distinguished from *C. ulrichi* by the rounded upper terminations of the protuberances and the greater number of tubercles per plate in *C. faberi*, particularly on the ambulacral coverplates.

Specimens

CFMUC 8821. Holotype of *Carneyella faberi* (Miller), *in* Miller and Dyer (1894, p. 156, pl. 8, fig. 24, 25). Whitewater Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Halfway between Versailles and Osgood, Indiana. C. L. Faber Collection. 17.2 mm axial by 17.2 mm transverse diameter.

Text fig. 15A, B, pl. 17, fig. 10, 11.

The holotype is an extremely disrupted specimen. Only the general outline of most major thecal structures can be seen. Text figure 15B outlines the individual thecal plates whereas text figure 15A roughly delimits the location of the ambulacra, interambulacra, and oral region. The prosopon is well preserved on many of the plates.

USNM 87162. Holotype of *Agelacrinus vetustus* Foerste (1914, p. 429–441, pl. 3, fig. 1). Greendale member, Cynthiana Formation, Trenton Group, Mohawkian Series, Upper Ordovician. South side of the Kentucky River at Clays Ferry, 14 miles south of Lexington, Kentucky. 12.5 mm axial by 12.3 mm transverse diameter.

Pl. 17, fig. 12, 13.

This specimen has collapsed, but only a few areas are disrupted. All major structures are distinct. The thecal prosopon is well preserved with the exception of the highest parts of the ambulacra, which have been more extensively etched; this removed most of the perradial ridges of the coverplates and also the ridges of the oral area. A thin layer of matrix covers most of the theca and hides some of the plate boundaries. Further cleaning would damage the delicate prosopon.

USNM S-3965. Holotype of *Carneyella foerstei* Bassler and Shideler, *in* Bassler (1936, p. 8, pl. 6, fig. 7, 8). Arnheim Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Russellville, Ohio. 25.4 mm axial by 23.9 mm transverse diameter.

Pl. 18, fig. 1–5.

This large specimen has collapsed, disrupting some of the interambulacrals. The specimen has been etched, but most of the prosopon is preserved. Some of the protuberances have been lost during weathering.

Discussion of previous investigation

S. A. Miller (1894) based the species *Agelacrinus faberi* on a single disrupted specimen (pl. 17, fig. 10, 11). He cited the tuberculate prosopon and the lack of any small outer rim plates as distinctive. Foerste (1914, p. 441) thought that "the type is too poorly preserved to merit description," but then proceeded to describe it in extreme detail and to ostensibly demonstrate that all recognizable structures were identical in construction to *Carneyella pilea.* Foerste pointed out that the proximal peripheral rim plates are not unusually large and that the lack of the small outer rim plates is due to preservation. However, Foerste interpreted the tuberculate prosopon to be a covering of *Dermatostroma papillata* and therefore not related to the specimen.

In the pages immediately preceding his redescription of *Agelacrinus faberi* Miller, Foerste (1914) described his species *Agelacrinus vetustus,* here placed in synonymy with *Carneyella faberi* (pl. 17, fig. 12, 13). Foerste contrasted his new species with *C. pilea*: (1) its occurrence in the Cynthiana Formation stratigraphically below most other edrioasteroids in the Cincinnati Arch region (according to Foerste the most significant feature of the specimen); (2) the presence of perradial ridges on the ambulacral coverplates; (3) the narrow width and short length of the coverplates and; (4) the less curved ambulacra. All of these fall within the normal range of variation of *Carneyella pilea,* but the specimen is distinct from that species on the basis of its prosopon, which agrees with that of *Carneyella faberi.* Foerste again described this as a covering of some form of *Dermatostroma.* He noted that the tuberculation was restricted to the plates of the edrioasteroid, and curiously, did not extend onto the surrounding surface of the underlying brachiopod, but this he explained as evidently due to the mobility of the edrioasteroid. Foerste (1914, p. 439) even noted the distal change in prosopon, citing: " in fact, for some reason this stroma does not actually reach the extreme margin of the theca but is separated from the latter by a very narrow space along which the vertical ridges belonging to the outermost rows of very small marginal plates are exposed."

