Text fig. 34, pl. 36, fig. 1-3.

The holotype is well preserved. Floorplates have been lost from ambulacrum III, which exposes the inner side of the coverplates. A few floorplates are crushed in the other ambulacra. The oral frame is slightly abraded but not disrupted. The anal structure lies to the right of center of interambulacrum 5 (left from the inner surface view). Etching has removed some surficial features, especially the smaller basal ridges of the distal rim plates.

GSC 14680-2. Paratype of *Isorophusella pleiadae* (Sinclair and Bolton) (1965, pl. 11, fig. 4, 5, 6). 5.7 mm axial by 6 mm transverse diameter.

Pl. 36, fig. 5.

This individual, considerably smaller than the holotype, appears to retain thecal proportions characteristic of a young adult. The ambulacral-interambulacral areas are proportionately smaller, and the oral area and the rim proportionately larger than is common in adults. Plate boundaries are less clear in this specimen, but the thecal structures appear identical to those of the holotype. The anal structure is very close to the left side of ambulacrum V. Etching has removed most of the basal ridges from the distal plates of the rim.

GSC 14680-3. Paratype of *Isorophusella pleiadae* (Sinclair and Bolton) (1965, pl. 11, fig. 5, 6). 8.4 mm axial by 8.8 mm transverse diameter.

Pl. 36, fig. 6.

This specimen is the largest of the type series, but has been disrupted. Only ambulacrum I, parts of interambulacra 1 and 5, the anal structure, and one segment of the rim are intact.

GSC 14680-4. Paratype of *Isorophusella pleiadae* (Sinclair and Bolton) (1965, pl. 11, fig. 5, 6). 5.5 mm axial by 5.6 mm transverse diameter.

Pl. 36, fig. 7.

This is a well-preserved specimen with all of the ambulacral floorplates preserved. The oral frame and stone canal passageway are very well preserved. A small section of the left posterior rim has been lost. Etching has removed all but the larger basal ridges of the proximal rim plates.

GSC 14680-5. Paratype of *Isorophusella pleiadae* (Sinclair and Bolton) (1965, pl. 11, fig. 5, 6). 7 mm axial by 7.2 mm transverse diameter.

Pl. 36, fig. 8.

This specimen is only slightly disrupted, but lacks the floorplates of ambulacra II and IV. The theca has been more deeply etched than the others, and details are obscure. The oral frame and the hydropore structures are relatively well preserved, as is the anal area.

GSC 14680-6. Paratype of *Isorophusella pleiadae* (Sinclair and Bolton) (1965, pl. 11, fig. 3, 5, 6). 6.1 mm axial by 6.2 mm transverse diameter.

Pl. 36, fig. 9.

In this specimen, ambulacra II and IV are missing several floorplates, and those of I and III are poorly preserved. The oral frame and stone canal passageway are both intact. Etching has again removed most of the distal rim plate basal ridges.

GSC 14680-7. Paratype of *Isorophusella pleiadae* (Sinclair and Bolton) (1965, pl. 11, fig. 3, 6). 5.7 mm axial by 5.7 mm transverse diameter.

Pl. 36, fig. 10.

This individual, like paratype 14680-2, appears to be less fully developed than the others. It is a young adult. The specimen is not in good condition, for many of the plates are partially crushed and etched. The anal structure is well preserved.

Discussion

The seven type specimens appear to represent a distinct species, as suggested by the small thecal diameters and adult thecal proportions.

The species is referable to *Isorophusella* on the basis of: the slight ambulacral curvature with I, II, III contrasolar, IV, V solar; the shorter length of ambulacrum IV; and the regularity of the double biseries of ambulacral coverplates.

RANGE AND OCCURENCE: Richmond Group, Cincinnatian Series, Upper Ordovician of Anticosti Island, Quebec.

Genus *Hemicystites* Hall, 1852

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

1852 *Hemicystites* Hall, J., Nat. Hist. New York, pt. VI, Palaeontology 2: 245-246, 335, pl. 51, fig. 18-20.

1854 *Hemicystites* Hall, Billings, E., Canadian Jour. Industry, Sci. and Art: 273.

1855 *Agelacrinus* Vanuxem, Roemer, F. [*partim*], *in* Lethaea Geognostica, H. G. Bronn, 3rd edition, Stuttgart, Bd. 1, pt. 2, Palaeo-Lethaea, 2: 277.

1857 *Hemicystites* Hall, Pictet, F.-J., Traité de Paléontologie ou Histoire Naturelle des Animaux Fossils, 2nd edition, Paris, 4: 305-306 [*non* pl. 99, fig. 25].

1860 *Agelacrinites* Vanuxem, Chapman, E. J. [*partim*], Canadian Jour. Industry, Sci. and Arts (n.s.), 5: 360-365.

1862 *Agelacrinus* Vanuxem, Dujardin, F. and Hupé, H. [*partim*], Histoire Naturelle des Zoophytes Echinodermes, Paris: 84 [*non* pl. 5, fig. 8].

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

1871 *Hemicystites* Hall, J. [*partim*], New York State Mus., 24th Ann. Rept. (adv. pub.): explanation of pl. 2.

1872 *Hemicystites* Hall, J. [*partim*], New York State Mus., 24th Ann. Rept.: 216.

1873 *Hemicystites* Hall, Meek, F. B. [*partim*], Geol. Surv. Ohio, v. 1, Geology and Palaeontology, pt. 2, Palaeontology, sect. 1: 53-54.

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

1894 *Hemicystites* Hall, Miller, S. A. and Gurley, F. E., Illinois State Mus. Bull. 5: 13.

1896b *Hemicystis* Hall, Haeckel, E. [*partim*], Die Amphorideen und Cystoideen, Leipzig, 1: 111-112 [*non* pl. 3, fig. 27-28].

1899 *Hemicystites* Jaekel, O. [*partim*], Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 49.

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

1903 *Hemicystis* Hall, Delage, Y. and Herouard, E. Traité de Zoologie Concréte, T. 3, Echinodermes, Paris: 415.

1915 *Hemicystites* Hall, Bassler, R. S. [*partim*], United States Nat. Mus. Bull. 92, 1: 605-606.

1935 *Hemicystites* Hall, Bassler, R. S. [*partim*], Smithsonian Misc. Coll. 93 (8): 7.

1936 *Hemicystites* Hall, Bassler, R. S. [*partim*], Smithsonian Misc. Coll. 95 (6): 10-11, pl. 4, fig. 5-6.

1938 *Hemicystites* Hall, Bassler, R. S. [*partim*], Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 110.

1943 *Hemicystites* Hall, Bassler, R. S. and Moodey, M. W. [*partim*], Geol. Soc. America, Spec. Pap. 45: 202, 204.

1946 *Hemicystites* Hall, Wilson, A. E. [*partim*], Geol. Surv. Canada Bull. 4: 20.

1958a *Hemicystites* Hall, Ehlers, G. M. and Kesling, R. V. [*partim*], Jour. Paleont. 32 (5): 933-934.

1965 *Hemicystites* Hall, Sinclair, G. W. and Bolton, T. E. [*partim*], Geol. Surv. Canada Bull. 134 (3): 38-39.

1966 *Hemicystites* Hall, Regnéll, G. [*partim*], *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U162 [*non*] text fig. 118-3, 120-5a, 125-7, 126-11.

TYPE SPECIES: *Hemicystites parasiticus Hall*, 1852.

Diagnosis

Isorophidae with: ambulacra straight, wide; ambulacral coverplates forming alternating double biseries; interambulacrals squamose, imbricate.

Description

The domal theca of *Hemicystites* is small and averages less than 10 mm in diameter.

The oral region includes four primary orals, two pairs of shared coverplates, one hydropore oral, and at least one right lateral secondary oral, arranged as in other Isorophidae.

The ambulacra are short, wide, and straight. The ambulacral coverplates form a double biseries of alternating pairs of large primary and smaller secondary plates. The perradial parts of the coverplates may be flexed upward to form a rounded axial ridge which extends the length of the ambulacra along the perradial lines. The ambulacral floorplates are uniserial and trough-shaped.

Interambulacral areas are restricted in size by the broad ambulacra, are covered with squamose, imbricate plates and are small to moderate in size in proportion to thecal diameter.

The prominent valvular anal structure is formed by regularly alternating inner and outer circlet plates.

The peripheral rim is typical of the family.

Discussion

Hall's (1852) original description of the genus and the type species, *H. parasiticus*, summarized only major thecal characters that separated the new taxa from other major echinoderm groups. A very generalized drawing of *H. parasiticus* accompanied the text. Under additions and corrections in the same volume (p. 355), Hall explains that *Hemicystites* " is apparently identical with *Agelacrinites* of Vanuxem [1842], the description and figure of which I had overlooked at the time this volume was written."

E. Billings (1854), F. Roemer (1855), F. J. Pictet (1857), and Dujardin and Hupé (1862) concurred with Hall and recognized Hall's species as an *Agelacrinites*. As was pointed out by Meek (1873), the subsequent equating of the two genera may in part be explained by the erroneous illustration of an *Isorophus cincinnatiensis* (then placed in *Agelacrinites*) as an example of *Hemicystites parasiticus* by Pictet (1857) and by Dujardin and Hupé (1862).

By 1866 Hall was disposed to consider *Hemicystites* as a distinct genus. He also described *Agelacrinus (Hemicystites) stellatus* in 1866. In Hall's (1871) publication of the plate of illustrations for that work, he lists *Hemicystites stellatus* and also a new species, *Hemicystites* (s.g. *Cystaster*) *granulatus*. Detailed drawings of both species were presented. The text and plate were republished together in 1872, with the two species cited as *Hemicystites* (s.g. *Cystaster) granulatus* and *Agelacrinus (Hemisystites) stellatus*. These are relatively common species and both conform to the genus *Cystaster*. On the other hand, Hall's (1852) illustration of *Hemicystites parasiticus* does not accurately portray the plating of the oral area and represents ambulacral coverplates as a single biseries rather than the actual double biseries. Specimens of *H. parasiticus* are rare. Unfortunately, most workers have used *Cystaster stellatus* or *C. granulatus* to represent the generic characters of *Hemicystites*. Meek (1973) and Miller (1877, 1889) both included the *Cystaster* species in *Hemicystites*. Haeckel (1896) even cited "*Hemicystites*, (= *Cystaster*) *granulatus*, Hall" as the type species of the genus. He characterized the genus exclusively on its sack- or disk-shape and straight ambulacra.

Jaekel (1899) recognized *Cystaster* as a distinct genus, but retained *C. stellatus* in *Hemicystites*. He also transferred several Bohemian species described by Barrande (1887) into *Hemicystites*. Jaekel's generic appraisal cited the small thecal size and hemispherical shape, the weak, imbricate thecal plates, and the short, straight ambulacra.

Bassler (1935, 1936) examined the holotype and several topotypes of *H. parasiticus*, but he described *Hemicystites* as having an oral-ambulacral structure like that of *Carneyella*. The supposed presence of only three primary orals, two anterior and one large central posterior, was the prime taxobasis of Bassler's new family Hemicystitidae. He excluded *Cystaster granulatus* and *Cystaster stellatus* from *Hemicystites*, and proposed the genus *Cincinnatidiscus* for *Cystaster stellatus*. However, he included 11 other species in *Hemicystites*, many of which agreed with his concept of the genus, but none of which show the structure of the type species. All are here removed from *Hemicystites*.

Bassler and Moodey (1943) repeated the Bassler (1935, 1936) assignment of the 11 species to *Hemicystites*, and added the American species *Hemicystites eckeli* Cullison and Prouty (1939). This last species has not been studied here, but apparently belongs to some other genus. Following Jaekel's lead, four European species described by Barrande (1887) under the genus *Agelacrinites* were also included in *Hemicystites*, along with two other European species. These have not been restudied here and their assignment is questionable.

Wilson (1946) adhered to Bassler's interpretation of *Hemicystites* and cited the short, broad, straight ambulacra and an oral area supposedly like that of *Carneyella* as the generic taxobases.

Ehlers and Kesling (1958) recognized the hydropore oral as one of the peristomial plates in *Hemicystites* and in all supposedly related genera that are included in Bassler's Hemicystitidae. Their emended description of that family was apparently based on species other than *Hemicystites parasiticus*, for the oral region was again characterized as having only three large primary orals.

Regnéll (1966) summarized earlier descriptions of *Hemicystites*, and recognized only three primary orals and the hydropore oral as the primary oral series. *Cryptogoleus chapmani* was illustrated as a supposedly typical species of *Hemicystites*.

Hemicystites Hall is a typical Isorophidae, as is shown by the double biseries of ambulacral coverplates and the oral area with four primary orals, two pairs of lateral shared coverplates, one hydropore oral, and at least one secondary oral plate. The numerous species with carneyellid oral and ambulacral structures that formerly have been referred to the genus, are not congeneric. Several European species, particularly those from Bohemia described by Barrande (1887), may possibly correspond to *Hemicystites parasiticus*. At this stage, however, *Hemicystites parasiticus* is the only species that can definitely be retained in the genus.

RANGE AND OCCURRENCE: Clinton Group, Niagaran Series, Middle Silurian of New York.

Hemicystites parasiticus Hall, 1852
Text fig. 35; plate 37

1852 *Hemicystites parasitica* Hall, J., Nat. Hist. New York, pt. VI, Palaeontology 2: 246, pl. 51, fig. 18-20.

1855 *Agelacrinus parasiticus* (Hall), Roemer, F., *in* Lethaea Geognostica, H. G. Bronn, 3rd edition, Stuttgart, Bd. 1, pt. 2, Palaeo-Lethaea, 2: 277.

1857 *Hemicystites parasitica* Hall, Pictet, F.-J., Traité de Paléontologie ou Histoire Naturelle des Animaux Fossils, 2nd edition, Paris, 4: 306 [*non* pl. 99, fig. 25].

1860 *Agelacrinites parasiticus* (Hall), Chapman, E. J., Canadian Jour. Industry, Sci. and Art (n.s.), 5: 360-365.

1862 *Agelacrinus parasiticus* (Hall), Dujardin, F. and Hupé, H., Histoire Naturelle des Zoophytes Echinodermes, Paris: 84 [*non* pl. 5, fig. 8].

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

1872 *Hemicystites parasiticus* Hall, J., New York State Mus., 24th Ann. Rept.: 216.

1873 *Hemicystites parasiticus* Hall, Meek, F. B., Geol. Surv. Ohio, v. 1, Geology and Palaeontology, pt. 2, Palaeontology, sect. 1: 53-54.

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

1896b *Hemicystis parasitica* Hall, Haeckel, E., Die Amphorideen und Cystoideen, Leipzig, 1: 112.

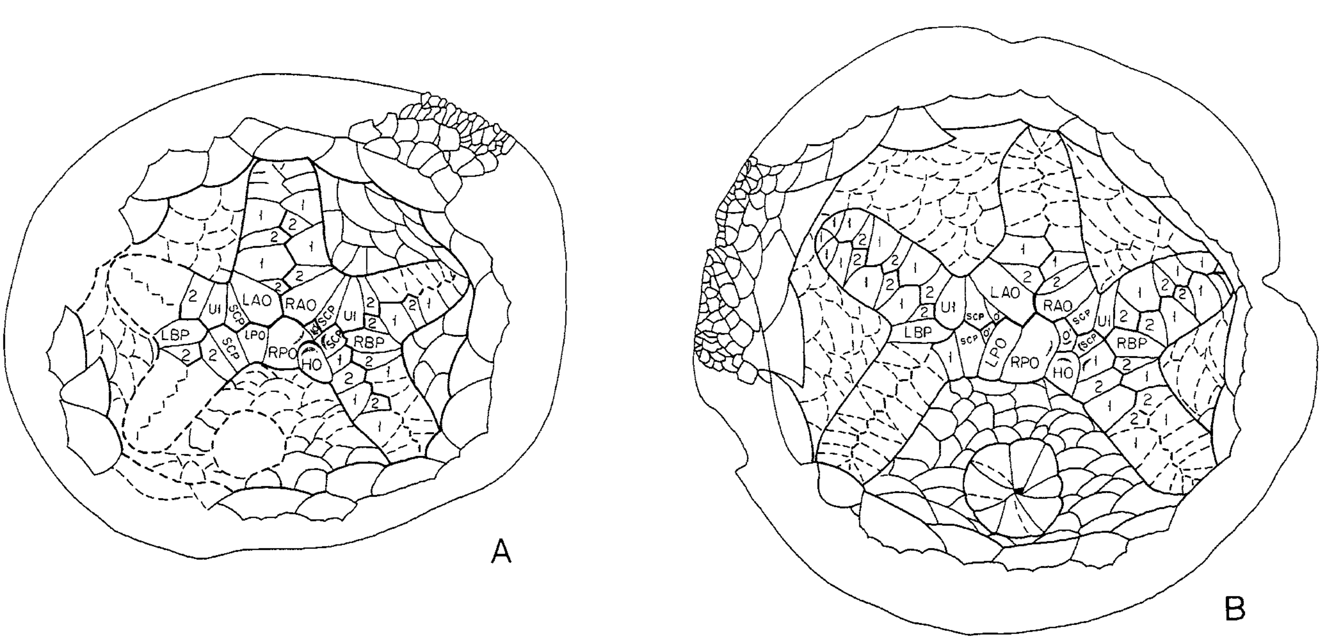
1899 *Hemicystites parasiticus* Hall, Jaekel, O., Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 49.

1915 *Hemicystites parasiticus* Hall, Bassler, R. S., United States Nat. Mus. Bull. 92, 1: 606.

1936 *Hemicystites parasiticus* Hall, Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 11, pl. 4, fig. 5, 6.

1938 *Hemicystites parasiticus* Hall, Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 110.

1943 *Hemicystites parasiticus* Hall, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45, 204.



Text figure 35. *Hemicystites parasiticus* Hall, 1852.
A. USNM S-3183-B, (x 12), pl. 37, fig. 3. B. USNM S-3183-A, (x 12), pl. 37, fig. 2.
HO, hydropore oral plate; LAO, left anterior primary oral plate; LBP, left lateral bifurcation plate; LPO, left posterior primary oral plate; o', secondary oral plate; RAO, right anterior primary oral plate; RBP, right lateral bifurcation plate; RPO, right posterior primary oral plate; SCP, lateral shared coverplate; U1, unpaired primary ambulacral coverplate; 1, primary ambulacral coverplate; 2, secondary ambulacral coverplate.

1965 *Hemicystites parasiticus* Hall, Sinclair, G. W. and Bolton, T. E., Geol. Surv. Canada Bull. 134 (3): 38-39.

1966 *Hemicystites parasiticus* Hall, Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U162.

Diagnosis

A *Hemicystites* with: small domal theca; one or more secondary orals; hydropore opening on top of small protuberance formed by four or five of the six hydropore structure plates; secondary ambulacral coverplates commonly large, some approaching size of primaries; coverplates perradially arched to form median ridge along ambulacra, which continues along the transverse and anterior oral midlines; interambulacral plates squamose, imbricate, moderate in size in proportion to thecal diameter; valvular anal structure large.

Description

The theca of *Hemicystites parasiticus* is small, apparently averaging 6 or 7 mm in diameter. One broken specimen may have been over 10 mm in diameter.

The two anterior primary orals are large, subequal in size, and symmetrically disposed across the anterior oral midline (text fig. 35A, B, pl. 37, fig. 2, 3). The right posterior one is the largest primary oral and is perradially in contact with both anterior orals. The small left posterior primary is restricted to the far left part of the central oral area. One pair of lateral shared coverplates flank each side of the central primary orals. One member of each pair is distally in contact with the perradial end of one of the two lateral bifurcation plates.

A single, small, posterior, right lateral secondary oral lies between the perradial tips of the right posterior primary oral and the right posterior shared coverplate (text fig. 35A, B). However, an opposing, anterior, right lateral secondary oral may be present in some individuals, forming a right lateral pair of secondaries. A left lateral pair of secondaries which lie between the perradial ends of the two left primary orals and the left lateral pair of shared coverplates may also be present (text fig. 35B).

The perradial parts of all the oral area plates arch upward to form a prominent central ridge that extends along the transverse and anterior oral midlines. These are continuous with the central ridges of the ambulacra.

The oral frame is formed by the proximal ambulacral floorplates and probably by intrathecal extensions from the primary orals as well (pl. 37, fig. 7, 8).

The hydropore structure is formed by the hydropore oral, the right posterior primary oral, the posterior right lateral shared coverplate, the posterior right lateral secondary oral, and the proximal two posterior coverplates of ambulacrum V. The two ambulacral coverplates are not in contact with the opening, but both are conspicuously shortened when they meet the hydropore oral, which intrudes into the edge of the ambulacrum.

The hydropore opens on the summit of a small, highly elevated protuberance formed by the four plates which surround the opening. The contiguous parts of these plates are highly elevated in a manner similar to the perradial arching of the orals and the ambulacral coverplates. The right posterior primary oral and the hydropore oral form the posterior two-thirds of the protuberance. The anterior third is formed by the adradial parts of the posterior, right lateral shared coverplate and perhaps also by the adradial end of the posterior right lateral secondary oral. The opening appears to be a small, crescentic slit on the summit of the tubercle and opens along the contact of the right posterior primary oral, the right posterior shared coverplate, and the hydropore oral plate. The posterior right lateral secondary oral may also be in contact with the opening. The opening possibly bifurcates in some individuals so as to extend along the junction between the posterior primary oral and the adjacent proximal edge of the right lateral secondary oral.

The ambulacra are short, wide, and straight. The secondary ambulacral coverplates are somewhat smaller than the primaries. The more distal secondaries are commonly much smaller than the adjacent primaries, as are some of the proximal secondaries. However, other proximal secondaries appear to be large, and approach the size of adjacent primaries. The secondaries commonly reach the adradial suture line externally. Alternation of the pairs of primary and secondary sets appears to be somewhat irregular. Ambulacra II and IV each appear to have a large proximal unpaired primary oral on the anterior side between the proximal pair of secondary coverplates and the anterior lateral shared coverplates of the oral area.

The adradial two-thirds of the coverplates are inclined at a low angle to the surface of the adjacent interambulacra and produce a gradual upward rise of the ambulacral structures above the interambulacra. However, the perradial thirds of the coverplates are sharply arched upward and form proximal axial ridges which extend the length of the ambulacra. These axial ridges are confluent with the transverse and anterior oral midline ridges formed by similar perradial flexure of the oral plates.

The uniserial, trough-shaped ambulacral floorplates are rectangular in plan view and are elongate normal to the ambulacral axes. The distal one or two floorplates are somewhat smaller and form the rounded, blunt ambulacral terminations.

The interambulacra are restricted in extent by the broad ambulacra. The squamose, imbricate plates are of average size in comparison with other edrioasteroids of the same size.

The valvular anal structure is unusually large in proportion to the size of interambulacrum 5. It appears to have 12 to 14 large triangular plates arranged as regularly alternating members of an inner and an outer circle. The proximal tips of the anals are flexed upward and form a small central elevation. The entire structure may have been a cone-shaped protuberance before thecal collapse.

The peripheral rim includes five or six circlets of plates. The large plates of the proximal circlet are distributed as alternating proximal and distal subcirclet members. The distal rim circlets are less regular. Vertical ridges may be present on the bases of the larger geniculate plates.

External plate surfaces appear to have been smooth.

Specimens

USNM S-3183 (A-K). Topotypes of *Hemicystites parasiticus* Hall (1852). *Homocrinus* beds, Rochester Shale, Clinton Group, Niagaran Series, Middle Silurian. Lockport, New York.

USNM S-3183-A. Illustrated Specimen of *H. parasiticus* by Bassler (1936, pl. 4, fig. 6). 7 mm axial by 7 mm transverse diameter.

Text fig. 35B, pl. 37, fig. 2.

The theca of the specimen has collapsed, but only a few of the interambulacrals have been intensely disrupted. Slight lateral shifting of the orals and ambulacral coverplates also appear to have occurred. A small crack separates a posterior segment of the peripheral rim from the remainder of the theca. Plate boundaries are more or less distinct, but the specimen has been etched, particularly in the oral and ambulacral areas. Thus external plate shapes and sizes have been differentially altered.

USNM S-3183-B. 5.3 mm axial by 6.2 mm transverse diameter.

Text fig. 35A, pl. 37, fig. 3.

This specimen is the best preserved of the topotypes. The theca has collapsed, but little disruption has occurred. However, slight lateral shifting of plates has affected the oral and ambulacral areas. The anal structure is considerably disrupted and appears to have been abraded. Superficial etching has differentially altered some external features.

USNM S-3183-C. 6.8 mm axial by 4.3 transverse diameter.

Pl. 37, fig. 4.

The specimen has collapsed, disrupting interambulacrals and some of the ambulacral elements. The anal structure is jumbled. The theca is laterally compressed, although apparently this is due mostly to mode of growth. Plates are only slightly etched.

USNM S-3183-D-1. 7.5 mm axial by 7.8 mm transverse diameter.

Pl. 37, fig. 8.

This individual exposes the inner side of the oral surface. Unfortunately it is poorly preserved. The ambulacral floorplates have been crushed into the ambulacral tunnels along axial fractures. This creates the false appearance of a double biseries of floorplates. The oral frame is crushed and plate boundaries are completely obscured. Only the anals and some of the interambulacral plates are well preserved. The peripheral rim is little disrupted, but the exposed basal surfaces of the geniculate plates appear to have been extensively etched. Remnants of what appear to have been vertical basal ridges are seen on some of these plates.

USNM S-3183-D-2. 5.2 mm axial by 5 mm transverse diameter.

Pl. 37, fig. 7.

This is a second specimen that exposes the inner side of the oral surface. It is poorly preserved. The ambulacral floorplates are crushed and the oral frame is completely obscured; parts of the interambulacra and the rim are moderately well preserved.

USNM S-3183-D-3. 6.9 mm greatest diameter by 6 mm diameter.

Pl. 37, fig. 9.

This fragmentary and poorly preserved specimen exposes the inner side of the oral surface. The size of the fragment suggests that the individual was larger than other known specimens, perhaps over 10 mm in diameter.

USNM S-3183-E. 6.7 mm axial by 6.1 mm transverse diameter.

Pl. 37, fig. 5.

This deeply etched specimen has collapsed, but little plate disruption has occurred. All major thecal structures are preserved.

USNM S-3183-F. 5 mm axial by 4.8 mm transverse diameter.

Pl. 37, fig. 6.

The theca of this specimen has collapsed, but only the interambulacrals have been disrupted. Oral and ambulacral plating is similar to that of the other topotypes. However, the peripheral rim appears somewhat larger proportionately than in the other specimens, and the ambulacra-interambulacra somewhat smaller. Combined with the small thecal diameter, this suggests that the specimen is less fully developed than the others; it may be a young adult.

UCMP 37217. Topotype of *H. parasiticus*. *Homocrinus* beds, Rochester Shale, Clinton Group, Niagaran Series, Middle Silurian. Lockport, New York. Kopf Collection. 7.4 mm axial by 7.2 mm transverse diameter.

Pl. 37, fig. 10, 11.

This specimen is from the USNM S-3183 topotype series described above and was traded by R. S. Bassler to M. Kopf in 1941. The theca has collapsed and is partially deformed by the underlying costae of the brachiopod on which it rests. A prominent crack extends across the posterior half of the theca. The specimen has been only slightly etched, therefore most surficial features are well preserved. Slight lateral shifting of the orals and ambulacral coverplates has modified plate arrangement in some areas. The anal area and parts of the rim are notably well preserved.

Discussion of previous investigation

The original description of *Hemicystites parasiticus* by Hall (1852) emphasized general thecal features that separate this species from other major echinoderm groups. Taxonomically important characters mentioned include: small domal theca; imbricate interambulacrals; straight ambulacra; and a valvular anal structure with an inner and outer circlet of alternating plates. In addition, Hall (1852, p. 246) described "a porous tubercle near the apex on the side opposite the ovarian orifice [anal structure], and near this the minute oral orifice, with an obscure pore below and near it . . . The oral orifice is so minute and obscure that little can be said of it more than that near the porous tubercle, on the side opposite the conspicuous ovarian pyramid, there is a triangular orifice and near it a circular depression or pore." Examination of an unretouched photograph of the holotype suggests that Hall's "oral orifice" is a slight separation between the raised perradial ends of the primary orals. The "triangular orifice" is the slightly disrupted and etched hydropore opening on top of the hydropore tubercle. The third opening mentioned as an "obscure pore" appears to be a preservational irregularity adjacent to the adradial end of the left posterior shared coverplate.

The drawing accompanying Hall's description is quite generalized. The ambulacra taper proximally to a small oral area in which plate boundaries are obscure. Ambulacral coverplates are shown as a regularly alternating single biseries. The anal structure is diagrammatic, but does show an inner and outer circlet of plates. Only one specimen was illustrated, but Hall notes that several others were at hand.

Discussion

The present description of *Hemicystites parasiticus* is based upon 13 topotypes. The location of the holotype is unknown. However, Bassler (1936) had access to it and published the first photograph of it. Detailed comparison of the topotypes to an unretouched enlargement of Bassler's photograph, found in the United States National Museum (pl. 37, fig. 1), confirms the conclusion that the topotypes are conspecific with the holotype.

The few well-preserved topotypes establish the basic plate structure of the species. Unfortunately, minor lateral slippage of the oral-ambulacral series and other preservational irregularities leaves doubt as to the number of secondary orals, the number of plates forming the hydropore tubercle, and the regularity of alternation of the primary and secondary coverplate pairs. Moreover, one fragmentary specimen may have been over 10 mm in diameter, suggesting that average adult thecal diameter could have been greater than recorded here.

One of the most diagnostic features of *H. parasiticus* is the perradial flexure of the oral-ambulacral plate series which forms prominent axial ridges along the ambulacra and across the oral area. No other agelacrinid is known to develop comparable large perradial ridges, and their significance is unknown.

RANGE AND OCCURRENCE: Rochester Shale, Clinton Group, Niagaran Series, Middle Silurian of New York.

Genus *Rectitriordo* Bell, gen. nov.

TYPE SPECIES: *Rectitriordo kirkfieldensis* Bell, *sp. nov.*

Diagnosis

Isorophidae with: ambulacra straight; ambulacral coverplates forming regular triple biseries.

Description

Rectitriordo is monotypic. The type species is represented by three partially disrupted specimens in which the ambulacral structure is well preserved, but the oral area and hydropore structures are incomplete. The genus is distinguished from other Isorophidae by the straight ambulacra with a regular triple biseries of ambulacral coverplates that includes three sets of coverplates.

ETYMOLOGY: *Rectitriordo* is compounded from the Latin *rectus*, *tres*, and *ordo* meaning straight, three, and series, referring to the straight ambulacra with a triple biseries of coverplates.

Rectitriordo kirkfieldensis Bell, *sp. nov.*
Text fig. 36, 37; plate 38.

Diagnosis

A *Rectitriordo* with: highly arched, domal theca; oral area including approximately 13 secondary orals; ambulacra straight; ambulacral coverplates a regular triple biseries; interambulacrals squamose, imbricate, and relatively large; distal rim plates subtriangular.

Description

The domal theca of *Rectitriordo kirkfieldensis* is nearly hemispherical. The largest specimen recorded is 31.5 mm in diameter (text fig. 36A, pl. 38, fig. 1, 2).

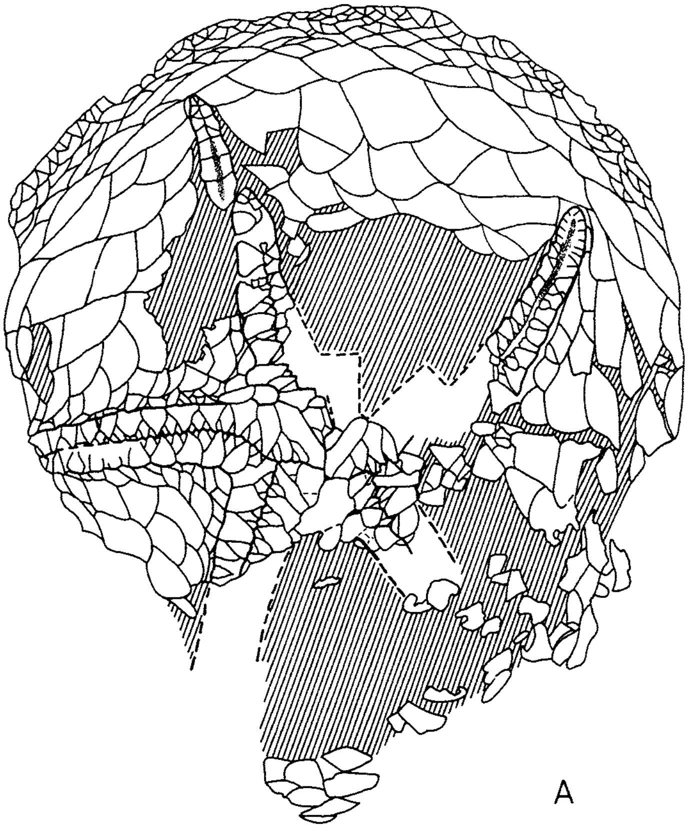
The oral area is preserved only in the holotype, where it is partially disrupted. The plates are tentatively identified in text fig. 36B. The four primary orals are central in position, but the right posterior primary is unusually large. It extends across the entire posterior edge of the area, in contact with both the hydropore structure and the

Text figure 36. *Rectitriordo kirkfieldensis* Bell, *sp. nov.* Holotype, UCMP 40476.

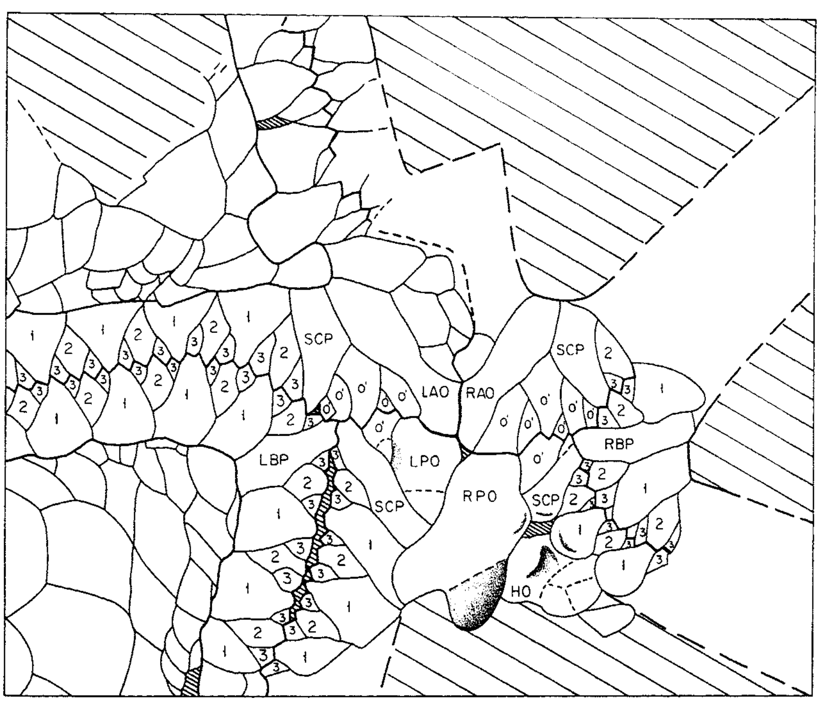
A. Oral surface, (x 4), pl. 38, fig. 2. Ambulacral floorplate trough, exposed where coverplates are missing, is stippled.

B. Oral area and adjacent structures, (x 10), pl. 38, fig. 4. Adradial intrathecal part of the right posterior primary oral plate is stippled.

HO, hydropore oral plate; LAO, left anterior primary oral plate; LBP, left lateral bifurcation plate; LPO, left posterior primary oral plate; o', secondary oral plate; RAO, right anterior primary oral plate; RBP, right lateral bifurcation plate; RPO, right posterior primary oral plate; SCP, lateral shared coverplate; 1, primary ambulacral coverplate; 2, secondary ambulacral coverplate; 3, tertiary ambulacral coverplate.



A



B

proximal plates of ambulacrum I. Therefore, the left posterior primary oral is restricted to the left central part of the area and does not reach the adradial suture line.

Two pairs of lateral shared coverplates appear to be present. The opposing alternate members of each pair are separated perradially by secondary orals. The two posterior shared coverplates are perradially in contact with the lateral bifurcation plates. The anterior members perradially abut proximal ambulacral coverplates distal to the bifurcation plates.

Five or six lateral anterior secondary orals and one lateral posterior secondary lie along both the right and left sides of the transverse oral midline. These plates perradially separate the lateral shared coverplates and the primary orals. The two anterior groups of secondaries reflect the pattern of the three sets of ambulacral coverplates.

A small node appears to be present in the left posterior oral region, formed by the contiguous elevated margins of three plates: the left posterior primary oral, the left posterior shared coverplate, and the left posterior lateral secondary oral.

The hydropore structure appears to be formed by the right posterior primary oral, the hydropore oral, the right posterior shared coverplate, and the proximal primary coverplate of the posterior side of ambulacrum V (text fig. 36A, B). Plate margins surrounding the opening appear to have been highly elevated.

The straight ambulacra taper gradually (text fig. 36A, pl. 38, fig. 1, 2). The ambulacral coverplates form a triple biseries of alternating plate pairs. The primary coverplates are large and subtriangular in external outline. Opposing alternate members of each pair are in contact across the perradial line. Adjacent primaries are in contact adradially and restrict the external parts of the other two sets of coverplates to the medial part of the ambulacra.

One pair of secondary coverplates lies between each pair of primaries. These secondaries are subrhomboidal in plan view and intermediate in size. The angular perradial ends of opposing alternate pair members are in contact perradially. The external adradial ends of these plates are also angular, wedged between the lateral edges of the adjacent primaries; therefore they end externally before reaching the adradial suture line. However, one specimen suggests that the secondaries may reach the adradial suture line externally in the distal parts of the ambulacra.

