straight, coverplates large, forming a single alternating biseries; interambulacrals large, thick, polygonal, tessellate; valvular anal structure formed by one circllet of plates.

Description

Hadrochthus is monotypic. Therefore, separation of generic and specific taxobases is uncertain. Features outlined in the above diagnosis are in part inferred to be of generic rank from established taxobases for other Isorophina genera.

ETYMOLOGY: *Hadrochthus* is compounded from the Greek *hadros*, meaning stout or thick, in reference to the large size and great thickness of the thecal plates, and *ochthos*, meaning mound, in reference to the domal theca.

RANGE AND OCCURRENCE: Mason City Member, Shell Rock Formation, Upper Devonian of Iowa.

Hadrochthus commensalus Bell, sp. nov.

Text fig. 60; plate 57

Diagnosis

A *Hadrochthus* with: medium-sized, highly convex, domal theca; oral area formed by three large primary orals, two pairs of lateral shared coverplates, four secondary orals, and one small hydropore oral; small hydropore protuberance formed by two plates; anal plates large and triangular.

Description

The medium-sized, highly convex, domal theca of *H. commensalus* reaches 15 mm in diameter.

The oral area includes 14 plates (text fig. 60 A, B). Three large primary orals form the center, all adradially in contact with the adjacent interambulacra. Two are anterior primaries which meet each other laterally along the proximal end of the anterior oral midline. A single, very large posterior primary oral meets both anterior primaries along the center of the transverse oral midline. However, it may be offset to the right and abut a larger

part of the right, than the left anterior oral. A small plate lies adjacent to the proximal part of the left side of the large posterior primary oral. Perradially this plate abuts a large sector of the proximal end of the left anterior primary oral. This small element, tentatively identified here as a secondary oral, might represent a fourth primary oral, homologous to the left posterior primary oral found in the *Isorophidae*.

Two pairs of lateral shared coverplates flank the central primaries along the transverse oral midline, with one pair on each side. These shared coverplates reach the adradial suture line where they are laterally in contact with the adjacent primary orals. One pair of secondary orals—one plate anterior and one posterior to the transverse midline—perradially separates each of the two pairs of shared coverplates from the central primaries. Two small anterior secondary orals lie along the anterior oral midline between the anterior orals and the proximal coverplates of ambulacrum III. The two anterior secondaries may lie on the left side of the midline, or they may be opposed, one on each side. A small right posterior hydropore oral completes the oral sequence. Proximally it abuts the right distal margin of the large posterior primary oral. Laterally it abuts the adradial end of the second, and sometimes also part of the first proximal posterior coverplate of ambulacrum V.

The hydropore structure (text fig. 60 A, B) involves only two plates. It is a small, semi-integrated elevation arising from the posterior slope of the oral rise. The anterior side is formed by the right posterior end of the large posterior primary oral. The adjacent left anterior margin of the small hydropore oral forms the posterior side of the structure. The contiguous edges of these two plates are thickened and form a small, elongate elevation. The hydropore opening lies along the summit of the protuberance at the junction of the two plates. Commonly the opening is arcuate and convex proximally (text fig. 60B). In one specimen it appears to be sinuous (text fig. 60A).

The wide ambulacra are straight and drape down the highly convex upper oral surface to the proximal margin of the peripheral rim. The ambulacral coverplates form a single alternating biseries. Each coverplate is large and subpentagonal, with a pointed perradial end. Adjacent coverplates laterally abut along vertical sutures.

The inner sides of the coverplates are inadequately known, having been observed only in partially disrupted specimens. Large, bladelike intra-ambulacral extensions are produced into the large ambulacral tunnel from the perradial ends of the coverplates. The length and shape of the inner parts of these extensions are unknown. The adradial ends of the coverplates abut the adjacent thick interambulacrals along nearly vertical adradial

sutures. These adradial faces may be modified by a groove incised into the edge of the coverplates which extends the length of the adradial face of each coverplate. A corresponding rounded ridge may be present on the opposing edge of each interambulacral. The inner adradial ends of the coverplates rest on the upper lateral margins of the ambulacral floorplates. The coverplates apparently end adjacent to the edges of the floorplates and thus are not produced inward as intrathecal extensions.

A single isolated ambulacral floorplate is preserved on the disrupted lower side of the holotype (pl. 57, fig. 2). It suggests that the uniserial floorplates are trough-shaped. The upper side is convex downward, with narrow lateral margins that slope inward less steeply than the sides of the deep central trough. These lateral margins apparently abut the inner adradial ends of the overlying coverplates. The inner sides of the floorplates appear to be evenly convex inward, without lateral nodes.

The interambulacrals are large, unusually thick, polygonal plates which abut along vertical sutures.

The valvular anal structure lies near the center of interambulacrum 5. It is formed by seven or eight large, thick, triangular plates which apparently form a single circlet.

The peripheral rim includes five circlets of plates. The very large plates of the proximal circlet, and the much smaller ones of the second are externally elongate concentric with the thecal margin. Plates of the following three circlets progressively diminish in size outward and are elongate radially.

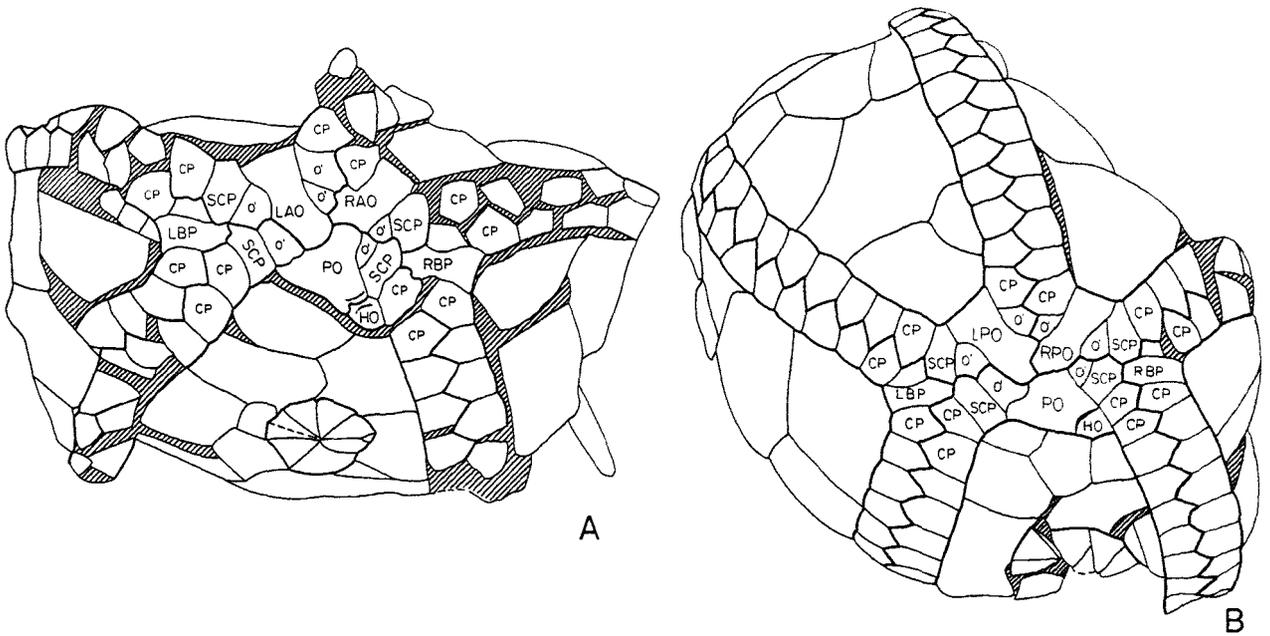
Most thecal plates appear to be smooth externally. However, two disrupted interambulacrals, preserved on the lower side of the holotype, have been shoved into the thecal cavity and were thus protected from abrasion. These bear large, rounded tubercles. Although the outer ends of the tubercles are large, they are attached to the plates by short, narrow, constricted "necks." All of the specimens of this species are much abraded. Thus it is not impossible that large tubercles may have been present on many of the plates, but have been lost.

Specimens

SUIC 80002, 80003, 32293, 32299. Middle of the Mason City member, Shell Rock Formation, Senecan Series, Upper Devonian. Thomas William Quarry, NW $\frac{1}{4}$, sec. 28, T. 96 N., R. 18 W., Floyd County, 3 miles southwest of Norra Springs, Iowa.

SUIC 80002. Holotype of *Hadrochthys commensalus* Bell. 14.7 mm axial by 13.8 mm transverse diameter.

Text fig. 60B, pl. 57, fig. 1-3.



Text figure 60. *Hadrochthys commensalus* Bell, sp. nov.

A. Paratype (1), SUIC 80003, (x 6), pl. 57, fig. 4.

B. Holotype, SUIC 80002, (x 6), pl. 57, fig. 1.

CP, ambulacral coverplate; HO, hydropore oral plate; LAO, left anterior primary oral plate; LBP, left lateral bifurcation plate; o', secondary oral plate; PO, posterior primary oral plate; RAO, right anterior primary oral plate; RBP, right lateral bifurcation plate; SCP, lateral shared coverplate.

The holotype preserves the central part of the upper oral surface with little plate disruption. However, the distal parts of the oral surface, including most of the right anterior third of the theca, have been folded under the upper side. The peripheral rim is missing. The oral and hydropore areas are well preserved, along with most of ambulacra I, II, III, and V. Only the proximal end of IV is not disrupted. Interambulacra 1 and 2 are well preserved also. The anal structure is disrupted, with some of the posterior plates missing. The upper surface of the specimen has been severely abraded.

The lower side of the specimen preserves several disrupted plates which have been pushed into the thecal cavity; these include one ambulacral floorplate and two interambulacrals which bear large external nodes. The specimen is believed to have rested on the theca of a cystoid, *Adocetocystis williamsi*.

SUIC 80003. Paratype (1) of *H. commensalus*. 15.1 mm axial by 15 mm transverse diameter.

Text fig. 60A, pl. 57, fig. 4-7.

The specimen has been laterally compressed. One surface, referred to here as upper, preserves the oral

area, ambulacra I, II, IV, and V, interambulacra 1, 4, and 5, and the anal structure. The reverse, or lower, side preserves the proximal parts of ambulacrum III and interambulacra 2 and 3. The remainder of the theca, including the peripheral rim, is missing.

The oral area, hydropore structure, anal structure, and proximal parts of ambulacra I and V are well preserved, with their plates nearly in place. Other thecal elements are disrupted to varying degrees, although most of the plates of interambulacrum 5 are nearly in place. The specimen has been extensively abraded. Although now free, it is believed to have been attached to the theca of a cystoid, *Adocetocystis williamsi*.

SUIC 32293. Paratype (2) of *H. commensalus*. 11.7 mm axial by 11 mm transverse diameter.

Pl. 57, fig. 8-10.

This specimen has collapsed; the oral surface is depressed and has been pushed anteriorly. The distal parts of ambulacra II, III and IV, and interambulacra 2 and 3 have overridden the anterior section of the peripheral rim. Although many of the plates are disrupted, the oral

area and parts of the ambulacra preserve the plate relationships. The posterior half of the peripheral rim is well preserved. Ambulacrum III, which arches out over the anterior edge of the theca, has been separated from adjacent interambulacra and exposes the grooved adradial ends of the coverplates along the left side of the ambulacrum. The specimen is resting on a paratype (SUIC 32293) of the cystoid *Adocetocystis williamsi*.

SUIC 32299. Paratype (3) of *H. commensalus*. 7.1 mm axial by 6.5 mm transverse diameter.

Pl. 57, fig. 11, 12.

This specimen is partially collapsed and irregularly compressed. It retains some of the original convexity of the oral surface, but the distal parts of the ambulacra and interambulacra have been crushed inward along the proximal margin of the peripheral rim. Many plates are disrupted, but the proximal parts of ambulacra I, III, IV, and the center of V preserve the coverplate relationships. The two anterior primary orals and some of the anal area plates are identifiable. The specimen is resting on a paratype (SUIC 32299) of the cystoid *Adocetocystis williamsi*.

Discussion

Thecal plating in *Hadrochthys commensalus* Bell is simple. As in specimens in the Lebetodiscina, the ambulacral coverplates form a single alternating biseries. Moreover, the oral area includes relatively few plates with primary orals differentiated, and the hydropore structure is formed by only two plates. However, *H. commensalus* lacks ambulacral coverplate passageways, and the anal structure is valvular. Therefore it is included here within the suborder Isorophina, but does

not appear to belong to either of the two families recognized in this study. With only a single species exhibiting these features, it seems unwise to propose a new family, thus *H. commensalus* is not assigned to a family here.

As the only species of Isorophina known to have a single alternating biseries of coverplates (in the adult stage), *H. commensalus* may be either primitive or highly specialized. In view of the unusual thickness of the thecal plates and the apparently commensal relationship with the cystoid *Adocetocystis williamsi*, *H. commensalus* is thought to be a highly specialized form.

Evidence for the suggested commensal relationship between *H. commensalus* and the cystoid *Adocetocystis williamsi* is circumstantial. All specimens of *H. commensalus* appear to have been attached to the theca of one of these cystoids. All of the specimens are from a single locality. Koch and Strimple (1968) have presented a detailed reconstruction of this site, apparently an intertidal or perhaps very shallow subtidal area. The substrate is an eroded limestone surface with large, rounded knobs of limestone separated and undercut by deep, interconnected solution channels. The cystoids attached to the undersides of the knobs, and apparently were able to extend out and upward above the knobs for feeding. Thousands of specimens of another edrioasteroid species (*Agelacrinites hanoveri* Thomas, 1924) are found resting on the upper surface of the limestone knobs. Thus favorable substrate conditions existed for edrioasteroid growth within the area, but *H. commensalus* occurs only on cystoid thecae. Therefore, it seems that some type of commensal relationship existed between *H. commensalus* and the cystoid, without which the edrioasteroid was not able to survive.

RANGE AND OCCURRENCE: Shell Rock Formation, Seneca Series, Upper Devonian of northcentral Iowa.

Suborder and Family Uncertain:

(?) *Hemicystites carbonarius* Bassler, 1936

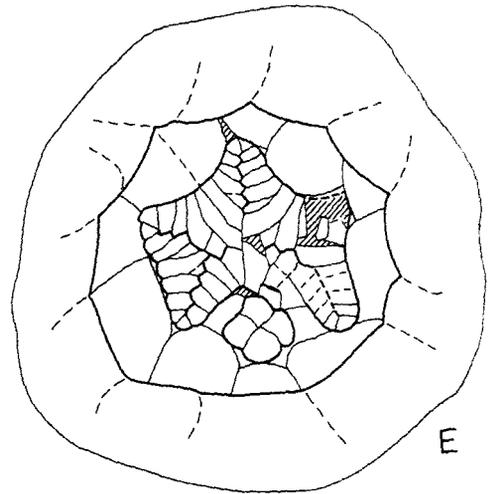
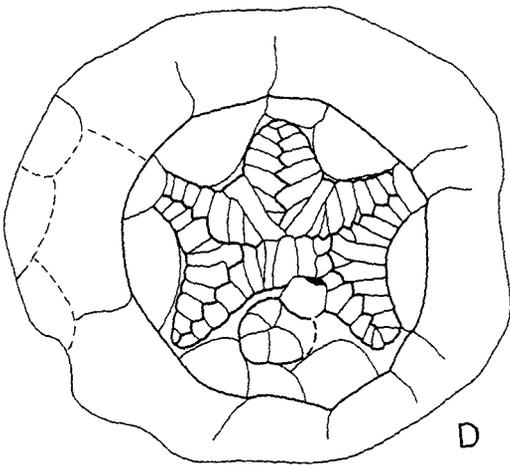
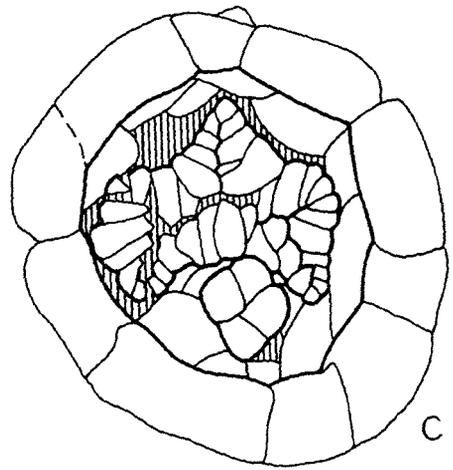
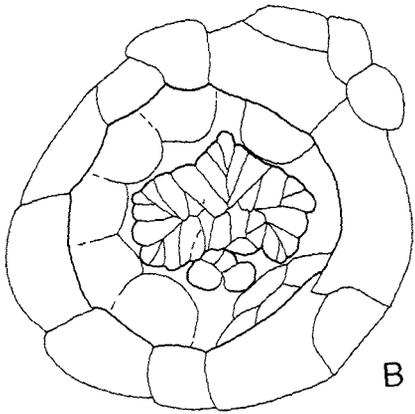
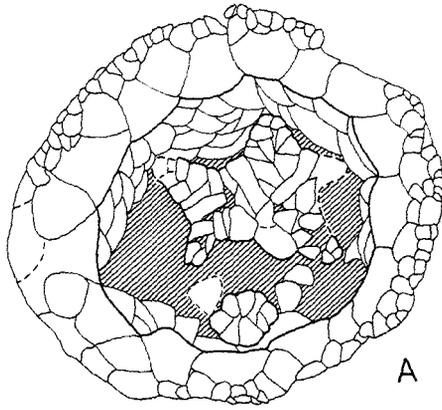
Text fig. 61A; plate 55, fig. 7-10

- 1936 *Hemicystites(?) carbonarius* Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 15, pl. 4, fig. 10-11.
 1943 *Hemicystites(?) carbonarius* Bassler, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 203.
 1944 *Hemicystites(?) carbonarius* Bassler, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, pl. 49, fig. 14.

Text figure 61.

- A. *Hemicystites carbonarius* Bassler, 1936, type series specimen, USNM 91837-b-6, (x 15), pl. 55, fig. 10.
 B-E. *Agelacrinites hanoveri* Thomas, 1924.
 B. Juvenile, SUIC 35162, (x 20), pl. 55, fig. 11.
 C. Juvenile, SUIC 1906, (x 15), pl. 55, fig. 13.
 D. Juvenile, SUIC 35163, (x 15), pl. 55, fig. 14.
 E. Juvenile, SUIC 35164, (x 15), pl. 55, fig. 12.

FAMILY UNCERTAIN



Description

Hemicystites carbonarius is known from eight specimens, seven of which preserve only the peripheral rim and a completely disrupted central thecal area. The single individual with partially preserved oral surface features is a juvenile (text fig. 61A). The theca is domal; the largest specimen is 10.5 mm in diameter. The oral region appears to include four or five large plates in the juvenile. An asymmetrical, right posterior bulge in the oral area outline suggests the presence of a hydropore structure. The five ambulacra appear to be straight. Ambulacral coverplates may form a double biseries. Interambulacrals are squamose, imbricate plates. The anal structure lies in the posterior part of interambulacrum 5 and is formed by at least six subtriangular plates.

The peripheral rim includes approximately five circlets. Plates of the proximal circlet are very large and alternate as proximal and distal subcirclet members. These and the smaller plates of the following two circlets are extremely elongate concentric with the thecal margin. The tiny plates of the distal two circlets are radially elongate.

Specimens

USNM 91837. Type series of *Hemicystites carbonarius* Bassler (1936, p. 15, pl. 4, fig. 10, 11). Bluefield shale, Bluefield Group, Chesterian Series, Mississippian [not Pennsylvanian as listed by Bassler, 1936, and authors]. Four-fifths of a mile east of Addis Valley, West Virginia. Two fragments that were originally one slab.

Fragment A. Two specimens. (Pl. 55, fig. 7.)

A-1. 10.5 mm greatest diameter by a perpendicular of 10.5 mm (Pl. 55, fig. 8.)

A-2. 6.6 mm greatest diameter.

Fragment B. Six specimens. (Pl. 55, fig. 9.)

B-1. 9.4 mm greatest diameter by a perpendicular of 7.3 mm.

B-2. 7.0 mm greatest diameter.

B-3. 8.2 mm greatest diameter.

B-4. 4.8 mm greatest diameter.

B-5. 4.2 mm greatest diameter.

B-6. 3.5 mm axial by 4.2 mm transverse diameter. (Pl. 55, fig. 10.)

Text fig. 61A, pl. 55, fig. 7-10.

All eight specimens of *H. carbonarius* are resting upon a fragment of a large "cephalopod shell" (Bassler, 1936, p. 15) that was originally one larger fragment, now broken into two pieces. All specimens have collapsed. Seven of the eight are poorly preserved; the peripheral rim is the only interpretable feature in any of these. The eighth specimen is only partially disrupted, but it is a juvenile.

Discussion

Hemicystites carbonarius Bassler (1936) is here restricted to the type specimens that are too poorly preserved to define the species characters or even to allow recognition of generic or familial relationships. Bassler's generic assignment of *Hemicystites carbonarius* seems unlikely in view of the great difference in age between his Mississippian specimens and the Middle Silurian *Hemicystites parasiticus* Hall.

Order EDRIOASTERIDA Bell, *ord. nov.*

Diagnosis

Edrioasteroidea with: "echinoidal" shaped theca, ambulacra extended past ambitus into subambital zone; oral frame formed by large, compound plates, five radial, five interradial; hydropore structure located along right posterior margin of oral area, opening sutural but elongate perpendicular to suture line so as to penetrate adjacent plates; ambulacra including alternating biseries of coverplates without intrathecal or intra-ambulacral extensions; and biserial floorplates with sutural passageways which connect ambulacral tunnel with thecal cavity.

Description

The Edrioasterida have a semigloboid, "echinoidal" theca that can be divided into five areas: the upper oral surface, which ends at the ambitus; the subambital zone; the resting zone; the incurved zone; and the distal membrane. The center of the upper oral surface is nearly horizontal; the distal parts gradually increase in inclination down to vertical plates at the ambitus. The subambital zone gradually constricts in diameter downward. It forms approximately one-third of the total thecal height. In the subambital zone, the sides of theca curve inward toward the center of the lower side. The resting zone lies distal to the subambital zone. Only one or two plates wide, this area is parallel to the horizontal, central upper oral surface, and the exterior sides of the plates of the resting zone are parallel to, and apparently rest on, the underlying substrate. Distal to the resting zone the thecal surface curves upward, away from the substrate, and inward toward the center of the theca for a short distance. A thick membrane, imbedded with numerous minute platelets, is attached to the distal edges of the innermost plates of the incurved zone. This plated membrane apparently extended downward toward, and was probably attached to, the substrate. It is not continuous across the lower surface, and a large, circular, central gap is surrounded by the attached distal edge of the plated membrane.

The oral area, hydropore structure, proximal parts of the ambulacra, and the anal structure are on the upper oral surface. Distally the ambulacra extend past the ambitus into the subambital zone, but either terminate or curve laterally before they reach the resting zone.

The oral area includes external covering orals, which are continuous with the ambulacral coverplate series, and the externally exposed parts of the oral frame. The

covering orals form the center of the area and are similar to the ambulacral coverplates in size and shape. They apparently vary in number. Perradially the orals form the transverse and anterior oral midlines. Adradially they meet the externally exposed parts of the oral frame and form a submarginal suture line on the thecal surface; distally this suture line is continuous with that between the adradial ends of the ambulacral coverplates and exposed parts of the ambulacral floorplates.

The large central oral frame is formed by 10 compound plates, each formed by the fusion of numerous plates; a minimum of 55 fused elements constitute the frame of *Edrioaster bigsbyi*. The proximal margin of the frame is pentagonal to ovoid, transversely elongate, and surrounds the pentagonal to oval central lumen. The lumen extends downward from the proximal ends of the ambulacral tunnels to open into the underlying thecal cavity. The distal margin of the frame is subpentagonal in outline and is continuous with the five radiating ambulacra.

Five frame plates are radial and lie at the proximal ends of the ambulacra, and five are interradial. Each radial plate is formed by the fusion of several proximal pairs of the biserial ambulacral floorplates of the adjacent ambulacrum. They expand proximally, both inward and laterally. Adjacent radials may be in contact around the innermost proximal part of the frame rim, under the interradial elements. These radials also extend distally out under the proximal, unfused ambulacral floorplates.