Bassler (1936) reillustrated the type specimens of both *Carneyella faberi* (Miller) and *Carneyella vetusta* (Foerste). His brief description of the two specimens noted that the tubercles were prosopon and not a *Dermatostroma* covering. However, Bassler did not contrast the two types.

Bassler and Shideler (*in* Bassler, 1936) proposed the species *Carneyella foerstei,* here also placed in synonymy with *Carneyella faberi.* Their description of the new species, based on a single individual (pl. 18, fig. 1–5), contrasted it only with *Carneyella ulrichi* Bassler and Shideler, and made no mention of either *Carneyella vetusta* or *C. faberi.* Their specimen has the typical *C. faberi* prosopon.

Discussion

Carneyella faberi is represented by only three specimens, all adults, widely separated stratigraphically. It is possible that many more specimens have been collected but not identified because of the effects of abrasion and etching. The tubercles have been lost from various plates of all three specimens and commonly leave almost no trace of their original presence. The remnants of missing tubercles are small, because of the constriction of the tubercle bases, and thus resemble the small, rounded nodes of *C. pilea*. Because *C. pilea* and *C. faberi* differ only in prosopon, it seems reasonable to suspect that many of the deeply etched specimens identified as *C. pilea* may actually be *C. faberi*. Moreover, the prosopon of *C. faberi* may be much more subdued in juveniles and young adults, which makes their identification difficult. Several of the smaller specimens here placed in *C. pilea* appear to have proportionately more prominent nodes than normal adults, and yet the tubercles and ridges are not nearly as prominent as those of *C. faberi*.

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

Carneyella ulrichi Bassler and Shideler, 1936

Text fig. 16; plate 18, fig. 6-10

1936 *Carneyella ulrichi* Bassler and Shideler, *in* Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 8, pl. 6, fig. 5, 6.

1943 *Carneyella ulrichi* Bassler and Shideler, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 198.

Diagnosis

A *Carneyella* with: large, clavate tubercles with acuminate distal extremities; tubercles numerous on larger interambulacrals and rim plates but restricted to a single, central tubercle on most ambulacral coverplates.

Description

Carneyella ulrichi differs from *C. pilea* and *C. faberi* only in the character of its prosopon. The holotype and only known specimen is 20 mm in diameter (pl. 18, fig. 6–10).

The clavate tubercles of *C. ulrichi* look conical and taper to a sharp, distal tip, but each tubercle constricts sharply where it joins the underlying plate and forms a short "neck" below the conical "head" (text fig. 16A, B). These tubercles contrast with those of *C. faberi*, which are distally rounded and more obviously clavate, with the constricted basal neck longer and more apparent.

As in *C. faberi*, the greatest number of tubercles in *C. ulrichi* occur on the largest thecal plates, which are the distal interambulacrals and the proximal rim plates. Each of these has approximately 25 nodes. The distal small plates of the peripheral rim lack nodes but have small elongate ridges like those in the other two species of *Carneyella*. The smaller proximal interambulacrals have fewer tubercles per plate, but these tubercles become progressively larger, with the largest near the center of the theca. The most proximal interambulacral plates have only one or two large tubercles.