The tertiary coverplates are small, subrhomboidal, and restricted to the axis of the ambulacra. One pair of tertiaries lies adjacent to each side of each secondary pair and separates them perradially from the tips of the primaries. Thus there are two pairs of tertiary coverplates for each pair of primaries or secondaries. The sequence of coverplates encountered along the serrate perradial line is: primary, tertiary, secondary, tertiary, primary, etc.

Disrupted specimens suggest that the secondary coverplates extend adradially under the adjacent primaries, at least as far as the adradial sutures. Both sets of plates are beveled along the zone of overlap and fit tightly together. The tertiary plates appear to be limited to the axial ambulacral area and their external form apparently reflects the total extent of these plates. Both the primaries and secondaries apparently extend past the lateral margin of the floorplates into the thecal cavity as intrathecal extensions.

The floorplates are uniserial, trough-shaped, and subrectangular in plan view, elongate normal to the ambulacral axis. The concave central part of the upper side of each floorplate forms a broad trough along the axis of the ambulacrum. Lateral margins of the upper side are nearly horizontal along the articulation zone with the overlying coverplates.

The interambulacral plates are squamose and imbricate. The central and distal plates of each interambulacrum are relatively large in proportion to thecal diameter. Moreover, these plates may be unusually thick.

The valvular anal structure is formed by large, subtriangular plates, perhaps 18 or more, which alternate as inner and outer circlet members (text fig. 37B, pl. 38, fig. 9, 10).

The peripheral rim includes five or six circlets of plates (text fig. 37A). The large, externally squamose plates of the proximal circlet alternate as proximal and distal subcirclet members. The more distal circlets of the rim are less ordered than the proximal. The plates are triangular to subtriangular; and commonly, adjacent plates have their apices reversed in direction, one pointing proximally, the next one distally. The most distal circlet appears to be formed by pairs of triangular plates with the apices of the two plates together. Combined, the two plates of each pair form a larger subtriangular unit which points proximally.

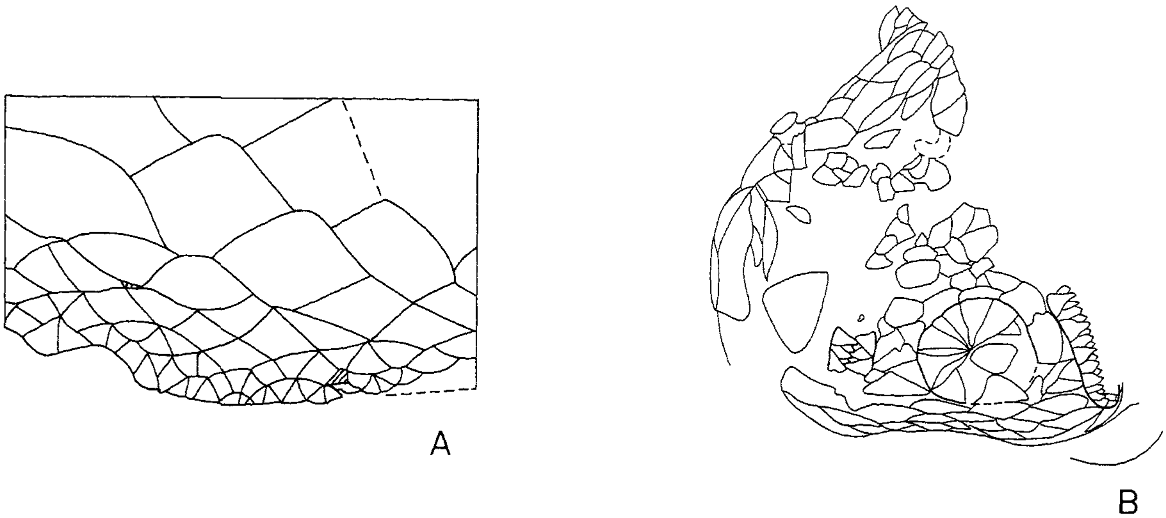
The thecal plates of *Rectitriordo kirkfieldensis* appear to have been smooth externally.

Specimens

UCMP 40476. Holotype of *Rectitriordo kirkfieldensis* Bell. "Hull Limestone," Trenton Group, Mohawkian Series, Middle Ordovician. Quarry 3 miles north of Kirkfield, Ontario. Kopf Collection. 27.6 mm axial by 25.3 mm transverse diameter; 31.5 mm greatest diameter, 8 mm high.

Text fig. 36A, B, 37A, pl. 38, fig. 1-6.

The central part of the oral surface has collapsed inward, but the distal third of the ambulacral-interambulacral areas and the peripheral rim remain in life orienta-



Text figure 37. ***Rectitriordo kirkfieldensis*** **Bell, *sp. nov.***

A. Segment of the peripheral rim, holotype, UCMP 40476, (x 6), pl. 38, fig. 3.
B. USNM S-3889-G, (x 6), pl. 38, fig. 10.

Large sectors of the theca are missing, including al structure, much of interambulacra 2, 3, 4, and 5, acra IV and V, and the posterior half of the periph- im. Most plates of the oral area and hydropore ıre appear to be present, but slight lateral shifting ; collapse and later fracturing of some of these makes identification tentative. The proximal parts of .acra I and II are well preserved. The coverplates ıissing from the distal sector of ambulacrum III, exposes the upper sides of the floorplates. The nal plates of interambulacrum 1 and the distal plates erambulacra 2 and 3 are also well preserved. Sev- egments of the anterior half of the peripheral rim oderately well preserved, although many of the distal t plates appear to be missing, even from the well-pre- l segments.

M S-3889-G. Paratype of *Rectitriordo kirkfieldensis* " Hull Limestone," Trenton Group, Mohawkian ;, Middle Ordovician. Quarry 3 miles north of Kirk- Ontario. 10.6 mm greatest diameter by 6.7 mm. ‹t fig. 37B, pl. 38, fig. 9, 10.

is individual is one of several housed with the type nens of *Foerstediscus parvus* Bassler (USNM ;9) (= *Foerstediscus grandis* Bassler, 1935). The men is a disrupted fragment, but small segments of ılacra I and V are preserved along with half of the structure, which is completely missing in the holo-

USNM S-3894-D. Paratype of *Rectitriordo kirkfieldensis* Bell. " Hull Limestone," Trenton Group, Mohawkian Series, Middle Ordovician. Quarry 3 miles north of Kirk-field, Ontario. 12.4 mm axial by 12.5 mm transverse diameter.

Pl. 38, fig. 7, 8.

The specimen is housed with Bassler's illustrated speci-men of *Cryptogoleus multibrachiatus* (Raymond) (USNM S-3894-A). The theca has collapsed and several large sec-tors are missing. Many of the remaining plates have been partially disrupted during collapse. However, segments of the peripheral rim, interambulacrum 2, and ambulacra II and III are fairly well preserved. Some of the oral plates can be identified. The plates of the peripheral rim appear to be more rounded than in the holotype and sug-gest that the distinctive triangular shape is developed dur-ing later adult growth.

Discussion

Rectitriordo kirkfieldensis is unique in being the only Isorophidae with straight ambulacra and a regular triple biseries of coverplates. Apparently the disposition of the secondary oral plates is also distinctive, but poor preser-vation makes definitive description of these impossible. Likewise, the hydropore structure is inadequately known. The distinctive triangular shape of the distal rim plates and the relatively large size of the interambulacrals also characterize the species, at least in large adults.

The tertiary series of ambulacral coverplates introduces a decidedly different plate group not found in species with single or double biseries of ambulacral coverplates. Both primary and secondary coverplates extend to the adradial suture of the ambulacra, at least internally, if not externally. The inner surfaces of both articulate with the lateral margins of the underlying floorplates. In contrast, the tertiary coverplates are entirely axial, apparently held in place by tight suturing to adjacent primary and secondary coverplates. Therefore, functionally, the tertiaries may be considered accessory ambulacrals as opposed to the integrated, articulating primaries and secondaries.

ETYMOLOGY: The species is named after the type locality, Kirkfield, Ontario.

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

Genus *Curvitriordo* Bell, gen. nov.

TYPE SPECIES: *Isorophus kentuckyensis* Bassler, 1936.

Diagnosis

Isorophidae with: ambulacra curved, I-IV contrasolar, V solar; ambulacral coverplates forming a triple biseries.

Description

Curvitriordo is represented by two inadequately known species. *C. kentuckyensis* is based on two poorly preserved specimens, *C. shideleri* on only the fragmentary holotype. The domal theca ranges from 17 to 28 mm in diameter.

The oral area appears to contain four primary orals, one hydropore oral, two pairs of lateral shared coverplates, and several secondary orals. The hydropore structure is formed by the right posterior primary oral, the hydropore oral, and perhaps four or five other plates of the oral-ambulacral series.

The genus is characterized by the structure and disposition of the ambulacra. Ambulacral curvature is pronounced, I-IV contrasolar, V solar. Distally the moderately long, tapering ambulacra become concentric with the proximal margin of the rim. Three sets of coverplates form a triple biseries of alternating pairs of plates.

The squamose, imbricate interambulacrals are relatively small and numerous. The valvular anal structure and the distinct peripheral rim appear similar in structure to other Isorophidae.

Discussion

Curvitriordo is proposed here to include two species formerly placed in the genus *Isorophus*. Both have three series of ambulacral coverplates which form a triple biseries that contrasts with the double biseries of coverplates characteristic of *Isorophus*. The ambulacral curvature in *Curvitriordo* separates this genus from the straight-rayed *Rectitriordo*, the only other Isorophidae with a triple series of coverplates.

ETYMOLOGY: *Curvitriordo* is compounded from the Latin *curvus*, *tres*, and *ordo* meaning bent, three, and series, referring to the curved ambulacra with a triple biseries of coverplates.

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

Curvitriordo kentuckyensis (Bassler), 1936

Text fig. 38; plate 39, fig. 1-7.

1936 *Isorophus kentuckyensis* Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 18-19, pl. 6, fig. 10.

1943 *Isorophus kentuckyensis* Bassler, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 205.

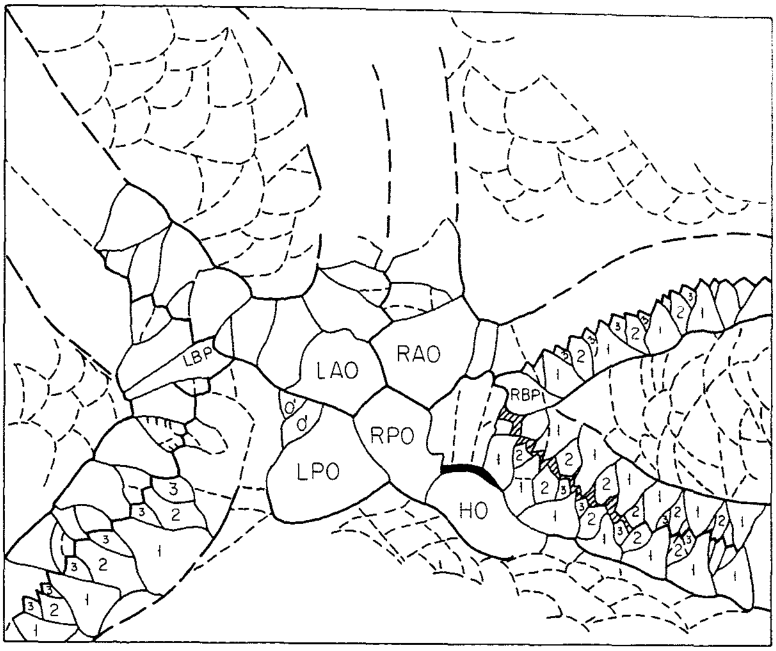
Diagnosis

A *Curvitriordo* with: triple biseries of ambulacral coverplates formed by regularly alternating pairs of three sets of plates, opposing alternate pair members in contact perradially.

Description

Curvitriordo kentuckyensis is known from only two poorly preserved individuals (pl. 39, fig. 1-7). The domal theca appears to have been highly arched before collapse. Thecal diameters are 25 and 28 mm.

The oral region includes four large central primary orals (text fig. 38). The left posterior primary is more central and perradially meets both the right and left anterior orals. A large hydropore oral abuts the right edge of the right posterior primary oral and extends distally along the posterior side of the proximal part of ambulacrum V. Two pairs of lateral shared coverplates are probably present. Two small, lateral secondary orals flank the left margin of the left posterior primary oral.



Text figure 38. *Curvitriordo kentuckyensis* (Bassler), 1936.
Holotype, USNM S-3967-A, oral area and adjacent structures, (x 10), pl. 39, fig. 3.
HO, hydropore oral plate; LAO, left anterior primary oral plate; LBP, left lateral bifurcation plate; LPO, left posterior primary oral plate; o′, secondary oral plate; RAO, right anterior primary oral plate; RBP, right lateral bifurcation plate; RPO, right posterior primary oral plate; 1, primary ambulacral coverplate; 2, secondary ambulacral coverplate; 3, tertiary ambulacral coverplate.

Other secondaries appear to be present, but individual identification is tentative.

The slitlike hydropore extends from the right edge of the right posterior primary oral along the anterior margin of the hydropore oral. The anterior edge of the opening is formed by the adradial ends of several plates, presumably the right posterior shared coverplate, perhaps a secondary oral, and one or two proximal posterior coverplates of ambulacrum V.

The relatively long ambulacra taper gradually (pl. 39, fig. 1, 2, 6, 7). The contrasolar curvature of ambulacra I-IV and solar curvature of V is pronounced and the distal parts are concentric with the proximal margin of the peripheral rim.

Three sets of ambulacral coverplates form a triple biseries (text fig. 38). The large primary coverplates are subtriangular in external view. Opposing alternate members of each pair are usually in contact perradially. Adjacent primaries are commonly in contact adradially and restrict the other sets to the more axial part of the ambulacra.

The secondary coverplates are subrhomboidal in external plan view. The angular perradial ends of opposing alternate pair members are in contact along the perradial line. The adradial ends are often angular, wedged between the contiguous adradial bases of adjacent primaries. In other areas, the adradial ends of the secondaries are blunt and externally in contact with the adradial suture line, and thereby separate the adradial bases of adjacent primaries. Pairs of secondaries alternate regularly with pairs of primaries.

The small tertiary coverplates are subrhomboidal. One pair lies adjacent to each side of each secondary pair and separates the perradial tips of the secondaries from adjacent primaries. Thus two pairs of tertiaries are present for each pair of primaries or secondaries. The sequential arrangement along the perradial line is primary, tertiary, secondary, tertiary, primary, etc.

The numerous squamose, imbricate interambulacrals are relatively small in proportion to thecal diameter.

The valvular anal structure is formed by triangular plates, perhaps 16 to 18, alternating as inner and outer circlet members.

The peripheral rim includes six or seven circlets. Some of the more distal rim plates appear to be moderately angular and approach the triangular external shape of the rim plates of *Rectitriordo kirkfieldensis*. However, unlike the latter, the pointed ends of all the angular rim plates of *Curvitriordo kentuckyensis* appear to be directed proximally.

The exterior surfaces of the thecal plates appear to be smooth.

Specimens

USNM S-3967 (A-B). Slab with the types of *Curvitriordo kentuckyensis* (Bassler) (1936). Woodburn-Greendale Formation contact zone. Trenton Group, Mohawkian Series, Middle Ordovician. Lair Station, Kentucky.

USNM S-3967-A. Holotype of *Curvitriordo kentuckyensis* (Bassler) (1936, pl. 6, fig. 10). 25.2 mm axial by 25.7 mm transverse diameter.

Text fig. 38, pl. 39, fig. 1-5.

The theca of this large specimen has completely collapsed, and some lateral plate slippage has occurred. The large number of nearly vertical distal interambulacrals suggests that the theca was highly arched before collapse. The specimen has been deeply etched, obscuring most plate detail. However, a majority of the plate boundaries in the oral region and surrounding proximal ambulacral-interambulacral areas are tentatively recognized (text fig. 38). Plates are missing from a large sector of interambulacrum 5 and parts of 1, 2, and 3. The peripheral rim plates are distinct in some areas.

USNM S-3967-B. Paratype of *Curvitriordo kentuckyensis*. 28.7 mm axial by 28.2 mm transverse diameter.

Pl. 39, fig. 6, 7.

A second, very poorly preserved specimen is resting near the holotype on the same small slab. The theca has collapsed and the center of the oral surface has moved laterally toward the right anterior margin of the rim. Extensive etching has rendered many plate boundaries indistinct. A large crack extends through the theca, and a large section of the left posterior oral surface is missing. The ambulacral coverplate pattern can be seen in small segments of the remaining ambulacra. Much of the peripheral rim is fairly well preserved.

Discussion

Bassler (1936, p. 19) described the species as having "the general characteristics of *Isorophus* and related to *Isorophus holbrooki* but differing in that the arms are shorter, less curved and the interambulacral plates are smaller, less regular and more imbricating."

Curvitriordo kentuckyensis (Bassler) does resemble species of *Isorophus* in general thecal construction, but the three sets of coverplates which form a triple biseries separate this species. The disposition of the coverplates, with opposing alternate plate pair members in contact perradially separates *Curvitriordo kentuckyensis* from *C. shideleri*, the only other species in the genus.

Some irregularity may occur in the coverplate sequence of *C. kentuckyensis*. Occasionally the opposing alternate members of the primary coverplate pairs appear to be separated perradially by tertiary coverplates. Observed irregularities may be preservational. The oral area and hydropore structure plate disposition may also be useful taxonomically at the specific level, but these areas are poorly preserved in both specimens.

The large thecal diameter, high convexity of the oral surface, and the long ambulacra suggest that the two specimens of *C. kentuckyensis* are mature adults, perhaps even unusually large for the species.

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

Curvitriordo shideleri (Bassler), 1936
Text fig. 39; plate 39, fig. 8-9.

1936 *Isorophus shideleri* Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 19, pl. 6, fig. 9.

1943 *Isorophus shideleri* Bassler, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 205.

Diagnosis

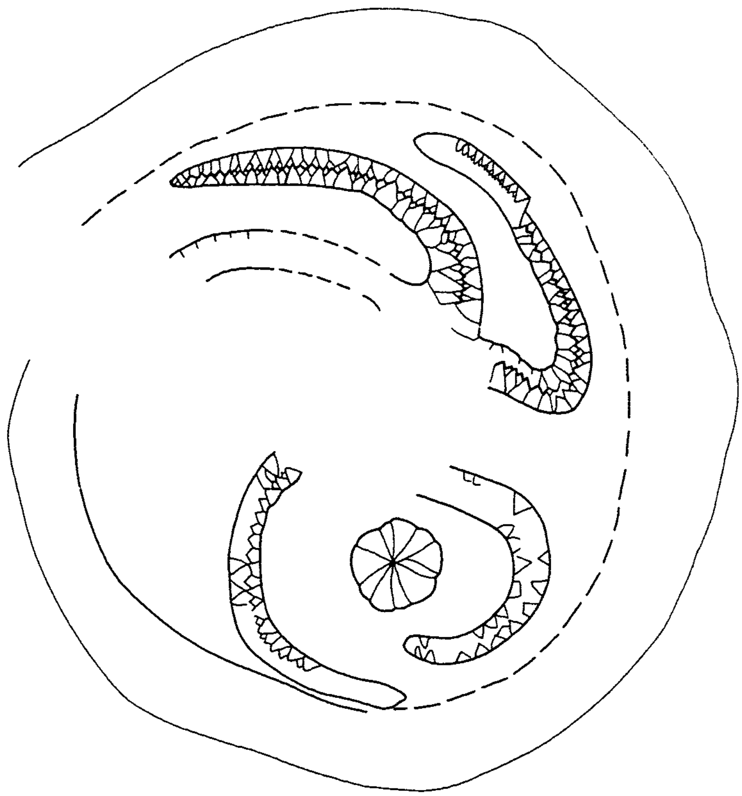
A *Curvitriordo* with: triple biseries of ambulacral coverplates formed by alternating pairs of three sets of plates, opposing pair members of primary and secondary series separated perradially by pairs of tertiary coverplates.

Description

Curvitriordo shideleri (Bassler) is known only from the poorly preserved holotype in which the oral area and hydropore structure plates are completely disrupted (text fig. 39, pl. 39, fig. 8, 9). The domal theca appears to have been highly convex and is 17 mm in diameter.

The ambulacra are long and taper gradually (text fig. 39). Curvature is pronounced and the distal parts are concentric with the proximal margin of the peripheral rim. The distal tip of ambulacrum V appears to curve slightly back toward the oral region and approaches the posterior edge of the anal structure.

The triple biseries of ambulacral coverplates consist of three sets of plates. The primary coverplates are large and subtriangular in external outline. Adjacent primaries are



Text figure 39. ***Curvitriordo shideleri*** **(Bassler), 1936.**
Holotype, USNM S-3958, (x 6), pl. 39, fig. 9.

usually adradially separated by the adradial ends of the alternate secondary coverplates. The opposing alternate members of each pair of primaries are separated perradially by a pair of tertiary coverplates.

The secondary coverplates are intermediate in size and externally are subtriangular to subrhomboidal in outline. They alternate with the primaries. The subtriangular secondaries reach the adradial suture line and separate the adradial bases of the alternate primaries. The subrhomboidal secondaries are angular adradially, wedged between the two adjacent primaries which are in contact adradially. Opposing alternate pair members of the secondary series are also separated perradially by a pair of tertiary coverplates.

The small tertiary coverplates are confined to the axial part of the ambulacra. Subrhomboidal in shape, these coverplates are the only set in which opposing alternate pair members are perradially in contact. One pair of tertiaries is inserted between the perradial tips of opposing alternate members of both the primary and secondary coverplate series. Thus there are twice the number of pairs of tertiaries as primaries or secondaries. The sequence encountered along the perradial line is: primary, tertiary, secondary, tertiary, primary, etc.

The squamose, imbricate interambulacrals are relatively small in proportion to thecal diameter.

The valvular anal structure is formed by an inner and an outer circlet of alternating, triangular plates. In the holotype (text fig. 39), six outer and five inner plates are seen. Apparently the sixth inner circlet plate is hidden by lateral slippage of the two adjacent outer circlet plates.

The peripheral rim is formed by five or six circlets of plates. The more distal plates appear to be angular and approach the triangular shape found in the rim plates of *Rectitriordo kirkfieldensis*.

Plate exteriors appear to have been smooth.

Specimen

USNM S-3958. Holotype of *Curvitriordo shideleri* (Bassler) (1936, pl. 6, fig. 9). Elkhorn Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Just west of Hamburg, Indiana. 16.6 mm axial by 17.1 mm transverse diameter.

Text fig. 39, pl. 39, fig. 8, 9.

The holotype has collapsed, shifting the central oral surface toward the left edge of the theca. A large part of the right side of the theca is missing, including a small section of the rim, interambulacra 1 and 2, and ambulacrum II. The oral area and the hydropore structure are completely disrupted. Plates of the peripheral rim are generally well preserved. The arrangement of the ambulacral coverplates is preserved in the remaining ambulacra.

Discussion

Bassler (1936, p. 19) originally described the species as a typical *Isorophus*, but with " long, much curved, extremely narrow rays made up of unusually small plates and separated by many comparatively small interambulacrals." The species is here included in *Curvitriordo* on the basis of the ambulacral curvature pattern and the triple biseries of ambulacral coverplates. The perradial separation of opposing alternate pair members of the primary and secondary coverplate sets serves to differentiate *C. shideleri* from *C. kentuckyensis*, in which the opposing alternate pair members of all three series of coverplates are perradially in contact.

RANGE AND OCCURRENCE: Richmond Group, Cincinnatian Series, Upper Ordovician of Hamburg, Indiana.

Family AGELACRINITIDAE Chapman, 1860

Type genus: *Agelacrinites* Vanuxem, 1842

Diagnosis

Isorophina with: domal or clavate theca; oral plates commonly numerous, primary orals usually undifferentiated; hydropore structure commonly a large, polyplated, isolated protuberance posterior to central oral rise; ambulacral coverplates forming cyclic series or mixtures of cyclic and biserial sets; interambulacral plates squamose and imbricate or polygonal and tessellate.

Description

The Agelacrinitidae vary greatly in size; average adult thecae are only 8 or 9 mm in some species, whereas diameters reach 50 mm in others. Both domal and clavate thecae are known.

External oral area plating varies from species that have relatively few plates (approximately 15) with distinct primary orals, to species with numerous orals which lack differentiated primary oral plates. The numerous orals of the latter type commonly reflect the ambulacral coverplate pattern and distally appear to grade into the coverplate sequence. One or more differentiated hydropore orals may be included in the oral area. The oral frame, which underlies the external orals, is formed by the five proximal floorplates of the ambulacra. The frame may include intrathecal extensions from the primary orals in those species in which the primary orals are externally differentiated.

Agelacrinitidae hydropore structures range from small protuberances, semi-integrated with the central oral rise, to large, elongate, isolated prominences which are distal to the oral rise. Semi-integrated types are formed by relatively few oral-ambulacral series plates and include one or more hydropore orals. The larger, isolated protuberances are formed by many plates, commonly including: posterior orals, specialized small hydropore plates distal and adjacent to the posterior orals, and modified proximal plates of interambulacrum 5 that have been incorporated into the oral area.

The ambulacral coverplates commonly occur in cyclic sets composed of two to seven plates per cycle. Occasionally the coverplates are a mixture of cyclic and biserial sets. One species (?)*Postibulla jasperensis* possibly has only a single biseries of coverplates.

The uniserial ambulacral floorplates may meet one another along vertical sutures or they may be imbricate with the proximal edge of each overlapping the distal edge of the adjacent proximal plate. Large lateral nodes often project into the thecal cavity from the inner sides of the floorplates.

The interambulacral plates of domal Agelacrinitidae are commonly squamose and imbricate. However, domal species may have polygonal interambulacrals which approach a tessellate relationship in the centers of the interambulacra. In all domal forms the interambulacrals that lie distal to the ambulacra are squamose and imbricate, and distally intersect the proximal rim plates. Clavate Agelacrinitidae commonly have thick, polygonal, tessellate interambulacrals. Adjacent to the ambulacra, oral area, and anal structure, these plates may become more squamose and imbricate slightly. Distal to the ambulacra the polygonal interambulacrals grade into imbricate plates which are commonly extremely thin, elongate, and subrectangular in outline. These form the pedunculate part of the theca, which extends down to the proximal plates of the basal, peripheral rim.

The valvular anal structure commonly includes an inner and outer circlet of triangular plates. The overlapping plates of the outer circlet regularly alternate with the inner ones. The lateral edges of contiguous anals are beveled to fit tightly together along the zone of overlap. Some species apparently modify this common Isorophina plan and add an extra inner circlet of plates.

The peripheral rim includes two or three proximal circlets of geniculate plates which are externally squamose and elongate concentric with the thecal margin. These are surrounded by several circlets of progressively smaller, radially elongate plates. The rim plates that form the transition zone between the concentrically and the radially elongated plates are squamose and without any characteristic form. The large plates of the proximal circlet are commonly arranged as alternate proximal and distal subcirclet members.

Discussion

Kesling and Ehlers (1958, p. 925) summarize usage of the taxon family Agelacrinitidae, including the incorrect spellings by most early authors based on the misspelling of *Agelacrinites* Vanuxem as " *Agelacrinus*." As they recorded, Clarke (1901) used the correct spelling, predating Bassler's (1935) claim to the family name. However, Chapman (1860) was actually the first to define the family Agelacrinitidae, and he included all then known edrioasteroid species in one genus, *Agelacrinites*.

The suborder Isorophina Bell is essentially equal to the family Agelacrinitidae as emended by Bassler (1936), Kesling and Ehlers (1958), and Regnéll (1966). The family Agelacrinitidae Chapman is here restricted to the more advanced species of the suborder, whereas the older species are included in the family Isorophidae Bell.

Morphologically the Agelacrinitidae is the most diverse family of edrioasteroids. Thecal shapes include both domal and clavate types. The oral region may include relatively few plates, with primary orals differentiated, or numerous small orals may be present, and these reflect the ambulacral coverplate pattern.

The hydropore structure may be a small prominence, semi-integrated with the central oral rise and formed by relatively few oral-ambulacral series plates. In other Agelacrinitidae it is a large, isolated rise formed by numerous plates, including modified interambulacrals. Apparently this latter form is derived from the former. Juveniles suggest that the hydropore migrates during growth and enlarges through the incorporation and modification of adjacent proximal interambulacrals, until it stands as a separate, large mound, posterior to the central oral rise.

Ambulacral coverplate patterns are diverse and range from mixtures of sets of biserial and cyclic plates to cyclic sets of coverplates. Apparently small intra-ambulacral coverplate extensions are developed in some species, but not in others. The coverplates are overlapped adradially by adjacent interambulacrals, but they appear to end at the upper lateral margins of the underlying floorplates. Thus intrathecal extensions may be lacking throughout the family. Unfortunately, the externally hidden ambulacral tunnel and adradial parts of the coverplates are inadequately known.

The uniserial ambulacral floorplates vary from thick, axially elongate plates which abut along vertical sutures to relatively thin, imbricate, trough-shaped ones. Floorplates have been observed in only a few Agelacrinitidae species, but apparently both abutting and imbricating types occur within the same genus *(Lepidodiscus)*. If so, this variability is in marked contrast to the Lebetodiscina, in which imbricating, as opposed to abutting, floorplates are a familial taxobasis.

The well-developed valvular anal structure, with an inner and outer circlet of alternating, tightly fitting, triangular plates, is common in the Agelacrinitidae. However, the structure occasionally includes three circlets. In the Isorophidae, only two circlets of plates are found in the valvular anal structure.

Postibulla jasperensis is questionably included in the Agelacrinitidae. It appears to have only a single biseries of coverplates and few, regularly arranged oral plates. The holotype and only known specimen may be a juvenile, suggesting that additional sets of coverplates and orals were forthcoming during growth.

Published descriptions of several species not included in this study suggest that they belong to the Agelacrinitidae. Three of these are of special interest. *Agelacrinites hanoveri* Thomas (1924) is found in the Middle Devonian, Shell Rock Formation of north-central Iowa. The type specimens have been misplaced and were thus unavailable for study. However, thousands of specimens from a quarry near the type locality have been collected (see *Hadrochthus commensalus* for description of stratigraphic and geographic location). The species appears to be closely related to the genus *Postibulla*, but may represent a new genus. The species occurs on the upper surface of large limestone knobs separated and undercut by interconnected solution channels. This substrate and the associated fauna suggest an intertidal or very shallow subtidal environment for this occurrence (Koch and Strimple, 1968, p. 12-15).

Many of the specimens of *Agelacrinites hanoveri* Thomas are juveniles. Among these are specimens equal in size to the type specimen of *Timeischytes megapinacotus* Ehlers and Kesling (1958). As noticed by Strimple (personal communication, 1968), these young *Agelacrinites hanoveri* are essentially identical in plate structure to the types of the Ehlers and Kesling species (text fig. 61B-E, pl. 55, fig. 11-15). Thus *T. megapinacotus* is believed to be conspecific with *A. hanoveri*.

Agelacrinites hybolopus Fraunfelter and Utgaard (1970) occurs in the Pennsylvanian Jamestown Cyclothem of southern Illinois. The published account of this species suggests affinities to the genus *Postibulla*. This species, and unnamed fragmentary specimens from New Mexico (see description at end of Isorophida) are the only two described edrioasteroids from the Pennsylvanian.

RANGE AND OCCURRENCE: Erian Series, Middle Devonian into Virgilian Series, Upper Pennsylvanian of North America (and probably Britain, Europe, and Russia).

Genus *Agelacrinites* Vanuxem, 1842

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

1848 *Agelacrinites* Vanuxem, Forbes, E. [*partim*], Geol. Surv. Great Britain and Mus. Practical Geology, London, Mem. 2 (2): 519-521.

1851 *Agelacrinus* Vanuxem, Roemer, F. [*partim*], Decheniana 8: 370-375.

1857 *Agelacrinus* Vanuxem, Pictet, F.-J. [*partim*], Traité de Paléontologie ou Histoire Naturelle des Animaux Fossils, 2nd edition, Paris, 4: 305.

1860 *Agelacrinites* Vanuxem, Chapman, E. J. [*partim*], Canadian Jour. Industry, Sci. and Art (n.s.) 5: 358-365.

1862 *Agelacrinus* Vanuxem, Dujardin, F. and Hupé, H. [*partim*], Histoire Naturelle des Zoophytes Echinodermes, Paris: 83-85.

1867 *Agelacrinus* Vanuxem, Hall, J., New York State Mus., 20th Ann. Rept.: 299.

1868 *Agelacrinites* Vanuxem, Meek, F. B. and Worthen, A. H. [*partim*], Philadelphia Acad. Nat. Sci., Proc. 5: 357-358.

1870 *Agelacrinus* Vanuxem, Hall, J., New York State Mus., 20th Ann. Rept. (revised edition): 344-345.

1873 *Agelacrinites* Vanuxem, Meek, F. B. and Worthen, A. H. [*partim*], Geol. Surv. Illinois, v. 5, Geology and Palaeontology, pt. 2, Palaeontology of Illinois: 515.

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

1896b *Agelacystis* Haeckel, E., Die Amphorideen und Cystoideen, Leipzig, 1: 114, pl. 3, fig. 30.

1899 *Agelacrinites* Vanuxem, Jaekel, O. [*partim*], Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 49-51.

1900a *Agelacrinus* Vanuxem, Bather, F. A., *in* A Treatise on Zoology, E. R. Lankester (ed.), London, pt. III, Echinoderma: 207, fig. 3.

1901 *Agelacrinites* Vanuxem, Clarke, J. M. [*partim*], New York State Mus. Bull. 49 (2): 182-198.

1910 *Agelacrinus* Vanuxem, Grabau, A. W. and Shimer, H. W. [*partim*], North American Index Fossils, Invertebrates, New York, 2: 472.

1914 *Agelacrinus* Vanuxem, Foerste, A. F. [*partim*], Denison Univ., Sci. Lab. Bull. 17 (art. 14): 399-456, pl. 6, fig. 3.

1924 *Agelacrinites* Vanuxem, Thomas, A. O. [*partim*], Iowa Geol. Surv., Ann. Rept. 29: 420-421.

1935 *Agelacrinites* Vanuxem, Bassler, R. S. [*partim*], Smithsonian Misc. Coll. 93 (8): 7.

1936 *Agelacrinites* Vanuxem, Bassler, R. S. [*partim*], Smithsonian Misc. Coll. 95 (6): 15-16, pl. 1, fig. 18.

1938 *Agelacrinites* Vanuxem, Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 36.

1943 *Agelacrinites* Vanuxem, Bassler, R. S. and Moodey, M. W. [*partim*], Geol. Soc. America, Spec. Pap. 45: 195.

1944 *Agelacrinites* Vanuxem, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, pl. 49, fig 22.

1953 *Agelacrinus* Vanuxem [*non* Billings], Piveteau, J., Traité de Paléontologie, Paris, 3: 652-653, text fig. 3.

1958b *Agelacrinites* Vanuxem, Ehlers, G. M. and Kesling, R. V. [*partim*], Univ. Michigan, Contrib. Mus. Paleont. 14 (15): 271-272.

1960 *Agelacrinites* Vanuxem, Kesling, R. V. [*partim*], Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 139-192.

1966 *Agelacrinites* Vanuxem, Regnéll, G. [*partim*], *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U167-U169, text fig. 128-6.

TYPE SPECIES: *Agelacrinites hamiltonensis* Vanuxem, 1842.

Diagnosis

Agelacrinitidae with: domal theca, 15 or more oral plates, including two or more apparently differentiated primaries and one large hydropore oral; hydropore structure semi-integrated, formed by few plates; ambulacra curved, I-III contrasolar, IV-V solar, coverplates in alternating two-plate cycles; interambulacrals large, subpolygonal, slightly imbricate; valvular anal structure with two circlets of regularly alternating plates.

Description

Adult diameters of over 30 mm are recorded for the type species of *Agelacrinites.*

The oral plates appear to vary in number and arrangement; 15 or more are commonly present (pl. 40, fig. 2, 7). Two large anterior primary orals, and perhaps two large posterior primaries, are externally differentiated from the other orals by their size. A single large hydropore oral forms a prominent distal bulge in the oral area outline and extends along the proximal posterior margin of ambulacrum V.

The hydropore structure lies in the right posterior part of the oral area (pl. 40, fig. 1, 2, 7-9). Plates surrounding the opening are raised to form a low, elongate mound, semi-integrated with the central oral rise. The structure involves three or more plates: the single, elongate hydropore oral forms the entire posterior side of the structure; and two or more oral-ambulacral series plates form the anterior side and lateral extremities of the structure.

The ambulacra of *Agelacrinites* are long and moderately narrow. Ambulacral coverplates form two-plate cyclic sets. The two-plate sets on each side of the perradial line are offset by half their width; the primary plates of one side lie opposite the secondaries of opposing cycles. Thus the alternating two-plate cycles form a broadly undulating, zigzag perradial line. Occasionally anomalous coverplates may interrupt the regularity of this sequence.

The trough-shaped floorplates meet along vertical sutures. The upper faces of the floorplates are evenly concave downward, except for the nearly horizontal lateral margins which form a wide zone of articulation with the overlying bases of the coverplate. The evenly convex-inward, inner faces of the floorplates appear to be smooth.

The subpolygonal interambulacrals are slightly imbricate. Sutures between contiguous plates are often nearly vertical; the zone of overlap is very small, particularly in the centers of the interambulacra.

The valvular anal structure is formed by an inner and outer circlet of triangular plates that alternate and are beveled to fit tightly together. Only the central parts of the inner circlet plates are exposed between the broadly overlapping edges of the outer circlet plates.

The peripheral rim includes two or three circlets of larger plates that are elongate concentric with the thecal margin, and two or three irregular, distal circlets of smaller, radially elongate plates. The large plates of the proximal circlet regularly alternate as proximal and distal subcirclet members.

Prosopon of large ridges and nodes occurs in the type species.