The interradial frame plates lie between the radials. These elements are formed by the fusion of ambulacral floorplates and the proximal interambulacral plate of each interambulacrum. Each interradial includes floorplates from both adjacent ambulacra. Apparently, opposing members of the most proximal pairs of biserial floorplates of each ambulacrum separate along the per radial suture line. Opposing plates of the pair migrate laterally away from each other and become incorporated into different interradial frame plates. Thus each interradial includes floorplates from one side of the biseries of both adjacent ambulacra. These floorplates are fused to each other and form the proximal ends of the interradials. The adradial ends of these fused "half pairs" of floorplates are also fused to the adjacent proximal plate of each interambulacrum to form a single, large interradial plate of the frame.

Viewed externally, when oral coverplates are in place, only the interradial plates of the frame are ex-

Unfortunately, the coverplates are not preserved in the known specimens, which are only molds of the upper oral surface. It may well be that these specimens are conspecific with *Edriophus levis*.

Dinocystis barroisi is separated generically from other Edrioasterida by the contrasolar curvature of all five ambulacra. Moreover, the resting and incurved zones of

the theca appear to be formed by squamose, imbricate plates. This species is also represented only by molds, with the ambulacral and oral covering plates not preserved.

RANGE AND OCCURRENCE: Middle Ordovician of eastern North America and Europe.

Family EDRIOASTERIDAE BATHER, 1898

Type genus: *Edrioaster* Billings, 1858

Characters of the Order.

Genus *Edrioaster* Billings, 1858

- 1842 [non] *Agelacrinites* Vanuxem, L., Nat. Hist. New York, pt. IV, Geology 3: 158, fig. 80.
- 1854 *Agelacrinites* Vanuxem, Billings, E. [partim], Canadian Jour. Industry, Sci. and Art: 271-273 [non text fig. 10-12].
- 1857 *Cyclaster* Billings, E. [partim], Geol. Surv. Canada, Rept. Progress 1853-1856: 292-294.
- 1858a *Edrioaster* Billings, E. [partim], Geol. Surv. Canada, Fig. and Descriptions of Canadian Organic Remains, dec. 3: 82-83, 85, pl. 8, fig. 1, 1a, 2, 2a.
- 1860 *Agelacrinites* Vanuxem, Chapman, E. J. [partim], Canadian Jour. Industry, Sci. and Art (n.s.), 5: 361-365.
- 1889 *Edrioaster* Billings, Miller, S. A., North American Geology and Palaeontology, Cincinnati: 242.
- 1894 *Aesiocystites* Miller, S. A. and Gurley, F. E., Illinois State Mus. Bull. 5: 13-15, pl. 2, fig. 10-12.
- 1896b *Edriocystis* Haeckel, E. [partim], Die Amphorideen und Cystoideen, Leipzig, 1: 117-118, pl. 3, fig. 35-36.
- 1899 *Edrioaster* Billings, Jaekel, O. [partim], Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 44-46, pl. 2, fig. 4, 4a.
- 1900a *Edrioaster* Billings, Bather, F. A. [partim], in A Treatise on Zoology, E. R. Lankester (ed.), London, pt. III, Echinoderma: 209, text fig. 6-1, -2, -3; *Aesiocystis* Miller and Gurley, *idem*, *ibid.*: 208-209.
- 1903 *Edrioaster* Billings, Delage, Y. and Herouard, E., Traite de Zoologie Concrete, T. 3, Echinodermes, Paris: 414-415, text fig. 548-550.
- 1903 *Edrioaster* Billings, Steinmann, G., Einführung in die Paläontologie, Leipzig: 192-193, text fig. 264D,E.
- 1907 *Edrioaster* Billings, Steinmann, G., Einführung in die Paläontologie, 2nd edition, Leipzig: 213-214, text fig. 299D, E.
- 1908 *Edrioaster* Billings, Bather, F. A. [partim], Geol. Mag. (n.s.), dec. 5, 5: 543-550.
- 1914 *Edrioaster* Billings, Bather, F. A. [partim], Geol. Mag. (n.s.), dec. 6, 1: 115-125, 162-171, text fig. 1, 3-4, pl. 10, fig. 1-11, pl. 11, fig. 1-2, pl. 13, pl. 14, fig. 1-3.
- 1915a *Edrioaster* Billings, Bather, F. A. [partim], Geol. Mag. (n.s.), dec. 6, 2: 211-215, 259-266, text fig. 1a.
- 1915b *Edrioaster* Billings, Bather, F. A. [partim], Geol. Mag. (n.s.), dec. 6, 2: 316-322.
- 1915c *Edrioaster* Billings, Bather, F. A. [partim], Geol. Mag. (n.s.), dec. 6, 2: 393-403, text fig. 3.
- 1915 *Edrioaster* Billings, Bassler, R. S. [partim], United States Nat. Mus. Bull. 92, 1: 473-474; *Aesiocystites* Miller and Gurley, *idem*, *ibid.*: 19.
- 1935 *Edrioaster* Billings, Bassler, R. S. [partim], Smithsonian Misc. Coll. 93 (8): 9.
- 1938 *Edrioaster* Billings, Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 92.
- 1943 *Edrioaster* Billings, Bassler, R. S. and Moodey, M. W. [partim], Geol. Soc. America, Spec. Pap. 45: 201-202.
- 1944 *Edrioaster* Billings, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131-133, pl. 49, fig. 24.
- 1946 *Edrioaster* Billings, Wilson, A. E., Geol. Surv. Canada Bull. 4: 22.
- 1953 *Edrioaster* Billings, Piveteau, J., Traité de Paléontologie, Paris, 3: 654-655, text fig. 7-8.
- 1960 *Edrioaster* Billings, Kesling, R. V. [partim], Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 145-146, text fig. 1, 14a [non pl. 1, fig. 1-2].
- 1963 *Edrioaster* Billings, Müller, A. H., Lehrbuch der Paläozoologie, Bd. 2, Invertebraten, Teil 3, Jena, East Germany: 280, text fig. 386.
- 1966 *Edrioaster* Billings, Regnéll, G. [partim], in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U171, text fig. 111, 116-1, 118-1, 119-1, 3, 120-1, 131-1a, b.

TYPE SPECIES: *Cyclaster bigsbyi* Billings, 1857.

Diagnosis

Edrioasteridae with: oral plates similar to ambulacral coverplates in size and shape; right posterior hydropore structure plate intruding into proximal posterior edge of ambulacrum V, abutting, but free from floorplates; ambulacra curved, I-IV contrasolar, V solar, elevated above interambulacra with adradial edges steep, ambulacral coverplates in single alternating biseries; plates of distal cirlet of incurved zone large.

Description

Only the type species, *Edrioaster bigsbyi*, is placed in the genus without question. Thus, for diagnostic purposes the genus is essentially monotypic and has the characters of the type species. Separation of generic and specific traits is uncertain. The features cited in the above diagnosis are in part inferred to be of generic rank from taxobases established for other edrioasteroid genera.

Discussion

Billings (1854) reviewed published descriptions of "Trenton limestone" edrioasteroids, and described additional new specimens that he had examined. Included was a reconstruction (1854, fig. 10), based on several specimens and labeled *Agelacrinites* from the Trenton Limestone, Bytown, Canada. His specimens apparently represent two species, *Edrioaster bigsbyi* (Billings) and *Edriophus levis* (Bather). The reconstruction is dominated by features of the latter, with the ambulacra all curved solarly and the thecal plates smooth. Billings concluded that large, "globoid" Trenton species apparently belonged to a new genus which fit published descriptions of neither *Agelacrinites* Vanuxem (1842) nor *Hemicystites* Hall (1852).

Billings later proposed (1857) the genus *Cyclaster* (type species *C. bigsbyi* Billings). The following year he substituted the name *Edrioaster* for the preoccupied *Cyclaster*. Billings' generic description (1857, p. 292) was brief: "body sessile, circular, discoid, covered with numerous irregularly polygonal plates; mouth large, subpentagonal [oral frame]; five ambulacral areas, each composed of two series of oblong plates [floorplates] and having two rows of large pores which penetrate to the interior."

Billings apparently included in his new genus specimens recognized here as representing four species of three genera. In the generic discussion he refers to Sowerby's 1825 illustration of a then unnamed specimen of *Lebetodiscus dicksoni* and to the type specimen of *Edriophus buchianus* (Forbes) (1848). In addition, Billings' description of the type species, *Cyclaster bigs-*

byi, includes specimens representing not only *Edrioaster bigsbyi* (Billings), but also specimens of *Edriophus levis* (Bather), *i.e.*, specimens with some ambulacra (I-IV) curved contrasolarly and with tuberculate plates, as in *Edrioaster bigsbyi*, and others with all ambulacra curved solarly and the thecal plates smooth, as in *Edriophus levis*.

Billings (1858) not only introduced the name *Edrioaster*, but also "corrected" part of his 1857 description. He here reports four rows of ambulacral "pores" rather than two. The original two rows identified by Billings as pores lie along the sutures between floorplates at the perradial edge of the zone of articulation with the overlying coverplates. Sutural passageways do extend into the thecal cavity along these zones, each originating at the base of a small pit centered over the floorplate sutures. Two lower rows of small pits, perradial to these upper pits, are found near the perradial floorplate suture line, with one along each side of the floor of the ambulacral trough. The lower pits are also centered over the lateral sutures between the floorplates and are connected to the upper pits by a deep groove that extends along the floorplate lateral sutures. However, in contrast to Billings' description, these end blindly. Thus only one set of passageways is developed on each side of each ambulacrum.

Billings (1858) also mentioned that in 1857 he had misinterpreted Forbes' description of *Agelacrinites buchianus* and thus erroneously referred a specimen of *Agelacrinites dicksoni* to the genus *Edrioaster*. It is ironic that this specimen, collected by Bigsby, had inspired the trivial name *bigsbyi*, but fortunately it had not been designated type of the new species.

Edrioaster Billings was a commonly accepted genus during the last half of the 19th century. However, Chapman (1860) referred *E. bigsbyi* to *Agelacrinites*, and Haeckel (1896) arbitrarily changed the spelling of the generic name to *Edriocystis*.

Miller and Gurley (1894) proposed the genus *Aesiocystites* for a new species, *A. priscus*. The few available specimens of this species are poorly preserved, but appear to conform to the generic traits of *Edrioaster*.

Bather published a series of papers (1898-1915) describing in great detail several edrioasteroid species, including *Edrioaster bigsbyi* (Billings), *Edriophus buchianus* (Forbes), and *Edriophus levis* (Bather). Bather included all three species, plus *Edriophus saratogensis* (Ruedemann) in the genus *Edrioaster*. His emended generic diagnosis (1914, p. 170) recorded: "An Edrioasteroid with pores of subjective groove within the tract protected by coverplates; with interradials all tessellate and separated from the central apical region by a frame of stouter plates; on the apical face

the peripheral plates are variable in size but not minute, the central plates are minute and tend to imbricate." Ambulacral curvature, coverplate shapes, thecal size, and prosopon were relegated to trivial taxobases.

Bassler (1935) emended the diagnosis of *Edrioaster* and restricted the genus to species with ambulacra curved I-IV contrasolar, V solar. However, in spite of his definition he listed *Agelacrinites buchianus*, *Edrioaster levis*, and *Edrioaster saratogensis* as species belonging to *Edrioaster*, although all three have ambulacra I-IV curved solarly.

Recent references to *Edrioaster* have been based on Bather's description without restudy of specimens. Most comprehensive is Regnéll's (1966, p. U171) diagnosis, which recognizes variable ambulacral curvature but suggests that species with solar curvature "possibly should be separated generically."

Edrioaster is here restricted to species with ambulacra curved I-IV contrasolar, V solar. Only the type, *E. bigsbyi*, is included with certainty. *Aesiocystites priscus* is included with question, owing to the poor preservation of all available specimens which has obscured the details of most plate boundaries in the critical oral-ambulacral series.

RANGE AND OCCURRENCE: Trenton Group, Middle Ordovician of eastern North America.

Edrioaster bigsbyi (Billings), 1857

Text fig. 62-63; plate 58-59

- 1854 *Agelacrinites* sp. Billings, E. [partim], Canadian Jour. Industry, Sci. and Art: 271-273 [non text fig. 10-12].
- 1857 *Cyclaster bigsbyi* Billings, E. [partim], Geol. Surv. Canada, Rept. Progress 1853-1856: 293-294.
- 1858a *Edrioaster bigsbyi* (Billings), E. [partim], Geol. Surv. Canada, Fig. and Descriptions of Canadian Organic Remains, dec. 3: 82-83, 85, pl. 8, fig. 1, 1a, 2, 2a.
- 1860 *Agelacrinites bigsbyi* (Billings), Chapman, E. J., Canadian Jour. Industry, Sci. and Art (n.s.) 5: 361-365.
- 1896b *Edriocystis bigsbyi* (Billings), Haeckel, E., Die Amphoriden und Cystoideen, Leipzig, 1: 117-118, pl. 3, fig. 35-36.
- 1899 *Edrioaster bigsbyi* (Billings), Jaekel, O., Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 44-46, pl. 2, fig. 4, 4a.
- 1900a *Edrioaster bigsbyi* (Billings), Bather, F. A., in A Treatise on Zoology, E. R. Lankester (ed.), London, pt. III, Echinoderma: 209, text fig. 6-1, -2, -3.
- 1903 *Edrioaster bigsbyi* (Billings), Delage, Y. and Herouard, E., Traité de Zoologie Concrète, T. 3, Echinodermes, Paris: 414-415, text fig. 548-550.
- 1903 *Edrioaster bigsbyi* (Billings), Steinmann, G., Einführung in die Paläontologie, Leipzig: 192-193, text fig. 264D-E.
- 1904 *Edrioaster bigsbyi* (Billings), Spencer, W. K., Royal Soc. London, Proc. 74: 31-46.
- 1907 *Edrioaster bigsbyi* (Billings), Steinmann, G., Einführung in die Paläontologie, 2nd edition, Leipzig: 213-214, text fig. 299D-E.
- 1908 *Edrioaster bigsbyi* (Billings), Bather, F. A., Geol. Mag. (n.s.), dec. 5, 5: 543-550.
- 1914 *Edrioaster bigsbyi* (Billings), Bather, F. A., Geol. Mag. (n.s.), dec. 6, 1: 115-125, 162-171, text fig. 1, 3-4, pl. 10, fig. 1-11, pl. 11, fig. 1-2, pl. 13, pl. 14, fig. 1-3.
- 1915a *Edrioaster bigsbyi* (Billings), Bather, F. A., Geol. Mag. (n.s.), dec. 6, 2: 211-215, 259-266, text fig. 1a.
- 1915b *Edrioaster bigsbyi* (Billings), Bather, F. A., Geol. Mag. (n.s.), dec. 6, 2: 316-322.
- 1915c *Edrioaster bigsbyi* (Billings), Bather, F. A., Geol. Mag. (n.s.), dec. 6, 2: 393-403, text fig. 3.
- 1915 *Edrioaster bigsbyi* (Billings), Bassler, R. S., United States Nat. Mus. Bull. 92, 1: 474.
- 1928 *Edrioaster bigsbyi* (Billings), Hussey, R. C., Univ. Michigan, Contrib. Mus. Paleont. 3 (4): 77-79, pl. 1, fig. 4.
- 1936 *Edrioaster bigsbyi* (Billings), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): pl. 1, fig. 1.
- 1943 *Edrioaster bigsbyi* (Billings), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 201.
- 1944 *Edrioaster bigsbyi* (Billings), Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 133, pl. 49, fig. 24.
- 1946 *Edrioaster bigsbyi* (Billings), Wilson, A. E., Geol. Surv. Canada Bull. 4: 22.
- 1953 *Edrioaster bigsbyi* (Billings), Piveteau, J., Traité de Paléontologie, Paris, 3: 654-655, text fig. 7-8.
- 1960 *Edrioaster bigsbyi* (Billings), Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 145-146, text fig. 1, 14a [non pl. 1, fig. 1-2].
- 1963 *Edrioaster bigsbyi* (Billings), Müller, A. H., Lehrbuch der Paläozoologie, Bd. 2, Invertebraten, Teil 3, Jena, East Germany: 280, text fig. 386.
- 1966 *Edrioaster bigsbyi* (Billings), Regnéll, G., in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U171, text fig. 111, 116-1, 118-1, 119-1, 3, 131-1a, b.

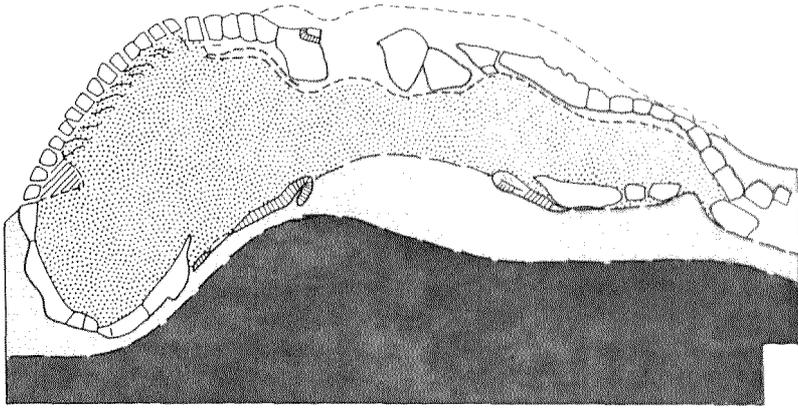
Diagnosis

An *Edrioaster* with: large, "echinoidal" theca; nine or more oral plates; ambulacral coverplates subpentagonal, perradial ends pointed; interambulacrals large, polygonal, tessellate, periproct formed by several irregular circlets; thecal plates with large, rounded, external nodes.

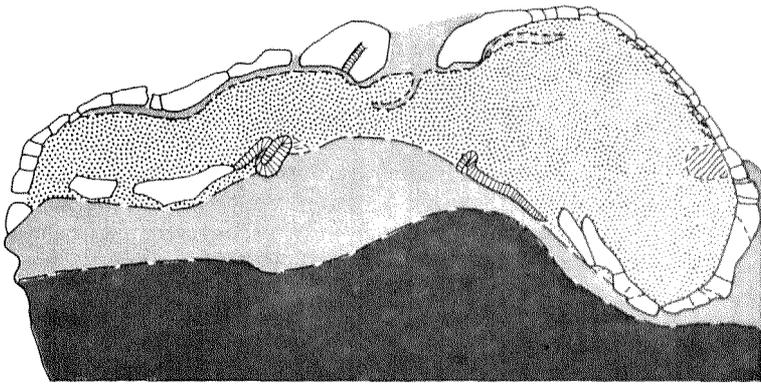
Description

The theca of *Edrioaster bigsbyi* (Billings) reaches diameters of over 45 mm (reconstruction, text fig. 2).

The oral plates which cover the central oral area are missing or disrupted in available specimens. However, Bather (1914) illustrated a now missing individual that preserves seven oral plates. His specimen, obviously



A



B

Text figure 62. *Edrioaster bigsbyi* (Billings), 1857

A. Lectotype, GSC 1407, (x 4), pl. 58, fig. 4. Axial cross section view.

B. Lectotype, GSC 1407-A, (x 4), pl. 58, fig. 5.

Dark shading marks firm carbonate substrate; light shading marks softer, dark shale which buried the specimen; dotted pattern marks fine-grained, light-colored carbonate filling of thecal cavity.

missing at least two additional orals, suggests that nine or more orals form the central oral area. The orals are similar in shape and size to the proximal ambulacral coverplates. Four or five central orals may be somewhat larger than the others. Distally the oral plates appear to grade into the proximal ambulacral coverplate series without apparent division between the two sets of plates.

The oral frame of *E. bigsbyi* is poorly exposed in available specimens (pl. 58, fig. 1-5, pl. 59, fig. 5). Distally the frame is pentagonal in outline and confluent with the ambulacral structures. The proximal rim of the frame appears to be subpentagonal with five large, rounded lobes surrounding the central lumen. However, only the outline of the inner side of the frame has been seen as an impression through the distal membrane of the lower side of the theca (pl. 59, fig. 2, 8, 10).

The frame comprises 10 compound plates, five radials, and five interradials. Each of the five radials is formed by the fusion of three or four pairs of proximal floorplates from the adjacent ambulacrum (text fig. 62A, B, pl. 58, fig. 2-5). These pairs of floorplates are fused to one another both laterally and perradially, obliterating the sutures. However, four to six passageways penetrate each compound radial. These passageways are believed to be homologous to the floorplate passageways of the ambulacral floorplates, and thus mark the position of the now fused sutures between the floorplate components of the radial plates of the frame.

The compound radial plates extend inward proximally to form the radial sectors of the thick proximal wall of the rim of the frame. The innermost edge of each radial extends into the thecal cavity more than twice as far as the adjacent (nonfused) proximal floorplates of the ambulacra. Distally each radial becomes thinner and narrower, and this tapered part extends out under the proximal three or four pairs of floorplates of the adjacent ambulacrum. The center of the upper surface of this tapered, distal sector of each radial is exposed axially where the proximal two or three pairs of nonfused floorplates of the adjacent ambulacrum are perradially separated, with the opposing members of each pair pulled away from one another along the perradial suture.

The five interradial frame plates alternate with the radials. Each compound interradial is formed by the fusion of four proximal floorplates and a large proximal interambulacral plate. The floorplates form the proximal sector of the compound interradial and the interambulacral plate forms the distal part. The floorplates that are incorporated into the interradial plates represent "half-pairs," *i.e.*, the opposing pair members of two pairs of proximal floorplates of each ambulacrum have

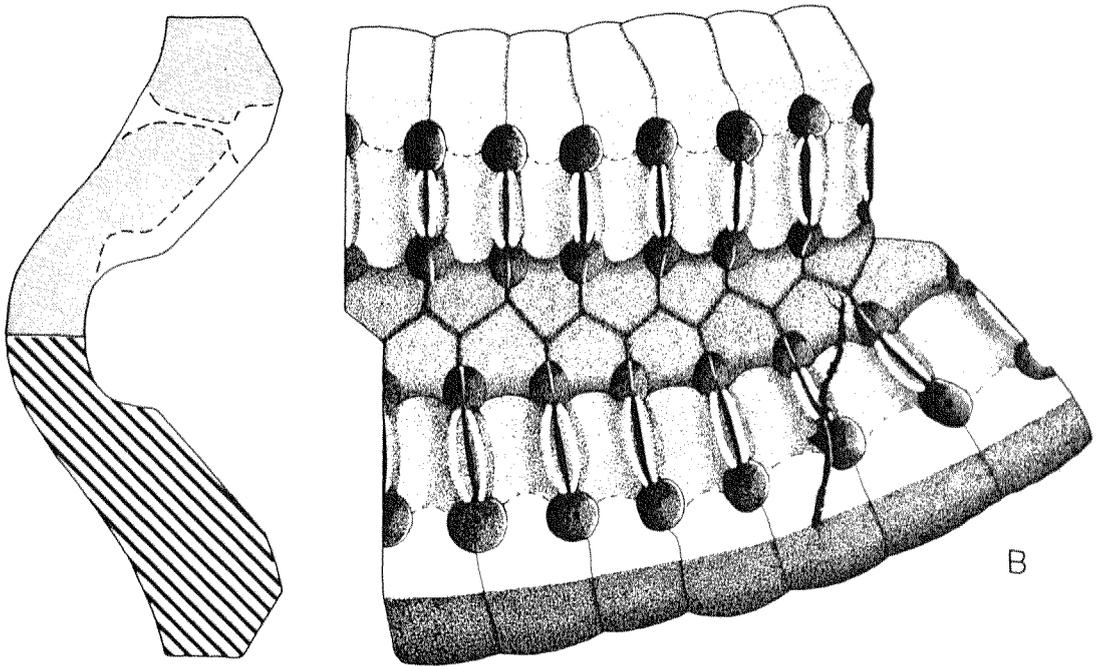
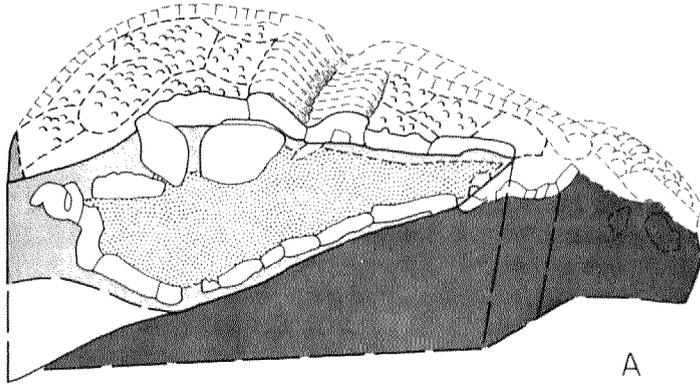
been separated perradially and those on one side of the perradial line have been incorporated into the interradial plate which flanks one side of the ambulacrum, whereas the opposing members of the pairs of floorplates have been incorporated into the interradial which flanks the other side of that ambulacrum. Three passageways penetrate the proximal end of each interradial and demonstrate that four floorplates have been fused together laterally, two from each adjacent ambulacrum. These fused floorplates are proximally enlarged and extend inward more than twice as far as the adjacent proximal unfused floorplates of the ambulacra. The interradial sectors of the inner rim of the frame are formed by the proximal inner ends of the fused floorplates of each interradial plate. The inner edge of the rim of the frame is thus formed by alternating radials and interradials. The upper parts of the fused floorplates of the interradials about the proximal, lateral edges of the proximal nonfused floorplates of each adjacent ambulacrum. Adradially the fused floorplates of the proximal part of the compound interradial are fused to the proximal plate of the adjacent interambulacrum. This interambulacral forms the largest part of the compound interradial plate and extends distally much further than the adjacent compound radial plates of the frame.

