Lebetodiscus "*loriformis*," which is not borne out by the type specimen. This mistake is evidently the origin of Regnéll's (1966) erroneous statement that tessellate interambulacral plates occur in the genus *Lebetodiscus.*

Discussion

Lebetodiscus dicksoni is represented by only 13 known individuals, of which 10 were available for the present study. Fortunately, several are well preserved and allow nearly complete determination of external plate arrangement and surficial features. No individuals exposing the inner side of the oral surface are known, but several specimens are partially disrupted and reveal features normally hidden from view. Moreover, saw cuts in two specimens (GSC 1407-B, ROM 161-t-a) expose cross section views of the ambulacral structure, and the loose ambulacral fragment of GSC 1412 exposes both inner and outer surfaces.

A few major thecal features of *Lebetodiscus dicksoni* remain inadequately known. The most obvious of these are the oral frame and the stone canal passageway. The peripheral rim is poorly preserved in most specimens, which is rather unusual, as the rim is normally one of the best preserved features. The unusually high angle at which the rim intersects the substrate in several of the specimens may account for this occurrence. A nearly vertical rim would be subject to disruption and loss of plates during collapse.

The coverplate passageways in *Lebetodiscus dicksoni* are the largest of any yet encountered within the Lebetodiscina. It seems likely from the proximity of the external foramina of the passageways to the lateral depression series of the coverplates that their function may be interrelated. The most rational correlation between them would be the water vascular system. Apparently in this suborder the radial water canals extended beneath the ambulacra, along the lower side of the ambulacral floorplates. Each large primary radial canal would seem to have branched laterally along its length, sending alternate branch canals to the inner foramen of each passageway. Thus one branch canal would have entered each of the passageways through the inner foramen, extended upward through the passageway to the exterior of the theca, and made its exit through the external foramen.

The course of the branch canals upon reaching the external foramen is far from clear. The rows of lateral depressions are apparently related to their emergence. The most obvious explanation envisions the large branch radial canal, after emerging from the external foramen, abruptly turning outward and downward to follow the trough along the suture line between adjacent coverplates. Possibly this external branch canal sent out a series of smaller lateral branches from both sides, one into each of the external lateral depressions along the coverplate margins. The subcircular shape of these basinlike depressions suggest that the small branches may have been distally bulbous. The external part of this supposed extension of the hydrovascular system would thus have been featherlike.

As discussed in the introductory section on respiration, these external extensions of the hydrovascular system are thought to be respiratory structures. As in all Lebetodiscina, these extensions would permit respiration whether the ambulacra were open or closed.

The passageways which lie between the oral area coverplates appear to descend into the central lumen of the oral frame, and therefore would be divorced from the radial canals. As suggested by the apparent closure of the external openings of some of these by the secondary oral plates, these oral passageways would appear to be nonfunctional, for they lack extensions from the hydrovascular system. The oral covering plates in all edrioasteroids appear to have originated as modified ambulacral coverplates, hence the oral area passageways may be relict structures.

Coverplate movement in *Lebetodiscus dicksoni* was inhibited by the thickness of the coverplates, by the interlocking large proximal intra-ambulacral extensions, and by their basal overlap onto the underlying floorplates. The edge of the lower part of each coverplate adjacent to the ambulacral tunnel appears to have rested in a small depression on the sloping lateral margin of the floorplate. Thus the coverplate bases must have rotated within these depressions as the perradial ends of the nearly vertical coverplates moved laterally outward, away from the perradial line. The small ridges along the lower edges of the floorplate depressions would inhibit all but slight rotation. Moreover, the intrathecal part of the coverplate would abut the lateral edge of the floorplate after only moderate movement. Thus it appears that the coverplates, when open, formed only a small perradial gap.

The interlocking intra-ambulacral extensions of the coverplates necessitate very little if any differential movement between adjacent plates, and the coverplates appear to have been sutured together by tissue as in all Lebetodiscina. Thus the hydrovascular extensions which passed up through the coverplate passageways would not have been "pinched" during coverplate movement. The perradial ends of the nearly vertical coverplates apparently swung laterally outward along with adjacent coverplates, moving almost simultaneously. Opening must have begun at the distal tip of the ambulacrum, as described for *Carneyella pilea*, sweeping in a broad undulation toward the oral area.

The small ridges developed on the inner, perradial ends of the coverplates may have aided in food gathering. The extremely limited range of coverplate movement suggests that even when the coverplates were fully open, the ridges would remain close to those of the opposing, alternate coverplates, and the ridge tips probably were still slightly interdigitating. Thus the ridges might have functioned as a straining device for entering particles. Alternately, the ridges may have served as current directors. It is not impossible that the ridges acted as dividers for ciliary tracts that ran down the inner sides of the coverplates to the food groove at their base. Such tracts may have directed food particles down to the central food groove. With the ridges as dividers, a quite complex system of currents may have been developed.

It is interesting that perradial ridges also occur on the inner surface of oral plates as well as on the ambulacral coverplates. These produce serrate oral midlines in etched specimens. Apparently there are more than three ridges on each large oral plate. If so, these ridges may indicate that the primary oral plates are compound and were formed by the fusion of two or more individual ambulacral coverplates. Plate compounding in edrioasteroids is otherwise known only in the formation of the oral frame elements of the Edrioasterida.

A rather perplexing feature found in this species is the row of depressions along the distal margins of many of the interambulacral and some of the marginal plates of the theca (text fig. 3A, B, 4A-C; pl. 1, fig. 1, 10, 11; pl. 2, fig. 3, 6). Although observed thus far only in small areas, the depressions apparently occur on all of the interambulacral plates and perhaps on at least the larger plates of the peripheral rim. The depressions, which do not extend through the plates, form either a single or a double arcuate row across the distal edge of the plate, along the zone overlapped by the adjacent distal plate. Thus in nondisrupted individuals the depressions are either hidden, or, at best, only partly exposed, and falsely appear to be passageways into the theca along the suture line (*i.e.*, " sutural pores " of authors). Each such depression is a subcircular to elongate oval pit in the upper surface of the plate and thus is not a pore or passageway. These depressions might be muscle apodemes related to the expansion and contraction of the imbricate plates of the theca. However, the lower surface of the overriding parts of the imbricating plates do not appear to have any complementary structures (muscle seats) above or near the depressions.

RANGE AND OCCURRENCE: Trenton Limestones, Middle Ordovician, Ottawa region, Ontario (including Peterborough, Ontario), and Mercer County, Kentucky. [For those specimens from the Ottawa region with accurate data, the stratigraphic occurrence of all known specimens is " Cobourg beds " (= the " Cystid beds, about 180 feet below the top of the Trenton "). The Kentucky specimen is listed as Lower Trenton.]

Genus *Foerstediscus* Bassler, 1935

1935 *Foerstediscus* Bassler, R. S., Smithsonian Misc. Coll. 93 (8) : 6, pl. 1, fig. 12.

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1966 *Foerstediscus* Bassler, Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: 165, text fig. 115-1, 120-2b, 125-6, 126-5.

TYPE SPECIES: *Foerstediscus grandis* Bassler, 1935.

Diagnosis

Lebetodiscidae with: highly convex domal theca; oral area with several secondary orals; hydropore structure formed by first three coverplates of ambulacrum V and one or more modified interambulacral plates; ambulacra curved, I-V solar; coverplate passageways large, external foramina elliptical; coverplate lateral depression series present.

Description

The oral surface of the theca is highly convex, the marginal peripheral rim commonly almost vertical. Only a few specimens preserve the rim flared out against the substrate.

The oral area is formed by three primary plates, two anterior and one posterior, two pairs of lateral shared coverplates and several secondary orals (text fig. 5A, pl. 3, fig. 5). The inner part of the oral area has not been observed, but as in other Lebetodiscidae, probably includes a large oral frame.

The hydropore structure is similar to that found in *Lebetodiscus dicksoni* (text fig. 5A,D, pl. 3, fig. 115, pl. 4, fig. 1–8). It is formed by the proximal, posterior three would remain close to those of the opposing, alternate coverplates, and the ridge tips probably were still slightly interdigitating. Thus the ridges might have functioned as a straining device for entering particles. Alternately, the ridges may have served as current directors. It is not impossible that the ridges acted as dividers for ciliary tracts that ran down the inner sides of the coverplates to the food groove at their base. Such tracts may have directed food particles down to the central food groove. With the ridges as dividers, a quite complex system of currents may have been developed.

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TYPE SPECIES: *Foerstediscus grandis* Bassler, 1935.

Diagnosis

Lebetodiscidae with: highly convex domal theca; oral area with several secondary orals; hydropore structure formed by first three coverplates of ambulacrum V and one or more modified interambulacral plates; ambulacra curved, I-V solar; coverplate passageways large, external foramina elliptical; coverplate lateral depression series present.

Description

The oral surface of the theca is highly convex, the marginal peripheral rim commonly almost vertical. Only a few specimens preserve the rim flared out against the substrate.

The oral area is formed by three primary plates, two anterior and one posterior, two pairs of lateral shared coverplates and several secondary orals (text fig. 5A, pl. 3, fig. 5). The inner part of the oral area has not been observed, but as in other Lebetodiscidae, probably includes a large oral frame.

The hydropore structure is similar to that found in *Lebetodiscus dicksoni* (text fig. 5A,D, pl. 3, fig. 115, pl. 4, fig. 1–8). It is formed by the proximal, posterior three coverplates of ambulacrum V and one or more modified interambulacral plates. The opening is bounded primarily by two plates. Most of the anterior side is formed by the adradial end of the proximal posterior coverplate of ambulacrum V. The posterior side is bounded mainly by the anterior edge of the largest and most posterior interambulacral plate. One or more additional interambulacrals may also be included in the structure. The second proximal ambulacral coverplate, which is occasionally also in contact with the opening, and the third are always reduced in length (adradial-perradial), and both abut the right end of the large posterior interambulacral hydropore plate which intrudes into the edge of the ambulacrum.

The five ambulacra all curve in a solar direction. The proximal parts are straight for a short distance before the gradual curvature is initiated. The tips of the ambulacra always remain widely separated from the nearest part of the adjacent ambulacrum. The ambulacra form high ridges on the theca, owing to the thickness of the coverplates.

The coverplate passageways are large. The external foramina are somewhat more elongate normal to the ambulacral axis than in *Lebetodiscus,* and thus are less obvious from external view. Remnants of the lateral depression series of the coverplates found in *Foerstediscus* suggest structures similar to those of *Lebetodiscus,* but unfortunately, all known specimens are deeply etched, which obscures the details of these depressions.

The interambulacrals are moderately large, squamose, imbricating plates. The interambulacrals of *Foerstediscus* appear to lack the marginal depressions of *Lebetodiscus.*

The anal periproct lies in the posterior interambulacrum. Its position is specifically variable.

The peripheral rim is formed by squamose plates. During collapse these are depressed equally with the interambulacrals and this obscures the boundary between the rim and the interambulacra.

Both smooth and pustulose species of *Foerstediscus* occur.

Discussion

Bassler (1935) used the direction of ambulacral curvature in *Foerstediscus* as the primary character separating it from *Lebetodiscus.* He also mentioned the degree of curvature and the length and width of the ambulacra, although all three of these features are related to the size and age of the specimens. Bassler also thought that the interambulacrals were polygonal and nonimbricate. In 1936, Bassler noted as "essential" generic features the direction of ambulacral curvature and the "mosaic" (tessellate) arrangement of the interambulacrals. However, he included in the genus one species (*F. parvus,* here placed in synonymy with *F. grandis*) for which he described squamose, imbricate interambulacrals. All three species included in *Foerstediscus* in this work have squamose, imbricate interambulacrals.

The general aspect of *Foerstediscus* is quite unlike *Lebetodiscus* because of the opposing direction of ambulacral curvature. Otherwise they are remarkably similar. The only other major distinction between them is the presence of the depressions on the interambulacral and rim plates of *Lebetodiscus,* which appear to be unique to that genus.

In the new species *F. solitarius,* the hydropore structure appears to involve only a single large interambulacral plate rather than two or three, as in the other two species of this genus and in *Lebetodiscus.* Unfortunately, the species is known from a single collapsed specimen. Therefore, this apparently unique hydropore structure could include unseen elements.

The only known report of a specimen assigned to this genus that is not discussed below is by Branson (1941), who reported a *Foerstediscus sp.* from the Richmondian, Upper Ordovician of McHenry County, Illinois. Unfortunately, the specimen has not been located and the brief description, without illustration, does not allow speculation as to its true nature.

RANGE AND OCCURRENCE: Trenton Group, Middle Ordovician to lower Keyser Formation, Upper Silurian, of Minnesota, Kentucky, Pennsylvania, and Ontario.

Foerstediscus grandis Bassler, 1935

Text fig. 5; plate 3, 4

1935 *Foerstediscus grandis* Bassler, R. S., Smithsonian Misc. Coll. 93 (8) : 6, pl. 1, fig. 12.

1936 *Foerstediscus grandis* Bassler, R. S., Smithsonian Misc. Coll. 95 (6) : 9-10; *Foerstediscus parvus* Bassler, *ibid.*: 10, pl. 2, fig. 6, 7.

1938 *Foerstediscus grandis* Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 99.

1943 *Foerstediscus grandis* Bassler, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 202; *Foerstediscus parvus* Bassler, *idem, ibid.*: 202.

1966 *Foerstediscus grandis* Bassler, Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: 165.

Diagnosis

A *Foerstediscus* with: several secondary oral plates; hydropore structure formed primarily by four plates; anus near center of interambulacrum 5; thecal plates covered with large nodes.

Description

The domal theca is highly convex upward, although somewhat less so than in *Lebetodiscus dicksoni.* Thirteen specimens are known, varying from young adults 5 to 7 mm in diameter to an individual 32.5 mm. Average adult diameter appears to be in the range of 20 to 25 mm.

The oral region includes several secondary orals, but these are not clearly defined in any of the specimens, all being severely etched. These plates appear to be best preserved in specimen ROM 543t-a. Text fig. 5B illustrates the maximum number of secondary orals that may be present in that specimen. Text fig. 5A shows an enlargement of the oral area on which dashed lines represent all problematic lineations; these may be either suture lines or fractures; solid lines mark definite plates and represent the minimum number of secondary orals that may occur in that individual. The following description of secondary orals is thus tentative.

The secondary orals are of three groupings — two lateral and one anterior. The lateral groups lies between the primary orals and the shared coverplates, and include an anterior and a posterior section separated by the transverse oral midline. Both anterior and posterior parts include a central secondary oral, approximately one-third the size of the adjacent shared coverplates, in external view. One or more smaller secondary oral plates flank the large central secondary along the transverse oral midline. The posterior sections of both lateral groupings include two small secondaries, one flanking each side of the large central secondary oral, and thus form three-plate groupings. In the anterior sector of the right lateral grouping only one small secondary plate is present; this is on the proximal side of the larger secondary oral. The anterior section of the left lateral grouping has a small secondary on both sides of the larger secondary. Thus only the anterior section of the right lateral group is unique, having only one large and one small secondary oral.

The anterior grouping of secondary orals lies along the anterior oral midline. It includes a single large secondary oral on the right side of the midline and is flanked distally by a small secondary oral. These plates are opposed by one or two small secondary orals on the left side of the midline.

Assuming that all small secondary orals described above are plates, not fragments of larger elements, a total of 15 secondary plates may be present in the oral region, *i.e.*, four large laterals, one large anterior, and 10 small ones. The most questionable of these plates are: the small one in the anterior part of the left lateral grouping, distal to the larger secondary oral of that group, and the proximal small plate on the left side of the anterior group. Both of these may represent pieces of larger plates.

Most of the smaller specimens of *F. grandis* appear to include all five large secondary orals found in the larger adult (ROM 543t-a), but only a few of the smaller secondaries. This may be due to preservation, for all the small specimens are etched, or possibly the smaller secondaries were added late in ontogeny.

The hydropore structure is elevated above the plates of interambulacrum 5 and juts out from the posterior side of ambulacrum V as a low, rounded mound approximately half as high as the ambulacrum. Prior to thecal collapse it was probably almost level with the interambulacrals. The structure includes two interambulacrals and three ambulacral coverplates. The interambulacrals form the posterior side of the structure and both are elongate parallel to ambulacrum V. The anterior side of the distal interambulacral plate forms the posterior edge of the hydropore, whereas the anterior interambulacral forms only the proximal tip of the opening. The anterior edge of the opening is formed by the enlarged adradial edge of the proximal coverplate of ambulacrum V. The second coverplate, greatly reduced in adradial-perradial length, forms only the distal tip of the opening. The third ambulacral coverplate is also reduced in length, and as does the second, abuts the edge of the large posterior interambulacral which intrudes into the side of ambulacrum V. This third coverplate is entirely separated from the hydropore, and except for being shortened, looks much like a normal coverplate.

The hydropore structure of *Foerstediscus grandis* appears to be much like that found in *Lebetodiscus dicksoni.* However, specimens of both are scarce, and in most of these the hydropore structures are disrupted. Thus the similarity may be more apparent than real.

The ambulacral coverplates and coverplate passageways of *Foerstediscus grandis* appear to be nearly identical to those of *Lebetodiscus dicksoni.* However, in *F. grandis* at least four small surficial plates not found in *L. dicksoni* flank the two lateral bifurcation plates, one on either side of each element along the perradial line (text fig. 5A-C). These small plates extend only a short distance below the thecal surface and are wedged between the upper edges of the bifurcation plates and adjacent proximal coverplates. They cover the external foramina of the passageways which flank each side of the two bifurcation plates. In some specimens they appear to seal off the external foramen of the passageway, whereas in others they restrict the opening to one or two smaller openings along the lateral edges of the small plates. In specimen ROM 543t-a there appear to be two small plates flanking each side of the right bifurcation plate, although as shown in text fig. 5A these may be single plates fractured during preservation.

A few ambulacral floorplates of *Foerstediscus grandis* have been observed in partially disrupted specimens. They appear to be quite similar to those described for *Lebetodiscus dicksoni*.

The squamose, imbricate interambulacrals are of moderate size.

Large, rounded nodes, irregular in distribution, cover the exteriors of the interambulacrals and larger peripheral rim plates. These nodes produce a very distinctive appearance (pl. 3, fig. 3; pl. 4, fig. 9, 10). This prosopon appears to be limited to these plates; orals and ambulacral coverplates apparently are smooth.

Specimens

USNM S-3191. Holotype of *Foerstediscus grandis* Bassler (1935, p. 6, pl. 1, fig. 6). Curdsville Formation, Trenton Group, Mohawkian Series, Middle Ordovician. Near Troy, Woodford County, Kentucky. 23.5 mm axial by 24.4 mm transverse diameter.

Text fig. 5C, pl. 3, fig. 1, 2.

The holotype is partially disrupted and extensively etched, but fortunately, the taxonomically significant features of the specimen can be recognized. A large part of the anterior edge of the theca is missing, including peripheral rim plates, the distal parts of ambulacra III and IV, and interambulacra 2, 3, and 4. Two floorplates are exposed at the broken end of ambulacrum IV. The extreme surficial etching of this specimen has dissolved away most of the outer surface of the theca. The coverplate passageways are seen only along the posterior proximal part of ambulacrum II and the right proximal part of ambulacrum III. In these two areas the upper parts of the passageways have been etched away, which exposes a subsurficial view of their lower parts. Only remnants of the lateral basin series are preserved. The nodose prosopon is preserved only in the proximal part of interambulacra 3 and 4.

One additional complicating factor in the description of the holotype is the presence of numerous small bits of beekite, which obscure the underlying plates. It has proved impossible to remove these without cleaving the underlying calcite plates. Beekite covers several parts of the oral region and hydropore area.

ROM 543t-a. "Trenton Limestones," Trenton Group, Mohawkian Series, Middle Ordovician. Kirkfield, Ontario. Collected by J. Townsend. 20 mm axial by 20.5 mm transverse diameter.

Text. fig. 5A, B, pl. 3, fig. 3-5.

This individual, labeled "*Edrioaster bigsbyi*" in the collection, is the best preserved adult representative of *Foerstediscus grandis* available. Partial plate disruption in a small part of the left posterior sector of the theca exposes a unique lateral view of several of the ambulacral coverplates and their associated passageway structures. Surficial etching apparently concentrated on the ambulacral coverplates and has left only remnants of the lateral depression series. The characteristic nodose prosopon is well preserved. This specimen provides the only moderately complete view of the oral region and hydropore structure.

UCMP 40433, 40434, 40435, 40436. Four specimens of *F. grandis*. "Trenton Limestones," Trenton Group, Mohawkian Series, Middle Ordovician. Quarry at Kirkfield, Victoria County, Ontario (probably from near the floor of the quarry). Kopf Collection.

UCMP 40433. 33 mm axial by 28.7 mm transverse diameter.

Pl. 4, fig. 9.

The completely collapsed theca of this specimen has been extensively etched and the right third of the specimen is missing. The peripheral rim is well preserved in two sectors. Several lateral views of the ambulacral coverplates and their passageway structures are exposed in the disrupted distal part of ambulacrum III. The tips of the ambulacra remain widely separated from the nearest part of the adjacent ambulacra despite the large size of the individual. Accessory plates are seen adjacent to the bifurcation plate. This is the largest known representative of the species.

Text figure 5. *Foerstediscus grandis* Bassler, 1935

A-B. ROM 543t-a.

- A. Oral region (x 10), pl. 3, fig. 5. Ambulacral coverplate intrathecal extensions are stippled; intra-ambulacral extensions are separated from the main body of the coverplates by dashed lines. AO, anterior primary oral plate; CP, ambulacral coverplate; HCP, hydropore ambulacral coverplate; HI, hydropore interambulacral plate; LBP, left lateral bifurcation plate; o', secondary oral plate; PO, posterior primary oral plate; RBP, right lateral bifurcation plate; SC, lateral shared coverplate.
- B. Oral surface, (x 4), pl. 3, fig. 4. Ambulacral floorplates with large dots; lateral view of two disrupted ambulacral coverplates with stippled pattern, coverplate passageways blackened.

C. Holotype, USNM S-3191, (x 4), pl. 3, fig. 2.

D. USNM S-3889-A, (x 9), pl. 4, fig. 2.

A few ambulacral floorplates of *Foerstediscus grandis* have been observed in partially disrupted specimens. They appear to be quite similar to those described for *Lebetodiscus dicksoni.*

The squamose, imbricate interambulacrals are of moderate size.

Large, rounded nodes, irregular in distribution, cover the exteriors of the interambulacrals and larger peripheral rim plates. These nodes produce a very distinctive appearance (pl. 3, fig. 3; pl. 4, fig. 9, 10). This prosopon appears to be limited to these plates; orals and ambulacral coverplates apparently are smooth.

Specimens

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The holotype is partially disrupted and extensively etched, but fortunately, the taxonomically significant features of the specimen can be recognized. A large part of the anterior edge of the theca is missing, including peripheral rim plates, the distal parts of ambulacra III and IV, and interambulacra 2, 3, and 4. Two floorplates are exposed at the broken end of ambulacrum IV. The extreme surficial etching of this specimen has dissolved away most of the outer surface of the theca. The coverplate passageways are seen only along the posterior proximal part of ambulacrum II and the right proximal part of ambulacrum III. In these two areas the upper parts of the passageways have been etched away, which exposes a subsurficial view of their lower parts. Only remnants of the lateral basin series are preserved. The nodose prosopon is preserved only in the proximal part of interambulacra 3 and 4.

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UCMP 40433. 33 mm axial by 28.7 mm transverse diameter.

Pl. 4, fig. 9.

The completely collapsed theca of this specimen has been extensively etched and the right third of the specimen is missing. The peripheral rim is well preserved in two sectors. Several lateral views of the ambulacral coverplates and their passageway structures are exposed in the disrupted distal part of ambulacrum III. The tips of the ambulacra remain widely separated from the nearest part of the adjacent ambulacra despite the large size of the individual. Accessory plates are seen adjacent to the bifurcation plate. This is the largest known representative of the species.

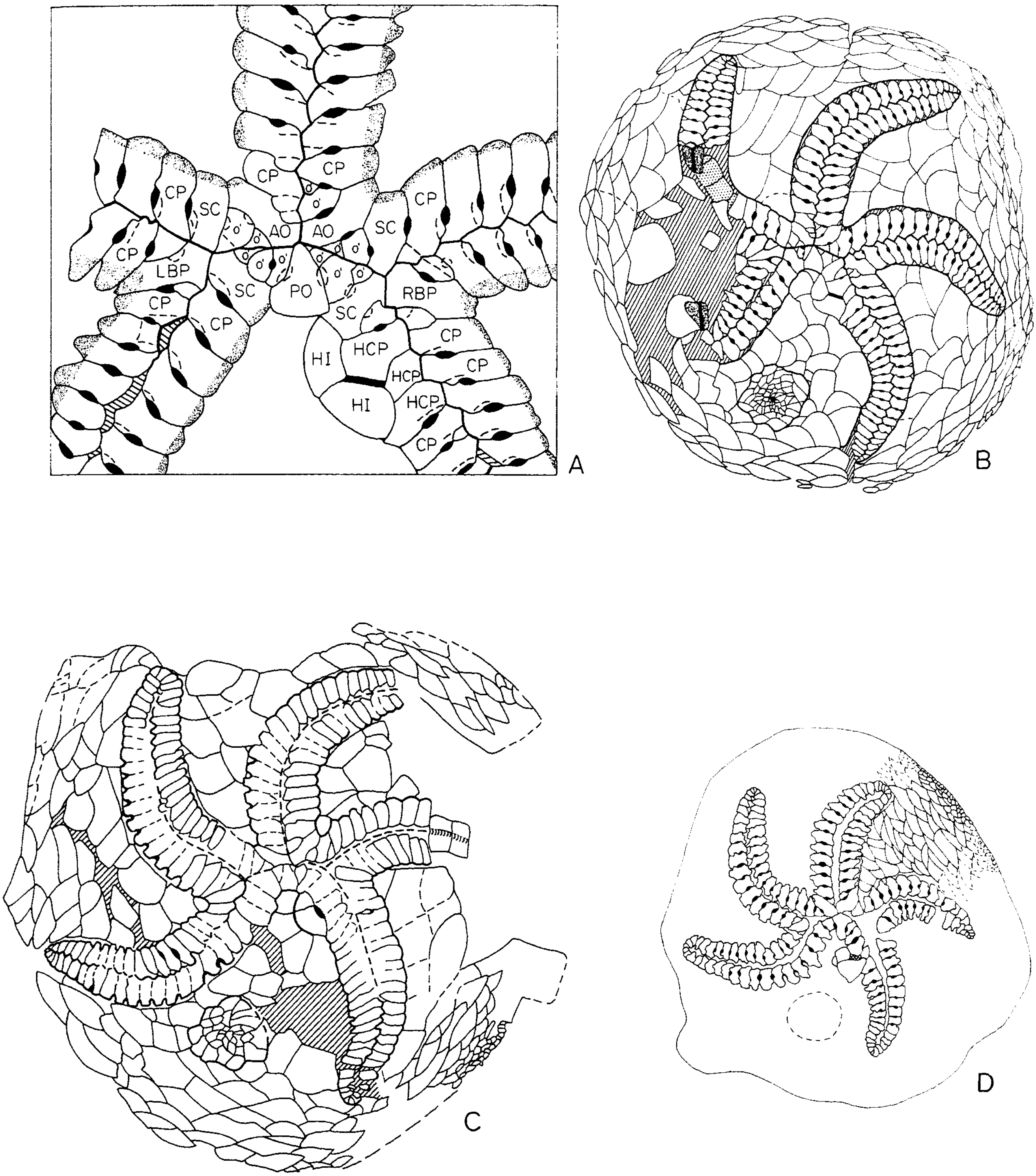
Text figure 5. *Foerstediscus grandis* Bassler, 1935

A-B. ROM 543t-a.

- A. Oral region (x 10), pl. 3, fig. 5. Ambulacral coverplate intrathecal extensions are stippled; intra-ambulacral extensions are separated from the main body of the coverplates by dashed lines. AO, anterior primary oral plate; CP, ambulacral coverplate; HCP, hydropore ambulacral coverplate; HI, hydropore interambulacral plate; LBP, left lateral bifurcation plate; o', secondary oral plate; PO, posterior primary oral plate; RBP, right lateral bifurcation plate; SC, lateral shared coverplate.
- B. Oral surface, (x 4), pl. 3, fig. 4. Ambulacral floorplates with large dots; lateral view of two disrupted ambulacral coverplates with stippled pattern, coverplate passageways blackened.

C. Holotype, USNM S-3191, (x 4), pl. 3, fig. 2.

D. USNM S-3889-A, (x 9), pl. 4, fig. 2.


CP
SC
AO
O'
PO
LBP
RBP
HI
HCP
A
B
C
D

UCMP 40434. 24.6 mm axial by 26.7 mm transverse diameter.

Pl. 4, fig. 10.

This specimen is poorly preserved. It is both deeply etched and partially disrupted. However, the peripheral rim is nearly complete. Moreover, remnants of the lateral depression series and the nodose prosopon are preserved.

UCMP 40435, 40436. Two poorly preserved specimens that probably belong to this species.

The above four specimens rest directly on a firm carbonate substrate which is highly irregular, with large, rounded knobs separated by deep, interconnected channels. This surface is quite similar to the one described by Koch and Strimple (1968) [see *Hadrochthus commensalus*] and probably represents an intertidal or very shallow subtidal environment.

USNM S-3889 (A-F). Six specimens of *F. grandis* illustrated as the types of *Foerstediscus parvus* Bassler (1936, p. 10). "Hull, Trenton Limestones," Trenton Group, Mohawkian Series, Middle Ordovician, Kirkfield, Ontario.

Seven specimens in the United States National Museum bear the number 3889. Two of these were illustrated by Bassler (1936) as "cotypes" of *F. parvus*. Of the five other specimens stored with the two illustrated ones, one belongs to a different species.

USNM S-3889-A. "Cotype" of *F. parvus* Bassler (1936, p. 10, pl. 2, fig. 6). 7.4 mm axial by 7.3 mm transverse diameter.

Text fig. 5D, pl. 4, fig. 1, 2.

The specimen has collapsed, accentuating the interambulacral plate overlap. A small part of the left edge of the theca is missing, and the anal structure is partially disrupted. Extensive surficial etching has removed the exteriors of the ambulacral coverplates and has exposed the entire length of the passageways. Remnants of the nodose prosopon and coverplate lateral depression series are preserved in a few areas. Only the larger orals are clearly defined. The right anterior part of the peripheral rim is well preserved.

USNM S-3889-B. "Cotype" of *F. parvus* Bassler (1936, p. 10, pl. 2, fig. 7). 6.8 mm axial by 6.2 mm transverse diameter.

Pl. 4, fig. 3.

In this specimen thecal collapse accentuates interambulacral plate imbrication. The plate surfaces are so deeply etched that all external features have been destroyed.

USNM S-3889-C. Type series specimen of *F. parvus* Bassler (1936). 6.2 mm axial by 7 mm transverse diameter.

Pl. 4, fig. 4, 5.

This is the best preserved of the six *F. grandis* specimens numbered USNM 3889. The theca has collapsed, disrupting some interambulacrals, and surficial etching has removed some plate detail. However, secondary orals are seen on the left half of the oral region, and the hydropore plates can be recognized.

USNM S-3889-D. Type series specimen of *F. parvus* Bassler (1936). 7.1 mm greatest diameter by 4.5 mm.

Pl. 4, fig. 6, 7.

The theca has collapsed, has been etched, and is missing ambulacra II and III. Four secondary orals are preserved in the oral area.

USNM S-3889-E. Type series specimen of *F. parvus* Bassler (1936). 9 mm axial by 5.6 mm transverse diameter.

Pl. 4, fig. 8.

This is a fragmentary, severely disrupted and etched specimen.

USNM S-3889-F. Type series specimen of *F. parvus* Bassler (1936). Approximately 5.4 mm diameter (specimen in two pieces glued together).

The theca of this individual is poorly preserved, but four secondary orals are seen in the oral area.

YPM 28452 (old 2361). One of 10 edrioasteroids labeled "*Edrioaster.*" "Lower Trenton Limestones," Trenton Group, Mohawkian Series, Middle Ordovician. Curd's farm, Mercer County, Kentucky. Fischer Collection, donated to Yale by O. C. Marsh. 17 mm axial by 21 mm transverse diameter.

Pl. 3, fig. 6.

This specimen of *Foerstediscus grandis* is replaced by beekite, which destroys nearly all details of the plating. However, the thecal shape and morphologic structures are intact. The ambulacral coverplates are distinct, owing to the external convexity of each. Parts of both the left and right sides of the theca are missing, along with fragments from along a break through the center which includes most of the oral area. The theca is only partially collapsed, with most thecal elements only slightly disrupted. The most significant aspect of this *F. grandis* specimen is its occurrence: among the other nine specimens from this collection are eight specimens of *Edrioaster priscus* and one *Lebetodiscus dicksoni*. Thus all three species occur together, apparently in the same environment.

Discussion of previous investigation

Bassler's (1935) description of his *Foerstediscus grandis* primarily included generic features which he thought differentiated *Foerstediscus* from *Lebetodiscus*. Since he used only the holotype, all features mentioned, such as thecal diameter and the degree of interambulacral plate imbrication, apply only to that specimen.

In 1936 Bassler added two new species to *Foerstediscus*, of which *F. parvus* seems to be based on small individuals of *F. grandis*. Bassler (1936, p. 10) described *F. parvus* as differing " from the genotype in the small size of the theca, about 6 mm in diameter, the general delicacy of its parts, and the more imbricate nature of its interambulacral plates."

The types of Bassler's *F. parvus* are young adults of *F. grandis*, which was based on a large adult holotype. The smaller specimens have collapsed, accentuating the interambulacral plate imbrication. Extensive etching has altered the appearance of the thecal plates, particularly the ambulacral coverplates, but remnants of the passageways and lateral depression series are preserved. A few of the characteristic external nodes are also preserved on several interambulacral plates.

Discussion of description

Foerstediscus grandis is best represented by specimen ROM 543t-a, which preserves most of the taxonomically important thecal features including secondary oral plates, the lateral depression series, and the nodose prosopon. Unfortunately, the inner surface features of the theca which include the oral frame, inner sides of the ambulacral floorplates, and the ambulacral tunnel side of the ambulacral coverplates have not been observed.

The small plates which flank the perradial sides of both lateral bifurcation plates are of unknown significance. Quite surficial in extent, they end only a short distance below the ambulacral surface. They lie directly over the external foramina of the passageways which flank the two bifurcation plates, and therefore they may have been related to some specialized function of these individual passageways.

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

Foerstediscus splendens Bassler, 1936

Text fig. 6; plate 5

1936 *Foerstediscus splendens* Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 10, pl. 7, fig. 13.

1943 *Foerstediscus splendens* Bassler, Bassler, R. S. and Moodey. M. W., Geol. Soc. America, Spec. Pap. 45: 202.

1960 *Foerstediscus splendens* Bassler, Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 162-163, text fig. 8, pl. 7, fig. 1, 2.

1966 *Foerstediscus splendens* Bassler, Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: 165, text fig. 115-1, 120-2b, 125-6, 126-5.

Diagnosis

A *Foerstediscus* with: oral region including 12 secondary orals; hydropore formed by three ambulacral and four interambulacral elements; thecal plates smooth.

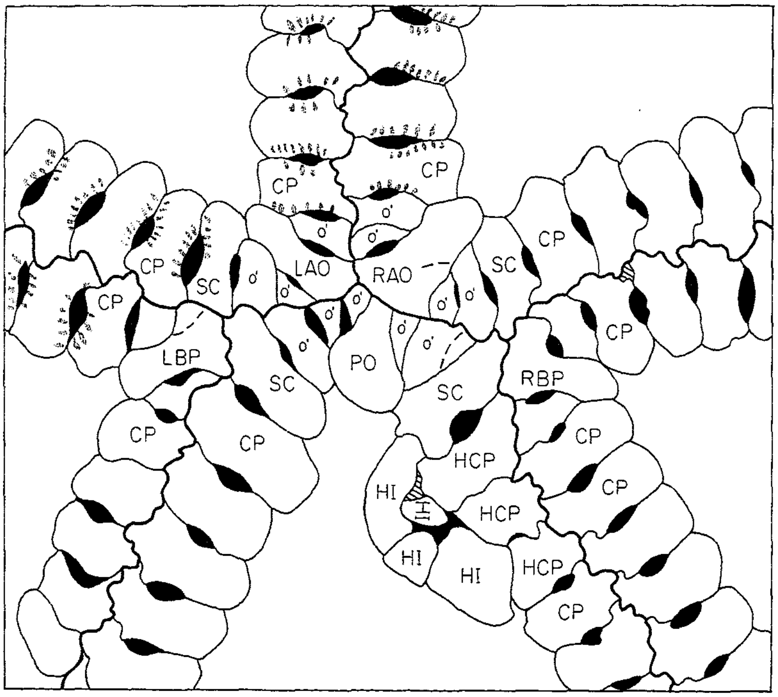
Description

F. splendens is represented only by the holotype. In this specimen, the domal theca is highly convex and the oral surface distally reflexed. Apparently the specimen is resting on a very small, hard object. Thus the peripheral rim apparently flexed beneath the upper oral surface as the individual " overgrew " the size of the resting area. This contorted the thecal shape. The maximum thecal diameter is 27.8 mm, but this figure does not include the reflexed rim and gives a deceptively small reading for comparison with other species.