Discussion

As the first formally proposed edrioasteroid genus, *Agelacrinites* Vanuxem (1842) was broadly defined. For the next two decades nearly all edrioasteroid species were included in *Agelacrinites; e.g.*, Forbes (1848), Roemer (1851), Pictet (1857), Chapman (1860), and Dujardin and Hupé (1862).

In 1867 Hall redescribed the type species of *Agelacrinites* in detail. This description and Hall's contemporaneous descriptions of several other edrioasteroid species initiated the gradual restriction of the generic taxobases for *Agelacrinites.* Ambulacral width, length, disposition, and number; interambulacral plate morphology; thecal shape; and peripheral rim development were accepted as generic criteria from 1870 through the 1920's. Using only these criteria, numerous species were placed in *Agelacrinites.* Bassler (1935) suggested that the degree of interambulacral plate imbrication, the width of the peripheral rim, and the number of ambulacra vary intraspecifically in all edrioasteroids. On the other hand, he thought valid generic taxobases should include ambulacral plate structure, oral area plating, and direction and degree of ambulacral curvature. Bassler's criteria have been accepted by most subsequent authors. So defined, *Agelacrinites* since 1935 has included all species with: domal theca; oral plates small, numerous and without definite order; ambulacra long, narrow, curved, I-III contrasolar, IV-V solar; interambulacrals squamose or polygonal, imbricating or tessellate; and peripheral rim with several rows of plates.

As suggested by Ehlers and Kesling (1958), Kesling (1960) and Regnéll (1966), the oral plating, hydropore structure, and the ambulacral coverplate pattern are also prime generic taxobases. Thus, in agreement with the type species, *Agelacrinites* is here further restricted to include only those species with: a moderate number of orals which include differentiated anterior and perhaps posterior primary orals; hydropore structure semi-integrated with the oral rise and including a large hydropore oral plate; ambulacral coverplates in an alternating, two-plate cyclic series; and valvular anal structure with an inner and outer circlet of plates. *Agelacrinites hamiltonensis* is the only species included in this study that strictly conforms to the genus.

RANGE AND OCCURRENCE: Skaneateles Formation, Hamilton Group, Erian Series, Middle Devonian of New York.

Agelacrinites hamiltonensis Vanuxem, 1842

Text fig. 40–41; plate 40, plate 41, fig. 1–5

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

1848 *Agelacrinites hamiltonensis* Vanuxem, Forbes, E., Geol. Surv. Great Britain and Mus. Practical Geology, London, Mem. 2 (2): 520-521.

1851 *Agelacrinus hamiltonensis* Vanuxem, Roemer, F., Decheniana 8: 370-375.

1857 *Agelacrinus hamiltonensis* Vanuxem, Pictet, F.-J., Traité de Paléontologie ou Histoire Naturelle des Animaux Fossils, 2nd edition, Paris, 4: 305.

1860 *Agelacrinites hamiltonensis* Vanuxem, Chapman, E. J., Canadian Jour. Industry, Sci. and Art (n.s.) 5: 360-365.

1862 *Agelacrinus hamiltonensis* Vanuxem, Dujardin, F. and Hupé, H., Histoire Naturelle des Zoophytes Echinodermes, Paris: 84.

1867 *Agelacrinus hamiltonensis* Vanuxem, Hall, J., New York State Mus., 20th Ann. Rept.: 299.

1868 *Agelacrinites hamiltonensis* Vanuxem, Meek, F. B. and Worthen, A. H., Philadelphia Acad. Nat. Sci., Proc. 5: 357-358.

1870 *Agelacrinus hamiltonensis* Vanuxem, Hall, J., New York State Mus., 20th Ann. Rept. (revised edition): 344-345.

1871 *Agelacrinus hamiltonensis* Vanuxem, Hall, J., New York State Mus., 24th Ann. Rept. (adv. pub.): pl. 2, fig. 14-15.

1872 *Agelacrinus hamiltonensis* Vanuxem, Hall, J., New York State Mus., 24th Ann. Rept.: pl. 6, fig. 14-15.

1873 *Agelacrinites hamiltonensis* Vanuxem, Meek, F. B. and Worthen, A. H., Geol. Surv. Illinois, v. 5, Geology and Palaeontology, pt. 2, Palaeontology of Illinois: 515.

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

1896b *Agelacystis hamiltonensis* (Vanuxem), Haeckel, E., Die Amphorideen und Cystoideen, Leipzig, 1: 114, pl. 3, fig. 30.

1899 *Agelacrinites hamiltonensis* Vanuxem, Jaekel, O. Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 51.

1900a *Agelacrinus hamiltonensis* Vanuxem, Bather, F. A. *in* A Treatise on Zoology, E. R. Lankester (ed.), London, pt. III, Echinoderma: 207, fig. 3.

1901 *Agelacrinites hamiltonensis* Vanuxem, Clarke, J. M., New York State Mus., Bull. 49 (2): 182-198, pl. 10, fig. 6.

1903 *Agelacrinus hamiltonensis* Vanuxem, Delage, Y. and Herouard, E., Traité de Zoologie Concréte, T. 3, Echinodermes, Paris: 414-415, text fig. 551.

1910 *Agelacrinus hamiltonensis* Vanuxem, Grabau, A. W. and Shimer, H. W., North American Index Fossils, Invertebrates, New York, 2: 472.

1914 *Agelacrinus hamiltonensis* Vanuxem, Foerste, A. F., Denison Univ., Sci. Lab. Bull. 17 (art. 14), 399-456, pl. 6, fig. 3.

1924 *Agelacrinites hamiltonensis* Vanuxem, Thomas, A. O., Iowa Geol. Surv., Ann. Rept. 29: 420.

1936 *Agelacrinites hamiltonensis* Vanuxem, Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 15-16, pl. 1, fig. 18.

1938 *Agelacrinites hamiltonensis* Vanuxem, Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 36.

1943 *Agelacrinites hamiltonensis* Vanuxem, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 195.

1944 *Agelacrinites hamiltonensis* Vanuxem, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, pl. 49, fig. 22.

1953 *Agelacrinus hamiltonensis* Vanuxem, Piveteau, J., Traité de Paléontologie, Paris 3: 652-653, text fig. 3.

1958b *Agelacrinites hamiltonensis* Vanuxem, Ehlers, G. M. and Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 14 (15): 271-272.

1960 *Agelacrinites hamiltonensis* Vanuxem, Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 143.

1966 *Agelacrinites hamiltonensis* Vanuxem, Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U167-U169, text fig. 128-6.

Diagnosis

Agelacrinites with: large theca; oral plate arrangement variable; hydropore structure formed by large hydropore oral plus two to five oral-ambulacral series plates; two-element coverplate sets in regular to irregular cycles; interambulacrals proportionately large; thecal plates with prominent to subdued ridge and node prosopon.

Description

The domal theca of adult *Agelacrinites hamiltonensis* reaches diameters of over 32 mm. The species is known from only 22 adult and 10 poorly preserved juvenile specimens.

The oral area averages 15 to 20 plates, which are somewhat variable in arrangement (text fig. 40A, B, 41D). Apparently two large anterior primary orals form the central anterior part of the area. Two large plates, perhaps primary orals, form the central posterior margin of the region. These posterior plates may centrally meet the anterior primaries, or they may be separated from them by several smaller orals, hence the identification of posterior primary orals as homologous to those found in the Isorophidae is questionable. Approximately five lateral secondary orals flank both the right and left side of the central oral plates. In addition, one to three secondary orals separate the anterior primary orals from the proximal coverplates of ambulacrum III.

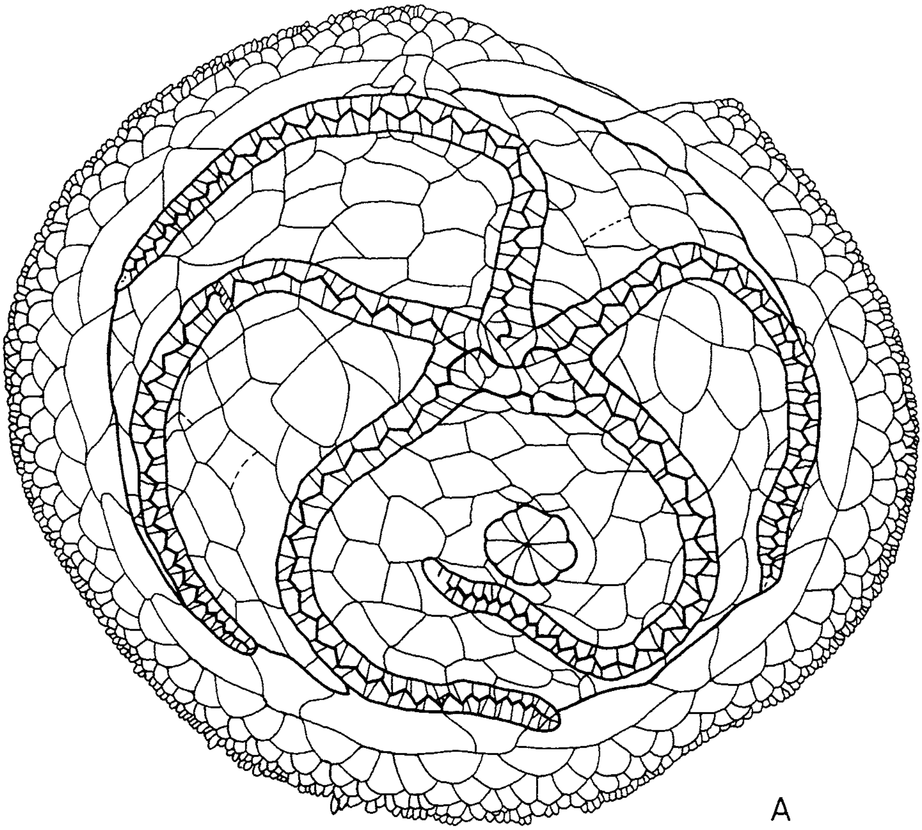
Text figure 40. *Agelacrinites hamiltonensis* Vanuxem, 1842.

Lectotype, NYSM, 362-A.

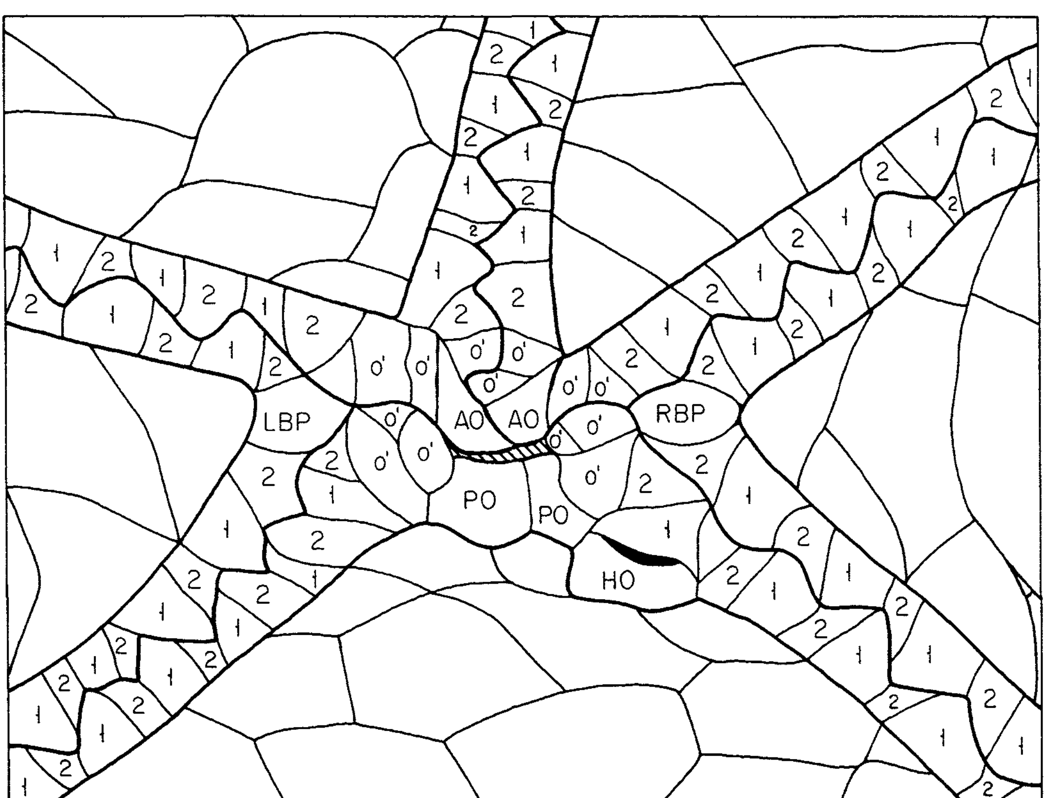
A. Oral surface, (x 4), pl. 40, fig. 1.

B. Oral area and adjacent structures, (x 12), pl. 40, fig. 2.

AO, anterior primary oral plate; HO, hydropore oral plate; LBP, left lateral bifurcation plate; o′, secondary oral plate; PO, posterior primary oral plate; RBP, right lateral bifurcation plate; 1, primary series ambulacral coverplate; 2, secondary series ambulacral coverplate.



A



B

The hydropore structure (text fig. 40B, 41D) forms a prominent distal bulge in the oral area outline. Participating plates are elevated and form a low mound that is semi-integrated with the central oral rise. A single, large hydropore oral extends along the proximal posterior edge of ambulacrum V. In addition to this large hydropore oral, the structure may include two to five adjacent plates of the oral-ambulacral series. The posterior side of the elongate, slitlike opening is bounded entirely by the anterior margin of the hydropore oral. The anterior edge of the opening is formed primarily by the adradial end of the (?) proximal primary coverplate of the posterior side of ambulacrum V. The hydropore opening may be limited to the boundary between these two plates (text fig. 40B), or it may extend proximally to intersect the right margin of the large, right posterior oral plate (text fig. 41D). In both cases, the adjacent margin of this oral plate is elevated and forms part of the hydropore prominence. Specimen USNM 85190-A suggests that several other proximal coverplates of ambulacrum V are shortened adradially along their zone of contact with the hydropore oral and are thereby included in the structure. In contrast, only three plates, the right posterior oral, the hydropore oral, and the opposing large primary coverplate, appear to form the entire hydropore structure in the lectotype (text fig. 40B).

The oral frame and adjacent stone canal passageway have been observed in one moderately well preserved specimen and several other poorly preserved individuals (pl. 41, fig. 1, 2). The transversely elongate oral frame extends into the thecal cavity below the ambulacra. The five proximal ambulacral floorplates form the radial parts of the structure; each is enlarged proximally and extends downward into the thecal cavity and also extends laterally to make contact with the adjacent floorplates of the frame. The upper extremities of the frame interradii, between ambulacra II-III and III-IV, are formed by downward tapering, wedge-shaped intrathecal extensions from the two large, anterior primary orals. Interradii between ambulacra I-II and IV-V are formed entirely by the enlarged proximal floorplates. The two posterior floorplates are not in contact across the posterior interradius. This sector includes only the intrathecal extensions from two or more large posterior oral plates. These extensions are relatively short and extend downward only a short distance, thereby forming a pronounced posterior gap in the frame. The central lumen, surrounded by the frame, opens downward into the thecal cavity and also laterally into the area beneath interambulacrum 5 through the posterior gap in the frame. Large, bladelike extensions may extend proximally into the central lumen from the two posterior floorplates or from the adjacent intrathecal extensions of the oral plates.

The stone canal passageway leads downward from the hydropore and opens directly into the thecal cavity (pl. 41, fig. 1, 2). It is a rapidly expanding, funnel-shaped passageway, formed by the proximal two floorplates of ambulacrum V and adjacent intrathecal extensions of several (?) plates. The inner end of the passageway appears unusually large; it extends across the entire width of the floorplates and bulges into the cavity beneath interambulacrum 5.

Ambulacral curvature is commonly gradual, initiated near the proximal end of the ambulacrum. The rate of curvature is greatest where the ambulacra approach and become concentric with the proximal margin of the rim.

The ambulacral coverplates form a two-plate cyclic series with opposing sets alternating along the ambulacra (text fig. 40A). The large primary coverplates are subrectangular, with straight adradial margins, parallel or moderately converging lateral sides, and an angular perradial end. Occasionally the lateral margins converge rapidly and merge with the pointed perradial end to form a subtriangular plate outline. The smaller secondary plates lie along the proximal side of the primaries. Each is subrectangular to subtriangular, with a straight adradial margin and parallel or converging lateral sides. The perradial end slopes toward the adjacent distal primary so that together, the two plates form a single, wide, perradial point. The perradial line is thus an undulating zigzag line, with each broad point formed by both plates of each cycle.

The regularity of the coverplate pattern and perradial line undulation may be interrupted by modifications of the secondary coverplate shapes. Occasionally the secondaries are angular perradially and form a discrete perradial point. In this case, each major undulation includes two points — the larger primary, and a less prominent, proximal, secondary point. Moreover, some of the secondary plates may become nearly as large as the adjacent primaries, further altering the perradial line.

The distal sectors of the ambulacra include only primary coverplates which form an alternating, single biseries. The secondaries are intercalated later along the proximal margin of each primary. In some specimens secondaries first appear three or four primary plates from the tip of the ambulacrum. In others, the entire distal fourth of the ambulacrum appears to lack secondaries.

Text figure 41. *Agelacrinites hamiltonensis* Vanuxem, 1842.

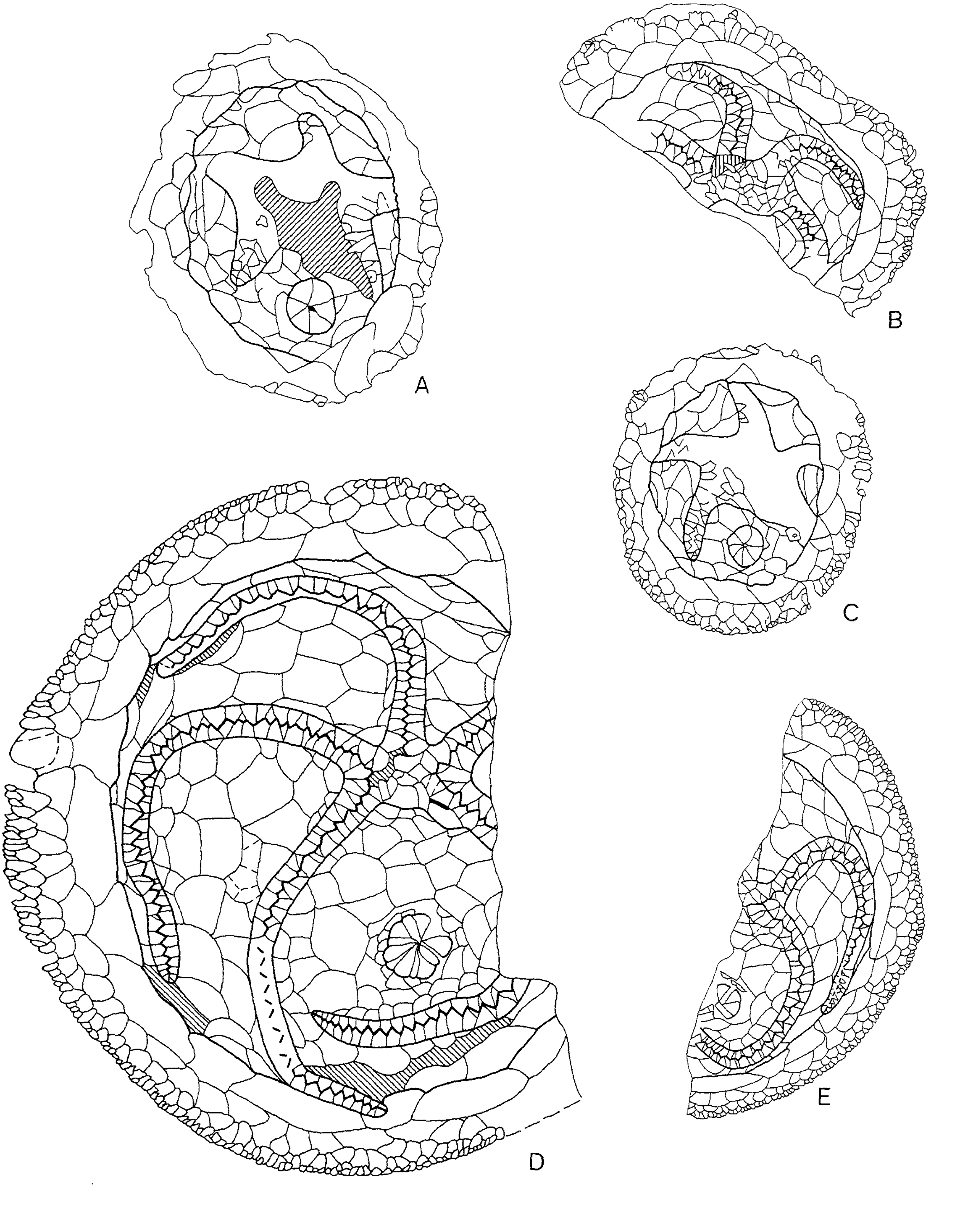
A. Lectoparatype (4), juvenile, NYSM 362-E, (x 15), pl. 40, fig. 3

B. Lectoparatype (2), small adult, NYSM 362-C, (x 6), pl. 40, fig. 5.

C. Lectoparatype (3), juvenile, NYSM 362-D, (x 10), pl. 40, fig. 4

D. USNM 85190-A, (x 4), pl. 40, fig. 7.

E. Lectoparatype (1), NYSM 362-B, (x 3), pl. 40, fig. 6.



Initially, the secondaries may be limited to the axial part of the ambulacrum, at least externally. However, they quickly increase in size, and one or two plates proximal to their insertion zone they extend to the adradial suture line.

The coverplate pattern in the largest observed specimen of *Agelacrinites hamiltonensis* appears to vary from the above description (text fig. 41D, pl. 40, fig. 7). The secondary coverplates commonly form discrete perradial points. Moreover, additional plates appear to be present in the proximal parts of the ambulacra. These may be extra secondary series plates, with two added between each two primaries, or they may represent an irregular, third set of plates which form a three-plate cycle. Some of the smaller plates in the proximal parts of four of the ambulacra do not reach the adradial suture line externally, and further suggest that three distinct sets of plates are present. However, in ambulacrum III of this specimen most proximal coverplates are nearly equal in size, and each forms a discrete perradial point. Thus the sequence resembles a single alternating biseries. The coverplate modifications in this specimen could represent gerontic adult traits. However, their variability from one ambulacrum to another suggests that this is merely an anomalous individual. Moreover, other specimens nearly as large as this do not appear to develop these coverplate variations.

A single specimen of *Agelacrinites hamiltonensis* exposes the inner, ambulacral tunnel side of several proximal coverplates. The latex pull seen in pl. 40, fig. 8, replicates the impressions of the inner coverplate surfaces. Although mediocre preservation obscures details, the ambulacral coverplates appear to have small, bladelike intra-ambulacral extensions developed on their perradial sectors. Each extension is straight, produced directly downward into the ambulacral tunnel. Thus, unlike the proximally flexed intra-ambulacral blades of the Isorophidae, the extensions of *Agelacrinites hamiltonensis* do not underlap the adjacent coverplates. Apparently each large coverplate has a larger central blade flanked by two smaller, lateral blades. When closed, the extensions of opposing coverplates apparently interdigitate beneath the perradial line.

Adradially the ambulacral coverplates are slightly overlapped by adjacent interambulacrals. The lower surfaces of the coverplates rest on the nearly horizontal lateral margins of the underlying floorplates. All coverplates appear to end adjacent to the lateral margins of the floorplates, and thus apparently lack intra-ambulacral extensions such as those developed in the Isorophidae.

The floorplates are rectangular in plan view, elongate normal to the ambulacral axis. Contiguous floorplates abut along vertical sutures. Their inner surfaces are evenly convex inward, with the upper surfaces concave downward except for the nearly horizontal lateral articulation zones. A low, rounded ridge may be developed along the upper lateral zones, and may perhaps be related to the coverplate articulation.

The valvular anal structure has 16 to 18 triangular plates, which alternate as inner and outer circlet members. Outer circlet plates broadly overlap the inner plates along tightly fitting, beveled edges, and leave only a narrow central strip of the inner plates externally exposed. Interambulacral plates which surround the anal area are small and form an irregular bordering circlet.

The peripheral rim includes four to six circlets of plates. The proximal circlets are segregated into alternating proximal and distal subcirclet members; the overlapping distal plates are externally much larger than the alternate proximals. Plates of the proximal two or three circlets are elongate concentric with the thecal margin. The small plates of the distal two or three circlets are radially elongate.

Prominent vertical ridges are developed on the basal surfaces of the larger geniculate rim plates (pl. 41, fig. 1, 5). Commonly, individual ridges extend across the entire basal surface, although occasionally shorter ridges are set between the distal parts of the larger ones. Each ridge is broad proximally, and tapers rapidly to a thin blade that extends across the distal two-thirds of the plate base. Some ridges are nearly straight, whereas others flex distally, their course diverging from the plate centers. Each large, proximal circlet plate appears to have five to nine ridges. Smaller rim plates have fewer ridges.

Large, irregular ridges and nodes lend a distinctive appearance to the thecal plates of many *Agelacrinites hamiltonensis*. Development is variable, pronounced in some adults but subdued in other adults and all juveniles. In some specimens nearly all plates bear the prosopon except for the nearly smooth proximal rim plates. In other individuals it may be limited to interambulacrals and distal rim plates.

Specimens

NYSM 362 (A-E). Type series of *Agelacrinites hamiltonensis* Vanuxem (1842, fig. 80). Chenango Sandstone member, Skaneateles Formation, Hamilton Group, Erian Series, Middle Devonian. Colgate University Campus Quarry, Hamilton, New York.

The small sandstone slab preserves six *A. hamiltonensis* resting on a fragment of a smooth pelecypod valve. All are molds of the external oral surface.

NYSM 362-A. Lectotype of *Agelacrinites hamiltonensis*. 27.7 mm axial by 32.3 mm transverse diameter.

Text fig. 40A, B, pl. 40, fig. 1, 2.

This is the largest complete specimen in the type series and is here designated the lectotype. The theca has collapsed. but little plate disruption has occurred. Slight lateral shifting of plates in and around the oral region may have altered external plate shapes and locations. Latex casts of the specimen show most external features, although suture lines are somewhat obscured in the critical oral area and hydropore structure. Text fig. 40A, B depicts probable plate boundaries. Each ambulacral coverplate appears to be centrally domed, so that lateral suture lines between adjacent coverplates lie in deep depressions. The perradial line between opposing coverplates is marked by a narrow, slightly elevated ridge that extends the length of the ambulacrum. These ridges suggest that the perradial coverplate margins were slightly elevated, although the ridges might also be preservational features. Thecal prosopon is prominently developed in this individual.

NYSM 362-B. Lectoparatype (1) of *A. hamiltonensis.* 26.8 mm along break, 12.2 mm normal to break.

Text fig. 41E, pl. 40, fig. 6.

Lectoparatype (1) lies adjacent to the lectotype; the two specimens touch along a small segment of their peripheral rims. This specimen preserves only the right half of the theca, including: ambulacra IV, most of V, and a small segment of III; interambulacra 4, and parts of 3 and 5; the partially disrupted right half of the oral-hydropore structure area; most of the disrupted anal structure; and the right half of the peripheral rim. Preservation is similar to that of the lectotype, although thecal collapse has caused more extensive plate disruption in this individual.

NYSM 362-C. Lectoparatype (2) of *A. hamiltonensis.* 12.4 mm diameter parallel to break, 6.1 mm normal to break.

Text fig. 41B, pl. 40, fig. 5.

This lectoparatype is a small adult. The left posterior third of the theca is missing, and the remainder of the specimen is partially disrupted and rather poorly preserved. Oral area plates outlined in text fig. 41B appear to be fragmented. Irregularities in the ambulacral coverplate pattern may be preservational.

NYSM 362-D. Lectoparatype (3) of *A. hamiltonensis.* 5.5 mm axial by 5 mm transverse diameter.

Text fig. 41C, pl. 40, fig. 4.

This lectoparatype is a juvenile. The theca has collapsed, but the major structural units appear to be only slightly disrupted. Unfortunately, most individual plate boundaries are indistinct. This and the following juvenile demonstrate the relatively increased size of the oral-hydropore region, the anal structure, and the peripheral rim in young individuals. The ambulacra and interambulacral areas are proportionately small. These juvenile characteristics correspond with the growth series features observed in other edrioasteroid species.

NYSM 362-E. Lectoparatype (4) of *A. hamiltonensis.* 4.7 mm axial by 3.9 mm transverse diameter.

Text fig. 41A, pl. 40, fig. 3.

Lectoparatype (4) is a small juvenile. Most plate boundaries are indistinct. but the outlines of major thecal structures are visible. Plates have been totally obscured in a large irregular area that includes much of the oral region and ambulacrum V. Anals, interambulacrals, some rim plates, and a few ambulacral coverplates are tentatively outlined in text fig. 41A.

NYSM 362-F. Lectoparatype (5) of *A. hamiltonensis.* 20.8 mm long.

This specimen is a small segment of the peripheral rim of a large adult.

USNM 85190. Topotypes of *A. hamiltonensis.* Chenango Sandstone member, Skaneateles Formation, Hamilton Group, Erian Series, Middle Devonian. Colgate University Campus Quarry, Hamilton, New York. G. A. Cooper. collector.

Ten small slabs of Chenango sandstone bearing 26 specimens of *A. hamiltonensis* (eight juveniles and 18 adults) are included under this number. One specimen preserves a few weathered plates; all others are molds. Descriptions are based primarily on latex pulls of these specimens, which include both external and internal oral surface casts.

USNM 85190-A. 32.9 mm axial by 24.2 mm (broken) transverse diameter.

Text fig. 41D, pl. 40, fig. 7.

This large topotype is missing the right third of the theca, and a large crack extends across the posterior rim. Collapse has partially disrupted some orals and distal interambulacrals. However, most of the ambulacral coverplates appear to be well preserved. Proximally, the coverplate cycle in four of the ambulacra appears to include a third, irregular series of plates. Moreover, nearly all of these proximal plates form discrete perradial points, and some of the smaller plates are restricted to the axial parts of the ambulacra. Ambulacrum III is unique, for all of the proximal plates are nearly equal in size. This creates the appearance of a single alternating biseries of coverplates. The medial sectors of all the ambulacra exhibit the common two-plate cycles. Distally, the primary coverplates form a single alternating biseries, the secondary coverplates first appearing far from the distal tips of the ambulacra. Prosopon is subdued in this specimen; apparently it developed only on the larger interambulacrals.

USNM 85190-B. 26.5 mm axial by 29.2 mm transverse diameter.

Pl. 40, fig. 8, 9.

This topotype is unique in preserving some of the original thecal plates. The specimen lies with the external oral surface toward the matrix, and originally only the inner sides of the thecal plates were exposed. Loss of many plates, but preservation of others, provides a composite view of the individual which includes both internal and external features.

A latex pull made in 1969 (pl. 40, fig. 8) exposes the following features: the exterior oral surface of most of the peripheral rim; interambulacra 1, 2, and 5; the anal structure; the oral and hydropore area; and some of the ambulacral coverplates; also, the impressions of the ambulacral tunnel surfaces of the proximal and medial coverplates of ambulacra II-V; the inner surfaces of the plates of interambulacrum 3 and parts of 2 and 4; and the impressions of the basal surfaces of a small section of peripheral rim plates. The numerous small holes in the latex pull apparently resulted from a thin coating of glue that preserves the remaining plate calcite, which is extremely soft. Although the amount of detail preserved is variable owing to the weathered condition of the plate calcite, this specimen demonstrates the presence of intraambulacral extensions on the ambulacral tunnel surfaces of the coverplates.

A gutta-percha squeeze of this specimen (pl. 40, fig. 9) made prior to 1941, found in the University of Cincinnati's Kopf Collection, shows that more original plate material was once present. In contrast with the 1969 pull, this squeeze preserves the impressions of the inner surfaces of the ambulacral floorplates in the proximal parts of ambulacra III and IV. The squeeze also provides a three-dimensional view of the ambulacral tunnel filling in the proximal part of ambulacrum III.

USNM 85190-G. Small slab with four *A. hamiltonensis* specimens resting on a pelecypod valve.

USNM 85190-G-1. Largest of the four specimens. 22 mm axial by 24.7 mm transverse diameter.

Pl. 41, fig. 3, 4.

This large specimen is incomplete; the right posterior third of the theca is now missing. The full thecal diameter was apparently over 30 mm. Significantly, the ambulacral coverplate pattern is clearly a two-plate cyclic series with adjacent primary and secondary plates uniting to form a single perradial point. Thus the coverplate sequence in this large adult is like that of the lectotype, but contrasts with the apparently unusual proximal sequence in specimen USNM 85190-A. This specimen is also noteworthy for its nearly smooth plate exteriors, which contrast with the pronounced development of nodes and ridges in other specimens.

USNM 85190-G-2, G-3, G-4. Three other typical *A. hamiltonensis* adults.

USNM 85190-I. 19.5 mm axial by 19.7 mm transverse diameter.

Pl. 41, fig. 1, 2.

This topotype is an impression of the inner side of the oral surface. Preservation is variable. The floorplates of ambulacra I, II, and V, some of the interambulacrals, and many of the peripheral rim plates are well preserved. The structure of the oral frame is somewhat indistinct, but better preserved here than in any other known individual examined. The stone canal passageway is also visible, but plate boundaries are difficult to identify.

USNM 85190-J. 22.5 mm long by 11 mm wide.

Pl. 41, fig. 5.

This specimen, which exposes the inner side of the oral surface, is a fragment of the left posterior part of the theca. It includes the distal floorplates of ambulacra I, II, and V, interambulacral plates, and the adjacent sector of the peripheral rim. The vertical ridges on the basal surfaces of the peripheral rim plates are well preserved.

The remainder of the topotypes examined include:

USNM 85190-C	Slab with eight juveniles.
USNM 85190-D	One medium-sized adult.
USNM 85190-E	Slab with three small adults.
USNM 85190-F	Slab with two fragmentary specimens which expose the inner surface of the theca.
USNM 85190-H	Slab with four small adults which expose the inner side of the oral surface.
YPM 28454	One adult specimen originally from the USNM 85190 series, apparently donated to Yale University.

Discussion

Agelacrinites hamiltonensis Vanuxem (1842) was the first formally named edrioasteroid species. It was based on the molds of six specimens, three of which are fragments, that rest on the smooth surface of a large pelecypod valve. Vanuxem (1842, p. 158) interpreted the six individuals and the resting surface as " one system," and thus unique in being the only colonial " crinoidal fossil." The original description noted the shape, size, position, and prosopon of the six specimens and continued, " near the center of the largest and perfect medallion [the lectotype] are five branching arms, like those of an asteria or starfish, between two of which and those which are most expanded, is a star [anal structure] which probably was the mouth of the animal." Fortunately, Vanuxem included a woodcut (image reversed left to right) that accurately depicts many of the thecal features, although the orals and ambulacral coverplates are difficult to interpret.

A. hamiltonensis was frequently cited by early workers in subsequent descriptions of new edrioasteroid species. Recognizing the individuality of the type series specimens, most authors used Vanuxem's illustration of the lectotype as the basis for interpretation of trivial characteristics. In 1867, Hall redescribed the species in detail and in 1871 he presented a new drawing of the lectotype. The description presented here contrasts with Hall's interpretation in that he recognized: only a single alternating biseries of ambulacral coverplates, oral area with only six plates, and interambulacrals abutting. No mention was made of the hydropore structure.

Hall's description and drawing of *A. hamiltonensis* have been accepted as definitive by most authors. The description presented here is the first account since Hall's that is based upon a restudy of the type specimens. The discovery of undescribed topotype specimens housed in the United States National Museum has substantially increased understanding of thecal structures and variations within the species.

Agelacrinites hamiltonensis is represented by relatively few specimens. All are preserved as molds, and descriptions are based primarily on latex pulls prepared from them. The identification of individual suture lines is difficult in areas of small, complexly arranged plates such as the oral region, hydropore structure, and in part, the ambulacra. Thus the apparent variability in the number and arrangement of the orals and hydropore structure plates may be at least partially preservational. The supposed presence of a third series of ambulacral coverplates in specimen USNM 85190-A, and the described irregularities in the basic two-plate cyclic series of other specimens, cannot be established with certainty, owing to the mode of preservation.

Plate boundaries are especially difficult to see in the smaller juveniles. Only the changes in areal dominance of the major thecal structures is definitely established by these specimens.

RANGE AND OCCURRENCE: Skaneateles Formation, Hamilton Group, Erian Series, Middle Devonian of Hamilton, New York.

Genus *Krama* Bell, *gen. nov.*

TYPE SPECIES: *Hemicystites devonicus* Bassler, 1936

Diagnosis

Agelacrinitidae with: domal theca; 16 or more oral plates, including 4 large primary orals, one hydropore oral, and lateral secondary orals that resemble ambulacral coverplates; hydropore structure semi-integrated; ambulacra of moderate width, curved I-III contrasolar, IV-V solar, ambulacral coverplate sequence a combination of cyclic sets and biserial pairs; interambulacrals squamose, imbricate; valvular anal structure formed by alternating inner and outer circlet plates.

Description

The genus *Krama* is monotypic, and therefore separation of generic and specific taxobases is uncertain. Features outlined in the above diagnosis are inferred to be of generic rank from taxobases for related Agelacrinitidae genera.

ETYMOLOGY: *Krama* is Greek meaning mixture, and refers to the mixture of cyclic and biserial sets of coverplates.

RANGE AND OCCURRENCE: Traverse-Hamilton Groups. Erian Series, Middle Devonian of eastern Michigan and western Ontario.

Krama devonicum (Bassler), 1936

Text fig. 42-45; plate 41, fig. 6-8, plate 42, 43

1936 *Hemicystites devonicus* Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 14, pl. 7, fig. 1; *Agelacrinites southworthi* Bassler, *idem, ibid.*: 16, pl. 4, fig. 12.

1943 *Hemicystites devonicus* Bassler, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 203; *Agelacrinites southworthi* Bassler, *idem, ibid.*: 196.