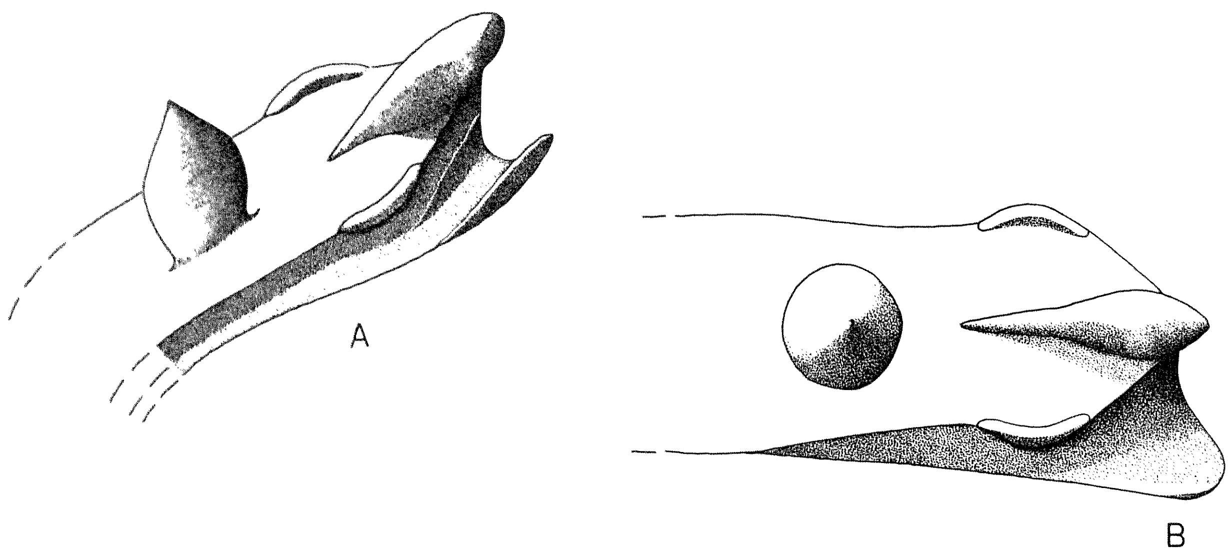
The ambulacral coverplates commonly have a single large tubercle which is between the adradial end of the perradial ridge of the coverplate and the adradial suture line (text fig. 16A, B). Occasionally two tubercles occur on one coverplate, in which case one is much larger than the other, but neither is as large as the single tubercles of the adjacent coverplates. Each large coverplate tubercle is slightly inclined to the surface of the coverplate and leans toward the perradial end of the plate. The coverplates, when closed, are slightly inclined upward, toward the perradial line. The angle of inclination of each tubercle to the surface of the underlying coverplate offsets the upward perradial slope of the coverplate, and the coverplate tubercles project upward vertically.

The two anterior primary oral plates each have a single large tubercle near the distal edge of the plate. These are inclined perradially like the coverplate tubercles, and offset the upward slope of the oral plate so that the oral plate nodes also project upward vertically. The large posterior primary oral has four tubercles, two large and two small. One large tubercle is near the center of the plate, the other is in the right posterior corner. The two small nodes lie along the left edge of the plate.

Each anal plate has a large, pointed tubercle at the upper tip of the plate. These are also so inclined to the surface of the plates that they project upward vertically.

In addition to the tubercles, *C. ulrichi*, like *C. faberi*, has elongate perradial ridges on the ambulacral coverplates. These taper more or less evenly and lack the marked constrictions adradial to their perradial tips that are found in *C. faberi* (text fig. 15C, D). In *C. ulrichi*, the perradial tip of each ridge projects beyond the perradial tip of the underlying coverplate and thereby crosses over the perradial line (text fig. 16A, B).

Both lateral adradial edges of the angular perradial part of each coverplate bear small lateral ridges which flank the adradial extremity of the central perradial ridge. As in *C. faberi*, the lateral ridges of adjacent coverplates are



Text figure 16. *Carneyella ulrichi* Bassler and Shideler, 1936

A-B. Reconstruction of an ambulacral coverplate from the holotype USNM S-3964.

A. Oblique lateral view.

B. Exterior surface plan view.

in contact and thus form the most proximal point of contact between laterally contiguous coverplates. These ridged plate edges extend laterally further than the more adradial central part of the coverplate, owing to the constriction in plate width along the external foramina of the sutural passageways. The small, lateral coverplate ridges of *C. ulrichi* appear to be identical to those of *C. faberi*, although they may be somewhat more subdued in the latter.