The compound frame plates thus represent numerous fused elements. The five radials each have six to eight fused floorplates and the five interradials each represent four fused floorplates and one interambulacral. Thus 50 to 60 individual floorplates and five interambulacral plates are included in the structure.

When proximal ambulacral coverplates and the oral covering plates are in place, the upper, adradial ends of the fused floorplate sectors of each interradial plate of the frame remain exposed externally. Like the adradial portions of the adjacent ambulacral floorplates, these are abruptly elevated above the level of the interambulacrals

Text figure 63. *Edrioaster bigsbyi* (Billings), 1857

- A. Lectotype, GSC 1407-A, (x 3), pl. 58, fig. 6. Lateral cross section view cutting ambulacrum II and adjacent structures. Dark shading marks firm carbonate substrate; light shading marks softer, dark shale which buried the specimen; dotted pattern marks fine-grained, light-colored carbonate filling of thecal cavity.
- B. Lectoparatype, GSC 1407-E, (x 10), pl. 58, fig. 12. Segment of one ambulacrum exposing the upper surface of the floorplates. A cross section of the ambulacrum is shown at the left end of the specimen. The shaded upper floorplate exposes the proximal sutural face of the plate, with the sutural passageway, groove, and pits. The striped lower floorplate face is a section through the center of the alternate, opposing floorplate.



and form a small ridge that is continuous with the ambulacral ridges. The distal margin of this ridge marks the line of fusion of the floorplates with the proximal interambulacral plate of each interambulacrum, although all traces of the original suture have been obliterated.

The hydropore is a small, elliptical opening along the right posterior margin of the oral area, shared by two plates (pl. 59, fig. 5). It is elongate normal to the suture between two plates—the interambulacral part of the posterior interradial plate of the oral frame, and an adjacent, posterior, polygonal plate. The left anterior margin of this posterior plate abuts the right posterior margin of the posterior interradial frame plate. Its right edge intrudes into the adradial edge of the proximal, posterior side of ambulacrum V where it abuts one or two proximal floorplates which are thus shorter than adjacent floorplates. Distally this posterior plate abuts interambulacrals. This posterior hydropore plate is constant in position from one specimen to another and is considered to be part of the oral series, as are the modified interambulacral plates that are incorporated into the compound interradial frame plates. The edges of the two hydropore structure plates are thickened around the opening and form a small, raised rim.

The stone canal passageway leads inward from the hydropore and penetrates both plates of the hydropore structure. It appears to extend obliquely inward in a proximal direction; it is thus housed primarily by the posterior interradial frame plate. The inner edge of this posterior interradial is enlarged and apparently modifies the inner end of the passageway, but this area is inadequately exposed in available specimens.

The five long, broad ambulacra extend from the oral region, past the ambitus, into the subambital thecal zone. All are curved, I-IV contrasolar, V solar. Curvature is uneven; the proximal upper surface parts are commonly straight or nearly so, followed by pronounced curvature immediately distal to the ambitus. The distal parts of the ambulacra extend along the subambital zone concentric with the ambitus. Ambulacrum V commonly curves back onto the upper oral surface and ends near the left posterior edge of the anal area. The proximal upper oral surface parts of the ambulacra may be gently curved, often in the direction opposite to the pronounced direction of distal curvature. Bather (1914, p. 122) presented detailed descriptions of these minor proximal undulations in several specimens. His data show the proximal flexures of each ambulacrum to vary in degree and even in direction from one specimen to another, and thereby to have no taxonomic importance. Moreover, in partially inflated specimens such as the lectotype, these proximal parts are nearly straight, suggesting that much of the apparent minor curvature is preservational, produced during thecal depression.

The ambulacra form low, rounded ridges on the thecal surface. Their adradial edges are steeply inclined and rise abruptly from the adjacent interambulacra.

The ambulacral coverplates form a single alternating biseries. Each plate is subpentagonal; the perradial end is pointed and interdigitates with the opposing alternate coverplates to form a prominent zigzag perradial line (pl. 59, fig. 15, 16). Lateral sides are straight and parallel, and they extend normal to the ambulacral axis. The slightly convex adradial ends of the coverplates meet the exposed adradial ends of the ambulacral floorplates and form subtly scalloped submarginal suture lines with the exposed parts of the floorplates. The lower edge of the adradial ends of the coverplates are beveled to fit tightly against the slightly inwardly sloping, upper lateral surface of the floorplates, along the articulation zone. Otherwise the coverplates appear to be of uniform thickness, without intra-ambulacral extensions. Commonly the coverplates are either lost or collapsed into the ambulacral groove during preservation.

Bather (1914, p. 162) described an additional set of coverplates which he termed "accessory coverplates." He described them as small plates wedged between the adradial ends of the coverplates and floorplates, and supposedly lying adjacent to the lateral adradial edges of the coverplates. These elements occur only sporadically along the ambulacra and are supposedly often hidden from view. Topotype GSC 1407-D has these elements in the proximal parts of ambulacra I and II. The coverplates are slightly disrupted and overlap one another laterally. Wherever one of these small plates occurs, the adradial corner of the adjacent coverplate is unusually rounded. It now appears that these supposed plates are merely fragments broken from the coverplates during preservation.

The biserial ambulacral floorplates are elongate and subrectangular in plan view (text fig. 63B). Their perradial ends are pointed and form a central zigzag floorplate perradial suture. The long, straight lateral edges of each floorplate are nearly parallel to one another and extend normal to the ambulacral axis. The adradial ends are irregularly convex outward and abut adjacent interambulacrals. Each floorplate lies directly under a corresponding coverplate. Thus lateral sutures of the plates and the zigzag perradial lines of both series are aligned one above the other. The adradial ends of the longer floorplates extend past the ends of the coverplates, and are thereby exposed externally between the adradial and submarginal ambulacral suture lines.

The floorplates form a broad, central ambulacral trough. Opposing alternate floorplates slope downward from the zone of articulation with the coverplates to the center of the ambulacral trough. The rate of slope is

gradual along the upper sides of the trough. However, a short, steeply inclined zone flanks the nearly horizontal perradial area and thus a narrow U-shaped trough is incised into the center of the broad ambulacral trough.

The sectors of the floorplates which form the upper lateral margins of the deep ambulacral trough are nearly horizontal and slope perradially only slightly. This is the articulation zone on which the bases of overlying coverplates rest. The zone lies partly along, and partly adradial to, the upper ends of the floorplate passageways. Adradial to the coverplate articulation zone, the floorplates slope away from the ambulacral trough and form the externally exposed adradial zone of the floorplates. The pronounced adradial slope of this area forms the abrupt sides of the externally elevated ambulacra which rise above the adjacent interambulacra.

The floorplates are thickest under the articulation zone, thinning conspicuously toward their perradial ends (text fig. 63A, B). Thus the internal, inward convexity of the ambulacra is less pronounced than the external corresponding concavity of the ambulacral trough. Perradially, opposing alternate floorplates abut along vertical sutures. Adradially they abut adjacent interambulacrals along vertical or perhaps oblique sutures which may slope toward the ambulacral axis.

The floorplate passageways begin in small, subcircular, steep-walled pits which are centered over the lateral sutures between adjacent floorplates. These pits lie along the perradial edge of the coverplate articulation zone. Their adradial ends are partly roofed by the bases of the overlying coverplates, whereas the perradial sides of the pits are open into the upper lateral margin of the ambulacral tunnel. The passageways extend inward from the floor of these pits along the floorplate sutures. Their inner ends expand and open into the thecal cavity as sutural depressions elongate normal to the ambulacral axis. Bather (1914, p. 124) reported these inner surface depressions to be larger than the upper pits.

The small pits which mark the upper ends of the floorplate passageways form two rows along each ambulacrum, one flanking each edge of the ambulacral tunnel. Two additional rows of pits, perradial to the passageway pits, also occur (text fig. 63A, B). One row of these lower depressions lies along each steep wall of the central, U-shaped, axial depression in the center of the broad ambulacral trough. These subcentral pits are less clearly defined than the passageway pits and their perradial edges open toward the central axial trough.

The upper and lower rows of pits on each side of the ambulacrum are connected by deep grooves which extend along the lateral sutures of the floorplates. Moreover, a shallower groove flanks each side of each sutural groove. The three grooves extend toward the

center of the ambulacral trough parallel to one another, normal to the ambulacral axis. A small ridge separates each shallow lateral groove from the adjacent deep sutural groove.

The lower series of less well-defined pits ends blindly, but apparently misled earlier workers to suggest that four, rather than only two, rows of passageways penetrate each ambulacrum. The floorplate grooves, which extend along the walls of the ambulacral trough between the upper and lower lateral pits, were first described by Bather (1914, p. 123). In contrast with the above description, he reported that the shallower grooves which flank each sutural groove diverge as they extend downward toward the center of the ambulacral trough.

The perradial edges of the floorplates are slightly depressed and form a subtle groove along the zigzag perradial suture line. The lateral edges of the floorplates, perradial to the lower pits, are also slightly depressed and thus form very subtle grooves that extend from the lower pits along the lateral sutures to intersect the perradial suture line grooves at each zigzag point.

Interambulacral plates are large, polygonal, and tessellate. Smaller polygonal plates, continuous with the interambulacrals, form the resting and proximal part of the incurved thecal zones.

The resting zone is two or three plates wide. Distal to these, three or four irregular circlets form the incurved zone of the theca which is flexed upward above the substrate and extends inward toward the center of the theca. The last (distal) circlet includes approximately 12 large plates which form a well-ordered circlet. The distal margins of these plates taper to a thin edge. The proximal edge of the lower surface membrane is attached to the distal tapered edge of these large plates. This membrane is imbedded with numerous minute plates, slightly elongate concentric with the thecal margin. The membrane apparently flexed downward and was attached to the substrate. The membrane is not in evidence across the center of the lower surface, and a small central zone surrounded by the distal margin of the plated membrane thus represents the aboral surface of the theca. The five-part lobation of the basal membrane described by Bather (1914) is merely the impression of the inner edge of the oral frame seen through the membrane which is pressed against that structure during thecal collapse.

The periproct lies in the posterior part of the upper oral surface part of interambulacrum 5. It includes a large number of plates that are smaller than the surrounding interambulacrals. These form three or four irregular circlets. The central plates are elongate and subtriangular and may be more regular.

External thecal plate surfaces are covered by rounded nodes which occur irregularly on the plates. This pustular prosopon appears to be limited to upper oral surface and subambital thecal zones; the plates of the resting and incurved zones are apparently smooth externally.

Specimens

GSC 1407, 1407-A, 1407 C-H. Eight pieces representing six specimens. "Cobourg beds, Trenton Limestone," Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario.

The collection of the Geological Survey of Canada now includes six specimens of *Edrioaster bigsbyi* (GSC 1407). Two of these are from Billings' (1858) original type series and were illustrated in his publication. Bather (1914) designated specimens GSC 1407, 1407-A, which are two pieces of one individual, as the "holotype," *i.e.*, lectotype. The other specimen, illustrated by Billings (GSC 1407-E, 1407-F, two fragments of one specimen) is thus a lectoparatype. The other four specimens are topotypes and may have been in Billings' original type series; they were not illustrated by him.

When Bather restudied *Edrioaster bigsbyi* he indicated that the collection of the Geological Survey of Canada included 10 specimens. Bather's description was based on three of these, to which he referred as "A," "B," and "C." These three individuals, plus a fourth, are now missing. However, Bather's "B" and "C" closely resemble specimens GSC 1407-D and GSC 1407-C, respectively. Most of Bather's work was based on specimen "A"; his drawing of this specimen (see text fig. 2) suggests that it is better preserved than any of the remaining individuals.

GSC 1407, 1407-A. Lectotype of *E. bigsbyi* (Billings) (1857, p. 293-294, 1858, pl. 8, fig. 1, 1a).

1407. 39.3 mm "axial" (along cut surface) by 20.5 mm "transverse" diameter (normal to cut section, from oral area out to edge of theca).

Text fig. 62A, pl. 58, fig. 1, 3, 4.

1407-A. 37.2 mm "axial" (along axial line cut section) by 11.5 mm normal to axial cut, out to second lateral cut.

Text fig. 62B, 63A, pl. 58, fig. 1, 2, 5, 6.

The lectotype exposes the upper oral surface of the theca. It has been cut into three sections; one is now missing. One cut nearly follows the axial midline of the theca, slicing the proximal part of ambulacrum III, the oral area, interambulacrum 5, and part of the anal structure. The right half of the theca is labeled GSC 1407 (pl. 58, fig. 1). The left side of the theca was cut a second time along its left edge. The cut extends through

the distal parts of interambulacra 1 and 2 and the distal upper oral surface sector of ambulacrum II. The small left edge fragment of the specimen is missing. The large fragment, which preserves most of the left half of the theca, is labeled GSC 1407-A (pl. 58, fig. 1). The cut surfaces of this specimen expose sectional views of both upper oral surface plates and also the thecal zones below the ambitus.

The specimen is only partially collapsed and retains most of the original thecal shape. All oral and ambulacral coverplates are missing, which exposes the ambulacral tunnel surface of the floorplates and the upper parts of the oral frame plates. The ambulacral and interambulacral plates are nearly in life position. Resistant matrix obscures part of the specimen. Abrasion has modified the floorplate pits and grooves, and has also broken the upper edges of some elements, particularly the posterior floorplates of ambulacrum V. The left posterior edge of the theca is missing, including the ambital part of ambulacrum I and adjacent interambulacrals. The anal structure is disrupted. The prominent nodose prosopon is preserved on the interambulacrals.

The axial section of GSC 1407 (text fig. 62A, pl. 58, fig. 4) shows: (1) the sutural passageways which extend between the floorplates of the right side of ambulacrum III, (2) a sectional view of the anterior radial oral frame plate, with an oblique view of the upper end of one passageway which extends down the sloping proximal side of the plate [this groove is open to the central lumen along its upper side, but the oblique view makes it appear to be a small tube partly roofed by the plate]; (3) sectional views of the posterior interradiial frame plate and the proximal tips of two other frame elements; (4) sectional views of the posterior interambulacral plates and a few of the anals; (5) sectional views of the plates that form the resting and incurved zone of the theca with the posterior plates partially disrupted; (6) sectional views of the partially disrupted, lower surface, plated integument which extends toward the center of the lower surface and then curves downward toward the substrate.

The opposing side of the axial cut, seen on specimen GSC 1407-A, exposes a slightly different view, for it is separated from the first by the width of the cutting instrument. It exposes (text fig. 62B, pl. 58, fig. 5): (1) a more central view of ambulacrum III floorplates proximal to the passageways; (2) a sectional view of the anterior radial oral frame plate; (3) a sectional view of the posterior interradiial oral frame plate which exposes one of the passageways that penetrate this compound plate; (4) sectional views of posterior interambulacrals, resting zone, and incurved zone plates; and (5) a sectional view of the basal flexible membrane which has curled back on

itself distally, but is still attached proximally to the thin, distal edge of the distal circlet of plates of the incurved zone. Both axial section views of the lectotype preserve a series of thin, curved slivers of calcite immediately beneath the floorplates of ambulacrum III. Most are convex toward the oral area, but some recurve and are S-shaped in sectional view. Apparently one calcite sliver is present for each ambulacral floorplate. If they are not preservational in origin, the relationship of these slivers to other thecal structures is unknown.

The lateral section view of GSC 1407-A (text fig. 63A, pl. 58, fig. 6) exposes a cross section view of ambulacrum II and adjacent interambulacral plates. Interambulacrals adjacent to the anterior side of the ambulacrum are disrupted and the resultant oblique section view gives the deceptive appearance of large, thick plates adjacent to and under the ambulacral plates. The lower part of the section exposes plates of the subambital zone.

GSC 1407-E, F. Lectoparatype of *E. bigsbyi* (Billings) (1857, p. 293, 294, 1858, pl. 8, fig. 2, 2a).

1407-E. 17.7 mm along cut by 20.9 mm normal to cut.

Text fig. 63B, pl. 58, fig. 7, 11-13.

1407-F. 18.2 mm along cut by 5.8 mm normal to cut.

Pl. 58, fig. 7-10.

The lectoparatype is a small fragment of a large specimen that preserves the subambital sectors of two ambulacra and a few adjacent interambulacrals. Only ambulacral floorplates are preserved. The fragment was cut in two so as to separate the two ambulacral segments. The upper edge of the ambulacrum on specimen GSC 1407-F has been ground obliquely and then polished to expose sectional views of the adradial parts of the floorplates. Grinding was deep enough along the left proximal four floorplates to expose the floorplate passageways which extend from the ambulacral tunnel into the thecal cavity.

The upper sides of the ambulacral floorplates are well preserved in both ambulacra and expose the upper and lower rows of pits as well as the grooves and ridges connecting these pits. The subtle central perradial line groove is also preserved and is connected to the lower pits by the shallow lateral sutural grooves between adjacent floorplates. This specimen clearly demonstrates that the two shallow lateral grooves flanking the deep sutural groove which connects the upper and lower pits are parallel and do not diverge downward as described by Bather.

GSC 1407-C. Topotype of *E. bigsbyi*. 36 mm axial by 35 mm transverse diameter.

Pl. 59, fig. 1-5.

This specimen exposes both the upper and lower sides of the theca, but it is depressed and the inner surfaces of the upper and lower sides are pressed together. The upper side preserves most of the upper oral surface except for the distal part of the right anterior margin of the theca. Most oral and ambulacral coverplates are missing, except for the proximal coverplates of ambulacrum V. However, these are partially disrupted and collapsed down into the ambulacral trough. Many ambulacral floorplates are well preserved and completely free of matrix in ambulacrum II. Some of the ambulacrals are displaced, apparently having been disrupted during thecal collapse. Interradial plates of the oral frame are partially exposed and reveal the upper ends of the passageways and associated grooves which mark the line of fusion between the floorplates which form these compound elements. The hydropore is apparently enlarged by abrasion and only remnants of the small rim are preserved. The right posterior hydropore plate is clearly not fused to the proximal ambulacrals, but does intrude into the edge of the ambulacrum. Interambulacrals are only slightly disrupted. The anal structure plates are partially jumbled but apparently formed three or four irregular circlets. The distal tip of ambulacrum V curves back onto the upper surface and ends near the anal structure in interambulacrum 5.

The lower surface of the specimen preserves the collapsed subambital, resting, and incurved thecal zones. The distal parts of ambulacra I-IV and adjacent interambulacra of the subambital zone are partially disrupted. The resting and incurved zones appear to total only three irregular circlets of plates. The distal circlet of the incurved zone is formed by 11 large plates. The basal flexible membrane is poorly preserved.

GSC 1407-D. Topotype of *E. bigsbyi*. 43 mm axial by 41.8 mm transverse diameter.

Pl. 59, fig. 15-17.

This specimen is buried in matrix and only part of the depressed upper oral surface of the theca is exposed. Ambulacra I, II, III, and V are seen along with the interambulacral plates of 1, 2, and 3. A small segment of ambulacrum IV curves back up onto the upper oral surface in interambulacrum 3. The oral region is disrupted, along with the proximal plates of ambulacrum V. This individual preserves the ambulacral coverplates, but they have been twisted laterally during preservation and are now imbricated with adjacent coverplates. The nodose prosopon is preserved on the interambulacrals, ambulacral coverplate, and the few oral coverplates. Small elements described by Bather as "accessory coverplates" lie between the adradial ends of the coverplates and underlying floorplates. These

appear to be the broken adradial corners of the coverplates and thus are not discrete plates.

GSC 1407-G. Topotype of *E. bigsbyi*. 38.4 mm axial by 29.1 mm transverse diameter.

Pl. 59, fig. 7-12.

This specimen exposes both the upper and lower sides of the completely collapsed theca. Parts of the ambital area are missing, including the right posterior third of the theca and a small segment of the left anterior zone. The ambulacral coverplates are missing, thereby exposing the floorplates and oral frame elements. These are not well preserved, but show partially eroded pit rows and grooves. Interambulacrals preserve the nodose prosopon. The lower surface of this specimen exposes the collapsed resting and incurved zone plates. Moreover, parts of the basal flexible membrane are preserved. The minute, elongate platelets imbedded in this membrane are well preserved. They are elongate concentric with the thecal margin and proximally imbricate. The integument is "lobate," reflecting the large oral frame plates which are pressed against the inner side of the membrane. The distal edge of the membrane is not well preserved in this specimen, but apparently attached to substrate. It thus surrounded a small, central, open basal zone, the aboral surface of the theca.

GSC 1407-H. Topotype of *E. bigsbyi*. 32.4 mm long by 23 mm wide.

Pl. 59, fig. 13, 14.

This specimen has been laterally compressed, hiding the lower surface of the theca between the two halves of the upper oral surface. Compression followed a line through interambulacrum 4, the oral area, and ambulacrum II. One side of the specimen exposes interambulacra 2, 3, part of 4, ambulacrum III, and parts of II and IV. The opposing surface exposes interambulacra 5 and 1, and parts of ambulacra I, II, IV, and V.

Many of the thecal plates have been partly dissolved, exposing impressions of the inner surfaces of these plates that were preserved in the matrix which fills the thecal cavity. Some of the ambulacral coverplates are preserved in segments of the ambulacra, but all are collapsed down into the ambulacral trough. The anal structure is disrupted. The nodose prosopon is well preserved on both interambulacrals and ambulacral coverplates.

UMMP 10347. Illustrated Specimen of *E. bigsbyi* by Hussey (1928, p. 78, pl. I, fig. 4). Trenton Group, Mohawkian Series, Middle Ordovician. Escanaba River, 3 miles north of Escanaba, Michigan. Locality 8,

zone 2, 1927 expedition of Museum of Paleontology, University of Michigan. 33.5 mm axial by 25.6 mm transverse diameter.

Pl. 59, fig. 6.

This specimen preserves only the left half of the upper oral surface of the theca. Some ambulacral coverplates are preserved, others are missing and expose the upper ambulacral tunnel sides of the floorplates. Thecal prosopon is well preserved. This specimen extends the range of species into Michigan.

Discussion

Billings' (1854) description of an *Agelacrinites* outlined the major features of what was to become *Edrioaster bigsbyi*. An accompanying illustration reconstructs the dominant structures of what is now *Edriophus levis* (Bather). In 1857, Billings described *Cyclaster bigsbyi*. Included in this definition are: thecal shape, ambulacral floorplate and coverplate structure, floorplate passageway structures, and interambulacral and anal area plating. However, Billings described ambulacral curvature as variable—contrasolar in some, but all solar in others, and thecal plates either smooth or pustulose. This analysis incorporated traits of both *Edrioaster bigsbyi* and *Edriophus levis*. Billings (1857) referred to several specimens but did not illustrate any of them.

In 1858 Billings revised his original description and replaced the preoccupied *Cyclaster* with *Edrioaster*. In this paper he suggested that each ambulacrum had four rows of floorplate passageways. He (1857) had already established the presence of sutural passageways leading inward from the upper rows of floorplate pits. Apparently this led him to suppose that similar passageways led from the two lower rows of pits which he observed in better preserved specimens. This latter assumption was shown to be erroneous by Bather (1914); passageways led inward only from the upper pits.