1944 *Hemicystites devonicus* Bassler, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, pl. 49, fig. 23.

1958b *Agelacrinites southworthi* Bassler, Ehlers, G. M. and Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 14 (15): 271-272.

1960 *Hemicystites devonicus* Bassler, Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 159-160, pl. 10, fig. 5-7; *Agelacrinites* sp. B, *idem, ibid.*: 149-150, text fig. 2, pl. 5, fig. 1-2; *Agelacrinites southworthi* Bassler, *idem, ibid.*: 150-151, pl. 5, fig. 3-4.

1966 *Agelacrinites* sp. B. Kesling, Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: text fig. 120-4.

Diagnosis

A *Krama* with: moderate-sized theca; oral plates including two anterior and two posterior primaries; semi-integrated hydropore structure formed by three or more plates; ambulacral coverplate series including alternate cyclic series of three sets of plates and one late, fourth set added as biserial pairs; squamose, imbricate interambulacrals relatively large in proportion to thecal diameter; large triangular anals arranged as alternate inner and outer circlet members, with elevated, acuminate tips forming central anal protuberance.

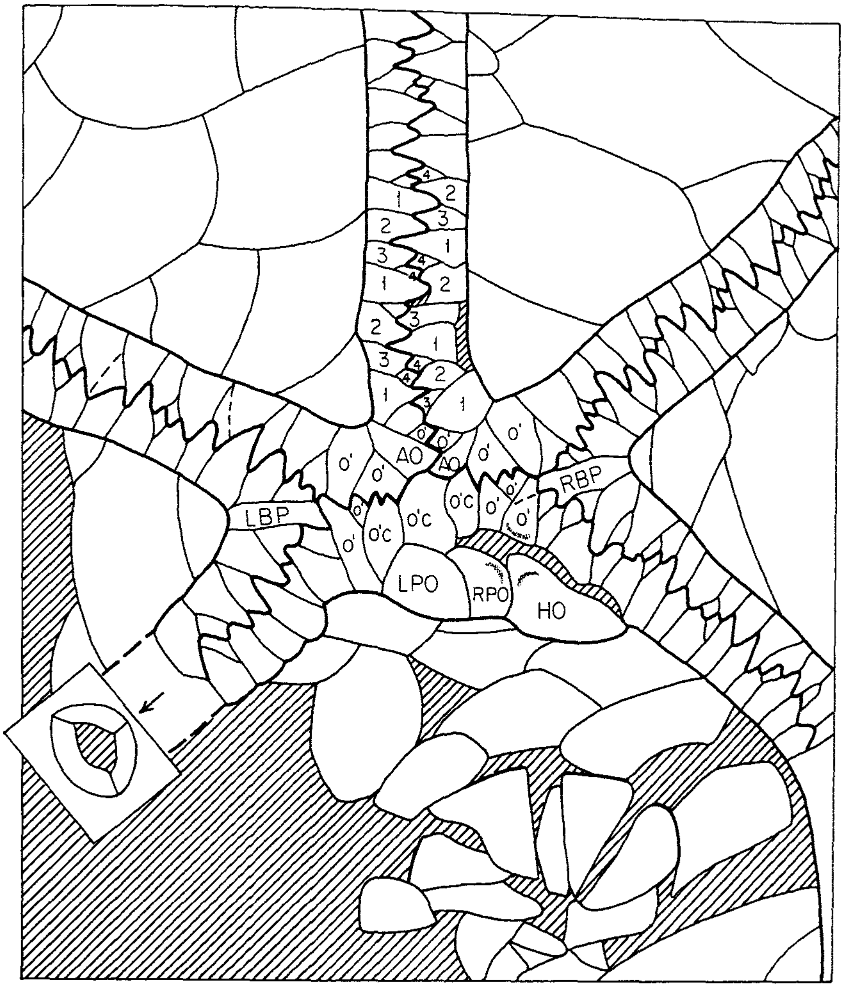
Description

The domal theca of *Krama devonicum* (Bassler) is moderate in size; the maximum known diameter approaches 18 mm.

The oral area is composed of approximately 20 plates in large adults (text fig. 42). Oral plate number and disposition change during ontogeny. In small specimens four primary orals (two anterior and two posterior) form the center of the oral area (text fig. 44A, B). All four are adradially in contact with adjacent interambulacra and extend proximally to the central transverse oral midline. The two subequal anteriors are symmetrically disposed on either side of the anterior oral midline. The right posterior is larger than the other primaries and perradially abuts both anterior primary orals. The left posterior is the smallest primary and perradially abuts only the left side of the left anterior primary. A single, moderate-sized hydropore oral lies adjacent to the right posterior edge of the right posterior primary oral and forms a distal bulge in the oral area outline which extends along the posterior proximal part of ambulacrum V. Secondary orals distally flank the central primaries, four or more on each side along the transverse oral midline, and two along the anterior oral midline. Thus oral plates total 15 or 16 in the smaller specimens.

In the largest adult specimen (USNM S-3478, text fig. 42), the oral area includes 20 or more plates. The two anterior primary orals remain distinct and are located in the same position as in younger specimens. However, some of the lateral secondary orals are larger than either anterior primary. The two large posterior primary orals have apparently shifted position and no longer meet the anterior primaries perradially. Three moderately large " central secondary orals " lie between the anterior margins of the posterior primaries and the transverse oral midline. The middle " central secondary " is largest. Perradially it abuts both anterior primaries and forms the center of the transverse oral midline. The posterior margin of this plate meets the anterior edge of both posterior primaries. The right " central secondary " perradially abuts the right anterior primary oral, and before thecal collapse it apparently also abutted the right posterior primary oral. The left " central secondary " posteriorly meets the left posterior primary oral but perradially it is in contact with an anterior lateral secondary oral. The large hydropore oral lies adjacent to the right margin of the right posterior primary oral and extends distally along the proximal posterior margin of ambulacrum V. Additional secondary orals flank the central oral plates, two along the anterior oral midline and four or more on each side along the transverse oral midline. The lateral secondaries in part reflect the pattern of the ambulacral coverplate series and appear to grade distally into the proximal coverplate series without a distinct break. Therefore, the distinction between distal orals and proximal coverplates is obscure, and the exact number of lateral secondary orals is indeterminate.

A medium-sized adult (UMMP 57679, 8 mm diameter, text fig. 45B) suggests that the central separation of the anterior and posterior primary orals is accomplished late in ontogeny by proximal migration of lateral secondary orals. In this individual the two anterior primaries are larger than adjacent secondaries, with one disposed on each side of the anterior oral midline. Meeting perradially, they form the anterior edge of the central transverse oral midline. The two large posterior primaries form most of the central posterior oral area. Adradially they form the posterior margin of the oral area, but perradially they are separated from the anterior orals. Centrally, the separation is an open gap between the primaries, perhaps accentuated somewhat during thecal collapse. But laterally, two secondary orals, which formerly flanked the right and left posterior orals, have apparently migrated both anteriorly and proximally. The right secondary, apparently ahead of the left, completely separates the right anterior and posterior primaries. The left plate separated only the distal parts of the two left primary orals. Continued posterior movement of the two posterior primaries, coupled



Text figure 42. ***Krama devonicum*** **(Bassler), 1936.**

Oral area and adjacent structures, USNM S-3478, (x 15), pl. 43, fig. 11. Inset at the broken end of ambulacrum I is a vertical cross section view of the most distal preserved plates of ambulacrum I.

AO, anterior primary oral plate; HO, hydropore oral plate; LBP, left lateral bifurcation plate; LPO, left posterior primary oral plate; o', secondary oral plate; o'c, central secondary oral plate; RBP, right lateral bifurcation plate; RPO, right posterior primary oral plate; 1, primary set ambulacral coverplate; 2, secondary set ambulacral coverplate; 3, tertiary set ambulacral coverplate; 4, quaternary set ambulacral coverplate.

with continued proximal migration of the lateral secondaries, would produce the oral plate arrangement seen in the larger adult (text fig. 42).

The hydropore structure of *Krama devonicum* lies in the right posterior distal bulge of the oral region. It is semi-integrated with the central oral rise; the adjacent margins of plates surrounding the opening are elevated to form a low, moundlike protuberance along the distal edge of the oral rise. At least three plates participate directly in its formation. The posterior side includes the proximal part of the hydropore oral and the right margin of the right posterior primary oral. The anterior side of the mound is formed primarily by the adradial end of one elongate plate of the oral-ambulacral series that opposes the junction between the hydropore oral and the right posterior primary. This anterior plate is either a posterior right lateral secondary oral, or the proximal primary coverplate of the posterior side of ambulacrum V. One or two oral-ambulacral series plates that flank this central anterior one may be adradially elevated and thereby also participate directly in the structure. In addition, one or more of the proximal coverplates of the posterior side of ambulacrum V may be adradially shortened where they meet the adjacent right anterior edge of the hydropore oral plate, and thus are indirectly included in the hydropore complex.

In young individuals, the hydropore protuberance is formed entirely by the hydropore oral, the right posterior primary oral, and the opposing oral-ambulacral series plate. The hydropore is a small, triangular gap between these three plates at the summit of the prominence. In larger specimens, both the opening and the elevated protuberance appear to be elongated parallel to the axis of ambulacrum V, and may include additional plates of the oral-ambulacral series which are adjacent to the initial anterior element.

The ambulacra are curved; I-III contrasolar, IV-V solar. In young adults the ambulacra curve gradually, whereas in larger specimens the proximal parts are nearly straight. The distal tip of each ambulacrum remains separated from the adjacent ray by several interambulacrals. Distally, ambulacrum V may curve proximally toward the anal structure in large individuals.

The ambulacral coverplate series, when fully developed (text fig. 43H, 44C), contains four sets of plates. The initial three sets are disposed in alternating cyclic series; the final set forms biserial pairs which are inserted into the cyclic series. In mature segments of the ambulacra, the primary plates are largest and triangular in outline, with wide adradial bases and pointed perradial tips. The plates of the second set are the next largest, often two-thirds the size of the primaries. They vary from broad-based triangular plates to elongate subtriangular ones with straight adradial margins, nearly parallel sides, and a pointed perradial end. These plates lie adjacent to the proximal margins of the primary plates of the next distal cycle. The tertiary plates are somewhat smaller than the secondaries, but usually not less than half the size of the primaries. They range from subtriangular plates that broadly abut the adradial suture line, to subrhombic forms that are angular both perradially and adradially. The latter may extend to the adradial suture line or end before intersecting it. The tertiaries lie between the primary and secondary plates of each cycle.

These first three sets of coverplates complete the cyclic part of the mature coverplate series. Cycles on opposite sides of the perradial line alternate, offset by half a cycle width. Thus the pointed perradial tips of the primary plates fit between the pointed tips of contiguous tertiary and secondary plates of opposing cycles (text fig. 44C). The offset three-plate cycles yield a broadly undulating perradial line, but the large, discrete, angular tips of each cycle plate form sharp perradial serrations which partially mask the broader undulations.

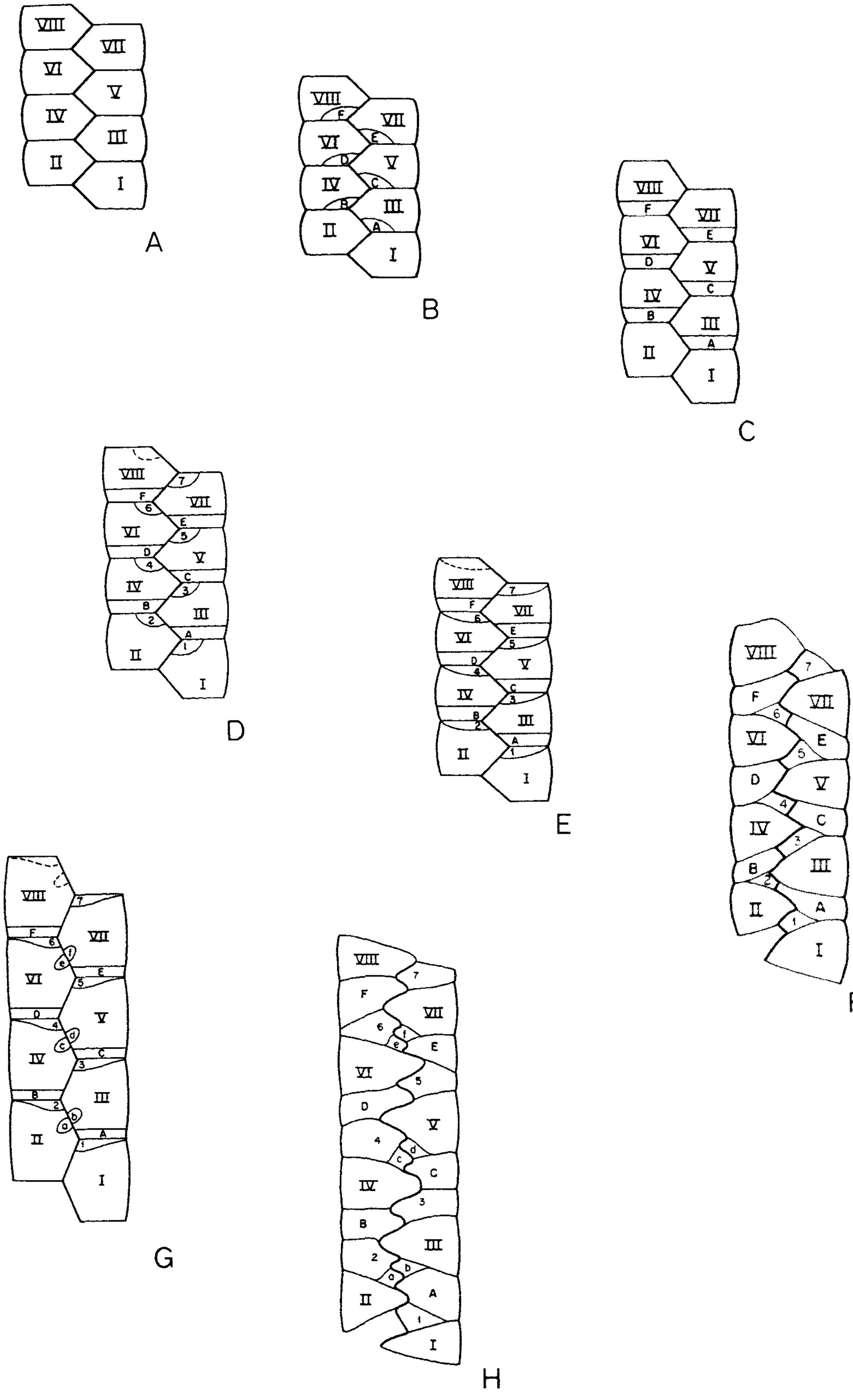
The quaternary plates are small and are restricted to the axial part of the ambulacra. Each is rhombic and pointed, both perradially and adradially (text fig. 44C). The quaternaries are added as biserial pairs inserted into the fully formed, three-plate cycles. Opposing pair members are perradially in contact and thus lie in different parts of the offset, opposing cycles. As one looks along the ambulacra in a distal direction, the adradial end of each right quaternary is seen inserted between the pointed perradial tip of each right tertiary plate and the tip of the adjacent right primary plate of the following distal cycle (text fig. 44C). The adradial end of the left member of the quaternary pair is inserted between the tips of the primary and the adjacent tertiary plate of each left cycle. The pointed perradial tip of the left member of the quaternary pair lies adjacent and proximal to the tip of the right plate.

The ontogenetic development of the coverplate sequence is schematically depicted in text fig. 43A-H. Primary coverplates are developed singly at the distal tip of the ambulacra and shift alternately left and right to form an alternating biserial pattern (text fig. 43A, UMMP 57677). Apparently specimens less than 2 mm in diameter include only primary coverplates.

Formation of secondary coverplates begins after four or five primary plates are present on each side of the perradial line. The first secondary plate is introduced adjacent to the distal margin of the proximal primary coverplate. At approximately the same time, a new primary plate is added at the distal tip of the ambulacrum. Thus the zone of secondary coverplate insertion is perpetually four or five primary plates from the distal tip of the ambulacrum. The secondaries are added alternately along the ambulacra, with one adjacent to the distal edge of each primary. When first developed, each secondary is a small, rhombic element, restricted to the medial part of the ambulacrum. Rapidly increasing in size, they become subtriangular in outline as their bases widen after reaching the adradial suture line (text fig. 43B, C).

Text figure 43. *Krama devonicum* (Bassler), 1936.

Schematic reconstruction of ambulacral coverplate development. The proximal end of each ambulacral segment is the bottom of the illustration. A through E depict the development of the cyclic primary set (Roman numerals), secondary set (capital letters), and tertiary set (Arabic numbers) of ambulacral coverplates. F is a regularized drawing of actual plate shapes seen at this stage of development. G shows the addition of the quaternary set (small letters) as pairs of coverplates. H is a regularized drawing of actual plate shapes where all four sets of coverplates have developed.


A
B
C
D
E
F
G
H

Development of the tertiary coverplates parallels that of the secondaries (text fig. 44D-F). Their formation begins in the proximal part of the ambulacra after four or five alternate sets of secondaries have been developed. Corresponding insertions of new secondaries maintain the zone of tertiary coverplate emplacement four or five secondary plates proximal to the zone of secondary plate formation. Each tertiary is inserted along the distal margin of each primary, and thereby separates the primary and secondary coverplates of each cycle. Initially the small, rhombic tertiaries are limited to the axial part of the ambulacra. They gradually increase in size and extend toward the adradial suture line. The tertiaries commonly maintain the rhombic shape and end before reaching the adradial suture line in all but very large adults. Text fig. 43F represents actual plate shapes in the proximal part of the ambulacra of UMMP 57679, approximately 8 mm in diameter, and shows the typical three-plate cyclic pattern in medium-sized adults. The holotype is in the same stage of ambulacral coverplate development (text fig. 44D).

Quaternary plate development, which begins proximally, is initiated late in adult development after numerous three-plate cycles are complete (text fig. 43G). The rate of quaternary plate pair insertion is apparently more rapid than development of the cyclic plates. Thus the zone of quaternary plate insertion gradually migrates closer to the zone of tertiary plate insertion. For example, the ambulacral sequence in UMMP 4796, 14.5 mm in diameter (text fig. 45C, D), contains only numerous three-plate cycles throughout the long ambulacra. In contrast, the entire proximal halves of the ambulacra in USNM S-3478, 17.5 mm in diameter (text fig. 42, 44C), have quaternary plate pairs.

Individual cyclic coverplates continue to increase in size as the quaternary pairs are added. The secondaries expand adradially and become nearly triangular in outline. The once rhombic tertiaries commonly become subtriangular as their adradial bases intersect the adradial suture line and widen. In contrast, the quaternaries apparently remain small, rhombic plates, and are always confined to the axial parts of the ambulacra (text fig. 42, 43H).

Modifications of the ambulacral coverplate pattern are encountered occasionally. As one looks along the ambulacra in a distal direction, the proximal primary coverplate may be seen on the left side of the perradial line rather than on the right, its usual position. The relative proximal-distal location of the opposing, interdigitating, pointed perradial tips of the coverplates is thus reversed, with the perradial tip of the right, rather than the left member of the quaternary pair of plates lying proximal to the opposing quaternary plate, and so on (ambulacrum II, text fig. 42). In addition to plate reversals, the secondary and tertiary plates occasionally become unusually large and approach the size of adjacent primary coverplates. Small extraneous plates occasionally appear in the coverplate sequence, although these may be fragments of adjacent coverplates that were broken during preservation (text fig. 44C).

The primary coverplates laterally overlap adjacent secondary and tertiary ones, and the contiguous margins of these plates are beveled to fit tightly together. In fully developed adults, all three plates of the cyclic series commonly reach the adradial suture externally, and their bases rest upon the lateral margins of the underlying floorplates. In smaller adults the tertiaries may end externally before reaching the adradial suture line, but apparently they extend under the adjacent overlapping coverplates and internally make contact with the inner edge of the lateral floorplate margin. Only small, newly formed secondary and tertiary plates are confined to the axial part of the ambulacra, both externally and internally. In contrast, all quaternary coverplates are limited to the axial ambulacral area, both externally and internally.

The inner surfaces of the coverplates are inadequately known. Intra-ambulacral extensions apparently are developed on the primary, secondary, and perhaps tertiary coverplates, but their shape and size has not been determined. Adradially, the coverplates end adjacent to the edges of the underlying floorplates and apparently lack intrathecal extensions. The adradial ends of the coverplates are overlapped by the upper edges of adjacent interambulacral plates, whereas the lower parts of these interambulacrals abut the adradial faces of the coverplates. A pronounced groove is incised into the abutted adradial face of each coverplate, apparently facilitating articulation between the coverplates and the lower, abutting part of the adjacent interambulacral plates.

The ambulacral floorplates, seen only in disrupted specimens, are uniserial, trough-shaped, and meet one another

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Text figure 44. *Krama devonicum* (Bassler), 1936.

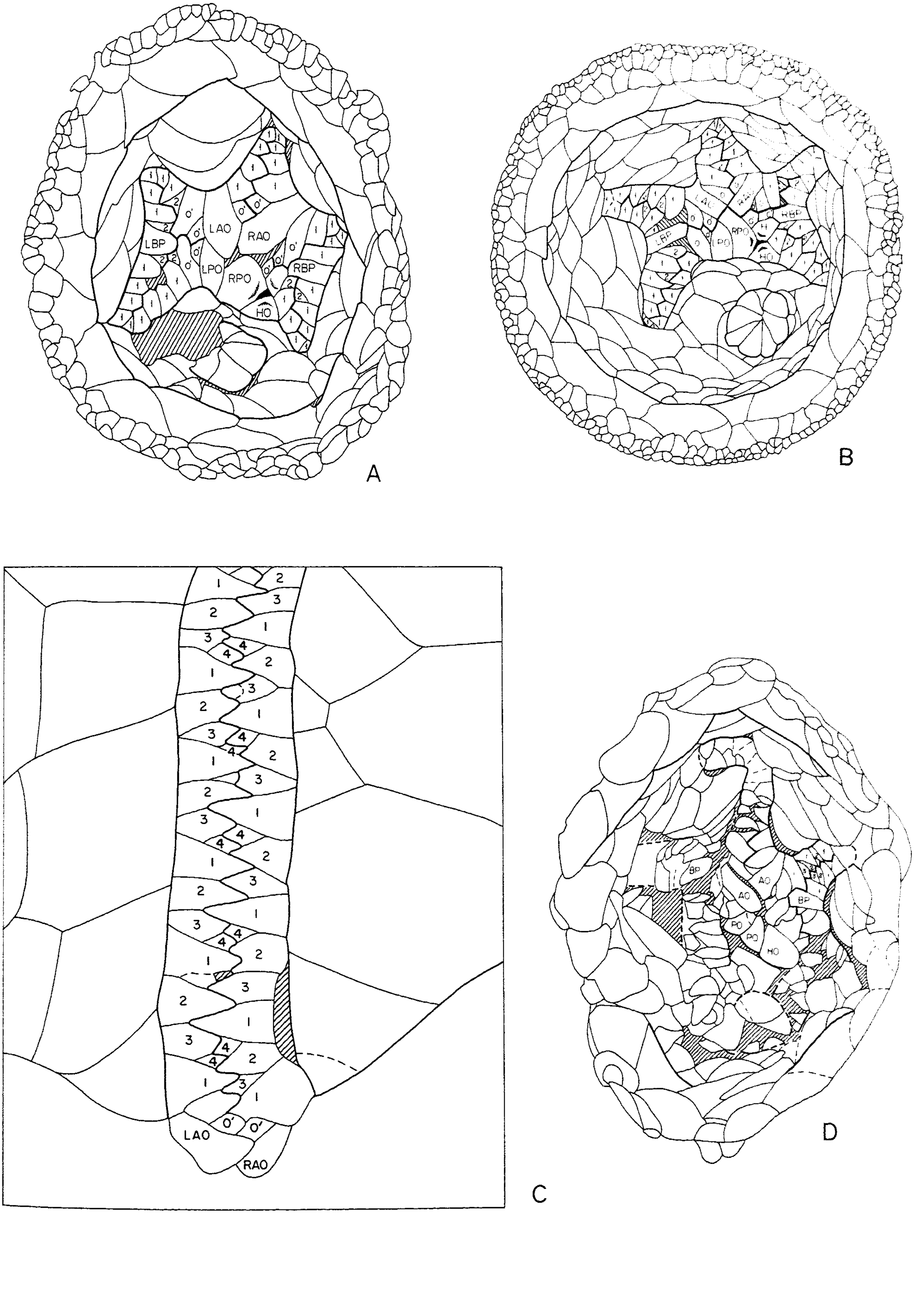
A. Juvenile, UMMP 35390, (x 30), pl. 41, fig. 7.

B. Juvenile, UMMP 21123, (x 18), pl. 42, fig. 1.

C. Ambulacrum III, USNM S-3478, (x 25), pl. 43, fig. 9.

D. Holotype, UMMP 17295, (x 15), pl. 41, fig. 6.

AO, anterior primary oral plate; BP, lateral bifurcation plate; HO, hydropore oral plate; LAO, left anterior primary oral plate; LBP, left lateral bifurcation plate; LPO, left posterior primary oral plate; o′, secondary oral plate; PO, posterior primary oral plate; RAO, right anterior primary oral plate; RBP, right lateral bifurcation plate; RPO, right posterior primary oral plate; 1, primary set ambulacral coverplate; 2, secondary set ambulacral coverplate; 3, tertiary set ambulacral coverplate; 4, quaternary set ambulacral coverplate.


A
LAO
RAO
LPO
RPO
LBP
RBP
HO
B
LAO
LPO
RPO
LBP
RBP
HO
C
LAO
RAO
D
BP
AO
PO
HO

along vertical sutures. The inner surfaces are evenly convex inward. The upper surfaces are concave downward except for the lateral adradial margins, which slope gently and form a moderately wide articulation zone upon which the bases of the overlying coverplates rest (insert, text fig. 42). These lateral margins slope toward the ambulacral trough in specimen UMMP 4796 (pl. 43, fig. 1-2) but appear to slope away from the trough in USNM S-3478 (insert, text fig. 42).

The squamose interambulacral plates are imbricate and moderately large in proportion to thecal diameter.

The valvular anal structure of *Krama devonicum* includes approximately 16 triangular plates, alternating as inner and outer circlet members. Outer circlet plates broadly overlap inner ones and leave only a narrow central strip of each inner plate exposed externally. The central, pointed tips of the anals are flexed upward to form a small, conical protuberance in the center of the anal structure. The basal ends of the anal plates are grooved, like the adradial ends of the ambulacral coverplates, and apparently aid in articulation of the anals with the adjacent abutting interambulacrals (pl. 43, fig. 1-3).

The peripheral rim is formed by four to six circlets. The large proximal circlet plates regularly alternate as proximal and distal subcirclet members. Plates of this and the following circlet are elongate concentric with the thecal margin, whereas the distal two to four circlets are formed by radially elongate plates.

External plate surfaces are smooth, except for the extremely fine pustulation reflecting the microstructure of the plates.

Specimens

UMMP 17295, UMMP 35390, UMMP 21123, UMMP 21203, UCMP 36118, UMMP 57078, UMMP 4796, UMMP 57679.

Holotype and seven topotypes of *Krama devonicum* (Bassler). Ferron Point Formation (Long Lake Beds), Traverse Group, Erian Series, Middle Devonian. Abandoned shale pit of the Alpena Portland Cement Company, SE¼, Sec. 18, T. 32 N., R. 9 E., Alpena County, about 7 miles north of Alpena, Michigan.

UMMP 17295. Holotype of *Krama devonicum* (Bassler) (1936, p. 14, pl. 7, fig. 1, as *Hemicystites devonicus*). H. H. Hindshaw, collector. 6.6 mm axial by 4.8 mm transverse diameter.

Text fig. 44D, pl. 41, fig. 6.

The holotype is a small, poorly preserved specimen. Thecal collapse and lateral compression have disrupted most of the plates. Many outer rim plates have been eroded away, and the oral region plates are centrally abraded. The ambulacral curvature pattern is discernible, and the three-plate cyclic coverplate pattern is preserved in the proximal part of ambulacrum IV. The quaternary coverplates are not present in this young adult. The four primary orals, hydropore oral, and some of the secondary orals are outlined in text fig. 44D.

UMMP 35390. Topotype of *Krama devonicum* illustrated by Kesling (1960, pl. 10, fig. 7, as a juvenile *Hemicystites devonicus*). 2.8 mm axial by 2.5 mm transverse diameter.

Text fig. 44A, pl. 41, fig. 7, 8.

This well-preserved topotype is a young juvenile. The theca has collapsed, but little plate disruption has occurred. All five ambulacra are distinct, but curvature has not yet been initiated. Each ambulacrum includes four or five sets of primary coverplates. Proximal secondary coverplates are present in ambulacra I, II, and V, but have not yet appeared in ambulacra III and IV. The oral area is formed by the four primary orals, the right posterior hydropore oral, two anterior secondary orals, and four or five lateral secondaries on each side of the central primaries. Three plates form the hydropore protuberance: the right posterior primary oral, the hydropore oral, and the single, opposing oral-ambulacral series plate. Interambulacrals are few in number, each is relatively large in proportion to thecal diameter. The partially disrupted anal structure includes approximately eight plates. The peripheral rim is formed by the proximal circlet of large plates and two or three poorly ordered distal circlets.

UMMP 21123. Topotype of *Krama devonicum* illustrated by Kesling (1960, pl. 10, fig. 6, as a juvenile *Hemicystites devonicus*). 4.4 mm axial by 4.6 transverse diameter.

Text fig. 44B, pl. 42, fig. 1, 2.

Although nearly twice the size, this juvenile is about equal in development to the above specimen. Thecal collapse has shifted the oral-ambulacral series toward the right anterior edge of the rim. Apparently it moved as a

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Text figure 45. *Krama devonicum* (Bassler), 1936.

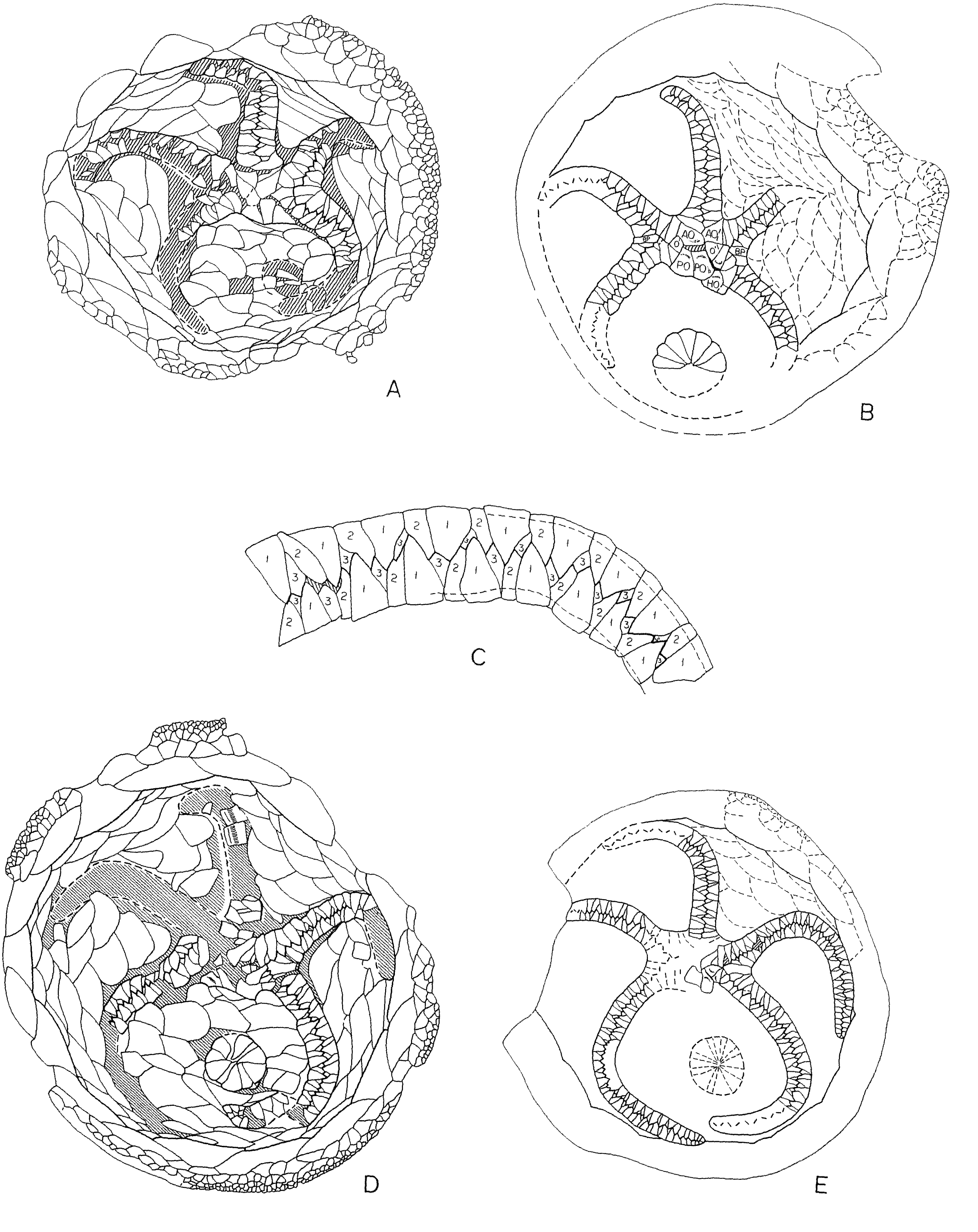
A. UMMP 21203, (x 10), pl. 42, fig. 7.

B. UMMP 57679, (x 10), pl. 42, fig. 9. AO, anterior primary oral plate; BP, lateral bifurcation plate; HO, hydropore oral plate; o', secondary oral plate; PO, posterior primary oral plate.

C. Ambulacrum V, UMMP 4796, (x 20), pl. 43, fig. 3. Proximal end is to the left. 1, primary set ambulacral coverplate; 2, secondary set ambulacral coverplate; 3, tertiary set ambulacral coverplate.

D. UMMP 4796, (x 6), pl. 43, fig. 1.

E. UMMP 57677-A, (x 6), pl. 43, fig. 5.


AO
AO'
O
O'
BP
BP
PO
PO
HO
A
B
C
D
E

unit, and only the distal interambulacrals are disrupted. Ambulacra I, II, and III show slight curvature. Each ambulacrum includes four to six primary coverplate sets, and one to three proximal secondary coverplates. The plating of the oral area and hydropore structure is identical to that of UMMP 35390. However, interambulacral plates are more numerous in this specimen than in the last. The anus includes eight plates, and the peripheral rim three or four circlets. The pointed tips of the anals are flexed upward and form a small conical mound in the center of the anal structure. Minute external plate pustulation is seen in enlarged photographs.

UMMP 57678. Topotype of *Krama devonicum.* G. C. McIntosh, collector (May, 1967). 6.8 mm axial by 6.7 mm transverse diameter.

Pl. 42, fig. 4.

In this partially disrupted specimen, the theca has collapsed, and most of the left-half plates proximal to the rim are disrupted. The right side of the oral region, the hydropore structure, ambulacra IV and V, most of the anal structure, and the anterior half of the peripheral rim are well preserved. All ambulacra curve, but the degree is less pronounced than in larger individuals. All three sets of cyclic coverplates have formed in the proximal parts of the ambulacra, but the tertiary plates are small and are restricted to the axial part of the ambulacra. A short distance from the oral region only the primary coverplates reach the adradial suture line externally, with the secondaries also restricted to the axial region. The anal structure appears to include 14 plates, whose pointed tips form a small, central protuberance. The rim is formed by four circlets of plates.

UCMP 36118. Topotype of *Krama devonicum.* Kopf Collection. 4.4 mm axial by 6 mm transverse diameter.

Pl. 42, fig. 5, 6.

Large sections of the anterior and posterior parts of the theca are missing. The complete specimen appears to have been over 6 mm in diameter. Plates in the posterior third of the specimen are depressed below the level of the anterior elements. Ambulacral curvature is slight. Proximally, the coverplate series includes primary, secondary, and tertiary plates, but only the primaries reach the adradial suture line regularly. The distal halves of the ambulacra appear to include only primary coverplates. Ten triangular anals form the anal structure; their pointed tips are raised to form a small, central, conical prominence.

UMMP 21203. Topotype of *Krama devonicum* illustrated by Kesling (1960, pl. 5, fig. 2, as *Agelacrinites* sp. B). 7.2 mm axial by 7.6 mm transverse diameter.

Text fig. 45A, pl. 42, fig. 7, 8.

This small adult is partially disrupted. Some of the interambulacrals and rim plates have been lost, and the plates of interambulacra 1, 2, and 5, the anal structure, and the distal parts of all the ambulacra are disrupted. However, the three-element coverplate cycles are well preserved in the proximal parts of ambulacra III, IV, and V. The specimen appears to include all typical adult features, with the exception of the quaternary coverplates and the perradial separation of the primary orals.

UMMP 57679. Topotype of *Krama devonicum.* G. C. McIntosh, collector (May, 1967). 7.8 mm axial by 8.5 mm transverse diameter.

Text fig. 45B, pl. 42, fig. 9-11.

This topotype has collapsed, disrupting many of the distal parts of the theca. However, the oral region, the hydropore structure, the proximal two-thirds of the ambulacra, interambulacrum 4, and a segment of the peripheral rim are well preserved. Distal displacement of the two posterior primary orals has begun here, with concurrent proximal migration of lateral secondary orals. The coverplate sequence includes all three plates of the cyclic sets, but the tertiary plates, and distally the secondaries, are confined to the axial part of the ambulacra. The anal structure apparently includes 14 plates. Four circlets of rim plates are present.

UMMP 4796. Topotype of *Krama devonicum* illustrated by Kesling (1960, pl. 5, fig. 1, as *Agelacrinites* sp. B). 14.6 mm axial by 14.5 mm transverse diameter.