The ambulacral coverplates of *C. ulrichi* differ from those of *C. faberi* by having: (1) a single large tubercle with an acuminate distal tip (as opposed to several rounded tubercles); and (2) a large but evenly tapered perradial ridge that overhangs the perradial tip of the plate (in contrast with the unevenly tapered ridge of *C. faberi* that does not overhang).

The perradial edges of the oral plates are thickened and form prominent anterior and transverse oral midline ridges. A prominent raised rim also surrounds the hydropore. These features in *C. ulrichi* appear identical to their counterparts in *C. faberi*.

Specimen

USNM S-3964. Holotype of *Carneyella ulrichi* Bassler and Shideler, *in* Bassler (1936, p. 8, pl. 5, fig. 5, 6). Bellevue Formation, Maysville Group, Cincinnatian Series, Upper Ordovician. Railroad cut south of Maysville, Kentucky. 20.3 mm axial by 16.4 mm transverse diameter.

Pl. 18, fig. 6-10.

The large holotype, and only known specimen of *Carneyella ulrichi*, rests on a highly convex brachiopod (*Hebertella*) and has collapsed. Moreover, the theca has slumped toward its left anterior side and the more central plates have overridden the left side of the peripheral rim. The distal parts of ambulacra I, II, and III are thus flexed under the upper side of the theca. The underfolded area is severely disrupted. The plates of the right side of the theca are relatively undisturbed. The prosopon is variably preserved. The tubercles and ambulacral coverplate ridges, both perradial and lateral, are well preserved over much of the theca. The tubercles in the lower depressed areas are better preserved than those on the higher plates. Pitting is preserved on a few of the large proximal plates of the peripheral rim.

Discussion

The single specimen of *Carneyella ulrichi* is striking. The well-preserved tuberculate prosopon is clearly exposed by the nearly complete removal of matrix during weathering. It differs from *C. faberi* in having sharply pointed tubercles which are less abundant on the ambulacral coverplates. However, it is not impossible that these apparent differences represent intraspecific variation. Additional specimens are needed to substantiate the seemingly unique character of the *C. ulrichi* prosopon.

RANGE AND OCCURRENCE: Bellevue Formation, Maysville Group, Cincinnatian Series, Upper Ordovician of Maysville, Kentucky.

(?) *Carneyella valcourensis* Clark, 1920

Plate 18, fig. 11, 12

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

1943 *Carneyella valcourensis* Clark, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 198.

Description

Carneyella valcourensis Clark is based upon a single specimen which is so extensively disrupted that determination of specific and even most generic characters is questionable. The specimen is small, and the domal theca is laterally compressed so that the inner sides of opposing edges of the oral surface are now in contact with each other. Anterior and posterior have not been determined.

The disrupted oral region lies along the line of thecal flexure at the top of pl. 18, fig. 11. A single ambulacrum is moderately well preserved, whereas the other four (?) are completely disrupted. It appears to be formed by a single biseries of alternating plates similar to those of other Carneyellidae. Some of the coverplate passageways are visible and one displaced coverplate which now is in the oral area exposes a lateral view of one side of a passageway. The ambulacra appear to have been curved, in keeping with the *Carneyella* assignment.

The interambulacra are formed by squamose, imbricate plates. The periproct is not visible. The anal zone depicted in Clark's (1920) original illustration is an area of disrupted interambulacral (?) plates that have been extensively fractured and etched. There is no indication that this zone of minute granules of calcite represents the anal area.

The margin of the oral surface appears to have been a normal peripheral rim, although now extensively disrupted. Several large proximal rim plates have pitted surfaces.

Specimen

MCZ 532. Holotype of *Carneyella valcourensis* Clark (1920, p. 69-71, fig. 1). Chazy Limestone (Valcour or Pamelia), Chazyan Series, Middle Ordovician. Valcour Island, New York. 11.1 mm greatest length (along the line of the one well-preserved ambulacrum) by a perpendicular dimension of 10.1 m.

Pl. 18, fig. 11, 12.