The oral area includes 12 secondary oral plates in addition to the three primary orals and two pairs of lateral shared coverplates (text fig. 6). As in *F. grandis*, the secondary orals are in three groups, two lateral and one anterior. Two sizes of secondaries occur, the larger ones externally about one-third the size of the adjacent shared coverplates, the smaller secondaries at most half the size of the larger ones. The anterior halves of the two lateral groups, anterior to the transverse oral midline, are each formed by one large secondary and a smaller one on its proximal side. The posterior half of the left lateral grouping includes one large secondary flanked proximally by two smaller ones; the most proximal of these lies almost directly over the oral pole. The posterior half of the right lateral grouping includes one larger secondary oral and one smaller one proximal to it. (Possibly another small secondary flanks the distal margin of the larger secondary, although this supposed plate appears to be a broken fragment of the larger.)

The anterior grouping of secondary orals lies along the anterior oral midline and consists of one larger secondary oral plate on each side of the midline, and a single smaller secondary oral along the proximal side of the right, larger secondary oral.

The secondary oral plate arrangement in the single specimen of *F. splendens* is thus quite like that of *F. grandis*. The nearly central location in the oral area of the small proximal plate in the posterior half of the left lateral grouping appears to be due to slight lateral shifting of the orals during collapse, with the perradial tip of the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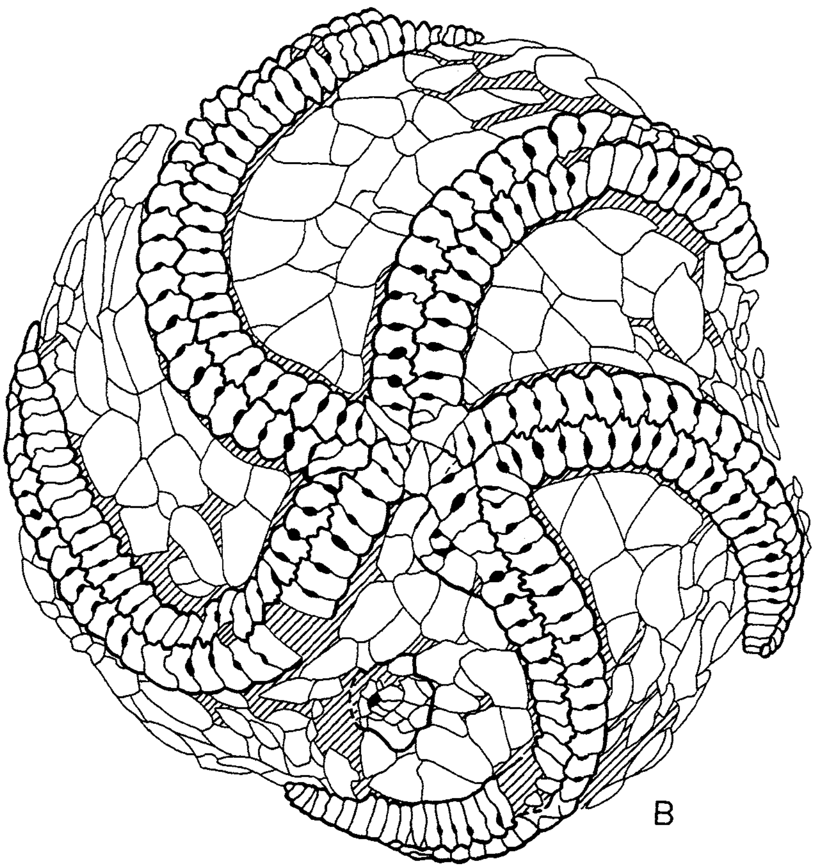


B

large primary posterior oral having moved somewhat to the right.

The hydropore structure forms a low, rounded hump which extends outward from the proximal posterior edge of ambulacrum V, distal to the oral region. Although elevated above the adjacent interambulacrals, the top of this mound is slightly less than half as high as the top of the adjacent ambulacrum. The structure includes four interambulacrals and the proximal posterior three coverplates of ambulacrum V (text fig. 6A, B, pl. 5, fig. 3, 4). The adradial ends of the proximal two coverplates appear to form the left, or anterior side of the hydropore. The coverplate passageway to be expected between these two coverplates appears to be absent or externally closed. The third coverplate is removed from the opening, but is adradially shortened and abuts the large, most posterior interambulacral plate of the structure which extends into the edge of the ambulacrum. Three of the interambulacral hydropore plates comprise the semicircular, posterior, interambulacral side of the structure; these encompass the small fourth interambulacral. This small plate appears to be rotated 90 degrees from its life position. It thus appears to be elongate transversely, whereas originally it was axially elongate. Apparently it lay between the adradial end of the most proximal coverplate and the opposing most proximal interambulacral of the hydropore structure. When the small, rotated interambulacral is returned to its supposed life position, the hydropore appears to have been bounded anteriorly by the adradial ends of the proximal two coverplates. The posterior side was formed by all four interambulacrals, although the anterior two bounded only the anterior tip of the opening, whereas the posterior two formed most of the opening's posterior margin. Plate margins surrounding the opening are thickened and form a prominent raised rim.

Kesling (1960) gave a different interpretation of the hydropore morphology of this specimen. The major difference lies in the interpretation of the nature of the small, supposedly displaced interambulacral. Kesling described it as being fused to the large proximal interambulacral plate to form a " buckle-shaped " element. Resolution of this difference of opinion requires new material to supplement the unique holotype.

The ambulacra of *F. splendens* are nearly identical to those of the type species; they are long, highly elevated, and evenly curved solarly. The distal tips remain widely separated from the adjacent ambulacra even though the holotype is a large adult. Distally the ambulacra extend under the upper side of the theca because of the distal contortion of the domal theca.

The structure of the ambulacra is typical of the genus. The thick coverplates and associated passageways are nearly vertical, the elliptical external foramina of the passageways are large. An exceptional view of one passageway is seen in the proximal part of ambulacrum V. The right posterior shared coverplate is slightly displaced and exposes nearly the entire length of the passageway which flanks the distal edge of that plate.

Remnants of the lateral depression series are found along the suture lines between many of the coverplates. However, the exterior central ridges of most of the coverplates have been planed off by erosion, which also destroyed the exterior parts of the lateral depression series. Approximately eight depressions lie along each side of a coverplate. These are variable in width and depth. Those on opposite sides of a lateral suture line may be opposite, alternate, or both.

As in *F. grandis*, four small, unpaired plates are included in the ambulacra of *F. splendens*, one flanking each side of the perradial ends of the two lateral bifurcation plates. These four plates are centered over the external foramina of the passageways which flank the bifurcation plates. Three of these cause the passageways to bifurcate and open through two small foramina, one on each side of the small plate. The fourth plate, between the left lateral bifurcation plate and the proximal posterior coverplate of ambulacrum II, appears to restrict the passageway opening to an elongate slit which flanks the distal edge of the small plate.

The ambulacral perradial lines are complexly undulatory. The bluntly angular perradial ends of the biserial coverplates form a major zigzag pattern. However, the etched coverplates expose the upper ends of the large, proximal intra-ambulacral extensions and also the ends of the small, vertical perradial ridges on the ambulacral tunnel sides of the coverplates. These impose multiple small serrations on the perradial line. Although seen only from the exterior sides of the etched coverplates, the perradial ridges appear to be identical to those of *Lebetodiscus dicksoni*, *i.e.*, three per coverplate — one large central ridge flanked by two smaller ones.

The ambulacral floorplates have not been observed in this species.

Text figure 6. *Foerstediscus splendens* Bassler, 1936

Holotype, USNM 4079

A. Oral region, (x 9), pl. 5, fig. 4. Lineations thought to be fractures are dashed. CP, ambulacral coverplate; HCP, hydropore ambulacral coverplate; HI, hydropore interambulacral 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; SC, lateral shared coverplate.

B. Oral surface, (x 4), pl. 5, fig. 2.

The interambulacral plates are large, squamose, and imbricate. The type specimen suggests that this species has somewhat larger interambulacrals than *F. grandis*. The posterior interambulacrum is partially disrupted, obscuring the details of the anal structure. However, it appears to be a typical periproct.

The peripheral rim, mostly hidden, appears to be like that of other Lebetodiscidae.

The interambulacral and rim plates are smooth. This lack of prosopon, perhaps more so than any other feature, sets the species apart from *F. grandis*.

Specimen

USNM S-4079. Holotype of *Foerstediscus splendens* Bassler (1936, p. 10, pl. 7, fig. 13). Top of the *Rhinidictya* bed, Decorah Formation, Mohawkian Series, Middle Ordovician. Ford Plant, St. Paul, Minnesota. 27.4 mm axial by 27.8 mm transverse diameter.

Text fig. 6A, B, pl. 5, fig. 1-6.

The theca preserves much of the original oral surface convexity. Plates are partially disrupted along the marginal zone where the upper oral surface plates are reflexed under the upper side of the theca. Interambulacrum 5, including the anal area, is partially disrupted. Etching and abrasion has affected the orals and ambulacral coverplates, but the interambulacrals appear well preserved.

Discussion

Bassler's (1936) original description of *Foerstediscus splendens* records only preservational features of the holotype and the suggestion that the ambulacra are longer, more curved, and contain more coverplates than those of *F. grandis*. These ambulacral characters are due to the difference in size of the holotypes of the two species, *F. splendens* being the larger, older adult.

Foerstediscus splendens appears to be closely related to *F. grandis*. The two species are separated mainly on the basis of the prosopon; *F. grandis* has nodose thecal plates, whereas *F. splendens*' plates are smooth. Details of the oral and hydropore regions may serve further to differentiate the two species, although these areas are only tentatively described, owing to the limited number of specimens and their somewhat unsatisfactory preservation.

One noteworthy feature of the holotype of *F. splendens* is the exceptionally clear preservation of stroma canals. Commonly the stroma canals of edrioasteroid plates are filled by secondary calcite. Differential etching of this secondary calcite and the original plate calcite commonly forms a minute pitting or "pustulation" on the plate surfaces. In this specimen many of the canals are filled with pyrite, apparently the result of a microreducing environment produced by the decaying tissue in the labyrinthine canals. Under magnification, when viewed in xylene, the pyrite fillings of many of the canals can be traced deep into the interior of the plates.

Foerstediscus solitarius Bell, *sp. nov.*

Text fig. 7; plate 6

Diagnosis

A *Foerstediscus* with: four or more secondary oral plates; hydropore structure formed by four plates; periproct near the oral area in proximal part of interambulacrum 5; thecal plates smooth.

Description

F. solitarius is known only from the holotype, a deeply etched specimen. The domal theca is small, 11.2 mm the greatest diameter (text fig. 7).

The oral area includes at least four small secondary orals (text fig. 7B, pl. 6, fig. 5). The single posterior primary oral appears to be displaced, shoved anteriorly between the central ends of the two anterior primary orals. Two moderately large secondary orals, one on either side of the anterior oral midline, perradially separate the anterior orals from the proximal pair of coverplates of ambulacrum III. A slightly smaller secondary lies between the perradial tips of the right anterior primary oral and the adjacent right anterior shared coverplate. A tiny secondary oral is inserted between the perradial end of the posterior primary oral and the left posterior lateral shared coverplate. Possibly two other secondary orals are present, one flanking each side of the perradial tip of the left anterior shared coverplate. These are thought to be broken fragments of the larger adjacent plates, delineated by dashed lines in text fig. 7B, but these lineations could be interpreted as sutures.

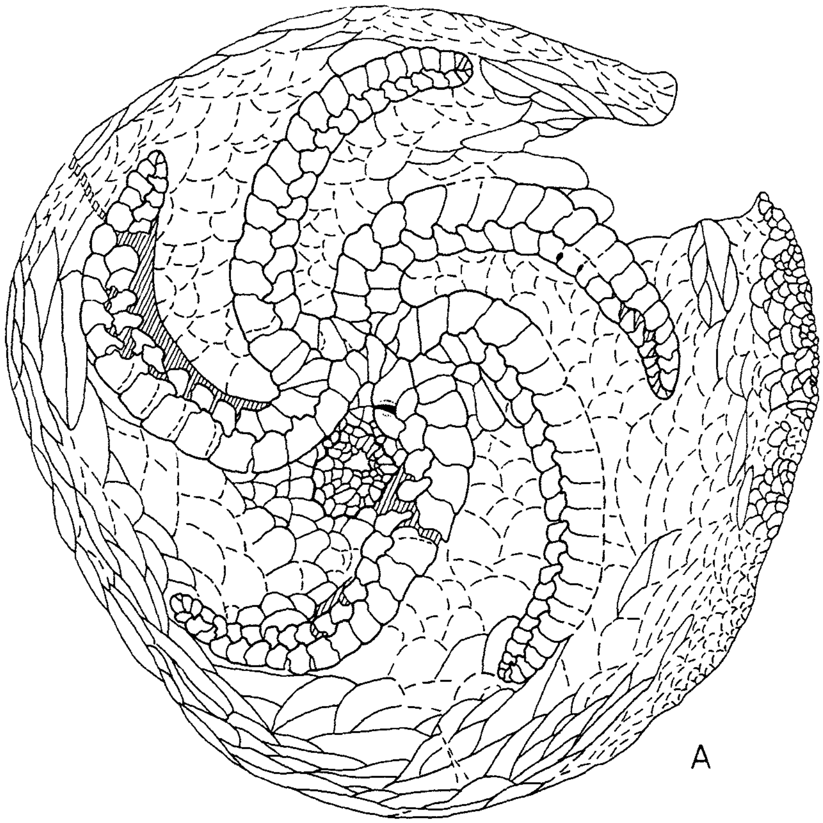
The hydropore structure lies along the proximal posterior edge of ambulacrum V, squeezed between the central oral rise and the anal structure (pl. 6, fig. 3, 5). The

Text figure 7. *Foerstediscus solitarius* Bell, *sp. nov.*

Holotype, USNM 140853.

A. Oral surface, (x 10), pl. 6, fig. 1.

B. Oral region, (x 20), pl. 6, fig. 5. CP, ambulacral coverplate; HCP, hydropore ambulacral coverplate; HI, hydropore interambulacral 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; SC, lateral shared coverplate.



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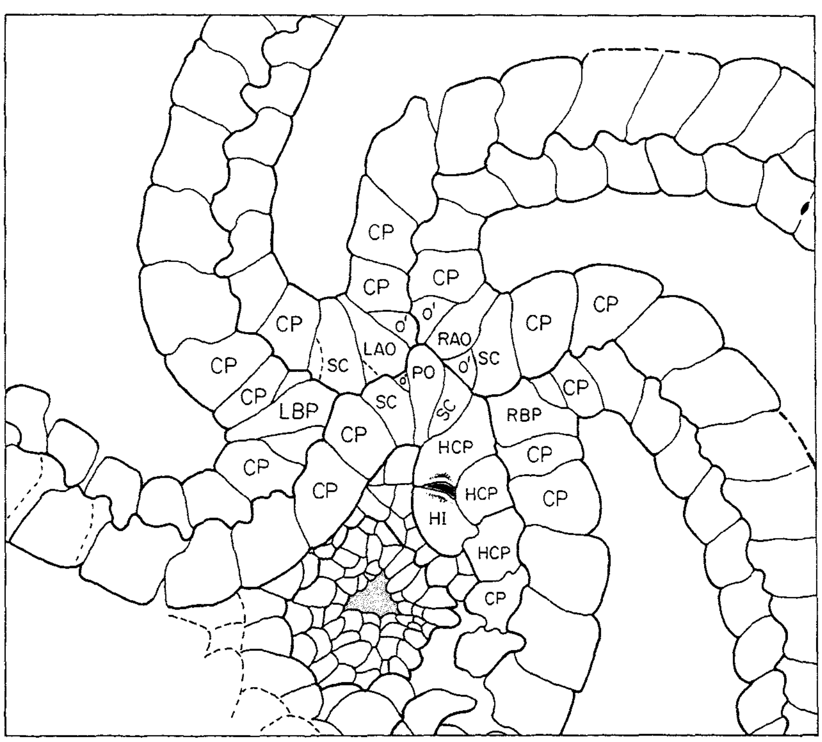


B

area is depressed in the holotype, which has partially disrupted the plates and makes interpretation tentative. It appears to be formed by four plates. A single large interambulacral forms the posterior interambulacral side of the structure. Its right anterior edge bounds the posterior side of the opening. The anterior side of the hydropore is formed primarily by the adradial end of the proximal posterior coverplate of ambulacrum V. The adradial end of this plate is enlarged and juts out into interambulacrum 5. The distal part of the distended area forms the anterior side of the opening. The second and third posterior coverplates of ambulacrum V are adradially shortened and abut the right edge of the interambulacral hydropore plate which intrudes into the edge of the ambulacrum in this area. The second coverplate forms the right end of the hydropore, but the third does not make contact with the opening.

The ambulacra appear to be similar to those of the other two species of *Foerstediscus.* However, the coverplates are extensively etched, which has obliterated the lateral depression series and most of the sutural passageways. Remnants of the latter are most clearly seen in ambulacra I and III. Removal of the perradial parts of the coverplates has exposed the upper ends of the etched proximal intraambulacral extensions. In contrast with other species of *Foerstediscus, F. solitarius* appears to have only three of the small surficial ambulacral plates which flank the perradial edges of the two lateral bifurcation plates. The posterior side of the right lateral bifurcation plate appears to be bounded only by the proximal ambulacral coverplate, without an intervening surficial perradial plate.

The squamose, imbricate interambulacrals may be somewhat smaller in proportion to thecal diameter than in other *Foerstediscus* species.

The periproct is unique, for it lies in the anterior part of interambulacrum 5. Only a few small interambulacrals separate it from the proximal parts of ambulacra I and V, and the distal edge of the oral region. The anals are elevated and form a high, subconical mound.

The peripheral rim is like that of other *Foerstediscus* species. It is well exposed only along the right margin of the theca and apparently includes six or seven irregular circlets.

The external plate surfaces appear to have been smooth.

Specimen

USNM 140853. Holotype of *Foerstediscus solitarius* Bell, *sp. nov.* Lower part of the Keyser Formation, Cayugan Series (Pridolian), Upper Silurian. Double quarry on the southeastern side of Route 96, near Hyndman, Pennsylvania (Locality 5 of Bowen, 1967, p. 65). P. W. Goodwin and E. J. Anderson Collectors. 11.0 mm axial by 11.2 mm transverse diameter.

Text fig. 7A, B, pl. 6, fig. 1-5.

The specimen has collapsed, apparently increasing the imbrication of the interambulacrals and causing slight shifting of orals, hydropore plates, and some ambulacral coverplates. The theca has been extensively etched, which has dissolved away the exteriors of the ambulacral coverplates. Large, rounded masses of secondary beekite cover parts of the interambulacra. A small section of the anterior thecal margin is missing, including rim plates and a few distal plates of interambulacrum 2.

Discussion

In contrast with the other species of *Foerstediscus,* the anal area of *F. solitarius* lies in the proximal part of interambulacrum 5, rather than near the center of that area. Moreover, only four secondary orals are thought to be present. This contrasts with the more numerous secondary orals of the other two species of the genus. Otherwise the morphology of this Upper Silurian species is remarkably similar to that of the Ordovician species. It would appear that the genus was a very conservative one, showing remarkably little modification over a long time span.

The specimen comes from a carbonate sequence described by Goodwin and Anderson (in press) as a very shallow, moderately low energy, near-shore marine environment.

ETYMOLOGY: The trivial name *solitarius* is Latin for alone, isolated (the collectors suggested " lonelius "), and refers to its isolation from the Ordovician members of the genus.

RANGE AND OCCURRENCE: Lower Keyser Formation, Upper Silurian of Pennsylvania.

Genus *Belochthus* Bell, *gen. nov.*

TYPE SPECIES: *Belochthus orthokolus* Bell, *sp. nov.*

Diagnosis

Lebetodiscidae with: domal theca; oral area with at least several large secondary oral plates; large primary oral plates externally sagittate; hydropore structure including at least two ambulacrals and one enlarged interambulacral plate; ambulacra straight; coverplate passageways oblique, elliptical external foramina narrow.

Description

Belochthus is monotypic, and therefore differentiation of generic and specific taxobases is uncertain. The features outlined in the generic diagnosis are inferred to be of generic rank from established taxobases of other Lebetodiscidae.

ETYMOLOGY: *Belochthus* is compounded from the Greek *belos* arrow, referring to the sagittate exterior of the primary orals, and *ochthos* mound, referring to the domal thecal shape.

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

Belochthus orthokolus Bell, *sp. nov.*

Text fig. 8; plate 8

Diagnosis

A *Belochthus* with: oral area with three large secondary oral plates; ambulacra moderately short, wide, and straight, distally separated from proximal margin of peripheral rim by numerous interambulacral plates; interambulacral areas large; periproct near center of posterior interambulacrum; thecal plates smooth.

Description

The domal theca of *B. orthokolus* appears to have been moderately convex in life, but has completely collapsed in all known specimens. The maximum known diameter is 15.5 mm.

The oral area, although partially disrupted in all known adults, appears to include three large secondary orals (text fig. 8E, pl. 7, fig. 3). One large secondary flanks each side of the single primary posterior oral. Unusually large for secondary orals, these plates extend from the transverse oral midline out to the posterior adradial suture line of the oral area. The third secondary is smaller, inserted between the perradial ends of the right anterior primary oral and right anterior shared coverplate. It is in contact only with the transverse oral midline.

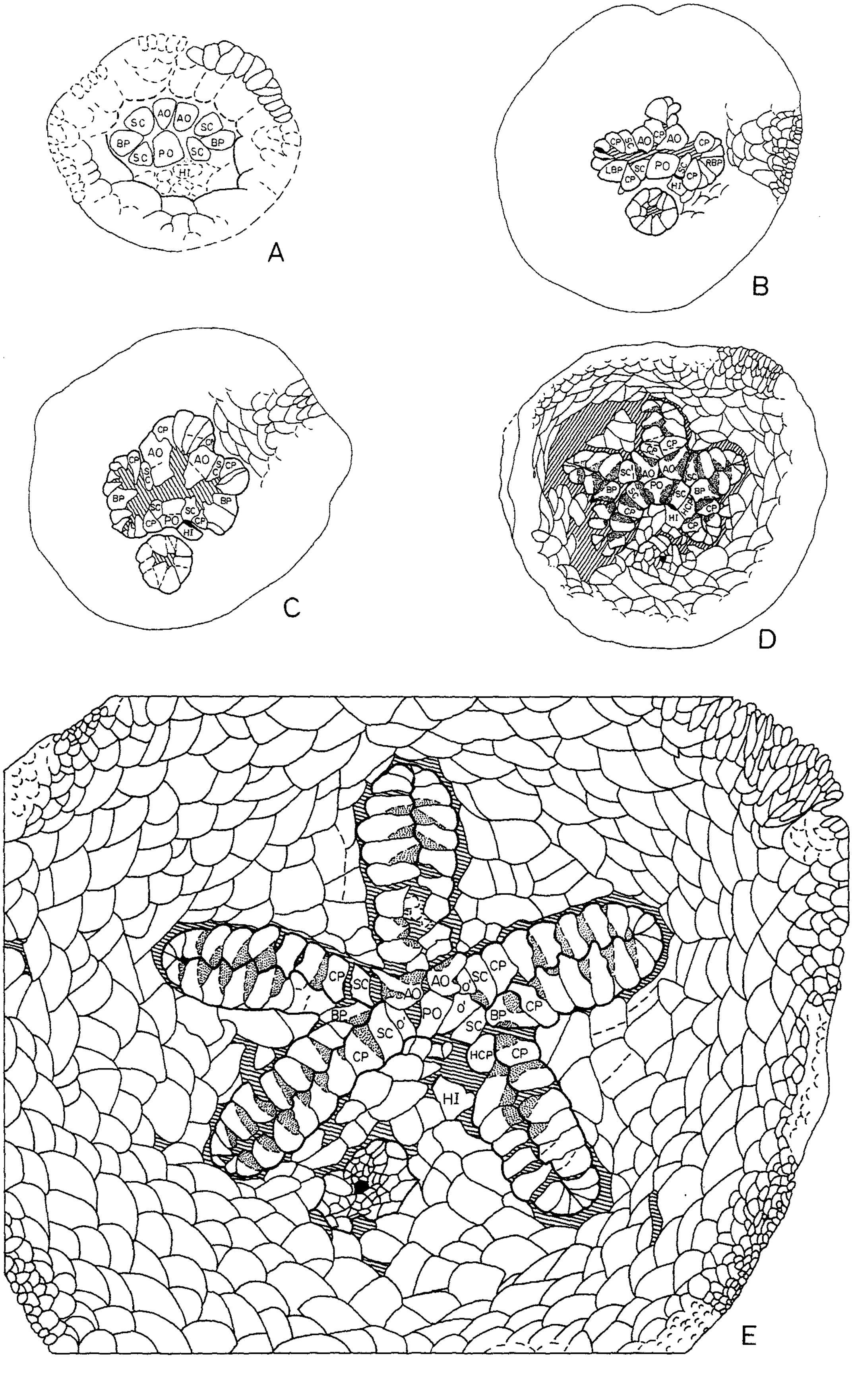
The pronouncedly sagittate external shape of the three primary orals in *B. orthokolus* is distinctive (pl. 7, fig. 1–3). The external foramen of the sutural passageway which flanks each side of each oral is large and elongate. The oral plate width is constricted adjacent to the foramina, and forms a long, central, posterior shaft. The wide perradial end of each primary forms the " head " of the " arrow."

The hydropore structure is partly disrupted in all adults but appears to include at least two ambulacrals and one large interambulacral plate. The anterior ambulacral side of the structure is formed by the adradial ends of the right posterior lateral shared coverplate and the proximal posterior coverplate of ambulacrum V. Additional ambulacrals may have been included. One interambulacral forms most or all of the posterior interambulacral side of the hydropore. This element is considerably larger than the surrounding interambulacrals. No suggestion of a raised rim has been observed.

The ambulacra are straight, moderately wide, and taper little along their length. The terminations are blunt. The ambulacra are unusually short and are separated distally from the proximal margin of the peripheral rim by interambulacrals which form a zone five to eight plates wide.

The biserial ambulacral coverplates are somewhat thinner than in *Lebetodiscus* or *Foerstediscus.* Their nearly flat to moderately convex external surfaces lie oblique to the thecal surface and form moderately elevated ambulacral ridges on the thecal surface. Thus the coverplate passageways are also oblique. Their structure is similar to that of *Lebetodiscus* and *Foerstediscus,* although the external foramina are narrower and more elongate. The two lateral ambulacral bifurcation plates are also externally sagittate, owing to the central constriction formed by the adjacent passageway foramina. However, the sagittate shape of the bifurcation plates is more subtle than that of the primary orals.

The intra-ambulacral extensions of the ambulacral coverplates appear to be similar to those of other Lebetodiscidae, but larger. These bladelike flanges extend proximally from the ambulacral tunnel edge of the coverplates and curve upward under the adjacent coverplate. The perradial tips of these extensions underlap the alternate coverplate on the opposite side of the perradial line by slipping under the distal part of perradial tip of the alternate plate. Thus both adjacent and alternate coverplates are interlocked when the coverplates are closed. Moreover, the intra-ambulacral extensions apparently are developed along the entire length of the ambulacral tunnel


A
B
C
D
E
SC
AO
PO
BP
HI
CP
LBP
RBP
HCP
O'

surface of the coverplate. Largest perradially, they decrease in width adradially and merge with the edge of the coverplate just above the adradial suture. Thus the coverplate extensions of *B. orthokolus* are longer than those of *Lebetodiscus* or *Foerstediscus*, which merge with the coverplate surface approximately halfway from the perradial to the adradial line. Here, as in other Lebetodiscidae, the outer surface of the intra-ambulacral extensions forms the inner side of the upper ends of the sutural passageways. Because these are adradially-perradially larger in *B. orthokolus*, they form a longer part of the passageway. Therefore, the distal member of every two adjacent coverplates forms more of the passageway than the proximal one, unlike *Lebetodiscus* or *Foerstediscus*, in which the passageways are shared subequally.

The squamose, imbricate interambulacrals are of moderate size. The interambulacra are proportionately large, formed by numerous plates. They extend distal to the ambulacra and form a wide zone five to eight plates deep between the distal tips of the ambulacra and the proximal circlet of peripheral rim plates.

The periproct is slightly offset toward the left side of interambulacrum 5. It includes several irregular circlets of plates which diminish in size toward the center.

The peripheral rim includes approximately five to seven irregular circlets of squamose plates. The large plates of the proximal three or four circlets are elongate concentric with the thecal margin, whereas the progressively smaller plates of the distal two or three circlets are radially elongate.

External thecal plate surfaces appear to be smooth, but are somewhat etched in all known specimens.

Specimens

ROM 18874. Holotype of *Belochthus orthokolus* Bell. *sp. nov.* "Trenton Limestone," Trenton Group. Mohawkian Series. Middle Ordovician. Ottawa. Ontario. J. E. Narroway Collection. 14 mm axial by 15 mm transverse diameter.

Text fig. 8E, pl. 7, fig. 1–3.

The theca has completely collapsed, but only a few plates have been differentially moved; those include the posterior orals, the hydropore structure plates, and the anals. Interambulacrals which flank the adradial sutures have been pulled away from the coverplates along most of the ambulacra. The remainder of the plates appear only slightly disrupted, although the surface of all have been etched. This is the only mature adult specimen known.

ROM 28179. Paratype (1) of *Belochthus orthokolus* Bell, *sp. nov.* "Trenton Limestone," Trenton Group, Mohawkian Series. Middle Ordovician. Peterborough, Ontario. J. Townsend Collection. 6.7 mm axial by 6 mm transverse diameter.

Pl. 7, fig. 4, 5.

The theca has collapsed; the right anterior part is disrupted and apparently crushed. Many of the ambulacral coverplates are partially disrupted, and the upper surfaces of others have been broken off. The specimen has been moderately etched. Size indicates that the specimen is a young adult.

NYSM 12773. Paratype (2) of *Belochthus orthokolus* Bell, *sp. nov.* "Trenton Limestone," Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario. 5.4 mm axial by 5.6 mm transverse diameter.

Text fig. 8D, pl. 8, fig. 6. 7.

This, like paratype (1), is a young adult just in the process of acquiring full adult characters. The specimen is well preserved except for the disruption of interambulacrals, especially in the left half of the theca. The ambulacral, oral, and hydropore plates are only slightly, if at all disrupted. The plates of this specimen may not have been etched.

USNM S-3894-C. Paratype (3) of *Belochthus orthokolus* Bell. *sp. nov.* "Trenton Limestone." Trenton Group. Mohawkian Series. Middle Ordovician. Kirkfield, Ontario. 9 mm axial by 9.2 mm transverse diameter.

Pl. 7, fig. 6, 7.

This individual was included with the type specimens of *Cryptogoleus multibrachiatus* (Bassler) in the United States National Museum. The theca has collapsed and it has been deeply etched, which has obliterated much of the plating. However, this specimen extends the distribution of the species to the Kirkfield region, for this is one of the few species that occurs at both Kirkfield and Ottawa, Ontario.

Text figure 8. ***Belochthus orthokolus*** **Bell, *sp. nov.***

A. Juvenile, NYSM 12774, (x 40), pl. 8, fig. 1.
B. Juvenile, ROM 160t-c-2, (x 40), pl. 8, fig. 3.
C. Juvenile, ROM 160t-c-1, (x 20), pl. 8, fig. 5.
D. Paratype (2), young adult, NYSM 12773, (x 10), pl. 8, fig. 7.
E. Holotype, adult, ROM 18874, (x 11), pl. 7, fig. 2. Coverplate intra-ambulacral extensions are separated from the main body of the plates by dashed lines and are stippled.

AO, anterior primary oral plate; BP, lateral bifurcation plate; CP, ambulacral coverplate; HCP, hydropore ambulacral coverplate; HI, hydropore interambulacral plate; LBP, left lateral bifurcation plate; o', secondary oral plate; PO, posterior oral plate; RBP, right lateral bifurcation plate; SC, lateral shared coverplate.

Juveniles

NYSM 12774. "Trenton Limestones," Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario. 0.8 mm axial by 1.1 mm transverse diameter.

Pl. 8, fig. 1.

This is the smallest known representative of the species. Along with the other juveniles, it is described in detail in the section on ontogeny. The theca is well preserved, with little plate disruption and only moderate etching. Unfortunately, this specimen proved extremely difficult to photograph.

ROM 160t-c. Two specimens of *B. orthokolus* on one slab (accompanied by many *Isorophusella incondita*). "Trenton Limestone," Trenton Group, Mohawkian Series, Middle Ordovician. Peterborough, Ontario.

ROM 160t-c-1. 2.6 mm axial by 2.8 mm transverse diameter.

Text fig. 8C, pl. 8, fig. 4, 5.

This individual lies only a few millimeters from the following specimen but is not nearly as well preserved. The collapsed theca has been deeply etched, removing over half the thickness of most plates. The major thecal structures can be identified when the specimen is under xylene.

ROM 160t-c-2. 1.3 mm axial by 1.3 mm transverse diameter.

Text fig. 8B, pl. 8, fig. 2, 3.

This individual has collapsed, but little plate disruption has occurred. The exterior of the theca has been abraded and etched; the plates are distinct only when under xylene.

Ontogenetic development

The ontogeny of *B. orthokolus* is recorded by three juveniles, one young adult, and the mature adult holotype (text fig. 8A-E). The oral and ambulacral features of the young individuals are unusually clear, because of the squamose rim plates which are equally depressed with the distal interambulacrals. In contrast, juveniles of species with geniculate rim plates are often difficult to interpret because the central upper oral surface collapses below and often partly under the elevated rim and is thereby hidden from view.

In the smallest specimen (NYSM 12774, text fig. 8A, pl. 8, fig. 1), 0.8 mm axial by 1.1 mm transverse diameter, the peripheral rim dominates the theca and forms approximately two-thirds of the oral surface. Within the central third, only nine plates of the oral-ambulacral series are apparent; interambulacrals and anals are indistinct. Three large primary orals form the center of the area — two anterior and one larger posterior plate. A grouping of three plates flanks each side of the central orals along the transverse thecal axis. The central one is largest and lies somewhat distal to the other two; it is thought to be the lateral bifurcation plate, and the two smaller, more proximal plates would then be the lateral shared coverplate pair. Apparently none of the ambulacral coverplates has developed.

The outline of the central oral-ambulacral series group is distinctly three-part and produces a triradiate symmetry with two lateral radii and one anterior radius. The lateral radii are much longer than the anterior radius, and are extended by the shared coverplate pairs and bifurcation plates. The anterior radius is marked only by a small hump formed by the two large anterior primary orals.

Two or three elongate plates are questionably visible posterior to the oral plates but proximal to the rim plates. A dark area (under xylene) occurs between one of these and the adjacent orals, just to the right of the posterior primary oral. Perhaps this indicates the hydropore. The other elongate plates may represent disrupted anals.

The second specimen (ROM 160t-c-2, text fig. 8B, pl. 8, fig. 2, 3), 1.3 mm axial by 1.3 mm transverse diameter, is far advanced over the first (text fig. 8A). The peripheral rim is still dominant and forms about half the total area of the oral surface. The central oral surface includes at least 24 plates of the oral-ambulacral series and 12 or more anals. The oral-ambulacral series forms a distinct triradiate symmetry with two dominant lateral radii and one shorter anterior radius. However, the two lateral radii have bifurcated and initiated the independent development of each of the four lateral ambulacra.