Text fig. 45C-D, pl. 43, fig. 1-3.

This specimen is a moderately large adult. The coverplates of ambulacra II and III, and the distal parts of I and IV are disrupted, as are most of the oral plates. Several sections of the distal rim circlets are missing. However, the three-element cyclic series of coverplates is well preserved in parts of ambulacra I, IV, and most of V (text fig. 45D). Quaternary coverplates have still not begun to develop. Lateral displacement of adjacent interambulacrals has exposed the grooved, adradial ends of most of the ambulacral coverplates, and the grooved basal edges of the anals. The upper surfaces of two floorplates are exposed in ambulacrum III where the coverplates have been lost. Secondary orals may separate the anterior and posterior primary orals, although disruption of this area partially obscures the oral plate relationships. Approximately 12 triangular plates form the anal structure; each is centrally elevated to form a conical mound. The rim includes five plate circlets. Minute surficial plate pustulation is apparent in the enlarged photographs (pl. 43, fig. 3).

MMP 57677. Three specimens of *Krama devonicum* ›sting on a convex brachiopod valve previously encrusted ith bryozoa. Arkona Shale, about 25 feet below the ›ntact with the Hungry Hollow Formation, Hamilton roup, Erian Series, Middle Devonian. Lot No. 8, ›rthwest bank of Ausable River, 3 miles north-northeast : Arkona, Middlesex County, Ontario.

MMP 57677-A. Largest of three. 13.5 mm axial by 2.6 mm transverse diameter.
Text fig. 45E, pl. 43, fig. 4, 5.
The specimen is a moderately large adult. The theca as collapsed, but the plates are well preserved except for e partially disrupted oral area and a small missing seg-ent of the left thecal margin. This individual is essen-ally equal in stage of development to the last. In this ›ecimen the distal parts of ambulacra I and IV are well :eserved and demonstrate the mode of coverplate addi-on. The distal tips include only primary coverplates, six eight on each side of the perradial line. Secondary ates are developed in the next sector, inserted alternately ong the perradial line, adjacent to the distal edge of each :imary. Tertiary plates first appear after four (ambu-crum I) to six (ambulacrum II) secondary sets are :esent. Thus the zone of tertiary plate insection is sepa-ated from the distal tip of the ambulacrum by approxi-ately 12 sets of primary coverplates. The anal struc-re appears to include 15 plates in this specimen.

MMP 57677-B. 8 mm axial by 8.6 mm transverse ameter.
This individual is a small adult. The theca is poorly :eserved except for the three-plate cyclic sets of ambu-cral coverplates in II, IV, and V. The grooved adradial ›ds of the coverplates are exposed in the distal part of nbulacrum V.

SNM S-3478. Large adult *Krama devonicum* (Bassler). he holotype of *Agelacrinites southworthi* Bassler (1936, 16, pl. 4, fig. 12) and illustrated by Kesling (1960, pl. fig. 3). Arkona Shale, 20 to 30 feet below the Encrinal imestone (Hungry Hollow Formation) Hamilton Group, rian Series, Middle Devonian. Marsh's Mills, Arkona, ntario. 17.5 mm axial by 17.8 mm transverse diameter.
Text fig. 42, 44C, pl. 43, fig. 6-11.
The largest known specimen of *Krama devonicum,* this dividual is the only representative in which the final, ıaternary set of ambulacral coverplates has developed. he specimen is well preserved. Only partial thecal col-pse has occurred, which caused slight disruption of the terambulacrals. The medial part of ambulacrum I is issing, along with the adjacent plates of interambulacra 1 and 5. The anal structure is also disrupted. The remainder of the oral and ambulacral plates appear essentially undisturbed, except for the right posterior primary oral and adjacent hydropore oral plates. These elements have slipped toward the left posterior margin of the theca, and thus the left margin of the right posterior primary oral has slipped beneath the right edge of the left posterior primary oral. This movement has opened a small gap along the anterior margins of both the hydropore oral and right posterior primary oral plate. The broken end of ambulacrum I reveals an oblique cross section of both the coverplates and a floorplate (insert, text fig. 42). Quaternary ambulacral coverplates are present in the proximal one-half to two-thirds of all the ambulacra. Distal to the quaternary plates, the three-plate cyclic series of coverplates is like that of smaller adults. Distally, first the tertiary, then the secondary coverplates are lost, the distal tips being formed by four or five pairs of primary plates. In the well-preserved oral region, the anterior and posterior primary orals are separated by three intervening secondary orals. Some of the lateral secondary orals are quite large and form multiple perradial points, perhaps suggesting that they were formed by the fusion of two or more adjacent secondary orals.

USNM 94643. Juvenile *Krama devonicum* illustrated by Kesling (1960, pl. 5, fig. 4, as a young *Agelacrinites southworthi).* Labeled " Widder " at Thedford, Ontario. " G. A. Cooper is uncertain about the history of this edrioasteroid [probably collected by Mr. Southworth] but states that the matrix resembles the Arkona Shale instead of the younger Middle Devonian Widder formation " (Kesling, 1960, p. 151). 5 mm axial by 5.2 mm transverse diameter.

Pl. 42, fig. 3.

This well-preserved, small specimen has collapsed, but plate disruption is confined to slight separation of a few of the proximal elements. Surficial abrasion has smoothed many of the plates, particularly in the hydropore region. The specimen is similar to the other two described juveniles, UMMP 35390 and UMMP 21123. The oral area includes four abutting primary orals, one right posterior hydropore oral, two anterior secondary orals, and four or five lateral secondary orals on each side of the central primaries. The hydropore structure is formed by the right posterior primary oral, the hydropore oral, and the one oral-ambulacral series plate which opposes the junction between the hydropore oral and right posterior primary. The adjacent plate margins appear to have been elevated to form a small hydropore protuberance, but abrasion has obscured its original height. The anal structure includes nine or ten plates, and the rim has four circlets of plates.

Discussion of previous investigation

Bassler (1936, p. 14) described *Hemicystites devonicus* as a small edrioasteroid with: rather large interambulacrals and orals; exceptionally short, straight, rapidly tapering ambulacra with broad oral extremities, only four or five coverplates per row; and other thecal features as in *Hemicystites* [*i.e.*, three primary and no secondary orals, coverplates in a single alternating biseries, interambulacrals squamose and imbricate]. He illustrated only the holotype. In contrast with Bassler's description, a plate-tracing of that specimen, text fig. 44D, shows: the oral region has many plates and an adjacent, semi-integrated hydropore structure; and the ambulacra are curved, with coverplates forming a three-plate cyclic series.

In the same paper, Bassler (1936, p. 16) described *Agelacrinites southworthi* [= *Krama devonicum* (Bassler)], based on one specimen, USNM S-3478. Bassler characterized the species as being like *Agelacrinites hamiltonensis* but with large, squamose, smooth interambulacrals, and ambulacra shorter than, but similar to those of *A. hamiltonensis* [*i.e.*, curved, I-III contrasolar, IV-V solar, and apparently following Hall's description, with a single, alternating biseries of coverplates]. As seen in text fig. 42, a plate tracing of that specimen, Bassler apparently overlooked the complex plating of the oral-hydropore area and the intricate mixture of cyclic and biserial ambulacral coverplates.

Kesling (1960) described the hydropore structures of *Hemicystites devonicus*, *Agelacrinites southworthi*, and a species referred to as *Agelacrinites* sp. B. All seven specimens included by Kesling in these three species are here recognized as *Krama devonicum* (Bassler). The hydropore of *Hemicystites devonicus* was described from three specimens, including the partially disrupted holotype, which is a young adult, and two juvenile topotypes (UMMP 21123 and UMMP 35390). Kesling included the hydropore oral and one to three opposing plates of the oral-ambulacral series in the structure, but apparently excluded the right posterior primary oral, which is included here. No mention was made of the elevation of the hydropore plates into a small protuberance, although it is pronounced in both juveniles. As interpreted here, only three plates are actually in contact with the hydropore opening in these two young *Krama devonicum* specimens; they are the hydropore oral, the right posterior primary oral, and the one plate of the oral-ambulacral series directly opposite the junction between them.

Kesling's interpretation of the oral plates and hydropore structure of *Agelacrinites southworthi*, based on the holotype and one small specimen which he assigned to that species, differs significantly from that presented here. He described the right posterior primary oral as subtriangular, abutting the left posterior primary along a prominent straight suture line, and elevated to form a " vaulted structure." As seen in pl. 43, fig. 10, the right posterior primary has apparently slipped under the left primary, and thus Kesling's " vaulting " is preservational. "The right plate [here the hydropore oral], subtriangular and transversely elongate, has its right anterior border indented parallel to the convex end of the adjacent ambulacral [V] plate. The hydropore seems to be between the indentation in the right posterior peristomial plate [the hydropore oral] and the adjacent part of ambulacrum V" (Kesling, 1960, p. 151). As seen in pl. 43, fig. 10, both the right posterior primary oral and the adjacent hydropore oral are distally displaced, which leaves a gap between them and the opposing ambulacrals that obscures the hydropore location. The hydropore structure is here thought to lie between the elevated proximal, or "left" anterior edge of the hydropore oral, the adjacent elevated right anterior edge of the right posterior primary oral, and the elevated adradial margin of the oral-ambulacral series plate opposite the junction between these two (text fig. 42, pl. 43, fig. 10, 11). Prior to preservational plate slippage, the elevated margins of these three plates appear to have formed a small protuberance with the hydropore opening along the summit, as described here for other specimens of *Krama devonicum* as well. The following one or two ambulacral coverplates distal to the elongate plate of the oral-ambulacral series may have been slightly elevated also, which suggests that the opening continued distally between these elements and the opposing anterior edge of the hydropore oral.

Kesling's other specimen of *Agelacrinites southworthi* (USNM 94643, pl. 42, fig. 3) has a relatively small hydropore oral which lies adjacent to the right posterior edge of the right posterior primary oral. The hydropore opening is formed by these two plates and the adradial end of the elongate oral-ambulacral series plate, which opposes their junction. The adjacent corners of the two orals and the adradial margin of the opposing plate appear to have been elevated to form a protuberance with the opening at the summit, but erosion has partially leveled the area. Kesling, overlooking or disregarding the smaller hydropore oral, recognized only two posterior orals. He suggested that the right plate was the "homologue " of the combined right posterior oral and hydropore oral plates of the adult (USNM S-3478). He thought the opening was along the edge of this plate, apparently referring to the perradial edge, where a small preservational gap separates it from the anterior primary orals. The junction between the two posterior primary orals is slightly elevated. This is interpreted here as preservational tilting of the plates, whereas Kesling identified this as a " vaulted structure" like the one he described in specimen USNM S-3478.

Kesling's location of the hydropore in the juvenile USNM 94643 lies "slightly ahead of the suture line between the two posterior primary orals, whereas his placement of the opening in the adult USNM S-3478 is posterior to or "behind" this suture line. Thus he suggested that the opening migrated distally during ontogeny. Relative to the oral pole, the hydropore does shift somewhat distally during growth, owing to the increase in size and number of the secondary orals. However, the same three plates — the hydropore oral, the right posterior primary oral, and the opposing oral-ambulacral series plate — always surround the opening. It is possible, however, that the opening may actually lengthen distally somewhat during growth, and extend farther along the anterior edge of the hydropore oral in large adults to include the next one or two ambulacral series plates as well.

Two additional specimens of *Krama devonicum* (UMMP 4796; text fig. 45C,D, pl. 43, fig. 1-3; and UMMP 21203 text fig. 45A, pl. 42, fig. 7, 8) were included in Kesling's hydropore study under the label *Agelacrinites* sp. B. As seen in the text figures, the disrupted oral area and hydropore region are difficult to interpret in both, although apparently they are consistent with the structure found in better preserved specimens of *Krama devonicum* (text fig. 42, 45B). In both, the two posterior orals and the right posterior hydropore oral plate are tentatively recognized. In the smaller (UMMP 21203), the anterior and posterior primary orals apparently were perradially in contact, whereas in the larger (UMMP 4796) the lateral secondary orals had probably migrated between the primaries, as in specimen USNM S-3478. Kesling's reconstruction of *Agelacrinites* sp. B deviates from the description presented here, in that: (1) the oral plating, in which the two anterior primary orals are not distinct, but a large, central anterior oral is shown meeting the proximal coverplates of both sides of ambulacrum III; (2) the elongate shapes of the posterior oral plates; (3) the indication of a posterior oral ridge formed by the supposedly upturned contiguous edges of the two posterior orals; (4) the hydropore structure, shown as formed by only the right anterior edge of the hydropore oral and one large, opposing plate of the oral-ambulacral series [thereby deleting the right edge of the right posterior primary oral, which actually extends laterally to meet the opposing oral-ambulacral series plate]; and (5) the inclusion of a border of extremely narrow, elongate plates which flank the ambulacra and surround the anal structure [which actually represent the exposed, grooved, adradial faces of the coverplates and anals]. In spite of the somewhat fragmentary condition of both specimens, Kesling accurately portrays the complex three-element cyclic pattern of the ambulacral coverplates, including the distal absence of the tertiary and secondary plates. However, both sets are shown ending at approximately the same point. Kesling considered *Agelacrinites* sp. B as closely allied to *Agelacrinites southworthi* and separated the two on the supposed presence of the narrow bordering plates of the ambulacra [*i.e.*, the exposed adradial edges of the coverplates] and the wider ambulacra of *Agelacrinites* sp. B. The latter difference is the result of the differing sizes of the specimens, because the interambulacra increase in width more rapidly than the ambulacra during growth.

Other references to specimens of *Krama devonicum* include: a reillustration of the holotype and summary of Bassler's original description by Shimer and Shrock (1944); mention of the squamose interambulacrals of *Agelacrinites southworthi* by Ehlers and Kesling (1958); and a reillustration of Kesling's 1960 reconstruction of *Agelacrinites* sp. B by Regnell (1966); included with his summary of Kesling's hydropore structure study.

Discussion

The twelve described specimens of *Krama devonicum* (Bassler) represent a moderately complete growth series which includes three juveniles (2.5 to 5 mm in diameter) and nine adults, ranging from small to large individuals (6 to 17.8 mm in diameter). Earliest ontogenetic stages are unknown. In the smallest juvenile (2.5 mm in diameter), all major structural units of the theca are distinct. The oral-hydropore area, anal structure and rim are proportionately large, whereas the ambulacral-interambulacral sector of the theca is relatively small compared to that of adults. As the ambulacra lengthen and the interambulacra increase in area, the oral-hydropore area, the anal area, and the rim become proportionately smaller, although still increasing in absolute size. Interambulacra increase in width relatively faster than do the ambulacra, so that proportionately, the ambulacra decrease in width during growth.

The oral region, when first observed, includes: four very large primary orals, two anterior and two posterior, which are perradially in contact; one small, right posterior hydropore oral; and 10 to 12 secondary orals, two anterior and four or five laterals on each side of the central primaries. During growth the primaries decrease somewhat in relative size, whereas the hydropore oral increases greatly. Secondary orals increase slowly in total number, and some increase in size relative to the primaries. The exact number of secondaries is difficult to determine because the lateral secondaries reflect the ambulacral coverplate pattern which obscures the break between the lateral orals and proximal ambulacral coverplates. Apparently large adults include a minimum of 15 secondaries, versus the 10 to 12 of the youngest known juveniles. During the continuing growth of adults, apparently when the theca reaches 8 to 10 mm in diameter, lateral secondary orals, which originally flank the posterior primaries, migrate anteriorly and proximally as the posterior orals migrate posteriorly. When migration is complete, two or three secondary orals lie between the perradial edges of the anterior and posterior primaries.

In the youngest known specimen the posterior side of the hydropore protuberance is formed by the contiguous corners of the hydropore oral and the right posterior primary oral. The anterior side includes only the adradial margin of an elongate plate of the oral-ambulacral series which lies opposite the junction between the two posterior plates. During growth, the hydropore structure appears to shift slightly in a distal direction along the posterior side of ambulacrum V, because of the increasing size and number of oral plates. Although the same three plates continue to participate in the structure throughout adult development, possibly one or two proximal posterior coverplates of ambulacrum V, distal to the original single anterior plate, may also flank the anterior side of the opening and thereby lengthen it distally.

The ambulacra are short, broad, and straight in the youngest known juvenile. Four to six sets of primary coverplates are included in each ambulacrum of specimens 2.5 to 4 mm in diameter. Secondary coverplates are first inserted near the oral area after four to six primary sets are present, apparently when the theca is approximately 2 mm in diameter. Ambulacral curvature appears to be initiated as the theca approaches 4 mm in diameter. Tertiary coverplates first appear after four to six secondary sets have formed; the theca is then somewhere between 4 and 6 mm in diameter. These three sets of cyclic coverplates continue to develop and ambulacral curvature continues to increase without change until very late in adult development. When the theca is approximately 15 mm in diameter, quaternary plate pair development is initiated. Addition of quaternaries apparently proceeds rapidly and fills the entire proximal half to two-thirds of each ambulacrum by the time the theca reaches 17.8 mm in diameter.

The interambulacrals are proportionately large, even in juveniles. Numbers increase continuously throughout growth by the proliferation of new plates along the ambulacral adradial suture lines.

The anal structure grows from eight plates, when first observed in the juveniles, to approximately 16 in large adults. Development of new plates seems to be erratic, without apparent correlation to thecal diameter. Peripheral rim development proceeds by the addition of new circlets, from three in the youngest known specimens to five or six in adults.

In contrast to the moderately complete understanding of external thecal features of *Krama devonicum*, knowledge of most inner surface features is lacking. Ambulacral floorplates are seen only in two specimens which expose partial views of a few plates. The oral frame, stone canal passageway, and inner surface features of other thecal structures have not been observed.

Krama devonicum is the only edrioasteroid in which secondary oral plate migration during adult development results in the perradial separation of anterior and posterior primary orals. The addition of a new set of coverplates late in adult development is also uncommon. Moreover, the biserial pair arrangement of these late coverplates contrasts to the cyclic arrangement of the earlier coverplate series and produces a unique mixture of coverplate patterns.

RANGE AND OCCURRENCE: Traverse-Hamilton Groups, Erian Series, Middle Devonian of eastern Michigan and western Ontario.

Genus *Postibulla* Bell, *gen. nov.*

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

Diagnosis

Agelacrinitidae with: domal theca; oral area with many plates, primaries not differentiated; large, elevated, posterior oral protuberance present; hydropore protuberance semi-integrated, including three or more plates; ambulacra narrow, curved, I-III contrasolar, IV-V solar, coverplates steeply inclined to thecal surface, with two or three sets forming irregular cycles; interambulacrals squamose, imbricate; anal structure highly elevated and conical, with three circlets of plates.

Description

Postibulla includes small to medium-sized, domal edrioasteroids. The oral area is formed by many plates. Most of the oral plates are variable in size and shape, and their arrangement appears to be variable intraspecifically. Lateral and anterior orals reflect the pattern of the ambulacral coverplate series and thus appear to grade into the coverplate series. Therefore, separation of distal orals from proximal ambulacrals and determination of the total oral plate number is impossible. Differentiation of primary orals is not apparent in adults. Along the posterior margin of the region, four or more plates are flexed upward to form a prominent, protruding, axially elongate ridge—the posterior oral protuberance. Equal in elevation to the center of the oral rise, the protuberance extends distally into the proximal part of interambulacrum 5. It lies along the axial midline of the theca, and, in effect, the central suture line of the protuberance extends the anterior oral midline directly across the posterior half of the oral region. The structure is distinct even in juveniles. Two of the posterior plates that form the protuberance are consistently larger than any other orals.

The hydropore structure lies in the right posterior part of the oral region between the posterior oral protuberance and the proximal posterior edge of ambulacrum V. Plate margins surrounding the opening are flexed upward to form a conical or ovate prominence which rises above the distal part of the central oral rise. The hydropore, varying from a subtriangular gap to an elongate arcuate slit, lies at the summit of the prominence. In younger individuals the hydropore structure involves three or four plates, whereas four or five are commonly included in larger adults.

Each ambulacrum is a narrow, highly elevated ridge that rises above the adjacent interambulacra. Perhaps accentuated during collapse, the ambulacral elevation results primarily from the high angle inclination of the coverplates to the adjacent thecal surface.

The ambulacral coverplate pattern appears to be an irregular cyclic series of two sets of plates. A third series may be included in large adults. Large primary coverplates laterally overlap alternate secondary coverplates and form a two-plate cyclic sequence along each side of the ambulacrum. In mature parts of the ambulacra, the secondary coverplates are commonly almost as large as primaries (externally), and thus mask their identity. Each coverplate commonly forms a discrete perradial point. Cycles on opposite sides of the perradial line alternate and are offset by half a cycle width.

The broad interambulacra are covered by numerous, squamose, imbricate plates.

The anal structure is a high conical mound formed by three somewhat irregular circlets of plates. The triangular to subtriangular anals are steeply inclined to the surrounding thecal surface, as are the ambulacral coverplates. Outer circlet plates overlap the more or less regularly alternating plates of the second circlet along beveled margins. The pointed tips of a third, innermost circlet of anals are commonly exposed in the center of the anal structure. Lateral slippage of the highly inclined anals commonly obscures the original plate arrangement.

The peripheral rim includes five or six circlets. The large plates of the proximal circlet regularly alternate as proximal and distal subcirclet members in some species, but not in others.

Thecal plates have smooth exteriors in all known species.

Discussion

Postibulla embraces several species previously placed in *Agelacrinites*. Species of both genera have domal thecae, numerous oral plates, ambulacra curved I-III contrasolar, IV-V solar, cyclic ambulacral coverplates, and imbricating interambulacrals. But in contrast with *Agelacrinites*, species of *Postibulla* (1) develop a unique, prominent, posterior oral protuberance; (2) have steeply inclined coverplates which form externally narrow, high ambulacra; and (3) have three circlets of anal plates which form a highly elevated, conical protuberance. These three features also separate *Postibulla* species from *Krama devonicum*, which exhibits similar thecal form and ambulacral disposition. Moreover, the mixture of cyclic sets and biserial pairs of coverplates is unique to *Krama devonicum*.

Limited irregularities in the ambulacral coverplate pattern are not uncommon throughout the Agelacrinitidae, but in *Postibulla* they seem to dominate. Perhaps much of this apparent irregularity is preservational. The steep inclination of the coverplates may dictate instability during thecal collapse and thereby facilitate random lateral slippage of individual plates, which would disrupt the original order. Moreover, the relatively large size of the secondary coverplates obscures recognition of coverplate patterns. The anal structure of *Postibulla* resembles more the loose, irregular periproct found in the Lebetodiscina than the valvular structure of other Agelacrinitidae. Like the ambulacral coverplates, the steeply inclined anals may be unstable during collapse, thus promoting preservational disruption of the structure. In the least disrupted specimens, the outer circlet plates appear to overlap the alternate second circlet ones along tightly fitting, beveled margins, and thus form a well-ordered valvular structure. However, the inclusion of a third, inner circlet of plates commands the recognition of this structure as unique among the Agelacrinitidae.

ETYMOLOGY: *Postibulla* is compounded from the Latin *post*, behind, and *bulla*, knob or swelling, referring to the posterior oral protuberance.

RANGE AND OCCURRENCE: Erian Series, Middle Devonian to Kinderhookian Series, Mississippian of Michigan, Alberta, and Iowa.

Postibulla legrandensis (Miller and Gurley), 1894

Text fig. 46; plate 44

1894 *Agelacrinus legrandensis* Miller, S. A. and Gurley, F. E., Illinois State Mus. Bull. 5: 15-16, pl. 3, fig. 13-14.

1897 *Agelacrinus legrandensis* Miller and Gurley, Miller, S. A., Second Appendix to North American Geology and Palaeontology, Cincinnati: 733.

1901 *Agelacrinites legrandensis* Miller and Gurley, Clarke, J. M., New York State Mus. Bull. 49 (2): 182-198.

1936 *Agelacrinites legrandensis* Miller and Gurley, Bassler, R. S., Smithsonian Misc. Coll. 95 (6): pl. 4, fig. 16.

1943 *Agelacrinites legrandensis* Miller and Gurley, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 196.

Diagnosis

A *Postibulla* with: small theca; posterior part of posterior oral protuberance formed by three plates; hydropore structure formed by four or more plates, including two posterior ones.

Description

The domal theca of adult *Postibulla legrandensis* (Miller and Gurley) averages 8 or 9 mm in diameter, the largest recorded specimen approximately 10 mm (pl. 44).

The oral area includes many plates equal to or smaller than the proximal ambulacral coverplates (text fig. 46B). Oral plate arrangement appears variable. Plate shapes are similar to the ambulacral coverplates, thus the boundary between the distal orals and proximal ambulacrals is indistinct.

The posterior oral protuberance is formed by three or more average-sized orals and two large plates (text fig. 46B, pl. 44, fig. 11). All are flexed upward to form the high, nearly vertical sides of the elongate prominence. Opposing protuberance plates meet centrally to form a nearly straight central suture line along the summit. It extends from the transverse oral midline directly across the posterior half of the oral area, along the axial midline of the theca. Commonly abrasion has leveled off the summit of the protuberance, leaving a flattened, nearly horizontal summit with a central gap that separates opposing plates.

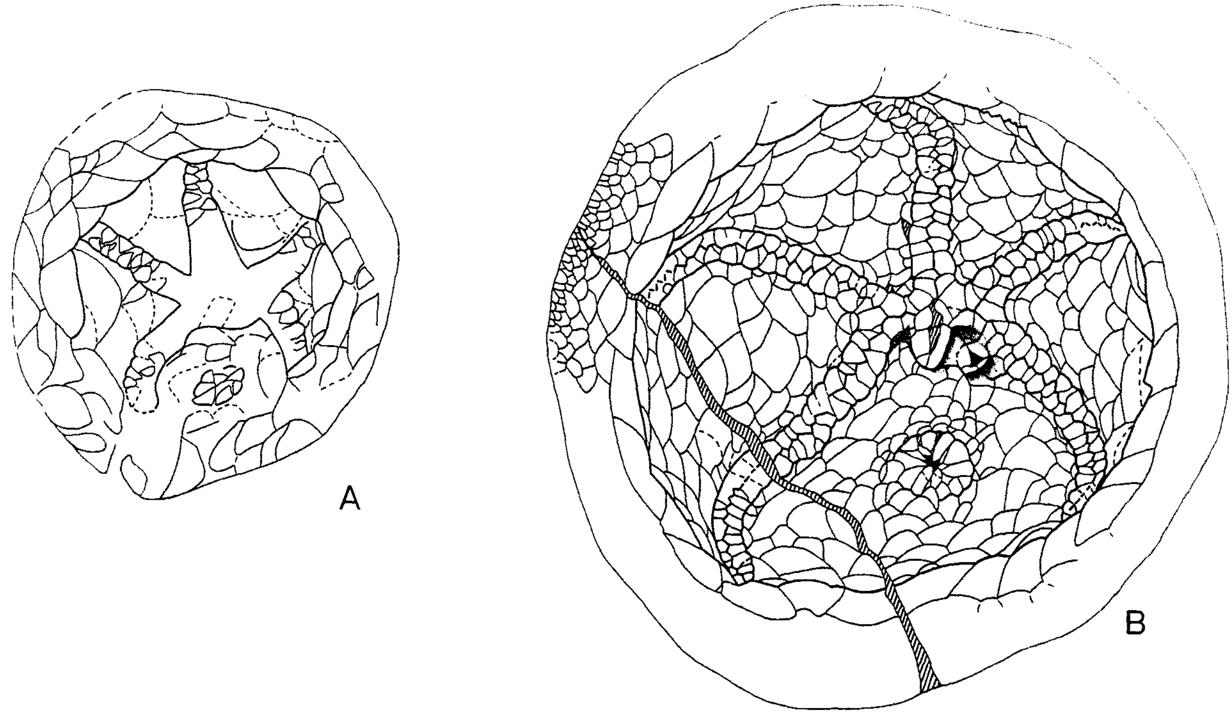
The arrangement of the protuberance plates varies among observed specimens. Commonly a single, very large oral forms the posterior two-thirds of the right side (text fig. 46B). Two opposing plates — a proximal large plate and a small distal one—form the left posterior side. The anterior third of the protuberance is formed by two or four opposing, average-sized orals. Their posterior margins lie adjacent to the large posterior plates; their anterior edges form the center of the transverse oral midline.

The hydropore structure is a small, conical prominence (text fig. 46B, pl. 44, fig. 10). The posterior half includes two medium-sized plates which apparently are a hydropore oral and one modified interambulacral. The left side of the elevation is formed by the pointed right margin of the large right plate of the posterior oral protuberance. The right anterior side includes one large, adradially expanded plate of the oral-ambulacral series, and perhaps one (? or more) plate of the oral-ambulacral series which flanks the distal side of the expanded plate. The contiguous margins of the hydropore plates are upturned and form the conical elevation. (Thus the large, right posterior plate of the oral protuberance is saddle-shaped; it is elevated both along its elongate left and its pointed right side, and the center of the plate forms a deep trough that separates the oral protuberance from the hydropore mound.) The hydropore was apparently an arcuate slit lying at the summit of the hydropore structure. Commonly abrasion has enlarged the opening into a subtriangular gap between the opposing plates.

The curvature of the narrow ambulacra is variable. It may be even throughout from near the proximal ends, or it may be uneven, with long, nearly straight proximal sectors followed by pronounced curvature as the ambulacra approach the peripheral rim. The distal tip of each ambulacrum remains widely separated from the other ambulacra, even in large adults.

The ambulacral coverplate series appears to be cyclic, and includes two or three sets of coverplates. Large primary coverplates are subtriangular to subrectangular in outline, and perradially angular. Somewhat smaller secondary plates flank the primaries. Commonly almost as large as the primaries, the secondary plates are subtriangular to subrectangular. Each may form a discrete perradial point, or its perradial margin may slope toward the adjacent primary, so that the two plates unite to form a single, broad, perradial point. Commonly two plates, nearly identical in size and shape, lie between successive primary coverplates. Both have the appearance of secondaries. In other cases only one secondary separates successive primaries. Thus two types of cycles are present: one with two plates — one primary and one secondary; the other with three plates — one primary and two secondaries. The occurrence of these two types of cycles appears to be random along the ambulacra.

In mature sectors of the ambulacra small, rhombic coverplates are also present occasionally. Lacking any apparent regularity, these plates may represent atypical secondaries or perhaps a new, third set of coverplates that are inserted late in ambulacral development. The degree to which lateral plate slippage during thecal collapse has contributed to the apparent irregularity of



Text figure 46. *Postibulla legrandensis* (Miller and Gurley), 1894

A. Lectoparatype, juvenile, CFMUC 6495-B, (x 15), pl. 44, fig. 2.
B. GSC 25143, (x 15), pl. 44, fig. 9.

the coverplate sequence is uncertain, but appears to be great.

The ambulacral floorplates have been observed in one disrupted specimen tentatively identified as a *Postibulla legrandensis* (pl. 44, fig. 5). The floorplates are uniserial and abut along vertical sutures. Each is rectangular in outline, elongate normal to the ambulacral axis. The upper surface of the trough-shaped plate is concave downward, except for the nearly horizontal lateral margins which slope slightly toward the ambulacral axis. These margins apparently form a broad surface of articulation upon which the bases of the overlying coverplates rested. The convex-inward, inner sides of the floorplates appear to bear small lateral nodes that extend into the thecal cavity, with at least one on each side of each plate.

The numerous, squamose, imbricate interambulacrals are relatively small in proportion to thecal diameter.

The anal structure is formed by at least 20 plates in large adults. Outer circlet elements appear to alternate regularly with second circlet plates, whereas plates of the third, or innermost, circlet are fewer in number than each of the two outer circlets and they appear to occur sporadically.

The peripheral rim is formed by five or six circlets of plates. The large plates of the proximal circlet occasionally alternate as proximal and distal subcirclet members. More commonly, one lateral margin of each plate lies proximal to the adjacent rim plate, whereas the other is distal to its neighbor. Thus subdivision of the proximal circlet plates into two subcirclets is incomplete.

Specimens

CFMUC 6495. Type series of *Postibulla legrandensis* (Miller and Gurley) (1894, p. 15-16, pl. 3, fig. 13-14, as *Agelacrinus legrandensis*). LeGrand beds, Hampton Formation, Easley Group, Kinderhookian Series, Mississippian. LeGrand, Marshall County, Iowa.

CFMUC 6495-A. Lectotype of *Postibulla legrandensis*. 7.3 mm axial by 7.2 mm transverse diameter.
Pl. 44, fig. 1.

The lectotype is poorly preserved. The theca has collapsed and many of the plates are disrupted; the right half of the theca has been severely crushed. A small fracture separates the posterior edge of the theca from the remainder. Plate structure can be interpreted in parts of ambulacra I and II, interambulacra 1, 2, and part of 5, and in the left anterior half of the rim. Only the original outline of ambulacra III-V is visible. The specimen does have five ambulacra, although V is particularly difficult to locate, which thereby explains Miller's and Gurley's original description of only four ambulacra. The anal structure is not visible.

CFMUC 6495-B. Lectoparatype of *Postibulla legrandensis*. 3.8 mm axial by 3.6 mm transverse diameter.

Text fig. 46A, pl. 44, fig. 2.

The second specimen of the type series is a juvenile and lies near the lectotype on the same small piece of limestone. The theca has collapsed, causing partial disruption of many plates. All five ambulacra are visible; II and III are nearly straight, whereas I, IV, and V show slight curvature. Each ambulacrum includes approximately eight to ten sets of coverplates. Most of the coverplates are primaries, but a few secondaries may be included proximally. The orals, anals, and interambulacrals are disrupted. The anterior half of the rim is well preserved and is composed of three or four circlets of plates.

GSC 25143 (old 9011, S-3881). Topotype. LeGrand beds, Hampton Formation, Easley Group, Kinderhookian Series, Mississippian. LeGrand, Marshall County, Iowa. 5.9 mm axial by 6.4 mm transverse diameter.

Text fig. 46B, pl. 44, fig. 9-10.

This topotype is a medium-sized adult. The theca has collapsed, but only the distal interambulacrals and tips of ambulacra III-V have been extensively disrupted and have slipped beneath the proximal edge of the rim plates. A crack extends through the left posterior part of the theca. The plates of the oral-ambulacral series and the anals appear to be partially disturbed, owing to random lateral slippage. The upper parts of the plates of the posterior oral protuberance have been abraded, leveling the summit of that structure. Plate boundaries in the anterior half of the hydropore structure are obscure. One of the older numbers assigned to this specimen (S-3881) corresponds to the United States National Museum number for other topotypes, and suggests that the specimen was originally included in that collection.

USNM S-3881. Topotypes of *Postibulla legrandensis* (Miller and Gurley), five slabs, eight specimens. LeGrand beds, Hampton Formation, Easley Group, Kinderhookian Series, Mississippian. LeGrand, Marshall County, Iowa.

USNM S-3881-A-1. Illustrated Specimen of *P. legrandensis* by Bassler (1936, pl. 4, fig. 13, as *Agelacrinites legrandensis*). 9.5 mm axial by 8.6 mm transverse diameter.

Pl. 44, fig. 14.

The theca of this large adult has collapsed and the distal interambulacrals and ambulacrals have slipped under the proximal rim plates. Orals and many ambulacrals have been abraded, partially obscuring the plate boundaries. The abraded posterior oral protuberance appears to include five plates—three posterior and two anterior. The hydropore opening is unusually large, owing to erosion of the upper ends of the four or five plates that form the tubercle. The ambulacral coverplate pattern is visible in many sectors of the ambulacra. The anal structure is partially disrupted.

USNM S-3881-A-2. Topotype. 8.5 mm axial by 8.3 mm transverse diameter.

Pl. 44, fig. 4.

This small adult is on the slab with A-1. Collapse has accentuated the interambulacral plate imbrication. The posterior part of the theca is deeply depressed, and the left posterior sector of the rim is missing. The posterior oral protuberance is well preserved, except for abrasion of the upper surface. The cyclic sequence of ambulacral coverplates is preserved in ambulacra III-V. The anal structure shows the outer circlet plates overlapping alternately the second circlet plates. The tips of four or five anals of the inner third circlet are exposed centrally.

USNM S-3881-B-1. Topotype. 8.1 mm axial by 8.1 mm transverse diameter.

Pl. 44, fig. 6, 7.

This topotype is another moderately well preserved adult with a collapsed theca. Interambulacra 2 and 4 are disrupted distally. The posterior oral protuberance and the hydropore structure are well preserved except for erosion of the upper ends of the central plates of each structure. The ambulacral coverplate sequence is preserved, although distally the opposing coverplates are separated perradially.

USNM S-3881-B-2. Topotype. 5.6 mm axial by 5.8 mm transverse diameter.

Pl. 44, fig. 3.

This small adult has collapsed, but only distal interambulacrals and ambulacrals are disrupted. Ambulacral curvature is less pronounced than in larger adults. Erosion has leveled the tops of the hydropore and posterior oral protuberances.

USNM S-3881-C-1. Topotype. 7.1 mm axial by 7.9 mm transverse diameter.

Pl. 44, fig. 8.

This collapsed adult is missing the right anterior sector of the rim. Abrasion has leveled the upper ends of the oral and ambulacral series plates. The anals are in part laterally separated because of thecal collapse.

USNM S-3881-E. Topotype. 9 mm greatest diameter by a perpendicular of 6 mm.

Pl. 44, fig. 5.

This fragment of a large adult is tentatively identified as *Postibulla legrandensis*. Only the right half of the theca is preserved, and here etching and abrasion have removed all oral-ambulacral series covering plates. The upper sides of the floorplates are partially exposed. Secondary calcite fills the ambulacral trough and preserves the impressions of the inner surfaces of the coverplates.

NYSM 12777. Topotype. LeGrand beds, Hampton Formation, Easley Group, Kinderhookian Series, Mississippian. LeGrand, Marshall County, Iowa. 10.2 mm axial by 10.9 mm transverse diameter.

Pl. 44, fig. 11-13.