Billings' 1858 paper included the first illustrations of the type specimens of *Edrioaster bigsbyi*. Of the two illustrated, that on pl. 3, fig. 1, 1a, was designated the lectotype by Bather (1914, p. 116); the other, plate 3, fig. 2, 2a, a lectoparatype. (The lectotype had been cut into three pieces when Billings' illustration was prepared, for fig. 1a is an axial section view of specimen GSC 1407.) The small fragment of the left side was apparently missing then also.

Bather's (1914) reinterpretation of *Edrioaster bigsbyi* was very complete. This came after he had described the related species *Edrioaster levis* and *Dinocystis barroisi* and redescribed *Edrioaster buchianus* (Forbes). Bather's extensive description of *Edrioaster bigsbyi* was based primarily on three specimens from the Geological Survey

of Canada, which are now missing, supplemented by three British Museum specimens. It covered most important thecal features. Among the few significant differences between Bather's and the present redescription of *Edrioaster bigsbyi* are the following seven items: (1) The ambulacra extend into the subambital zone, but this area was still elevated above the sea floor; only the resting zone was in contact with the substrate. Thus the ambulacra did not come into contact with the sea floor as Bather suggested. (2) The basal membrane was flexible and distally attached to the underlying substrate. There is no evidence that it extended entirely across the lower side of the theca as Bather suggested. (3) The interradial plates of the oral frame include not only fused floorplates, as noted by Bather, but also the fused proximal plate of each interambulacrum. (4) The hydropore penetrates the interambulacral part of the posterior interradial plate of the oral frame, and a second, modified, right proximal "interambulacral" or hydropore plate, which intrudes into the proximal posterior edge of ambulacrum V. Thus the two plates of the hydropore structure are modified interambulacrals that belong to the oral-ambulacral series; Bather described both hydropore plates as interambulacrals. (5) Bather's "accessory coverplates," small, triangular elements supposedly lying between the adradial ends of the coverplates and underlying floorplates, are interpreted here as fragments of the adradial corners of the biserial ambulacral coverplates, in spite of Bather's rejection of this interpretation. (6) Bather described the upper and lower rows of ambulacral floorplate pits and the deep sutural groove connecting them. However, he described the two shallow grooves that flank each deep sutural groove as diverging downward. The lectoparatypes clearly show that all three grooves are parallel and extend normal to the ambulacral axis. Bather also described the passageways as mere "pin-pricks," although the narrowest diameter seen in exposed sectional views averages .22 mm. (7) The nodose prosopon described by Bather on the external surfaces of the interambulacrals also covers the orals and the ambulacral coverplates.

Bather described all of the specimens he studied in great detail; he gave extensive analyses of size ranges of individual structural elements and of the minor proximal undulations of the ambulacra. Bather's statistics suggest that such features vary intraspecifically.

Later works have relied upon Bather's descriptions and illustrations of *Edrioaster bigsbyi* as definitive for the species. Moreover, many texts and summary works have used Bather's description as diagnostic of the characters of all edrioasteroids. Bather's reconstruction of *E. bigsbyi* has been refigured many times in these summary works as typifying the class.

Discussion

Edrioaster bigsbyi (Billings) is not a common or "typical" edrioasteroid, in spite of the impression that frequent citation has created. The related species, *Edriophus levis* (Bather) is not uncommon and has often been misidentified as *Edrioaster bigsbyi*.

Four fundamental thecal features are not well exposed in the few available specimens of *Edrioaster bigsbyi*. First, the perradial ends of the ambulacral coverplates are crushed in all specimens; the supposedly single, angular perradial ends are perhaps more complex. Second, the oral coverplates are missing or disrupted in all known specimens. Third, the plates of the oral frame may not be fully revealed in the partially covered and sectional views seen in the specimens illustrated here. Fourth, the inner elliptical ends of the floorplate passageways are known only in Bather's (1914) illustrations, not on the specimens now available.

The complex series of ambulacral floorplate pits and grooves suggest several possible alternative functions. The seemingly most plausible interpretation suggests a dual function. Extensions from the central radial canals, which extend under the ambulacral floorplates, passed upward through the sutural passageways into the upper series of pits. Bulbous, distensible vesicles would have been housed in these upper pits. Their expansion would have exerted pressure against the lower surfaces of the overlying coverplates and thus opened these plates to expose the food groove for feeding. Lateral tubules apparently extended from these upper vesicles downward along the deep sutural grooves, ending in extensible podia housed in the lower pits. These probably were extended upward during feeding and were used as food-gathering devices. The thin-walled podia no doubt also functioned as respiratory structures, with gases and perhaps fluids exchanged with the sea water through their thin walls.

Bather's interpretation of the floorplate structures contrasts with the above. He thought the radial water canals extended along the floor of the ambulacral tunnels, on the upper surfaces of the floorplates. Lateral branches supposedly extended along the lateral sutural grooves up to the upper pits. Here each branch connected to a podial structure with a tubule extending into the theca via the sutural passageways. This ended in an internal ampulla. Large, extensible podia arose from the upper pits. These supposedly pushed open the coverplates and then functioned as food-gathering and respiratory structures. Bather's interpretation suggests no function for the lower pits. Moreover, the hydropore opens through the stone canal into the thecal cavity and no evidence has been found to suggest that radial canals passed up through the central lumen to reach the prox-

imal ends of the ambulacral tunnels. Thus the radial canals are here assumed to lie under the ambulacral floorplates in the thecal cavity. This corresponds to their position in the *Lebetodiscina*. Bather's suggestion that large, extensible podia were housed in the upper pits is functionally problematic. The coverplates articulate with the floorplates along the zone housing the pits and almost completely roof them over, even when open, and thus leave little room for the upward extension of podia. Neither of the above two interpretations explains the two shallower grooves which flank each deep sutural groove that extends between the upper and lower rows of floorplate pits.

The coverplates of *Edrioaster bigsbyi* rest upon the floorplates and appear to lack intrathecal and intra-ambulacral extensions. Thus it is conceivable that they could be moved individually, in sequence, or randomly, or they may have moved as a unit, all opening and closing at once. Thus, unlike the *Isorophida*, their structure did not limit movement to a fixed pattern.

RANGE AND OCCURRENCE: Trenton Group, Middle Ordovician, of Ontario and Michigan.

Edrioaster priscus (Miller and Gurley), 1894

Plate 60, fig. 1-6

- 1894 *Aesiocystites priscus* Miller, S. A. and Gurley, F. E., Illinois State Mus. Bull. 5: 13-15, pl. 2, fig. 10-12.
 1915 *Aesiocystites priscus* Miller and Gurley, Bassler, R. S., United States Nat. Mus. Bull. 92, 1: 19.
 1943 *Edrioaster priscus* (Miller and Gurley), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 202.

Diagnosis (tentative)

An *Edrioasteridae* with: small "echinoidal" theca; ambulacra curved, I-IV contrasolar, V solar, curvature uneven, long proximal parts straight, distal parts curved abruptly, distal tips directed back toward oral area; thecal plates smooth.

Description

All known specimens of *Edrioaster priscus* (Miller and Gurley) are replaced by beekite, which has destroyed most plate sutures. Only major structural units of the theca are recognizable. The whereabouts of the four specimens of the type series is unknown. Three specimens from the same area as the type are illustrated here.

The theca is relatively small; diameters range from 15 to 19 mm. The upper oral surface of the "echinoidal"

theca is highly convex. The subambital zone appears to be very narrow, and the ambulacra appear to extend beyond it onto the resting zone. This appearance may be due to preservational compression of the lower thecal zones. The incurved zone is also narrow and leaves a relatively large, nonplated central area on the lower surface. A membrane similar to that of *Edrioaster bigsbyi* may have been attached to the distal plates of the incurved zone and presumably extended downward and attached to the substrate.

The oral region includes oral covering plates that are continuous with the ambulacral coverplate series and oral frame plates. The oral frame is transversely elongate and surrounds an ovoid central lumen that leads from the proximal ends of the ambulacral tunnels down into the thecal cavity. Presumably it is formed by 10 compound plates, five radial and five interradial.

The hydropore structure is probably similar to that of *Edrioaster bigsbyi*, but cannot be confidently identified on the available specimens.

The five ambulacra rise abruptly above the adjacent interambulacra and form prominent ridges on the thecal surface. The ambulacra are curved, I-IV contrasolar, V solar, but curvature is limited to the distal quarter of each ambulacrum. The proximal parts are straight and are draped down over the convex upper oral surface. They extend into the subambital and perhaps also the resting zone. The distal segments curve abruptly, with the distal tip of each directed back toward the oral region. However, all appear to end in the subambital zone and none recrosses the ambitus onto the upper oral surface.

Remnants of the contact faces between ambulacral plates suggest that the biserial coverplates and floorplates are similar to those found in *Edrioaster bigsbyi*.

The interambulacral plates appear to be large, polygonal, and tessellate. These plates are continuous with the apparently polygonal tessellate plates of the resting and incurved thecal zones.

The anal structure, apparently a periproct, is located near the distal edge of the center of the upper oral surface part of interambulacrum 5. It may be slightly elevated to form a low, rounded mound.

Thecal plate surfaces appear to have been smooth.

Specimens

YPM 28455, 28456 (old 2361). Two of seven specimens from one locality. "Lower Trenton," Trenton Group, Mohawkian Series, Middle Ordovician. Curd's farm, Mercer County, Kentucky. Fischer Collection, O. C. Marsh, donor.

YPM 28455. 16.3 mm axial by 17.1 mm transverse diameter by 10.7 mm high.

Pl. 60, fig. 6.

The type locality is listed by Miller and Gurley only as Mercer County. Therefore, this and the following specimens may be topotypes.

This individual appears to be only slightly, if at all depressed, and thus preserves the original thecal shape. Oral and ambulacral coverplates are preserved along most of the length of the ambulacra. Only the outline of the oral area, ambulacra, and anal structures are distinct, for nearly all plate sutures have been destroyed.

YPM 28456. 19.1 mm axial by 17.8 mm transverse diameter, 11.3 mm high.

Pl. 60, fig. 1-3.

The specimen apparently preserves the original inflated shape of the theca. Oral and most ambulacral coverplates are missing, exposing the central oral lumen, the upper side of the oral frame, and the ambulacral grooves. Remnants of the ambulacral coverplates suggest an alternating biseries similar to that of *Edrioaster bigsbyi*. A few sutures between the apparently alternating, biserial floorplates have been identified, and suggestions of the upper ends of floorplate passageways are present. Interambulacral plate suture lines are preserved in some areas, and the slightly disrupted anal structure is preserved in interambulacrum 5.

The lower side of the specimen preserves the distal parts of ambulacra I, III, IV, and V, which show the pronounced distal curvature. The incurved thecal zone is partially visible. Matrix obscures the center of the lower side.

CFMUC 33380. "Curdsville, Trenton Limestone," Trenton Group, Mohawkian Series, Middle Ordovician. 1.5 miles south of High Bridge, Mercer County, Kentucky. 15.2 mm axial by 13.6 mm transverse diameter by 10 mm high.

Pl. 60, fig. 4, 5.

This is an incomplete specimen; the left third of the theca is missing. Ambulacra III, IV, and V, and part of I are preserved with the coverplates in place. All sutures have been destroyed. The lower side of the specimen may preserve part of an attachment membrane which extends from the incurved zone down toward the substrate.

Discussion

Miller and Gurley (1894) based the species *Aesiocystites priscus* on four specimens and illustrated two of these. Both the generic and specific descriptions were brief and generalized. Features included were: thecal shape, oral area and ambulacral disposition, and anal structure location. They also described: alternating biserial ambulacral coverplates; orals similar to ambulacral coverplates; deep ambulacral grooves beneath coverplates; and interambulacrals polygonal and abutting. The new genus *Aesiocystites* was contrasted with *Hemicystites*.

Subsequent to Bather's (1914) description of *Edrioaster bigsbyi*, most authors have considered *Aesiocystites* to be a junior synonym of *Edrioaster* (i.e., Bassler, 1935; Bassler and Moodey, 1943; Regnéll, 1966). The thecal shape, the course of the ambulacra, and the suggested structure of the ambulacral plates support this conclusion. Unfortunately, until specimens that preserve the plates are located, this interpretation remains questionable.

It is not impossible that specimens identified as *Edrioaster priscus* are young adults of *Edrioaster bigsbyi*. The only observable thecal features separating the two species are thecal size, details of the thecal shape, and the nature of ambulacral curvature. All of these could be explained as ontogenetic.

RANGE AND OCCURRENCE: Trenton Group, Mohawkian Series, Middle Ordovician, of Mercer County, Kentucky.

Genus *Edriophus* Bell, gen. nov.

- 1842 [non] *Agelacrinites* Vanuxem, L., Nat. Hist. New York, pt. IV, Geology 3: 158, fig. 80.
- 1854 *Agelacrinites* Vanuxem, Billings, E. [partim], Canadian Jour. Industry, Sci. and Art: 271-273, text fig. 10-12.
- 1857 *Cyclaster* Billings, E. [partim], Geol. Surv. Canada, Rept. Progress 1853-1856: 292-294.
- 1858a *Edrioaster* Billings, E. [partim], Geol. Surv. Canada, Fig. and Descriptions of Canadian Organic Remains, dec. 3: 82-83, 85.
- 1899 *Edrioaster* Billings, Jaekel, O. [partim], Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 44-46, text fig. 9.
- 1914 *Edrioaster* Billings, Bather, F. A. [partim], Geol. Mag. (n.s.), dec. 6, 1: 115-125, 162-171, text fig. 2, pl. 12, fig. 1-2.
- 1915a *Edrioaster* Billings, Bather, F. A. [partim], Geol. Mag. (n.s.), dec. 6, 2: 211-215, 259-266.
- 1915b *Edrioaster* Billings, Bather, F. A. [partim], Geol. Mag. (n.s.), dec. 6, 2: 316-322.
- 1915c *Edrioaster* Billings, Bather, F. A. [partim], Geol. Mag. (n.s.), dec. 6, 2: 393-403.

- 1943 *Edrioaster* Billings, Bassler, R. S. and Moodey, M. W. [partim], Geol. Soc. America, Spec. Pap. 45: 201, 202.
 1960 *Edrioaster* Billings, Kesling, R. V. [partim], Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 147-148, pl. 1, fig. 1-4.

TYPE SPECIES: *Edrioaster levis* Bather, 1914.

Diagnosis

An Edrioasteridae with: oral plates similar to and continuous with ambulacral coverplates; right posterior plate of hydropore structure apparently fused to proximal posterior floorplates of ambulacrum V; ambulacra curved, I-V solar; ambulacral coverplates forming a single alternating biseries, each perradially elevated.

Description

Only the type species, *Edriophus levis* (Bather), is placed in the genus without question. Thus for diagnostic purposes the genus is essentially monotypic and has the characters of the type species; separation of generic and specific traits is uncertain. The features cited in the above diagnosis are in part inferred to be of generic rank from taxobases established for other edrioasteroid genera.

Discussion

The genus *Edrioaster* Billings originally included species with ambulacra curved I-IV contrasolar, V solar, as well as those with I-V solar. The latter type includes three species: *Edrioaster levis* Bather, *Edrioaster saratogensis* Ruedemann, and *Agelacrinites buchianus* Forbes. Only the first is represented by well-preserved specimens, and is here selected as the type species of the new genus *Edriophus*.

The direction of ambulacral curvature is the most apparent difference between *Edriophus* and *Edrioaster*. Other generic differences probably include the structure of the oral frame, structure of the hydropore plates, the shape of the ambulacral coverplates, the ambulacral groove structures formed by the floorplates, and perhaps the features of the oral plates.

Unfortunately, with only one well-known species, the amount of variability in supposedly generic features is uncertain. *Edriophus saratogensis* is represented by only a few fragmentary specimens, all preserved as molds, and is of no help in establishing generic features. *Edriophus buchianus* is known from two incomplete specimens which were not available during this study. Bather's detailed description of that species establishes the ambulacral curvature as like that of *Edriophus levis*. Other thecal features mentioned by Bather are quite similar to those seen in *Edriophus levis*, and thus it is not

impossible that the two are conspecific. Unfortunately, the ambulacral coverplates of *Edriophus buchianus* are unknown. Therefore, even restudy of the type specimens is not likely to resolve this problem.

ETYMOLOGY: *Edriophus* is compounded from the Greek *Edrio*, seat, and *ophis*, serpent, in reference to the sinuous perradial ridge formed by the tips of the ambulacral coverplates of this "seat-star."

RANGE AND OCCURRENCE: Trenton Group, Mohawkian Series, Middle Ordovician of New York and Ontario.

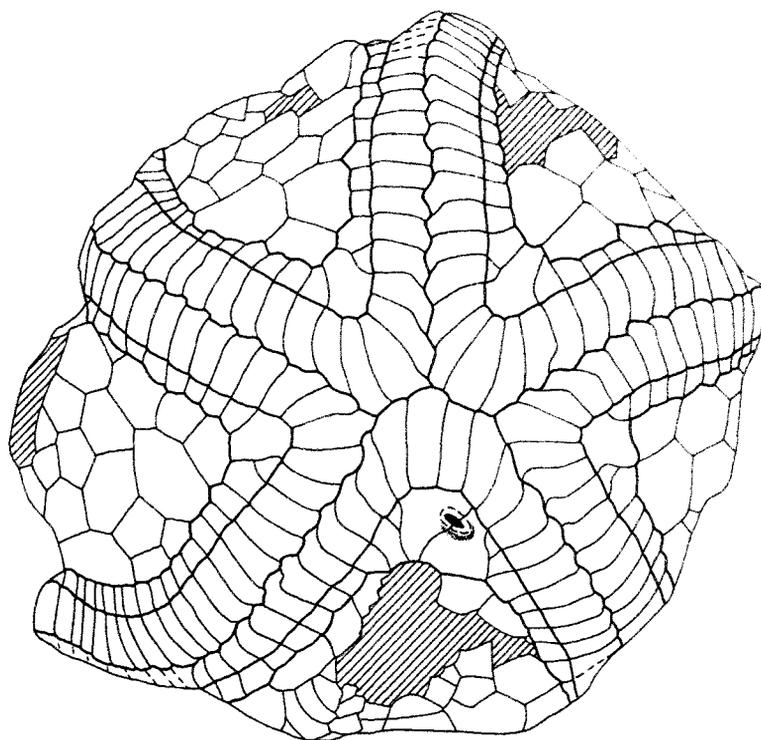
Edriophus levis (Bather), 1914

Text fig. 64; plate 61-63

- 1854 *Agelacrinites* sp. Billings, E. [partim], Canadian Jour. Industry, Sci. and Art: 271-273, text fig. 10-12.
 1857 *Cyclaster bigsbyi* Billings, E. [partim], Geol. Surv. Canada, Rept. Progress 1853-1856: 293-294.
 1858a *Edrioaster bigsbyi* (Billings), E. [partim], Geol. Surv. Canada, Fig. and Descriptions of Canadian Organic Remains, dec. 3: 82-83, 85.
 1914 *Edrioaster levis* Bather, F. A., Geol. Mag. (n.s.), dec. 6, 1: 115-125, 162-171, text fig. 2, pl. 12, fig. 1-2.
 1915a *Edrioaster levis* Bather, F. A., Geol. Mag. (n.s.), dec. 6, 2: 259-266.
 1943 *Edrioaster levis* Bather, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 202.
 1960 *Edrioaster levis* Bather, Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 147-148, pl. 1, fig. 1-4.
 1966 *Edrioaster levis* Bather, Regnéll, G., in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: text fig. 115-2.

Diagnosis

An *Edriophus* with: large theca, approximately 10 orals, with four central orals apparently larger than other orals; orals raised perradially to form a small ridge along oral midlines; oral frame formed by five compound interrational oral frame plates that are partly exposed externally, and five compound radial frame plates that lie in part below the interradians; radials in contact around inner edge of frame rim; ambulacral coverplates perradially elevated to form a distinct perradial ridge; proximal side of perradial end of each coverplate produced proximally as a small lobe; interambulacrals large, polygonal, tessellate; periproct formed by several irregular circlets of plates, the central elements larger, elongate; thecal plates smooth.



Text figure 64. *Edriophus levis* (Bather), 1914
UCMP 40479, (x 4), pl. 62, fig. 1.

Description

The "echinoidal" theca of *Edriophus levis* (Bather) is large, averaging 40 mm in diameter, with larger individuals over 55 mm (text fig. 64).

The oral area includes approximately 10 covering orals which are continuous with the ambulacral coverplate series (pl. 61, fig. 4, pl. 62, fig. 3, 5, 9, 10). Three or four central orals are somewhat larger than the others. Two are anterior, with one on either side of the anterior oral midline. These centrally abut one or two large posterior plates along the center of the transverse oral midline. The central orals are flanked by smaller plates that are about equal in size to the proximal ambulacral coverplates. Commonly one pair of the smaller orals lies adjacent to each side of centrals along the transverse oral midline, proximal to the point of bifurcation of the two lateral pairs of ambulacra. A third pair lies along the anterior midline and separates the central orals from the adjacent proximal coverplates of ambulacrum III. Occasionally one of these smaller anterior orals may reach the transverse oral midline, and thus it separates the two larger anterior central orals. The orals

are perradially raised and form a small, distinct ridge along each of the oral midlines.

The large, transversely elongate oral frame of *Edriophus levis* is subpentagonal in outline, being distally continuous with the ambulacra (pl. 61, fig. 2, 5, 7-9). The proximal margin is ovoid and surrounds the large central lumen which extends down from the proximal ends of the ambulacral tunnels and opens into the thecal cavity. The five compound radial plates are formed by the fusion of three or more pairs of proximal ambulacral floorplates. Four passageways penetrate each radial plate and mark the fused lateral sutures between the floorplate components of these compound plates. The radials are enlarged proximally and extend both downward into the thecal cavity and laterally; the inner proximal edges of adjacent radial elements are in contact around the innermost proximal edge of the frame rim. Only the two posterior radials are not in contact; the lower edge of the posterior interradial forms this part of the frame rim. Distally the radials extend out under the proximal three or four pairs of ambulacral floorplates of the contiguous ambulacra. The radials

taper gradually and each has a blunt termination. Small, triangular sectors of the upper sides of the distal parts of the radials, pointed distally, are exposed when the oral frame is viewed from above with the oral and proximal ambulacral coverplates removed. These wedges are seen between the perradially separated, opposing members of the proximal two or three pairs of ambulacral floorplates.

The five compound interradiial frame plates alternate with the radials. Each is formed by the fusion of approximately six floorplates and the proximal plate of each interambulacrum. As in *Edriaster bigsbyi*, the floorplates incorporated into each interradiial plate are "half-pairs." The originally opposed members of the proximal three pairs of floorplates in each ambulacrum were separated perradially. Opposing members were thus incorporated into different interradiials, with pair members of the right side fused into the adjacent interradiial to the right, and pair members of the left side into the adjacent interradiial on the left. Commonly five passageways penetrate each interradiial plate, marking the fused sutures between the six floorplates. The fused floorplates are also fused adradially to the proximal plate of each interambulacrum.

The interradiial frame plates lie adjacent to the upper part of the alternate radials and also extend above the radials so that the adradial ends of the floorplate sectors and all of the interambulacral plate sectors of each interradiial are exposed externally, distal to the ends of the oral coverplates. Except in the posterior interradius, the inner proximal ends of the interradiials are wedged between the adjacent radials. They end before reaching the inner edge of the frame rim which is formed by the laterally expanded radial plates. In the posterior interradius, the interradiial plate does reach the inner frame edge and separates the inner ends of the two adjacent posterior radials.

The oral frame of *Edriophus levis* is thus formed by 60 or more fused floorplates and five fused interambulacrals. It differs from the frame of *Edriaster bigsbyi* not only by the addition of at least two extra floorplates in each interradiial, but also by the greater proximal expansion of the radials, which are laterally in contact under the interradiials (except posteriorly) around the inner edge of the frame rim. Moreover, the externally exposed adradial ends of the frame plates slope gradually down to the interambulacra, and thus do not form a steeply sloping, abrupt border as in *Edriaster bigsbyi*.