The oral-ambulacral series plates are not well preserved. Many are separated perradially from opposing plates, and several appear irregular in size and shape relative to adjacent elements. Thus the specimen seems to have been differentially etched, and this, combined with the effect of thecal collapse, makes interpretations uncertain.

The three large, thick primary orals are central, but the left anterior primary appears to be laterally displaced to the left and is no longer in contact with the right anterior primary. Shared coverplates flank the central orals; one pair is on the left, but on the right only the posterior plate is preserved. The left anterior element was apparently lost during preservation and this leaves a gap along the right edge of the left anterior primary oral.

Distal to the left pair of shared coverplates are seven ambulacral elements. The largest of these, on the posterior side of the group, would from its size appear to be the left ambulacral bifurcation plate. If so, only one large and one tiny coverplate form ambulacrum I, whereas two pairs of coverplates form ambulacrum II. On the right side of the central orals the larger bifurcation plate lies at the distal edge of the left group; ambulacra IV and V have three coverplates each. Ambulacrum III appears to have five coverplates. Those on the left side of the midline look much larger than those on the right, owing to differential etching and collapse. The hydropore may be represented by an elongate darkened area (under xylene) along the posterior adradial edge of the right posterior shared coverplate. A large interambulacral plate bounds the posterior side of the darkened area. The right margin of this plate also abuts the adradial end of the proximal posterior coverplate of ambulacrum V, although the darkened area does not appear to extend along this zone.

The anal structure, posterior to the oral area, is formed by approximately 12 plates that are irregular in size and shape, and loosely grouped into one or two circlets which form a periproct. The relative size of the structure is very large in comparison to that of adults.

The third individual of the series (ROM 160t-c-1, text fig. 8C, pl. 8, fig. 4, 5), 2.6 mm axial by 2.8 mm transverse diameter, is far advanced over the stage seen in the second specimen (text fig. 8B). Unfortunately, the outer sides of the oral surface plates have been removed by erosion and etching. This exposes a subsurficial view of the individual which does not reveal the external shape and size of these plates. The specimen is described as it appears now, without the missing exterior.

The peripheral rim and distal interambulacrals occupy about half of the thecal surface area. Approximately 30 plates of the oral-ambulacral series are present. The three large primary orals are clearly defined, although they are widely separated from one another perradially owing to the loss of the upper parts of the plates. The subsurficial view thus exposes the upper ends of large intrathecal extensions of the orals which extend downward from their inner perradial edges toward the interior of the theca. It is assumed, from correlation with related species, that these extensions participate in the formation of the oral frame, each fitting into the structure between the upper parts of the proximal ambulacral floorplates. The dashed line across the orals in the text fig. 8B suggests the dividing line between the body of the plates and the intrathecal extensions, the latter represented by the proximal ends of the plates.

One pair of lateral shared coverplates flanks each side of the central primary orals along the transverse oral midline. The plate immediately adjacent to the left side of the posterior primary oral would seem to be the left posterior shared coverplate. However, this could be a secondary oral plate and the next distal plate the shared coverplate. If so, ambulacrum I has only five coverplates, not six as suggested below.

Ambulacrum I includes six plates, diminishing in size distally along the ambulacrum. Those on the right side of the midline appear to be larger than the opposing plates. Ambulacrum II has five coverplates, all rather small. Ambulacrum III contains four relatively large and subequal plates. (The small plate distal to the right anterior primary oral could also be a coverplate.) Ambulacra IV and V each have three plates. Thus the ambulacra appear to develop at differing rates, although comparison with other juveniles suggests no consistent pattern.

One large interambulacral plate adjacent to the proximal part of ambulacrum V is probably a hydropore interambulacral, although the region is very obscure. Under xylene, a darkened zone exists between the edge of this large plate and the adjacent part of the ambulacrum.

The large anal structure is seen in interambulacrum 5. Although highly etched, the periproct is clearly much larger proportionately at this stage than in an adult. Moreover, the individual anal plates appear larger.

NYSM 12773, paratype (2), 5.4 mm axial by 5.6 mm transverse diameter, text fig. 8D, pl. 8, fig. 6, 7, is considered to be a young adult. Most thecal features are identical to those seen in the larger adult holotype, although the proportional sizes of the structures remain in a transitional state between those found in juveniles and adults. However, the secondary orals may be absent and the ambulacra appear to taper, whereas in the adult the ambulacra are nearly uniform in width throughout and terminate bluntly.

The most significant aspect of the growth series of *B. orthokolus* is the ontogenetic change in symmetry. The earliest stage is characterized by a triradiate plan. The two lateral radii originate at the center of the oral region and are distally extended by the shared coverplate pairs and lateral ambulacral bifurcation plates. The anterior radius is marked by a small anterior hump on the transversely elongate oral area, formed by the two large anterior primary orals. The next glimpse of development shows a continuation of the triradiate plan, with all three radii elongated but the anterior one still subordinate. As the two lateral radii bifurcate to form the five-part symmetry of the adults, the anterior axis becomes essentially equal in size to the other ambulacra. The five-part symmetry becomes apparent as the theca approaches 2.5 to 3 mm diameter.

The growth series also shows progressive changes in relative size of major thecal structures; the peripheral rim, oral area, and anal structure decrease in proportional size, the ambulacra and interambulacra progressively increase. Thus juveniles can be separated from adults by the relative size of the thecal structure, even when preservation is poor and the plate boundaries obscure.

Discussion

The holotype and only known large adult of *Belochthus orthokolus* was discovered at the Royal Ontario Museum under the name "*Hemicystites narrowayi.*" An extensive literature search failed to reveal any edrioasteroid species with the trivial name *narrowayi* although an asteroid species *Hudsonaster narrowayi* is on record. It appears that this is a manuscript name of an earlier unknown worker. *B. orthokolus* may be easily identified by the distinctive sagittate shape of the primary orals and lateral ambulacral bifurcation plates, and also by the extensive development of the interambulacrals distal to the tips of the straight, short ambulacra. Unfortunately, the inner oral surface structures are not exposed in the few available specimens. Moreover, the hydropore structure is disrupted in the four adult specimens, and the oral region is partially disrupted.

Cystaster granulatus is the only other Lebetodiscidae in which the ambulacra do not closely approach the proximal margin of the peripheral rim. However, *C. granulatus* is clavate and those interambulacrals distal to the ambulacra form a downward constricting pedunculate zone which separates the upper oral surface ambulacra from the basal peripheral rim. The theca of *Belochthus orthokolus* is clearly domal, although the large distal zone of interambulacrals suggests it may have been highly convex upward before collapse.

The external sides of the ambulacral coverplates appear to be nearly flat in adults, but are convex in small specimens, like those of most other Lebetodiscidae. This may reflect ontogenetic change or is perhaps preservational, the convex exteriors of adult coverplates having been removed by surficial etching as in the holotype of *Foerstediscus splendens*. No suggestion of a lateral depression series has been observed in *B. orthokolus*.

ETYMOLOGY: The trivial name *orthokolus* is compounded from the Greek *orthos* straight, and *kolon* arm; denoting the straight ambulacra.

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

Genus *Streptaster* Hall, 1872

1842 [*non*] *Agelacrinites* Vanuxem, L., Nat. Hist. New York, pt. IV, Geology 3: 158, fig. 80.

1866 *Agelacrinus* Vanuxem, Hall, J. [*partim*], New York State Mus., 20th Ann. Rept. (adv. pub.): 7-8.

1871 *Agelacrinus* Vanuxem, Hall, J. [*partim*], New York State Mus., 24th Ann. Rept. (adv. pub.): pl. 2, fig. 11-13.

1872 *Agelacrinus* (*Streptaster*) Hall, J., New York State Mus., 24th Ann. Rept.: 215, pl. 6, fig. 11-13.

1873 *Agelacrinites* Vanuxem, Meek, F. B. [*partim*], Geol. Surv. Ohio, v. 1, Geology and Palaeontology, pt. 2, Palaeontology, sect. 1: 57, pl. 3, fig. 7a, b.

1878 *Agelacrinus* Vanuxem, Miller, S. A. and Dyer, C. B., Cincinnati Soc. Nat. Hist., Jour. 1 (1): 27, pl. 1, fig. 9.

1889 *Agelacrinus* Vanuxem, Miller, S. A., North American Geology and Palaeontology, Cincinnati: 221-222.

1896b *Agelacrinus* Vanuxem, Haeckel, E. [*partim*], Die Amphorideen und Cystoideen, Leipzig, 1: 112-113.

1899 *Agelacrinites* Vanuxem, Jaekel, O. [*partim*], Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 50.

1900a *Streptaster* Hall, Bather, F. A., *in* A Treatise on Zoology, E. R. Lankester (ed.), London, pt. III, Echinoderma: 207-208.

1914 *Streptaster* Hall, Foerste, A. F., Denison Univ., Sci. Lab. Bull. 17 (art. 14): 399-454, pl. 1, fig. 7a-b, pl. 4, fig. 2, 3.

1915 *Streptaster* Hall, Bassler, R. S., United States Nat. Mus. Bull. 92, 2: 1199.

1918 *Streptaster* Hall, Williams, S. R., Ohio Jour. Sci. 19 (1): 61-73, pl. 3, fig. 19, pl. 5, fig. 31, pl. 8, fig. 47, 48.

1935 *Streptaster* Hall, Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 5.

1936 *Streptaster* Hall, Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 9.

1938 *Streptaster* Hall, Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 176.

1943 *Streptaster* Hall, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 208.

1960 *Streptaster* Hall, Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 163-164, text fig. 9, pl. 6, fig. 1, 2.

1966 *Streptaster* Hall, Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U167, text fig. 117-2, 120-3-b, 125-3, 130-2.

TYPE SPECIES: *Agelacrinus vorticellata* Hall, 1866.

Diagnosis

Lebetodiscidae with: domal theca, convex oral surface dominated by high ambulacral ridges; oral region including secondary oral plates; hydropore structure formed by one large interambulacral plate and two ambulacral coverplates; ambulacra contrasolarly curved, long, wide, and high; coverplates columnar, forming high, steep-sided ambulacral ridges which commonly obscure all other external thecal structures; large conical spines mounted in basins atop ambulacral coverplates; coverplate passageways open externally along most of their length; interambulacrals squamose and imbricate; periproct plates elongate, possibly bearing spines.

Description

Streptaster, as recognized here, is monotypic. Therefore, differentiation of generic and specific taxobases is uncertain. Features outlined in the above generic diagnosis are inferred to be of generic rank from established taxobases of other Lebetodiscidae.

Discussion

The date of publication of the name *Streptaster* requires explanation. *Agelacrinus vorticellata,* the type species of the genus, was originally described by Hall in 1866. The description was published in an advance printing of a paper intended to be included in the 20th Annual Report of the State Cabinet of Natural History of New York. The advance printing included only the text and no illustrations. The completed paper did not appear in the intended publication, but rather was transferred to the 24th Annual Report (1872). However, in 1871 a second advance printing of the paper was issued. This included the plates and additions to the text, but not the original parts of the paper published in 1866. The plates included two specimens assigned to this species, the holotype and a second individual not mentioned in the original description. The plate explanations listed the name as "*Agelacrinus* (   ) *vorticellatus,*" with a blank between the parentheses. Finally, in 1872, the paper was reprinted in its entirety in the 24th Annual Report of the Cabinet of Natural History of the State of New York. The text remained unchanged, but the plate explanation contained the designation "*Agelacrinus (Streptaster) vorticellatus* Hall, 1866." Thus the name *Streptaster* dates from 1872, having been proposed at that time as a subgenus of *Agelacrinites.*

Throughout the later part of the 19th century, *Streptaster vorticellatus* was referred to the genus *Agelacrinites.* Around 1900, following Bather's lead, most workers adopted the name *Streptaster,* but on the generic rather than the subgeneric level.

RANGE AND OCCURRENCE: Cincinnatian Series, Upper Ordovician, Ohio, Indiana, and Kentucky.

Streptaster vorticellatus (Hall), 1866

Text fig. 9; plate 9, 10

1866 *Agelacrinus vorticellata* Hall, J., New York State Mus., 20th Ann. Rept. (adv. pub.) : 7-8.

1871 *Agelacrinus vorticellatus* Hall, J., New York State Mus., 24th Ann. Rept. (adv. pub.) : pl. 2, fig. 11-13.

1872 *Agelacrinus (Streptaster) vorticellatus* Hall, J., New York State Mus., 24th Ann. Rept.: 215, pl. 6, fig. 11-13.

1873 *Agelacrinites vorticellatus* Hall, Meek, F. B., Geol. Surv. Ohio, v. 1, Geology and Palaeontology, pt. 2, Palaeontology. sect. 1: 57, pl. 3, fig. 7a, b.

1878 *Agelacrinus septembrachiatus* Miller, S. A. and Dyer, C. B., Cincinnati Soc. Nat. Hist., Jour. 1 (1) : 27, pl. 1, fig. 9.

1889 *Agelacrinus septembrachiatus* Miller and Dyer, Miller, S. A., North American Geology and Palaeontology, Cincinnati: 222; *A. vorticellatus* Hall, *idem, ibid.*: 222.

1896b *Agelacrinus vorticellatus* Hall, Haeckel, E., Die Amphorideen und Cystoideen, Leipzig, 1: 112-113.

1899 *Agelacrinites septembrachiatus* Miller and Dyer, Jaekel, O., Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 50; *Agelacrinites vorticellatus* Hall, *idem, ibid.*: 50.

1914 *Streptaster vorticellatus* (Hall), Foerste, A. F., Denison Univ., Sci. Lab. Bull. 17 (art. 14): 411-450; *Streptaster reversata* Foerste, *idem, ibid.*: 405-453, pl. 4, fig. 3; *Streptaster septembrachiatus* (Miller and Dyer), *idem, ibid.*: 420-450, pl. 1, fig. 7a-b, pl. 4, fig. 2.

1918 *Streptaster vorticellatus* (Hall), Williams, S. R., Ohio Jour. Sci. 19 (1) : 63, pl. 5, fig. 31, pl. 8, fig. 47; *Streptaster reversata* Foerste, *idem, ibid.*: 65, pl. 3, fig. 19; *Streptaster septembrachiatus* (Miller and Dyer), *idem, ibid.*: 63.

1935 *Streptaster vorticellatus* (Hall), Bassler, R. S., Smithsonian Misc. Coll. 93 (8) ; 5; *Streptaster reversatus* Foerste, *idem, ibid.*: 5; *Streptaster septembrachiatus* (Miller and Dyer), *idem, ibid.*: 5.

1936 *Streptaster septembrachiatus* (Miller and Dyer), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 9; *Streptaster reversata* Foerste, *idem, ibid.*: 9.

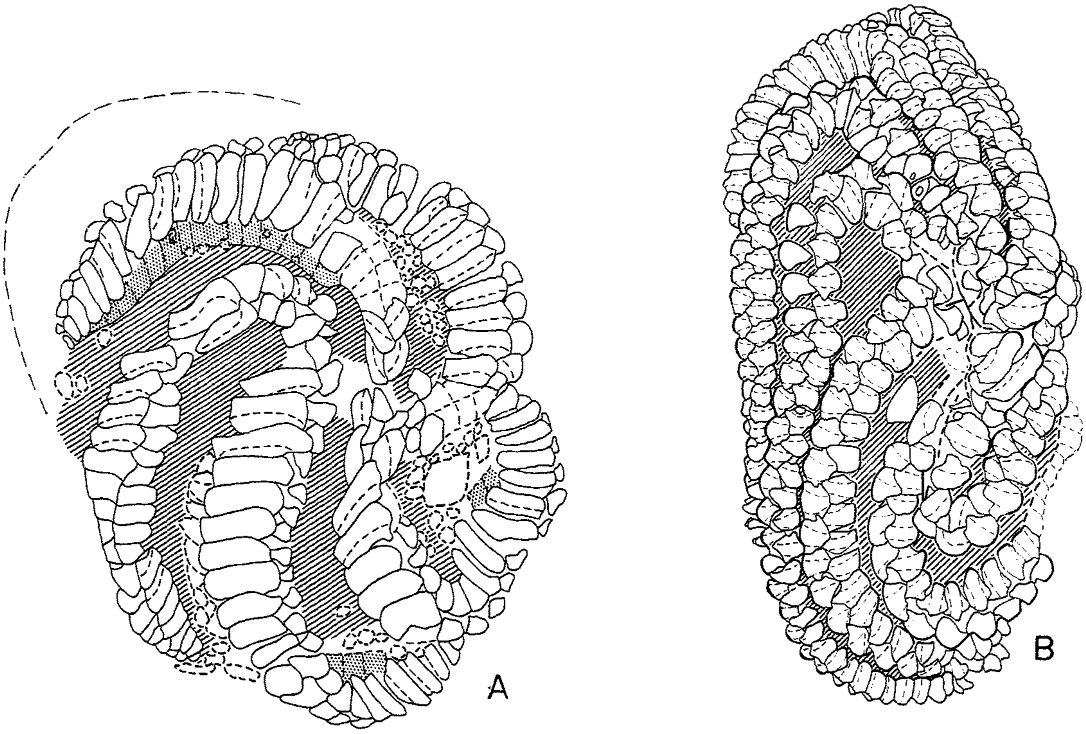
1943 *Streptaster vorticellatus* (Hall), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 208; *Streptaster reversatus* Foerste, *idem, ibid.*: 208; *Streptaster septembrachiatus* (Miller and Dyer), *idem, ibid.*: 208.

1960 *Streptaster sp.* cf. *S. vorticellatus* (Hall), Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 163-164, text fig. 9, pl. 6, fig. 1, 2; *Streptaster reversata* Foerste, *idem, ibid.*: 163; *Streptaster septembrachiatus* (Miller and Dyer), *idem, ibid.*: 163-164.

1966 *Streptaster vorticellatus* (Hall), Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: 167, text fig. 125-3, 130-2; *Streptaster reversatus* Foerste, *idem, ibid.*: U167; *Streptaster septembrachiatus* (Miller and Dyer), *idem, ibid.*; U167.

Diagnosis

A *Streptaster* with: secondary oral plates apparently variable; hydropore structure formed by second and third proximal posterior coverplates of ambulacrum V and one large interambulacral; ambulacra highly curved, distal tips near adjacent ambulacra; spines atop ambulacral coverplates varying in size independently of variations in diameter of underlying columnar coverplates; spine basins developed on upper ends of coverplates; interambulacral plates varying in shape, each with large external node; peripheral rim commonly reflexed under upper side of theca: interambulacrals and rim plates having external



Text figure 9. *Streptaster vorticellatus* (Hall), 1866

A. MCZ 520, (x 6), pl. 9, fig. 3. Ambulacral floorplates are marked by the dotted pattern.

B. MCZ 514, (x 4), pl. 9, fig. 7-9. The anterior edge of the theca may be the left edge of the plate tracing. Dashed lines separate the main body of the ambulacral coverplates from the intra-ambulacral extensions.

nodes or protuberances which vary in shape, size, and frequency.

Description

The domal theca of *Streptaster vorticellatus* is dominated by the long, wide, and extremely high ambulacra (text fig. 9A, B, pl. 9, 10). During thecal collapse, even slight lateral shifting of the ambulacral coverplates totally hides other thecal structures. The oral area, hydropore structure, anal area, and even the interambulacral areas, are exposed only in exceptional specimens and remain inadequately known. In an unusually high percentage of specimens, the peripheral rim is flexed under the upper side of the theca, and the specimen rests on an object smaller than the thecal diameter. Average adult diameter is approximately 15 mm, the largest known just over 23 mm.

The oral plates rise above the level of the interambulacra and form a central oral rise, but apparently its summit lies well below the tops of the proximal ambulacral ridges. Although commonly hidden, the oral area appears to include several secondary oral plates. The number and position of the secondary orals is questionable, although at least seven different secondary orals have been identified tentatively in various individuals. Their diversity may be preservational, or may represent intraspecific variation.

The oral plates are elongate and subtriangular in outline. They are inclined toward the thecal surface and slope upward to meet perradially, in contrast with the columnar, vertical. ambulacral coverplates. Prominent sutural passageways flank both sides of each primary oral plate.

The oral frame is moderately well exposed in one specimen of *S. vorticellatus* (pl. 9, fig. 10, 11), and is similar to that found in other Lebetodiscina. It is transversely elongate, but less so than is known for any other Lebetodiscina. The proximal margin is nearly subcircular in outline and surrounds the central lumen. Distally the frame is subpentagonal, continuous with the five ambulacra. The proximal rim of the frame extends down into the thecal cavity further than any other structure.

The frame is formed by the enlarged proximal floorplates of all five ambulacra and the intrathecal extensions of the three primary orals. The anterior half of the frame includes the floorplates of ambulacra II–III–IV. These are enlarged proximally and extend inward and laterally. The inner proximal edge of floorplate III is laterally in contact with the anterior tips of floorplates II and IV, and forms the innermost edge of the interradial parts of the frame rim. However, large intrathecal extensions from the right and left anterior primary orals are wedged between the upper parts of the floorplates and form all but the inner edge of the two anterior frame interradii.

The posterior half of the frame includes the proximal floorplates of ambulacra I and V. The anterior sides of these two floorplates abut the posterior lateral edges of floorplates II and IV and form the two lateral frame interradii. The inner parts of the two lateral bifurcation plates, which overlie the lateral interradii, may form part of the uppermost edge of the frame. The two posterior floorplates (I, V) are not in contact across the posterior interradius. The center of the posterior side is formed by the intrathecal extension from the primary posterior oral. This extension ends far above the inner edges of the floorplate parts of the frame, and thereby leaves a large opening which affords direct lateral access from the central lumen into the thecal cavity beneath interambulacrum 5.

The hydropore structure includes at least three elements: a large interambulacral plate, and the second and third coverplates of the posterior side of ambulacrum V (pl. 9, fig. 4-6, pl. 10, fig. 8, 9). The enlarged adradial end of the second posterior coverplate of ambulacrum V juts out into interambulacrum 5, with the proximal edge much further out than the distal. The distal side of this adradial extension, oriented nearly parallel to the transverse oral midline, forms the anterior edge of the elongate, slitlike hydropore. The posterior side of the opening is formed by a large interambulacral which lies distal to the adradial extension of the second coverplate. This interambulacral, twice the size of any surrounding interambulacrals, is domed outward and gives the plate a bulbous appearance. The large interambulacral element has an intricate groove and ridge structure sculpted into the nearly vertical sutural face which abuts the opposing adradial edge of the second ambulacral coverplate (pl. 9, fig. 6, pl. 10, fig. 9). The groove appears to form a canal which leads from the hydropore down to the beginning of the passageway for the stone canal. The third posterior coverplate of ambulacrum V is shorter than the others (normal to the ambulacral axis), and abuts the right margin of the large hydropore interambulacral plate which intrudes into the edge of ambulacrum V.

The passageway for the stone canal is exposed in the same specimen in which the oral frame is seen (pl. 9, fig. 10, 11). Kesling (1960) first identified the structure on this specimen, although as he pointed out, it was first noted by Foerste in 1914 (under the designation *S. septembrachiatus*). Unfortunately, the structure is not well preserved and most sutures are only questionably identified. Apparently the first and second floorplates of ambulacrum V are involved, along with the inner parts of the large interambulacral hydropore plate.

The contrasolar curvature of the long, broad ambulacra begins immediately distal to the oral region and continues along the length of the ambulacra. In large specimens the distal parts of adjacent ambulacra become concentric with each other and with the thecal margin. The large columnar coverplates form exceptionally high, steep-sided ambulacral ridges that completely dominate the thecal surface. Commonly in collapsed specimens only the ambulacral coverplates are visible.

The columnar coverplates reach an unprecedented height. The external surface of each extends nearly vertically from the interambulacrum up to the summit of the ambulacrum. There it curves sharply in a perradial direction and forms a nearly horizontal upper surface. Thus the alternating biseries of coverplates forms an ambulacral ridge with steep, nearly vertical lateral walls, surmounted by a flat, nearly horizontal upper surface.

The bladelike intra-ambulacral extensions which arise from the proximal inner edges of the coverplates are similar to those of other Lebetodiscidae. They extend proximally inward and the proximal tips are reflexed outward to abut the inner distal edge of the adjacent, next proximal, coverplate. The outer surface of each extension forms the inner ambulacral tunnel side of the upper end of the coverplate passageway (the part which is visible through the external foramen). The extensions are widest perradially and taper in width downward. Thus the distal side of the adjacent, proximal coverplate progressively forms more of the inner wall of the passageway. Approximately halfway down to the underlying floorplate, the passageway is formed subequally by the two adjacent coverplates. The proximal perradial tip of each intra-ambulacral extension, as in most other Lebetodiscina, extends a short distance under the distal edge of the perradial tip vertical. ambulacral coverplates. Prominent sutural passageways flank both sides of each primary oral plate.

The oral frame is moderately well exposed in one specimen of *S. vorticellatus* (pl. 9. fig. 10, 11), and is similar to that found in other Lebetodiscina. It is transversely elongate, but less so than is known for any other Lebetodiscina. The proximal margin is nearly subcircular in outline and surrounds the central lumen. Distally the frame is subpentagonal, continuous with the five ambulacra. The proximal rim of the frame extends down into the thecal cavity further than any other structure.

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The posterior half of the frame includes the proximal floorplates of ambulacra I and V. The anterior sides of these two floorplates abut the posterior lateral edges of floorplates II and IV and form the two lateral frame interradii. The inner parts of the two lateral bifurcation plates, which overlie the lateral interradii, may form part of the uppermost edge of the frame. The two posterior floorplates (I, V) are not in contact across the posterior interradius. The center of the posterior side is formed by the intrathecal extension from the primary posterior oral. This extension ends far above the inner edges of the floorplate parts of the frame, and thereby leaves a large opening which affords direct lateral access from the central lumen into the thecal cavity beneath interambulacrum 5.

The hydropore structure includes at least three elements: a large interambulacral plate, and the second and third coverplates of the posterior side of ambulacrum V (pl. 9, fig. 4-6, pl. 10, fig. 8, 9). The enlarged adradial end of the second posterior coverplate of ambulacrum V juts out into interambulacrum 5, with the proximal edge much further out than the distal. The distal side of this adradial extension, oriented nearly parallel to the transverse oral midline, forms the anterior edge of the elongate, slitlike hydropore. The posterior side of the opening is formed by a large interambulacral which lies distal to the adradial extension of the second coverplate. This interambulacral, twice the size of any surrounding interambulacrals, is domed outward and gives the plate a bulbous appearance. The large interambulacral element has an intricate groove and ridge structure sculpted into the nearly vertical sutural face which abuts the opposing adradial edge of the second ambulacral coverplate (pl. 9, fig. 6, pl. 10, fig. 9). The groove appears to form a canal which leads from the hydropore down to the beginning of the passageway for the stone canal. The third posterior coverplate of ambulacrum V is shorter than the others (normal to the ambulacral axis), and abuts the right margin of the large hydropore interambulacral plate which intrudes into the edge of ambulacrum V.

The passageway for the stone canal is exposed in the same specimen in which the oral frame is seen (pl. 9, fig. 10, 11). Kesling (1960) first identified the structure on this specimen, although as he pointed out, it was first noted by Foerste in 1914 (under the designation *S. septembrachiatus*). Unfortunately, the structure is not well preserved and most sutures are only questionably identified. Apparently the first and second floorplates of ambulacrum V are involved, along with the inner parts of the large interambulacral hydropore plate.

The contrasolar curvature of the long, broad ambulacra begins immediately distal to the oral region and continues along the length of the ambulacra. In large specimens the distal parts of adjacent ambulacra become concentric with each other and with the thecal margin. The large columnar coverplates form exceptionally high, steep-sided ambulacral ridges that completely dominate the thecal surface. Commonly in collapsed specimens only the ambulacral coverplates are visible.

The columnar coverplates reach an unprecedented height. The external surface of each extends nearly vertically from the interambulacrum up to the summit of the ambulacrum. There it curves sharply in a perradial direction and forms a nearly horizontal upper surface. Thus the alternating biseries of coverplates forms an ambulacral ridge with steep, nearly vertical lateral walls, surmounted by a flat, nearly horizontal upper surface.

The bladelike intra-ambulacral extensions which arise from the proximal inner edges of the coverplates are similar to those of other Lebetodiscidae. They extend proximally inward and the proximal tips are reflexed outward to abut the inner distal edge of the adjacent, next proximal, coverplate. The outer surface of each extension forms the inner ambulacral tunnel side of the upper end of the coverplate passageway (the part which is visible through the external foramen). The extensions are widest perradially and taper in width downward. Thus the distal side of the adjacent, proximal coverplate progressively forms more of the inner wall of the passageway. Approximately halfway down to the underlying floorplate, the passageway is formed subequally by the two adjacent coverplates. The proximal perradial tip of each intra-ambulacral extension, as in most other Lebetodiscina, extends a short distance under the distal edge of the perradial tip of the alternate coverplate, across the perradial line, and thereby firmly interlocks the coverplates together when they are closed.

The coverplate passageway system of *S. vorticellatus* is apparently unique. Individual passageways appear to remain open externally along their entire length because the external lateral edges of adjacent coverplates never quite make contact with one another. Thus an elongate slit opens into each passageway; it extends from the upper edge of the ambulacrum down to the level of the adjacent interambulacral plates (pl. 9, fig. 3, 4, 7-9, pl. 10, fig. 1, 3, 12, 14). The inner foramina of the passageways are formed by the intrathecal ends of the coverplates, as in related species. However, their location in relation to the floorplates is different. The inner foramina lie above the level of the floorplate margins rather than adjacent to them as in other Lebetodiscidae (pl. 9, fig. 11). This unique condition is due to the coverplates' resting upon the upper lateral edges of the floorplates. In most other species the coverplates rest partially on the upper lateral edges of the floorplates, but also extend beyond them. Thus the inner foramina of the passageways in other Lebetodiscina lie adjacent and lateral to the floorplates, rather than above them as in *S. vorticellatus.*

The lower, basal ends of the coverplates, which rest on the lateral margins of the underlying floorplates, are much smaller than the external, upper parts of the plates. Immediately after reaching the level of adjacent interambulacrals, the coverplates constrict, and the thecal cavity side curves inward toward the edge of the floorplate. When viewed from the inner surface, the entire base of each coverplate is seen to rest on the floorplate, whereas the upper part of the plate can be seen projecting outward beyond its edge (pl. 9, fig. 10, 11). The inner foramina of the passageways lie between the coverplates along this upwardly enlarging zone, above the floorplates but beneath the interambulacrals.

The interambulacral plates adjacent to the ambulacra play an important part in the passageway system. The adradial edges of these plates act as the outer wall of the passageways where they enter the theca. In effect, they separate the inner foramina from the long upper part of the passageway which is open to the exterior along its entire length. Thus the passageways are two large " foramina " connected by a very short tube. Depression of the interambulacrals during thecal collapse commonly exposes the entire passageway structure and a lateral view of the underlying floorplates.

The uniserial floorplates are trough-shaped and imbricate, each floorplate proximally overlapping the distal half of the adjacent one (pl. 9, fig. 10, 11, pl. 10, fig. 5). Coverplate pairs correspond to individual floorplates with nearly one pair to one floorplate. However, the floorplates are slightly shorter than the combined length of a pair of coverplates, and therefore the location of the coverplates on the floorplates changes along the length of the ambulacrum.

Mounted atop each ambulacral coverplate of *S. vorticellatus* is a relatively large, conical, movable spine (pl. 10, fig. 1, 3, 6, 7, 11, 12). Spine shapes and sizes are quite variable. Commonly the spines are broad based and taper evenly upward to a pointed, distal extremity. The diameter of the base varies from approximately one-half to one-eighth that of the top of the coverplate on which it rests. Some wider based spines are nearly two-thirds as long as the height of the underlying coverplate. Narrower based spines may be only one-tenth the height of the coverplate. Spines also occur on the oral plates, although these appear to be much smaller than those of adjacent proximal ambulacral coverplates.

The spines rest in basinlike depressions on the nearly horizontal upper surfaces of the columnar coverplates (pl. 10, fig. 1, 3, 6, 12). The depressions also exhibit a considerable range in form, and appear to vary from broad, shallow, uniform depressions, evenly dished into the surface of the coverplates, to deep, steep-sided depressions in which the lateral perradial edge of the basin opens toward the perradial line. The shallow open depressions would allow the spines great freedom of movement, but this may be illusory and due to erosion of the deeper basins, the open perradial side of which would suggest that spine movement was restricted to a back and forth motion obliquely across the ambulacral axis.

The interambulacra of *S. vorticellatus* are narrow regions squeezed between the long, wide, and highly curved ambulacra. Interambulacral plates in general appear to be squamose and imbricate, although the proximal plates in many specimens may be subpolygonal and only slightly overlapping. Unfortunately, the interambulacral plates are usually hidden by the slightly disrupted columnar ambulacral coverplates. Commonly large irregular protuberances cover the external surfaces of the interambulacral plates, obscuring their definition and creating the appearance that the interambulacra are formed by granular plates. This prosopon ranges from rounded tubercles to irregular mounds in different parts of the same individual (pl. 10, fig. 1, 8, 10, 12). A similar prosopon extends onto the proximal plates of the peripheral rim although it diminishes rapidly outward in both size and abundance of the nodes.

The anal structure lies slightly proximal to the center of interambulacrum 5. Although rarely exposed, it appears to be a periproct formed by several circlets of elongate plates. Spines seem to be present on the upper tips of the anals.

The peripheral rim is formed by five to eight circlets of squamose plates, the plates diminishing in size distally (pl. 10, fig. 14). Plates of the proximal two or three circlets are elongate concentric with the thecal margin; the distal four or five circlets are formed by small, radially elongate plates.

Specimens

AMNH 1192. Holotype of *Streptaster vorticellatus* (Hall) (1866, p. 7, 8; 1871; pl. 2, fig. 11). Maysville Group, Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. 10.3 mm axial by 10.4 mm transverse diameter.

Pl. 9, fig. 1, 2.

The holotype is extremely poorly preserved. The collapsed theca is moderately complete and no major plate disruption has occurred, but the exterior has been deeply etched. This etching does not appear to be the typical natural etching so commonly encountered in the edrioasteroids. The specimen may have been prepared with a caustic which removed most external detail. In its present state, the holotype reveals little other than gross thecal features. The specimen is resting upon a small pelecypod.

This poor specimen is clearly to be regarded as the holotype, as shown by a careful examination of the original description of the species which Hall (1866) mentioned was based on a single specimen, less than half an inch in diameter. In Hall's 1871 presentation, this specimen was illustrated together with another, somewhat larger individual. Moreover, in the original description Hall clearly indicates the presence of interambulacral and rim plates in the holotype, whereas the second specimen does not preserve these features.

MCZ 520 (old 3876). Illustrated Specimen of *Streptaster vorticellatus* (Hall) (1871, pl. 2, fig. 13); incorrectly illustrated as the holotype by Meek (1873). "Shales of the Hudson River Group," Maysville Group, Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. 13.2 mm axial by 14.5 mm transverse diameter.

Text fig. 9A, pl. 9, fig. 3.

This individual, figured by Hall (1871) along with the holotype, clearly played no part in the original description. The specimen is rather poorly preserved; most of the interambulacral plates and all of the rim plates are missing, along with anals and the interambulacral part of the hydropore structure. All five ambulacra are represented by partially disrupted and etched coverplates.

USNM 87164. Holotype of *Streptaster reversata* Foerste (1914, p. 451-453, pl. 3, fig. 2). "Lower Eden," Cincinnatian Series, Upper Ordovician. West of [railroad] Trestle 15, 2 miles west of Million, Kentucky. 21.7 mm along the broken edge by 11.2 mm normal to the break.

Pl. 9, fig. 4-6.

This specimen is a fragment which preserves only the posterior third of the theca. It includes most of ambulacra I, V, and part of II, but just the tip of III. Interambulacrum 5 is preserved, along with parts of 1 and 2, and the posterior third of the peripheral rim.