Discussion

The poorly preserved holotype of Clark's *Carneyella valcourensis* appears to belong to the Carneyellidae and probably to the genus *Carneyella*. The name *C. valcourensis* is here restricted to the holotype.

Genus *Cryptogoleus* Bell, *gen. nov.*

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

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

1860 *Agelacrinites* Vanuxem, Chapman, E. J. [*partim*], Canadian Jour. Industry, Sci. and Art (n.s.) 5: 358-365, text fig. 1.

1861 *Agelacrinites* Vanuxem, Chapman, E. J. [*partim*], Canadian Jour. Industry, Sci. and Art (n.s.) 6: 516, text fig. 86.

1864 *Agelacrinites* Vanuxem, Chapman, E. J. [*partim*], A Popular and Practical Exposition of the Minerals and Geology of Canada, Toronto: 110, text fig. 86.

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

1901 *Agelacrinites* Vanuxem, Clarke, J. M. [*partim*], New York State Mus., Bull. 49 (2): 189, 191.

1908 [*non*] *Lebetodiscus* Bather, F. A., Geol. Mag. (n.s.), dec. 5, 5: 550, pl. 25, fig. 1.

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

1915 *Lebetodiscus* Bather, Raymond, P. E. [*partim*], Ottawa Naturalist 29 (5-6): 53-62, pl. 1, fig. 2-5.

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

1918 *Agelacrinites* Vanuxem, Shideler, W. H. [*partim*], Ohio Jour. Sci. 19 (1): 58.

1918 *Agelacrinites* Vanuxem, Williams, S. R. [*partim*], Ohio Jour. Sci. 19 (1): 62-65, pl. 5, fig. 28, 30.

1921 *Carneyella* Foerste, Raymond, P. E. [*partim*], Geol. Surv. Canada, Mus. Bull. 31 (Geol. Series 38): 7–12, pl. 2, fig. 8, pl. 3, fig. 3–7.

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): 10–14, pl. 3, fig. 1, 2, 9, pl. 4, fig. 3, 4, pl. 5, fig. 10; *Carneyella* Foerste, *idem* [*partim*], *ibid.*: 7, pl. 7, fig. 15.

1943 *Hemicystites* Hall, Bassler, R. S. and Moodey, M. W. [*partim*], Geol. Soc. America, Spec. Pap. 45: 202–204; *Carneyella* Foerste, *idem* [*partim*], *ibid.*: 198.

1944 *Hemicystites* Hall, Shimer, H. W. and Shrock, R. R. [*partim*], Index Fossils of North America, New York: 131, pl. 49, fig. 15.

1946 *Hemicystites* Hall, Wilson, A. E. [*partim*], Geol. Surv. Canada, Bull. 4: 20; *Carneyella* Foerste, *idem* [*partim*], *ibid.*: 19–20.

1960 *Hemicystites* Hall, Kesling, R. V. [*partim*], Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 161–162, text fig. 7.

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

TYPE SPECIES: *Lebetodiscus chapmani* Raymond, 1915.

Diagnosis

Carneyellidae with: ambulacra straight; terminations commonly penetrating proximal peripheral rim circlet; external foramina of coverplate passageways slitlike.

Description

The domal theca of *Cryptogoleus* ranges in average adult thecal diameter from 10 to 18 mm.

The oral area is formed by two anterior and one large posterior primary oral and a single hydropore oral plate (text fig. 17B). These are similar in size, shape, and arrangement to the oral plates of *Carneyella.* The two lateral ambulacral bifurcation plates perradially abut the central primary orals. The transverse and anterior oral midlines are straight. The hydropore oral forms a right posterior bulge in the outline of the oral region which extends outward along the proximal posterior edge of ambulacrum V.