This large adult has collapsed, partially disrupting the interambulacral plates. Plates of the oral-ambulacral and anal series are well preserved, although the upper surfaces of the plates of the posterior oral protuberance have been eroded and form a large central gap between opposing plates. The hydropore tubercle is well preserved and apparently only slightly abraded.

Discussion

Miller and Gurley (1894) differentiated *Agelacrinus legrandensis* from other *Agelacrinites* by the small thecal size and by the occurrence of only four ambulacra, three contrasolar, one solar. Based on two specimens (CFMUC 6495-A, B), one adult and one juvenile, they also recorded the domal thecal shape; the squamose, imbricate interambulacral and rim plates; the narrow, ridgelike ambulacra; the numerous small orals; and the disrupted anal structure. The larger specimen (CFMUC 6495-A), here designated the lectotype, is poorly preserved but five ambulacra are present, I-III contrasolar, IV-V solar (pl. 44, fig. 1). The five ambulacra are more easily observed in the smaller lectoparatype (pl. 44, fig. 2). The taxonomically important ambulacral coverplate pattern is preserved in part of ambulacrum III of the lectotype. The equally important structure of the oral region, the posterior oral protuberance, the hydropore, and the anal area are not recognizable in the type specimens.

Bassler (1936, p. 16, pl. 4, fig. 13) illustrated a moderately well preserved topotype of *Agelacrinites legrandensis*. He noted the presence of five ambulacra as "normal" but made no mention of the posterior oral protuberance, hydropore structure, ambulacral coverplate pattern, or the anal area construction.

In *Postibulla legrandensis* (Miller and Gurley) the external thecal plating appears to vary intraspecifically in several taxonomically important structures. Oral plates are small, numerous, and lack apparent regularity. The posterior oral protuberance includes seven or nine plates with the anterior third being formed either by two or four plates. Plates participating in the hydropore structure vary from four to five, or (?)six. The ambulacral coverplate sequence includes primary and secondary coverplates variably arranged in two- or three-plate cycles. Distribution of the differing cycles appears to be random along the ambulacra. In large adults a third set of coverplates may occur sporadically in the proximal parts of the ambulacra. Preservational distortion of these steeply inclined plates of the oral-ambulacral series can account only for part of this variation. Thus plating variability appears to be basic to the species. Other distinguishing features include the small adult thecal size and the proportionately small size of the numerous interambulacrals.

RANGE AND OCCURRENCE: Hampton Formation, Easley Group, Kinderhookian Series, Mississippian of LeGrand, Iowa.

Postibulla keslingi Bell, *sp. nov.*

Text fig. 47; plate 45, fig. 1-10

1960 *Agelacrinites* sp. A. Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 148-149, pl. 4, fig. 1-5.

Diagnosis

A *Postibulla* with: medium-sized theca; posterior part of posterior oral protuberance formed by two large plates; hydropore structure formed by four plates, including one large posterior plate.

Description

The domal theca of *Postibulla keslingi* Bell is of moderate size; recorded adult diameters reach 13 mm.

The oral area in all adult specimens examined is partially disrupted, but it appears to be formed by numerous small plates (text fig. 47A-C). These small orals reflect the pattern of the ambulacral coverplate series in size and shape. Thus the orals appear to grade into the ambulacrals without apparent break. Only the four to six plates that form the posterior oral protuberance are constant in position. The contiguous parts of these plates are upturned and form the highly elevated, elongate protuberance. The posterior two-thirds of the protuberance is formed by two large opposing plates, one right, the other left. They meet centrally along a straight to moderately sinuous suture line which approximates the position of the axial midline of the theca. The anterior third of the structure is commonly formed by two small opposing plates. Their posterior margins abut the two large posterior protuberance plates, and their anterior margins form the central section of the transverse oral midline (text fig. 47A, B). Occasionally an additional pair of small plates may lie between the anterior and posterior pairs and raise the total to six protuberance plates (text fig. 47C, pl. 45, fig. 7). The suture line between opposing plates of the protuberance extends to the central oral pole, where it intersects the transverse oral midline and aligns with the posterior end of the anterior oral midline.

In juveniles, the oral area is formed by fewer plates than in adults. Moreover, two large anterior primary orals are distinct (text fig. 47A, pl. 45, fig. 9). The posterior oral protuberance is proportionately larger in younger specimens, where it is formed by only one pair of small anterior plates and two very large posterior plates.

Four or more plates form the hydropore tubercle in the right posterior part of the oral region (text fig. 47A-C). A single large hydropore oral forms the entire posterior side of the structure. The right side of the large right plate of the posterior oral protuberance forms the left side of the hydropore tubercle. The adradial ends of two medium-sized plates of the right posterior oral-ambulacral series complete the structure; they lie opposite the anterior edge of the large hydropore oral plate. The contiguous margins of the hydropore plates are upturned and form the oblong elevated tubercle with the slitlike hydropore opening along the summit. Probably because of preservational disruption the orientation of the tubercle (and the opening) appears to vary, either paralleling the axis of ambulacrum V, or being nearly normal to that axis (text fig. 47A-C). As in *P. legrandensis*, both the right and left margins of the large right plate of the posterior oral protuberance are upturned, with the plate participating in both the hydropore structure and the posterior oral protuberance Thus the central part of this saddle-shaped plate forms a deep trough separating the two structures.

Ambulacral curvature is even, and is initiated near the oral region. Distally the ambulacra remain separated from one another by many interambulacrals, and commonly they are also separated from the proximal margin of the peripheral rim by an unusually large number of interambulacrals, even in larger adults.

The ambulacral coverplates form an irregular series of alternating large and small plates (text fig. 47A-C, pl. 45, fig. 1-10). They are apparently grouped into irregular, alternating cycles, but no consistent pattern of plate disposition is apparent. On each side of the perradial line, in the proximal parts of the ambulacra, large subtriangular plates alternate with smaller subrhombic plates. The latter do not reach the adradial suture line externally. One medium-sized, subrhombic plate lies adjacent to each large subtriangular plate. A third, smaller rhombic plate is occasionally also present. Thus, proximally there appear to be large primary coverplates and smaller secondary coverplates which form both two- and three-plate cycles, but without apparent regularity.

The small rhombic and medium-sized subrhombic plates (? secondaries) occur only in the proximal one-half to two-thirds of the ambulacra. Distally, all plates are large and subtriangular and broadly intersect the adradial suture line. However, two slightly different sizes of plates are sometimes present, with larger plates more or less regularly alternating with smaller ones. These perhaps represent two different sets of coverplates. If so, the slightly smaller plates may be a secondary set inserted between the larger primaries very near the distal tips of the ambulacra. Proximally all these coverplates are nearly equal in size and thus not readily distinguished as different sets. If two sets are present distally, the small rhombic and subrhombic proximal coverplates represent a tertiary set, and each coverplate cycle would contain: one primary followed by one or two tertiaries, followed by one secondary, then one or two more tertiaries, thereby totaling four to six plates per cycle. All coverplates form discrete perradial points and thus obscure any cyclic pattern in the course of the perradial line.

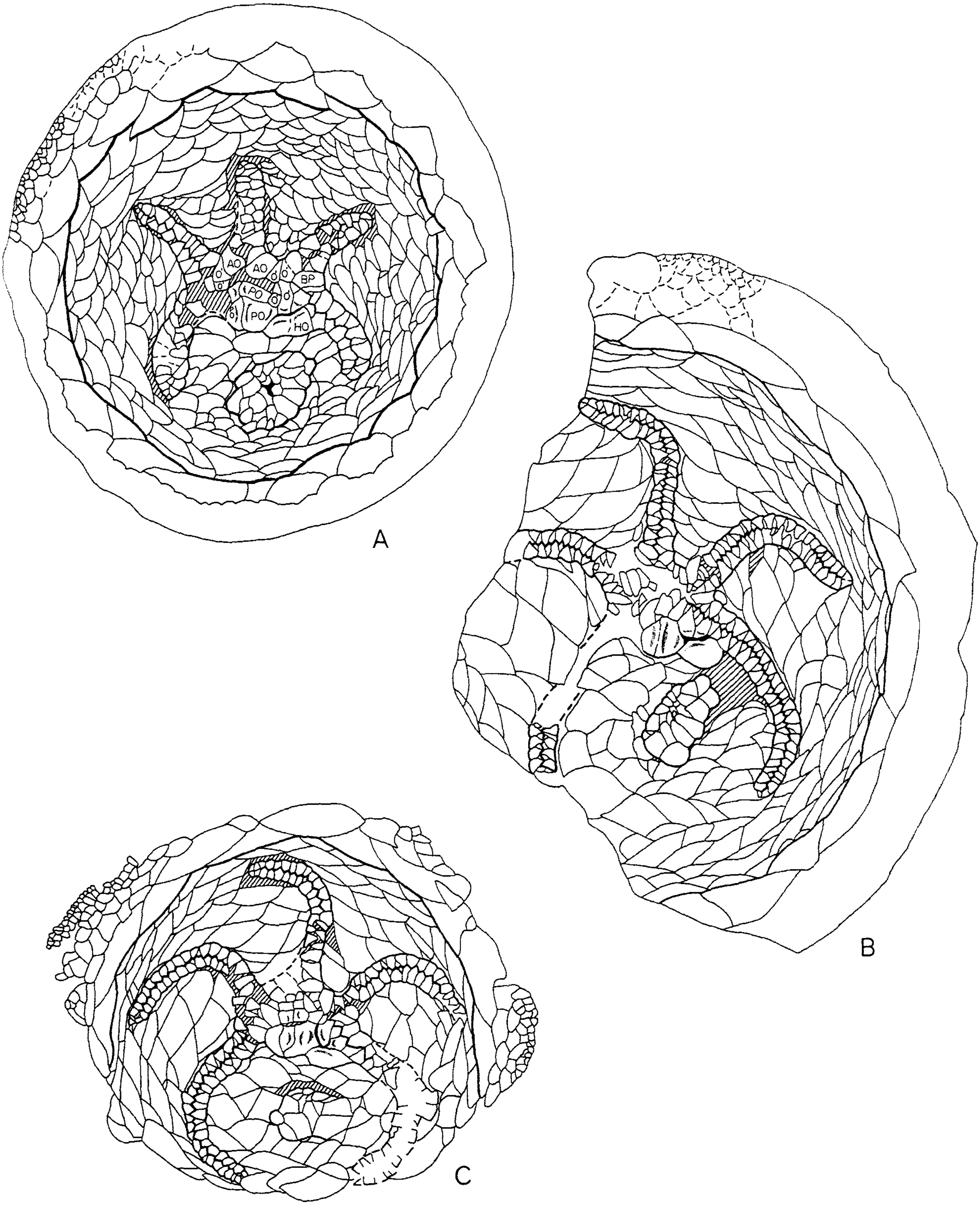
The large subtriangular coverplates laterally overlap adjacent smaller ones. Apparently all but the small rhombic plates extend under adjacent larger plates and internally meet the adradial suture. Adjacent interambulacrals overlap the adradial ends of the large ambulacral coverplates. The coverplates appear to end near the lateral margins of the underlying ambulacral

Text figure 47. *Postibulla keslingi* Bell, *sp. nov.*

A. Paratype (3), UMMP 35379, (x 18), pl. 45, fig. 3.
AO, anterior primary oral plate; BP, lateral bifurcation plate; HO, hydropore oral plate; o′, secondary oral plate; PO, posterior primary oral plate.

B. Holotype, UMMP 35387, (x 9), pl. 45, fig. 1.

C. Paratype (1), USNM 111225, (x 10), pl. 45, fig. 7.


AO
AO
BP
PO
PO
HO
A
B
C

floorplates, without forming large intrathecal extensions. Intra-ambulacral extensions, developed on the ambulacral tunnel surfaces of the coverplates, are suspected but have not been clearly observed.

The ambulacral floorplates are uniserial and trough-shaped, and have been observed only in cross section in one broken specimen (pl. 45, fig. 1).

The numerous interambulacral plates are squamose and imbricate. Rather small in younger specimens, they appear to increase rapidly in size during ontogeny and become medium-sized in proportion to thecal diameter in larger adults.

The anal structure, disrupted in all known specimens, appears to include three circlets of plates. The outer circlet plates are large, very wide-based, triangular plates that overlap and apparently alternate with the second circlet anals. Only the tips of a few plates which form a third, innermost irregular circlet have been observed (pl. 45, fig. 1, 5).

Five or six circlets form the peripheral rim. The large plates of the proximal circlet alternate in position to form proximal and distal subcirclets.

External plate surfaces are smooth except for the minute pustulation seen in enlarged photographs; these are related to the microstructure of the plates.

Specimens

UMMP 35387, USNM 111225, UMMP 35377, UMMP 35379, UMMP 35389. Upper part of the Ferron Point Formation, Traverse Group, Erian Series, Middle Devonian. Abandoned shale pit of the Alpena Portland Cement Company, SE¼, Sec. 18, T. 32 N., R. 9 E., Alpena County, about 7 miles north of Alpena, Michigan.

UMMP 35387. Holotype of *Postibulla keslingi* Bell, *sp. nov.*, illustrated by Kesling (1960, pl. 4, fig. 1, 2, as *Agelacrinites* sp. A). 12.2 mm axial by 9.5 mm transverse diameter.

Text fig. 47B, pl. 45, fig. 1, 2.

The left side of the holotype is missing, including part of ambulacra I, II, interambulacra 1, 2, 5, and the entire left half of the peripheral rim. The missing thecal area has left a faint trace of its outline on the underlying brachiopod (Kesling, 1960, pl. 4, fig. 1, 2). Collapse has disrupted distal interambulacrals, some oral plates, and most of the proximal coverplates of ambulacrum I. However, the remaining ambulacra preserve the coverplate pattern. The posterior oral protuberance and the hydropore structure are well preserved. The anal structure is deeply depressed, and the plates partially disrupted. In spite of preservational distortion, the specimen records the taxonomically critical structures. It is the largest known representative of the species.

USNM 111225. Paratype (1) of *Postibulla keslingi*. 7.6 mm axial by 8.9 mm transverse diameter.

Text fig. 47C, pl. 45, fig. 7-9.

The theca of this adult has collapsed, accentuating the imbrication of the interambulacrals and causing some lateral shifting of the oral and ambulacral plates. Most of the plates of the distal circlets of the peripheral rim have been lost, along with some of the posterior, proximal plates of the rim. Surficial etching may have accentuated the minute pustulation that reflects the microstructure of the plates. This minute surficial irregularity includes elongate grooves and channels on many of the ambulacral coverplates. The anal structure and surrounding interambulacrals are much depressed, thus disrupting the anal plate arrangement. The ambulacral coverplate pattern, the arrangement of the plates of the posterior oral protuberance, and the hydropore structure are moderately well preserved.

UMMP 35377. Paratype (2) of *Postibulla keslingi* Bell, illustrated by Kesling (1960, pl. 4, fig. 3, as *Agelacrinites* sp. A). 8.8 mm axial by 9.2 mm transverse diameter.

Pl. 45, fig. 5, 6.

The specimen is nearly complete, but much of the collapsed theca is covered by a thin layer of tenacious matrix that obscures plate boundaries. Only the larger ambulacral coverplates are distinct. The posterior oral protuberance appears to include six plates — two large posterior ones and two pairs of small anterior ones. However, the right anterior part of the protuberance is crushed. Thus the supposed left central plate could be the anterior end of the broken large left posterior plate. Ambulacral curvature is less pronounced in this adult; I and III are nearly straight. The anal plate arrangement is obscure.

UMMP 35379. Paratype (3) of *Postibulla keslingi* Bell, illustrated by Kesling (1960, pl. 4, fig. 4, as *Agelacrinites* sp. A). 5.3 mm axial by 5.1 mm transverse diameter.

Text fig. 47A, pl. 45, fig. 3, 4.

The specimen is a young adult or an advanced juvenile. Thecal collapse has accentuated interambulacral plate imbrication and caused some oral-ambulacral plate disruption, particularly in the hydropore structure and the left side of the oral region. Two large anterior primary orals form the center of the anterior side of the oral region. The posterior oral protuberance includes only four plates; the two posterior plates are proportionately larger than in a large adult.

The hydropore oral plate also appears exceptionally large. The ambulacra are short and extend only halfway to the proximal margin of the rim. Two sets of coverplates form an irregular, alternating, two-plate cyclic series, with the primary plates only slightly larger than the secondaries. The anal plates apparently form three circlets.

In contrast to most other young edrioasteroids, the interambulacral areas are relatively large in proportion to thecal diameter. They extend distal to the ambulacra and form a broad zone that separates the ambulacra from the rim. The peripheral rim is formed by approximately four circlets of plates.

UMMP 35389. Topotype of *Postibulla keslingi* Bell, illustrated by Kesling (1960, pl. 4, fig. 5, as *Agelacrinites* sp. A). 2.9 mm axial by 2.7 mm transverse diameter.

Pl. 45, fig. 10.

This individual is a poorly preserved juvenile, probably a *Postibulla keslingi*. It is collapsed, partially obscured by matrix and somewhat abraded so that many thecal plates are difficult to identify. The peripheral rim dominates. The oral area is proportionately larger than in adults. The posterior oral protuberance may include only the two large posterior plates. The ambulacra are short and straight, with four to six pairs of coverplates per ambulacrum. Interambulacral plates are indistinct, and the anal structure is disrupted. Only three or four circlets of plates form the peripheral rim.

Discussion

Specimens here designated *Postibulla keslingi* Bell, *sp. nov.* were first described by Kesling (1960) as *Agelacrinites* sp. A. Primarily interested in hydropore structures, Kesling concentrated on that feature. He included both juveniles (UMMP 35389, 35379) and an adult (UMMP 35387), and suggested that the hydropore structure migrated distally along the posterior side of ambulacrum V during ontogeny, involving different plates in adults than in juveniles. Admittedly, additional plates are present between the hydropore tubercle and the center of the oral region more often in larger adults than in juveniles, but these may be new elements rather than modified hydropore plates. Moreover, it is difficult to distinguish between distal orals and proximal coverplates in this species because of the similarity in shapes and sizes of the two series. Thus identification of homologous ambulacral coverplates in individuals of differing size is tentative. Together with the partially disrupted condition of all of the available specimens, these factors make Kesling's proposed hydropore migration highly speculative.

Kesling (1960, p. 149) further supposed that the posterior oral protuberance, or "vaulted structure" as first described by him, "may have operated like a hinge, with the larger plate [right posterior saddle-shaped element] lifting to admit water through the hydropore along its right edge." The posterior oral protuberance includes not only the two large posterior plates described by Kesling, but also one or two pairs of anterior plates that extend the structure to the center of the oral region. Thus it appears to be functionally integrated with the central oral region, or the underlying oral frame and oral lumen. Movement of the large right posterior plate seems improbable, although not impossible. The function of the posterior oral protuberance remains uncertain.

Postibulla keslingi resembles *P. legrandensis* but differs in the plate structure of the posterior oral protuberance, the hydropore structure, and the ambulacral coverplate pattern. Perhaps also significant is the relatively wide separation of the ambulacra from the proximal margin of the peripheral rim, the great width of the bases of the outermost anal plates, and the increase in proportional size of the interamblacrals in larger adults.

ETYMOLOGY: The species is named in honor of R. V. Kesling for his outstanding work with edrioasteroids.

RANGE AND OCCURRENCE: Ferron Point Formation, Traverse Group, Erian Series, Middle Devonian of the Alpena area, Michigan.

(?)*Postibulla jasperensis* (Harker), 1953

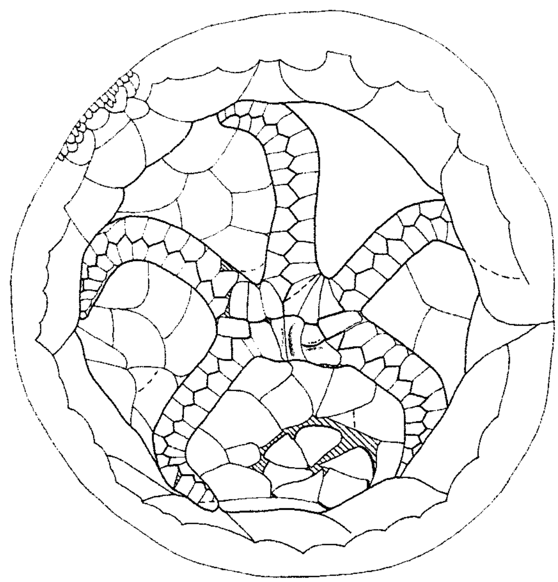
Text fig. 48; plate 45, fig. 12-14

1953 *Agelacrinites jasperensis* Harker, P., Jour. Paleont. 27 (2): 288-289, text fig. 1.

Description

Postibulla jasperensis (Harker) is represented by one small specimen, 7.6 mm in diameter, probably a young adult or an advanced juvenile in which plate development is incomplete.

The oral region includes four elongate plates which meet centrally; these are perhaps primary orals (text fig. 48, pl. 45, fig. 14); three or four additional elongate orals flank the central four on each side, along the transverse oral midline. A single, small, anterior oral lies along the anterior oral midline, distal to the two large anterior central orals. The two central posterior orals meet along upturned lateral margins and form a small posterior oral protuberance. Its straight central



Text figure 48. *Postibulla jasperensis* (Harker), 1953
Holotype, GSC 10051, (x 10), pl. 45, fig. 13.

suture line parallels the axial midline of the theca and aligns with the posterior end of the anterior oral midline.

The arcuate, slitlike hydropore is believed to lie along the junction between two plates in the right posterior corner of the oral region. The posterior plate (? hydropore oral) lies between the distal right margin of the right posterior central oral and the adradial ends of the proximal two posterior coverplates of ambulacrum V. The opposing anterior hydropore plate is a medium-sized, posterior, right lateral secondary oral. The margins of the two plates bounding the supposed hydropore are thickened and form a low, transversely elongate mound.

The ambulacra are moderate in width, and curved I-III contrasolar, IV-V solar. The coverplates appear to form a single alternating biseries of subrectangular plates with wide, pointed perradial ends. Each coverplate is inclined to the adjacent interambulacral surface and angles vary from 30 to 45 degrees. Thus the coverplates form high ambulacral ridges.

The interambulacral plates are very large in proportion to thecal diameter and few in number. They are subpolygonal to squamose, and abut or slightly overlap adjacent interambulacrals.

The large anal structure is formed by six or more large, triangular plates, grouped into a (?)single circlet.

The relatively wide peripheral rim includes approximately four circlets of plates. Plates of the proximal circlet are very large and alternate more or less regularly as proximal and distal subcirclet members.

External plate surfaces are smooth.

Specimen

GSC 10051. Holotype of *Postibulla jasperensis* (Harker) (1953, p. 288-289, fig. 1, as *Agelacrinites jasperensis*). Upper Banff Formation, 135 feet below the Banff-Rundle contact, Kinderhookian Series, Mississippian. Morro Creek, just south of Jasper-Edmonton highway, about 10 miles north of Jasper, Alberta. 7.6 mm axial by 7.6 mm transverse diameter.

Text fig. 48, pl. 45, fig. 12-14.

The specimen has collapsed; the distal interambulacrals and ambulacrals have slipped under the proximal plates of the rim. The oral and anal plates are partially disrupted, but other thecal elements appear to be only slightly disturbed. A few rim plates are missing from the right side of the theca.

Discussion

The relative size of the thecal structures in the holotype of *Postibulla jasperensis* suggests that the specimen is not fully developed. The oral area, anal structure, and peripheral rim are proportionately larger than is common in adult edrioasteroids. However, the combined ambulacral-interambulacral areas dominate the theca, and ambulacral curvature has developed, which suggests that the specimen is at least a young adult.

The presence of a small posterior oral protuberance seems to link the specimen to species of *Postibulla*. However, the single biseries of ambulacral coverplates and the relatively few oral and hydropore structure plates contrast with both the generic and even the familial and subordinal taxobases. Thus the specimen could represent a young individual of a very large species in which additional sets of coverplates and more oral-hydropore series plates would have appeared later in ontogeny. More likely is the interpretation that this form represents a specialized genus in which all but the primary ambulacral coverplates have been suppressed along with a corresponding reduction in number of orals and hydropore plates.

RANGE AND OCCURRENCE: Banff Formation, Kinderhookian Series, Mississippian, of the Jasper area, Alberta.

(?)*Postibulla alpenensis* (Bassler), 1936
Plate 45, fig. 11

1936 *Lepidodiscus alpenensis* Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 20, pl. 3, fig. 3.

1943 *Lepidodiscus alpenensis* Bassler, Bassler, R.S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 206.

Specimen

UMMP 17296. Holotype of *Postibulla alpenensis* (Bassler) (1936, p. 20, pl. 3, fig. 3, as *Lepidodiscus alpenensis*). Presque Isle division of the Long Lake Formation (Ferron Point Formation), Traverse Group, Erian Series, Middle Devonian. Quarry of the Alpena Portland Cement Company, Alpena, Michigan. 8.6 mm axial by 6.8 mm transverse diameter.

Description and discussion

The species is based on a single, poorly preserved specimen (pl. 45, fig. 11). The domal theca has collapsed and is laterally compressed. Most of the oral, hydropore, and ambulacral coverplates are jumbled, along with many interambulacrals and the anal plates. The five narrow ambulacra are curved, I-III contrasolar, IV-V solar. The distal part of a prominent posterior oral protuberance is preserved and is formed by two very large opposing plates, similar to those of *Postibulla keslingi*. The squamose imbricating plates of interambulacrum 2 are less disrupted than others. The anal plates are centrally separated and form a gaping opening in the center of the anal area. Approximately four or five circlets of plates form the peripheral rim.

Bassler (1936, p. 20) reported that the specimen "shows clearly four ambulacra curved to the left and the fifth, the right posterior, to the right, as well as the strongly imbricating plates of typical *Lepidodiscus*." The small thecal size was cited as diagnostic at the species level. However, ambulacrum IV, which is very poorly preserved, appears to curve solarly, not contrasolarly. Thus the ambulacral curvature and other interpretable thecal features, particularly the posterior oral protuberance, suggest that this specimen belongs to *Postibulla*. Unfortunately, the critical ambulacral coverplate pattern, the hydropore structure, and the oral area plating are too poorly preserved to allow definition of specific characters.

Genus *Discocystis* Gregory, 1897

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

1858 *Agelacrinus* Vanuxem, Hall, J., Iowa Geol. Surv. Rept., 1855-1857, v. 1, pt. 2, Palaeontology: 696, pl. 25, fig. 18.

1883 *Echinodiscus* Worthen, A. H. and Miller, S. A., Geol. Surv. Illinois, v. 7, Geology and Palaeontology, sect. 2, Palaeontology of Illinois: 335.

1889 *Echinodiscus* Worthen and Miller, Miller, S. A. [*partim*], North American Geology and Palaeontology, Cincinnati: 241.

1897 *Discocystis* Gregory, J. W., Geol. Soc. London, Quart. Jour. 53: 131.

1897 *Ageladiscus* Miller, S. A. [*partim*], Second Appendix to North American Geology and Palaeontology, Cincinnati: 734.

1901 *Discocystis* Gregory, Clarke, J. M. [*partim*], New York State Mus., Bull. 49 (2): 182-198.

1904 *Discocystis* Gregory, Klem, M. J. [*partim*], St. Louis Acad. Sci., Trans. 14: 73; *Echinodiscus* Worthen and Miller, *idem*, *ibid*.: 73.

1935 *Discocystis* Gregory, Bassler, R. S. [*partim*], Smithsonian Misc. Coll. 93 (8): 8.

1936 *Discocystis* Gregory, Bassler, R. S. [*partim*], Smithsonian Misc. Coll. 95 (6): 21.

1938 *Discocystis* Gregory, Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 88.

1943 *Discocystis* Gregory, Bassler, R. S. and Moodey, M. W. [*partim*], Geol. Soc. America, Spec. Pap. 45: 200.

1944 *Discocystis* Gregory, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, pl. 49, fig. 19-20.

1958b *Discocystis* Gregory, Ehlers, G. M. and Kesling, R. V. [*partim*], Univ. Michigan, Contrib. Mus. Paleont. 14 (15): 271.

1966 *Discocystis* Gregory, Regnéll, G. [*partim*], *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U169, text fig. 113-3 (?), 128-3(?).

TYPE SPECIES: *Echinodiscus optatus* Worthen and Miller, 1883 = *Agelacrinus kaskaskiensis* Hall, 1858.

Diagnosis

Agelacrinitidae with: clavate theca; numerous oral plates; large hydropore protuberance separated from central oral rise; ambulacra long, narrow, curved, I-IV contrasolar, V solar, coverplates in three- or four-plate cyclic series; interambulacrals large, polygonal, tessellate; valvular anal structure with two circlets of plates.

Description

The genus *Discocystis*, as recognized here, is monotypic. Therefore, separation of generic and specific taxobases is uncertain. Features outlined in the above diagnosis are in part inferred to be of generic rank from taxobases established for related Agelacrinitidae genera.

Discussion of previous investigation

The status of the name *Discocystis* is problematic. Clarke (1901) recorded most of the revelant information. Hall (1858) described and illustrated *Agelacrinus kaskaskiensis* based upon a single specimen from the Chester Group, Mississippian, Kaskaskia, Illinois. The holotype (pl. 46, fig. 1-7) preserves the upper side of the oral surface, including the oral region, hydropore structure, five ambulacra (I-IV contrasolar, V solar), cyclic ambulacral coverplates, and large, polygonal, tessellate interambulacrals. As noted by Meek and Worthen (1868), only five ambulacra are present, not six as described by Hall.

> In 1883 Worthen and Miller introduced the generic term, *Echinodiscus*, with a single species, *E. optatus*, from the Chester limestone of Illinois. [The specimen illustrated is fragmentary, and exposes only part of the lower, pedunculate zone, and one section of the ambitus of a clavate theca.] Of itself it serves to define nothing, affording no clue either to generic or specific structures. As establishing either species or genus it is practically worthless. Notwithstanding this fact, the definition given of both species and genus is full and clear, describing all the main features of the theca and ambulacra. One cannot fail of conviction, nor therein be far from the truth, that in the preparation of this account the authors were relying mainly on the original specimen of *Agel. kaskaskiensis* Hall, which belonged to the Worthen collection. That *Ech. optatus* W. and M. is not the same thing as *A. kaskaskiensis* has not been proven, and every indication favors the presumption that it is. Sidelight is thrown on this proposition by two facts, viz., that in the description of *Echinodiscus* and *E. optatus*, the remotest reference to *A. kaskaskiensis* is avoided, and also that in the edition of Miller's *North American Geology and Palaeontology* (1889) next succeeding the date of Worthen and Miller's publication, *A. kaskaskiensis* is referred to *Echinodiscus*.
>
> (Clarke, 1901, p. 185-186.)

Gregory (February 1897) proposed *Discocystis* as a substitute term for *Echinodiscus*, which had been used twice before for other echinoderms (Leske, 1778, and d'Orbigny, 1854). Miller (1897) also noted this circumstance, and proposed the name *Ageladiscus*, but his work did not appear until October 1897 (Clarke, 1901, p. 187). Thus *Discocystis* has priority.

Subsequent to, and in agreement with, Clarke's 1901 analysis, *Discocystis optatus* (Worthen and Miller) has been recognized as a junior synonym for *Discocystis kaskaskiensis*. The occurrence of the type specimens of these two taxa lends support to Clarke's thesis; both specimens are from Chester Group limestones of southern Illinois. However, the etched and abraded holotype of *D. optatus* exposes only part of the lower pedunculate zone of the theca and one extremely etched ambulacral segment. The rather vague cyclic coverplate pattern appears to contain three plates, as in *D. kaskaskiensis*, but this is still uncertain (pl. 47, fig. 6-8). There now seems no compelling reason to consider it different from *D. kaskaskiensis*.

Previous accounts of *Discocystis* have been based upon specimens of *D. kaskaskiensis* and include the original diagnosis of *Echinodiscus*; and the type species is *D. kaskaskiensis*, of which *D. optatus* is a junior synonym.

The alternative approach would be to recognize *D. optatus* as a valid species, represented only by the fragmentary holotype; thus *Discocystis* would become a problematical genus represented only by its type species, *D. optatus*. This approach would require the proposal of yet another generic name for *D. kaskaskiensis*. Such proliferation of generic names, combined with restriction of *Discocystis* to an essentially meaningless species, would seem only to increase confusion.

RANGE AND OCCURRENCE: Chester Group, Mississippian of southern Illinois.

Discocystis kaskaskiensis (Hall), 1858

Text fig. 49, 50; plate 46, plate 47, fig. 1-8

1858 *Agelacrinus kaskaskiensis* Hall, J., Iowa Geol. Surv. Rept., 1855-1857, v. 1, pt. 2, Palaeontology: 696, pl. 25, fig. 18.

1860 *Agelacrinites kaskaskiensis* Hall, Chapman, E. J., Canadian Jour. Industry, Sci. and Art (n.s.), 5: 360-365.

1868 *Agelacrinites kaskaskiensis* Hall, Meek, F. B. and Worthen, A. H., Philadelphia Acad. Nat. Sci., Proc. 5: 357.

1873 *Agelacrinites kaskaskiensis* Hall, Meek, F. B. and Worthen, A. H., Geol. Surv. Illinois, v. 5, Geology and Palaeontology, pt. 2, Palaeontology of Illinois: 514-515.

1876 *Agelacrinus kaskaskiensis* Hall, Quenstedt, F. A., Petrefaktenkunde Deutschlands, Tübingen, 4 (12): 708.

1879 *Agelacrinites kaskaskiensis* Hall, Sladen, W. P., Geol. Soc. London, Quart. Jour. 35: 748-750.

1883 *Echinodiscus optatus* Worthen, A. H. and Miller, S. A., Geol. Surv. Illinois, v. 7, Geology and Palaeontology, sect. 2, Palaeontology of Illinois: 336-337, pl. 31, fig. 9.

1889 *Echinodiscus kaskaskiensis* (Hall), Miller, S. A., North American Geology and Palaeontology, Cincinnati: 241.

1894 *Echinodiscus kaskaskiensis* (Hall), Keyes, C. R., Missouri Geol. Surv. 4 (1): 133, pl. 18, fig. 3.

1901 *Discocystis kaskaskiensis* (Hall), Clarke, J. M., New York State Mus., Bull. 49 (2): 182-198, text fig. 1.

1904 *Echinodiscus kaskaskiensis* (Hall), Klem, M. J., St. Louis Acad. Sci., Trans. 14: 73.

1910 *Agelacrinus (Discocystis) kaskaskiensis* (Hall), Grabau, A. W. and Shimer, H. W., North American Index Fossils, Invertebrates, New York, 2: 373.

1936 *Discocystis kaskaskiensis* (Hall), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 21-22, pl. 1, fig. 4, pl. 1, fig. 5 (?), pl. 3, fig. 4-5 (?), [*non* 6], pl. 7, fig. 11(?).

1938 *Discocystis kaskaskiensis* (Hall), Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 88.

1943 *Discocystis kaskaskiensis* (Hall), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 200-201.

1944 *Discocystis kaskaskiensis* (Hall), Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, (?) pl. 49, fig. 19-20.

1958b *Discocystis kaskaskiensis* (Hall), Ehlers, G.M. and Kesling, R. V., Univ. Michigan, Contrib. Mus.Paleont. 14 (15):271.

1966 *Discocystis kaskaskiensis* (Hall), Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U169, text fig. 113-3(?), 128-3(?).

Diagnosis

A *Discocystis* with: large theca; numerous small oral plates, primary orals undifferentiated; large hydropore protuberance formed by several plates, including at least three large posterior plates.

Description

The clavate theca of *Discocystis kaskaskiensis* is large, with diameters of the gibbous upper oral surface reaching 50 mm.

The numerous oral plates, seen only in the crushed oral area of the holotype (text fig. 49A, pl. 46, fig. 3) are similar in size to the proximal ambulacral coverplates and appear to reflect the ambulacral coverplate pattern. Thus the oral series appears to grade distally into the proximal ambulacral series without apparent break, and this obscures the total number of orals present. The regularity of the oral plate arrangement has not been determined. Primary orals are not differentiated externally.

The hydropore structure lies distal to the central oral rise and extends from the axial midline of the theca postero-laterally along the proximal, posterior side of ambulacrum V (text fig. 49A). The structure has been observed only in the holotype, where it is partially disrupted and the upper ends of the plates have been extensively crushed (pl. 46, fig. 3). Apparently the 10 (or more) plates that form the structure extend upward and produce a high, large, elongate elevation. The elongate, slitlike hydropore extends along the summit. The posterior side is formed by three or four large plates that are apparently modified interambulacrals or multiple hydropore orals. The distal part of the anterior side of the structure is formed by the adradial ends of several proximal posterior coverplates of ambulacrum V. The proximal anterior part appears to be formed by several orals, but these apparently do not extend perradially to the transverse oral midline. The proximal, or left, end of the prominence is separated from the central oral rise by a deep groove. The right end of the structure appears to merge with the proximal part of ambulacrum V, although a shallow but distinct trough separates the two equally elevated zones.

The ambulacra are long, narrow, and curved, I-IV contrasolar, V solar (pl. 46, fig. 1, 2). Curvature is variable; it may be initiated near the proximal ends in some, whereas in others, long proximal sectors are straight. Distally the long ambulacra become concentric with the ambitus of the upper oral surface. Each extends along the distal edge of the adjacent ambulacrum, separated from it by only a few interambulacrals. The distal tip of ambulacrum V curves proximally, away from the ambitus, and extends into interambulacrum 5, where it ends near the left posterior side of the anal structure.

The ambulacral coverplate series is cyclic (text fig. 50A-C). Cycles on opposite sides of the perradial line alternate, offset by half a cycle length. The plates in each cycle form a single, wide, perradial point, yielding a broadly undulating, zigzag, perradial line. Small points formed along the perradial edges of the cycle plates superimpose fine serrations on the broad, perradial undulations.