The specimen, here placed in *S. vorticellatus*, has reversed (solar) curvature for ambulacrum V. This allows a clear view of the plates of interambulacrum 5 which are squamose and imbricate, and bear large irregular nodes. The anal periproct is formed by one or two irregular circlets of large, subtriangular, elongate plates. These form a conical protuberance. The ambulacral part of the hydropore structure is missing, but the large hydropore interambulacral is preserved and is much larger than any of the surrounding interambulacral elements. It rises above the surface of the interambulacrum to over half the height of adjacent ambulacral coverplates. The outer surface of the plate is convex. The adradial edge of the plate was apparently in contact with two coverplates, its proximal third with one, the distal two-thirds in contact with the next distal coverplate. The face of the interambulacral plate contacting the coverplates descends steeply toward the interior of the theca. Two upwardly convergent grooves are incised into this face. These intersect at a low angle at the upper edge of the plate. Where last observed near the lower covered part of this adradial face, the two grooves bend sharply inward, converging as they disappear from sight. These grooves apparently served as channels connecting the hydropore to the underlying stone canal passageway. The coverplate passageways and ambulacral spines of this specimen are typical of the species.

MCZ 514 (old 3875). Holotype of *S. septembrachiatus* (Miller and Dyer) (1878, p. 27, pl. 1, fig. 9). "Upper part of the Cincinnatian Series" (Richmond Group, Cincinnatian Series). Upper Ordovician. Near Waynesville, Ohio. 23.2 mm axial by 11.4 mm transverse diameter. 12.5 mm high.

Text fig. 9B, pl. 9, fig. 7-9.

This specimen is a large, moderately well-preserved *S. vorticellatus*, typical in all respects except for the occurrence of two additional ambulacra, a phenomenon known to occur in many edrioasteroid species. It cannot be determined which of the five primary ambulacra have bifurcated to form the extra rays. The specimen is resting on a small, elongate bryozoan colony. This results in an abnormal elongation of the theca which caused the peripheral rim and distal parts of the ambulacra to be reflexed as the edrioasteroid grew. The large size and increased number of ambulacra obscure nearly all the interambulacrals. The plates of the oral region are disrupted. An exceptionally large plate in one of the interambulacra may be the hydropore interambulacral. The anus is not visible. Parts of the peripheral rim are exposed adjacent to the underlying bryozoan, and a few of the distal plates of the interambulacral areas can be seen. Both have the knobby prosopon typical of the species.

The large, and still erect coverplates are well preserved. The spines seated atop these coverplates appear unusually small compared to the size of the coverplates. The spines are only sporadically present.

USNM 87165. Illustrated Specimen of *S. vorticellatus* by Foerste (1914, p. 420-421, pl. 1, fig. 7B, pl. 4, fig. 2 as *S. septembrachiatus*). Near the top of the Elkhorn Formation. Richmond Group, Cincinnatian Series, Upper Ordovician. From the falls west of Union Road, north of Eaton Pike, in the woods west of Dayton, Ohio (additional location information in Foerste, 1914). 22.2 mm axial by 22.5 mm transverse diameter.

Pl. 9, fig. 10, 11.

This specimen was illustrated and described by Foerste as a "normal" *S. septembrachiatus*. His species identification evidently was based more on stratigraphic position than morphology, for the specimen does not expose the taxonomically significant oral surface, and has only five ambulacra. The specimen reveals the inner side of the oral surface. Most of the interambulacral plates are missing, but the ambulacra are well preserved. The ambulacral floorplates and the lower, basal sections of the overlying coverplates are only slightly disrupted, and reveal the relationship of these two sets of plates. The description of the oral frame of *S. vorticellatus* is largely based on this individual. The inner surfaces of the squamose peripheral rim plates are also exposed.

AMNH 13267/1-C. "Lorraine Group" (Kope Formation), Eden Group, Cincinnatian Series, Upper Ordovician. 375 (?275) feet above the level of the Ohio River at Cincinnati, Ohio (the elevation in this and the following description is based upon the level of the Ohio River before the flood control dams were built). 15.6 mm axial by 14.7 mm transverse diameter.

Pl. 10, fig. 1–5.

This specimen is mostly free of matrix and exposes the exterior and part of the interior of the theca. Labels indicate that the specimen was studied and evidently prepared by Kesling, although he did not figure it. The distal margin of the oral surface is reflexed. This is due either to the small size of the unknown solid object on which it may have rested, or perhaps to postmortem shrinkage. The ambulacra and interambulacral regions are well preserved, but the oral and hydropore areas are obscure and their details questionable. Some coverplate spines are still in place. The spine basins vary from the deep, restrictive type to the open, shallow forms. The latter appear to be etched restrictive types and suggest that all such shallow basins are due to etching or erosion. Where the lower edge of the theca is broken, a sectional view of the coverplates resting on top of the floorplates is exposed (pl. 10, fig. 5).

AMNH 13267/1-E. "Lorraine Group" (Kope Formation), Eden Group, Cincinnatian Series, Upper Ordovician. 375 feet above the Ohio River level. Cincinnati, Ohio. 10.1 mm axial by 10.4 mm transverse diameter.

Pl. 10, fig. 6, 7.

This specimen is resting on general invertebrate wreckage including one large fragment of an *Isotelus* (trilobite). The oral area and the peripheral rim are moderately disrupted, but the remainder of the theca is well preserved, and includes several groups of ambulacral spines (pl. 10, fig. 7).

CFMUC 54065. Data unknown; the specimen appears preserved in the manner typical of other specimens from the Cincinnatian Series, Upper Ordovician, of the Cincinnati, Ohio area. 11.2 mm axial by 12 mm transverse diameter, 14.4 mm greatest diameter.

Pl. 10, fig. 13.

The specimen is highly distorted to conform to an elongate section of a ramose bryozoan on which it rests. This necessitated the reflexing of the distal rim and tips of the ambulacra. The living individual was therefore highly convex, and thecal collapse has severely disrupted many of the thecal elements. This has exposed many unusual views of the ambulacral coverplates. Deep coverplate spine basins are here preserved.

IUPC 10493. Fairmount member of the Fairview Formation, Maysville Group, Cincinnatian Series, Upper Ordovician. Specimen found in float about 10 feet stratigraphically higher than the "normal edrioasteroid layer" at the Forestville collecting site, Forestville, Ohio (Withamsville, Ohio-Kentucky quadrangle, 7.5 minute topographic sheet (1953), Ohio coordinate system: 397,300′; 1,474,700′). Collected by W. H. White, Jr. 9.8 mm axial by 11.2 mm transverse diameter.

Pl. 10, fig. 8, 9.

The specimen is a small, but typical *Streptaster vorticellatus*. Plate surfaces have been extensively etched. The specimen is noteworthy for the partly disrupted hydropore structure. The large interambulacral hydropore plate is partly displaced, and exposes the grooved adradial face which normally abuts the ambulacral hydropore plates. The groove development is like that described for specimen USNM 87164.

UCMP 24700. Arnheim Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Lawrenceburg, Indiana. 19.1 mm axial by 21.6 mm transverse diameter.

Pl. 10, fig. 14.

The specimen is large and well preserved except for the upper ends of the coverplates and the accompanying spines and spine basins, which have been extensively etched. The specimen clearly shows the peripheral rim and prosopon of the distal interambulacral plates.

UCMP 40438. Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio region. 11.7 mm axial by 13.9 mm transverse diameter.

Pl. 10, fig. 12.

This moderate-sized individual is missing a section of the posterior edge of the theca which divides ambulacrum I into two parts and creates the illusion that six, rather than five ambulacra are present. Distally the peripheral rim is reflexed. Noteworthy is the small size of the ambulacral spines in relation to the size of the underlying coverplates. The spine basins are deep.

UCMP 40437. Fairmount member, Fairview Formation, Cincinnatian Series, Upper Ordovician. North College Hill, Cincinnati, Ohio. 12.9 mm axial by 10.5 mm transverse diameter.

Pl. 10, fig. 11.

The theca is largely covered with matrix that has held the ambulacral spines in place atop the coverplates. The spines are large in proportion to the size of the underlying coverplates.

UCMP 26532. Upper Waynesville Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Wash bank, North branch, Cedar Creek, near Versailles, Indiana. 6.9 mm axial by 7.6 mm transverse diameter.

Pl. 10, fig. 10.

Plating detail is somewhat obscure in this specimen because of extreme etching, but the specimen is illustrated here because it is one of the rare examples of a young adult *S. vorticellatus*.

In addition to the above specimens, over 100 other *S. vorticellatus* have been examined in the course of this study. Unfortunately, most specimens are poorly preserved and add no information other than that provided by the above illustrated individuals.

Discussion of previous investigation

Hall (1866, 1871, 1872) characterized *S. vorticellatus* by the contrasolar curvature of the ambulacra and the narrowness of the interambulacra. He also noted general thecal features, including shape, size, anal area location, and the large, interlocking ambulacral coverplates. Meek (1873) reiterated Hall's description, stressing the height of the coverplates. He reillustrated one of Hall's specimens but not the holotype. This second specimen, which Hall figured (1871, 1872) but did not mention in the text, has since been commonly assumed to be the holotype.

Most authors have placed *S. vorticellatus* either in the genus *Agelacrinites* or in the genus *Streptaster*. Haeckel (1896) was mistaken in his citation of this as the type species of the genus *Agelacrinus* [sic].

Miller and Dyer (1878) proposed *Agelacrinus septembrachiatus* for a large individual with seven ambulacra, judging the number of ambulacra to be a specific criterion. The holotype differs from other *S. vorticellatus* only in the number of ambulacra. Specimens with an anomalous number of ambulacra are now known for several edrioasteroid species, and this development is not regarded as valid for species recognition. This has also been the interpretation of many authors, including Foerste (1914), Williams (1918), Bassler (1936), Ehlers and Kesling (1958), and Regnéll (1966).

The stratigraphic occurrence of the seven-rayed specimen, several hundred feet above the horizon of the type of *S. vorticellatus*, undoubtedly played an important role in Miller's and Dyer's decision to name a new species. Foerste (1914) assigned a second specimen to *S. septembrachiatus*. This was also from high in the Richmond Group (Upper Ordovician) but has only five ambulacra; thus Foerste suggested this individual was a " normal " *S. septembrachiatus*. The specimen exposes only the inner surface features; Foerste must therefore have based his identification on the stratigraphic occurrence. Foerste's description of this specimen (USNM 87165) includes a complete, accurate account of the oral frame, ambulacral floorplates, and stone canal passageway (although not so identified).

Foerste (1914) described *Streptaster reversata*, based on a single fragmentary specimen which preserves only the posterior third of the theca. The specimen appears to be a typical *S. vorticellatus* except for the solar curvature of ambulacrum V. This curvature is considered fortuitous in this individual, as was suggested by Regnéll (1966), and does not constitute a specific difference. Ambulacral curvature direction in edrioasteroids is recognized as generically and specifically consistent, but is not a sole determinant. Other morphologic traits in conjunction with curvature constitute the taxobases. In the fragmentary holotype and sole example of *S. reversata*, no features other than the direction of the ambulacral curvature differ from those found in typical *S. vorticellatus*. A similar fortuitous curvature reversal is known for one specimen of *Carneyella pilea*.

UCMP 24700. Arnheim Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Lawrenceburg, Indiana. 19.1 mm axial by 21.6 mm transverse diameter.

Pl. 10, fig. 14.

The specimen is large and well preserved except for the upper ends of the coverplates and the accompanying spines and spine basins, which have been extensively etched. The specimen clearly shows the peripheral rim and prosopon of the distal interambulacral plates.

UCMP 40438. Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio region. 11.7 mm axial by 13.9 mm transverse diameter.

Pl. 10, fig. 12.

This moderate-sized individual is missing a section of the posterior edge of the theca which divides ambulacrum I into two parts and creates the illusion that six, rather than five ambulacra are present. Distally the peripheral rim is reflexed. Noteworthy is the small size of the ambulacral spines in relation to the size of the underlying coverplates. The spine basins are deep.

UCMP 40437. Fairmount member, Fairview Formation, Cincinnatian Series, Upper Ordovician. North College Hill, Cincinnati, Ohio. 12.9 mm axial by 10.5 mm transverse diameter.

Pl. 10, fig. 11.

The theca is largely covered with matrix that has held the ambulacral spines in place atop the coverplates. The spines are large in proportion to the size of the underlying coverplates.

UCMP 26532. Upper Waynesville Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Wash bank, North branch, Cedar Creek, near Versailles, Indiana. 6.9 mm axial by 7.6 mm transverse diameter.

Pl. 10, fig. 10.

Plating detail is somewhat obscure in this specimen because of extreme etching, but the specimen is illustrated here because it is one of the rare examples of a young adult *S. vorticellatus*.

In addition to the above specimens, over 100 other *S. vorticellatus* have been examined in the course of this study. Unfortunately, most specimens are poorly preserved and add no information other than that provided by the above illustrated individuals.

Discussion of previous investigation

Hall (1866, 1871, 1872) characterized *S. vorticellatus* by the contrasolar curvature of the ambulacra and the narrowness of the interambulacra. He also noted general thecal features, including shape, size, anal area location, and the large, interlocking ambulacral coverplates. Meek (1873) reiterated Hall's description, stressing the height of the coverplates. He reillustrated one of Hall's specimens but not the holotype. This second specimen, which Hall figured (1871, 1872) but did not mention in the text, has since been commonly assumed to be the holotype.

Most authors have placed *S. vorticellatus* either in the genus *Agelacrinites* or in the genus *Streptaster*. Haeckel (1896) was mistaken in his citation of this as the type species of the genus *Agelacrinus* [sic].

Miller and Dyer (1878) proposed *Agelacrinus septembrachiatus* for a large individual with seven ambulacra, judging the number of ambulacra to be a specific criterion. The holotype differs from other *S. vorticellatus* only in the number of ambulacra. Specimens with an anomalous number of ambulacra are now known for several edrioasteroid species, and this development is not regarded as valid for species recognition. This has also been the interpretation of many authors, including Foerste (1914), Williams (1918), Bassler (1936), Ehlers and Kesling (1958), and Regnéll (1966).

The stratigraphic occurrence of the seven-rayed specimen, several hundred feet above the horizon of the type of *S. vorticellatus*, undoubtedly played an important role in Miller's and Dyer's decision to name a new species. Foerste (1914) assigned a second specimen to *S. septembrachiatus*. This was also from high in the Richmond Group (Upper Ordovician) but has only five ambulacra; thus Foerste suggested this individual was a "normal" *S. septembrachiatus*. The specimen exposes only the inner surface features; Foerste must therefore have based his identification on the stratigraphic occurrence. Foerste's description of this specimen (USNM 87165) includes a complete, accurate account of the oral frame, ambulacral floorplates, and stone canal passageway (although not so identified).

Foerste (1914) described *Streptaster reversata*, based on a single fragmentary specimen which preserves only the posterior third of the theca. The specimen appears to be a typical *S. vorticellatus* except for the solar curvature of ambulacrum V. This curvature is considered fortuitous in this individual, as was suggested by Regnéll (1966), and does not constitute a specific difference. Ambulacral curvature direction in edrioasteroids is recognized as generically and specifically consistent, but is not a sole determinant. Other morphologic traits in conjunction with curvature constitute the taxobases. In the fragmentary holotype and sole example of *S. reversata*, no features other than the direction of the ambulacral curvature differ from those found in typical *S. vorticellatus*. A similar fortuitous curvature reversal is known for one specimen of *Carneyella pilea*.

UCMP 24700. Arnheim Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Lawrenceburg, Indiana. 19.1 mm axial by 21.6 mm transverse diameter.
Pl. 10, fig. 14.

The specimen is large and well preserved except for the upper ends of the coverplates and the accompanying spines and spine basins, which have been extensively etched. The specimen clearly shows the peripheral rim and prosopon of the distal interambulacral plates.

UCMP 40438. Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio region. 11.7 mm axial by 13.9 mm transverse diameter.
Pl. 10, fig. 12.

This moderate-sized individual is missing a section of the posterior edge of the theca which divides ambulacrum I into two parts and creates the illusion that six, rather than five ambulacra are present. Distally the peripheral rim is reflexed. Noteworthy is the small size of the ambulacral spines in relation to the size of the underlying coverplates. The spine basins are deep.

UCMP 40437. Fairmount member, Fairview Formation, Cincinnatian Series, Upper Ordovician. North College Hill, Cincinnati, Ohio. 12.9 mm axial by 10.5 mm transverse diameter.
Pl. 10, fig. 11.

The theca is largely covered with matrix that has held the ambulacral spines in place atop the coverplates. The spines are large in proportion to the size of the underlying coverplates.

UCMP 26532. Upper Waynesville Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Wash bank, North branch, Cedar Creek, near Versailles, Indiana. 6.9 mm axial by 7.6 mm transverse diameter.
Pl. 10, fig. 10.

Plating detail is somewhat obscure in this specimen because of extreme etching, but the specimen is illustrated here because it is one of the rare examples of a young adult *S. vorticellatus.*

In addition to the above specimens, over 100 other *S. vorticellatus* have been examined in the course of this study. Unfortunately, most specimens are poorly preserved and add no information other than that provided by the above illustrated individuals.

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Hall (1866, 1871, 1872) characterized *S. vorticellatus* by the contrasolar curvature of the ambulacra and the narrowness of the interambulacra. He also noted general thecal features, including shape, size, anal area location, and the large, interlocking ambulacral coverplates. Meek (1873) reiterated Hall's description, stressing the height of the coverplates. He reillustrated one of Hall's specimens but not the holotype. This second specimen, which Hall figured (1871, 1872) but did not mention in the text, has since been commonly assumed to be the holotype.

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Williams (1918), Bassler (1935, 1936), and Regnéll (1966) all redescribed the basic features of *Streptaster vorticellatus* as being essentially in agreement with earlier descriptions. Williams suggested that *S. septembrachiatus* was merely an abnormal *S. vorticellatus,* although he did not indicate that *S. reversata* fell into the same category. On the other hand, Bassler not only accepted *S. septembrachiatus* as a distinct species, but even suggested that *S. reversata* belonged in the genus *Carneyella,* apparently disregarding the distinctive columnar ambulacral coverplates.

Kesling (1960) first accurately described the hydropore structure of a typical *Streptaster vorticellatus.* The present account differs only in terminology and a few new details revealed by additional specimens. Kesling's recognition of the stone canal passageway structure in Foerste's 1914 description of specimen USNM 87165 is still the only information on that structure.

The only significant error in previous descriptions of *S. vorticellatus* is the implication that the interambulacral plates are "granular," small, polygonal, and tessellate. In reality these plates are squamose and imbricate, but the large, irregular nodes on their exteriors create the false impression, especially in matrix-encrusted individuals, of a mosaic pattern of small plates.

Although readily visible in previously studied specimens, the large ambulacral spines of *S. vorticellatus* are reported here for the first time. Commonly these spines partly obscure the interlocking of the coverplates, yet this feature was accurately described by many earlier workers although the spines were overlooked. In fact, one of Hall's two lithographic illustrations (1872, pl. 6, fig. 13) records these spines along most of the length of the ambulacra.

Discussion

The most striking features of *Streptaster vorticellatus* are the extremely high, contrasolar ambulacra that dominate the entire oral surface and often totally obscure the remaining features of the theca. The ambulacral height results from the extreme vertical thickening of the coverplates, which produces their unique columnar shape. Also distinctive is the elongate slit between adjacent coverplates; hence the coverplate passageways are open to the exterior along the entire vertical wall of the exterior part of the ambulacrum.

The large, movable spines, seated in basins on the summit of the coverplates, appear to be unique to *Streptaster vorticellatus.* Other species may have similar spines, but they are delicate and appear to rest on the plate surfaces without well-formed basins. The deep, steep-sided spine basins no doubt restricted the direction of spine movement. Each deep basin lies along the distal margin of the nearly horizontal summit of the coverplate. The distal perradial edge of each basin is open along the perradial line. An erect spine seated in the deep basin would be restricted by the steep walls except along the distal perradial edge. Movement would be limited to rotation of the spine in an oblique distal direction, the upper end of the spine moving across the perradial line and backward between the perradial tips of the alternate two coverplates on the opposite side of the ambulacrum.

The limited range of possible spine movement would allow only two basic configurations of spines when the coverplates were closed, and two more when open. When coverplates were closed and the spines were vertically erect, they would form a single perradial row, their distal tips forming a slightly zigzag line due to the alternate positions of the opposing coverplates. If the spines were inclined toward the open side of the basins, each spine would extend between the perradial tips of the next two distal alternate coverplates on the opposite side of the ambulacrum, and thereby form a row of spines projecting obliquely upward and outward from either side of the ambulacrum. In this condition the ambulacrum would be protected along both sides by a row of laterally projecting spines.

When the coverplates were open (apparently forming only a narrow central gap between opposing coverplates), the spines would rest in the same two positions described above, but with a different effect: when erect, the spines would form a double row along the ambulacrum with a narrow central gap between the two rows. This condition would allow a clear passage of particulate matter into the food groove between the open coverplates. If the spines were inclined toward the open side of the basins, they would form an interdigitating gable over the gap. Such an arrangement might well have served as a coarse strainer above the food groove. Thus the spines may have aided in food selection in addition to their apparent protective capacity.

Streptaster vorticellatus occurs throughout the Cincinnatian Series (Upper Ordovician) in the Cincinnati Arch area. Several other species of edrioasteroids are common in this section, including Lebetodiscidae. However, *S. vorticellatus,* although found in the same formations as other Cincinnatian edrioasteroids, rarely is found on the same bedding planes. Perhaps the best illustration of this occurrence is the Forestville, Ohio site. A single bedding plane has yielded thousands of specimens of the four common Cincinnatian species, *Isorophus cincinnatiensis, Carneyella pilea, Cystaster granulatus,* and *C. stellatus,* but not a single example of *Streptaster vorticellatus.* However, several specimens of *S. vorticellatus* have been collected a few hundred feet away and not more than 10 feet stratigraphically above the densely populated layer.

S. vorticellatus are usually found resting on large, broken invertebrate skeletons in layers of organoclastic material that is coarser than that in which other Cincinnatian species are commonly found. The microfacies of the shallow Cincinnatian sea floor which best suited *S. vorticellatus* was probably an environment of somewhat higher energy than that preferred by other Cincinnatian edrioasteroids.

RANGE AND OCCURRENCE: Cincinnatian Series, Upper Ordovician of the Cincinnati Arch area, Ohio, Indiana, and Kentucky.

Genus *Cystaster* Hall, 1871

1852 [*non*] *Hemicystites* Hall, J., Nat. Hist. New York, pt. IV, Palaeontology 2: 245.

1866 *Agelacrinus (Hemicystites)* Hall, J. [*partim*], New York State Mus., 20th Ann. Rept. (adv. pub.): 8.

1871 *Hemicystites* (s.g. *Cystaster*) Hall, J., New York State Mus., 24th Ann. Rept. (adv. pub.): Explanation of pl. 2, fig. 1–6.

1872 *Agelacrinus (Hemicystites)* Hall, J., New York State Mus., 24th Ann. Rept.: 215–216, pl. 6, fig. 5–6; *Hemicystites* (s.g. *Cystaster)* Hall, *idem, ibid.*: Explanation of pl. 6, fig. 1-4.

1873 *Hemicystites* Hall, Meek, F. B., Geol. Surv. Ohio, v. 1, Geology and Palaeontology, pt. 2, Palaeontology, sect. 1: 52–54, pl. 3, fig. 8a-b; *Hemicystites (Cystaster)* Hall, *idem, ibid.*: 54, pl. 3, fig. 9a-b.

1889 *Hemicystites* Hall, Miller, S. A., North American Geology and Palaeontology, Cincinnati: 252.

1896b *Hemicystis* Hall, Haeckel, E. [*partim*], Die Amphorideen und Cystoideen, Leipzig: 111–112, pl. 3, fig. 27, 28.

1899 *Thecocystis* Jaekel, O., Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 43, pl. 1, fig. 1a-b; *Cystaster* Hall, *idem, ibid.*: 43–44, pl. 1, fig. 2, 2a; *Hemicystites* Hall, *idem* [*partim*], *ibid.*: 49.

1900a *Cystaster* Hall, Bather, F. A., *in* A Treatise on Zoology, E. R. Lankester (ed.), London, pt. III, Echinoderma: 207, fig. 2.

1906 *Hemicystites* Hall, Rowley, R. R., *in* Contribution to Indiana Palaeontology, G. K. Greene, 2 (2): 27–28, pl. 6, fig. 3, 4.

1910 *Hemicystites* Hall, Grabau, A. W. and Shimer, H. W., North American Index Fossils, Invertebrates, New York, 2: 473, fig. 1784-a, c.

1914 *Hemicystites* Hall, Foerste, A. F. [*partim*], Denison Univ., Sci. Lab. Bull. 17 (art. 14): 454–456, pl. 3, fig. 2a-b, pl. 6, fig. 6a-b; *Cystaster* Hall, *idem, ibid.*: 454, pl. 6, fig. 5a-d.

1915 *Hemicystites* Hall, Bassler, R. S. [*partim*], United States Nat. Mus. Bull. 92, 1: 605–607; *Hemicystites (Cystaster)* Hall, *idem, ibid.*: 606.

1918 *Thecocystis* Jaekel, O., Palaeontologische Zeitschr. 3: 112; *Cystaster* Hall, *idem, ibid.*: 112.

1935 *Cystaster* Hall, Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 3; *Cincinnatidiscus* Bassler, *idem, ibid.*: 3–4.

1936 *Cystaster* Hall, Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 4–5, pl. 1, fig. 14, pl. 2, fig. 3–5; *Cincinnatidiscus* Bassler, *idem, ibid.*: 5–6, pl. 2, fig. 10–12, pl. 3, fig. 11, pl. 5, fig. 4, 12.

1938 *Cincinnatidiscus* Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 66; *Cystaster* Hall, *idem, ibid.*: 82.

1943 *Cystaster* Hall, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 200; *Cincinnatidiscus* Bassler, *idem, ibid.*: 198–199.

1944 *Cystaster* Hall, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 129, pl. 49, fig. 9, 10; *Cincinnatidiscus* Bassler, *idem, ibid.*: 129, pl. 49, fig. 17, 18.

1953 *Cystaster* Hall, Piveteau, J., Traité de Paléontologie, Paris, 3: 652, fig. 2.

1960 *Cystaster* Hall, Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 165–166, fig. 10, pl. 9, fig. 1–6; *Cincinnatidiscus* Bassler, *idem, ibid.*: 167–169, pl. 8, fig. 1, 3, 4.

1966 *Cystaster* Hall, Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U165, text fig. 114-1, 120-3a, 125-5, 126-4; *Cincinnatidiscus* Bassler, *idem, ibid.*: U165, text fig. 125-1.

1967 *Cystaster* Hall, Kesling, R. V., Jour. Paleont. 41 (1): 201.

TYPE SPECIES: *Hemicystites (Cystaster) granulatus* Hall, 1871.

Diagnosis

Lebetodiscidae with: theca discoidal to clavate; oral area with no secondary orals; hydropore structure formed by one large and one very large interambulacral and the proximal two coverplates of the posterior side of ambulacrum V; ambulacra straight, in clavate forms draped down over convex upper surface to ambitus; external foramina of coverplate passageways large, elongate; interambulacrals squamose, imbricate, each with external nodes; anal periproct in proximal part of interambulacrum 5; delicate ambulacral spines may be present, apparently without articulatory basins.

Description

The thecal shape in *Cystaster* is singularly variable, and ranges from discoidal through most intermediates to clavate. The discoidal forms have steep, short sides which rise from the substrate to a nearly flat oral surface. In plan view they are commonly subpentagonal, the distal tips of the ambulacra marking the five angles. The fully clavate forms have an upper gibbous part with the oral area at the summit, the ambulacra draping down the upper surface but ending at the ambitus. Below the ambitus the theca constricts and forms a pedunculate zone which terminates at the substrate in an outward flaring basal peripheral rim. Between these two extremes a nearly complete spectrum of intermediate forms has been found. The missing segment of the gradational sequence is at the discoidal end of the series, between low subclavate forms, with only a short zone of constriction below the ambitus, and the true disklike forms.

Members of this genus are small in comparison to other Lebetodiscidae. In clavate forms the upper gibbous "head" is usually 6 mm to 8 mm in diameter, whereas thecal height is extremely variable, attaining a maximum of approximately 15 mm. The largest observed discoidal theca is approximately 11 mm in diameter.

The oral area of *Cystaster* includes only the three primary orals and two pairs of lateral shared coverplates common to all Lebetodiscidae (pl. 11, fig. 16). *Cystaster* is thus unique among the Lebetodiscidae in lacking secondary oral plates. The wide, elongate external foramina of the adjacent coverplate passageways impart a sagittate external shape to the primary oral elements that is noticeable in highly etched specimens but obscured in average specimens, owing to the great height of these plates.

The hydropore structure is formed by two enlarged interambulacrals and the two proximal posterior coverplates of ambulacrum V. The enlarged proximal adradial tip of the proximal coverplate extends into the adjacent part of interambulacrum 5. The posterior edge of this extended zone forms the anterior edge of the slitlike hydropore. The posterior side of the opening is formed by the anterior edge of the larger posterior hydropore interambulacral. The exterior of this plate bears a prominent, highly elevated, sickle-shaped ridge which masks the polygonal shape of the plate. This larger interambulacral intrudes into the edge of ambulacrum V, and abuts the shortened adradial edge of the second coverplate. This second coverplate may form the merest tip of the right end of the hydropore slit or may be entirely separated from the opening. The smaller of the two hydropore interambulacrals lies slightly anterior to, and to the left of the larger. It appears to form the left tip of the opening in some, but does not make contact with it in others. However, the smaller interambulacral always forms part of the underlying stone canal passageway.

The ambulacra are rectilinear and form high ridges on the thecal surface (pl. 12, fig. 8). These are proportionately higher than in *Foerstediscus* or *Lebetodiscus*, but lower than in *Streptaster*. The thick coverplates extend vertically upward from the interambulacra and abruptly curve perradially to terminate in wide horizontal surfaces which form the level summits of the ambulacral ridges. Thus the coverplates are similar in shape to those of *Streptaster*, but they are relatively lower and much wider in *Cystaster*. The coverplate width results in broad ambulacra which restrict the interambulacra to relatively narrow zones. Intra-ambulacral and intrathecal extensions of the coverplates are similar to those of other Lebetodiscidae.

The coverplate passageways extend inward nearly vertically between adjacent coverplates. The upper ends of the passageways open to the exterior through large, elongate foramina. The upper perradial end of each foramen is wide and clearly exposes the outer surface of the flexed, bladelike intra-ambulacral extension which forms the inner side of the upper end of the passageway. However, the outer lateral edges of adjacent coverplates, which form the outer side of each passageway, do not make contact until they near the adradial suture line. Thus an elongate slit which narrows adradially extends the perradial wide part of the external foramen down toward the adradial suture line.

The ambulacral floorplates are trough-shaped and imbricate; each floorplate proximally overlaps the distal edge of the adjacent element.

Interambulacral plates are small, squamose and imbricate. Since the interambulacra are restricted by the exceptionally wide ambulacra, their total area is relatively small in discoidal forms. In clavate individuals, the interambulacrals extend distal to the ambitus and form the constricted pedunculate zone which ends distally at the basal, flared, peripheral rim. As in *Streptaster*, interambulacrals falsely appear to be granular, tessellate plates. This is because of the prosopon of irregular, rounded protuberances which cover their exteriors. The density and prominence of this sculpture, especially in imperfectly cleaned specimens, conceals the squamose nature of the plates.

The periproct lies near the center of interambulacrum 5, and is formed by several loose, irregular circlets of plates. Commonly these are elongate and decrease in size toward the center of the area.

The distal peripheral rim comprises four to six circlets of plates which diminish in size distally. Plates of the proximal two or three circlets are elongate concentric with the thecal margin; the distal circlet plates are radially elongate.

In two specimens assigned to *Cystaster stellatus*, there are long, thin, delicate spines on the upper surface of some ambulacral coverplates. They are assumed to be generally present, but because of their fragility have usually been lost soon after death or by more recent erosion.

Discussion of previous investigation

Hall (1871) introduced the name *Cystaster* as a provisional subgenus under *Hemicystites* in an advance printing of his 1872 paper in the " 24th Annual Report of the New York State Cabinet of Natural History." It was monotypic, based on his new species *Hemicystites granulatus.* A footnote in the explanation accompanying plate 2 of the 1871 paper noted briefly that *Cystaster* was "saclike, composed of minute plates, and surmounted by five . . . ambulacral areas, each one consisting of two series of external plates separated by a narrow groove, and beneath these a more distant series separated by a wider median groove." Hall suggested that the " granular " nature of the plates and the possible " free " condition of one individual (in which the peripheral rim is missing and the broken pedunculate zone was shown as ending bluntly, pl. 11, fig. 1-3) were enough to provisionally separate the species as a new subgenus. Restudy of *Hemicystites parasiticus,* the type of that genus, has shown that it is not even closely related to *Cystaster granulatus. Hemicystites* [with a double biseries of ambulacral coverplates; without coverplate passageways; with oral area including primary orals, shared coverplates, and a hydropore oral; and with a valvular anus] is included in the suborder Isorophina.

Cystaster has been recognized by most modern authors as a distinct genus. Haeckel (1896) incorrectly cited *Hemicystites (Cystaster) granulatus* as the type species of *Hemicystis* [*sic*] (which is, in reality, *Hemicystites parasiticus* Hall, 1852, by original designation).

In 1899 Jaekel introduced the genus *Thecocystis* for his new species *T. sacculus.* He suggested that of Hall's original four figures of *Cystaster granulatus* only his figure 1 belonged to that species, whereas the other three (figures 2, 3, and 4 of plate 6; *i.e.,* plate 2 of the 1871 advance publication) were different. Thus he proposed *Thecocystis sacculus,* and cited Hall's figures 2, 3, and 4 of plate 6 as the type specimens of his new type species. Subsequent authors have rejected Jaekel's conclusions and placed *T. sacculus* in synonymy with *C. granulatus,* as is done here.

Jaekel based his assessment of Hall's work on interpretation of the Hall illustrations (drawings, not the specimens) and on two additional specimens that were available to him for study. As noted by Jaekel, Hall's figure 1, plate 6 does look different from figures 2, 3, and 4. However, this is not due to morphologic differences but rather to the differing views and modes of preservation of the individuals portrayed. The specimens seen in figures 2, 3, and 4 are viewed from an oblique angle and preserve the pedunculate zone at least partially distended. Moreover, these individuals all display the oral and ambulacral coverplates partly open along the perradial lines. This is a common occurrence in specimens of *C. granulatus,* and is apparently related to preservational compression of high thecae. In contrast, the individual represented in figure 1 shows the ambulacral coverplates closed and interlocking along the perradial line, and the theca depressed so as to hide the pedunculate zone.

Hall, (1871, 1872) had noted the difference in his specimens, although he erroneously concluded that the specimen in figure 1 retained " the external plates " of the ambulacra, whereas the other specimens had these supposed plates removed. Thus Hall described two sets of coverplates, one on top of the other. Regardless of the preservational differences between the specimens illustrated, Hall clearly described *Cystaster* as clavate, and therefore the examples of *C. granulatus* shown in figures 2, 3, and 4 of plate 6, would be the most typical representatives.

Hall's original specimen of plate 6, figure 1 is MCZ 515 (old 3878) in the Museum of Comparative Zoology. This specimen was mistakenly listed there as the one illustrated by Hall in plate 6, figure 5, one of the types of his *Hemicystites stellatus.* Comparison of the specimen with the original figure and description clearly shows that this is not the figure 5 specimen, whereas its size, preservation, and thecal detail appear to be identical to the one portrayed in figure 1. This specimen seems to be conspecific with the other three in the type lot, although it has collapsed vertically, flattening the oral surface. The depressed lower part of the theca, below the ambitus, is clearly constricted and forms the pedunculate region of the clavate theca. Thus the types of Jaekel's *Thecocystis sacculus* are conspecific with all of Hall's types of *Cystaster granulatus.*

Jaekel's (1899) illustrations of the two additional specimens, one identified as his *T. sacculus,* the second as a *Cystaster granulatus,* suggest an explanation for his confusion. The first (his *T. sacculus*) is a well-preserved, inflated, and clavate *Cystaster granulatus.* The ambulacrals and orals are widely separated along the perradial line. This individual is clearly conspecific with Hall's specimens illustrated in plate 6, figures 2, 3, and 4. Jaekel's other specimen (illustrated as *C. granulatus*) is a typical *Cystaster stellatus.* The theca is discoidal and the orals are tightly closed across the perradial lines. Therefore in plan view this specimen looks similar to that in figure 1 but not to the other three illustrated specimens. However, it is unclear why Jaekel did not immediately see the similarity of this specimen to the types of *C. stellatus* which were illustrated by Hall on the same plate. Thus Jaekel was correct in believing that he had two different species represented by his two specimens (but not two genera). Fortunately, most subsequent authors have not recognized Jaekel's new taxa, and therefore little confusion has resulted from them.