The hydropore is a small, elliptical opening along the right posterior margin of the oral area and is shared by two plates (text fig. 64; pl. 61, fig. 4; pl. 62, fig. 1-3, 9, 10; pl. 63, fig. 7, 8, 11, 13). It is elongate normal to the suture between the interambulacral part of the posterior interradiial of the frame and an adjacent right posterior

hydropore plate. The left margin of this posterior plate is fused to one or more (? three) floorplates of the proximal posterior side of ambulacrum V. Distally this plates abuts interambulacrals.

The hydropore may be shared equally by the two plates, or it may extend further into either plate. The rounded anterior end of the elongate opening is wider than the posterior end, which occasionally is pointed. The margins of both plates of the hydropore structure are thickened around the opening and form a small, distinct, raised rim.

The hydropore opens down into the stone canal passageway. This is apparently formed by the two plates of the hydropore structure. The passageway expands rapidly inward and opens into the thecal cavity by way of a large, elliptical to circular exit which lies adjacent to the distal edge of the right posterior margin of the oral frame.

The five long, broad ambulacra curve solarly. They extend outward from the oral area past the ambitus into the subambital thecal zone. Curvature is uneven; the proximal part of each is straight, but curvature is initiated gradually before the ambitus is reached. Distally they extend along the subambital zone concentric with the thecal margin. Occasionally the distal end of an ambulacrum may appear to curve back onto the upper oral surface, but this feature is found only in extremely depressed specimens, suggesting that it may be preservational.

The ambulacra are slightly elevated above adjacent interambulacra, but their adradial margins slope downward gradually and merge with the interambulacral areas.

The single alternating biseries of ambulacral coverplates roofs the ambulacral tunnel (text fig. 64, pl. 61, fig. 1, pl. 62, fig. 1-5, 7-10, pl. 63, fig. 1-13). The coverplates are more or less subrectangular. The adradial ends are straight or slightly convex outward. The straight, parallel sides extend normal to the ambulacral axis. The perradial ends of the coverplates are sinuous, each plate being centrally or distally concave, with the proximal part produced toward the oral area along the perradial line as a rounded to proximally angular lobe. The proximal perradial lobe of an opposing, alternate coverplate fits into the distal or central concavity of the coverplate. Moreover, the perradial ends of the coverplates are abruptly upturned and form a pronounced, narrow, median ridge which extends along the sinuous perradial line.

The elevation of the perradial ends of the coverplates, and their sinuous shape, each with a proximal lobe, apparently strengthens the coverplates when the ambulacra are closed. This is suggested by the common preservation of the ambulacral coverplates in place in

this species, whereas in *Edrioaster bigsbyi* these plates are commonly lost or disrupted.

The adradial ends of the coverplates rest on the upper surface of the floorplates and form a nearly straight, submarginal ambulacral suture line. The larger floorplates extend past the adradial ends of the coverplates and are exposed externally between the submarginal and adradial sutures. The lower edge of the adradial ends of the coverplates are beveled and fit tightly against the slightly inwardly sloping, upper lateral margin of the floorplates, along the articulation zone. Coverplates appear to be uniform in thickness and lack both intrathecal and intra-ambulacral extensions.

Bather (1914) described an additional series of small median ambulacral coverplates. These are not plates, but fragments of the upturned perradial ends of the coverplates.

The ambulacral floorplates form an alternating biseries (pl. 63, fig. 1, 2, 5, 6). Each plate is elongate and subrectangular in plan view. The pointed perradial ends of the alternating floorplates form a central, zigzag perradial suture. The long, straight, lateral edges of each floorplate are parallel to one another and extend normal to the ambulacral axis. The adradial ends abut adjacent interambulacrals along straight or slightly convex sutures. Adjacent floorplates may vary in length and thus form an irregular adradial suture line. This variability in length appears to be more common along the proximal parts of the ambulacra. Floorplates and coverplates correspond exactly, with each floorplate lying directly under a corresponding coverplate. Bather (1914) suggested that the coverplates were proximally offset from the floorplates, with each lying on parts of two floorplates and extending over the lateral suture between the two floorplates. This interpretation was apparently based upon specimens in which the coverplates were partially disrupted and crushed down into the ambulacral tunnel. Well-preserved specimens that have not been crushed preserve the coverplates over the floorplates, with the contact surfaces between coverplates lying directly above the lateral sutures between the floorplates.

The floorplates are similar in shape to those of *Edrioaster bigsbyi* (text fig. 63B). Opposing plates slope downward centrally and form a broad ambulacral trough. The slope is gradual along the upper sides of the trough. However, a short, steeply inclined zone flanks the nearly horizontal perradial area and thus forms a relatively narrow, U-shaped groove in the center of the broad trough.

The upper lateral margins of the floorplates are nearly horizontal and slope only slightly perradially. This is the articulation zone on which the beveled bases

of the overlying coverplates rest. It lies partly over and partly distal to the upper ends of the floorplate passageways. The adradial end of the zone is marked by the line of contact with the adradial ends of the coverplates, and forms the submarginal ambulacral suture line.

Adradial to the articulation zone, the externally exposed parts of the floorplates slope gradually downward toward the interambulacra. The floorplates abut adjacent interambulacrals along vertical sutures, and form the adradial suture line along the thecal surface.

The floorplates are thickest under the articulation zone and thin conspicuously toward their perradial ends. Thus the inwardly directed convexity of the inner side of the floorplates is less pronounced than the central concavity of the upper surface. The perradial contact of the alternate floorplates is by vertical sutures.

The floorplate passageways originate in small, rounded or elliptical pits centered over the lateral sutures between adjacent floorplates. These pits lie along the perradial edge of the articulation zone. Their adradial ends are partly roofed by the bases of the overlying coverplates, and their perradial sides open into the upper lateral edge of the ambulacral tunnel. The passageways extend inward from the floors of the pits along the sutures. Their inner ends expand rapidly and open into the theca as large, elliptical depressions along the sutures between adjacent floorplates; these depressions commonly exceed half the length of the floorplates.

The small upper pits of the passageways form two rows along each ambulacrum, one along each upper lateral edge of the ambulacral tunnel. As in *Edrioaster bigsbyi*, there are two additional rows of small depressions along each ambulacrum, perradial to the passageway pits. They lie along the steep walls of the U-shaped axial depression and are not as well defined as the upper pits. Their perradial side is open to the central trough. These depressions end blindly. They are not connected with passageways.

The upper and lower rows of pits are connected by deep grooves which extend along the lateral suture lines of the floorplates. Owing to partial erosion of all available specimens, additional details of the floorplate pits and connecting grooves are not known. The presence of lateral grooves flanking each sutural groove, such as those found in *Edrioaster bigsbyi*, has not been established.

The perradial edges of the floorplates may be slightly depressed to form a subtle groove along the zigzag perradial line of the floorplates. However, this groove is even less apparent than in *Edrioaster bigsbyi*.

Interambulacral plates are large, polygonal, and meet along vertical sutures. Smaller polygonal plates continuous with the interambulacrals form the resting

and proximal part of the incurved thecal zones. These distal zones have been observed only in collapsed specimens. Apparently their combined width is small and involves only two or three irregular circlets of plates. The distal circlet may be formed by somewhat larger plates than the adjacent one. As in *Edrioster bigsbyi*, a flexible membrane is attached to the distal edge of the last circlet and is likewise imbedded with numerous minute, squamose plates which are slightly elongate concentric with the thecal margin. The membrane extends downward, and its distal edge was apparently attached to the substrate. It thus surrounds a small, subcircular, central, nonplated area.

The periproct is located near the center of the upper oral surface part of interambulacrum 5 (pl. 61, fig. 1, pl. 62, fig. 6). It includes three irregular circlets. The outer two are formed by small, irregularly polygonal plates which distally abut large interambulacrals. The central circlet appears to be formed by elongate, sub-lanceolate plates which are acuminate centrally.

External thecal plate surfaces appear to be smooth.

Specimens

UCMP 40477-40480. Hull Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Quarry 3 miles north of Kirkfield, Ontario. (Specimens from near the floor of the quarry.) Kopf Collection.

UCMP 40477. 41.8 mm axial by 42.2 mm transverse diameter.

Pl. 61, fig. 1-6.

The specimen has collapsed; the upper and lower surface plates are pressed together. The upper oral surface is well preserved, although a few plates on the left side are missing. The hydropore structure is partly disrupted. The lower surface of the specimen is partly covered with matrix. The inner surface of the oral frame is exposed centrally. The inner sides of the proximal floorplates of ambulacrum V are exposed where the marginal plates are missing. The oral frame is partially disrupted; the inner lateral ends of adjacent radials are no longer in contact. The inner side of several posterior plates of the oral cover are exposed through the central lumen. One segment of the distal plated membrane is preserved adjacent to the oral frame under interambulacrum 3.

UCMP 40478. 39 mm axial by 39 mm transverse diameter.

Pl. 61, fig. 7-9.

This specimen has also collapsed, pressing the upper and lower surface plates together. The lower surface preserves the distal parts of the ambulacra; most of the

coverplates are missing and hence the ambulacral groove parts of the floorplates are visible. The inner sides of the adjacent subambital interambulacrals are also preserved intact. Centrally, the oral frame and proximal ambulacral floorplates are exposed. The oral frame is well preserved, and both the radial and parts of the interradial plates can be seen. The inner surfaces of two posterior oral covering plates are seen through the transversely elongate central lumen. The ambulacral floorplates show the large, elongate inner openings of the floorplate passageway.

UCMP 40479. 27.5 mm axial by 27 mm transverse diameter.

Text fig. 64, pl. 62, fig. 1-3.

This specimen is smaller than most other representatives of the species. It exposes only the upper side of the theca, but it is only partially collapsed and preserves most of the original convexity of the upper oral surface. The central plates of the upper oral surface are well preserved except for interambulacrum 5 and the anal structure; the orals and ambulacral coverplates are slightly pulled apart perradially, but ambulacral and oral midline ridges are preserved. The hydropore is surrounded by a raised rim. The anterior end of the opening is large and rounded, the posterior end acuminate. It is subequally shared by the two hydropore plates. Plate surfaces are minutely pustulose.

UCMP 40480. 55.3 mm axial by 51 mm transverse diameter.

Pl. 62, fig. 7-10.

This large individual exposes only the upper oral side of the collapsed theca. A large crack separates the disrupted anterior part of the theca from the posterior part. The oral region and proximal parts of the ambulacra and interambulacra are well preserved. Orals and ambulacral coverplates are in place. The perradial and oral midline ridges are well preserved. The hydropore structure is partly eroded. The opening is shared equally by the two plates, but the anterior part is much wider than the acuminate posterior end.

GSC 18659. Illustrated Specimen of *Edriophus lewis* by Sinclair (1964, AAPG Guidebook, pl. 3, fig. 21). Hull Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Quarry 3 miles north of Kirkfield, Ontario. 40 mm axial by 45 mm transverse diameter.

Pl. 63, fig. 1-6.

This specimen exposes the collapsed and partially disrupted upper oral surface. Ambulacral coverplates are missing along parts of ambulacra II, III, and IV, which exposes the ambulacral groove surfaces of the floorplates. Although partially eroded, these preserve

the upper and lower rows of pits and the connecting sutural grooves. When the specimen is under xylene, the recrystallized proximal coverplates of ambulacrum IV become transparent and reveal the upper lateral parts of the underlying floorplates. This view demonstrates that the adradial ends of the coverplates are located just adradial to the upper row of floorplate pits.

USNM S-3197 (A-B). Hull Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Quarry 3 miles north of Kirkfield, Ontario.

USNM S-3197-A. 55.7 mm axial by 55.4 mm transverse diameter.

Pl. 63, fig. 7, 8.

This specimen exposes the collapsed upper oral surface. Coverplates are preserved, but have partly caved into the ambulacral tunnel. Distal parts of the ambulacra and interambulacra are disrupted. The oral plates are well preserved and only slightly depressed, and the hydropore structure, with raised rim, is well preserved. It is subequally shared by both plates, although the anterior end is somewhat larger.

USNM S-3197-B. 52 mm axial by 53.5 mm transverse diameter.

Pl. 62, fig. 4, 5.

A second large specimen preserved in a manner similar to that of S-3197-A. The oral plates are well preserved.

USNM Acc. No. 212887. Hull Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Quarry 3 miles north of Kirkfield, Ontario. 43.7 mm axial by 49.6 mm transverse diameter.

Pl. 62, fig. 6.

This individual has collapsed, but is moderately well preserved and exposes the upper oral surface plates. The anal structure shows the two irregular outer circlets of smaller polygonal plates and the larger, elongate anals of the central circlet. A few plates are missing from the left posterior sector of the structure.

UMMP 5731. *Edriophus levis* illustrated by Kesling (1960, pl. 1, fig. 1, 2 as *Edrioaster bigsbyi*). Hull Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Quarry 3 miles north of Kirkfield, Ontario. 30.5 mm axial by 32.8 mm transverse diameter.

Pl. 63, fig. 9, 10.

This specimen was illustrated by Kesling (1960) as an *Edrioaster bigsbyi* to demonstrate the location and structure of the hydropore. This and other misidentifications have led to the erroneous conclusion that specimens of *Edrioaster bigsbyi* are common. The theca

is only partially collapsed; the upper oral surface retains its original convexity. The anterior third of the specimen is missing and the oral and proximal anterior thecal plates are crushed. The illustration that shows the specimen under xylene reveals the upper parts of three of the interradial oral frame plates.

UMMP 26428. Illustrated Specimen of *Edriophus levis* by Kesling (1960, pl. 1, fig. 3, 4). Hull Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Quarry 3 miles north of Kirkfield, Ontario. 38.8 mm axial by 47.6 mm transverse diameter.

Pl. 63, fig. 11-13.

The specimen exposes only the collapsed upper oral surface. Most of the interambulacra are disrupted or missing. Kesling illustrated an oral surface view (pl. 1, fig. 3, specimen whitened) and a close-up of the oral area and partially disrupted hydropore structure. An oral surface view of the specimen under xylene is presented here for comparison with Kesling's plate. The proximal part of ambulacrum I is well preserved (pl. 63, fig. 12). The coverplates are in place and their sinuous perradial ends are elevated and form the perradial ridge. The externally exposed adradial ends of the floorplates flank the adradial ends of the coverplates. The surfaces of the thecal plates appear to be minutely pustulose.

Over 50 other specimens of *Edriophus levis* were examined during this investigation. One (ROM 18854) is from the "Trenton Limestone" at Hull, Quebec. The others are all from the quarry 3 miles north of Kirkfield, Ontario, Kopf Collection, University of Cincinnati, Museum of Paleontology. The holotype of *Edriophus levis* designated by Bather (British Museum No. E. 15900) is listed as Trenton Limestone, Kirkfield, Ontario. It is probably from the quarry 3 miles north of town, and thus the other Kirkfield quarry specimens are probably topotypes.

Discussion

Specimens of *Edriophus levis* were first included in *Edrioaster bigsbyi* Billings. Billings' (1854) description of *Agelacrinites sp.* includes characters of both species. An accompanying "reconstruction" (1854, text fig. 10) depicts the upper oral surface of *Edriophus levis* which lacks ambulacral coverplates. Billings' 1857 and 1858 descriptions of *Edrioaster bigsbyi* also include characters of both *Edriophus levis* and *Edrioaster bigsbyi*; i.e., ambulacra all solar, or I-IV contrasolar, V solar, and thecal plates smooth or with large nodes.

Bather (1914) restricted *Edrioaster bigsbyi* to specimens with ambulacra curved I-IV contrasolar, V solar, and thecal plates with large nodes. He proposed the name *Edrioaster levis* for the others with ambulacra I-V solar and thecal plates smooth. Bather's detailed de-

scription of the new species and extensive comparison of it with *Edrioaster bigsbyi* includes most thecal features. The present redescription of *Edriophus levis* differs in only six features. (1) The hydropore opens down into the thecal cavity through the stone canal, which penetrates both plates of the hydropore structure—not merely the anterior one as suggested by Bather. Moreover, both hydropore plates are modified interambulacrals that have been incorporated into the oral-ambulacrals series. The anterior plate is the interambulacral part of the posterior interradial of the oral frame. The posterior plate is fused to the proximal posterior floorplate of ambulacrum V. Thus the hydropore location is described as in the right posterior extension of the oral area, not in the proximal part of interambulacrum 5. (2) The compound interradial plates of the oral frame include not only fused floorplates as Bather suggested, but also the proximal plate of each interambulacrum, which is fused to the adradial ends of the floorplates. (3) The ambulacral coverplates form a single alternating biseries. The irregular “median coverplates” described by Bather are perradial fragments of the large coverplates and not discrete plates. (4) The coverplates and floorplates correspond one to one, each coverplate being centered over a floorplate. Bather’s conclusion that the coverplates are proximally offset from the floorplates, with each coverplate over parts of two floorplates, was apparently based on partially disrupted specimens in which the coverplates had been shifted laterally and partly collapsed downward into the ambulacral tunnel. (5) The anal structure includes three irregular circlets of plates. Plates of the outer two are irregularly polygonal, but in contrast with Bather’s description, the plates of the central circlet are elongate. (6) Bather described the thecal plates as scrobiculate. Most specimens appear to have smooth plate surfaces. A few individuals do have minutely pustulose surfaces, but this appears to be due to differential weathering which reveals the microstructure of the plates; the stroma canals are now filled with more resistant secondary calcite, and thus stand in relief after etching.

Kesling (1960) described the hydropore opening, and suggested that it was essentially similar to that of *Edrioaster bigsbyi*. The hydropore plates “are closely associated with the peristomial region... If they are regarded as part of the ambulacra and peristomial region, then the hydropore is located within a posterior expansion of the peristomial region.” (Kesling, 1960, p. 147-148). This is in agreement with the present interpretation. It should be noted, however, that Kesling’s comparison of the hydropore structure of *Edrioaster bigsbyi* with that of *Edriophus levis* was based on two specimens, both examples of *Edriophus levis*.

Edriophus levis Bather is closely related to *Edrioaster bigsbyi*. Differences include ambulacral disposition, makeup of the oral frame and the hydropore structure, the shape of the ambulacral coverplates, details of the floorplate features, and prosopon. The coverplate shape would appear to denote significant functional difference, for the proximal extensions and pronounced elevation of the perradial ends of the coverplates apparently increased the strength of the coverplate series. Thus most specimens of *Edriophus levis* preserve the coverplates, whereas these elements are commonly missing from specimens of *Edrioaster bigsbyi*. This probably signifies weaker coverplate articulation in the latter and probably correlates with different modes of operation.

RANGE AND OCCURRENCE: Trenton Group, Middle Ordovician of Ontario.

(?) *Edriophus saratogensis* (Ruedemann), 1912

Text fig. 65; plate 60, fig. 7-14

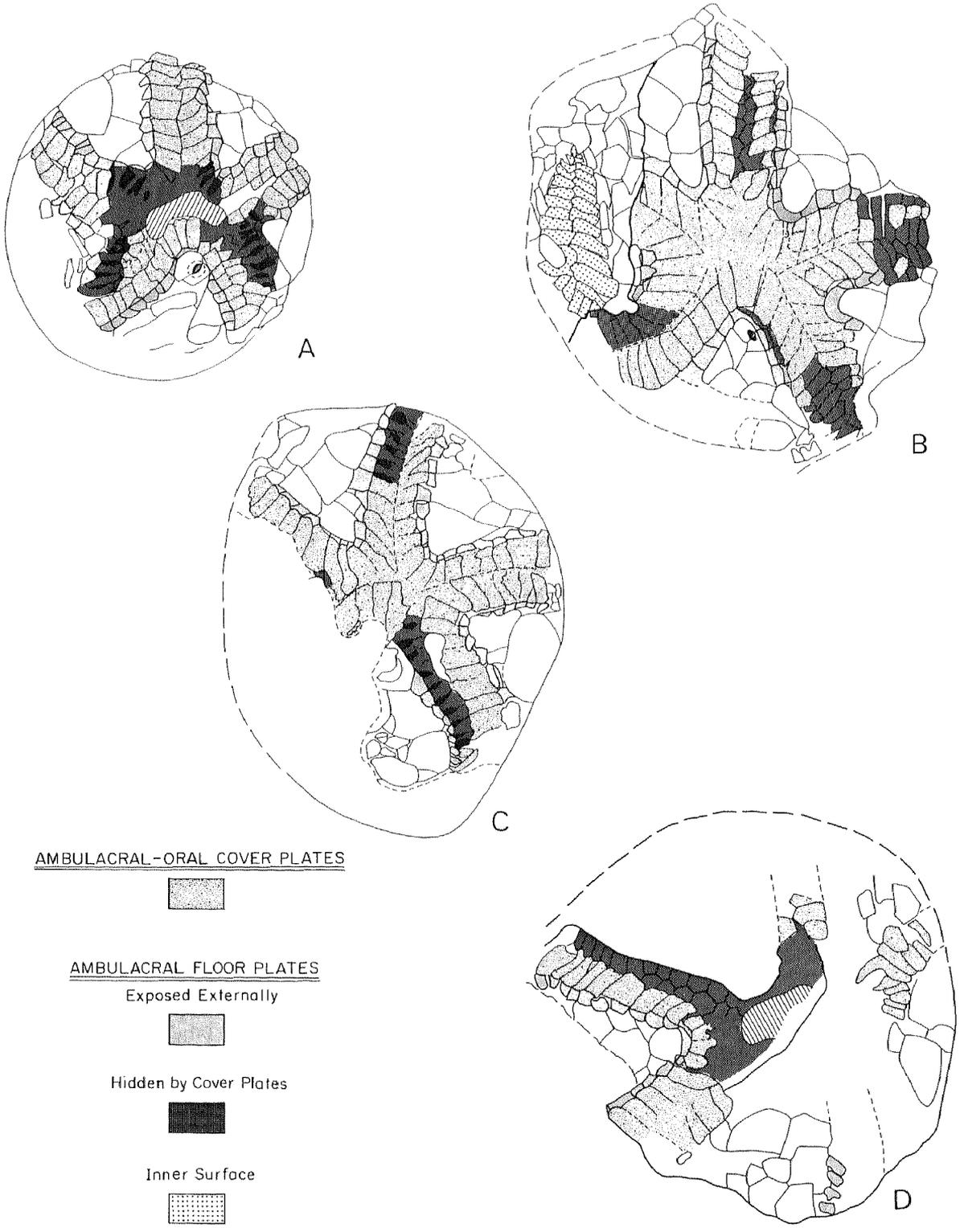
- 1912 *Edrioaster saratogensis* Ruedemann, R., New York State Mus., Bull. 162: 86-88, pl. 3, fig. 2-4.
 1914 *Edrioaster saratogensis* Ruedemann, Bather, F. A., Geol. Mag. (n.s.), dec. 6, 1: 162-171.
 1915 *Edrioaster saratogensis* Ruedemann, Bassler, R. S., United States Nat. Mus. Bull. 92, 1: 474.
 1943 *Edrioaster saratogensis* Ruedemann, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 202.

Diagnosis (tentative)

An Edrioasteridae with: small “echinoidal” theca; seven or more oral plates similar to and continuous with proximal ambulacral coverplates; hydropore elongate, penetrating two plates in right posterior oral area; ambulacra curved, I and probably II-V solar, coverplates forming a single alternating biseries; interambulacrals polygonal, tessellate; plates externally finely pustulose.

Text figure 65. (?) *Edriophus saratogensis* (Ruedemann), 1912

- A. Holotype, NYSM 7385, (x 5), pl. 60, fig. 7.
 B. Paratype (2), NYSM 7387, (x 5), pl. 60, fig. 11.
 C. Paratype (1), NYSM 7386, (x 5), pl. 60, fig. 9.
 D. NYSM 12779, (x 5), pl. 60, fig. 13.



Description

Edriophus saratogensis (Ruedemann) is represented by four semicomplete and three fragmentary specimens, all preserved as molds (text fig. 65A-D). Except for one small segment of the inner surface of the lower side, only the upper oral surface features are preserved.

The "echinoidal" theca is small, with diameters ranging from 10 to 17 mm. The upper oral surface is convex upward. Apparently a downwardly constricting subambital zone, which includes the distal ends of the ambulacra, was present below the ambitus. The resting and incurved zones, if both are developed, have not been observed.