The hydropore structure lies in the right posterior bulge of the oral area and is formed by four plates: the posterior primary oral, the hydropore oral, and the two proximal posterior coverplates of ambulacrum V (pl. 19, fig. 3, pl. 23, fig. 3, 6). As in *Carneyella,* the slitlike opening extends between the proximal edge of the hydropore oral and the adradial edge of the proximal posterior coverplate. The posterior primary oral forms the anterior edge of the left tip of the opening. The fourth plate in the structure (the second coverplate of ambulacrum V) is commonly separated from the opening, but it is reduced in length and its adradial end abuts the hydropore oral plate which juts into the side of the ambulacrum.

The inner structures of the oral region have not been observed in this genus. However, the external similarity of *Cryptogoleus* to *Carneyella* suggests similar oral frames.

The ambulacra of *Cryptogoleus* are straight or nearly so (pl. 19-23). Distally they reach the peripheral rim and in some cases even intrude into the proximal circlet of rim plates. The ambulacra are moderately wide and are only slightly elevated above the adjacent interambulacral plates in inflated individuals, because the coverplates lie nearly parallel to the thecal surface.

Externally, the coverplates are subrectangular with wide, angular perradial ends which interdigitate with alternate coverplates to form a zigzag perradial line. The adradial edge of each coverplate is straight. The two lateral edges are also nearly straight, being only slightly concave toward the center of the plate. The slight lateral concavity forms the edge of the extremely narrow, external foramen of the coverplate passageway. These slitlike external foramina in *Cryptogoleus* are so narrow that they are easily overlooked. Slight shifting of the coverplates during thecal collapse often totally obscures their presence. This contrasts with the external foramina of *Carneyella* which, although narrow, are relatively much wider and more conspicuous.

The inner sides of the ambulacral coverplates of *Cryptogoleus* are believed to be like those of *Carneyella,* although they have been observed only in outline, from lateral views. Apparently the proximal and distal edges of the coverplates have intra-ambulacral extensions. The distal extensions are small, narrow blades, whereas the proximal extensions are large, curved blades. These extend under and interlock with the adjacent proximal coverplate and also extend under the distal, perradial edge of the alternate coverplate across the perradial line. As in *Carneyella,* the outer (upper) surface of the curved proximal extension forms the inner surface of the upper end of each coverplate passageway. These proximal intra-ambulacral extensions of *Cryptogoleus* seem to be proportionately somewhat larger than those of *Carneyella.* The intrathecal extensions of the ambulacral coverplates and the inner foramina of the passageways have not been clearly seen in any *Cryptogoleus.*

The uniserial ambulacral floorplates are trough-shaped and the sutures between contiguous ones are oblique. The proximal edge of each broadly overlaps the next floorplate.

The interambulacrals are squamose and imbricate. The relative number and size varies specifically.

The anal structure lies near the center of the posterior interambulacrum and is commonly disrupted. However, in some specimens the anals appear to be more regular than in the common, loosely organized periproct. Only two or three circlets form the structure. The plates are large, elongate, and approach the triangular form seen in valvular anal structures. Adjacent anals fit snugly together but are not beveled, and the number of plates per circlet is quite variable — which suggests that it is better termed a periproct than a true valvular structure.

The peripheral rim is formed by five to eight circlets of plates. A circlet of transition plates separates the large proximal plates, which are externally elongate concentric with the thecal margin, from the smaller, distal, radially elongate plates. The transition plates have a distinctive shape at least in the type species.

The thecal plates are either smooth or pitted, and occasionally nodes are present.

Discussion

The genus *Cryptogoleus* embodies several of the " typical *Hemicystites* " species of authors. Restudy of the type species, *H. parasiticus* Hall, revealed that it was only superficially similar to the many other species that had been placed in the genus. *H. parasiticus* is here placed in the Isorophidae. Six species are assigned here to *Cryptogoleus*, of which four were originally defined by Raymond (1915). Two of these four are well established, the other two are monotypic and of doubtful status. *C. billingsi* (Chapman), 1860, is tentatively included here, but the holotype is now missing. The sixth species is new, although one of the type specimens had been illustrated as an example of *C. billingsi.*

The exterior of *Cryptogoleus* is well known, but the structure of the inner side has not been observed. Externally *Cryptogoleus* is quite similar to *Carneyella* with the exception of two features: the straight ambulacra, and the extremely narrow external foramina of the coverplate passageways. The anal structure is partially disrupted in most specimens, but where visible it suggests an intermediate condition between the periproct of all other Lebetodiscina and the valvular type of the Isorophina.