Along most of the length of the ambulacra each cycle includes three plates (text fig. 50B). Large primary plates are central. Each has a wide adradial base and an angular perradial tip which extends across the midline of the ambulacrum to form the center of the cycle point. Secondary set plates lie adjacent to the proximal side of the primaries, and their perradial margins slope toward the adjacent distal primary plate of the cycle. Smaller than the primaries along most of the length of the ambulacra, proximally these secondaries become nearly equal in size to the primaries. The tertiary coverplates flank the distal sides of the primaries and perradially slope proximally toward the adjacent primary plate of the cycle. The tertiaries are consistently smaller than the secondaries.

Small, rhombic "quaternary" plates may be added to the cycles proximally (text fig. 50A). They are inserted at the tips of the broad perradial point of a cycle and lie either between the tips of the adjacent primary and secondary set plates, or are inserted into a small notch formed in the center of the perradial tip of the primaries. Their occurrence appears to be erratic, as they have been observed in only one ambulacrum of the holotype.

Primary coverplates are developed at the distal tip of each ambulacrum. The zone of insertion of the plates of the secondary set is separated from the ambulacrum tip by only two or three pairs of primary plates. Each secondary is inserted along the proximal, perradial margin of a primary. The tertiary coverplates are inserted along the distal, perradial margins of the primaries and do not appear until numerous sets of primaries and secondaries have formed. Thus the zone of tertiary plate insertion lies far from the distal tip of the ambulacra. Apparently it commonly lies in the most highly curved part, where the ambulacra become concentric with the ambitus of the upper oral surface. The supposed quaternary plates are formed only in the proximal parts of the ambulacra and are developed late in adult ontogeny.

The adradial ends of the coverplates are overlapped by the adjacent interambulacrals. The upper adradial edge of each coverplate is depressed along the zone of overlap; a nearly vertical cliff separates the upper external plate surface from the rounded, sloping, adradial end. Text fig. 49C depicts an oblique view of a large coverplate and shows the rounded margin, increased thickness, and slightly concave base of the adradial part of the plate.

The trough-shaped ambulacral floorplates are axially elongate and rectangular in plan view (pl. 46, fig. 8, 9). Their upper sides are centrally concave downward and form a deep, central, axial trough. The lateral margins of this upper surface slope slightly toward the trough to form a narrow articulation zone upon which rest the bases of the overlying coverplates. The inwardly convex lower sides of the floorplates bear large lateral nodes which project obliquely downward into the thecal cavity. Each plate develops at least one node on each lateral margin. Additional smaller prominences may also be developed occasionally. Contiguous floorplates meet along vertical sutures.

The interambulacrals on the upper surface of the theca are large, thick, polygonal plates and abut one another along vertical sutures (pl. 46, fig. 1–3, 8, 9). Distal to the ambulacra, below the ambitus of the upper oral surface, the interambulacrals become progressively thinner and more elongate concentric with the ambitus (pl. 47, fig. 1, 2, 7, 8). In a zone beginning approximately seven to ten plates below the ambitus, the plates are subrectangular, extremely thin, elongate, and imbricate; these form vertical columns that include tens to hundreds of plates. The plate columns form the long, extensible, pedunculate zone. Presumably a small peripheral rim was developed at the base of the pedunculate zone and flared outward against the substrate.

The valvular anal structure lies proximal to the center of interambulacrum 5 (text fig. 49B, pl. 46, fig. 7). The outer circlet plates overlap the alternate, inner circlet ones along tightly fitting, beveled margins. However, the zone of overlap is rather narrow and most of the width of the inner circlet plates is visible externally. A total of 12 to 14 triangular plates are included in the adult anal structure.

External plate surfaces are smooth, except for a minute pustulation reflecting the microstructure of the plates.

Specimens

ISM 10037. Holotype of *Discocystis kaskaskiensis* (Hall) (1858, p. 696, pl. 25, fig. 18, as *Agelacrinus kaskaskiensis*). Kaskaskia Formation, Chester Group, Mississippian. Near Kaskaskia, Randolph County, Illinois. A. H. Worthen Collection, No. X-129. 31 mm axial by 31.5 mm transverse diameter.

Text fig. 49A, B, 50B, C, pl. 46, fig. 1–7.

The holotype is a partially disrupted specimen which exposes only the upper side of the oral surface, above the ambitus. The oral region and hydropore structure are partially disrupted. Extensive crushing has removed the upper parts of these plates. All five ambulacra are visible, but the coverplates are well preserved only in isolated sectors of each. The medial sector of ambulacrum IV is completely obliterated. Upper surface interambulacrals are mostly disrupted; the best preserved are found in interambulacrum 1. The anal structure is missing the distal parts of several posterior plates. Thecal plates below the ambitus are apparently missing, unseen even in areas where the upper surface plates have been lost.

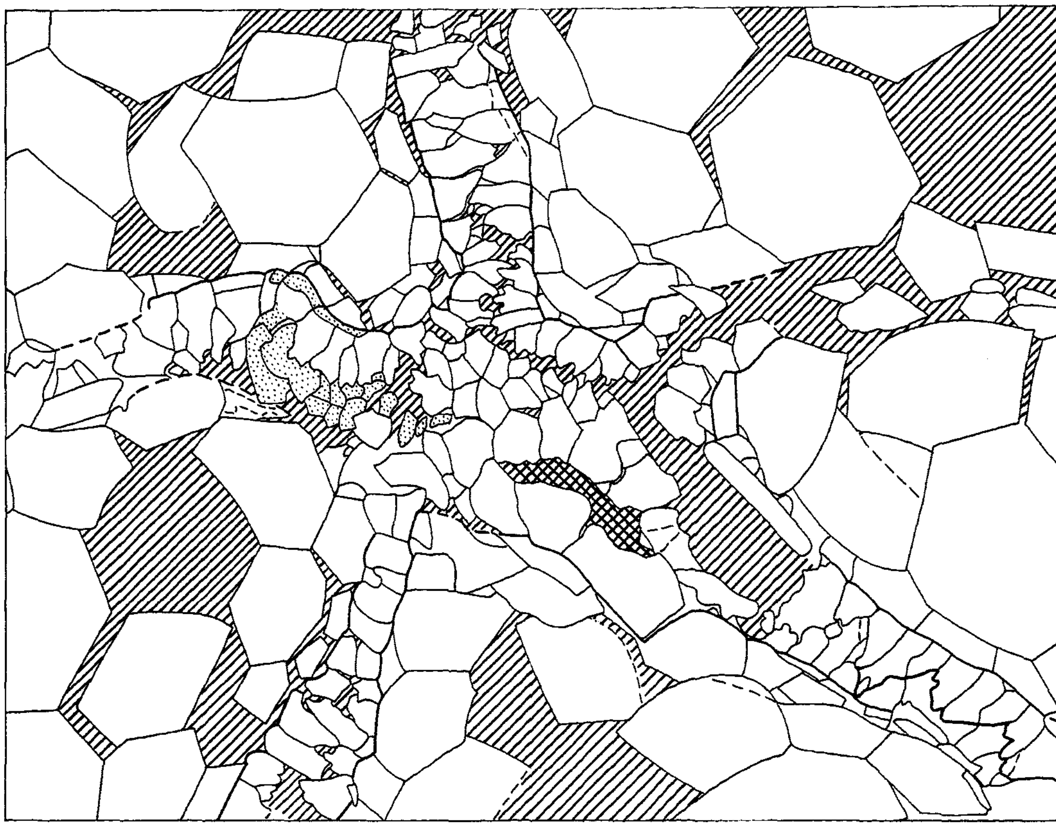
USNM S-3885. *D. kaskaskiensis*. Chester Group, Mississippian. Carter's Glade, Crittenden County, Kentucky. 44.9 mm greatest length.

Text fig. 50A, pl. 47, fig. 1–5.

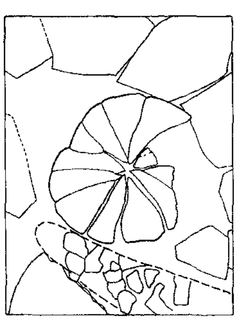
Text figure 49. *Discocystis kaskaskiensis* (Hall), 1858

A-B. Holotype, ISM 10037.
- A. Oral area and adjacent structures, (x 10), pl. 46, fig. 3. Plates in the left anterior oral area and proximal part of ambulacrum II, which have been depressed below the level of the surrounding elements, are marked by a dotted pattern.
- B. Anal area and adjacent structures, (x 5), pl. 49, fig. 7.

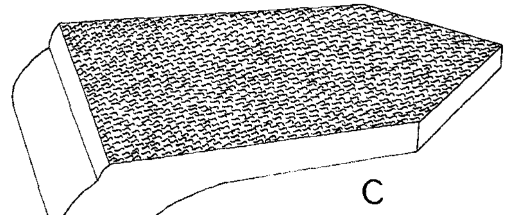
C. Reconstruction of a primary set ambulacral coverplate, oblique lateral view.



A



B



C

The specimen is a fragment of a large individual that was originally at least 50 mm in diameter. It preserves the external surface of a narrow zone of upper oral surface plates which includes the distal parts of two ambulacra and a few adjacent interambulacrals. The upper oral surface plates originally proximal to this marginal strip are missing and this exposes the inner sides of the plates that form the lower thecal zone, below the ambitus. This part of the specimen includes both the larger, thick plates immediately below the ambitus which form the transition zone, and the proximal part of about nine columns of thin, elongate, imbricate plates of the pedunculate zone.

The proximal part of the longer ambulacral segment preserves three-plate cycles of coverplates, whereas the long distal part of this ambulacrum, concentric with the ambitus, includes only two plates per cycle, the primary and secondary set plates. The distal tip of this ambulacrum is not exposed. A few ambulacral floorplates are exposed in the second fragmentary ambulacrum. Each has the deep central trough and less steeply sloping upper lateral margins or articulation surfaces. The upper sides of the large, inner surface nodes of the floorplates extend laterally beyond the plate margins. In the central sector of the larger ambulacral segment, where adjacent interambulacrals are missing, these nodes appear to be enlarged distally to form a broad support for the overlying inner sides of the interambulacrals.

USNM S-3883. *D. kaskaskiensis?* Stratigraphic and geographic occurrence unknown. (Label with specimen suggests that it may be from the St. Genevieve Limestone, Chester Group, Mississippian, near Huntsville, Alabama, but the matrix resembles that of the holotype from Kaskaskia, Illinois.) 44.2 mm axial by 26.4 mm transverse diameter.

Pl. 46, fig. 8, 9.

This fragmentary specimen exposes part of the inner side of the upper oral surface of a large individual. Preserved structures include: the oral frame and stone canal passageway; the proximal parts of ambulacra IV and V and about half of ambulacra I, II, and III; the proximal parts of the interambulacra, 2 and 5 the most complete; and most of the anal structure. The anterior tip of the specimen preserves the external surface of a few plates distal to the ambulacra; these hide the distal end of ambulacrum III. Siliceous beekite appears to have sporadically replaced some thecal plates.

This specimen is tentatively assigned to *D. kaskaskiensis*, although the ambulacral coverplates and other external oral surface features necessary for confirmation are not exposed. The inner surface structures of all of the clavate Agelacrinitidae are inadequately known, and thus cannot be used for specific identifications. The inner oral-ambulacral series structures of this specimen closely resemble those found in *Lepidodiscus laudoni*. But in contrast with that species, here the polygonal interambulacrals appear to be thicker, and the anal structure suggests that wide central sections of the inner circlet plates are exposed on the external oral surface. Both these features agree with the holotype of *Discocystis kaskaskiensis* and suggest that the specimens are conspecific. The following description of the inner surface features seen in this specimen is presented here rather than in the species description because of possible misidentification of the specimen.

The oral frame and stone canal passageway structures are somewhat obscure, thus their description is tentative. The large, transversely elongate, ovate oral frame underlies the oral area. It surrounds the large oval central lumen which extends from the proximal ends of the ambulacral tunnels directly downward, opening into the thecal cavity below. The frame is formed by the proximal floorplate of each ambulacrum, which is expanded both inwardly and laterally. The frame may also include intrathecal extensions of some oral area covering plates. The anterior half of the frame is semicircular, with laterally attenuated extremities. It is formed by the enlarged proximal floorplates of ambulacra II, III, and IV. If intrathecal extensions from the overlying oral plates participate in the formation of the two anterior interradii, they are obscure in this specimen. The arcuate posterior side of the frame is formed by the proximal floorplates of ambulacra I and V, and perhaps intrathecal parts of overlying posterior oral plates. The anterior edges of the two posterior floorplates are wide and meet the two lateral anterior floorplates of the frame along a wide zone of contact. This wide lateral contact zone produces the lateral attenuations of the frame. Intrathecal extensions do not participate in the formation of these two lateral frame interradii.

The two posterior floorplates apparently are not in contact across the posterior side of the frame and leave

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Text figure 50. *Discocystis kaskaskiensis* (Hall), 1858

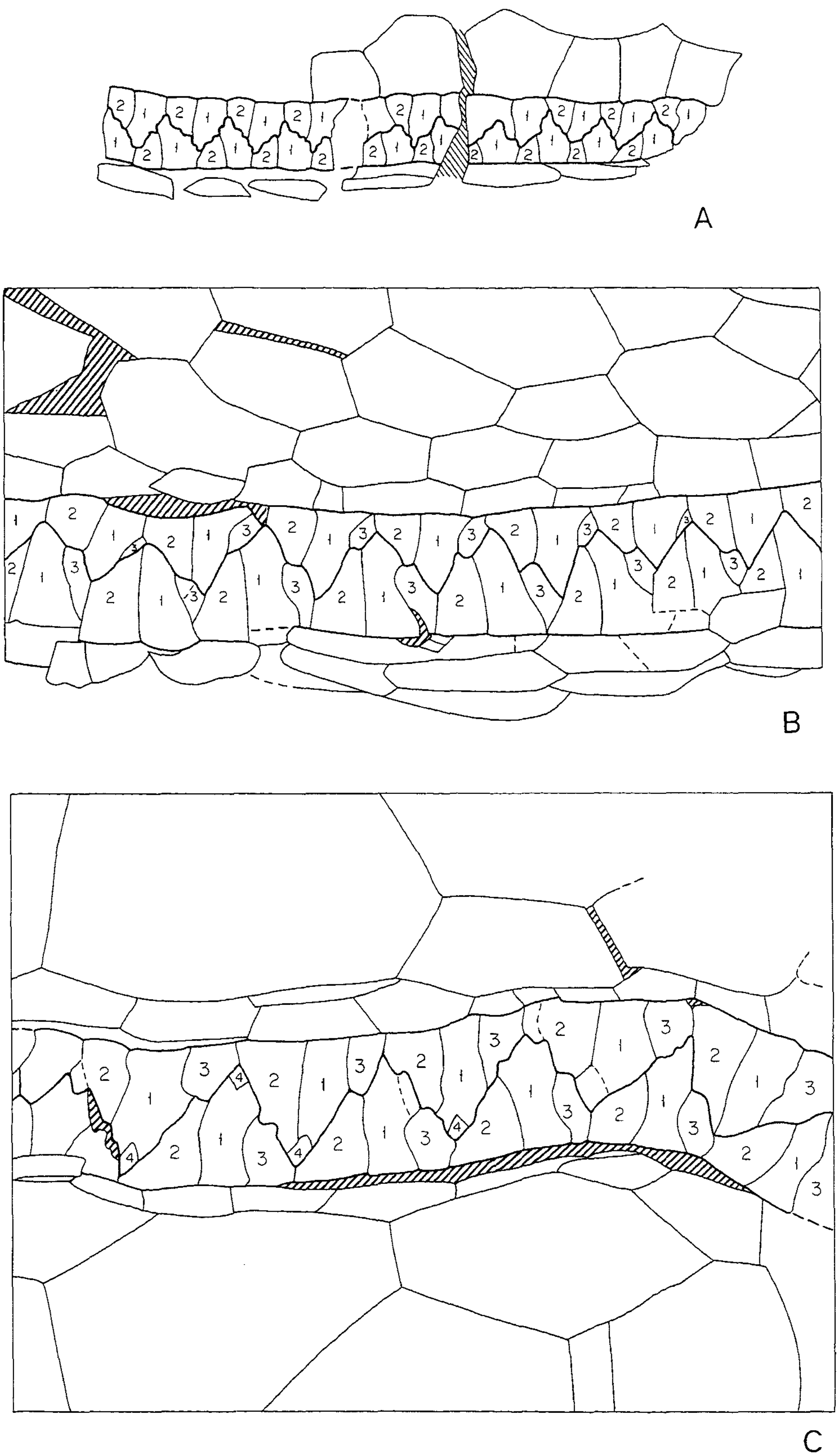
A. Segment of ambulacrum, USNM S-3885, (x 10), pl. 47, fig. 3. Proximal end of segment is to the left.

B-C. Holotype, ISM 10037.

B. Segment of ambulacrum III, (x 20), pl. 46, fig. 4. Proximal end of segment is to the left.

C. Segment of ambulacrum V, (x 20), pl. 46, fig. 6. Proximal end of segment is to the left.

1, primary set ambulacral coverplate; 2, secondary set ambulacral coverplate; 3, tertiary set ambulacral coverplate; 4, ?quaternary set ambulacral coverplate.


A
B
C

a large gap which laterally connects the central oral lumen to the thecal cavity beneath interambulacrum 5. The gap appears to be offset toward the right side of the frame (left side seen from below) and it distally intersects the inner end of the stone canal passageway. This gap exposes the inner ends of the posterior oral covering plates which thus appear to form the upper part of the posterior side of the frame, above the posterior gap. It is not impossible that this posterior frame gap is preservational and that the posterior floorplates originally extended straight across the posterior side.

The stone canal passageway extends into the thecal cavity along the right posterior margin of the oral frame (left as viewed from below). The inner end of the passageway appears to intersect the distal end of the supposed posterior frame gap. The diameter of the entire passageway appears to be large and only slightly increases inwardly. The structure is formed by eight or nine elements, which apparently are intrathecal parts of the hydropore structure plates and parts of the adjacent ambulacral floorplates.

ISGS (ISM) 2478. *Discocystis kaskaskiensis;* the holotype of *Echinodiscus optatus* Worthen and Miller (1883, p. 336-337, pl. 31, fig. 9). Chester Group, Mississippian. Pope County, Illinois. A. H. Worthen Collection. 24 mm greatest length by 21.2 mm wide.

Pl. 47, fig. 6-8.

This fragmentary specimen, imbedded in matrix, exposes about half of the lower pedunculate zone plates and a few interambulacrals of the transition zone below the ambitus. Along the ambital edge of the specimen one segment of an ambulacrum is exposed. The entire specimen is deeply etched and abraded, which obscures the exact location of many of the plate boundaries. The coverplates of the small ambulacral segment appear to be a three-plate cyclic series.

Discussion of previous investigation

Hall (1858, p. 696) described *Agelacrinus kaskaskiensis* as: discoidal; ambulacra six, radiating from a plated oral area; ambulacral coverplates subcuneiform, perradially "crenulate or poriferous," interlocking and forming a single alternating biseries, or with smaller intermediate plates; interambulacrals polygonal, flat. The accompanying drawing depicts six ambulacra, all curved contrasolarly, and tessellate interambulacrals.

Meek and Worthen (1969, p. 357), after restudying the holotype, noted that Hall's anomalous sixth ambulacrum "is the incurved extremity of the dextral [solar] right posterior ray." They cited the large, polygonal, tessellate interambulacrals as the "important character" separating *Agelacrinites kaskaskiensis* from their new Mississippian species, *Agelacrinites (Lepidodiscus) squamosus,* which has squamose, imbricate interambulacrals.

Worthen and Miller (1883) expanded and emended earlier descriptions of *Discocystis kaskaskiensis* under the name *Echinodiscus optatus*. The upper oral surface features were apparently described from Hall's holotype, and the features of the pedunculate zone of the lower surface from the fragmentary holotype of *Echinodiscus optatus* (= *Discocystis kaskaskiensis*; see generic discussion). Worthen and Miller (1883, p. 335) termed the thecal shape discoid, but also noted the "border . . . of narrow rim plates elongated in the direction of the circumference, and passing around upon the underside, forming a cylindrical nonsessile rim" [*i.e.*, the pedunculate zone of the theca, as the basal peripheral rim is missing]. They also reported that the ambulacra arise in three radii—one anterior and two lateral—each lateral radius bifurcating a short distance from the oral pole; ambulacral coverplates "composed on each side [of the perradial line] of alternately longer [primary] and shorter [secondary and tertiary] plates which interlock at the angular arch [perradial line], with each other and with smaller intercalated plates" [? irregular quaternaries, or tertiaries]; and "mouth" [oral area] central or subcentral, covered by numerous "larger and smaller" plates, supported internally by other elements [oral frame plates].

Miller (1889) listed Hall's *Agelacrinites kaskaskiensis* as a second species of *Echinodiscus,* along with *E. optatus*. The preempted name *Echinodiscus* was replaced by *Discocystis* Gregory (1897). Most subsequent works have referred to the species as *Discocystis kaskaskiensis* (Hall).

Although commonly cited in later works, only two papers added new data about *D. kaskaskiensis*. The first is Clarke's (1901) interpretation of the confused taxonomy in earlier works (see generic discussion). In the second paper, Bassler (1936) "corrected" Hall's (1858) drawing of the *D. kaskaskiensis* holotype and showed ambulacrum V curved solarly, with the distal tip extending back toward the oral area. He also refigured the original drawing of *Echinodiscus optatus* and described the specimen as conspecific with *Discocystis kaskaskiensis*. Moreover, Bassler figured four new specimens listed as *D. kaskaskiensis*: (1) (1936, pl. 3, fig. 4) an adult edrioasteroid, present location unknown, which exposes oral surface features similar to *D. kaskaskiensis*; however, the coverplate pattern cannot be determined from the illustration, and thus identification is questionable; (2) (1936, pl. 3, fig. 5) a broken specimen with only four ambulacra, present location unknown; the illustration suggests that the individual may be a *Lepidodiscus laudoni* (Bassler) (1936); (3)

(1936, pl. 3, fig. 6; USNM S-3884) a *Lepidodiscus laudoni* [see pl. 49, fig. 7-12]; (4) (1936, pl. 7, fig. 11) the collapsed pedunculate zone of a clavate edrioasteroid, perhaps a *D. kaskaskiensis*, present location unknown. Bassler correctly described the ambulacral floorplates as uniserial, although his conclusion was based upon a specimen (USNM S-3884) which is a *Lepidodiscus laudoni*.

Discussion

Discocystis kaskaskiensis is here described from four specimens, only two of which are identified with certainty. Externally, the plating of the oral area and hydropore structure remain inadequately described. Moreover, the cyclic ambulacral coverplate sequence commonly includes three plates, but a fourth proximal set, seen only in one ambulacrum of the holotype, suggests that development may be incomplete in this specimen. The holotype, about 31 mm in diameter, is significantly smaller than the projected 50 mm diameter of specimen USNM S-3885. Unfortunately, only distal parts of the ambulacra are preserved in the larger specimen.

The internal structures of *D. kaskaskiensis* are also inadequately represented in available specimens. The single individual which exposes the oral frame, the stone canal passageway, and the inner surfaces of ambulacral floorplates eludes positive identification. Moreover, the inner surface of the ambulacral coverplates has not been observed. However, the fine serrations developed along the perradial ends of the coverplates may indicate the presence of multiple intra-ambulacral extensions on the ambulacral tunnel surfaces of the coverplates.

RANGE AND OCCURRENCE: Chester Group, Mississippian of Illinois and Kentucky.

Genus *Lepidodiscus* Meek and Worthen, 1868

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

1868 *Lepidodiscus* Meek, F. B. and Worthen, A. H., Philadelphia Acad. Nat. Sci., Proc. 5: 357-358.

1873 *Lepidodiscus* Meek, F. B. and Worthen, A. H., Geol. Surv. Illinois, v. 5, Geology and Palaeontology, pt. 2, Palaeontology of Illinois: 513-515, pl. 16, fig. 1.

1879 *Lepidodiscus* Meek and Worthen, Sladen, W. P. [*partim*], Geol. Soc. London, Quart. Jour. 35: 749-750.

1883 [*non*] *Echinodiscus* Worthen, A. H. and Miller, S. A., Geol. Surv. Illinois, v. 7, Geology and Palaeontology, sect. 2, Palaeontology of Illinois: 335.

1891 *Echinodiscus* Worthen and Miller, Miller, S. A. [*partim*], Geol. Surv. Indiana, 17th Ann. Rept. (adv. pub.): 76, pl. 12, fig. 16.

1892b *Echinodiscus* Worthen and Miller, Miller, S. A., Geol. Surv. Indiana, 17th Ann. Rept.: 686, pl. 12, fig. 16.

1896b [*non*] "*Lepidodiscus* Hall," Haeckel, E., Die Amphorideen und Cystoideen, Leipzig, 1: 113-114.

1897 (Feb.) [*non*] *Discocystis* Gregory, J. W., Geol. Surv. London, Quart. Jour. 53: 131.

1897 (Oct.) *Ageladiscus* Miller, S. A. [*partim*], Second Appendix to North American Geology and Palaeontology, Cincinnati: 734.

1901 *Lepidodiscus* Meek and Worthen, Clarke, J. M. [*partim*], New York State Mus., Bull. 49 (2): 182-198; *Discocystis* Gregory, *idem* [*partim*], *ibid.*: 182-198; *Agelacrinites* Vanuxem, *idem* [*partim*], *ibid.*: 195-196, fig. 4-6.

1904 *Echinodiscus* Worthen and Miller, Klem, M. J. [*partim*], St. Louis Acad. Sci., Trans. 14: 73-74.

1935 *Lepidodiscus* Meek and Worthen, Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 8.

1936 *Lepidodiscus* Meek and Worthen, Bassler, R. S. [*partim*], Smithsonian Misc. Coll. 95 (6): 20, pl. 1, fig. 17; *Discocystis* Gregory, *idem* [*partim*], *ibid.*: 21, pl. 3, fig. 7-8.

1938 *Lepidodiscus* Meek and Worthen, Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 123.

1943 *Lepidodiscus* Meek and Worthen, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 206; *Discocystis* Gregory, *idem* [*partim*], *ibid.*: 201.

1944 *Lepidodiscus* Meek and Worthen, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, pl. 49, fig. 21.

1958b *Lepidodiscus* Meek and Worthen, Ehlers, G. M. and Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 14 (15): 265-276; *Discocystis* Gregory, *idem* [*partim*], *ibid.*: 265-276, pl. 1, fig. 1-4, pl. 2, fig. 1-2, pl. 3.

1958 *Lepidodiscus* Meek and Worthen, Kesling, R. V. and Ehlers, G. M. [*partim*], Jour. Paleont. 32 (5): 923-932, text fig. 1, pl. 119, fig. 1-3, pl. 120, fig. 1-6.

1960 *Discocystis* Gregory, Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 155, text fig. 4, pl. 3, fig. 1-3; *Lepidodiscus* Meek and Worthen, *idem, ibid.*: 155-157, text fig. 5, pl. 2, fig. 1-2.

1966 *Lepidodiscus* Meek and Worthen, Regnéll, G. [*partim*], *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U169, text fig. 120-6a, 130-4; *Discocystis* Gregory, *idem* [*partim*], *ibid.*: U169, text fig. 120-6a, 129-3, 130-5.

1968 *Discocystis* Gregory, Strimple, H. L. [*partim*], Iowa Acad. Sci., Proc. 73: 260-262, text fig. 1-4.

TYPE SPECIES: *Agelacrinites (Lepidodiscus) squamosus* Meek and Worthen, 1868.

Diagnosis

Agelacrinitidae with: theca highly convex and domal, or clavate; oral plates numerous, reflecting proximal coverplate pattern, primary orals undifferentiated; large, elongate hydropore protuberance separated from central oral rise, posterior side formed by many plates, anterior side formed by adradial ends of elongate orals; long ambulacra curved, I-IV contrasolar, V solar, coverplates forming alternating six-plate cycles; interambulacrals squamose, imbricate or polygonal, tessellate; valvular anal structure plates alternating as inner and overlapping outer circlet members.

Description

Lepidodiscus Meek and Worthen is represented by species of large size. Species with a clavate theca include an elongate, downwardly constricting pedunculate zone (below the ambitus of the upper gibbous region) formed by many columns of numerous, thin, elongate, subrectangular, imbricate plates. Both domal and clavate species develop a peripheral rim composed of several circlets of geniculate plates. The rim forms the margin of the upper oral surface in domal forms, whereas it is located at the base of the pedunculate zone in clavate species.

The transversely elongate oral region includes numerous plates. These imperfectly mimic the cyclic ambulacral coverplates in shape, size, and distribution. Thus, distally they appear to grade into the proximal ambulacrals without a distinct break and thereby obscure the total number of orals present. Primary orals are differentiated externally. Lateral orals greatly exceed the anteriors in number and produce the transversely elongate oral area outline.

The large, transversely elongate hydropore structure lies along the right posterior margin of the oral area. Participating plates are upturned to form the steep-sided, highly elevated protuberance which rises abruptly from the posterior edge of the central oral rise. Numerous plates, probably modified interambulacrals, form the posterior side of the elevation. The proximal part of the anterior side of the protuberance is formed by the adradial ends of elongate orals. These perradially extend to the transverse oral midline. The distal part of the anterior side of the prominence includes the adradial ends of several proximal, posterior coverplates of ambulacrum V. The elongate, slitlike hydropore opens along the junction between the anterior and posterior plates and extends along the summit of the protuberance.

The ambulacra are long and moderately narrow. Distally they become concentric with the margin of the theca, and commonly each extends distally along the distal edge of the adjacent ambulacrum and is separated from it by only a few interambulacrals. However, the distal part of ambulacrum V lies proximal to the distal part of I, with the tip curved proximally and ending near the posterior edge of the anal structure.

The ambulacral coverplates form six-plate cycles. Cycles on opposite sides of the perradial line alternate, offset by half the width of a cycle, and thereby produce a broadly undulating, zigzag perradial line. Individual cycle plates form small, discrete perradial points, and these superimpose a fine serration upon the broad perradial line undulations.

The uniserial ambulacral floorplates are trough-shaped; the convex-inward, inner surfaces bear large lateral nodes. The concave-downward, central part of the upper sides of these floorplates is flanked by gently sloping lateral margins; these are the articulation zones upon which the bases of the overlying coverplates rest. Contiguous floorplates abut one another along vertical sutures in some species. In others the sutures are oblique, with the proximal end of each floorplate broadly overlapping the distal margin of the next.

Interambulacral plates are squamose and imbricate in domal species, polygonal and tessellate to slightly imbricate in clavate forms.

The valvular anal structure includes an inner and an outer circlet of triangular to subtriangular plates. Outer circlet plates laterally overlap alternate inner circlet ones along tightly fitting, beveled edges.

The prominent peripheral rim is formed by six to eight circlets. Proximal circlet plates are the largest: distal circlet plates gradually diminish in size outward. The proximal two to four circlets are formed by plates externally elongate concentric with the thecal margin; the distal circlet plates are elongate radially. All but the tiny outer elements are geniculate.

External plate surfaces are smooth in all known species, except for the fine pustulation reflecting the plate microstructure.

Discussion of previous investigation

Meek and Worthen (1868) introduced *Lepidodiscus* as a subgeneric term for *Agelacrinites (Lepidodiscus) squamosus*. In describing the major thecal features of the species, they cited its squamose interambulacrals and the direction of ambulacral curvature as contrasting with the polygonal, tessellate interambulacrals and the differing ambulacral curvature of the type species of *Agelacrinites*, *A. hamiltonensis*, (as described by Hall). "It therefore certainly seems to us doubtful whether species differing in two such important characters as these are strictly congeneric. If they are not, then a new generic name should be applied to our species, . . . *Lepidodiscus* . . . At least we should think they ought to be separated subgenerically" (Meek and Worthen, 1868, p. 358). Their 1868 paper was republished in 1873 with the addition of a detailed line drawing of the holotype of *L. squamosus*.

Lepidodiscus was occasionally used as a subgenus (Hall, 1872; Miller, 1889; Grabau and Shimer, 1910), but most authors have used it at the generic level. Hall (1871, 1872) and many other authors transferred Ordovician species, including *Isorophus cincinnatiensis* (Roemer) and *Carneyella pilea* (Hall), from *Agelacrinites* to *Lepidodiscus* and thereby introduced strikingly different morphological characters into the generic descriptions. Foerste (1914, 1917) ended this practice by noting the obvious differences between the Ordovician forms and the Mississippian type species of *Lepidodiscus*, and by describing new genera for the Ordovician species.

New species have been occasionally assigned to *Lepidodiscus* (*e.g.*, *L. alleganius* Clarke, 1901, *L. alpenensis* Bassler, 1936). However, Meek's and Worthen's (1868) diagnosis (ambulacra I-IV contrasolar, V solar, interambulacrals squamose, imbricate) was used without modification until Kesling and Ehlers (1958) published a detailed account of the holotype of *Lepidodiscus squamosus*, which included description of the oral area plating, the hydropore structure, and the complex ambulacral coverplate cycles. Ehlers and Kesling (1958) redescribed the type specimens of *Discocystis laudoni* and reported that they differed from *Lepidodiscus squamosus* only in the nature of the interambulacral plates. Judging ambulacral coverplate pattern to be of major taxonomic importance, they questioned the use of squamose-imbricate versus polygonal-tessellate interambulacrals as a generic taxobasis for *Lepidodiscus*.

In agreement with Ehlers and Kesling (1958), *Discocystis laudoni* is here included in *Lepidodiscus*. The generic description has been modified to include (a) both clavate and domal thecae, and (b) both squamose-imbricate and polygonal-tessellate interambulacrals. The structure of the oral area and hydropore and the disposition of the ambulacral coverplates are now considered generic taxobases.

Several species other than those recognized here have been referred to *Lepidodiscus* as defined by Meek and Worthen. Among these are the following European species which are excluded from this investigation: *Lepidodiscus lebouri* Sladen (1879), *Lepidodiscus ephraemovianus* Bogolubov) (1926) [= *Agelacrinites ephraemovianus*], *Lepidodiscus fistulosus* Anderson (1939) [= *Anglidiscus fistulosus* (Anderson) according to Regnéll, 1950], *Lepidodiscus milleri* Sharman and Newton (1892). Published accounts of these species suggest that most (probably all) of them do not comply with the restricted generic diagnosis for *Lepidodiscus* presented here.

Discussion

Lepidodiscus includes species showing variability in three important characters that are constant in related genera. Most obvious is the inclusion of both domal and clavate thecae. Each form develops a distal peripheral rim, but the clavate theca includes an elongate, downwardly constricting zone below the ambitus. The numerous, thin, subrectangular plates which form the pedunculate zone appear to have no homolog in domal species. The second important variable is the occurrence of squamose, imbricate interambulacrals in domal forms, in contrast with the polygonal, tessellate interambulacrals of the upper oral surface of clavate types. Finally, the uniserial ambulacral floorplates are believed to be imbricate in domal forms, whereas they abut one another along vertical sutures in clavate species. Imbricate versus abutting floorplates is a familial taxobasis in the Lebetodiscina. Floorplate disposition is inadequately known throughout the Agelacrinitidae, but in all other species where observed, the floorplates abut along vertical sutures. Thus floorplate structure may have more taxonomic importance than it has received in this analysis of *Lepidodiscus*, which suggests further subdivision of the species here included in *Lepidodiscus*, or even eventually room for new genera.

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

Lepidodiscus squamosus Meek and Worthen, 1868

Text fig. 51; plate 47, fig. 9, 10, plate 48

1868 *Agelacrinites (Lepidodiscus) squamosus* Meek, F. B. and Worthen, A. H., Philadelphia Acad. Nat. Sci., Proc. 5: 357-358.

1873 *Agelacrinites (Lepidodiscus) squamosus* Meek, F. B. and Worthen, A. H., Geol. Surv. Illinois, v. 5, Geology and Palaeontology, pt. 2, Palaeontology of Illinois: 513-515, pl. 16, fig. 1.

1879 *Lepidodiscus squamosus* Meek and Worthen, Sladen, W. P., Geol. Soc. London, Quart. Jour. 35: 749-750.

1889 *Agelacrinus squamosus* Meek and Worthen, Miller, S. A., North American Geology and Palaeontology, Cincinnati: 222.

1899 *Agelacrinites squamosus* Meek and Worthen, Jaekel, O., Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 51.

1901 *Lepidodiscus squamosus* Meek and Worthen, Clarke, J. M., New York State Mus., Bull. 49 (2): 182-198; *Agelacrinites beecheri* Clarke, J. M., *ibid.*: 195-196, text fig. 4-6.

1910 *Agelacrinus (Lepidodiscus) squamosus* Meek and Worthen, Grabau, A. W. and Shimer, H. W., North American Index Fossils, Invertebrates, New York, 2: 473.

1914 *Agelacrinites beecheri* Clarke, Foerste, A. F., Denison Univ., Sci. Lab. Bull. 17 (art. 14): 417, pl. 1, fig. 2.

1936 *Lepidodiscus squamosus* Meek and Worthen, Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 20, pl. 1, fig. 17.

1938 *Lepidodiscus squamosus* Meek and Worthen, Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 123.

1943 *Lepidodiscus squamosus* Meek and Worthen, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 207; *Lepidodiscus beecheri* (Clarke), *idem*, *ibid.*: 206-207.

1944 *Lepidodiscus squamosus* Meek and Worthen, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, pl. 49, fig. 21.

1958b *Lepidodiscus squamosus* Meek and Worthen, Ehlers, G. M. and Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 14 (15): 265-276.

1958 *Lepidodiscus squamosus* Meek and Worthen, Kesling, R. V. and Ehlers, G. M., Jour. Paleont. 32 (5): 923-932, text fig. 1, pl. 119, fig. 1-3, pl. 120, fig. 1-6.

1960 *Lepidodiscus squamosus* Meek and Worthen, Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 155-157, text fig. 5, pl. 2, fig. 1-2.

1966 *Lepidodiscus squamosus* Meek and Worthen, Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U169, text fig. 130-4, 120-6a′.

Diagnosis

A *Lepidodiscus* with: large, highly elevated, domal theca; ambulacral floorplates imbricate; interambulacrals squamose, imbricate.