The oral area is formed by the oral covering plates and externally exposed parts of oral frame plates (text fig. 65A-C, pl. 60, fig. 7-12). Seven or more central oral covering plates roof the central oral lumen. These plates apparently are similar in size and shape to the proximal ambulacral coverplates. The orals are distally continuous with the ambulacrals. The three or four orals that lie in the center of the area and abut perradially may be somewhat larger than the others.

The transversely elongate oral frame surrounds the oval central lumen. This extends downward from the proximal ends of the ambulacral tunnels and opens into the thecal cavity below (text fig. 65A, D, pl. 60, fig. 7, 8, 13, 14). The frame appears to be similar to that of *Edriophus levis*, formed by five compound interradiial plates and presumably five compound radials, although the latter have not been seen. The interradiials appear to be formed by the fusion of four floorplates and the proximal plate of the adjacent interambulacrum. The upper ends of the passageways which mark fused sutures are exposed in four interradiials of specimen NYSM 7385. Apparently three passageways penetrate each plate, which suggests that four floorplates are fused together in each. Adradially these plates are fused to the proximal interambulacral plate. When the oral coverplates are in place, only the adradial edges of the floorplates and the adjacent fused interambulacral part of the interradiial plates are exposed externally. These adradial ends of the fused floorplates rise steeply above the interambulacrals and form an abrupt margin to the central oral rise. This abrupt margin is continuous with the steep adradial margins of the ambulacra.

The hydropore structure lies in the right posterior part of the oral region and is formed by two plates (text fig. 65A, pl. 60, fig. 7, 8). The left anterior one is the interambulacral part of the posterior interradiial plate of the oral frame. The right posterior element is a polygonal to subtriangular plate, apparently fused to the adradial ends of the proximal posterior floorplates of ambulacrum V.

The hydropore is a small elliptical opening which extends across and normal to the suture between the two plates of the hydropore structure. The opening is shared equally by both. A small raised rim may have surrounded the opening.

The five wide ambulacra are elevated above the interambulacra; their adradial margins are steeply inclined to the adjacent interambulacral plates (pl. 60, fig. 7-14). Proximally the ambulacra are straight. They extend past the ambitus onto the lower side of the theca. All appear to be curved. The curvature of ambulacrum I is known to be solar, and II-V are believed also to be solar, although the distal parts of these have not been clearly observed.

The coverplates form a single alternating biseries. The plates are believed to be subrectangular. Their adradial ends are straight and meet the externally exposed parts of the floorplates along the submarginal suture. The straight lateral margins of the coverplates are parallel and extend perradially normal to the submarginal suture line. The perradial ends of the coverplates are believed to be pointed, and interdigitate with the alternate coverplates to form a zigzag perradial line. However, the coverplates have been crushed downward into the ambulacral tunnels in all known specimens, making observation difficult.

The biserial alternating floorplates are subrectangular in outline (pl. 60, fig. 9-12). Their adradial ends are straight and parallel to the ambulacral axis. The straight lateral sides are parallel and extend normal to the adradial suture. Perradially these plates are bluntly pointed and form a median, zigzag, perradial floorplate suture line. The externally exposed adradial ends of the floorplates, adradial to the submarginal suture, slope steeply upward from the adjacent interambulacrals and form the abrupt adradial margins of the ambulacra. Perradially the floorplates slope downward from the submarginal suture and form a deep central ambulacral trough. Large, elongate depressions are formed along the sutures between adjacent floorplates. One row of depressions lies along the upper edge of each side of the ambulacral trough. Sutural passageways are believed to extend into the thecal cavity from the floor of each lateral depression. The inner sides of the floorplates appear to have sloped downward into the thecal cavity, thus the inner sides of the ambulacra are convex inward. Elongate depressions are also formed on the lower, thecal cavity sides of the floorplates along the sutures between the adjacent floorplates. These are believed to be the inner ends of the sutural passageways.

The interambulacrals are irregular polygonal plates and are relatively few in number. The central interambulacrals are large, whereas those flanking the ambulacra are much smaller.

A small part of the right side of the anal structure appears to be preserved in specimen NYSM 7386, near the center of interambulacrum 5. It includes several small, irregularly polygonal plates.

The external surfaces of the interambulacrals appear to have been covered with small pustules. The ambulacral coverplates may also have been pustulose.

Specimens

NYSM 7385, 7386, 7387, 12779. "Snake Hill shale and sandstone," Trenton Group, Mohawkian Series, Middle Ordovician. Loose slabs collected under the cliff on the shore of Lake Saratoga, Snake Hill, Saratoga County, New York.

All specimens are preserved as molds in a fine to medium "graywacke" sandstone. NYSM 7385 and 7386 are on one slab; NYSM 7387, 12779, and three other fragmentary specimens are preserved on a second.

NYSM 7385. Holotype of *Edriophus saratogensis* (Ruedemann) (1912, pl. 3, fig. 2, as *Edrioaster saratogensis*). 10.2 mm axial by 9.2 mm transverse diameter.

Text fig. 65A, pl. 60, fig. 7, 8.

The holotype preserves the upper oral surface of a small individual. It apparently retains most of the original convexity of the upper side of the theca. The ambulacra extend straight out from the oral region. Distally a slight solar curvature appears to be initiated as they disappear from sight. The left posterior edge of the specimen is disrupted, including ambulacrum I and the adjacent interambulacrals. Some of the oral and most of the ambulacral plates are preserved, but they have perradially collapsed downward into the ambulacral groove. Parts of the proximal margins of all but the posterior interradiial plates of the frame are exposed where oral covering plates are missing. These show the upper ends of the passageways, three per interradiial. A few proximal floorplates of ambulacra II and V are exposed. The hydropore structure has been partially disrupted, which gives the appearance that the opening is elongate parallel to the suture between the two plates of the hydropore structure. The plates of interambulacrum 2 are less disrupted than the others.

NYSM 7386. Paratype (1) of *Edriophus saratogensis* (Ruedemann) (1912, pl. 3, fig. 3, as *Edrioaster saratogensis*). 14 mm axial by 11.2 mm transverse diameter.

Text fig. 65C, pl. 60, fig. 9, 10.

This specimen preserves the upper oral surface of a partially collapsed and laterally compressed individual. The left posterior third of the theca is missing, includ-

ing interambulacrum 1 and half of 5, ambulacrum I and half of II, and the hydropore structure. Most of the oral covering plates are present. The preserved segments of the ambulacra include coverplates, but these have collapsed perradially into the ambulacral tunnel. The floorplates of the proximal posterior part of ambulacrum V are exposed and reveal the upper, elongate, sutural depressions which mark the upper ends of the sutural passageways. The plates of interambulacrum 2 are less disrupted than the others. Part of the right side of the anal structure appears to be preserved near the center of interambulacrum 5.

NYSM 7387. Paratype (2) of *Edriophus saratogensis* (Ruedemann) (1912, pl. 3, fig. 4, as *Edrioaster saratogensis*). 15 mm axial by 14 mm transverse diameter.

Text fig. 65B, pl. 60, fig. 11, 12.

This specimen has collapsed and is somewhat laterally compressed. It exposes the upper oral surface of the theca except for the left margin, where the plates of the upper oral surface are hidden beneath the thecal cavity filling which preserves the impression of the inner sides of a small section of the lower side of the specimen. This area includes the distal, solarly curved part of ambulacrum I. The upper oral surface preserves the proximal parts of all but ambulacrum II. Orals and ambulacral coverplates are preserved, but have collapsed perradially down into the ambulacral grooves. The median perradial ends of the coverplates of ambulacrum III are missing, exposing the perradial ends of the underlying floorplates. Floorplates are also exposed in the distal ends of the proximal sectors of ambulacra IV and V. The hydropore structure is present, although the two participating plates are slightly pulled apart. The inner surface of the distal floorplates of ambulacrum I shows the elongate inner opening of the sutural passageways.

NYSM 12779. Specimen on slab with paratype (2). 13.7 mm axial by 14.6 mm transverse diameter.

Text fig. 65D, pl. 60, fig. 13, 14.

This individual is very fragmentary and preserves only part of the collapsed upper oral surface. It includes most of the proximal part of ambulacrum II and small parts of the other four. It also exposes the proximal margin of the left anterior side of the oral frame and a few of the plates of interambulacrum 5. The collapsed ambulacral coverplates are preserved on the posterior side of ambulacrum II, whereas the anterior side exposes the partially eroded floorplates.

Three other fragments of edrioasteroids are preserved on the same slab as NYSM 7387 and 12779. These fragments preserve bits of the original calcite plates.

Discussion

Ruedemann's (1912) original description of this species outlined the major thecal structures. In contrast with the above description, he reported the ambulacra as "four solar and one contrasolar." The direction of curvature has been established only for ambulacrum I, as solar, but the slight curvature of the ambital and the distal upper oral surface parts of the other four ambulacra suggest that all are curved solarly. Ruedemann also described the "sub-ambulacral plates" [? floorplates] as polygonal or hexagonal, similar to the interambulacrals. The floorplates, where exposed, appear to be elongate, subrectangular and perradially pointed. Describing the anal structure, Ruedemann (1912, p. 87) reported it as "small, consisting of four triangular plates." The anal structure is seen only in

specimen NYSM 7386. It appears that only a few plates of the right edge of the structure are preserved. Ruedemann apparently assumed that these represented the complete structure.

Unfortunately, the few known specimens of this species are too incomplete and too poorly preserved to allow a definitive description of the species. If the ambulacra are all curved solarly, as the specimens suggest, it probably belongs to the genus *Edriophus*. If the specimens are full-sized adults, the species is readily distinguished from *Edriophus levis* by its small size. Difference in the structural details of the oral frame, ambulacral floorplates, and ambulacral coverplates would also be expected.

RANGE AND OCCURRENCE: Trenton Group, Middle Ordovician of Saratoga County, New York.

Bibliography

- Ami, H. M. 1884. List of Ottawa Fossils, with introduction (Table of Contents) or List of Fossils From Ottawa and Vicinity. Ottawa Field-Naturalists' Club, Trans. 5, 2(1):54-62.
- 1905. Appendix, Preliminary List of Fossil Organic Remains From the Potsdam, Beekmantown (Calciferos), Chazy, Black River, Trenton, Utica, and Pleistocene Formations Comprised Within the Perth Sheet (No. 119) in Eastern Ontario. Geol. Surv. Canada, Ann. Rept. (n.s.) 14(J):84.
- Anderson, F. W. 1939. *Lepidodiscus fistulosus* sp. nov. From the Lower Carboniferous Rocks, Northumberland. Geol. Surv. Great Britain, Bull. 1:67-81, text figs. 1-10, pl. 5.
- Barrande, J. 1887. Système Silurien du Centre de la Bohême, pt. 1: Recherches Paleontologiques, 7(1) Classe des Echinodermes. Ordre des Cystidées. (Ouvrage posthume de feu Joachim Barrande, publié par le Doct. W. Waagen) Prague: 233 p., 39 pls.
- Bassler, R. S. 1915. Bibliographic Index of American Ordovician and Silurian Fossils. United States Nat. Mus. Bull. 92, 2v.:1521 p.
- 1935. The Classification of the Edrioasteroidea. Smithsonian Misc. Coll. 93(8):11 p., 1 pl.
- 1936. New Species of American Edrioasteroidea. Smithsonian Misc. Coll. 95(6):33 p., 7 pls.
- 1938. Pelmatozoa Palaeozoica. Fossilium Catalogus I: Animalia. W. Quenstedt [ed.]. pars 83, Gravenhage, Holland: 194 p.
- and Moodey, M. W. 1943. Bibliographic and Faunal Index of Paleozoic Pelmatozoan Echinoderms. Geol. Soc. America, Spec. Pap. 45: 734 p.
- Bather, F. A. 1898. *Dinocystis barroisi*, n.g. et sp., Psammites du Condroz. Geol. Mag. (n.s.), dec. 4, 5:543-548, pl. 21.
- 1899a. A Phylogenetic Classification of the Pelmatozoa. British Assoc. Advancement Sci., Rept. 68th Meeting (Bristol, 1898) London:916-923.
- 1899b. The Horizon of *Dinocystis barroisi*, A Letter in Reply. Geol. Mag. (n.s.) dec. 4, 6:134-136.
- 1900a. The Edrioasteroidea (Chapter 12):205-216, 8 figs. In A Treatise on Zoology, E. Ray Lankester [ed.], pt. III, the Echinoderma (with J. W. Gregory and E. S. Goodrich), Adam and Charles Black, London.
- 1900b. *Edrioaster buchianus* Forbes sp. Geol. Mag. (n.s.) dec. 4, 7:193-204, pls. 8-10.
- 1908. *Lebetodiscus*, n.g. for *Agelacrinites dicksoni* Billings. Geol. Mag. (n.s.) dec. 5, 5:543-550, pl. 25.
- 1914. The Edrioasters of the Trenton Limestone (Parts 1 and 2). Geol. Mag. (n.s.) dec. 6, 1:115-125, 162-171, pls. 10-14.
- 1915a. Morphology and Bionomics of the Edrioasteroidea (Part 1 and 2). Geol. Mag. (n.s.) dec. 6, 2:211-215, 259-266, 1 text fig.
- 1915b. A Comparison with the Structure of Asterozoa. Geol. Mag. (n.s.) dec. 6, 2:316-322.
- 1915c. The Genetic Relations to Other Echinoderms. Geol. Mag. (n.s.) dec. 6, 2:393-403, 4 text figs.
- 1915d. Studies in Edrioasteroidea I-IX. Articles on Edrioasteroidea published in the *Geological Magazine* between 1898 and 1915 were reissued, including plates and retaining original pagination, with an added preface and index, as a book published by the author at "Fabo," Marryat Road, Wimbledon, England.
- Beaver, H. H. 1967. Morphology [of the Blastoids]:S300-S350. In Treatise on Invertebrate Paleontology, R. C. Moore [ed.], pt. S, Echinodermata 1, 2. Geol. Soc. America, Inc. and Univ. Kansas Press, Lawrence.
- Bernard, F. 1893. Elements de Paleontologie. Librairie J.-B. Bailliere et Fils, Paris, pt. 1:528 p., 266 text figs.
- Beyrich, E. 1846. Über *Agelacrinites* in Böhmen. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-kunde:192-194, pl. 3-B, figs. 8-9.
- Billings, E. 1854. On Some New Genera and Species of Cystidea From the Trenton Limestone (Second Paper). Canadian Jour. Industry, Sci. and Art: 268-274, text figs. 1-12.
- 1857. Report for the Year 1856, Fossils From Anticosti, and New Species of Fossils From the Lower Silurian Rocks of Canada. Geol. Surv. Canada, Rept. Progress 1853-1856:247-345.
- 1858a. On the Cystidea of the Lower Silurian Rocks of Canada. Geol. Surv. Canada, Fig. and Descriptions of Canadian Organic Remains, dec. 3:9-74, 26 text figs., pls. 1-7.

- Billings, E. 1958b. On the Asteriadae of the Lower Silurian Rocks of Canada. Geol. Surv. Canada. Fig. and Descriptions of Canadian Organic Remains, dec. 3:75-85, 2 text figs., pls. 8-10.
- Bogolubov, N. 1926. Sur la decouverte de *Agelacrinus ephraemovianus* n. sp. dans le devonien du gouvernement de Toula. Annuaire Société Paleontologique de Russie 4:33-38, 1 text fig.
- Bolton, T.E. 1970. Echinodermata From the Ordovician (*Pleurocystites*, *Cremacrinus*) and Silurian (*Hemicystites*, *Protaxocrinus*, *Macnamaratylus*) of Lake Timiskaming Region, Ontario and Quebec. Geol. Surv. Canada Bull. 187, Contrib. Canadian Paleont.:59-66, pls. 11-13.
- Branson, C. C. 1941. A New Edriasteroid From the Upper Ordovician of Northern Illinois. Illinois Acad. Sci., Trans. 34(2):166.
- Buch, L. von. 1845 (1846). Über Cystideen eingeleitet durch die Entwicklung der Eigenthümlichkeiten von *Caryocrinus ornatus* Say. K. Akad. Wiss. Berlin, Abhandl. 1844:89-116, pls. 1-2 (preprinted in 1845, regular issue in 1846).
- Carpenter, P. H. 1894. On Certain Points in the Morphology of the Cystidea. Linnean Soc. London, Jour., Zoology 24:1-52, pl. 1.
- Caster, K. E. 1967. Homoiostelea: S581-S627. In Treatise on Invertebrate Paleontology, R. C. Moore [ed.], pt. S, Echinodermata 1, 2. Geol. Soc. America, Inc. and Univ. Kansas Press, Lawrence.
- Chapman, E. J. 1860. On a New Species of *Agelacrinites* and on the Structural Relations of that Genus. Canadian Jour. Industry, Sci. and Art (n.s.) 5:358-365, 1 fig.
- 1861. A Popular Exposition of the Minerals and Geology of Canada, pt. 4, Some Remarks on Organic Remains, with Special Reference to Canadian Forms. Canadian Jour. Industry, Sci. and Art (n.s.) 6: 501-520, text fig. 86.
- 1864. A Popular and Practical Exposition of the Minerals and Geology of Canada. W. C. Chewett and Co., Toronto: 236 p., 253 text figs. (reprinting of Chapman's 1861-1863 series of articles of the same name).
- Clark, T. H. 1919. A Section in the Trenton Limestone at Martinsburg, New York. Mus. Comparative Zoology, Bull. 63(1):1-42, 1 pl.
- 1920. A New *Agelacrinitid* From the Chazy of New York. American Jour. Sci. 50:69-71.
- Clarke, J.M. 1901. New *Agelacrinites*. New York State Mus. Bull. 49, Paleontologic Papers (2):182-198, 7 text figs., pl. 10.
- Cuénot, L. 1948. Anatomie, Éthologie et Systématique des Échinodermes: 3-272, 312 text figs. In *Traité de Zoologie*, P.-P. Grassé [ed.], T. 11, Échinodermes, Stomocordés, Procordés. Masson and Co., Paris.
- Cullison, J. S. and Prouty, C. E. 1939. A New and Earlier Occurrence of the Edriasteroid Genus *Hemicystites*. Jour. Paleont. 13(5):524-525, 1 text fig.
- Cummings, E. R. 1908. The Stratigraphy and Paleontology of the Ordovician Rocks of Indiana. Indiana Dept. Geology and Nat. Resources, 32nd Ann Rept.: 605-1188, 55 pls.
- Delage, Y. and Herouard, E. 1903. *Traité de Zoologie Concrète*. T. 3, Les Échinodermes. Schleicher Freres and Co., Paris: 495 p., 565 text figs., 53 pls.
- Dujardin, F. and Hupe, H. 1862. *Histoire Naturelle des Zoophytes Echinodermes*. Librairie Encyclopedique de Roret, Paris: 629 p., 10 pls.
- Ehlers, G. M. and Kesling, R. V. 1958a. *Timeischityes*, A New Genus of Hemicystitid Edriasteroid From the Middle Devonian Four Mile Dam Limestone of Michigan. Jour. Paleont. 32(5): 933-936, 1 text fig., pl. 121.
- 1958b. Cyclic Pattern of Ambulacral Covering Plates in *Discocystis laudoni* and Its Taxonomic Implications. Univ. Michigan, Contrib. Mus. Paleont. 14(15):265-276, 3 pls.
- Fell, H. B. 1967. Echinoderm Ontogeny: S60-S85. In Treatise on Invertebrate Paleontology, R. C. Moore [ed.], pt. S, Echinodermata 1, 1. Geol. Soc. America, Inc. and Univ. Kansas Press, Lawrence.
- and Moore, R. C. 1966. General Features and Relationships of Echinozoans: U108-U118. In Treatise on Invertebrate Paleontology, R. C. Moore [ed.], pt. U, Echinodermata 3, 1. Geol. Soc. America, Inc. and Univ. Kansas Press, Lawrence.
- Fisher, D. W. 1951. A New Edriasteroid From the Middle Ordovician of New York, Jour. Paleont. 25(5):691-693, 2 figs.
- Foerste, A. F. 1914. Notes on *Agelacrinitidae* and *Lepadocystinae*, with Descriptions of *Thresherodiscus* and *Brockocystis*. Denison Univ., Sci. Lab. Bull. 17(14):399-487, 6 pls., 8 figs.
- 1917 (1916). Notes on Cincinnati Fossil Types. Denison Univ., Sci. Lab. Bull. 18(4):285-355 (dated 1916, but Raymond, 1921, reports the article was distributed on 5 April 1917).
- 1920. Racine and Cedarville Cystids and Blastoids with Notes on Other Echinoderms. Ohio Jour. Sci. 21(2):33-78, 4 text figs., pls. 1-4.

- Forbes, E. 1848. On the Cystideae of the Silurian Rocks of the British Islands. Geol. Surv. Great Britain and Mus. Practical Geology (London) Mem. 2(2):483-539, pls. 11-23.
- Fraunfelner, G. H. and Utgaard, J. 1970. Middle Pennsylvanian Edrioasteroid From Southern Illinois. Jour. Paleont. 44(2):297-303, 12 text figs., pls. 59-60.
- Grabau, A. W. and Shimer, H. W. 1910. North American Index Fossils, Invertebrates. A. G. Seiler and Co., New York, 2:909 p., text fig. 1211-1937.
- Grant, J. A. 1881. Descriptions of a New Species of *Porocrinus*. Ottawa Field Naturalists' Club, Trans. 2:42-45, 1 pl.
- Gregory, J. W. 1897. On *Echinocystis* and *Palaeodiscus*—Two Genera of Echinoidea. Geol. Soc. London, Quart. Jour. 53:123-136, 5 text figs., pl. 7.
- Haeckel, E. 1896a (1895). Die cambrische Stammgruppe der Echinodermen. Jenaische Zeitschr. für Natur-wiss. 30:393-404.
- 1896b. Die Amphorideen und Cystoideen. Beiträge zur Morphologie und Phylogenie der Echinodermen. Festschrift zum 70 Geburtstag von Carl Gegenbaur am 21. Aug. 1896, W. Engelmann, Leipzig, 1:179 p., 25 text figs., 5 pls.
- Hall, J. 1852. (Containing) Descriptions of the Organic Remains of the Lower Middle Division of the New York System. Nat. Hist. New York, pt. VI, Palaeontology 2:362 p., 85 pls.
- 1858. Palaeontology of Iowa. Iowa Geol. Surv. Rept., Embracing the Results of Investigations made During Portions of the Years 1855, 1856, 1857, v. 1, pt. 2, Palaeontology:473-724, text figs. 53-118, pls. 1-29.
- 1866. Descriptions of Some New Species of Crinoidea and Other Fossils. New York State Mus., 20th Ann. Rept. (adv. pub.):17 p.
- 1867. Notes on the Genus *Palaeaster* with Descriptions of Some New Species and Observations Upon Those Previously Described, Contributions to Palaeontology. New York State Mus., 20th Ann. Rept.: 283-299, pl. 9.
- 1870. Notes on the Genus *Palaeaster* with Descriptions of Some New Species and Observations Upon Those Previously Described, Contributions to Palaeontology. New York State Mus., 20th Ann. Rept. (revised edition): 324-345, pl. 9.
- 1871. Descriptions of Some New Species of Fossils, from the Shales of the Hudson River Group, in the Vicinity of Cincinnati, Ohio. New York State Mus., 24th Ann. Rept. (adv. pub.): 8 p., 4 pls.
- 1872. Descriptions of New Species of Crinoidea and Other Fossils From the Strata of the Age of the Hudson River Group and Trenton Limestone. New York State Mus., 24th Ann. Rept.: 205-224, pls. 5-8.
- Harker, P. 1953. A New Edrioasteroid From the Carboniferous of Alberta. Jour. Paleont. 27(2):288-289, text fig. 1.
- Hisinger, W. 1841. Lethaea Svecica seu Petrificata Sveciae, Supplementi secundi continuatio. Holmiae: 6 p., pls. 40-42.
- Hussey, R. C. 1928. Cystoids From the Trenton Rocks of Michigan. Univ. Michigan, Contrib. Mus. Paleont. 3(4):77-79, 1 pl.
- Hyman, L. H. 1955. The Invertebrates. V. 4 Echinodermata, The Coelomate Bilateria. McGraw-Hill, New York: 763 p.
- Jackson, R. T. 1912. Phylogeny of the Echini, with a Revision of Paleozoic Species, Boston Soc. Nat. Hist., Mem. (n.s., Boston Jour. of Nat. Hist.) 7:490 p., 256 text figs., 76 pls.
- Jaekel, O. 1895. Über die Organisation der Cystoideen. Verhandlungen der Deutschen Zoologischen Gesellschaft, J. W. Spengel [ed.], W. Engelmann, Leipzig:109-121.
- 1899. Stammesgeschichte der Pelmatozoen. Bd. 1, Thecoidea und Cystoidea, J. Springer, Berlin: 442 p., 88 text figs., 18 pls.
- 1918 (1921). Phylogenie und System der Pelmatozoen. Palaeontologische Zeitschr. 3(1):1-128, 114 text figs.
- James, U. P. 1875. Catalogue of Lower Silurian Fossils of the Cincinnati Group Found at Cincinnati and Vicinity — within a circuit of 40 or 50 miles. New Edition, Paleontology, Cincinnati: 8 p.
- 1878. Descriptions of Newly Discovered Species of Fossils From the Lower Silurian Formation — Cincinnati Group. The Paleontologist, Cincinnati, 1:1-7.
- 1879. Supplement to Catalogue of Lower Silurian Fossils of the Cincinnati Group. The Paleontologist, Cincinnati, 4:29-32.
- 1883. Descriptions of New Species of Fossils From the Cincinnati Group, Ohio and Kentucky. The Paleontologist, Cincinnati, 7:57-59, 2 pls.
- 1887. Genus *Agelacrinus* Vanuxem, *Agelacrinus holbrookii* James. Cincinnati Soc. Nat. Hist., Jour. 10:25-26, text figs. A-B.
- Kesling, R. V. 1960. Hydropores in Edrioasteroids. Univ. Michigan, Contrib. Mus. Paleont. 15(8): 139-192, 14 text figs., 13 pls.