Bassler (1935) proposed the genus *Cincinnatidiscus* with *Hemicystites stellatus* Hall as the type species. He indicated that the new genus was most closely related to *Cystaster*, but differed in its discoidal theca and squamose, imbricate interambulacrals from the clavate theca and supposedly "granular" interambulacrals of *Cystaster*. Bassler's genus was ill conceived, and conforms in all respects with *Cystaster*. Both *Cystaster granulatus* and *Cystaster stellatus* have squamose interambulacrals, but the prosopon in the former often obscures the underlying plate shapes. The single major distinction between the two is thecal shape, which is here judged to be a specific trait. In 1936 Bassler described a new species of *Cystaster* and two new species of *Cincinnatidiscus*. None of the three is recognized here as distinct. His *Cystaster ulrichi* and *Cincinnatidiscus turgidus* are synonyms of *Cystaster granulatus;* his *Cincinnatidiscus edenensis* appears indistinguishable from *Cystaster granulatus.*

Discussion

The two species here assigned to *Cystaster* are closely related and may be antipodal extremes of a gradational series. A "typical" *C. granulatus* is clavate and a "typical" *C. stellatus* is discoidal. But there is a nearly complete transitional series between the two thecal expressions. All of these moderately convex intermediates in which the lower parts of the theca are exposed have a short but definitely constricted pedunculate zone below the upper surface, which thus indicates that they are best attributed to *C. granulatus.* However, it is not unusual for the peripheral rim area of *C. stellatus* to be vertical or even slightly constricted below the upper surface of the theca, as if to initiate, but never actually form a pedunculate region. Whether or not the gradation between the two forms is absolutely complete remains to be shown.

For the present the species are recognized as distinct. Certainly the appearance of the two end members of the series is quite different. Even microenvironmental differences would appear to be ruled out as an explanation for thecal shape variability, for not only the two end expressions, but also intermediate forms are found within a few millimeters of one another (pl. 12, fig. 10). Occasionally the peripheral rims of specimens with different thecal shapes may even abut one another.

A possible explanation of the thecal variations, suggested by Caster (personal communication, 1969) is that one form represents the paedomorphic expression of the other. The known examples of juveniles with diameters of 3 mm or less are nearly impossible to separate specifically. The smallest known *Cystaster* specimens are commonly moderately convex, proportionately higher than adult *C. stellatus,* but lower than *C. granulatus.* The peripheral rim in these juveniles is almost vertical except for the distal circlets which flare outward upon contact with the substrate. Thus the theca does not clearly correlate with either adult form, and both adult shapes could easily be derived from this juvenile. Proliferation of plates above the rim could form the pedunculate zone for *C. granulatus,* increasing the convexity of the upper oral surface. Conversely, for *C. stellatus* the thecal diameter could be increased by the addition of plates to the peripheral rim, causing the upper oral surface to become nearly flat or only gently convex. It would appear that forms here called *C. stellatus* represent the paedomorphic form, which matures with little modification of the thecal shape except for an increase in diameter. Conversely, in view of the fact that oral surface curvature in juveniles is somewhat greater than in adult *C. stellatus, C. granulatus* might be considered a paedomorphic form of *C. stellatus.* In this case, typical *C. stellatus* would show a slight decrease in convexity during growth, whereas the paedomorphic expression of the species (or *C. granulatus*) would represent the maturation and accentuation of the moderate convexity of the young *C. stellatus.* However, if paedomorphism is the correct explanation, it seems more likely that the form represented by the individuals referred to here as *C. stellatus* are the paedomorphic expressions of *C. granulatus.*

RANGE AND OCCURRENCE: Trenton Group, Middle Ordovician through Richmond Group, Upper Ordovician of the Cincinnati Arch area, Indiana, Kentucky, Ohio.

Cystaster granulatus Hall, 1871

Text fig. 10; plate 11, plate 12, fig. 1-10

1871 *Hemicystites* (s.g. *Cystaster*) *granulatus* Hall, J., New York State Mus., 24th Ann. Rept. (adv. pub.): Explanation of pl. 2, pl. 2, fig. 1–4.

1872 *Hemicystites* (*Cystaster*) *granulatus* Hall, J., New York State Mus., 24th Ann. Rept.: Explanation of pl. 6, pl. 6, fig. 1–4.

1873 *Hemicystites* (*Cystaster*) *granulatus* Hall, Meek, F. B., Geol. Surv. Ohio, v. 1, Geology and Palaeontology, pt. 2, Palaeontology, sect. 1: 54, pl. 3, fig. 9a-b.

1889 *Hemicystites granulatus* Hall, Miller, S. A., North American Geology and Palaeontology, Cincinnati: 252.

1896b *Hemicystis granulata* Hall, Haeckel, E., Die Amphorideen und Cystoideen, Leipzig: 111–112, pl. 3, fig. 27, 28.

1899 *Thecocystis sacculus* Jaekel, O., Stammesgeschichte der Pelmatozoen, Bd. I, Thecoidea und Cystoidea, Berlin: 43, pl. 1, fig. 1a-b; *Cystaster granulatus* (Hall), *idem, ibid.*: 43–44, pl. 1, fig. 2, 2a.

1900a *Cystaster granulatus* (Hall), Bather, F. A., *in* A Treatise on Zoology, E. R. Lankester (ed.), London, part III, Echinoderma: fig. 2.

1910 *Hemicystites granulatus* (Hall), Grabau, A. W. and Shimer, H. W., North American Index Fossils, Invertebrates, New York, 2: 473, fig. 1784-c.

1914 *Cystaster granulatus* (Hall), Foerste, A. F., Denison Univ., Sci. Lab. Bull. 17 (art. 14): 454, pl. 6, fig. 5a-d.

1915 *Hemicystites (Cystaster) granulatus* Hall, Bassler, R. S., United States Nat. Mus. Bull. 92, 1: 606.

1935 *Cystaster granulatus* (Hall), Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 3.

1936 *Cystaster granulatus* (Hall), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 4, pl. 1, fig. 14; *Cystaster ulrichi* Bassler, *idem, ibid.*: 4–5, pl. 2, fig. 3–5; *Cincinnatidiscus turgidus* Bassler, *idem, ibid.*: 6, pl. 5, fig. 12.

1938 *Cystaster granulatus* (Hall), Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 82.

1943 *Cystaster granulatus* (Hall), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 200; *Cystaster ulrichi* Bassler, *idem, ibid.*: 200; *Cincinnatidiscus turgidus* Bassler, *idem, ibid.*: 199.

1944 *Cystaster granulatus* (Hall), Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 129, pl. 49, fig. 9, 10.

1953 *Cystaster granulatus* (Hall), Piveteau, J., Traité de Paléontologie, Paris, 3: 652, fig. 2.

1960 *Cystaster granulatus* (Hall), Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 165–166, text fig. 10, pl. 9, fig. 1–6.

1966 *Cystaster granulatus* (Hall), Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U165, text fig. 125-5, 126-4.

Diagnosis

A *Cystaster* with: clavate theca; ambulacra draped down upper side to ambitus; constricted lower pedunculate zone extended down to basal peripheral rim; larger hydropore interambulacral with a very prominent sickle-shaped ridge; interambulacral plates squamose and imbricate, but commonly appearing granular, because of the presence of prosopon.

Description

Cystaster granulatus is clavate. The ambulacra are rectilinear, but are draped downward on the highly convex upper oral surface and end at the ambitus (pl. 11, fig. 1-3). The downward constricting pedunculate zone varies greatly in length. Distally it meets the proximal margin of the basal peripheral rim which flares out against the substrate. The diameter of the distal edge of the peripheral rim commonly equals or exceeds the maximum diameter of the upper gibbous " head " of the theca. The ambulacral and oral plates are thick and consequently rise above the interambulacra. The conical anal structure also rises above the surrounding interambulacrum. The diameter of the gibbous thecal " head " averages 6 to 8 mm in adults. The maximum observed thecal height is approximately 15 mm.

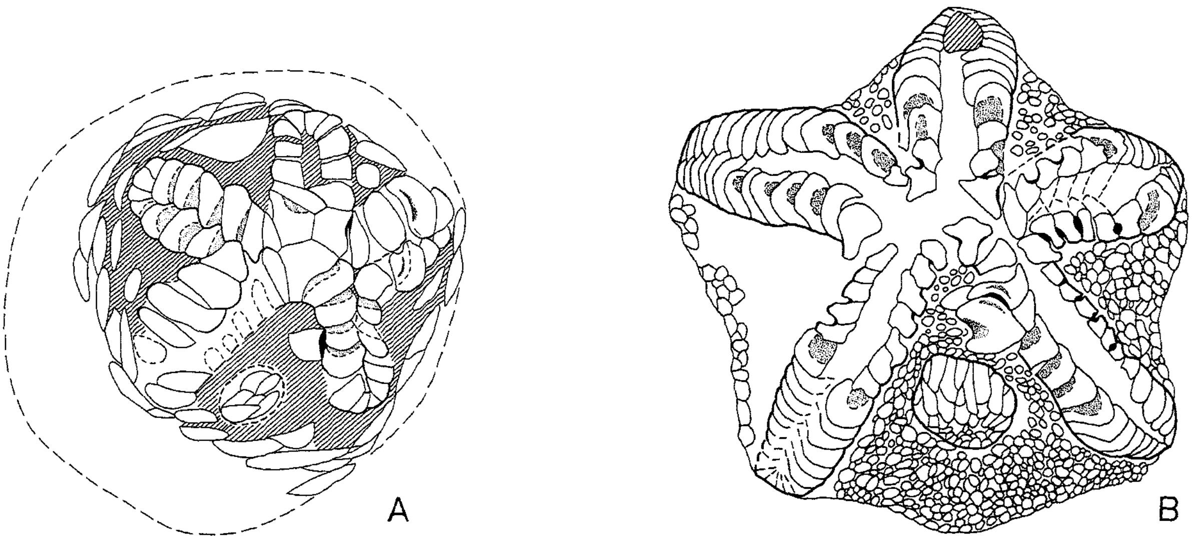
The oral plates of *C. granulatus* (three primary, two pairs of lateral shared coverplates) are commonly separated perradially during thecal collapse along the transverse and anterior oral midlines and expose the underlying oral frame and central lumen (pl. 12, fig. 2, 5-8). The frame appears to be formed by the proximal floorplates of the five ambulacra and the intrathecal extensions of the primary oral plates. It appears to be identical to that described in detail for *C. stellatus.*

The hydropore structure of *Cystaster granulatus* (as described for the genus) may differ from that of *C. stellatus* in only one respect: the large, sickle-shaped ridge on the exterior of the larger hydropore interambulacral may be larger in *C. granulatus* (text fig. 10B, pl. 12, fig. 1-3).

Kesling's (1960) description of the hydropore structure of *C. granulatus* differs in a few respects. Setting terminology differences aside, he depicted the ambulacral components of the structure essentially as presented here. However, he believed only one enlarged interambulacral plate was involved — the larger and more posterior of the two described here. No mention is made of the second interambulacral element. He also indicated that the larger interambulacral extends entirely across the anterior part of the posterior interambulacrum to end adjacent to the adradial edge of ambulacrum I, and he thought that the hydropore slit extended along the entire length of the anterior edge of the larger interambulacral plate.

Discrepancies between the two descriptions are minor and may be attributed to the current availability of a much larger suite of specimens than was available in 1960. The structure extends no more than three-fourths the distance across the anterior part of the posterior interambulacrum. The length of the slit is still questionable, but appears limited to the right two-thirds of the anterior edge of the larger interambulacral plate. The inclusion of a second enlarged interambulacral element in the structure can now be demonstrated in a number of specimens. This plate forms the left end of the structure, and is much smaller than the other hydropore interambulacral. Commonly it appears to be separated from the opening, but occasionally it may abut the left tip of the slit. The intrathecal part of this plate forms part of the underlying stone canal passageway.

The ambulacra of *Cystaster granulatus* appear to be identical to those of *C. stellatus*, although the coverplates are commonly preserved open, *i.e.*, separated along the perradial line. This is due to compression of the clavate theca. In both species the angular perradial ends of the biserial coverplates form a right-angled zigzag median line when they are closed. However, etching of the coverplates commonly exaggerates the undulations and may also produce a somewhat irregular path by exposing the



Text figure 10. *Cystaster granulatus* Hall, 1871

A. USNM 42138, (x 15), pl. 11, fig. 11. B. UCMP 40443, (x 10), pl. 12, fig. 3.

Dashed lines separate the main body of the ambulacral coverplates from their intra-ambulacral extensions.

upper ends of the underlying intra-ambulacral extensions on the proximal edges of these elements.

Interambulacral plates are small, squamose, and imbricate. However, their configuration is commonly masked by relatively large, irregular nodes which create the false impression of minute granular plates — the basis for the inappropriate trivial name.

The proximal plates of the peripheral rim, commonly hidden under the collapsed pedunculate zone, appear to bear nodes similar to those of the interambulacrals. This prosopon rapidly diminishes distally. The small distal rim plates commonly have a single elongate crest which extends the length of each plate.

It is possible that thin, delicate ambulacral spines were mounted on the flat summits of the coverplates in this species, as in *C. stellatus*, although no indication of spines has been seen. It must be noted, however, that of thousands of specimens of *C. stellatus* available for the present study, only two preserve the spines. No such quantity of material is available for *C. granulatus*.

Specimens

MCZ 521 (A, B, C). "Hudson River Group," probably Maysville Group, Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio.

MCZ 521-C. Lectotype of *Cystaster granulatus* Hall (1871, pl. 2, fig. 4). 6.2 mm axial by 4 mm transverse diameter; maximum height 11.3 mm.
Pl. 11, fig. 1-3.

MCZ 521-B. Lectoparatype of *C. granulatus* Hall (1871, pl. 2, fig. 3). 8.6 mm axial by 6.4 mm transverse diameter; height 5 mm.
Pl. 11, fig. 4, 5.

MCZ 521-A. Lectoparatype of *C. granulatus* Hall (1871, pl. 2, fig. 2). 6.3 mm axial by 4.3 mm transverse diameter; height 7.7 mm; maximum diameter of upper surface of theca 6.6 mm.
Pl. 11, fig. 6-8.

These specimens are three of the four used by Hall in the original description of the species. MCZ 521-C is here designated as the lectotype. It clearly shows the clavate thecal shape and other taxonomically significant features. MCZ 521-A and B are lectoparatypes. All three specimens are moderately well preserved, although the lower parts of the theca in all three are partially obscured by a thin covering of tenacious matrix. The upper sides of the thecae vary in completeness, since some parts of each individual have been lost.

The lectotype preserves the pedunculate zone in a distended state, although it is laterally compressed. The partially disrupted ambulacral coverplates and adjacent orals are broken along the right side of the theca. Contrary to the impression created by Hall's 1871 illustration, the specimen was obviously attached at the base of the pedunculate zone by a peripheral rim.

Lectoparatype MCZ 521-A is likewise compressed laterally and has a partially distended pedunculate zone. The gibbous " head " has been obliquely compressed and this partly disrupted the plates. The upper ends of many plates have been broken away.

Lectoparatype MCZ 521-B has the shortest pedunculate zone of the three. The upper oral surface remains moderately convex. Here again the upper ends of the ambulacral plates of the left side of the theca have been broken away. Ambulacra IV and V are the best preserved, although the coverplates have been etched. Plates of the oral region (despite breakage), the hydropore structure, and the periproct are distinct. Unlike the perradial disarticulated orals and ambulacrals of the other two, in this specimen they remain in a closed position and interlock across the perradial lines.

MCZ 515 (old 3878). Lectoparatype of *C. granulatus* Hall (1871, pl. 2, fig. 1). (?) Fairview Formation, Maysville Group, Cincinnatian Series, Upper Ordovician. 80 feet below the top of the hills, Cincinnati, Ohio. 9.4 mm axial by 8.9 mm transverse diameter.

Pl. 11, fig. 12, 13.

This specimen was found in the Museum of Comparative Zoology with types of *Cystaster stellatus.* The accompanying label indicated that the specimen was one of Hall's original specimens supposedly figured in plate 6, fig. 5 (*i.e.*, 1871, pl. 2, fig. 5) as *Hemicystites stellatus.* This specimen does not correlate with that illustration, but is identical in size, shape, and thecal detail to figure 1 of that plate and seems to be one of the original four specimens illustrated by Hall as types of *Cystaster granulatus.* This discovery has been critical in evaluating Jaekel's interpretation of Hall's work and the taxonomy proposed by Jaekel for Hall's illustrations.

The specimen has the orals and ambulacral coverplates tightly interlocked perradially. The upper surface has collapsed from its originally bulbous state to a nearly flat condition. The depressed pedunculate zone is preserved on the lower side of the specimen, although it is partly hidden by a fragment of the brachiopod on which the individual was resting. Surficial etching has removed most external details.

USNM 42138. Holotype of *Cystaster ulrichi* Bassler (1936, p. 4-5, pl. 2, fig. 3-5). Economy beds of the Eden [Kope] Formation, Eden Group, Cincinnatian Series, Upper Ordovician. West Covington, Kentucky. 4.4 mm axial by 3.9 mm transverse diameter.

Text fig. 10A, pl. 11, fig. 11.

The theca is as much domal as clavate, although collapse may have hidden the lower pedunculate zone. The specimen is surrounded distally by a faint pyrite film that appears to mark the location of a missing peripheral rim. The upper thecal surface has partially collapsed. The distal coverplates of ambulacrum III are missing, and the upper tips of the hydropore plates are gone. The relationships of this specimen and the following ones are discussed below.

USNM 87628 (A-C). Type specimens of *Cincinnatidiscus turgidus* Bassler (1936, p. 6). Whitewater Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Oxford, Ohio. Three individuals on one slab.

USNM 87628-A. Holotype (Bassler, 1936, pl. 5, fig. 12). 7.9 mm axial by 8.2 mm transverse diameter.

Pl. 11, fig. 9.

USNM 87628-B. 11.9 mm greatest diameter by a perpendicular of 11.1 mm.

Pl. 11, fig. 10.

USNM 87628-C. Small fragment of a third specimen.

Specimen A is a moderately well preserved clavate individual. Ambulacrum V, the hydropore, and the anal structure are missing. The pedunculate zone is completely hidden under the collapsed upper surface, but the upper surface is only slightly disrupted.

Specimen B is a second specimen on the same slab as A. Much of the upper theca is missing, exposing the peripheral rim. The outermost rim plates are radially elongate and each has a prominent, sharp-crested ridge which extends nearly its entire length. The next few rows of plates are elongate concentric with the thecal margin. Each of these plates bears one or more large nodes; these increase in size and abundance proximally.

* * *

Hundreds of individuals of *C. granulatus* were collected from a single bedding plane, all members of one population (referred to here as the Forestville population). A few examples are illustrated here to document morphology and variation.

UCMP 40439-40449. Fairmount member, Fairview Formation, Maysville Group, Cincinnatian Series, Upper Ordovician. North end of excavation for Beechmont Mall shopping center, opposite Anderson High School, Forestville, Ohio (Withamsville, Ohio-Kentucky quadrangle), 7.5 minute topographic sheet (1953), Ohio coordinate system: 397.300′; 1,474,700′, equals approximate center of 200-foot by 200-foot area [now under blacktop].

UCMP 40439. 5.2 mm axial by 5.6 mm transverse diameter; 3.6 mm high.

Pl. 11, fig. 20, 21.

This specimen has only four ambulacra. The mode of contact between these and the oral area suggests that the missing one is ambulacrum IV, with ambulacrum III distally displaced to the right of its normal position. The specimen is deeply etched, and the posterior interambulacrum is reflexed under the upper part of the theca so that the anus now lies below the ambitus. The large interambulacral hydropore plate is present but reduced in size by etching. The lower end of the pedunculate zone is covered with recalcitrant matrix.

UCMP 40440 (a, b). Two individuals on one slab, one large specimen with six ambulacra (a), and one small, normal, clavate specimen (b).

(a) 7.2 mm axial by 8 mm transverse diameter; 2.5 mm high.

Pl. 11, fig. 14, 15.

This is a six-rayed individual which is not particularly well preserved. The theca has collapsed vertically and the pedunculate zone is consequently hidden beneath the upper surface. The extra radius results from a splitting of ambulacrum II; the branch ambulacrum extends from the posterior side into interambulacrum 1. This specimen is the only *C. granulatus* with more than five ambulacra which is available for illustration, although four other similar variants from the same population have been observed. The occurrence of extra ambulacra appears to be more common in *Cystaster stellatus*, although this could be an accident of collecting rather than a statistically significant variation between the two species.

UCMP 40441. 3.8 mm axial by 4 mm transverse diameter.

Pl. 12, fig. 2.

This is a small, exceptionally well preserved individual. It affords a clear view of the hydropore slit which lies along the anterior edge of the large interambulacral hydropore plate and is bounded along its anterior margin by the posterior side of the enlarged adradial end of the proximal posterior coverplate of ambulacrum V. The sickle-shaped ridge on top of the hydropore plate stands in high relief. The periproct is preserved as a high, conical elevation distal and offset to the left of the hydropore. The ambulacral coverplates and the orals are disarticulated perradially, but the wide grooves are partially filled with matrix which obscures the inner surfaces of these plates.

UCMP 40442. Specimen broken from resting surface (brachiopod). 6.8 mm axial by 6.4 mm transverse diameter; by 2.8 mm high.

Pl. 11, fig. 18, 19.

The plates of this individual are well preserved, but the theca has collapsed, flattening the upper oral surface and compressing the pedunculate zone. The orals and ambulacral coverplates are interlocked perradially. The lower side of the specimen reveals the plates of the collapsed pedunculate zone and the basal peripheral rim which lies near the center of the lower surface.

UCMP 40443. 6.4 mm axial by 6.8 mm transverse diameter, 4.8 mm high.

Text fig. 10B, pl. 12, fig. 3, 4.

This specimen preserves the clearly exposed hydropore structure and conical periproct. Under xylene, sections of the coverplate passageways of the posterior side of ambulacrum I and IV are exposed where the upper ends of the coverplates have been lost.

UCMP 40444. 4 mm axial by 4.1 mm transverse diameter; 2 mm high.

Pl. 12, fig. 6.

This rather small individual is deeply etched; the coverplates are widely opened and thus their lower ends on opposite sides of each ambulacrum abut along the center of the ambulacrum. This hides the floorplates and creates the illusion that biserial floorplates are present. The perradial displacement of the inner ends of the coverplates from their life positions along the margins of the floorplates suggests that the coverplates formed only a narrow perradial gap when open. Wider opening would appear to have disrupted their inner ends.

UCMP 40445. 7.8 mm axial by 8 mm transverse diameter, 4 mm high.

Pl. 12, fig. 7.

This specimen, partially covered with tenacious matrix, retains the upper tips of the oral plates which are commonly broken off in specimens that are free of matrix.

UCMP 40446. 4.8 mm axial by 5.2 mm transverse diameter, approximately 4 mm high.

Pl. 12, fig. 5.

This small specimen is well preserved except for the presence of foreign ambulacral coverplates over interambulacrum 3. The orals and proximal ambulacral coverplates are widely separated perradially although the distal ambulacral coverplates are nearly closed.

UCMP 40447. 8 mm axial by 7.9 mm transverse diameter, approximately 4 mm high.

Pl. 12, fig. 1.

This large individual preserves closed coverplates in ambulacra I and V, but perradially disarticulated plates in the other three ambulacra. The oral plates are only slightly separated perradially, although the large primary posterior oral plate has been cleaved and the upper portion of the plate is now missing. The larger interambulacral hydropore plate is well preserved.

UCMP 40448. 5.6 mm axial by 5.2 mm transverse diameter, 1.6 mm high.

Pl. 11, fig. 16, 17.

This specimen demonstrates the common difficulty involved in the separation of the two species of *Cystaster*. The ambulacral coverplates and the oral elements remain tightly in contact perradially, rather than agape as is so common in *C. granulatus*. Thecal collapse has differentially depressed the upper oral surface; the right half is almost horizontal, whereas the left side retains some convexity. As a result, the ambulacra appear to extend horizontally out from the oral region and not to drape down the sides of the theca. Except for I and II, the ambulacra appear to end at the margin of a flat surface, as they do in *C. stellatus*. However, close inspection shows that a collapsed pedunculate zone is present, although it is now almost entirely hidden. If the lower edge of the specimen had been covered by matrix, it would be impossible to be sure whether the individual belonged to *C. granulatus*, or was merely a *C. stellatus* with the left part of the theca slightly depressed.

UCMP 40449 (a, b, c). Three specimens: (a) *C. stellatus* — 6.9 mm axial by 6.4 mm transverse diameter. (b) High *C. granulatus* — 5.5 mm axial by 5.7 mm transverse diameter. (c) Low *C. granulatus* — 7.3 mm axial by 7.6 mm transverse diameter.

Pl. 12, fig. 10.

This slab includes three edrioasteroids. They have been lighted obliquely in the photograph to demonstrate thecal elevation. The left posterior member of the trio is a typical *Cystaster stellatus;* the upper oral surface is only slightly convex; the peripheral rim is vertical proximally and then flares outward along the surface of the substrate. The right posterior specimen is a clavate *C. granulatus*; the upper surface of the theca is highly convex, but the lower pedunculate zone has collapsed. The anterior specimen is another *C. granulatus* and represents the "intermediate" variety. The upper part of the theca is more convex than that of *C. stellatus*, but not nearly as high as the other *C. granulatus* present. The pedunculate zone is hidden beneath the collapsed upper part of the theca and a small amount of matrix.

These three nearly contiguous individuals demonstrate that the differentiation of thecal shape was probably not due to environmental conditions, even on a microenvironmental level. Moreover, the differences cannot be assigned to preservational peculiarities, for the thecal forms are found here preserved together under the same conditions.

UCMP 40450. (?) Maysville Group, Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. 7.6 mm axial by 7.2 mm transverse diameter; 7.2 mm high.

Pl. 12, fig. 9.

This is a large, well-preserved individual. Oral plates are slightly agape, but the ambulacral coverplates are completely closed. Both the larger right posterior and smaller left anterior hydropore interambulacral plates are well preserved.

AMNH 13263/1-G. "Lorraine group of Hudson River shale" [Maysville Group, Cincinnatian Series], Upper Ordovician. 350 feet above river level, Cincinnati, Ohio. 5.2 mm axial by 5.6 mm transverse diameter, 4.8 mm high (width of upper gibbous part of theca as viewed in photograph: 6 mm).

Pl. 12, fig. 8.

This unusual specimen preserves the clavate theca in upright position, resting on a *Rafinesquina* (brachiopod). The pedunculate zone appears to be partially collapsed.

Discussion of previous investigation

Hall's (1871) original description of the subgenus *Cystaster* doubled as a description of the species *C. granulatus* until a second species was described and assigned to the genus. Bassler (1936) described *Cystaster ulrichi* and *Cincinnatidiscus turgidus* (here considered junior synonyms of *Cystaster granulatus). Cincinnatidiscus turgidus* is based on a large, moderately well preserved specimen (USNM 87628) which rests on a small slab with fragments of two other edrioasteroids, although Bassler made no note of them. The holotype is missing ambulacrum V and some of the adjacent interambulacrals, but it preserves the specific traits. The clavate theca and all observable plate details bespeak *Cystaster granulatus* rather than a separate species. No doubt the stratigraphic occurrence of this specimen in the upper part of the Richmond Group, well above most other *C. granulatus*, played an important part in its separation as a distinct species.

Bassler (1936, p. 4–5) described *Cystaster ulrichi* as differing from *C. granulatus* in having: "a shorter, broader sac forming the basal portion of the theca, and in the coarser and fewer plates covering the ambulacral areas . . ." The holotype (USNM 42138) is a juvenile, which accounts for the reduced number of ambulacral coverplates and the proportionately larger size of the individual elements. The shape of the theca is difficult to determine. The distal parts of the specimen are collapsed and the thecal plates in these areas are now highly imbricate. Since the specimen remains highly convex, it is reasonable to assume that the theca was clavate or nearly so. It is completely acceptable as a *C. granulatus*.

Discussion

The interambulacrals and the plates of the pedunculate zone of *Cystaster granulatus* are squamose and imbricate. The earlier descriptions of them as "granular" or minute polygonal plates apparently resulted from the numerous, irregular nodes covering the plate exteriors. Both etched and sectioned specimens have documented the underlying plates as moderate in size and squamose.

Unfortunately, the inner side of the theca is inadequately known, exposed only in a few poorly preserved specimens. Although several hundred specimens have been studied, only a few appear to be juveniles. Specimen USNM 42138, Bassler's *C. ulrichi* holotype, is the only juvenile in which plate boundaries are distinct (text fig. 10A). Even this specimen is too poorly preserved to allow confident analysis of juvenile traits.

RANGE AND OCCURRENCE: Eden Group through Richmond Group, Cincinnatian Series, Upper Ordovician of the Cincinnati Arch region, Indiana, Ohio, Kentucky.

Cystaster stellatus (Hall), 1866

Text fig. 11, 12; plate 12, fig. 11-22, plate 13

1866 *Agelacrinus (Hemicystites) stellatus* Hall, J., New York State Mus., 20th Ann. Rept. (adv. pub.): 8.

1871 *Hemicystites stellatus* (Hall), J., New York State Mus., 24th Ann. Rept. (adv. pub.): Explanation of pl. 2, pl. 2, fig. 5, 6.

1872 *Agelacrinus (Hemicystites) stellatus* Hall, J., New York State Mus., 24th Ann. Rept.: 215–216, pl. 6, fig. 5, 6.

1873 *Hemicystites stellatus* (Hall), Meek, F. B., Geol. Surv. Ohio, v. 1, Geology and Palaeontology, pt. 2, Palaeontology, sect. 1: 52–54, pl. 3, fig. 8a-b.

1889 *Hemicystites stellatus* (Hall), Miller, S. A., North American Geology and Palaeontology, Cincinnati: 252, fig. 328.

1899 *Hemicystites stellatus* (Hall), Jaekel, O., Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 49.

1906 *Hemicystites stellatus* (Hall), Rowley, R. R., *in* Contribution to Indiana Palaeontology, G. K. Greene, 2 (2): 28 pl. 6, fig. 3, 4.

1910 *Hemicystites stellatus* (Hall), Grabau, A. W. and Shimer, H. W., North American Index Fossils, Invertebrates, New York, 2: 473, fig. 1784-a.

1914 *Hemicystites stellatus* (Hall), Foerste, A. F., Denison Univ., Sci. Lab. Bull. 17 (art. 14): 454–456, pl. 6, fig. 6a-b; *Hemicystites carnensis* Foerste, *idem, ibid.*: 455–456, pl. 3, fig. 2a-b.

1915 *Hemicystites carnensis* Foerste, Bassler, R. S., United States Nat. Mus. Bull. 92, 1: 606; *Hemicystites stellatus* (Hall), *idem, ibid.*: 606–607.

1935 *Cincinnatidiscus stellatus* (Hall), Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 3–4.

1936 *Cincinnatidiscus (Hemicystites) stellatus* (Hall), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 5, pl. 2, fig. 11, 12; *Cincinnatidiscus (Hemicystites) carnensis* (Foerste), *idem, ibid.*: 5–6, pl. 5, fig. 4; *Cincinnatidiscus edenensis* Bassler, *idem, ibid.*: 6, pl. 2, fig. 10, pl. 3, fig. 11.

1938 *Cincinnatidiscus stellatus* (Hall), Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 66.

1943 *Cincinnatidiscus stellatus* (Hall), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 198–199; *Cincinnatidiscus carnensis* (Foerste), *idem, ibid.*: 198; *Cincinnatidiscus edenensis* Bassler, *idem, ibid.*: 198.

1944 *Cincinnatidiscus stellatus* (Hall), Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 129, pl. 49, fig. 17, 18.

1960 *Cincinnatidiscus stellatus* (Hall), Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 167–168, pl. 8, fig. 1; *Cincinnatidiscus carnensis* (Foerste), *idem, ibid.*: 168–169, pl. 8, fig. 3, 4.

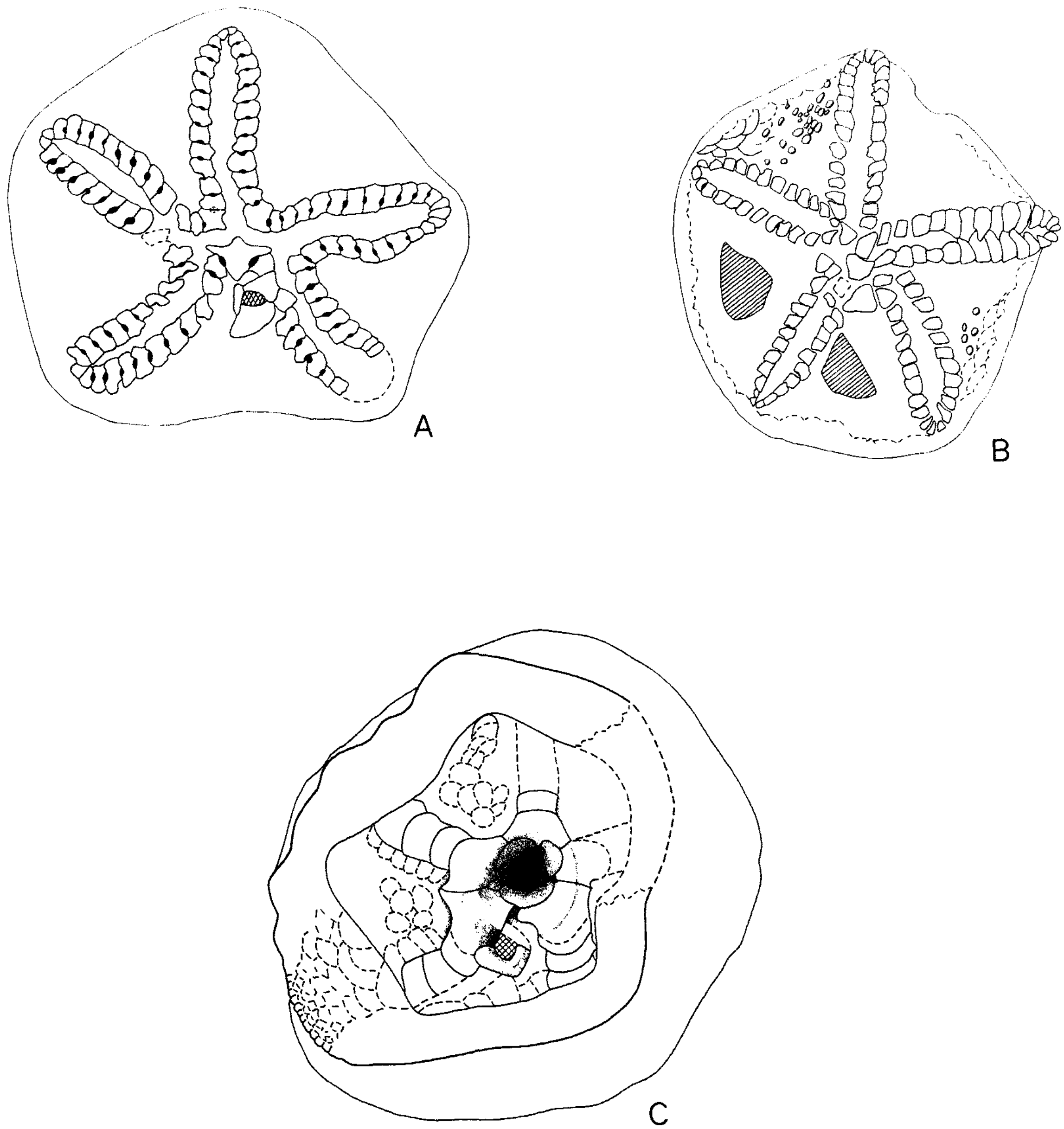
1966 *Cincinnatidiscus stellatus* (Hall), Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U165, text fig. 125-1.

Diagnosis

A *Cystaster* with: discoidal theca, with flat upper surface including ambulacra; external sickle-shaped ridge on larger interambulacral hydropore plate present but evidently only moderately prominent; interambulacrals squamose and imbricate, occasionally obscured by nodose prosopon.