Description

The theca of *Lepidodiscus squamosus* Meek and Worthen reaches at least 45 mm in diameter and was highly convex, with the oral surface nearly hemispherical before thecal collapse.

The oral area is formed by numerous plates. Text fig. 51B presents a tentative interpretation of oral area plating in the holotype, differentiating between plate boundaries (solid lines) and secondary fractures (dashed lines). Primary orals are not differentiated externally from other orals. Distally the oral plates reflect the pattern of the proximal, cyclic, ambulacral coverplate series and the orals appear to grade distally into the ambulacral sequence without a distinct break. Oral plate size and shapes are similar to the ambulacral coverplates and include large, intermediate, and small elements. Approximately 30 lateral orals and seven or eight anteriors are included. The relatively numerous lateral orals which lie proximal to the lateral bifurcation plates produce the pronounced transverse elongation of the area.

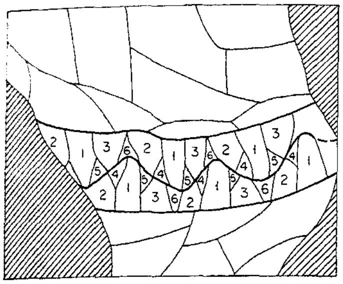
The hydropore structure (text fig. 51B, pl. 48, fig. 1) extends along the right posterior half of the oral region and the proximal posterior margin of ambulacrum V. Participating plates are flexed upward and form the steep, nearly vertical sides of the protuberance. The posterior side of the structure is formed by six or more plates. These may be interpreted as multiple hydropore orals that correspond to the single large hydropore oral found in some edrioasteroid species, or as modified interambulacrals that have been incorporated into the oral sequence. The proximal part of the anterior side of the structure is formed by the adradial ends of elongate oral plates. These perradially reach the transverse oral midline. The distal part of the anterior side is formed by the adradial ends of proximal, posterior coverplates of ambulacrum V. All of the anterior side plates of the oral-ambulacral series are centrally depressed and form a trough between the hydropore protuberance and the elevated oral area and ambulacrum V. The hydropore opening appears to have been an arcuate slit that extended along the summit of the protuberance.

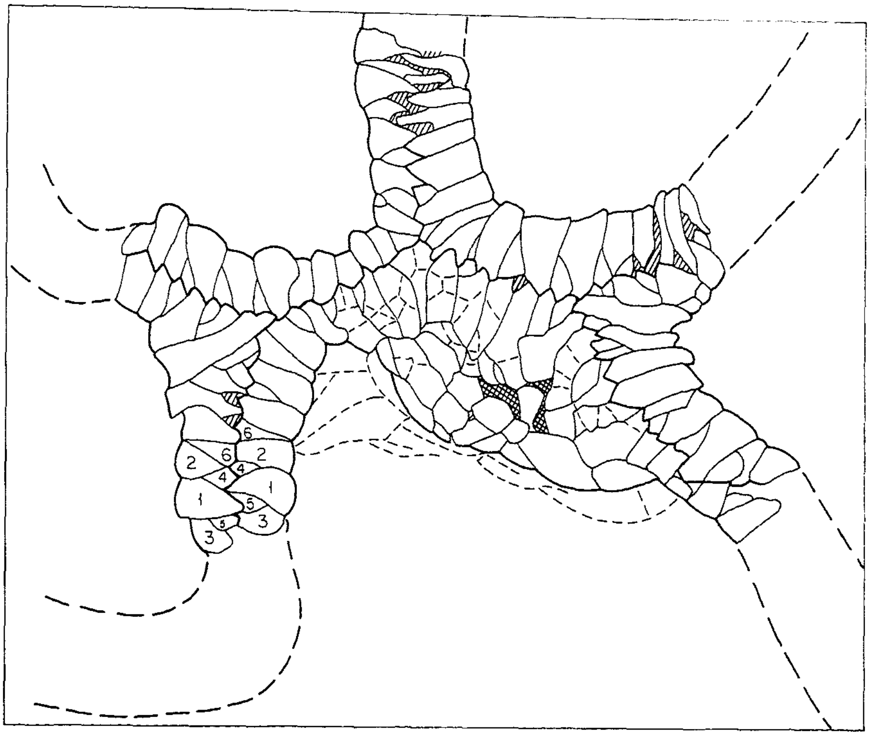
Distally, ambulacral curvature is consistent with the generic description: I-IV contrasolar, V solar. However, in the holotype the proximal parts of ambulacra I, II, III, and IV flex solarly before initiating the dominant contrasolar curvature. Proximally, ambulacrum V curves solarly, then slightly contrasolarly, before beginning the final distal solar curvature. Preservational distortion may account for some of these proximal sinuations in the holotype. In two other specimens, the proximal parts of the ambulacra appear to be essentially straight.

The ambulacral coverplate pattern is cyclic (text fig. 51A, B, pl. 48, fig. 1, 2, 6). The six-plate cycles on opposite sides of the perradial line alternate, offset by a length of half a cycle, and thereby produce the broadly undulating, zigzag perradial line.

As first described by Kesling and Ehlers [adjacent plates numbered consecutively]:

> the first [cycle plate] is short and subquadrate; the second is intermediate in length and irregularly hexagonal, its outer part subquadrate and its inner part acuminate; the fourth plate, the longest in the cycle, is subquadrate except that the inner corners are beveled; and the sixth plate is a mirror image of the second. The third plate is subrhombic, inserted between the second and fourth plates, with its inner apex forming a serration on the central line of the ambulacrum. The fifth plate is a mirror image of the third, lying on the opposite side of the long fourth plate. In most cycles the subrhombic third and fifth plates do not extend to





Text figure 51. *Lepidodiscus squamosus* Meek and Worthen, 1868

A. Proximal segment of ambulacrum III, YPM 24804-B, (x 10), pl. 48, fig. 6.
B. Holotype, oral area and adjacent structures, UMMP 5420, (x 10), pl. 48, fig. 1.
1 through 6 are the first through sixth sets of ambulacral coverplates, respectively.

the outside edge of the ambulacrum, but terminate along the side of the fourth plate.

(Kesling and Ehlers, 1958, p. 927-928)

In the proximal parts of the ambulacra the cyclic pattern is partially obscured by the differential enlargement of the cycle plates, and perhaps also occasionally by the insertion of irregular additional plates. Extraneous plates may also occur occasionally in the highly curved, medial ambulacral zones.

The distal tips of the ambulacra are too poorly preserved in specimens of *L. squamosus* to determine the sequence of coverplate insertions with certainty. It is probably similar to that of *L. laudoni,* which has a six-plate cycle nearly identical to that of *L. squamosus*. It appears that Kesling's and Ehlers' consecutive plate numbering corresponds to the sets of cyclic plates as follows: primary set plate = their fourth plate; secondary = their second; tertiary = their sixth; quaternary = their third; quintary = their fifth; and the sixth set plate = their first plate.

The intra-ambulacral surfaces of the coverplates have not been directly observed in *L. squamosus*. However, in extremely eroded sections of the holotype, the centers of the perradial ends of the coverplates appear to be thicker than the lateral edges and suggest the presence of bladelike intra-ambulacral extensions. Adradially, the coverplates appear to end adjacent to the lateral margins of the underlying floorplates, without development of intrathecal extensions.

The coverplates that form each cycle appear to be tightly sutured together laterally. It is unclear whether these sutures are vertical or oblique. Thus smaller plates of the cycle which externally end before reaching the adradial suture line, could reach the adradial suture internally.

Ambulacral floorplates have been observed in two specimens assigned to *L. squamosus* (pl. 48, fig. 3, 4, 7-11), but only a partial cross section of one floorplate is exposed in the holotype. Floorplates appear to be uniserial and trough-shaped. The upper surface is centrally concave downward; the upper lateral margins slope only slightly toward the ambulacral axis and form the nearly horizontal lateral articulation zones on which the bases of the overlying coverplates rest. The lower sides of the floorplates are convex downward. Large nodes are developed along the lateral margins of these inner surfaces, one on each side. They arise near the center of the upper edge of the inner surface of the floorplate and extend laterally outward into the thecal cavity. Sutures between contiguous floorplates are oblique, and the proximal margin of each overlaps almost the entire distal half of the next (pl. 48, fig. 11).

Interambulacrals are squamose, imbricate plates.

The valvular anal structure is offset toward the left side of interambulacrum 5. In the holotype it appears to be only a few plates away from ambulacrum I. However, at least part of this left lateral position appears to be preservational. In specimen YPM 24803, the anus lies much nearer the center of interambulacrum 5. The structure is formed by 14 large, triangular plates in the holotype, regularly alternating as inner, and overlapping outer, circlet members. The zone of overlap is of moderate width and exposes most of the upper surface of the inner plates. Several small triangular plates appear to be wedged between the larger anals in the holotype and perhaps represent new, incompletely formed anals.

The peripheral rim includes six to eight circlets of plates. The large plates of the proximal circlet may alternate as proximal and distal subcirclets. Plates of the proximal three circlets are elongate concentric with the thecal margin, whereas the plates of the distal circlets are radially elongate. Small vertical ridges are present on the basal surfaces of at least the large, proximal, geniculate rim plates.

External thecal plate surfaces are smooth except for fine pustulation reflecting the plate microstructure.

Specimens

UMMP 5420. Holotype of *Lepidodiscus squamosus* Meek and Worthen (1868, p. 357-358; 1873, p. 513-515, pl. 16, fig. 1). Edwardsville Formation, Osagean Series, Mississippian. Crawfordsville, Indiana. 45.2 mm axial by 33 mm transverse diameter.

Text fig. 51B, pl. 47, fig. 9, 10, pl. 48, fig. 1, 2.

The holotype is laterally compressed; at least some of this compression appears to be preservational. Originally highly domed, the theca has collapsed, disrupting interambulacrals and rim plates, and to a lesser extent, the ambulacra. A small part of the right anterior edge of the theca is missing, including a section of ambulacrum IV and the adjacent peripheral rim. The central oral region and hydropore structure has been extensively crushed, removing the upper parts of the plates and commonly fragmenting the remaining lower parts. The central segments of the ambulacra preserve the cyclic ambulacral coverplate pattern. Neither the proximal nor the distal parts of the ambulacra are well enough preserved to allow detailed analysis of the coverplate pattern.

A complete description of the specimen and its status as the holotype is given by Kesling and Ehlers (1958).

YPM 24803-24804. Two specimens of *Lepidodiscus squamosus;* the type specimens of *Agelacrinites beecheri* Clarke (1901, p. 195-196, fig. 4-6). Labeled "Lower Carbonic below the horizon of the Olean Conglomerate, Waverly." K. E. Caster suggests that the matrix and associated fauna are typical of the lowermost Mississippian *Syringothyris* zone, probably Cuyahoga Group, Kinderhookian-Osagean Series, Mississippian. "They probably came from the Yankee Bush Hill site, just north of Warren, Pennsylvania, where Charles Beecher and his friends collected so many of the perishoechinoids described by R. T. Jackson." (Personal communication, 1971.) Warren, Pennsylvania. C. E. Beecher, collector.

YPM 24803. (A) internal and (B) external mold of the specimen. (A) 27.4 mm axial by 23 mm transverse diameter. (B) 27.6 mm axial by 23.5 mm transverse diameter.

Pl. 48, fig. 7-13.

The specimen was only partially collapsed during preservation, and the upper oral surface remains convex upward. A large, central part of the theca is not preserved and leaves only the distal halves of the ambulacra and interambulacra, along with the anal structure and the peripheral rim.

The internal mold, and latex pulls prepared from it, reveal the imbricate floorplates which bear large lateral nodes. Vertical ridges are seen on the bases of the large, geniculate, proximal rim plates, with usually two or three near the center of each plate base. Distal rim plates appear to lack the basal ridges.

The cyclic ambulacral coverplate pattern is preserved by the external mold of the specimen. Smaller plates are difficult to identify along most of the preserved parts of the ambulacra, but are clear in a few segments (pl. 48, fig. 12,13). The broadly undulating perradial line is commonly apparent, and in some areas the perradial tips of the coverplates appear to have been flexed upward to form a small central ridge along the perradial line. The anal structure is preserved as a low, rounded, conical elevation near the center of interambulacrum 5.

YPM 24804 (A) internal and (B) external mold of a fragment of one specimen. (A) 20.5 mm long by 12 mm wide. (B) 18.8 mm long by 12 mm wide.

Text fig. 51A, pl. 48, fig. 3–6.

This specimen is a fragment of a large individual that includes the hydropore structure, the proximal parts of ambulacra III, IV, and V, interambulacra 3 and 4, and a small segment of the peripheral rim. Most of the details of the thecal plates have been obscured during preservation. The internal mold is very poorly preserved. The imbrication of the ambulacral floorplates can be seen only in ambulacrum V. Other features, including the basal ridges of the geniculate rim plates, are difficult to identify. The external mold preserves the shape of the hydropore protuberance, but individual plate boundaries are obscure. The cyclic ambulacral coverplate pattern is well preserved in a short segment of the central part of ambulacrum III (text fig. 51A). The coverplates appear to be perradially elevated in this individual also, and form a small, distinct perradial ridge.

Discussion of previous investigation

Meek and Worthen (1868, p. 357) described *Agelacrinites (Lepidodiscus) squamosus*: domal; ambulacra long, narrow, curved, I-IV contrasolar, V solar, coverplates in "two zigzag rows of very small pieces, with some irregular ones apparently not belonging properly to either row"; interambulacrals squamose, imbricate; anal structure near the left side of interambulacrum 5, including 10 laterally overlapping plates which form a "depressed cone"; "surface minutely granular." Citing the crushed and disrupted condition of the specimen, with question they suggested that the ambulacral coverplates closed over the ambulacra, the plates "interlocking" and with "pores arranged along them in a zigzag row between the pieces." A drawing of the holotype published by Meek and Worthen (1873) illustrates the dominant thecal structures and includes the varied ambulacral coverplates, which in some parts of the drawing closely resemble the individual cycle plates. The undulating perradial line is accurately depicted in all of the ambulacra.

Meek's and Worthen's description of *Lepidodiscus squamosus* was accepted without modification until Kesling and Ehlers (1958) presented a detailed redescription of the holotype. Included in this work was the first accurate account of the oral area, the hydropore structure, and the recognition of the complex six-plate cyclic ambulacral coverplate pattern. In contrast to the original description, Kesling and Ehlers reported that the coverplates were not interlocking across the perradial line, and that the holotype shows no evidence of ambulacral "pores."

Agelacrinites beecheri Clarke (1901) was based upon two specimens (YPM 24803, 24804) that preserve both internal and external molds of the two individuals. The original description notes thecal shape and size, ambulacral curvature and plating, and interambulacral and rim plating. Ambulacral coverplates were described as "triangular and interlocking along the median [perradial] line" (Clarke, 1901, p. 195). The imbrication of the ambulacral floorplates was cited as the important feature of the specimen, as those plates had been only rarely observed in other edrioasteroids. Clarke did not contrast his new species with other edrioasteroid species.

Occasional references to *Agelacrinites beecheri* include Foerste's (1914) acceptance of the imbricate nature of the ambulacral floorplates, accompanied by a republication of Clarke's (1901) drawing of them. Bassler (1935, 1936) and Bassler and Moodey (1943) referred the species to *Lepidodiscus* without explanation.

Discussion

The redescription of *Lepidodiscus squamosus* Meek and Worthen presented here is based upon the holotype and the two type specimens of Clarke's *Agelacrinites beecheri*. Restudy of the Clarke specimens revealed an ambulacral coverplate pattern identical to that of the holotype of *Lepidodiscus squamosus*. Other thecal structures, although incompletely preserved in the two specimens, also appear to be in complete agreement with *L. squamosus*.

Kesling's and Ehlers' detailed description of the holotype of *L. squamosus* included most thecal structures found in this species. The above redescription varies only in two significant aspects: the identification of the individual sets of ambulacral coverplates which form each cycle; and the description of the imbricate ambulacral floorplates, based on the specimens formerly called *Agelacrinites beecheri*. The occurrence of imbricate ambulacral floorplates in the Agelacrinitidae is known only from these two specimens.

RANGE AND OCCURRENCE: Lower Mississippian of Indiana and Pennsylvania.

Lepidodiscus laudoni (Bassler), 1936

Text fig. 52-54; plate 49, 50, plate 51, fig. 1-10

1936 *Discocystis laudoni* Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 21, pl. 3, fig. 7-8.

1943 *Discocystis laudoni* Bassler, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 201.

1958b *Discocystis laudoni* Bassler, Ehlers, G. M. and Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 14 (15): 265-276, pl. 1, fig. 1-4, pl. 2, fig. 1-2, pl. 3.

1960 *Discocystis laudoni* Bassler, Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 155, text fig. 4, pl. 3, fig. 1-3.

1966 *Discocystis laudoni* Bassler, Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U169, text fig. 120-6a, 129-3, 130-5.

1968 *Discocystis priesti* Strimple, H. L., Iowa Acad. Sci., Proc. 73: 260-262, text fig. 1-4.

Diagnosis

A *Lepidodiscus* with: large, clavate theca, pedunculate zone plates numerous, imbricate, thin and elongate, in vertical columns; cyclic ambulacral coverplates perradially raised, forming small, distinct perradial ridge; ambulacral floorplates abutting, each having two lower-surface, lateral nodes; central interambulacrals polygonal, tessellate.

Description

The theca of *Lepidodiscus laudoni* (Bassler) includes a broad, gibbous, upper oral surface, 30 to 40 mm in diameter, and an elongate, lower pedunculate zone (pl. 51, fig. 9, 10). The length of the extended pedunculate zone is apparently equal to or greater than the diameter of the upper oral surface. Total thecal height in specimens approximately 35 mm in upper oral surface diameter appears to have been approximately 50 mm in laterally compressed specimens which preserve the lower zone in an extended state.

The oral area is formed by numerous plates (pl. 49, fig. 6, pl. 50, fig. 2, pl. 51, fig. 2). Primary orals are not externally differentiated from other orals in adults. The various sized oral plates imperfectly mimic the proximal ambulacral coverplates in size, shape, and cyclic pattern. Thus, distally they appear to grade into the coverplate sequence without distinct break. Thirty or more lateral orals form the elongate transverse oral midline, proximal to the lateral bifurcation plates, whereas only about 10 anterior orals are present. Thus the oral area outline is transversely elongate, with the two lateral primary radii bifurcating far from the central oral pole. Total number, shapes, sizes, and arrangement of the oral plates appear to vary intraspecifically.

The large oral frame surrounds a transversely elongate, ovate, central lumen (pl. 50, fig. 12, pl. 51, fig. 3, 4). The lumen extends from the proximal ends of the ambulacral tunnels directly downward, and opens into the thecal cavity below. The frame, also transversely elongate, is ovoid proximally, but subpentagonal distally where it is confluent with the five radiating ambulacra. Plating of the oral frame is inadequately known. Apparently the frame is formed by the enlarged proximal floorplate of each ambulacrum, expanded inwardly and laterally. Adjacent floorplates are in contact around the central lumen. Intrathecal extensions from the overlying oral plates may also participate in frame formation, but these have not been observed in the specimens that expose the frame structure.

The hydropore structure (pl. 49, fig. 6) in large adults extends distally from the axial midline of the theca along the right posterior half of the oral area and the proximal posterior side of ambulacrum V. The posterior side of the mound is formed by three to six large plates, either modified interambulacrals incorporated into the oral area, or multiple hydropore oral plates. The anterior side of the hydropore structure is formed by the elevated, adradial ends of six or seven plates of the oral-ambulacral series. Perradially these plates form the posterior side of the right half of the transverse oral midline and the proximal part of the perradial line of ambulacrum V. The central parts of these plates are depressed and form a deep trough that separates the oral-ambulacral rise from the hydropore protuberance. One or two anterior plates which form the left end of the hydropore prominence may not reach the transverse oral midline because smaller, medial orals apparently lie proximal to these plates. The anterior edges of these smaller, central orals form the center of the posterior side of the transverse oral midline.

In younger adults (text fig. 52A, pl. 50, fig. 1, 2), the hydropore structure is formed by only three large posterior plates and four anterior ones. Apparently the additional plates in the anterior part of the hydropore structure seen in larger adults are the expanded adradial ends of small medial orals of the smaller specimens. These plates appear to increase rapidly in size during ontogeny, and extend adradially into the hydropore structure. Additional proximal posterior coverplates of ambulacrum V may also be incorporated into the adult structure. In some larger adults, the posterior side of the structure continues to be formed by only three large plates. In others, additional plates are added. These are probably new plates inserted into the structure between existing ones. Elevation of the hydropore protuberance may be less pronounced in smaller individuals.

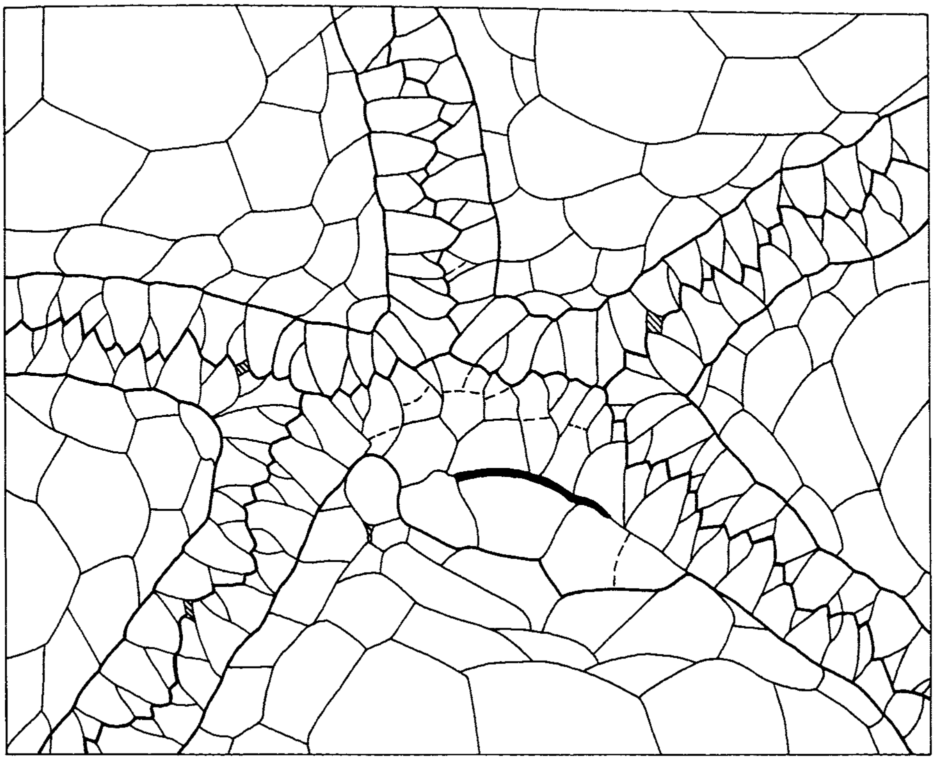
Poorly preserved stone canal passageways have been observed in two specimens (pl. 50, fig. 10-12, pl. 51, fig. 3, 4). Apparently expanding rapidly in diameter inwardly, the inner end of the funnel-shaped passageway is a large, ovate opening. The structure appears to

Text figure 52. *Lepidodiscus laudoni* (Bassler), 1936 SUIC 12545.

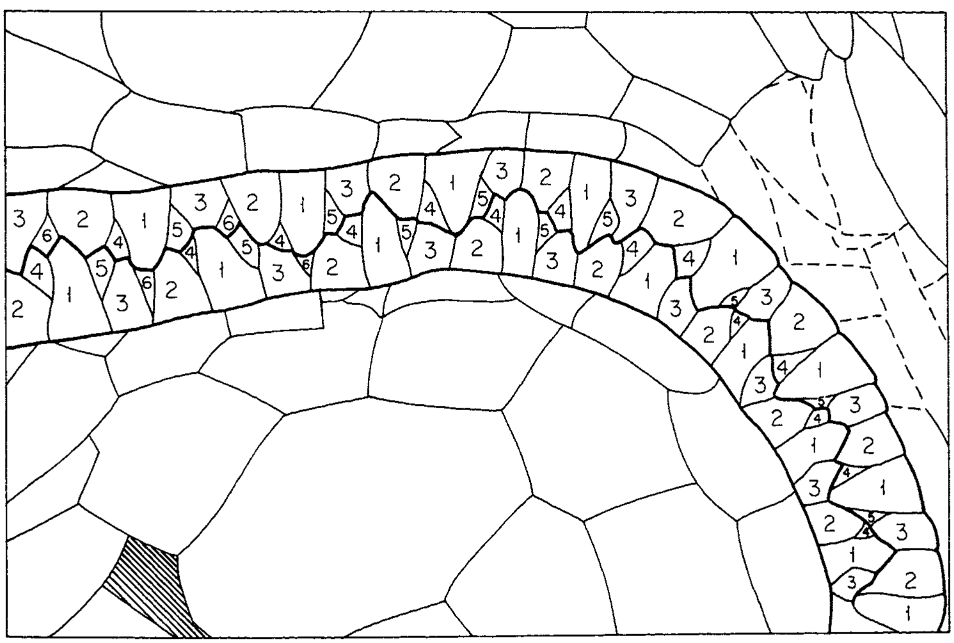
A. Oral area and adjacent structures, (x 20), pl. 50, fig. 2.

B. Segment of ambulacrum V, (x 25), pl. 50, fig. 4. Proximal end is to the left.

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



A



B

be formed by the proximal two floorplates of ambulacrum V and the intrathecal parts of several other elements, probably hydropore structure plates.

Curvature of the long, moderately narrow ambulacra is commonly uneven. A proximal straight sector is followed by pronounced curvature as the ambulacra become concentric with the ambitus of the upper oral surface.

The ambulacral coverplates form six-plate cycles; those on opposite sides of the perradial line alternate, offset by half the length of a cycle. The broadly undulating, zigzag perradial line is accentuated by the upturned perradial ends of the coverplates which form a small, sharply defined perradial ridge which extends the length of the ambulacra. The perradial edges of the individual plates of the cycle commonly align evenly and form the single, wide, smooth, perradial undulation for each cycle. However, any of the six plates of the cycle may form a discrete perradial point, and thereby superimpose small serrations on the broader undulations.

Coverplate shapes, sizes, and relative positions are similar to those of *L. squamosus* (text fig. 52B, 53A, B, pl. 49, fig. 3, 4, pl. 50, fig. 3, 4). Ehlers and Kesling (1958, p. 267) described these plates in detail, numbering them sequentially, proximal to distal:

> The first plate is small and short. It is located where the zigzag central line is near the edge of the ambulacrum. This plate is rectangular, . . . trapezoidal or pentagonal, . . . [or] deeply indented to fit around the apex of the central line. The second plate is typically subpentagonal . . . The third plate is small. It fits between the proximal parts of the second and fourth plate and borders on the central line. In most cycles it is triangular, . . . [or] subrhombic. The fourth plate is the longest and largest . . . The sides are parallel and more or less perpendicular to the edge of the ambulacrum, its proximal end . . . may be straight, bluntly tapering, sharply acuminate or, in rare cases, indented. The fifth plate is almost a mirror image of the third and is situated between the fourth and sixth plates; the sixth plate is a mirror image of the second.

The ambulacral coverplates of small adult specimens of *L. laudoni* more closely resemble the description for the coverplates given for *L. squamosus* than that presented above for *L. laudoni* (text fig. 52B, 53A, B). Notably, most plates form small but discrete perradial points which alter plate outlines to shapes more common in *L. squamosus*. Moreover, in small *L. laudoni*, plate shapes are more constant from cycle to cycle and the perradial elevation of the coverplates is less pronounced.

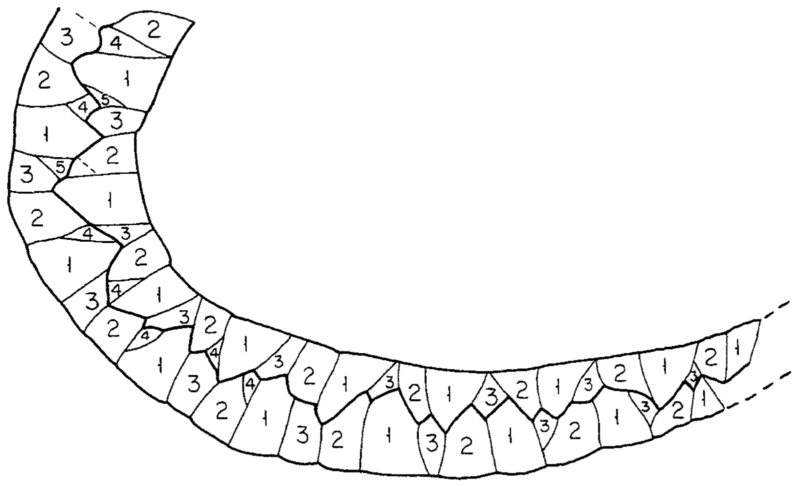
The mode of coverplate insertion and the sequential identity of the coverplate sets are preserved in the distal sectors of the ambulacra of two small adult *L. laudoni* (text fig. 53A). Coverplate sets are described below in order of insertion; parenthetic numbers refer to Ehlers' and Kesling's proximal to distal sequential numbering, cited above.

The first-formed, or primary, coverplates (fourth) are developed singly at the distal tip of each ambulacrum and move alternately left and right. Secondary coverplates (second) are inserted along the proximal margins of the alternating primaries. Their zone of insertion lies one or more primary plates from the distal tip of the ambulacrum. Next, tertiary set elements (sixth) are inserted along the distal margins of the alternate primaries. Their insertion zone lies two or three "two-plate cycles" proximal to the insertion zone of the secondaries. Coverplates of the quaternary set (third) are inserted between the perradial tips of primaries and secondaries, the insertion zone being four cycles proximal to that of the tertiaries. In contrast with the first three sets of plates, the tertiaries are confined to the perradial part of the ambulacrum and rarely enlarge sufficiently to reach the adradial suture line. Quintary, or fifth, set coverplates (fifth) follow, inserted between the perradial tips of plates of the primary and tertiary sets. Occasionally these plates are inserted in the same cycle as the quaternaries. Commonly their insertion zone lies one to three cycles proximal to the quaternary insertion zone. Like the quaternaries, plates of the quintary set are limited to the perradial part of the ambulacrum. The sixth, and final, set of coverplates (first) are inserted along the proximal side of the secondary set plates; the proximal margin of the sixth set plates is in contact with the distal edge of the tertiary plate of the adjacent next proximal cycle. These final elements are inserted three to six cycles proximal to the zone of insertion of the quintary set plates.

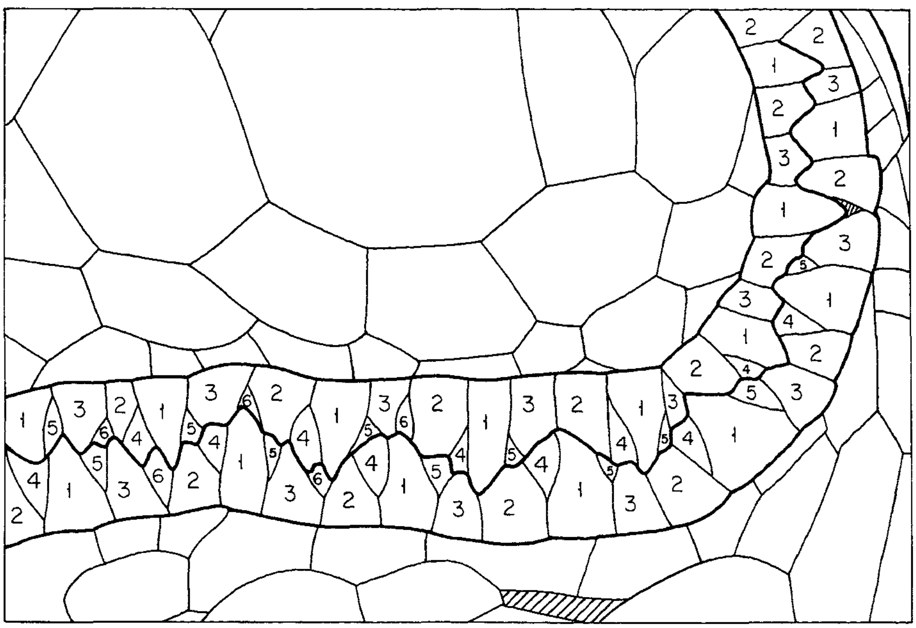
In larger adult specimens, the successive insertion zones tend to be separated by the minimum numbers of cycles cited above, whereas in younger specimens the maximum numbers are more common. Apparently in very large adults distal additions of primary coverplates nearly cease, and the following zones thus migrate distally until complete six-plate cycles are very near the distal tip of the ambulacrum.

Proximally, the cyclic coverplate pattern is less apparent, with many of the smaller cycle plates enlarged to nearly equal the size of the primary plates. Occasional cycle irregularities occur throughout the length of the ambulacrum; these are usually caused by the insertion of an extra coverplate and a corresponding modification of adjacent plate shapes. Occasional omissions of cycle plates are also encountered.

Bladelike intra-ambulacral extensions are produced inward from the ambulacral tunnel faces of the coverplates. The configuration of the inner parts of these



A



B

Text figure 53. ***Lepidodiscus laudoni*** **(Bassler), 1936**

A. Distal segment of ambulacrum I, SUIC 12546, (x 25), pl. 50, fig. 9. The distal end is to the right.
B. Central segment of ambulacrum IV, SUIC 12545, (x 25), pl. 50, fig. 3. The proximal end is to the left.

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

extensions are unknown. The adradial ends of the larger coverplates which externally reach the adradial suture line appear to be shaped similar to those of *L. squamosus* (text fig. 49C).

Small, thin, elongate interambulacrals laterally overlap the depressed upper adradial margins of the ambulacral coverplates. Irregular in the smaller adult specimens, these small interambulacrals are regularly spaced in the larger adults and extend furthest perradially over the central plates of each cycle. Thus the adradial suture lines of the ambulacra are sinuous in large adults. Commonly, adjacent large, thick interambulacrals extend under the thin adradial interambulacrals and abut the lateral edges of the ambulacral floorplates.

The thick, uniserial floorplates are subrectangular in plan view, and are axially elongate. Contiguous plates abut along vertical sutures. The upper surface of each floorplate is centrally concave downward, U-shaped in cross section, with steep lateral sides and a nearly horizontal central floor. Wide, upper lateral margins which form the articulation zones flank the central trough and slope slightly toward the trough. A small ridge appears to extend along each flat upper margin, parallel to the axis of the ambulacrum. Apparently it aids in the articulation of the floorplates with the bases of the overlying coverplates and may fit into a shallow groove in the bases of the overlying coverplates. The convex-inward, lower surfaces of the floorplates bear large lateral nodes. These project laterally outward and downward into the thecal cavity under the adjacent interambulacral plates. Two lateral nodes are developed on each floorplate, one on each side.

Adjacent interambulacral plates laterally abut the uppermost lateral margins of the lower surfaces of the floorplates. The zone of contact between these two sets of plates may be irregularly sinuous, with small nodes and depressions on the floorplate edges which fit into complementary grooves and ridges along the abutted margins of the interambulacrals (pl. 51, fig. 5-8). The small, thin interambulacrals that laterally overlap the adradial ends of the coverplates hide this floorplate-interambulacral plate junction in nondisrupted specimens.

The interambulacral plates are large, polygonal, and tessellate in the central sectors of the interambulacra. Marginally, they are more squamose and may imbricate slightly, particularly along the adradial suture line boundaries. Distally the interambulacrals extend past the ambitus of the upper oral surface onto the lower side of the upper, gibbous part of the theca. Immediately below the ambitus the interambulacrals become thinner, more elongate, and slightly imbricate. These plates of the transition zone form two or three irregular circlets. Distal to these, numerous, very thin, subrectangular plates, which are highly imbricate, are arranged in vertical columns that form the elongate pedunculate zone. The transition from polygonal-tessellate to elongate-imbricate takes place through three or four "circlets" of transition zone plates. This contrasts with the more gradual transition zone found in the clavate *Discocystis kaskaskiensis* in which seven or eight "circlets" of transition plates are required.

The valvular anal structure of *L. laudoni* comprises an inner and outer circlet of regularly alternating, triangular plates. Outer plates widely overlap inner ones along tightly fitting, oblique sutures and expose only a thin central strip of the inner plates. In large adults the bases of the outer plates are commonly in contact externally, the overlapped inner plates being exposed only in the more central sector of the structure. Thus, externally the inner anals commonly appear lanceolate. The external shape of the inner plates varies within the structure, owing to the variable degree of overlap by the outer plates. Large adults average 10 plates in each circlet.

A peripheral rim is formed at the base of the pedunculate zone. The large plates of the proximal circlet and the smaller plates of the following one or two circlets are elongate, concentric with the thecal margin. The small plates of the distal three or four circlets are radially elongate. Large vertical ridges are found on the bases of at least the large geniculate plates of the proximal circlet of the rim.

External plate surfaces are smooth.

Specimens

USNM S-3886 (A-B). Type series of *Lepidodiscus laudoni* (Bassler) (1936, p. 21, pl. 3, fig. 7, 8, as *Discocystis laudoni)*. Gilmore City Formation, Kinderhookian Series, Mississippian. Gilmore City, Iowa.

USNM S-3886-B. Lectotype of *L. laudoni* (Bassler). 29.4 mm axial by 30.1 mm transverse diameter.

Pl. 49, fig. 1-4.

The lectotype is incomplete, but preserves: the oral-hydropore region; the proximal parts of all the ambulacra, I and V complete; interambulacra 4 and 5; and the anal structure. These structures include most of the taxonomically important features, and thus the loss of the distal parts of ambulacra II-IV and interambulacra 1-3 do not hinder interpretation. The lower part of the theca is completely hidden. Thecal collapse has accentuated the height of the oral-ambulacral structures and has partially disrupted the interambulacrals. However, the oral-ambulacral plating has been only slightly disrupted, with the exception of minor plate shifting in the