- Kesling, R. V.** 1967. Edrioasteroid with Unique Shape From Mississippian Strata of Alberta. *Jour. Paleont.* 41(1):197-202, pl. 21, 2 text figs.
- and **Ehlers, G. M.** 1958. The Edrioasteroid *Lepidodiscus squamosus* (Meek and Worthen). *Jour. Paleont.* 32(5):923-932, 1 text fig., pls. 119-120.
- and **Mintz, L. W.** 1960. Internal Structures in Two Edrioasteroid Species, *Isorophus cincinnatiensis* (Roemer) and *Carneyella pilea* (Hall). *Univ. Michigan, Contrib. Mus. Paleont.* 15(14): 315-348, 4 text figs., 9 pls.
- Keyes, C. R.** 1894. Paleontology of Missouri (pt. 1). *Missouri Geol. Surv.* 4:271 p., 32 pls.
- Klem, M. J.** 1904. A Revision of the Paleozoic Palaeochinoidea, with a Synopsis of All Known Species. *St. Louis Acad. Sci., Trans.* 14:1-98, 6 pls.
- Koch, D. L. and Strimple, H. L.** 1968. A New Upper Devonian Cystoid Attached to a Discontinuity Surface. *Iowa Geol. Surv. Rept. of Investigations* 5:49 p., 9 text figs., 9 pls.
- Lebour, G. A.** 1876. Note, sur Deux Fossiles Du Calcaire Carbonifere du Northumberland: *Soc. Geol. Belge, Ann.* 3:21-24.
- MacBride, E. W.** 1906. Echinodermata: 425-623, text figs. 185-296. *In Cambridge Natural History.* S. F. Harmer and A. E. Shipley [ed.], v. 1. MacMillan and Co., London.
- Meek, F. B.** 1873. Descriptions of Invertebrate Fossils of the Silurian and Devonian Systems. *Geol. Surv. Ohio, v. 1, Geology and Palaeontology, pt. 2, Palaeontology, Sec. 1:1-243, pls. 1-23.*
- and **Worthen, A. H.** 1868. Remarks on Some Types of Carboniferous Crinoidea, with Descriptions of New Genera and Species of the Same, and One Echinoid. *Philadelphia Acad. Nat. Sci., Proc.* 5:335-359.
- 1873. Descriptions of Invertebrates From the Carboniferous System. *Geol. Surv. Illinois, v. 5, Geology and Paleontology, pt. 2, Paleontology of Illinois: 320-619, 32 pls.*
- Miller, S. A.** 1877. The American Paleozoic Fossils, a Catalogue of Genera and Species. Published by the author, Cincinnati: 253 p.
- 1882. Description of Three New Orders and Four New Families, in the Class Echinodermata, and Eight New Species (of other Fossils) From the Silurian and Devonian Formations. *Cincinnati Soc. Nat. Hist., Jour.* 5:221-231, pl. 9.
- 1889. North American Geology and Palaeontology for the Use of Amateurs, Students, and Scientists. Western-Methodist Book Concern, Cincinnati: 664 p., 1194 text figs.
- 1891. Paleontology. *Geol. Surv. Indiana, 17th Ann. Rept. (adv. pub.): 103 p., 20 pls.*
- 1892a. First Appendix to North American Geology and Palaeontology. Published by the author, Cincinnati: 665-718, text figs. 1195-1265.
- 1892b. Paleontology of Indiana. *Geol. Surv. Indiana, 17th Ann. Rept.: 611-705, 20 pls.*
- 1892c. Paleontology. *Geol. Surv. Indiana, 18th Ann. Rept. (adv. pub.): 76 p., 12 pls.*
- 1894. Paleontology. *Geol. Surv. Indiana, 18th Ann. Rept.: 257-333, 12 pls.*
- 1897. Second Appendix to North American Geology and Palaeontology. Published by the author, Cincinnati: 719-793, text figs. 1266-1458.
- and **Dyer, C. B.** 1878. Contributions to Paleontology. *Cincinnati Soc. Nat. Hist., Jour.* 1(1):24-40, 2 pls.
- and **Faber, C. L.** 1892. Some New Species and New Structural Parts of Fossils. *Cincinnati Soc. Nat. Hist., Jour.* 15(2):79-87, 1 pl.
- 1894. Description of Some Cincinnati Fossils. *Cincinnati Soc. Nat. Hist., Jour.* 17(3): 137-158, pls. 7-8.
- and **Gurley, F. E.** 1894. New Genera and Species of Echinodermata. *Illinois State Mus. Bull.* 5:5-53, 5 pls.
- Moore, R. C. and Fell, H. B.** 1966. Homology of Echinozoan Rays: U119-U131. *In Treatise on Invertebrate Paleontology, R. C. Moore [ed.], pt. U, Echinodermata 3, 1. Geol. Soc. America, Inc. and Univ. Kansas Press, Lawrence.*
- Müller, A. H.** 1963. *Lehrbuch der Paläozoologie. Bd. 2, Invertebraten, Teil 3, Arthropoda 2 — Stomochorda.* G. Fisher, Jena, East Germany: 698 p., 854 text figs.
- Neumayr, M.** 1881. Morphologische Studien über fossil Echinodermen. *Sitzungsberichte der kaiserlichen Akad. der Wiss. I, 84:143-175, 2 pls.*
- Philip, G. M.** 1963. The First Recorded Australian Edrioasteroid. *Australian Jour. Sci.* 26(1):25, text fig. 1.
- Pictet, F.-J.** 1857. *Traité de Paléontologie ou Histoire Naturelle des Animaux Fossiles.* 2nd edition, J.-B. Baillière et Fils, Paris, 4:768 p., 110 pls.
- Piveteau, J.** 1953. Classe des Edrioasteroides: 651-657, 10 text figs. *In Traité de Paléontologie.* J. Piveteau [ed.], v. 3. Masson et Co., Paris.
- Quenstedt, F. A.** 1876. Die Asteriden und Encriniden nebst Cysti- und Blastoideen. *Petrefaktenkunde Deutschlands, Tübingen, 4(12):561-742, pls. 90-114.*

- Raymond, P. E. 1915. Revision of the Canadian Species of *Agelacrinites*. Ottawa Naturalist 29(5-6):53-62, pl. 1.
- 1921. A Contribution to the Description of the Fauna of the Trenton Group. Geol. Surv. Canada, Mus. Bull. 31 (Geol. Series 38): 64 p., 11 pls.
- Regnéll, G. 1945. Non-Crinoid Pelmatozoa From the Paleozoic of Sweden, A Taxonomic Study. Meddelanden Från Lunds Geologisk-Mineralogiska Institution 108:255 p., 30 text figs., 15 pls.
- 1950. *Agelacrinites ephraemovianus* (Bogolubov) and *Lepidodiscus fistulosus* Anderson (Edrioasteroidea). Kungl. Fysiografiska Sällskapet Lund Handlingar 20(20):218-237, 2 text figs.; also reprinted as Skrifter Från Mineralogisk-och Paleontologisk-Geologiska Institutionerna, Lund. 3:1-14, 2 text figs.
- 1960a. (1959). Données Concernant Le Développement Ontogénétique des Pelamatozoaire du Paéozoïque (Échinodermes). Soc. Geol. France, Bull. serie 7, 1:773-783, 6 text figs.
- 1960b. "Intermediate" forms in early Paleozoic Echinoderms. International Geol. Congress, 21st Session (Norden, 1960) pt. 22, Intern. Paleont. Union, Copenhagen: 71-80.
- 1966. Edrioasteroids: U136-U173, text figs. 111-131. In Treatise on Invertebrate Paleontology, R. C. Moore [ed.], pt. U, Echinodermata 3, 1. Geol. Soc. America, Inc. and Univ. Kansas Press, Lawrence.
- Roemer, F. (C. F. Von) 1851. Beiträge zur Kenntniss der fossilen Fauna des devonischen Gebirges am Rhein. Decheniana (Verhandlungen des Naturhistorischen Vereins Rheinlands und Westfalens) 8:357-376, pls. 7-8.
- 1855. Uebersicht über die Gattungen der Cystideen: 210-280, 4 pls. In Lethaea Geognostica. H. G. Bronn, 3rd edition, Bd. 1, pt. 2, Palaeo-Lethaea, 2, Stuttgart.
- 1876. Lethaea Geognostica. Theil 1, Lethaea palaeozoica (Atlas), E. Schweizerbart'sche Verlagshandlung, Stuttgart: 62 pls.
- Rowley, R. R. 1906. (Descriptions of Fossils). In Greene, G. K., Contribution to Indiana Palaeontology 2(2):19-31, pl. 4-6.
- Ruedemann, R. 1912. The Lower Siluric Shales of the Mohawk Valley, New York State Mus. Bull. 162: 144 p., 30 text figs., 10 pls.
- Salter, J. W. 1866. Appendix, On the Fossils of North Wales. (To The Geology of North Wales by H. C. Ramsay) Geol. Surv. Great Britain, Mem. 2, 3 (1st edition):239-381, 19 text figs., 26 pls.
- Shideler, W. H. 1918. A Primitive Type of *Agelacrinites* From the Richmond. Ohio Jour. Sci. 19(1):58 (plates in the following publication by Williams, S. R. 1918. Ohio Jour. Sci. 19(1): 59-86, 9 pls.).
- Shimer, H. W. and Shrock, R. R. 1944. Index Fossils of North America. John Wiley and Sons, Inc., New York: 837 p., 303 pls.
- Sinclair, G. W. 1951. The Occurrence of Cystids in the Ordovician of Ontario and Quebec. Canadian Field Naturalist 65:176-179.
- and Bolton, T. E. 1965. A New Species of *Hemicystites*. Geol. Surv. Canada Bull. 134(3):35-39, pl. 11.
- Sladen, W. P. 1879. On *Lepidodiscus lebouri*, a New Species of Agelacrinitidae From the Carboniferous Series of Northumberland. Geol. Soc. London, Quart. Jour. 35:744-751, pl. 37.
- Sowerby, G. B. 1825. Notice of a Fossil Belonging to the Class Radiaria, Found by Dr. Bigsby in Canada. Zool. Jour., London, 2 (7, art. 37) p. 318-320, pl. 11.
- Spencer, W. K. 1904. On the Structure and Affinities of *Palaeodiscus* and *Agelacrinites*. Royal Soc. London, Proc. 74:31-46, 12 text figs., pl. 1.
- Stainbrook, M. A. 1937. New Echinoderms From the Devonian Cedar Valley Formation of Iowa. American Midland Naturalist 18(5):899-904, pl. 1.
- Steinmann, G. 1903. Einführung in die Paläontologie. W. Engelmann, Leipzig: 466 p., 817 text figs.
- 1907. Einführung in die Paläontologie. 2nd edition, W. Engelmann, Leipzig: 573 p., 902 text figs.
- and Doderlein, L. 1890. Elemente der Paläontologie, W. Engelmann, Leipzig, 2 v.: 848 p., 1030 text figs.
- Strimple, H. L. 1968. A New Edrioasteroid. Iowa Acad. Sci. Proc. 73:260-262, 4 text figs.
- Thomas, A. O. 1924. Echinoderms of the Iowa Devonian. Iowa Geol. Surv., Ann. Rept. 29:391-551, text fig. 60-80, pl. 35-54.
- Ubahgs, G. 1967. General Characters of Echinodermata: S3-S60. In Treatise on Invertebrate Paleontology, R. C. Moore [ed.], pt. S, Echinodermata 1, 1. Geol. Soc. America, Inc. and Univ. Kansas Press, Lawrence.
- Vanuxem, L. 1842. Survey of the Third Geological District. Nat. Hist. New York, pt. IV, Geology 3: 307 p., 80 text figs.

- Williams, S. R.** 1918. Concerning the Structure of the *Agelacrinites* and *Streptaster*, Edrioasteroidea of the Richmond and Maysville Divisions of the Ordovician. Ohio Jour. Sci. 19(1):59-86, 9 pls.
- Wilson, A. E.** 1941. Echinodermata of the Ottawa Formation of the Ottawa-St. Lawrence Lowland. Geol. Surv. Canada Bull. 4:61 p., 2 text figs., 6 pls.
- Worthen, A. H. and Miller, S. A.** 1883. Descriptions of New Carboniferous Echinoderms. Geol. Surv. Illinois, v. 5, Geology and Palaeontology, sec. 2, Palaeontology of Illinois: 327-338, pl. 31.
- Zittel, K. A. von.** 1879. Protozoa, Coelenterata, Echinodermata und Molluscoidea. Handbuch der Palaeontologie, Bd. 1, Palaeozoologie, 1(1), Oldenburg, München and Leipzig: 765 p., 558 text figs.
- 1895. Grundzüge der Palaeontologie (Palaeozoologie), Oldenburg, München, 8 v.; first part translated as Textbook of Paleontology by Eastman, C. R., 1896, with revision for Pelmatozoa by Wachsmuth, C., and others, New York, 8 v.; Reissue, 1900, London.
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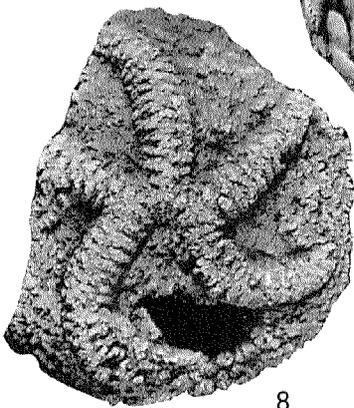
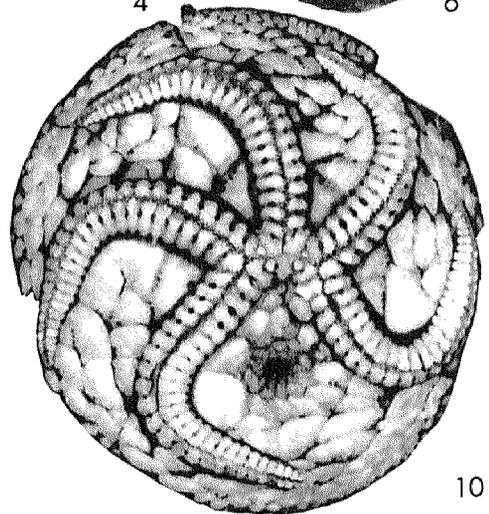
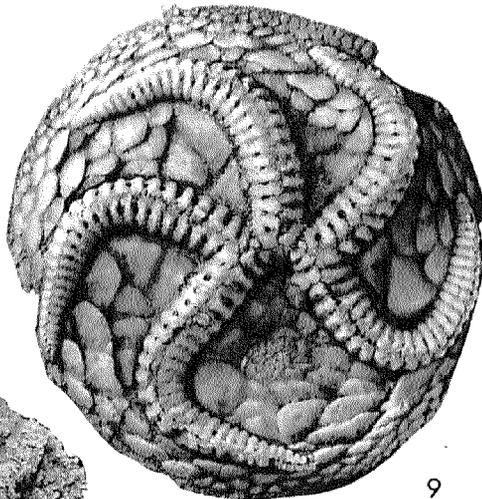
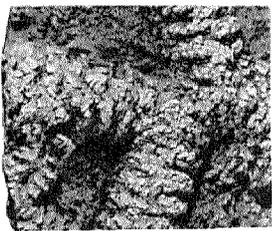
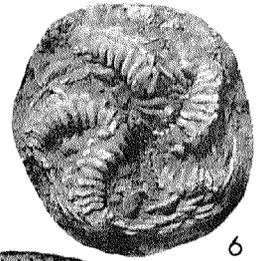
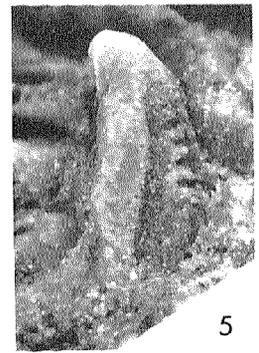
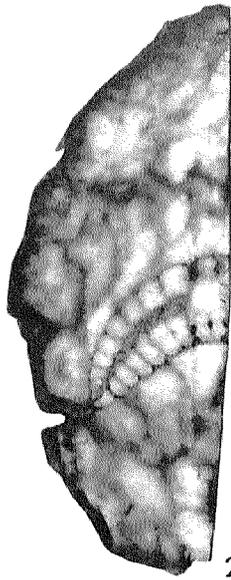
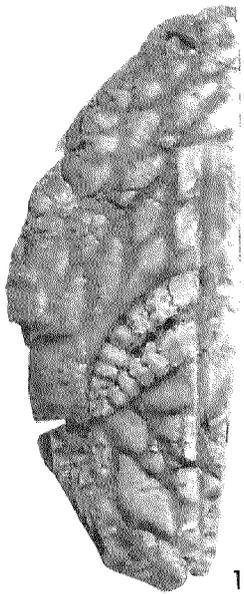
PLATES

Photographs have not been retouched. Where necessary, line drawings locate sutures. These are included as text figures and are identified in the plate legend. Each drawing was prepared by tracing an enlargement of the photograph seen in the corresponding plate figure. Photographs described as whitened show the specimen coated with a thin sublimate of ammonium chloride; those denoted as in xylene show the specimen submerged in xylene. Views labeled oral surface show the exterior of the upper side of that surface unless otherwise identified. Specimens are thought to be adults unless otherwise noted.

PLATE 1

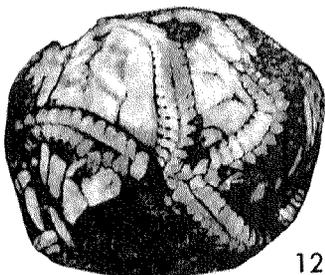
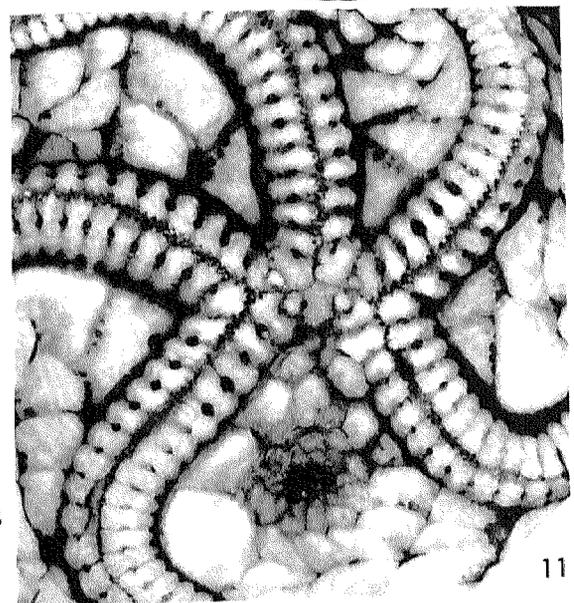
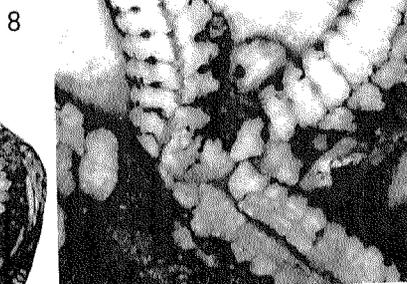
Lebetodiscus dicksoni (Billings), 1857

- 1-2. GSC 1407-B, holotype.
 1. Oral surface, $\times 6$, whitened.
 2. Oral surface, $\times 6$, in xylene (text fig. 3b).
- 3-5. ROM 18855-B.
 3. Oral surface, $\times 2$, whitened.
 4. Disrupted ambulacral coverplates that expose their ambulacral tunnel faces; each has three perradial ridges; the isolated interambulacral plate, right center, has two rows of submarginal, distal depressions, $\times 4$, whitened.
 5. Lateral view of isolated ambulacral coverplate, $\times 15$, whitened.
6. ROM 18855-A, oral surface, $\times 3$, whitened.
- 7-8. YPM 28451.
 7. Ambulacrum II with small posterior branch, $\times 5$, whitened.
 8. Oral surface, $\times 3$, whitened.
- 9-11. GSC 437.
 9. Oral surface, $\times 3$, whitened.
 10. Oral surface, $\times 3$, in xylene (text fig. 1A, 3A).
 11. Oral region, $\times 5$, in xylene.
- 12-13. ROM 18848-A.
 12. Oral surface, $\times 2$, in xylene.
 13. Oral area, $\times 5$, in xylene.



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PLATE 2

Lebetodiscus dicksoni (Billings), 1857

- 1-6. GSC 1414 [holotype of *Lepidoconia loriformis* (Raymond), 1915].
 1. Oral surface, $\times 2$, whitened.
 2. Oral surface, $\times 2$, in xylene (text fig. 4B).
 3. Oral region, $\times 5$, in xylene.
 4. Oblique view of ambulacrum II, $\times 8$, whitened (text fig. 4D).
 5. Oblique view of the proximal coverplates of ambulacrum I which have well-preserved lateral depression series, $\times 8$, whitened.
 6. Oblique view of right anterior segment of peripheral rim, $\times 6$, whitened (text fig. 4C).
- 7-9. ROM 161t-a-1 (= GSC 1415).
 7. Oral surface, $\times 2$, whitened.
 8. Oral surface, $\times 2$, in xylene (text fig. 4A).
 9. Oral region, $\times 6$, in xylene.
- 10-13. GSC 1412.
 10. Oral surface, $\times 2$, whitened.
 11. Oral surface, $\times 2$, in xylene.
 12. Proximal segment of ambulacrum IV, inner or thecal cavity side, proximal end up, $\times 15$, in xylene (text fig. 4E).
 13. Proximal segment of ambulacrum IV, exterior side, proximal end up, $\times 15$, in xylene (text fig. 4F).