Description

Cystaster stellatus is remarkably similar to the type species of the genus. The only external difference between the two forms is the thecal shape, and in this they may intergrade. Certainly the typical *C. stellatus* has a discoidal theca, with a flat or slightly convex upper surface, and a peripheral rim which is proximally vertical or steeply inclined and is distally flared outward in contact



Text figure 11. ***Cystaster stellatus*** **(Hall), 1866**

A. UCMP 40459, (x 9), pl. 13, fig. 6.

B. Lectotype, MCZ 523, (x 6), pl. 12, fig. 12.

C. Lower side, YPM 28453, (x 8), pl. 12, fig. 21.

with the substrate. In plan view the theca is commonly subpentagonal ,with the distal tip of each of the five ambulacra forming a corner of the pentagon. The ambulacra are highly elevated ridges which are confined to the flat oral surface. The discoidal theca of *C. stellatus* is quite different from the typically clavate *C. granulatus*, but the latter appears to grade from highly elevated clavate forms to low individuals which are almost discoidal, and thus closely approach *C. stellatus*.

The plate structure of the oral region and subjacent hydropore in *C. stellatus* appears nearly identical to that of *C. granulatus* (text fig. 11A, B). The only difference between the two is the apparently greater prominence of the sickle-shaped ridge on the larger interambulacral hydropore plate in *C. granulatus*. However, this region is commonly difficult to see in both species because of the small size of the theca and the disruption of the plates in this area. Commonly much of the hydropore structure is obscured by the adjacent high ambulacral elements.

The oral frame of *Cystaster stellatus*, seen only in one individual, appears to be similar to that of other Isorophida (text fig. 11C, pl. 12, fig. 21, 22). It most closely resembles the frame of *Streptaster* in being nearly circular, as opposed to the very transversely elongate, elliptical frames of such forms as *Carneyella* or *Isorophus*. The frame surrounds the subcircular central lumen which extends from the proximal ends of the ambulacral tunnels down into the thecal cavity.

The frame is formed by the enlarged proximal floorplates of the five ambulacra and the intrathecal extensions of at least the three primary oral plates. The floorplates are expanded both laterally and inwardly to form the radial parts of the frame and also the two lateral interradial areas (interambulacra 1 and 4) where the adjacent floorplates are broadly in contact. The anterior two interradii (interambulacra 2 and 3) are primarily formed by the wedge-shaped intrathecal extensions of the two anterior primary orals. These extend inward between the floorplates of ambulacra II-III and III-IV, but taper downward and end immediately above the inner rim of the frame. Thus adjacent anterior floorplates are in contact along the inner edge of the rim across the two anterior interradii. The posterior edge of the frame between the floorplates of ambulacra I and V, is formed only by the intrathecal extension of the posterior primary oral which does not extend inward nearly as far as the adjacent floorplates. This leaves a conspicuous posterior gap in the frame that directly connects the central lumen to the thecal cavity area under interambulacrum 5.

The inner end of the stone canal passageway lies along the distal, right posterior edge of the oral frame, adjacent to ambulacrum V (pl. 12, fig. 21, 22). It appears to be formed by the expanded posterior edge of the proximal floorplate of ambulacrum V and the intrathecal extensions of the two interambulacral hydropore plates.

The ambulacra of *Cystaster stellatus* extend straight out across the flat upper part of the theca. Their structure is identical to that of *C. granulatus*. However, the coverplates of *C. stellatus* are typically preserved in a closed position, tightly interlocked along the perradial line (text fig. 12C, D). In *C. granulatus* these plates are commonly open, having been disarticulated during collapse of the clavate theca.

The ambulacral floorplates are similar to those of other Lebetodiscina. The proximal third of each trough-shaped plate overlaps the distal margin of the adjacent plate. The proximal-distal length of the floorplates exceeds the proximal-distal length of a pair of ambulacral coverplates; hence the coverplate pairs are more numerous than the floorplates.

Since the coverplates' variation in size is not consistent along the length of the ambulacrum, they rest on different parts of the floorplates along a single ambulacrum, but without any consistent serial relationship.

The squamose imbricate interambulacral plates are more readily observed in *C. stellatus* than in *C. granulatus*. This supposed distinction between the two species may again be caused by the effects of preservation on the two different thecal forms. In some specimens, the interambulacrals of *C. stellatus* appear to be proportionately somewhat larger than in *C. granulatus*.

Two specimens of *C. stellatus* bear long, thin, and very delicate spines on the horizontal tops of the ambulacral coverplates (pl. 13, fig. 1-3). The location of the spines seems to be the same as in *Streptaster vorticellatus*, but no evidence of distinct basins for the bases of the spines has been observed. The spines evidently were mounted directly on the upper surface of the coverplates, one per plate.

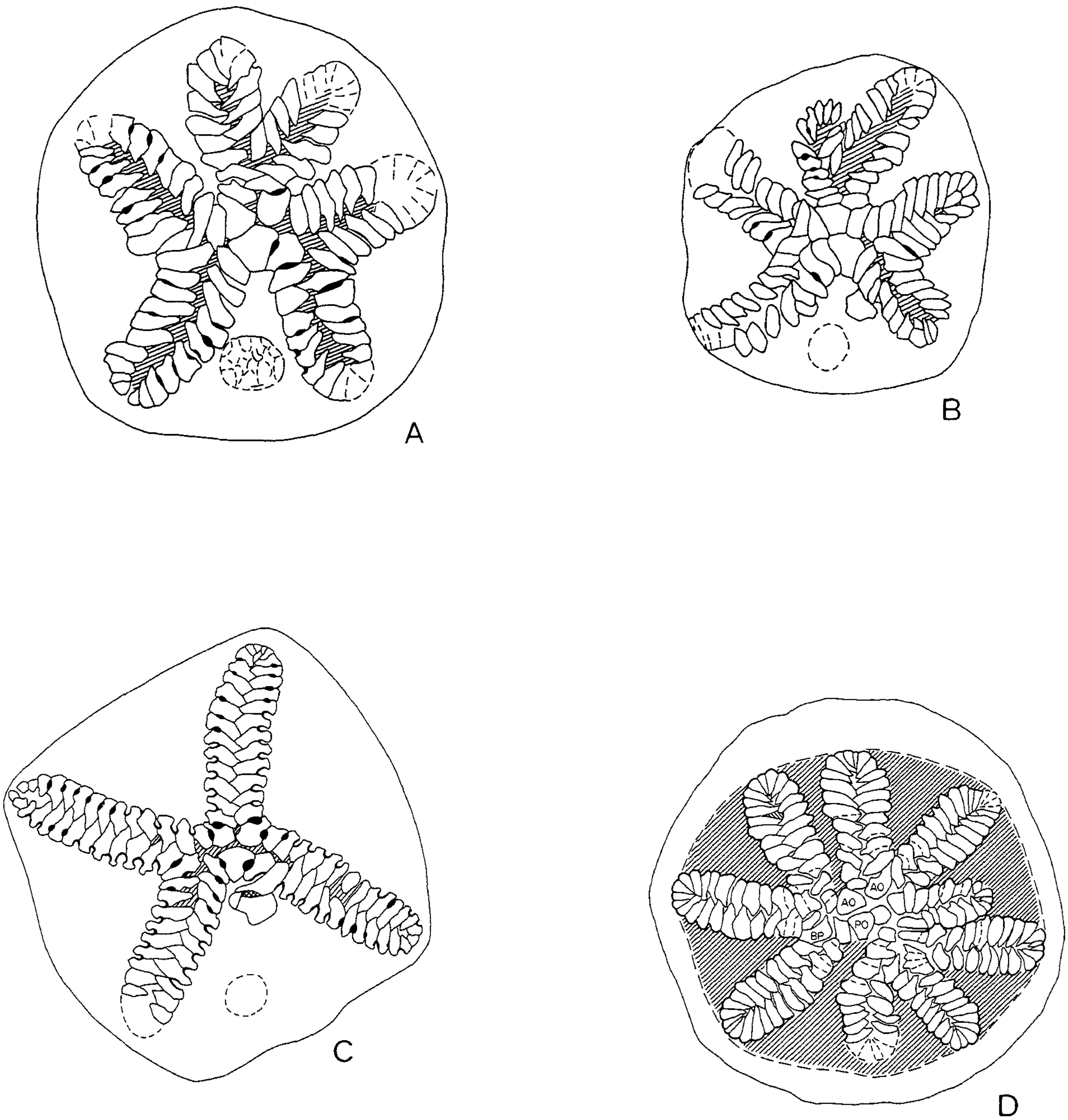
Specimens

MCZ 523 (old 3879). Lectotype of *Cystaster stellatus* (Hall) (1866, p. 8, 1871, pl. 2, fig. 6). "Shales of the Hudson River Group," (?) Fairview Formation, Maysville Group, Cincinnatian Series, Upper Ordovician. 80 feet below the top of the hills at Cincinnati, Ohio. 10 mm axial by 9.6 mm transverse diameter.

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

This is one of the two specimens used by Hall (1866) in the original species description and illustrated in the plate published in 1871. It is here designated the lectotype. The specimen is not as well preserved as Hall's other individual, but it is an adult whereas the other specimen is a juvenile.

The large theca has collapsed; the peripheral rim is obscure. The external ends of many plates are missing, in-



Text figure 12. ***Cystaster stellatus*** **(Hall), 1866**

A. USNM Acc. no. 258129-A, (x 10), pl. 13, fig. 13.

B. USNM Acc. no. 258129-B, (x 10), pl. 13, fig. 16.

C. UCMP 40452, (x 8), pl. 13, fig. 10.

D. UCMP 40458, (x 10), pl. 13, fig. 23.

AO, anterior primary oral plate; BP, left lateral bifurcation plate; PO, posterior primary oral plate.

cluding most of the coverplates, the orals, and the hydropore plates. The interambulacra are very poorly preserved, and no indication of the anal structure can be seen.

AMNH 1191-A. Lectoparatype of *C. stellatus* (Hall) (1866, p. 8: 1871, pl. 2, fig. 5). "Shales of the Hudson River Group," Maysville Group, Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. Resting on brachiopod with two other edrioasteroids. 4.4 mm axial by 4.4 mm transverse diameter.

Pl. 12, fig. 13.

This is the second of the two Hall specimens, and is a lectoparatype. The specimen is an advanced juvenile or young adult. The theca retains much of its original convexity. However, the entire upper surface has slumped as a unit slightly in an anterior direction, but little disruption of individual elements has occurred. The thecal plates are clearly defined. The oral region is proportionately a little larger than in adults, although all seven orals are clearly present at this stage. The ambulacra also reflect the youthful stage of development and possess only six or seven pairs of coverplates each. The hydropore region is unfortunately difficult to decipher, being the most poorly preserved area of the theca.

AMNH 1191-B. Tiny specimen on the same slab as and near the lectoparatype. 2.4 mm axial by 3.2 mm transverse diameter.

Pl. 12, fig. 14.

A small juvenile belonging to the genus *Cystaster*, and probably the species *C. stellatus*, is resting on the surface of the same brachiopod as the lectoparatype. Specific identification is difficult (if not impossible) in this size range. The major structural units of the theca can be seen, but the preservation is too poor to allow detailed interpretation of the plating.

AMNH 1191-D, E.

Two other *C. stellatus* occur in the collection of the American Museum of Natural History in the same lot with the lectoparatype of the species. The label indicates that they were acquired with the type and belong to the type series. However, Hall (1866) made no mention of additional specimens, and therefore they are certainly questionable types. Both individuals are average-sized adult specimens of *C. stellatus* and both are rather poorly preserved.

USNM 87163-A, B. Cotypes of *Cincinnatidiscus carnensis* (Foerste) (1914, p. 455-456, pl. 3, fig. 2A, B). "*Strophomena vicina* zone," Trenton Group, Mohawkian Series, Middle Ordovician. 20 feet above the level of the Ohio River (in 1914) on the creek flowing through Carntown, Pendleton County, Kentucky. Two specimens on one slab.

USNM 87163-A. 6.7 mm axial by 6.4 mm transverse diameter. Foerste (1914, pl. 3, fig. 2A).

Pl. 12, fig. 17, 18.

USNM 87163-B. 6.7 mm axial by 6.1 mm transverse diameter. Foerste (1914, pl. 3, fig. 2B).

Pl. 12, fig. 19, 20.

The two specimens, adjacent to one another on a small slab of limestone, show little evidence of plate disruption, and the ambulacral coverplates interlock tightly along the perradial lines. However, the surfaces of both specimens have been deeply etched, destroying or obscuring external details of most of the thecal plates. The oral plates are only questionably identifiable, and the hydropore and anal plates are obscure in both. The interambulacral and marginal parts of the theca have been stripped of their nodose prosopon, and even the suture lines of the underlying plates have been obscured by the extensive etching. The relationship of these and the following three specimens are discussed below.

USNM 34413-A, B, C. Type specimens of *Cincinnatidiscus edenensis* Bassler (1936, p. 6, pl. 2, fig. 10, pl. 3, fig. 11). Upper Eden beds (= Kope Formation), Eden Group, Cincinnatian Series, Upper Ordovician. South Clifton, Cincinnati, Ohio.

USNM 34413-A. Holotype of *Cincinnatidiscus edenensis* Bassler (1936, pl. 2, fig. 10, pl. 3, fig. 11). 8.3 mm axial by 8 mm transverse diameter.

Pl. 12, fig. 15.

USNM 34413-B. Paratype of *Cincinnatidiscus edenensis* Bassler (1936, pl. 3, fig. 11). 7.2 mm axial by 6.6 mm transverse diameter.

Pl. 12, fig. 16.

USNM 34413-C. Fragment of a third individual on the bryozoan fragment with Bassler's types of *Cincinnatidiscus edenensis*. 6.8 mm maximum diameter by 5.7 mm normal to maximum.

These three specimens occur together on a single fragment of a bryozoan colony and all are extensively etched. Only two were mentioned by Bassler, the third being merely a fragment. Of Bassler's two types, the paratype, specimen B, is the best preserved. The oral and hydropore plates of this individual can be recognized, although they are disrupted. All five ambulacra are preserved, but the plates are partially disrupted. The anal and interambulacral plates are mostly missing. Specimen A, the holotype, is even less complete. The orals are obscure, and of the hydropore structure only the larger interambulacral plate can be seen. The ambulacral coverplates are mostly disrupted, and many of the interambulacrals are missing.

UCMP 40451 (A, B). Upper 15 feet of Point Pleasant Limestone, Cynthiana Formation, Trenton Group, Mohawkian Series, Middle Ordovician. Quarry on Bear Creek Road, 0.1 mile north of the intersection of Route U.S. 52, about 3 miles east of Neville, Clairmont County, Ohio. (Moscow, Ohio-Kentucky quadrangle 7.5 minute topographic sheet. Ohio coordinate system: 296,300′; 1,526,-700′.)

UCMP 40451-A. 7.6 mm axial by 6.8 mm transverse diameter.

Pl. 13, fig. 1, 2.

UCMP 40451-B. 5.7 mm axial by 5.4 mm transverse diameter.

Pl. 13, fig. 3.

These two specimens rest adjacent to each other on a brachiopod fragment and preserve the only ambulacral coverplate spines known in *C. stellatus*. Both are well preserved, although the interambulacral and marginal plates are mostly vertical, disrupted during thecal collapse and thereby exposing the squamose, imbricate nature of these elements. The characteristic nodose prosopon of these is revealed along the edges of the specimens where the exteriors of some of the interambulacral plates are exposed. The thin, elongate, and extremely delicate spines appear to rest on the flat summits of the coverplates, with one per plate. The spines have been lost from the parts of the specimens in which all matrix has been removed.

YPM 28453 (old 2811). Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. 9.6 mm axial by 8.8 mm transverse diameter.

Text fig. 11C, pl. 12, fig. 21, 22.

This specimen exposes both the exterior and center of the inner surface of the theca. A clear view of the oral frame, the proximal ambulacral floorplates, and the inner end of the stone canal passageway are seen. This is the only *C. stellatus* which exposes the inner surface structures. Although there is no doubt that this is a *Cystaster*, the specific identification is problematic. Viewed from the upper side, the theca appears discoidal, and the coverplates are closed, as is most common in specimens of *C. stellatus*. From the lower surface, the theca looks to be slightly constricted proximal to the peripheral rim to form an exceptionally short pedunculate zone. This suggests that the theca was clavate and the individual should properly be placed in *C. granulatus*. Examination of the constricted area suggests it was more nearly vertical in life and that the apparent constriction is due to postmortem collapse. Therefore, this specimen is included here with *C. stellatus*. It serves as one more example of the difficulty in distinguishing between the two "species" assigned to the genus.

* * *

The following examples have been selected for their systematic importance from the hundreds of *C. stellatus* collected from the "Forestville, Ohio population." Only a few "normal" individuals are shown, but most of the "deviate" specimens have been included in order to show the range of variation encountered in one population.

UCMP 40452-40462, 40481-40482, USNM Acc. no. 258129 (A, B). Fairmount member, Fairview Formation, Maysville Group, Cincinnatian Series, Upper Ordovician. North end of excavation for Beechmont Mall shopping center, opposite Anderson High School, Route 125, Forestville, Hamilton County, Ohio. (Withamsville, Ohio-Kentucky quadrangle 7.5 minute topographic sheet [1953]. Ohio coordinate system: 397,300′; 1,474,700′; equals approximate center of a 200′ by 200′ area.)

UCMP 40452. 8.4 mm axial by 8 mm transverse diameter.

Text fig. 12C, pl. 13, fig. 9, 10.

Thecal plates are only slightly disrupted but have been much abraded. This individual has only four ambulacra; IV was not developed. Ambulacra III and V are shifted slightly from their normal position toward each other, but the combined interambulacrum 3–4 is almost as large as the areas occupied by these two interambulacra plus ambulacrum IV in normal specimens of comparable dimensions.

USNM Acc. no. 258129-A. 6.4 mm axial by 6.1 mm transverse diameter.

Text fig. 12A, pl. 13, fig. 12, 13.

This individual and the following one were collected from the Forestville population and donated to the United States National Museum. Both have six ambulacra; the additional radius arises from a bifurcation of ambulacrum III. In this individual the bifurcation is near the oral region. The two branches are subequal in size and diverge evenly from one another to form an additional interambulacrum along what would be the normal axis of ambulacrum III.

USNM Acc. no. 258129-B. 5.1 mm axial by 4.6 mm transverse diameter.

Text fig. 12B, pl. 13, fig. 16.

As in the above six-rayed specimen, the additional radius in this individual results from a splitting of ambulacrum III. But here the new ambulacrum is subordinate to the primary radius. It forms a small branch ambulacrum off the left side of ambulacrum III, which appears to divert ambulacrum II slightly to the right of its normal position.

UCMP 40453. 8 mm axial by 8.4 mm transverse diameter.
Pl. 13, fig. 11.

This individual has the normal five ambulacra plus a subordinate branch ambulacrum which extends from near the middle of the anterior side of ambulacrum I. The accessory ambulacrum is short and nearly at right angles to the anterior side of ambulacrum I. Ambulacrum I is slightly offset posteriorly distal to the bifurcation.

UCMP 40454. 4 mm axial by 4.4 mm transverse diameter.
Pl. 13, fig. 14, 15.

This is another six-rayed individual. It has an extra ambulacrum formed by the bifurcation of ambulacrum IV. The bifurcation is immediately distal to the normal bifurcation of ambulacra IV–V. The two ambulacra which replace IV are equally developed and diverge from each other evenly to form an extra interambulacral area along the normal axis of ambulacrum IV.

UCMP 40455. 8.8 mm axial by 8.7 mm transverse diameter.
Pl. 13, fig. 17, 18.

In this individual, also with six ambulacra, the new radius results from a double splitting of the right primary ambulacral axis. Two bifurcation plates are present immediately distal to the normal pair of shared coverplates on the right side of the oral region and form three right lateral ambulacra. The position of the ambulacra on the thecal surface suggests that ambulacrum V has bifurcated. The posterior of the three is unusual. Its proximal part extends toward interambulacrum 5 rather than toward the rim, then bends abruptly just proximal to its midpoint, directing the distal part toward the thecal margin.

UCMP 40456. 7.1 mm axial by 7.2 mm transverse diameter.
Pl. 13, fig. 20, 21.

This individual has seven ambulacral radii. Ambulacra I, II, and III are normal. Ambulacrum IV has two lateral subordinate branches, one from each side, which arise distal to the normal bifurcation of ambulacra IV and V. The distal part of ambulacrum V appears to lie closer to ambulacrum IV (and its branches) than is normally the case. This is a rather curious development, for one would expect a tendency for ambulacrum V to be diverted away from the somewhat congested area created by the extra ambulacra.

UCMP 40457. 5.6 mm axial by 6.1 mm transverse diameter.
Pl. 13, fig. 19.

This individual has eight ambulacra, of which five appear to be primary whereas three are subordinate branches off them. Ambulacrum I has a single lateral branch which arises from its posterior proximal zone and extends into interambulacrum 5. The branch is shorter than the main radius of ambulacrum I and ends distal to the midpoint of interambulacrum 5. Ambulacrum V has a lateral branch from each side of the main radius. The posterior, more proximal branch extends into interambulacrum 5 and appears to end as it abuts the proximal edge of the posterior branch of ambulacrum I. The anterior branch from ambulacrum V originates immediately distal to the point at which the posterior lateral branch arises. This branch is subequal in length to the distal part of ambulacrum V and the two elements diverge evenly.

UCMP 40458. 6.4 mm axial by 6.3 mm transverse diameter.
Text fig. 12D, pl. 13, fig. 22, 23.

This individual has nine ambulacra, eight of which extend to the rim of the theca. This is the largest number of ambulacra of any Isorophida included in this study. Ambulacra I, III, and IV appear to be normal. Ambulacrum II bifurcates immediately distal to its normal bifurcation from ambulacrum I; the two radii formed by this bifurcation are subequal in size and both extend to the peripheral rim. From the relative position of these two branches, one being quite close to ambulacrum III, it appears that the anterior radius is the extra one.

The area normally occupied by ambulacrum V includes four ambulacra. The posterior three are subequal in size from the point of divergence and all reach the thecal rim. Thus there is no indication which of the three represents the primary axis of ambulacrum V. The fourth branch is smaller than the other three. It is anterior to the three subequal branches and ends before reaching the thecal rim.

UCMP 40481. 7.3 mm axial by 7.9 mm transverse diameter.
Pl. 13, fig. 7.

UCMP 40482. 8.2 mm axial by 8.4 mm transverse diameter.
Pl. 13, fig. 8.

These two specimens are typical five-rayed individuals. Both have collapsed, and the interambulacral areas are depressed and somewhat disrupted. Ambulacral coverplates and orals are etched, and the intra-ambulacral extensions are exposed. The hydropore structure is slightly disrupted on both.

UCMP 40459, 40462.

The upper parts of the oral surface of these two specimens have been removed by grinding to expose subsurficial views of the upper theca and the coverplate passageways. The passageways are filled with secondary calcite, and when the specimen is properly oriented and under xylene these structures appear black in contrast with the white calcite of the surrounding coverplates.

UCMP 40459. 6.8 mm axial by 7.4 mm transverse diameter.

Text. fig. 11A, pl. 13, fig. 6.

This individual clearly shows many of the coverplate passageways. The oral and hydropore plates are also exposed in section view. Floorplates can be seen in ambulacrum II. Ambulacrum III reveals the inner, lower parts of the coverplates along the center of the ambulacrum. The squamose, imbricate thecal plates are visible in the interambulacral areas on the left half of the theca.

UCMP 40462. 7.8 mm axial by 6.4 mm transverse diameter.

Pl. 13, fig. 4, 5.

The subsurficial view of this specimen is closer to the oral surface than those above. It cuts into the tops of the ambulacral and oral plates and a small part of interambulacrum 5. The coverplate passageways are clearly seen in ambulacrum I.

Discussion of previous investigation

Hall's (1866) original description of *C. stellatus* outlined most major thecal features and the accompanying illustrations are remarkably accurate portrayals of the specimens. Meek (1873) published a description of two individuals of the same species, repeating Hall's description and adding details not mentioned by Hall, such as the nature of the anus and the biserial arrangement of the large ambulacral coverplates.

C. stellatus has been mentioned by many authors, but few have added new information to these early descriptions. Foerste's (1914) *Hemicystites carnensis*, here placed in synonymy with *C. stellatus*, was based on two individuals from the Trenton Group of Kentucky. They supposedly differ from *C. stellatus* in having ambulacra which appear to be nearly parallel-sided for their entire length and to terminate bluntly. This, according to Foerste, contrasts with the "swollen" ambulacra of *C. stellatus* which have a central gibbous part which gives them a petalate shape. However, it is now clear that these differing ambulacral shapes result from the mode of preservation of the ambulacral coverplates. Both conditions of ambulacra occur within a single population. Foerste thought his new species to be an early form of *C. stellatus*, and predicted that as more became known about *C. stellatus*, the closer to it his new species would probably be placed. It is apparent from Foerste's description that one of the important criteria used to separate *H. carnensis* from *C. stellatus* was the former's stratigraphic position well below the occurrence of any other members of the species known at the time.

Bassler's (1936) redescription of *Cystaster stellatus* included the first accurate portrayal of the primary orals. He also noted the variation in the number of ambulacra and illustrated a specimen with six radii. In this paper Bassler also described *Cincinnatidiscus edenensis*, based, as it now appears, on two disrupted and deeply etched *Cystaster stellatus*. The poorly preserved ambulacral coverplates led Bassler to think the ambulacra of his specimens were unique. From what is visible in the two type specimens, nothing indicates that they are not typical, but disrupted *Cystaster stellatus*. Bassler was undoubtedly influenced by the occurrence of these specimens somewhat lower stratigraphically than the horizon in which the species is most common.

Kesling (1960), in his general survey of edrioasteroid hydropores, was of the impression that there is a significant difference between that of *C. granulatus* and *C. stellatus*. From the considerable additional material now available, this conclusion seems invalid. His study tended to support Bassler's taxonomy, for he found no congeneric relationship between *C. granulatus* and *C. stellatus*, and for him *H. carnensis* appeared to be a valid species.

The large number of *Cystaster stellatus* now available has allowed a more complete interpretation of the characters of the species. One of the most significant features shown by the Forestville population is the variability in the number of ambulacra and the unacceptability of this trait as a specific taxobasis. From four to nine ambulacra have been seen in this species. Five is of course by far the most common number, but variants are by no means exceptionally rare. Among these, six is the most common condition, and the anterior axis is the most commonly bifurcated.

It is still unclear whether or not the interambulacrals of *C. stellatus* differ from those of *C. granulatus*. In forms attributed to the former. the nodose, granular prosopon is commonly less concealing and the outlines of the interambulacrals more clearly seen, and they seem to be relatively larger than in *C. granulatus*. The arcuate crest on the larger hydropore interambulacral plate seems to be more prominent in *C. granulatus*.

The coverplate spines, observed in two specimens of *C. stellatus*, have not been seen in *C. granulatus*. However, these spines have been seen in only two specimens out of more than two thousand *C. stellatus*. Half of the theca of these two specimens was exposed by weathering on the outcrop and reveals no spines. The other half was partially exposed by laboratory preparation (pl. 13, fig. 1-3) and preserves the spines *in situ* in the matrix. Thus it is evident that only under exceptional conditions are the spines preserved. It is most likely that all *C. stellatus*, and perhaps even all *C. granulatus*, had spines in life.

RANGE AND OCCURRENCE: Trenton Group through Richmond Group, Middle and Upper Ordovician of Indiana, Kentucky, Ohio.

Family CARNEYELLIDAE Bell, *fam. nov.*

Type genus: *Carneyella* Foerste, 1917

Diagnosis

Lebetodiscina with: domal theca; oral area with only three primary orals and one hydropore oral; hydropore in right posterior part of oral area, including oral and ambulacral plates; ambulacra forming low, rounded ridges on thecal surface; coverplates of moderate thickness (perpendicular to thecal surface); ambulacral tunnel wide and low; coverplate passageways oblique; passageway external foramina elongate, often slitlike; peripheral rim plates geniculate.

Description

The Carneyellidae have small to moderate-sized domal thecae. The oral area includes only the three large, central primary orals and a single large, right posterior hydropore oral plate. There are no shared coverplate pairs or secondary oral plates. Thus the proximal ambulacral coverplates and the perradial ends of the two lateral bifurcation plates (of the lateral ambulacral pairs) are in direct contact with the distal edges of the large, central primary orals.

The hydropore structure commonly involves four elements — the proximal two coverplates of the posterior side of ambulacrum V, the right edge of the large, posterior primary oral, and a large hydropore oral plate. The hydropore oral lies in the right posterior corner of the oral region and abuts the right side of the large, posterior primary oral plate. The anterior edge of this hydropore oral forms the posterior edge of the hydropore opening. The adradial edge of the proximal posterior coverplate of ambulacrum V forms most of the anterior edge of the hydropore opening. However, the left anterior tip of the opening is commonly formed by the posterior primary oral. The second proximal coverplate of the posterior side of ambulacrum V may form the right tip of the opening. Plates which surround the slitlike opening have thickened edges and form a raised rim around the hydropore.

The outer surface of each ambulacral coverplate is nearly parallel to the thecal surface and slopes gradually upward from the adradial suture to the perradial line.

The coverplate passageways of the Carneyellidae are directed obliquely inward, parallel to the outer surface of the coverplates. The external foramina are elongate, often slitlike openings which extend along most of the external length of the coverplates.

The uniserial ambulacral floorplates imbricate; the proximal edge of each overlaps the adjacent floorplate. The ambulacral tunnels, between the broad floorplates and nearly horizontal coverplates, are elliptical in cross section, transversely elongate, and low.

During thecal collapse the basal parts of the geniculate plates of the peripheral rim support the external parts and hold them nearly in life position, whereas the adjacent interambulacrals are depressed. Thus the proximal margin of the rim stands in high relief above the interambulacrals after collapse.

External plate surfaces are commonly smooth, but a few species are characteristically nodose or pitted.

Discussion of previous investigation

The family Carneyellidae equates conceptually with the family Hemicystitidae of authors. Bassler (1936) separated species here included in the order Isorophida into two families — a restricted Agelacrinitidae and his new family, the Hemicystitidae. The Hemicystitidae were described as having three large, central primary orals and two lateral bifurcation plates, forming a total of five orals. The Agelacrinitidae were described as having numerous small orals without definite order. Most species here included in the Lebetodiscina were included in Bassler's Hemicystitidae, whereas most Isorophina were included in his Agelacrinitidae.

Bassler's description of the Hemicystitidae oral area conforms to that of the Carneyellidae as defined here, although the two lateral bifurcation plates are considered ambulacrals rather than orals. Bassler apparently overlooked the hydropore oral. Ehlers and Kesling (1958) emended Bassler's diagnosis of the Hemicystitidae to include the hydropore oral.

The inclusion of lateral shared coverplates and secondary orals, and the lack of a hydropore oral plate excludes several species that have been included in Bassler's Hemicystitidae. They are here placed in a new family, the Lebetodiscidae. Most other Hemicystitidae species are here placed in the family Carneyellidae, with one important exception, *Hemicystites parasiticus*, the type species of *Hemicystites*. In erecting the family *Hemicystitidae*, Bassler apparently did not closely examine this species and assumed that it was similar in structure to numerous other species that erroneously have been included in *Hemicystites*. Restudy of *H. parasiticus* has shown that it has: an oral area with four primary orals, two pairs of lateral shared coverplates, secondary orals and a hydropore oral; also, a double alternating biseries of ambulacral coverplates without coverplate passageways. Therefore, all species except the type are here removed from *Hemicystites* and the genus is placed in the family Isorophidae. With the removal of *Hemicystites* from the group, *Carneyella* is selected as the type genus for the new family Carneyellidae, which includes the remainder of Bassler's Hemicystitidae species.

Discussion

The Carneyellidae includes two genera and 10 species. However, several of those species are questionable since they are based on few and poor specimens. Despite the seemingly large number of species included, the Carneyellidae show less diversity than the Lebetodiscidae, assuming that enough data are at hand to permit generalization.

A pronounced difference in external thecal appearance between the Carneyellidae and Lebetodiscidae is seen in the usual collapsed specimens. The geniculate rim plates of the Carneyellidae stand in relief above distal interambulacrals and form a high rim around the theca. In contrast, the peripheral rim of the Lebetodiscidae, formed by squamose plates, collapses with the interambulacrals and the thecal margin is evenly flattened.

The oral area of the Carneyellidae is formed by only four large plates, in contrast with the Lebetodiscidae, in which there are lateral shared coverplates and secondary orals in addition to the three primary orals. Moreover, the primary orals of the Lebetodiscidae are proportionately narrower than those of the Carneyellidae, and hydropore orals are absent. The three large and conspicuous primary orals in the Carneyellidae are very distinctive.

The hydropore structure of the Carneyellidae is in the posterior part of the oral area and is formed by oral and ambulacral elements. In the Lebetodiscidae the hydropore lies distal to the oral area along the proximal posterior edge of ambulacrum V, and is thus formed by ambulacral and interambulacral plates.

The ambulacral coverplates of the Carneyellidae are of moderate thickness; their external surfaces are nearly parallel to the thecal surface. Thus the coverplate passageways are also oblique and nearly parallel to the thecal surface. These features contrast sharply with the thick, almost vertical coverplates and passageways of the Lebetodiscidae. The pronounced elevation of the Lebetodiscidae ambulacra which results from the thick coverplates contrast with the low, rounded ambulacra of the Carneyellidae.

It is possible that the Lebetodiscidae evolved from the simpler Carneyellidae. This would involve the addition of plates lateral to the three primary orals of the Carneyellidae to form the more numerous orals of the Lebetodiscidae. The single large hydropore oral of the Carneyellidae may have migrated distally into the proximal part of interambulacrum 5, and in the process commonly incorporated additional interambulacrals as the structure moved distally from the oral region. The thin ambulacral coverplates of the Carneyellidae would have been greatly thickened to form the massive coverplates of the Lebetodiscidae. In the process the coverplate passageways and their external foramina were greatly enlarged. The " primitive " peripheral rim plates would have lost their geniculation in the reformation to achieve the highly elevated theca of the Lebetodiscidae.

Both families first appear at the same stratigraphic level, and if the Carneyellidae do represent a more generalized ancestral organization, the bifurcation in phylogeny took place long before the first records of the two families. In fact, the present data could be employed, perhaps with equal success, to derive the Carneyellidae from the Lebetodiscidae if the carneyellids did not in most respects conform better with current ideas on how generalized edrioasteroids looked.

RANGE AND OCCURRENCE: Chazy Group, Middle Ordovician through Richmond Group, Upper Ordovician of eastern North America (and probably Europe).

Genus *Carneyella* Foerste, 1917

1842 [*non*] *Agelacrinites* Vanuxem, L., Nat. Hist. New York, pt. IV, Geology 3: 158, fig. 80.

1866 *Agelacrinus* Vanuxem, Hall, J. [*partim*], New York State Mus., 20th Ann. Rept. (adv. pub.): 7.

1871 *Agelacrinus* Vanuxem, Hall, J. [*partim*], New York State Mus., 24th Ann. Rept. (adv. pub.): pl. 2, fig. 8–10.

1872 *Agelacrinus* Vanuxem, Hall, J. [*partim*], New York State Mus., 24th Ann. Rept.: 214-215, pl. 6, fig. 8-10.

1873 *Agelacrinites* Vanuxem, Meek, F. B. [*partim*], Geol. Surv. Ohio, v. 1, Geology and Palaeontology, pt. 2, Palaeontology, sect. 1: 56-57, pl. 3, fig. 5.

1889 *Agelacrinus* Vanuxem, Miller, S. A. [*partim*], North American Geology and Palaeontology, Cincinnati: 221-222.

1892 *Agelacrinus* Vanuxem, Miller, S. A. and Faber, C. L., Cincinnati Soc. Nat. Hist., Jour. 15 (2): 85-86, pl. 1, fig. 10; *Cyclocystoides* Salter and Billings, *idem, ibid.*: 85, pl. 1, fig. 13-15.

1894 *Agelacrinus* Vanuxem, Miller, S. A. and Faber, C. L. [*partim*], Cincinnati Soc. Nat. Hist., Jour. 17 (3): 156, pl. 8, fig. 24, 25.

1899 *Agelacrinites* Vanuxem, Jaekel, O. [*partim*], Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 49-50, text fig. 10, pl. 1, fig. 6.

1904 *Agelacrinus* Vanuxem, Spencer, W. K. [*partim*], Royal Soc. London, Proc. 74: 37-44, text fig. 8-12, pl. 1, fig. 2; *Lepidodiscus* Meek and Worthen, *idem, ibid.*: 37-44, text fig. 8-12, pl. 1, fig. 2.

1906 *Agelacrinus* Vanuxem, Rowley, R. R., *in* Contribution to Indiana Palaeontology, G. K. Greene, 2 (2): 27-28, pl. 6, fig. 1, 2.

1914 *Agelacrinus* Vanuxem, Foerste, A. F. [*partim*], Denison Univ., Sci. Lab. Bull. 17 (art. 14): 399-454, pl. 1, fig. 3a-c, 5a-d, pl. 2, fig. 1-4, pl. 3, fig. 1-4.

1915 *Agelacrinites* Vanuxem, Bassler, R. S. [*partim*], United States Nat. Mus. Bull. 92, 1: 20-21.

1917 *Carneyella* Foerste, A. F., Denison Univ., Sci. Lab. Bull. 18 (art. 4): 340-341.

1918 *Agelacrinus* Vanuxem, Williams, S. R. [*partim*], Ohio Jour. Sci. 19 (1): 59-81, pl. 1, fig. 3-7, pl. 2, fig. 10, pl. 3, fig. 19, pl. 7, fig. 45, pl. 9, fig. 53.

1920 *Agelacrinus* Vanuxem, Foerste, A. F., Ohio Jour. Sci. 21 (2): 60.

1920 *Carneyella* Foerste, Clark, T. H., American Jour. Sci. 50: 69-71, fig. 1.

1921 *Carneyella* Foerste, Raymond, P. E. [*partim*], Geol. Surv. Canada, Mus. Bull. 31 (Geol. Series 38): 7.

1935 *Carneyella* Foerste, Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 4, pl. 1, fig. 2, 3, 10.

1936 *Carneyella* Foerste, Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 6-9, pl. 2, fig. 13, 14, pl. 6. fig. 5-8; *Hemicystites* Hall, *idem* [*partim*], *ibid.*: 12–14, pl. 4, fig. 8, pl. 5, fig. 5-7; *Isorophus* Foerste, *idem* [*partim*], *ibid.*: 18, pl. 6, fig. 3, 4.

1938 *Carneyella* Foerste, Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 60.

1943 *Carneyella* Foerste, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 197-198; *Hemicystites* Hall, *idem, ibid.*: 203-204; *Isorophus* Foerste, *idem, ibid.*: 205.

1944 *Carneyella* Foerste, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, pl. 49, fig. 12.

1946 *Carneyella* Foerste, Wilson, A. E. [*partim*], Geol. Surv. Canada Bull. 4: 19-20.

1951 *Bassleridiscus* Fisher, D. W., Jour, Paleont. 25(5): 691-693, text fig. 1, 2.

1960 *Carneyella* Foerste, Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 166–167, text fig. 11, pl. 11, fig. 3–8.

1960 *Carneyella* Foerste, Kesling, R. V. and Mintz, L. W., Univ. Michigan, Contrib. Mus. Paleont. 15 (14): 315-348, text fig. 3-4, pl. 5, fig. 1, 2, pl. 6, fig. 1, 2, pl. 7, fig. 1-10, pl. 8, fig. 1-14.

1966 *Carneyella* Foerste, Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U165, text fig. 112-2, 117-3, 120-5a, 126-3, 129-1, 5.

TYPE SPECIES: *Agelacrinus pileus* Hall, 1866.

Diagnosis

Carneyellidae with: ambulacra curved, I-IV contrasolar, V solar.

Description

The domal theca of *Carneyella* varies in size from juveniles less than 1 mm in diameter to large adults over 20 mm; adult diameters average 15 mm.

The three primary oral plates are exceptionally large; the posterior one is nearly equal in size to the combined areas of the two anterior plates. The hydropore oral lies adjacent to the right margin of the primary posterior oral. Although also large, it is smaller than the adjacent posterior primary oral. The hydropore oral distorts the symmetry of the oral region by causing the right rear area to bulge outward along the posterior edge of ambulacrum V.

The three primary orals meet centrally. The anterior margin of the posterior primary oral abuts the posterior sides of both anteriors and forms a prominent transverse oral midline. This transverse midline extends out to the proximal tips of the two lateral bifurcation plates where it splits and becomes the perradial lines of the two pairs of lateral ambulacra. The abutting perradial sides of the two anterior primary orals form the anterior oral midline which extends normal to the transverse midline. The anterior midline is continuous with the perradial line of ambulacrum III. The contiguous edges of the three primary orals are thickened and form small ridges along the transverse and anterior oral midline. The midlines are nearly straight in *Carneyella*, in contrast with most edrioasteroids, in which these are serrated because of the perradial angularity of the oral plates.

The hydropore structure is formed by four plates; the posterior primary oral, the hydropore oral, and the two proximal posterior coverplates of ambulacrum V (text fig. 13). The two ambulacral coverplates are shortened normal to the ambulacral axis and adradially they abut the hydropore oral plate which projects into the posterior side of the ambulacrum. The slitlike hydropore is formed by three plates. The anterior edge of the hydropore oral forms the entire posterior side of the opening. The adradial edge of the proximal ambulacral coverplate forms most of the anterior edge of the slit, but the left end of the opening extends proximally past that plate and is formed by the right edge of the posterior primary oral. The shortened second posterior coverplate of ambulacrum V is not in contact with the opening. The thickened plate margins form a prominent raised rim which surrounds the hydropore slit.

The transversely elongate oral frame is formed by the proximal floorplates of the five ambulacra and the intrathecal extensions from the three primary orals. The details of the frame's structure are known only for *C. pilea* (pl. 16, fig. 1-3).

The ambulacra of *Carneyella* are curved, I-IV in a contrasolar direction and V solarly. The rate of curvature is variable; in some it is even, with the distal tips widely separated from adjacent ambulacra, whereas in others the rate increases as the nearly straight proximal parts approach and become concentric with the peripheral rim. In these the distal tip closely approaches the adjacent ambulacra.

The ambulacra are long and moderately wide. Inflated specimens indicate that the ambulacra were in life only slightly elevated above the adjacent interambulacra to form low, rounded ridges on the thecal surface.

The ambulacral coverplates are of moderate thickness and lie nearly parallel to the thecal surface. Each plate is elongate perpendicular to the ambulacral axis, and the exterior surface is subrectangular, with an angular perradial tip. The plate exterior is flat or gently arched.

A bladelike intra-ambulacral extension arises from the inner (ambulacral tunnel) side of both the proximal and distal edge of each coverplate (text fig. 14B). The distal extensions are simple blades that extend inward a short distance and make contact with the outer surface of the proximal end of the proximal intra-ambulacral extension from the adjacent coverplate. These distal intra-ambulacral extensions are confined to the perradial parts of the coverplates and diminish rapidly adradially.

The proximal intra-ambulacral extensions are much larger than the distal ones. They extend from the perradial tip more than halfway down to the adradial suture and gradually diminish in size to merge with the inner surface of the coverplate above the level of the floorplates. Each of these bladelike extensions arises from the proximal inner edge of the coverplate and extends proximally beneath the distal edge of the adjacent proximal coverplate. The proximal edge of the blade is flexed up and outward, and abuts the inner ambulacral tunnel surface of the distal lateral edge of the next coverplate, where it fits into a shallow groove. Thus the outer surface of the extension is convex inward, and the axis of the " trough " is parallel to the length of the coverplate. The perradial tip of the extension is widest and is also produced past the perradial tip of the coverplate, under the perradial line of the ambulacrum. It underlaps the perradial tip of the alternate coverplate on the opposite side of the ambulacrum. The proximal intra-ambulacral extensions thus interlock adjacent coverplates whether open or closed. Alternate opposing coverplates are locked together across the perradial line when closed, but the underlapping perradial tips of the extension slip out from under the alternate coverplates during opening.

The coverplates extend inward between the ambulacral floorplates and the edges of the adjacent interambulacral plates as intrathecal extensions which constrict in proximal-distal width as they enter the thecal cavity and then enlarge distally. The innermost tips of adjacent extensions are laterally in contact, or nearly so. The constriction forms a semicircular depression along each side of the intrathecal extension.

The ambulacral coverplate passageways extend from the thecal cavity to the thecal exterior between adjacent coverplates. A hemicylindrical groove is incised into both lateral sutural faces of each coverplate. The contiguous grooves between adjacent coverplates unite to form the tubular passageways. The upper end of each passageway is formed mostly by the more distal of two adjacent coverplates. The outer surface of the large proximal intra-ambulacral extension forms the inner side of the passageway. The distal intra-ambulacral extension from the adjacent proximal coverplate forms only the anterior edge of this upper end of the passageway where it abuts the proximal edge of the larger proximal extension. This upper part of the passageway is visible through the elliptical external foramen which opens along the more perradial segment of the suture between adjacent coverplates. The tubular passageway extends into the theca between the adjacent coverplates; the inner foramen is formed by the intrathecal extensions. The semicircular depression in each side of each extension marks the intersection of one side of each tubular passageway with the inner side of the coverplates. The two adjacent depressions unite to form the subcircular inner foramen.

The ambulacral floorplates are trough-shaped and nearly as wide as long (pl. 14, fig. 7, pl. 16, fig. 6). The sutures between contiguous floorplates are oblique and the proximal edge of each overlaps the distal edge of the adjacent floorplate. Thus the proximal and distal ends are arcuate in plan view. The upper surface of each floorplate is U-shaped in cross section: the broad central ambulacral groove extends the length of the plate. The upper lateral margins are slightly convex upward and form a rounded ridge along these edges of the floorplate. These bounding ridges apparently fit into a shallow corresponding groove in the lower surface of each overlying coverplate. This is the articulation zone between the two sets of plates.

The relationship of coverplate pairs to the underlying floorplates appears to vary along each ambulacrum. The floorplates taper very little except quite near the distal tip of the ambulacrum. Only the distal two or three last-formed floorplates are significantly reduced in length and width. In contrast, the coverplates decrease gradually in size toward the distal ends of the ambulacra. Thus the relative number of pairs of coverplates to floorplates increases distally.

The interambulacrals are squamose, imbricate plates without definite order.

The periproct lies near the center of interambulacrum 5. It includes several poorly ordered circlets of plates. The peripheral rim is commonly formed by five to eight circlets. Plates of the proximal three or four circlets are externally elongate concentric with the thecal margin; those of the outer circlets are elongate radially.

Thecal plates may be smooth, but are more commonly nodose.

Discussion

The genus *Carneyella* was proposed by Foerste (1917) for a group of Ordovician species that had been included in the genus *Agelacrinites.* He distinguished his new genus by the presence of five orals (three primary orals and two lateral bifurcation plates) and by the presence of a single biseries of ambulacral coverplates. Along with the type species *C. pilea,* Foerste placed in his genus all of the species here assigned to the two genera of the *Carneyellidae.* Foerste (1914, p. 400) had previously noted " it has long been recognized that a new generic term should be proposed for the Ordovician species usually referred to *Agelacrinus* or *Lepidodiscus.*" He had declined to do so at that time because R. S. Bassler was engaged in a restudy of the class, but by 1917 Foerste apparently grew tired of waiting.

Carneyella has been mentioned in many papers, but most descriptions apply only to the type species, *C. pilea.* Bassler (1935, 1936) described several new species which he assigned to *Carneyella,* but his brief generic description is like that of Foerste, except that he excluded the two lateral bifurcation plates from the oral region and listed only the three primary orals.

RANGE AND OCCURRENCE: Chazy Group, Middle Ordovician through Richmond Group, Upper Ordovician of eastern North America.

Carneyella pilea (Hall), 1866

Text fig. 13, 14; plate 14-16, plate 17, fig. 1-9

1866 *Agelacrinus pileus* Hall, J., New York State Mus., 20th Ann. Rept. (adv. pub.): 7.

1871 *Agelacrinus pileus* Hall, J., New York State Mus., 24th Ann. Rept. (adv. pub.): pl. 2, fig. 8-10.

1872 *Agelacrinus pileus* Hall, J., New York State Mus., 24th Ann. Rept.: 214-215, pl. 6, fig. 8-10.

1873 *Agelacrinites pileus* Hall, Meek, F. B., Geol. Surv. Ohio, v. 1, Geology and Palaeontology, pt. 2, Palaeontology, sect. 1: 56-57, pl. 3, fig. 5.

1889 *Agelacrinus pileus* Hall, Miller, S. A., North American Geology and Palaeontology, Cincinnati: 222.

1892 *Agelacrinus pileus* (?) Hall, Miller, S. A. and Faber, C. L., Cincinnati Soc. Nat. Hist., Jour. 15 (2): 85-86, pl. 1, fig. 10; *Cyclocystoides sp., idem, ibid.*: 85, pl. 1, fig. 13-15.

1899 *Agelacrinites pileus* Hall, Jaekel, O., Stammesgeschichte der Pelmatozoen, Bd. I, Thecoidea und Cystoidea, Berlin: 50, text fig. 10, pl. 1, fig. 6.

1904 *Agelacrinus pileus* Hall, Spencer, W. K., Royal Soc. London, Proc. 74: 39-42, text fig. 8-12, pl. 1, fig. 2; *Lepidodiscus pileus* Hall, *idem, ibid.*: 39-42, text fig. 8-12, pl. 1, fig. 2.

1906 *Agelacrinus pileus* Hall, Rowley, R. R., *in* Contribution to Indiana Palaeontology, G. K. Greene, 2 (2): 27-28, pl. 6, fig. 1, 2.

1914 *Agelacrinus pileus* Hall, Foerste, A. F., Denison Univ., Sci. Lab. Bull. 17 (art. 14): 399-454, pl. 1, fig. 5a-d, pl. 3, fig. 1-4.

1915 *Agelacrinites pileus* Hall, Bassler, R. S., United States Nat. Mus. Bull. 92, 1: 21.

1917 *Carneyella pileus* (Hall), Foerste, A. F., Denison Univ., Sci. Lab. Bull. 18 (art. 4): 340-341.

1918 *Agelacrinus pileus* Hall, Williams, S. R., Ohio Jour. Sci. 19 (1): 59-81, pl. 1, fig. 3-7, pl. 2, fig. 10, pl. 3, fig. 19, pl. 7, fig. 45, pl. 9, fig. 53.

1920 " *Agelacrinus* arm," Foerste, A. F., Ohio Jour. Sci. 21 (2): 60.

1921 *Carneyella pileus* (Hall), Raymond, P. E., Geol. Surv. Canada, Mus. Bull. 31 (Geol. Series 38): 7.

1935 *Carneyella cincinnatiensis* Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 4, pl. 1, fig. 10; *Carneyella pileus* (Hall), *idem, ibid.*: 4, pl. 1, fig. 2, 3.

1936 *Carneyella pileus* (Hall), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 6-7; *Carneyella nicklesi* Bassler, *idem, ibid.*: pl. 2, fig. 13; *Hemicystites curtus* Bassler, *idem, ibid.*: 12-13, pl. 4, fig. 8; *Hemicystites richmondensis* Bassler, *idem, ibid.*: 13-14, pl. 5, fig. 5-7; *Isorophus germanus* Bassler, *idem, ibid.*: 18, pl. 6, fig. 3, 4.

1938 *Carneyella pileus* (Hall), Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 60.

1943 *Carneyella pileus* (Hall), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 197-198; *Carneyella cincinnatiensis* Bassler, *idem, ibid.*: 197; *Carneyella nicklesi* Bassler, *idem, ibid.*: 197; *Hemicystites richmondensis* Bassler, *idem, ibid.*: 204; *Isorophus germanus* Bassler, *idem, ibid.*: 205.

1944 *Carneyella nicklesi* Bassler, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, pl. 49, fig. 12.

1946 *Carneyella pileus* (Hall), Wilson, A. E., Geol. Surv. Canada Bull. 4: 19-20.

1951 *Bassleridiscus mohawkensis* Fisher, D. W., Jour. Paleont. 25 (5): 691-693, text fig. 1, 2.

1960 *Carneyella pilea* (Hall), Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 166-167, text fig. 11, pl. 11, fig. 3-8.

1960 *Carneyella pilea* (Hall), Kesling, R. V. and Mintz, L. W., Univ. Michigan, Contrib. Mus. Paleont. 15 (14): 315-348, text fig. 3, 4, pl. 5, fig. 1, 2, pl. 6, fig. 1, 2, pl. 7, fig. 1-10, pl. 8, fig. 1-14.

1966 *Carneyella pileus* (Hall), Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U165, text fig. 112-2, 117-3, 120-5a, 126-3, 129-1, 5.

Diagnosis

A *Carneyella* with: sparse, small nodes on exterior surface of thecal plates.

Description

Adult *Carneyella pilea* average 16 mm in diameter. Occasionally individuals rest on irregular or elongate objects which distorts the domal theca to maintain contact between the peripheral rim and the underlying hard object. An extreme example of this contortion is an adult *C. pilea* attached to a crinoid stem (pl. 17, fig. 1-4).

The three primary orals and the hydropore oral are very large (text fig. 13). The thickened perradial edges form a small ridge along both the anterior and transverse oral midlines, but abrasion commonly removes all traces of these ridges. In some specimens the raised edges are very prominent and the exterior surface of the orals are concave.

The slitlike hydropore is formed mostly by the anterior edge of the hydropore oral and the adradial edge of the proximal posterior coverplate of ambulacrum V (pl. 14, fig. 11, pl. 16, fig. 7, 10). The opening terminates before reaching the adradial end of the second coverplate, but this plate is shortened adradially where it abuts the right margin of the hydropore oral which juts into the side of the ambulacrum. Proximally, the hydropore extends past the proximal edge of the first coverplate and along the boundary between the hydropore oral plate and the adjacent part of the primary posterior oral. The thickened plate margins form a conspicuous raised rim around the hydropore.

The oral frame of *Carneyella pilea* has been observed in several specimens that expose the inner side of the oral surface of the theca and also in successive polished surfaces. It is formed by the proximal floorplates of the five ambulacra and the intrathecal extensions of the primary oral plates (pl. 14, fig. 7, pl. 16, fig. 1-3). The proximal margin of the transversely elongate frame is subovate in plan view, and surrounds the central lumen. Distally the frame is subpentagonal, continuous with the five radiating ambulacra. The central oral lumen is subovoid and extends inward from the proximal ends of the ambulacral tunnels to open downward into the thecal cavity. All five ambulacral tunnels empty into the lumen, but those of each lateral pair (I-II, IV-V) lie close to one another whereas they are widely set apart from each other and from the anterior ambulacrum.

The anterior part of the frame is nearly semicircular, although both lateral sides flare outward and form a wide zone of contact with the posterior unit. The posterior part is broadly arcuate, the flared lateral extremities being nearly a continuation of the arc, rather than a distinct broadening as in the anterior side. The frame is thus ovate with the unequally curved anterior and posterior halves joined at attenuated lateral regions which impart a distinct transverse elongation.

The anterior half of the frame is formed by the floorplates of ambulacra II, III, and IV, and the intrathecal extensions of the two anterior primary oral plates. The three floorplates are proximally enlarged and expanded both inward and laterally to form the radial parts of the unit. The adjacent floorplates are in contact with each other along the innermost rim of the frame, across the two anterior interradii. All but these inner edges of the two interradii are formed by the wedge-shaped intrathecal extensions of the two anterior primary oral covering plates which extend inward between floorplates II-III and III-IV. Whereas the anterior sides of the floorplates of ambulacra II and IV are only slightly in contact with the proximal floorplate of ambulacrum III, the posterior sides of the two lateral floorplates flare outward and are in wide contact with the floorplates of the posterior half of the frame (I and V), and form the attenuated lateral extremities of the frame. The two lateral interradii (1 and 4) are thus formed entirely by floorplates.

Each of the intrathecal extensions of the two anterior primary orals has a marked bladelike ridge along the inner, proximal face of the extension; these ridges extend inward toward the center of the central lumen. They are largest at the upper end of the intrathecal extensions where they meet the inner surface of the plate which forms the roof of the central lumen. Each ridge extends down the center of the extension and diminishes in elevation until it merges with the main body of the extension near the inner rim of the frame.

The posterior part of the frame includes the proximal floorplates of ambulacra I and V, and the intrathecal extension of the large posterior primary oral. The anterior ends of the proximally enlarged floorplates flare out slightly, and broadly abut the two lateral anterior floorplates. The posterior sides of floorplates I and V are not in contact with each other across the posterior side of the frame. This central posterior area is formed by the broad intrathecal extension of the large posterior primary oral. It does not extend inward nearly as far as the other frame elements and thereby forms a conspicuous gap in the frame which laterally connects the central lumen to the thecal cavity underlying interambulacrum 5. The inner (central lumen boundary) proximal side of this posterior oral intrathecal extension has three vertical ridges (perpendicular to the surface of the extension). These extend proximally inward toward the center of the lumen. One ridge is formed along each lateral edge of the extension, adjacent to floorplates I and V. These ridges, although much smaller, are similar to those on the intrathecal extensions of the anterior primary orals. They are largest at the uppermost end of the extensions and gradually diminish in height inwardly. The third ridge lies along the center of the intrathecal extension. In contrast with the others, this ridge diminishes upward to merge with the uppermost part of the extension; it reaches its maximum proximal extension into the central lumen at its innermost tip, which appears to extend in a spinelike manner much further into the thecal cavity than any other part of the frame. Its total penetration is unknown because it is broken in all observed examples. This central ridge divides the posterior frame gap into two halves, thereby forming two parallel channels through the posterior side of the frame from the central lumen into the thecal cavity.

The passageway for the stone canal extends downward from the hydropore as an inwardly expanding funnel (pl. 16, fig. 1-3). Its upper part is formed by the inner sides of the four hydropore structure plates: the posterior primary oral, the hydropore oral, and the two proximal posterior coverplates of ambulacrum V. The lower part is formed by the adjacent posterior sides of the first two floorplates of ambulacrum V, and the distal edge of the innermost end of the intrathecal extension of the posterior primary oral. A more detailed account of the passageway structure is found in Kesling and Mintz (1960).

The rate of ambulacral curvature (I-IV contrasolar, V solar) in *C. pilea* is unusually variable. In some, the evenly curved ambulacra remain widely separated, whereas in others curvature is abrupt near the rim and the tips even appear to touch the side of the adjacent ambulacrum. This degree of intraspecific variation contrasts with species such as *Foerstediscus grandis*, in which the even rate of curvature has been employed as a specific taxobasis.

Structurally, the ambulacra, interambulacra, and periproct of *C. pilea* are like those of other species of *Carneyella*. Only the prosopon, described below, on the exterior of these plates is distinctive.

The peripheral rim comprises three outwardly intergradational series of plates. The proximal rim plates are elongate concentric with the thecal margin. The distal plates are small and radially elongated. Between these are transition plates which are ovate and slightly elongated radially. The shape of the transition plates is masked by a highly elevated, sagittate ridge. The proximal third of each plate forms the blunt " head of the arrow " which is anteriorly convex with a straight, transverse distal edge. A narrow, straight ridge extends distally from the proximal head along the center of the posterior two-thirds of the plate. The distal, lateral edges of the plate, on either side of the posterior shaft, are deeply depressed and overlapped by small, elongate plates of the next distal circlet. In nondisrupted specimens the proximal "head" appears to be a small, separate plate, slightly elongate concentric with the thecal margin. The central, distal shaft of each transition plate is flanked by small, radially elongate plates and thus appears to be a part of the most proximal circlet of radially elongate rim plates.

The plates of *Carneyella pilea* bear nodes or tubercles and are pitted (pl. 14, fig. 5, 10–13, 17, 18). The pitting is commonly preserved even in etched specimens. It varies

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Text figure 13. ***Carneyella pilea*** **(Hall), 1866**

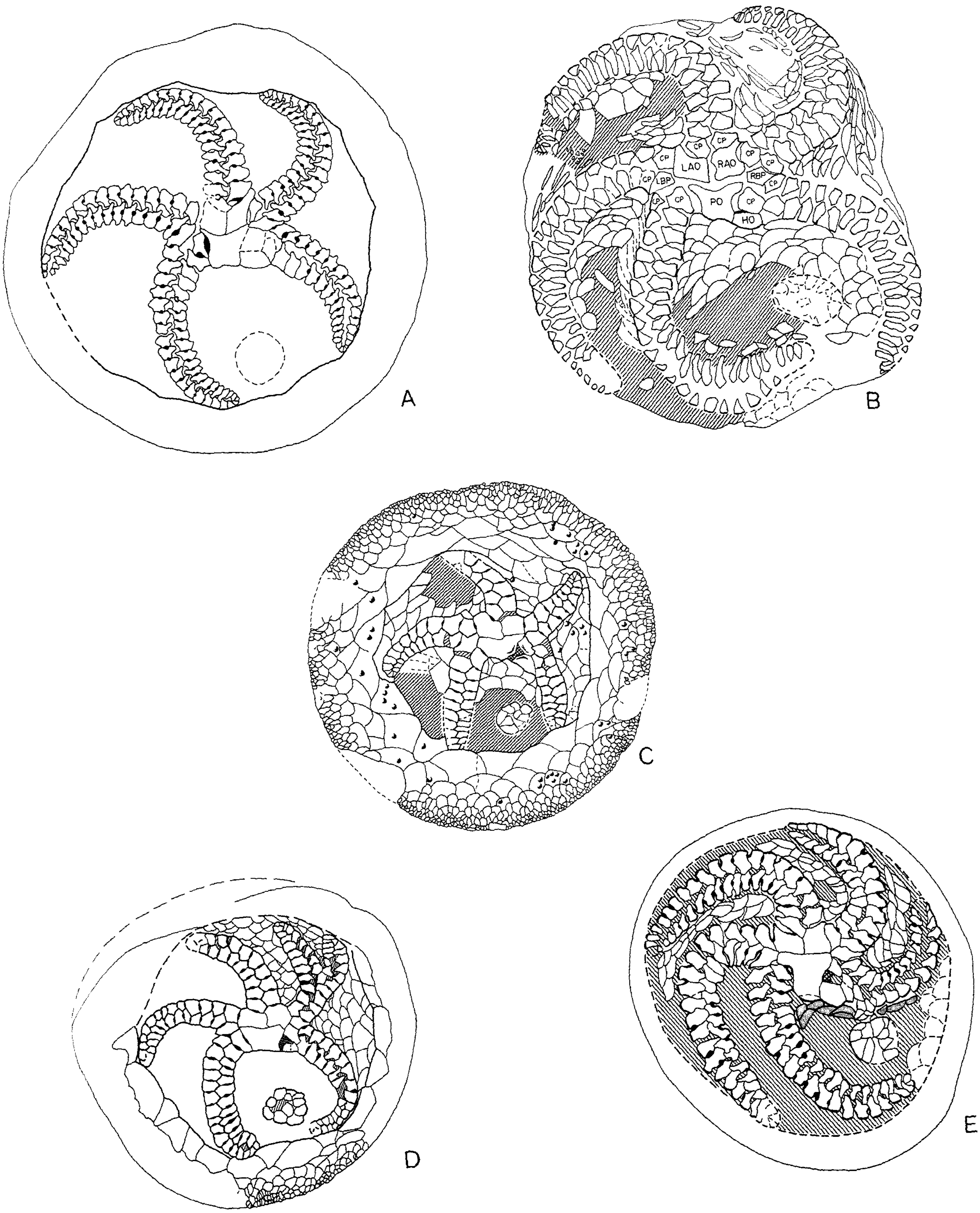
A. UCMP 40464, (x 4), pl. 17, fig. 8.

B. Lectotype, MCZ 516-A, (x 5), pl. 14, fig. 2. CP, ambulacral coverplate; HO, hydropore oral plate; LAO, left anterior primary oral plate; LBP, left lateral bifurcation plate; PO, posterior primary oral plate; RAO, right anterior primary oral plate; RBP, right lateral bifurcation plate.

C. CFMP 6504, (x 7), pl. 16, fig. 11.

D. USNM 40743-C, (x 6), pl. 14, fig. 8.

E. USNM 170362, (x 6), pl. 15, fig. 12. Interambulacral plates along the posterior side of ambulacrum V are shaded.


A
B
CP
LAO
RAO
RBP
LBP
PO
HO
C
D
E

from a coarse pattern visible to the unaided eye to micropitting that appears to be the surficial expression of the stroma canals intersecting the surfaces of the thecal plates.

Small, rounded to irregular nodes occur randomly on the interambulacral and rim plates. These are commonly removed by erosion or etching and leave no trace of their former presence. Individuals in which nodes are well preserved on half or more of the theca are exceptional.

Each ambulacral coverplate has a moderately large protuberance on the perradial tip of the plate (pl. 16, fig. 8–10). These elongate, ridgelike elevations extend upward from the tip of each coverplate and are highest perradially. Like the thecal nodes, these are frequently altered or removed by etching.

Specimens

MCZ 516-A. Lectotype of *Carneyella pilea* (Hall) (1866, p. 7, pl. 2, fig. 9). "Hudson River Group" (probably Maysville Group), Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. 16.1 mm axial by 15.5 mm transverse diameter.

Text fig. 13B, pl. 14, fig. 1, 2.

The type series of *Carneyella pilea* apparently includes seven specimens, some in the Museum of Comparative Zoology, others in the American Museum of Natural History. Hall illustrated only three specimens, but labels with the collections indicate that the other four were used by Hall (1866) for the original description. One of Hall's (1871) three illustrated specimens is missing; unfortunately, the original figures suggest it is the best preserved of the three. The remaining two illustrated individuals are poorly preserved, but MCZ 516-A is the better one and is here designated as the lectotype.

The lectotype is resting on a small bryozoan fragment, the distal parts of the peripheral rim flexed under the upper side and hidden from oral view. The interambulacral plates are collapsed and partially disrupted, but the ambulacra and oral area are well preserved; there is no sign of the anus. The theca is deeply etched and apparently has been damaged by improper preparation. All traces of the nodose prosopon are gone, and only remnants of the coverplate perradial ridges are visible.

AMNH 1193-A. Lectoparatype of *C. pilea* (Hall) (1866, p. 7; 1871, pl. 2, fig. 10). "Hudson River Group" (probably Maysville Group), Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. 11.1 mm axial by 15.6 mm transverse diameter (the axial diameter does not adequately reflect the size of the individual because of distortion of thecal shape).

Pl. 14, fig. 3–5.

The oral surface, which is normally convex upward, is doubled over along a nearly transverse axis which passes through the oral area and interambulacra 2 and 4. The anterior half of the theca is flexed under the posterior half and is mostly hidden from view. The specimen is resting upon a small, elongate bryozoan fragment and in life was flexed along the transverse axis to maintain contact with the narrow firm object. Upon burial the specimen was laterally compressed, accentuating the transverse folding. Only the posterior interambulacrum and ambulacra I and V are well preserved; the other areas are only partially visible. The proximal intra-ambulacral extensions of the coverplates and the coverplate passageways are exposed along the slightly disrupted ambulacra. Most of the prosopon has been lost, although one interambulacral plate retains a well-preserved node (pl. 14, fig. 5).

MCZ 518-A. (?)Lectoparatype of *C. pilea* (Hall) (1866, p. 7). "Hudson River Group" (probably Maysville Group), Cincinnatian Series, Upper Ordovician, Cincinnati, Ohio. 13.8 mm axial by 12.5 mm transverse diameter.

Pl. 14, fig. 6, 7.

This and the following two specimens are labeled as having been in Hall's original type lot. The right anterior third of the theca is missing. Both the outer and the inner sides of the remaining plates are exposed.

The exterior is well preserved, although etching has removed most of the nodes on the interambulacral plates. The raised perradial edges of the orals and the raised rim which surrounds the hydropore are well preserved. The external foramina of the coverplate passageways are clearly visible.

The inner side of the oral surface preserves the ambulacral floorplates and intrathecal extensions of the coverplates in ambulacra I, II, and III. The oral frame is somewhat disrupted. Most of the central ridge on the intrathecal extension of the primary posterior oral plate is preserved, and it extends far into the thecal cavity. It is unclear why Hall, if he had this individual, did not describe the features of the inner side of the theca.

MCZ 518-B. (?)Lectoparatype of *C. pilea* (Hall) (1866, p. 7). "Hudson River Group" (probably Maysville Group), Cincinnatian Series, Upper Ordovician, Cincinnati, Ohio. 13.8 mm axial by 14 mm transverse diameter.

This rather poorly preserved specimen is also thought to be one of Hall's original specimens.

AMNH 1193-C. (?)Lectoparatypes of *C. pilea* (Hall) (1866, p. 7). "Hudson River Group" (probably Maysville Group), Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. Two individuals on one brachiopod:

(1) 14.5 mm axial by 12 mm transverse diameter; (2) 12.8 mm diameter.

These two specimens are with the illustrated lectoparatype in the American Museum of Natural History collections. Both are poorly preserved.

USNM 40743 (A–D). Four specimens of *C. pilea*. Corryville Formation, Maysville Group, Cincinnatian Series. Upper Ordovician. Warren County, Ohio.

USNM 40743-A. Holotype of *Carneyella cincinnatiensis* Bassler (1935, p. 4, pl. 1, fig. 10). 13.1 mm axial by 13.5 mm transverse diameter.

Pl. 14, fig. 10–12.

The theca is completely collapsed and some interambulacral plates are missing. Many of the orals and ambulacral coverplates are partially disrupted. The plates, apparently little affected by etching, preserve the surficial pitting. the interambulacral and rim plate nodes, the raised edges of the orals and of the plates surrounding the hydropore, and many of the perradial ridges of the ambulacral coverplates. The partial disruption of many coverplates has distorted the shape of the external foramina of the passageways and exposed the proximal intra-ambulacral extensions of the coverplates.

USNM 40743-B. 10.8 mm axial by 10.5 mm transverse diameter.

Pl. 14, fig. 13.

This individual and the following two specimens were included in the United States National Museum collection with the holotype of Bassler's *Carneyella cincinnatiensis*. As is the above specimen, both are typical *Carneyella pilea* that preserve the external prosopon so commonly lost by etching. The transition plates of the peripheral rim are fully exposed where adjacent rim plates are disrupted.

USNM 40743-C. 9.4 mm axial by 11.1 mm transverse diameter.

Text fig. 13D, pl. 14, fig. 8, 9.

Six ambulacra have developed in this individual. The extra radius is formed by bifurcation of ambulacrum V. The prosopon has been partially removed by etching. The upper surface of the posterior primary oral has been cleaved and is missing, giving that plate an unusual appearance.

USNM 40743-D. 11.4 mm axial by 11.1 mm transverse diameter.

Pl. 14, fig. 14.

This specimen is deeply etched. Remnants of the surficial features are preserved.

USNM S-3876. Holotype of *Carneyella nicklesi* Bassler (1936, p. 7, pl. 2, fig. 13). Curdsville Formation, Trenton Group, Mohawkian Series, Middle Ordovician. Near Troy, Woodford County, Kentucky. 13.3 mm axial by 17.8 mm transverse diameter.

Pl. 14, fig. 17, 18.

This is a poorly preserved *Carneyella pilea*. A large section of the anterior part of the theca is missing and much of the remainder is partially covered with tenacious matrix. Deep etching has removed most of the prosopon, although the primary posterior oral retains the surficial pitting. The theca had been damaged by scraping in an attempt to remove some of the matrix.

USNM S-3959. Holotype of *Isorophus germanus* Bassler (1936, p. 18, pl. 6, fig. 3). Clarksville member, Waynesville Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Morrow, Ohio. 17.5 mm axial by 20 mm transverse diameter.

Text fig. 14E, pl. 15, fig. 9, 10.

This is a large *Carneyella pilea*. Thecal collapse has accentuated the height and partially disrupted the plates of the ambulacra and oral area. Etching and abrasion have removed most of the prosopon, although a few interambulacral nodes remain in depressed areas.

USNM S-3960. Paratype of *Isorophus germanus* Bassler (1936, p. 18, pl. 6, fig. 4). Clarksville member, Waynesville Formation, Richmond Group, Upper Ordovician. Oxford, Ohio. 20 mm axial by 20 mm transverse diameter.

Pl. 15, fig. 8.

This specimen, like the previous one, is a large but otherwise typical *Carneyella pilea*. The central part of the theca is well preserved, but most of the peripheral rim is missing. The surface has been extensively eroded and etched; only remnants of the prosopon are preserved.

USNM 42105. Holotype of *Hemicystites curtus* Bassler (1936, p. 12–13, pl. 4, fig. 8). Platteville Limestone, Black River Group, Middle Ordovician. Rockton, Illinois. 4.6 mm axial by 4.8 mm transverse diameter.

Text fig. 14C, pl. 14, fig. 16.

This small specimen is a juvenile *Carneyella pilea*. The specimen is only slightly disrupted, although the surface has been etched. The ambulacra, oral area, periproct, and peripheral rim are clearly defined. Only the interambulacral plates are indistinct.