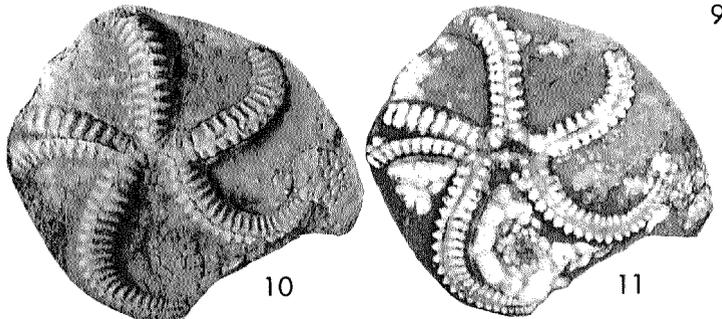
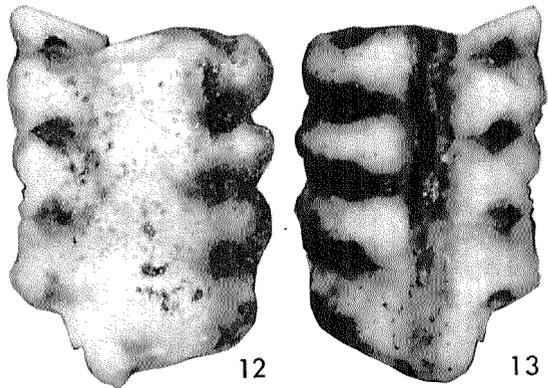
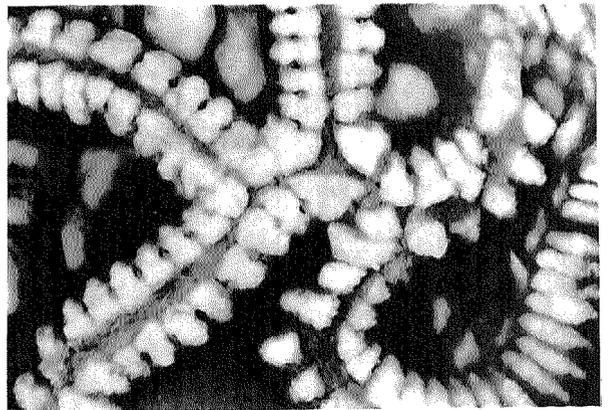
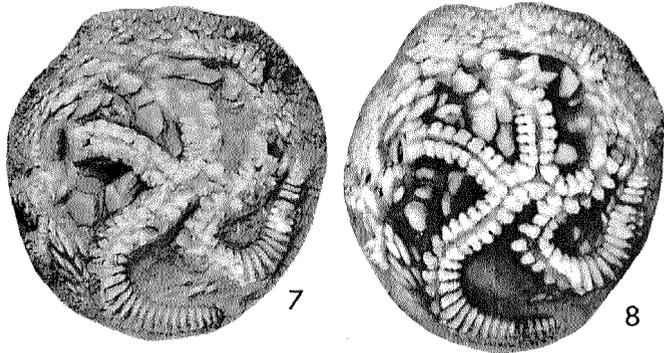
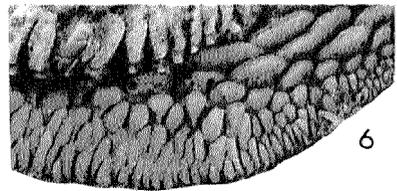
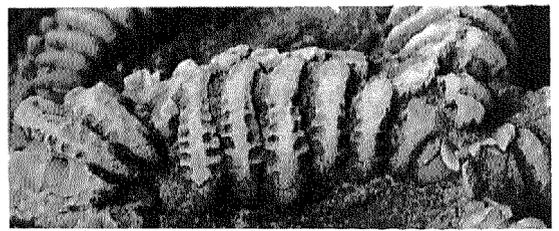
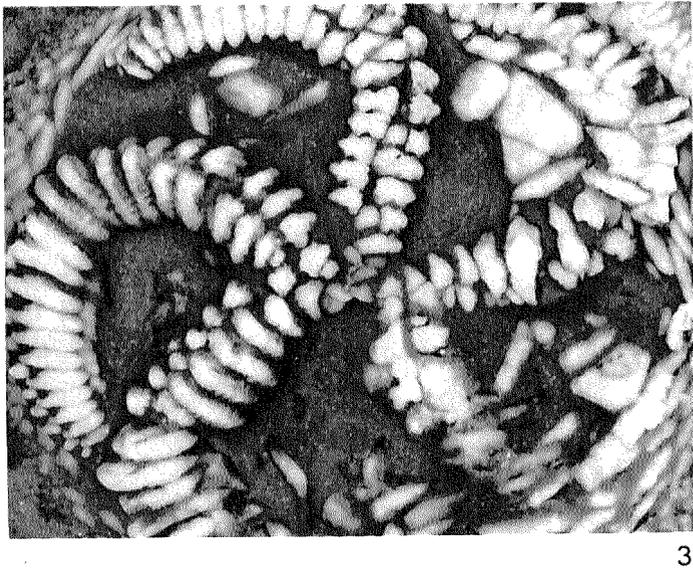
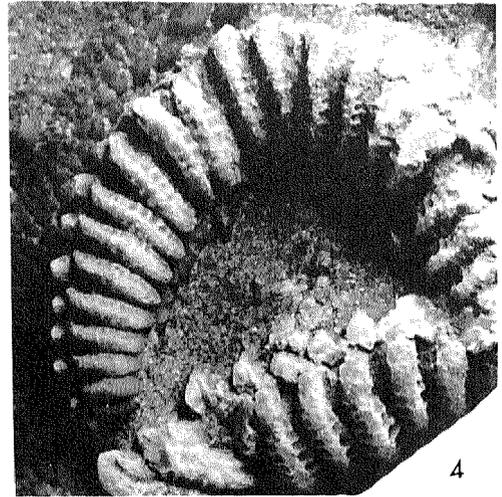
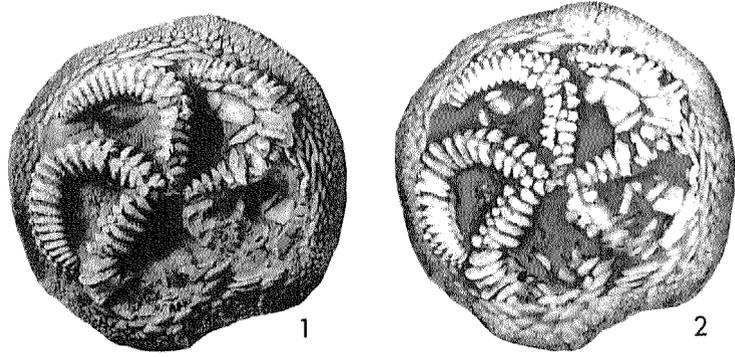


PLATE 3

Foerstediscus grandis Bassler, 1935

- 1-2. USNM S-3191, holotype.
 1. Oral surface, × 3, whitened.
 2. Oral surface, × 3, in xylene (text fig. 5C).
- 3-5. ROM 543t-a.
 3. Oral surface, × 4, whitened.
 4. Oral surface, × 4, in xylene (text fig. 5B).
 5. Oral region, × 9, in xylene (text fig. 5A).
6. YPM 28452, oral surface, × 3, whitened.

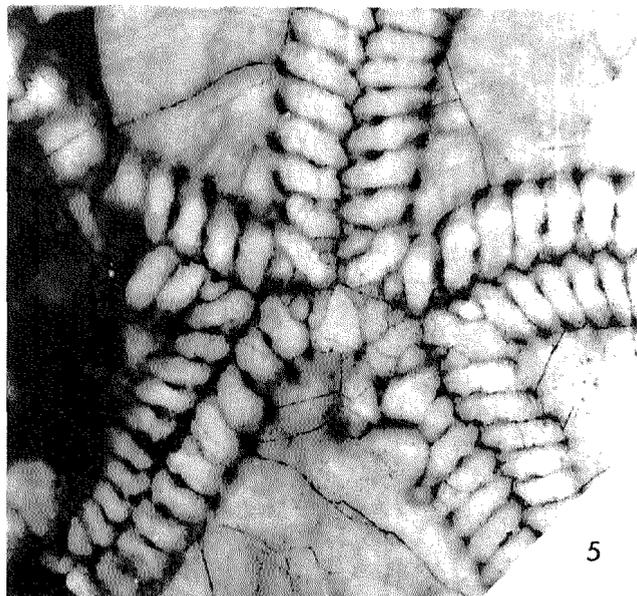
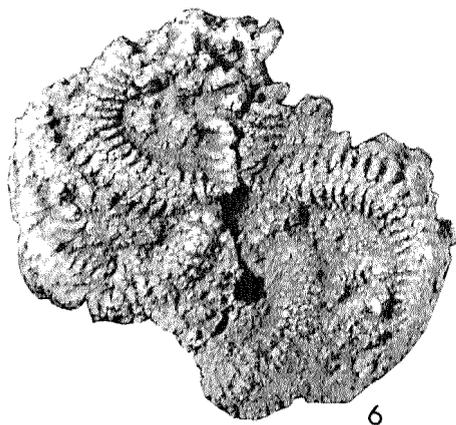
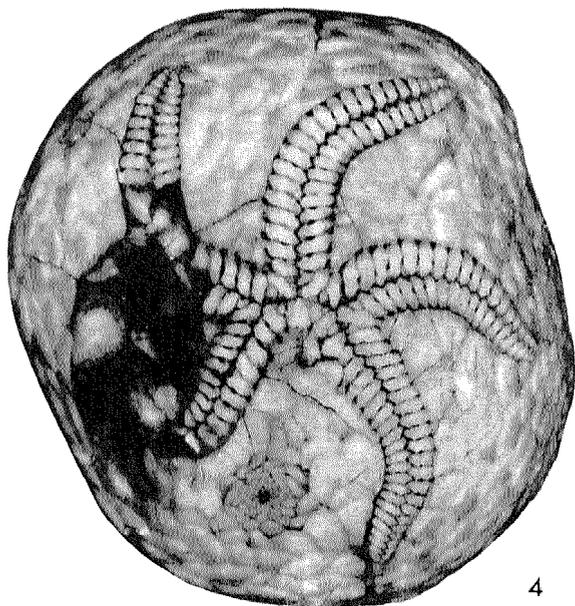
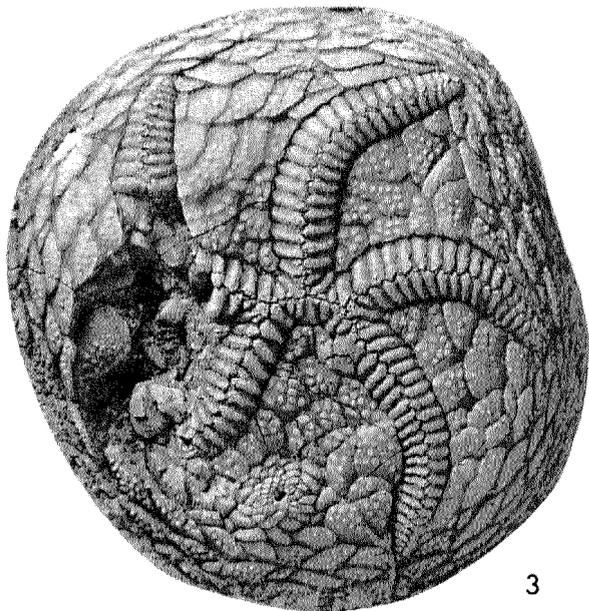
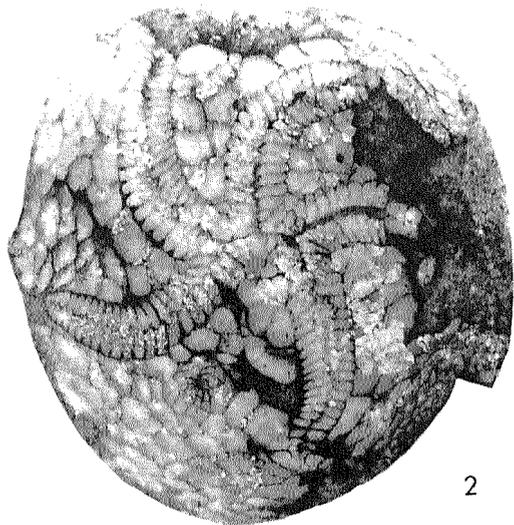
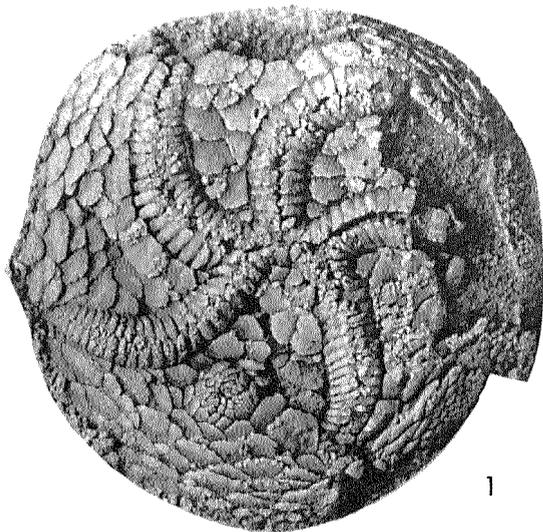


PLATE 4

Foerstediscus grandis Bassler, 1935

- 1-2. USNM S-3889-A ("cotype" of *Foerstediscus parvus* Bassler, 1936).
 1. Oral surface, $\times 7$, whitened.
 2. Oral surface, $\times 7$, in xylene (text fig. 5D).
3. USNM S-3889-B ("cotype" of *Foerstediscus parvus* Bassler, 1936), oral surface, $\times 7$, whitened.
- 4-5. USNM S-3889-C (Type series specimen of *Foerstediscus parvus* Bassler, 1936).
 4. Oral surface, $\times 7$, whitened.
 5. Oral surface, $\times 7$, in xylene.
- 6-7. USNM S-3889-D (type series specimen of *Foerstediscus parvus* Bassler, 1936).
 6. Oral surface, $\times 7$, whitened.
 7. Oral surface, $\times 7$, in xylene.
8. USNM S-3889-E (type series specimen of *Foerstediscus parvus* Bassler, 1936), oral surface, $\times 6$, whitened.
9. UCMP 40433, oral surface, $\times 2$, whitened.
10. UCMP 40434, oral surface, $\times 3$, whitened.

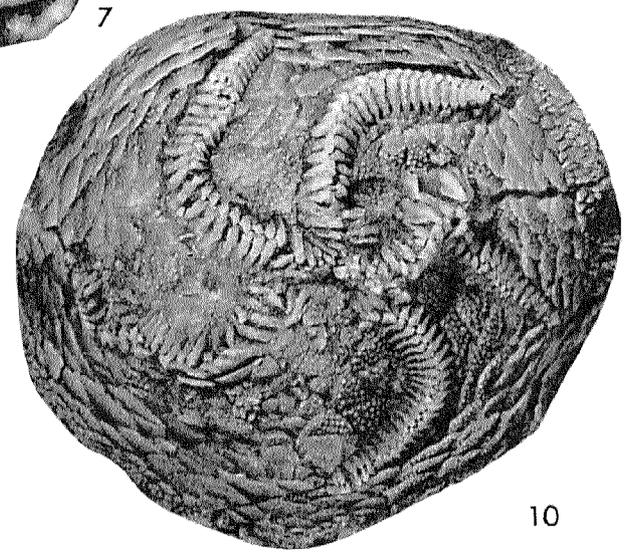
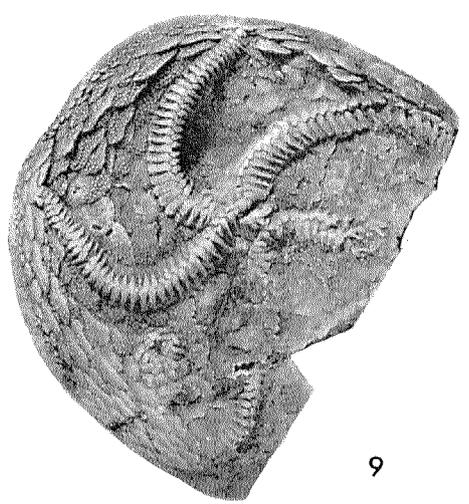
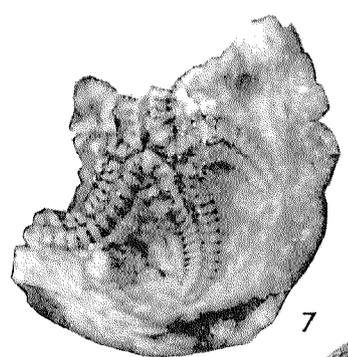
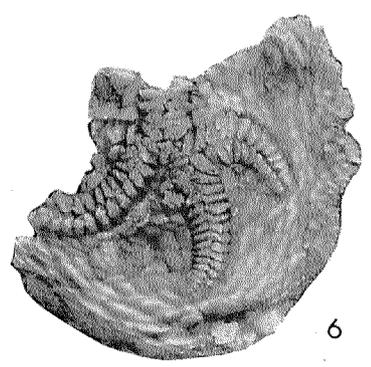
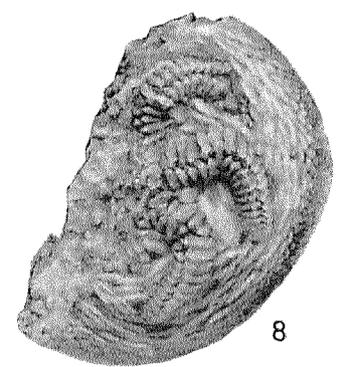
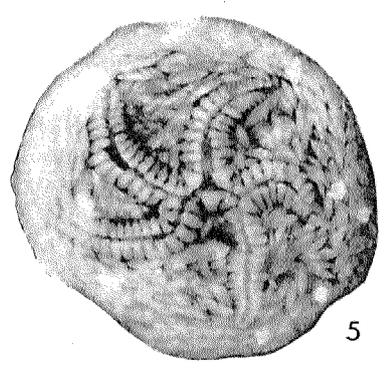
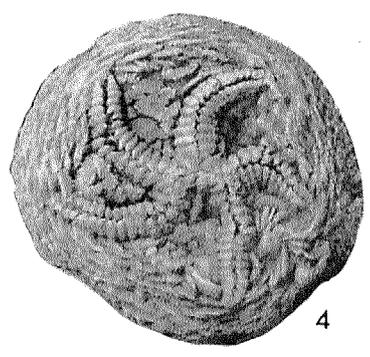
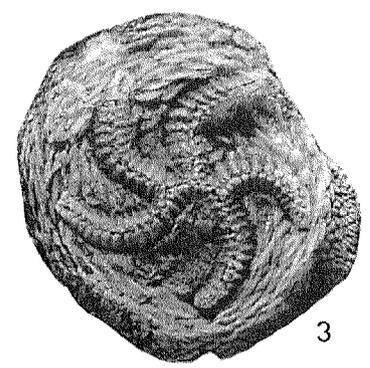
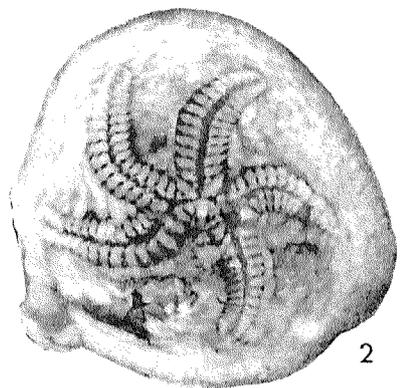
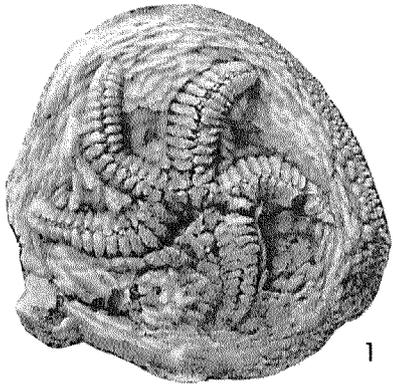


PLATE 5

Foerstediscus splendens Bassler, 1936

- 1-6. USNM S-4047, holotype.
 1. Oral surface, $\times 3$, whitened.
 2. Oral surface, $\times 3$, in xylene (text fig. 6B).
 3. Oral region, $\times 9$, whitened.
 4. Oral region, $\times 9$, in xylene (text fig. 6A).
 5. Segment of peripheral rim adjacent to tip of ambulacrum I, $\times 8$, whitened.
 6. Coverplate passageways and remnants of lateral depression series in proximal parts of ambulacra III and IV, $\times 8$, whitened.

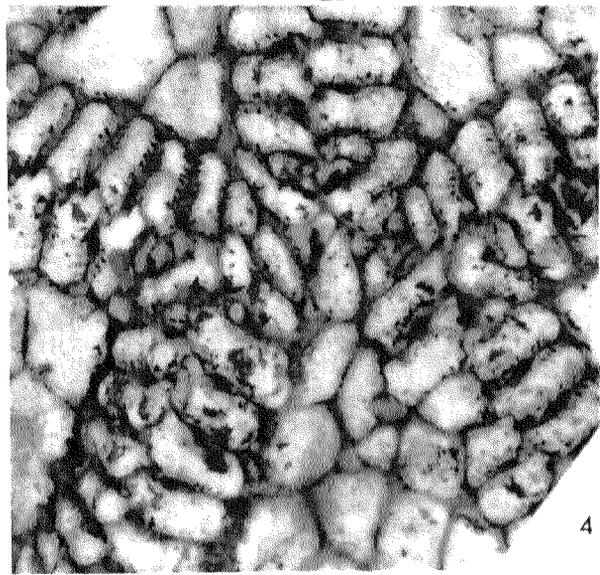
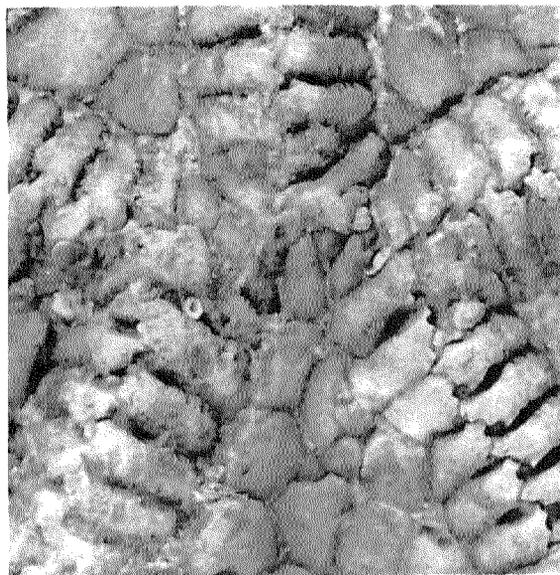
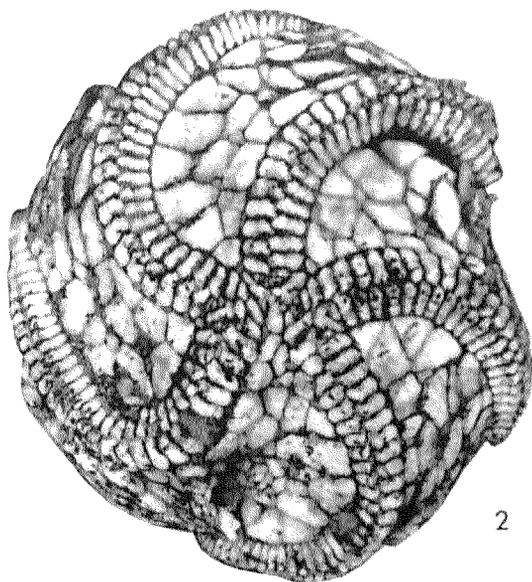
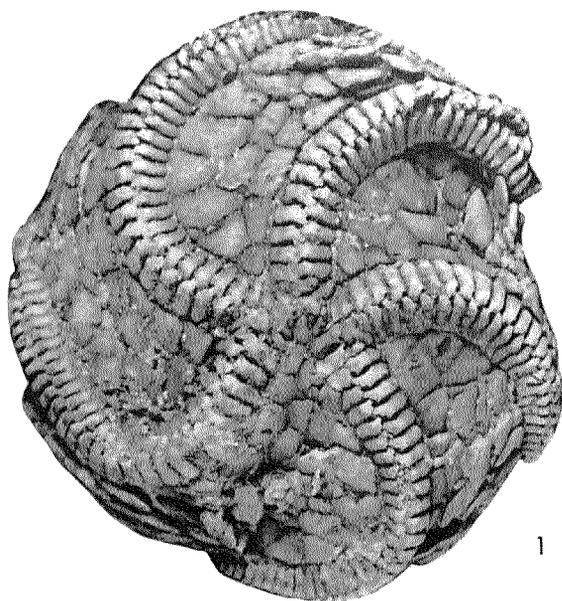


PLATE 6

Foerstediscus solitarius Bell, *sp. nov.*

- 1-5. USNM 140853, holotype.
 1. Oral surface, $\times 8$, whitened (text fig. 7A).
 2. Oral surface, $\times 8$, in xylene.
 3. Segment of peripheral rim distal to tip of ambulacrum III, $\times 20$, whitened.
 4. Oral region, $\times 15$, in xylene (text fig. 7B).
 5. Oral region, $\times 15$, whitened.