USNM 68333. "Cotype" of *Hemicystites richmondensis* Bassler (1936, p. 13, 14, pl. 5, fig. 7). Whitewater Formation, Richmond Group, Cincinnatian Series, Upper

Ordovician. Adams County, Ohio. 4.9 mm axial by 5.1 mm transverse diameter.

Pl. 15, fig. 7.

This specimen and the following five constitute Bassler's type series for *Hemicystites richmondensis*. All are juveniles or young adults of *Carneyella pilea*. Bassler illustrated only three of them; the other three are housed with the figured types. The largest of the specimens may be classed as a young adult rather than a juvenile.

Specimen USNM 68333 has been crushed and etched, although only the hydropore area is completely invisible. The prosopon is preserved in the depressed and protected parts of the theca and includes both nodes and pitting. In a few areas the nodes appear larger and more numerous than in typical *C. pilea*, suggesting that this individual might possibly belong to *Carneyella faberi* (Miller).

USNM 40742 (A1, A2, B). Three " cotypes " of *Hemicystites richmondensis* Bassler (1936, p. 13–14). Waynesville Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Warren County, Ohio.

USNM 40742-A-2. "Cotype" of *Hemicystites richmondensis* Bassler (1936, p. 13–14, pl. 5, fig. 5). 5 mm axial by 5.1 mm transverse diameter.

Text fig. 14A, pl. 15, fig. 6.

The specimen is partially crushed and etched. All major thecal structures can be recognized, and some of the surficial nodes and the pits are preserved.

USNM 40742-A-1. "Cotype" of *H. richmondensis* Bassler (not illustrated). 4.7 mm axial by 5.3 mm transverse diameter.

Pl. 15, fig. 5.

This individual rests on the same brachiopod as the last. It is a typical young *Carneyella pilea*.

USNM 40742-B. "Cotype" of *H. richmondensis* Bassler (not illustrated). 6.3 mm axial by 6.7 mm transverse diameter.

Pl. 15, fig. 4.

This rather poorly preserved individual is like USNM 68333 in seeming to have somewhat larger and more abundant nodes than average *Carneyella pilea*, which suggests that it might be a young *Carneyella faberi*.

USNM 42111-A, B. Two "cotypes" of *Hemicystites richmondensis* Bassler (1936, p. 13–14). Waynesville Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Versailles, Indiana (probably the large roadcut east of town on Route U.S. 50).

USNM 42111-A. (Bassler, 1936, p. 13–14, pl. 5, fig. 6). 6.7 mm axial by 6.9 mm transverse diameter.

Text fig. 14D, pl. 15, fig. 1, 2.

This is the best preserved of Bassler's type series. It is the second largest of the lot and is transitional between the young adult and juvenile stage. In spite of some etching and abrasion, the prosopon is preserved in protected, depressed areas.

USNM 42111-B. 7 mm axial by 8.4 mm transverse diameter.

Pl. 15, fig. 3.

This is the largest of Bassler's type series and is a young adult. The specimen is only slightly disrupted, but the prosopon is preserved only sporadically.

NYSM 10683. Holotype of *Bassleridiscus mohawkensis* Fisher (1952, p. 691–693, fig. 1, 2). Larrabee member. Kirkfield Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. One-fourth mile east of Manny Corners, a hamlet 2 miles northeast of Amsterdam, New York. 15.5 mm axial by 15 mm transverse diameter.

Pl. 14, fig. 15.

This is a typical *Carneyella pilea*. It rests upon a small ramose bryozoan. The peripheral rim has been flexed under the upper surface to maintain contact with the bryozoan. Thecal collapse, acting on the already distorted thecal shape, has accentuated the elevation of the ambulacra, partially disrupted the coverplates, and has preserved the distal parts of the ambulacra on the lower side of the theca.

USNM 170362. Float block of upper 15 feet of Point Pleasant Limestone, Cynthiana Formation, Trenton Group, Mohawkian Series, Middle Ordovician. Quarry section on Bear Creek Road, 0.1 mile north of the intersection

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Text figure 14. *Carneyella pilea* (Hall), 1866

A. Juvenile, USNM 40742-A-2, (x 10), pl. 15, fig. 6.

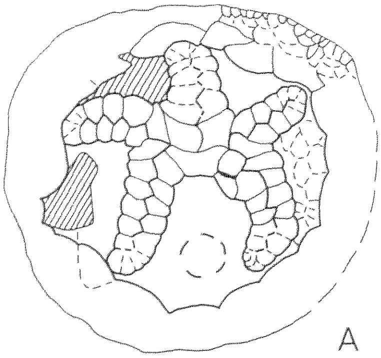
B. Lower side of the coverplates of ambulacrum I, CFMUC 8825, (x 20), pl. 16. fig. 4.

C. Juvenile, USNM 42105, (x 15), pl. 14, fig. 16.

D. Juvenile, USNM 42111-A, (x 10), pl. 15, fig. 2.

E. USNM S-3959, (x 4), pl. 15, fig. 10.

CP, ambulacral coverplate; HCP, hydropore ambulacral coverplate; HO, hydropore oral plate; LAO, left anterior primary oral plate; LBP, left lateral bifurcation plate; PO, posterior primary oral plate; RAO, right anterior primary oral plate; RBP, right lateral bifurcation plate.



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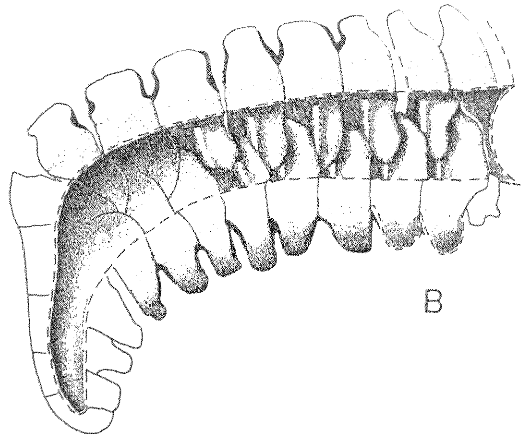

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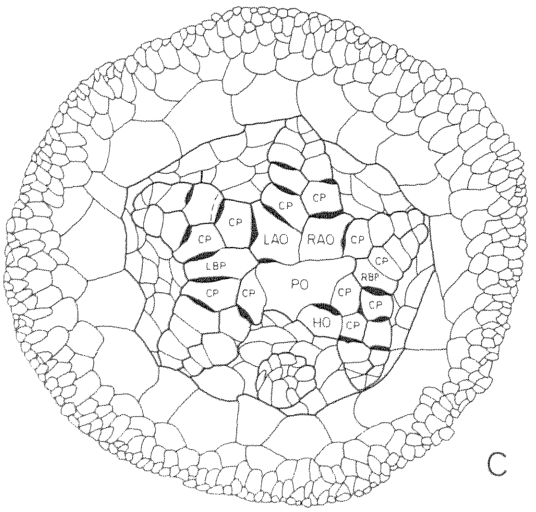
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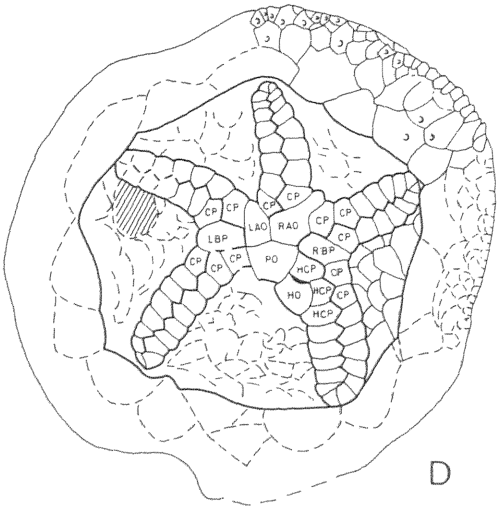
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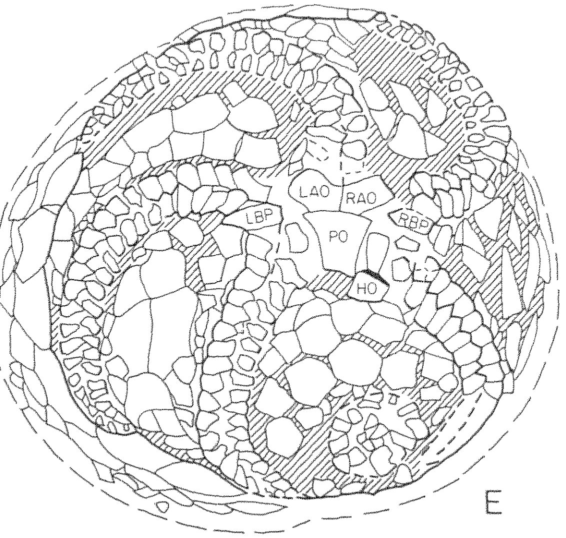
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E

with Route U.S. 52, about 3 miles east of Neville, Clairmont County, Ohio. (Moscow, Ohio-Kentucky quadrangle 7.5 minute topographic sheet, Ohio coordinate system: 296,275'; 1,526,725'.) 11.1 mm axial by 11.4 mm transverse diameter.

Text fig. 13E, pl. 15, fig. 11–13.

The theca is moderately complete, although most of the interambulacral plates are disrupted or missing. The exterior has been deeply etched, which removed the surface detail and in some areas obscured plate boundaries. The specimen appears to be a typical *Carneyella pilea* except for ambulacrum V, which is reversed and curves contrasolarly. It appears that ambulacrum V has a small, aborted branch which extends from the posterior side adjacent to the anal area. It is possible that this represents the primary axis of ambulacrum V which apparently stopped growing, whereas the secondary branch continued to lengthen and curved contrasolarly. It is also possible that this is one of the extremely rare variants in which a primary ambulacrum has a reverse curvature.

CFMUC 8886. Illustrated Specimen of *Carneyella pilea* as *Cyclocystoides sp.*, by Miller and Faber (1892, p. 85, pl. 1, fig. 13-15); *Agelacrinus cincinnatiensis* or *A. pileus*, by Foerste (1920, p. 60). " Hudson River Group " (probably Maysville Group), Cincinnatian Series, Upper Ordovician. Hills at Cincinnati, Ohio. Maximum length 10.2 mm.

Pl. 16, fig. 5, 6.

This is a small segment of one ambulacrum from a *Carneyella pilea* which includes several pairs of ambulacral coverplates, the underlying floorplates, and a few fragments of adjacent interambulacrals. Remarkably free of matrix, the coverplate-floorplate relationship is clearly exposed with both inner and outer foramina of the coverplate passageways. Each end of the ambulacral segment exposes a cross section of the structure.

CFMUC 8825. Illustrated Specimen of *Carneyella pilea* by Miller and Faber (1892, p. 85-86, pl. 1, fig. 10) as *Agelacrinus pileus.* " Hudson River Group " (probably Maysville Group), Cincinnatian Series, Upper Ordovician. Near top of hills at Cincinnati, Ohio. 17 mm axial by 16 mm transverse diameter.

Text fig. 14B, pl. 16, fig. 1-4.

The specimen exposes the inner side of the oral surface. It is incomplete, missing some interambulacral plates, most rim plates, and many ambulacral floorplates, including several of the proximal frame-forming ones. The inner ambulacral tunnel sides of the coverplates are seen where the floorplates are missing. Especially well preserved are the coverplates of ambulacrum I; text figure 14B shows the interlocking intra-ambulacral extensions.

CFMUC 54062. Probably Maysville Group, Cincinnatian Series, Upper Ordovician of the Cincinnati Arch region. 13.5 mm axial by 14.4 mm transverse diameter.

Pl. 16, fig. 12.

This specimen lacks adequate locality data but is illustrated to show the noncollapsed life configuration of the ambulacral-oral structures in relation to the interambulacral areas. The central part of the theca has slumped slightly toward the left but this appears to have distorted only the areas immediately proximal to the peripheral rim. The interambulacral areas remain elevated, collapse affecting only interambulacrum 5 around the anal structure. The ambulacra form low, only slightly raised, rounded ridges.

CFMP 6504. Maysville Group, Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. 9.8 mm axial by 9.8 mm transverse diameter.

Text fig. 13C, pl. 16, fig. 11.

This young adult has collapsed but only the interambulacra have been extensively disrupted. Some plates are etched but others preserve the pitting and nodose prosopon. The raised rim around the hydropore is well preserved.

UCMP 34535. Illustrated Specimen of *Carneyella pilea* by Kesling (1960, p. 166-167, pl. 11, fig. 3, 4). Bellevue Formation, Maysville Group, Cincinnatian Series, Upper Ordovician. Then vacant lot across street from Frisch's Big Boy Restaurant, Hamilton Avenue, North College Hill, Cincinnati, Ohio. Collected by William Deak, 1957. 15.7 mm axial by 15.4 mm transverse diameter.

Pl. 16, fig. 7.

Kesling used this and two other individuals from the North College Hill site to illustrate the hydropore structure in this species. This individual has collapsed and many of the plates are partially disrupted. The hydropore structure, including the raised rim, is well preserved and photogenic.

UCMP 34537. Illustrated Specimen of *Carneyella pilea* by Kesling (1960, p. 166-167, pl. 11, fig. 7, 8). Bellevue Formation, Maysville Group, Cincinnatian Series, Upper Ordovician. Then vacant lot across street from Frisch's Big Boy Restaurant, North College Hill, Cincinnati, Ohio. Collected by William Deak, 1957. 20.5 mm axial by 20 mm transverse diameter.

Pl. 16, fig. 8-10.

The second of Kesling's (1960) specimens has also collapsed, but the hydropore structure, with raised rim, is exceptionally clear. This specimen also preserves the oral midline ridges, the surficial pitting, and some of the nodes of the interambulacrals and rim plates.

UCMP 26324. Upper part of the Corryville Member, McMillan Formation, Maysville Group, Cincinnatian Series, Upper Ordovician. "Foot of Harrison Avenue, fill at Dent, across the valley west of the Tower Lake site, Dent, Ohio" (approximately 200 yards northeast of the intersection of Westwood Northern Blvd. and Harrison Ave., along the east edge of the town of Dent, just west of Cincinnati, Ohio). 16 mm axial by 13.8 mm transverse diameter (16.3 mm "long" by 12.8 mm "wide").

Pl. 17, fig. 1-4.

This unusual individual is resting upon a segment of crinoid stem. It illustrates the ability of domal edrioasteroids to modify thecal shape in response to the shape of the resting site. The opposing distal edges of the peripheral rim extend parallel to each other along most of their length and cross the stem abruptly at either end. The specimen has partially collapsed which disrupted a few areas, particularly the posterior interambulacrum. (An encrusting bryozoan is preserved on the surface of the crinoid stem segment opposite the edrioasteroid, possibly suggesting that the stem was vertical, in life position, during the life of the edrioasteroid.)

* * *

The following three specimens are selected representatives from the "Forestville population" which illustrate the morphology and variability of *Carneyella pilea.*

UCMP 40463-40465. Fairmount Member, Fairview Formation, Maysville Group, Cincinnatian Series, Upper Ordovician. North end of excavation for Beechmont Mall shopping center, opposite Anderson High School, Forestville, Hamilton County, Ohio. (Withamsville, Ohio-Kentucky quadrangle, 7.5 minute topographic sheet [1953], Ohio coordinate system: 397,300′; 1,474,700′; equals approximate center of a 200′ by 200′ area.)

UCMP 40463. 18.5 mm axial by 18.5 mm transverse diameter.

Pl. 17, fig. 5.

This is a large adult *Carneyella pilea* which has six ambulacra. The additional radius is formed by the bifurcation of ambulacrum IV immediately distal to the normal bifurcation point of ambulacra IV-V. The two branches diverge evenly from one another and form an interambulacral area along the normal axis of ambulacrum IV. The posterior branch is somewhat shorter than the anterior, but both are robust structures and neither is distinctly subservient to the other. The specimen has been deeply etched.

UCMP 40464. 21.3 mm axial by 20.8 mm transverse diameter.

Text fig. 13A. pl. 17, fig. 8, 9.

The theca has collapsed and some interambulacrals and rim plates are missing. The oral and hydropore areas are partially disrupted. Selective deep etching reveals a section view of the coverplate passageways which are clearly seen under xylene. The intra-ambulacral extensions of the coverplates are exposed perradially.

UCMP 40465. 16.6 mm axial by 16.4 mm transverse diameter.

Pl. 17, fig. 6, 7.

Only the posterior interambulacrum of this specimen has collapsed. The ambulacra and the oral area form only slightly raised, rounded ridges. The specimen has been extensively etched.

In addition to the above representatives of *Carneyella pilea,* over 500 other specimens were examined. These include a large number of individuals from both the Forestville and the North College Hill sites, as well as individuals from scattered localities around the Cincinnati Arch region.

Ontogeny

Several advanced juveniles and young adult *Carneyella pilea* suggest that at least the later stages of ontogeny for this species are quite similar to those of *Isorophusella incondita.* The advanced juveniles (USNM 42105, 68333, 40742-A-1, A-2, and B, 42111-A) contrast with adults in the proportionately large size of the peripheral rim, oral area, and periproct, whereas the ambulacra and interambulacra are relatively smaller (text fig. 14A, C, D). The ambulacra are short and straight or only slightly curved. In young adults (USNM 42111-B), the ambulacra and interambulacra become the dominant thecal structures and ambulacral curvature becomes progressively greater. Adults are characterized by the dominant ambulacra and interambulacra, whereas the peripheral rim, oral area, and anal structures each form a relatively small percentage of the total oral surface area (text fig. 13A, B). Ephebic ambulacra are distally concentric with the thecal margin. A few unusually large specimens (20 mm) suggest that gerontic forms differ only in their exceptionally large thecal diameter (text fig. 14E, pl. 15, fig. 8-10).

Discussion of previous investigation

Hall's (1866) original description of *Agelacrinus pileus* was unusually complete. He based the species on: shape of the theca; direction of curvature of the ambulacra;

single biseries of ambulacral coverplates; three large primary orals; four lateral ambulacra which originate as "pairs"; and central location of the anal structure ("ovarian aperture") in the posterior interambulacrum. In the subsequent description of the plate (1871), Hall recorded: "Along the depression at the summit of three of the rays may be seen the minute pores passing between the plates." His "pores" are the upper ends of the coverplate passageways which extend between the partially disrupted and deeply etched coverplates of his specimen. This observation has been overlooked or ignored by subsequent workers. In that plate explanation Hall also showed and called attention to "rounded nodes" on many of the interambulacral plates.

Meek (1873) redescribed Hall's *Agelacrinites pileus* and emphasized the lack of a second series of ambulacral coverplates (such as those in *Isorophus cincinnatiensis*). He also pointed out that the theca is domal (not semiglobose, as described by Hall, who illustrated only contorted specimens in which the peripheral rim was curved under the upper surface). Meek's specimens were etched and the nodose prosopon obscure; hence he described the plate exteriors as smooth.

Miller and Faber (1892) described the inner surface structure of *Carneyella pilea* from specimen CFMUC 8825 (pl. 16, fig. 1-4, text fig. 14B), which exposes the inner side of the oral surface. In the detailed description they reversed the terminology, *i.e.*, ambulacral floorplates are called covering elements and coverplates are called flooring elements. In standard terminology, they describe the interlocking inner sides of the ambulacral coverplates, the uniserial ambulacral floorplates, and the "subpentagonal" oral frame formed by the proximal ambulacral floorplates. Miller and Faber suggested that the innermost edge of the oral frame was flattened for attachment to the substrate. However, their specimen does not support this.

Spencer (1904) described *Carneyella pilea* from serial polished surfaces of a well-preserved specimen and a wax model restoration based on these. He described the ambulacral coverplates and floorplates as including "small interspaces between each covering plate," but denied the presence of passageways. He concluded that "*Agelacrinites*" has: (1) secondary triradiate symmetry formed by the fusion of ambulacra I-II and IV-V; (2) no regular numerical correspondence between ambulacral coverplates and floorplates; (3) orals derived from coverplates; (4) ambulacral floorplates forming the oral frame; and (5) no trace of a "madreporite" (*i.e.*, hydropore). Spencer's assessment of the coverplate-floorplate relationship, the derivation of the orals, and the construction of the oral frame agrees with current conclusions, whereas his contention that triradiate symmetry is secondary and that no hydropore is to be found are rejected here.

Foerste (1914) gave a detailed summary of the morphology of *Carneyella pilea*, including the first account of the hydropore and stone canal passageways (although he did not identify them as such). Most of Foerste's description agrees with that presented here except for two sets of "striations" on the articulating faces of the ambulacral coverplates (based on specimen CFMUC 8886, pl. 16, fig. 5, 6). These areas appear to be smooth. Foerste also described small vertical ridges on the inner sides of the peripheral rim plates of *Carneyella pilea*. However, he based this on what has proved to be a specimen of *Isorophus cincinnatiensis* (AMNH 13266/1-X, pl. 25, fig. 1, 2). As seen in several specimens, the rim plates of *Carneyella pilea* are squamose and the interior side is smooth.

Foerste (1914) also speculated on the life orientation of *Carneyella pilea* based on the presumed orientation of resting sites (concave-convex brachiopod shells) to current direction as related to the orientation of the edrioasteroid theca to the slope of the resting site surface. This, he contended, was indicated by the direction of thecal slump after death. He concluded that the theca was oriented to currents so as to provide maximum ease of feeding rather than for prevention of ambulacral contamination by excreta; and the direction of curvature of ambulacrum V, opposite the direction of the other four, evolved from the sloping substrate habitat of the edrioasteroids. Although Foerste's search for an ecologic and physiologic understanding was years ahead of his time, his conclusions seem to be unsupported by facts now at hand. Numerous specimens collected from a single bedding plane from the Forestville site appear to have been randomly oriented, and certainly in diverse positions on many types of hard surfaces of various configurations. His second suggestion seems to depend upon a neo-Lamarkian scheme of inheritance of acquired characteristics that can no longer be accepted.

Kesling (1960) identified the hydropore structure and the underlying stone canal passageway of *Carneyella pilea* that had been described but not identified as such by Foerste (1914). Kesling and Mintz (1960) summarized previous work on *C. pilea* and gave a detailed morphologic description based on external observations of both the inner and outer sides of the oral surface and also on serial polished surfaces of one individual. The only significant difference between their account and that given here is the identification of the coverplate passageway system described here. Minor discrepancies between their description and this one are related to specimen AMNH 13266/1-X, (pl. 25, fig. 1, 2), which exposes the inner side of the oral surface. Preparation of the individual with new techniques allowed removal of additional matrix and revealed that it is an *Isorophus cincinnatiensis* and not a *Carneyella pilea* as thought by Kesling and Mintz.

Bassler (1935, 1936) described five species which are here placed in synonymy under *Carneyella pilea.* The first, *Carneyella cincinnatiensis* Bassler (1935), was based on specimen USNM 40743-a and three additional unfigured specimens (b, c, d) (text fig. 13D, pl. 14, fig. 8-14). Bassler listed five characters: (1) theca " thin, depressed, almost flat "; (2) theca " attached by its entire aboral portion "; (3) " ambulacral plates . . . less elevated " (than in *C. pilea*); (4) " all the plates are rather papillose "; and (5) " only three oral plates " are present (in contrast with *Isorophus cincinnatiensis*). He referred to his new *Carneyella cincinnatiensis* a specimen illustrated by Hall (1871, pl. 2, fig. 7; = 1872, pl. 6, fig. 7). Hall's illustration depicts an *Isorophus cincinnatiensis,* except that the oral plates shown are those typical of *Carneyella pilea, i.e.,* three large primary orals. The oral region of Hall's specimen (AMNH 1194) is actually typical of *Isorophus cincinnatiensis,* formed by several plates including four primary orals. Bassler apparently examined only Hall's erroneous illustrations, and concluded from the three large orals that the specimen must belong to the genus *Carneyella* and not *Isorophus.* Bassler cited this illustration under his *Carneyella cincinnatiensis* as follows: " *Agelacrinus* (*Lepidodiscus*) *cincinnatiensis* Hall (*non* Roemer)." He thereby implied that the specimen belonged to the species *Carneyella cincinnatiensis* Bassler and not to Roemer's *Agelacrinus (Lepidodiscus) cincinnatiensis* (now *Isorophus cincinnatiensis*). This citation probably explains why Bassler selected the trivial name *cincinnatiensis,* in spite of the confusion it has created with the established name *Isorophus cincinnatiensis.*

Carneyella nicklesi Bassler (1936) was based on a large but poorly preserved *Carneyella pilea* (USNM S-3876, pl. 14, fig. 17, 18). Bassler (1936, p. 7) distinguished it from all other species of *Carneyella* by " its long, broad, much curved ambulacra, with about 20 short, wide covering plates in each row, and by the large, slightly imbricating, plainly visible interambulacral plates not obscured by surface ornamentation, which in this case consists of minute papillae arising from the finely punctate surface." These are all typical features of large *Carneyella pilea.*

Isorophus germanus Bassler (1936) was based on two specimens (USNM S-3959 and USNM S-3960, text fig. 14E, pl. 15, fig. 8-10). Both are quite large and typical *C. pilea.* Bassler's description of his new species is brief and contrasts this form with another species of *Isorophus* on the basis of thecal size, shape, number of plates, and anal structure. In these two types, the oral area with three large primary orals, the ambulacra with a single biseries of coverplates and coverplate passageways, and the anal periproct, all bespeak *Carneyella pilea,* and contrast with the structure of *Isorophus.*

Hemicystites curtus Bassler (1936) and *H. richmondensis* Bassler (1936) are both based on young specimens of *Carneyella pilea. H. curtus* was based on a single juvenile (USNM 42105) just under 5 mm in diameter, in which ambulacral curvature had just begun and the proportions of the major thecal structures are those of an advanced juvenile (text fig. 14C, pl. 14, fig. 16). Bassler cited the thecal proportions as distinguishing this individual from other species.

Hemicystites richmondensis Bassler (1936) was based on six specimens (USNM 68333, 40742, 42111), five juveniles and one young adult (text fig. 14A, D, pl. 15, fig. 1-7). The features Bassler described as characteristic of his species are characters of the youthful stage of development of *C. pilea.* Bassler's (1936, p. 14) contention that " it is not the young of some other edrioasteroid because the numerous specimens discovered all maintain the same maximum size," is not supported by measurements of the six specimens of the type series. Moreover, there is a progressive development from the smallest to the largest of the six individuals, although no mention is made of this in Bassler's description.

Bassleridiscus mohawkensis Fisher (1951) is also here placed in synonymy with *Carneyella pilea.* Fisher based his species, the type for his new genus, on a single individual (pl. 14, fig. 15) from the Middle Ordovician of New York which rests upon a fragment of a ramose bryozoan. The small, curved resting surface distorted the domal theca, and the distal parts of the ambulacra, interambulacra, and the peripheral rim are flexed under the upper side of the theca. The thecal contortion accounts for the " disco-globular " shape and long, strongly curved ambulacra that " extend onto the aboral surface " used by Fisher to differentiate the new genus and species from other forms with similar plate arrangements, such as undistorted *Carneyella pilea.*

Discussion

The study of over 500 specimens of *Carneyella pilea* has revealed only a few features not previously described. Most important is the coverplate passageway system, noted by Hall (1871) but overlooked since. The nodose prosopon is now believed to occur in all *Carneyella pilea,* although it is commonly obscured by surficial etching. The recognition of the wide range of thecal contortion which results from small or unusual resting areas accounts for several seemingly unique specimens (such as the type of *Bassleridiscus mohawkensis*). Knowledge of ontogeny necessarily broadens the taxobases.

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

Carneyella faberi (Miller), 1894

Text fig. 15; plate 17, fig. 10-13, plate 18, fig. 1-5

1894 *Agelacrinus faberi* Miller, S. A., *in* Miller, S. A. and Faber, C. L., Cincinnati Soc. Nat. Hist., Jour. 17 (3): 156, pl. 8, fig. 24, 25.

1914 *Agelacrinus faberi* Miller, Foerste, A. F., Denison Univ., Sci. Lab. Bull. 17 (art. 14): 441-444, pl. 1, fig. 3a-c, pl. 3, fig. 4; *Agelacrinus vetustus* Foerste, *ibid.*: 439-441, pl. 3, fig. 1.

1915 *Agelacrinites faberi* Miller, Bassler, R. S., United States Nat. Mus. Bull. 92, 1: 20; *Agelacrinites vetustus* Foerste, *idem, ibid.*: 21.

1918 *Agelacrinus faberi* Miller, Williams, S. R., Ohio Jour. Sci. 19 (1): 64.

1936 *Carneyella faberi* (Miller), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 9; *Carneyella vetustus* (Foerste), *idem, ibid.*: 7, pl. 2, fig. 14; *Carneyella foerstei* Bassler and Shideler, *idem, ibid.*: 8, pl. 6, fig. 7, 8.

1943 *Carneyella faberi* (Miller), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 197; *Carneyella foerstei* Bassler and Shideler, *idem, ibid.*: 197; *Carneyella vetusta* (Foerste), *idem, ibid.*: 198.

Diagnosis

A *Carneyella* with: large, clavate tubercles having rounded distal extremities, numerous on interambulacral and rim plates, but only two to seven per ambulacral coverplate.

Description

Carneyella faberi is represented by only three specimens in which the domal theca ranges from 12 to 25 mm in diameter (pl. 17, fig. 10-13, pl. 18, fig. 1-5). It differs from *C. pilea* only in the character of the prosopon. Whereas *C. pilea* has small, irregular nodes on the interambulacrals and rim plates, *C. faberi* has numerous large tubercles.

The tubercles are commonly clavate, the bulbous upper part connected to the underlying plate by a short, distinctly constricted zone (text fig. 15C, D, pl. 18, fig. 4, 5). The distal tips are usually rounded, although some appear pointed. All three known specimens show evidence of etching, thus it is not impossible that most of the nodes were originally sharply pointed like those of *Carneyella ulrichi.*

The number of tubercles per plate varies with the size and type of thecal plate involved. The largest plates of the interambulacra and peripheral rim average 25 nodes per plate, whereas smaller, average-sized plates in these areas have only 20. The ambulacral coverplates bear from two to seven nodes per plate. The larger proximal coverplates have six or seven. Oral plates appear to bear from 10 to 15 nodes each.

The tubercles vary greatly in size, as exemplified by ambulacral coverplates which are usually dominated by two or three large nodes, the other three or four so small that they are almost obscured by the larger tubercles (text fig. 15 C, D, pl. 18, fig. 3, 4).

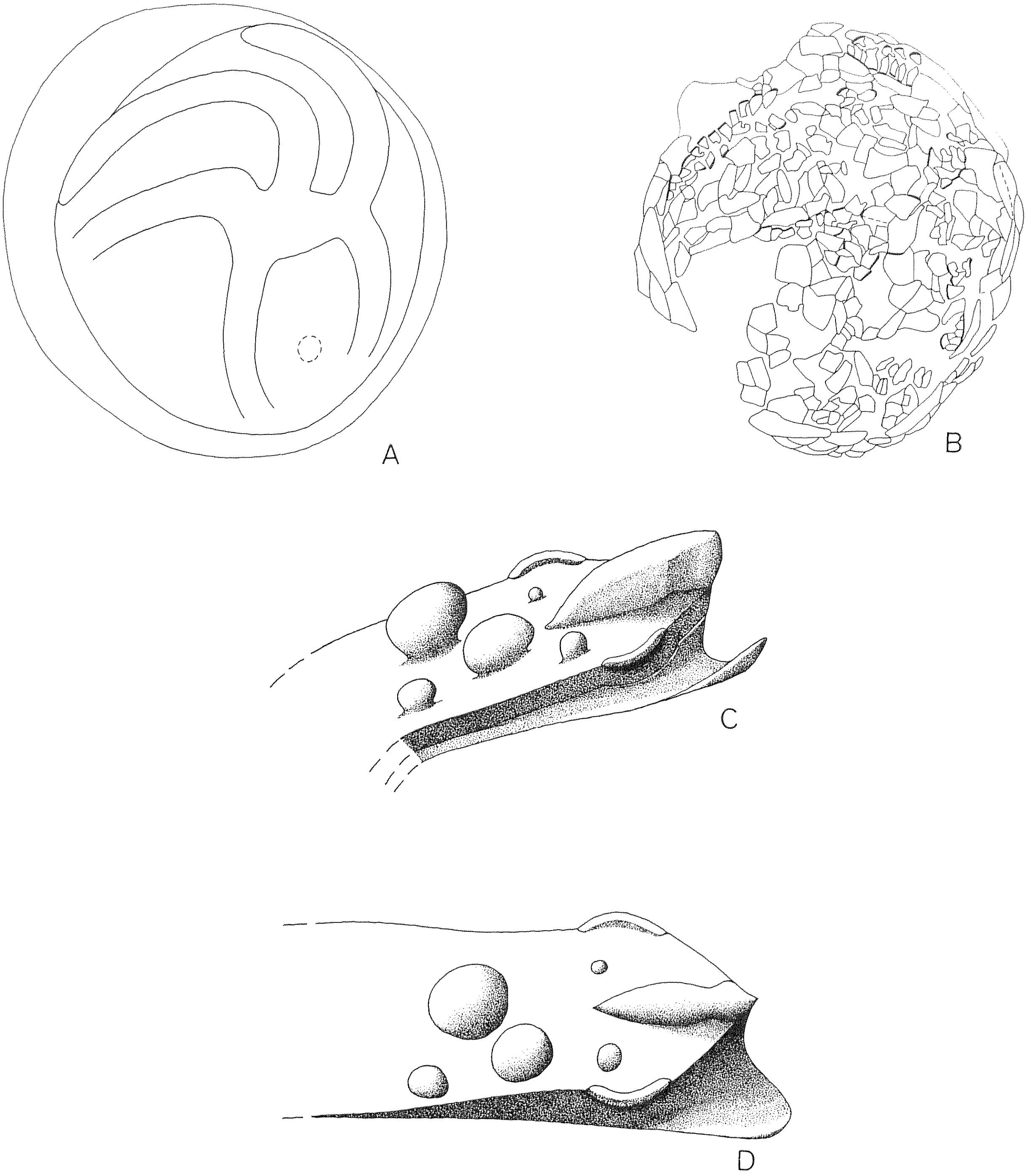
The ambulacral coverplates, like those of *Carneyella pilea*, have râised perradial ridges which extend parallel to the length of the coverplate, normal to the ambulacral axis (text fig. 15C, D). These perradial ridges are more highly elevated than those of *C. pilea*, and appear to have a sharp lateral constriction adradial to the perradial tip of the ridge. In addition to the large central ridge, each coverplate has two smaller ridges, one along each side of the adradial end of the angular perradial margin of the plate (text fig. 15C, D). These two lateral ridges, which parallel and flank the adradial end of the large central ridge, form the most perradial point of contact between adjacent coverplates. The width of each coverplate across the lateral ridged zone is equal to the width of the coverplate along the adradial suture line. The ridged part of the plate therefore extends laterally further than the central section of the coverplate (immediately adradial to the lateral ridges) because of the constriction in external plate width along the external foramen of the coverplate passageway. The ambulacral coverplates are thus very "ornate," with large and small tubercles, a large central perradial ridge and two smaller lateral ridges at the perradial end of the external foramina of the coverplate passageways.

The external edges of all three oral plates are steeply upturned along the transverse and anterior oral midline, and form highly elevated ridges. These oral midline ridges occur in *Carneyella pilea* but are more subdued.

A prominent raised rim surrounds the hydropore slit. It is formed by the upturned edges of the adjacent plates, as in *C. pilea*. In addition, the hydropore oral and the enlarged proximal coverplate of ambulacrum V have ridges that extend outward normal to the rim (pl. 18, fig. 5).

Small vertical ridges are also present on the distal tips of the anal plates and the outermost small plates of the peripheral rim.

Carneyella faberi can be distinguished from *C. pilea* solely on the basis of prosopon. Both species have external nodes and ridges, but these features in *C. faberi* are larger and more numerous. The surficial pitting of *C. pilea* appears to be less prominent than that of *C. faberi*, although this may be due to preservation. *C. faberi* is



Text figure 15. *Carneyella faberi* (Miller), 1894

A-B. Holotype, CFMUC 8821.

A. Sketch outlining major thecal structures, (x 4).

B. Oral surface, (x 4), pl. 17, fig. 10.

C-D. Reconstruction of an ambulacral coverplate.

C. Oblique lateral view.

D. Exterior surface plan view.