In this anal structure only two or three circlets of plates are present; the anals are large and subtriangular; the total number of plates in the structure is intermediate; and the contiguous edges of the anals fit closely together but are not beveled. This periproctal structure may reflect limited respiratory anal pumping. Such an interpretation would correlate with the unusually small size of the external openings of the coverplate passageways — which suggests rather small external hydrovascular branches whose respiratory role may therefore have been reduced.

ETYMOLOGY: *Cryptogoleus* is compounded from the Greek *crypto* = hidden, and *goleos* = hole, referring to the slit-like external foramina of the passageways.

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

Cryptogoleus chapmani (Raymond), 1915

Text fig. 17, 18; plate 19, 20.

1915 *Lebetodiscus chapmani* Raymond, P. E., Ottawa Naturalist 29 (5–6): 58–59, pl. 1, fig. 3.

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

1918 *Agelacrinites rectiradiatus* Shideler, W. H., Ohio Jour. Sci. 19 (1): 58.

1918 *Agelacrinites rectiradiatus* Shideler, Williams, S. R., Ohio Jour. Sci. 19 (1): 65, pl. 5, fig. 28, 30.

1921 *Carneyella chapmani* (Raymond), Raymond, P. E., Geol. Surv. Canada, Mus. Bull. 31 (Geol. Series 38): 9–10, pl. 2, fig. 8, pl. 3, fig. 6.

1935 *Hemicystites chapmani* (Raymond), Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 7; *Hemicystites rectiradiatus* (Shideler), *idem, ibid.*: 7.

1936 *Hemicystites (Lebetodiscus) chapmani* (Raymond), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 11–12, pl. 3, fig. 9; *Hemicystites (Agelacrinites) rectiradiatus* (Shideler), *idem, ibid.*: 14, pl. 5, fig. 10.

1943 *Hemicystites chapmani* (Raymond), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 203; *Hemicystites rectiradiatus* (Shideler), *idem, ibid.*: 204.

1944 *Hemicystites (Lebetodiscus) chapmani* (Raymond), Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, pl. 49, fig. 15.

1946 *Hemicystites chapmani* (Raymond), Wilson, A. E., Geol. Surv. Canada, Bull. 4: 20.

1960 *Hemicystites chapmani* (Raymond), Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 161–162, text fig. 7.

1966 *Hemicystites chapmani* (Raymond), Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U162, text fig. 120-5a, 125-7, 126-1; *Hemicystites rectiradiatus* (Shideler), *idem, ibid.*: text fig. 118-3.

Diagnosis

A *Cryptogoleus* with: large, domal theca averaging 18 mm in diameter; hydropore with prominent raised rim: ambulacra straight or slightly curved, direction variable: ambulacra tapering distally but terminations blunt and impinging upon proximal circlet of rim plates; central interambulacral plates large; transition plates of the peripheral rim distinctive; interambulacral and rim plates smooth or foveolate.

Description

The theca of *Cryptogoleus chapmani* ranges from an average of 18 mm up to 22 mm diameter in the largest known specimen. This species is distinctly larger than others assigned to the genus (text fig. 17B, pl. 19, fig. 1. 2).

The hydropore structure of *Cryptogoleus chapmani* differs from that of other *Cryptogoleus* species in that a prominent raised rim surrounds the opening. Although partially disrupted in all specimens, the opening appears to be arcuate (pl. 19, fig. 3, pl. 20, fig. 11). It extends along the anterior edge of the hydropore oral and continues around the left side of the plate to end near the posterior interambulacrum. The anterior side of the opening is flanked by the adradial edge of the proximal coverplate of ambulacrum V and along its left end by the right edge of the posterior primary oral. In some specimens it appears that the right end of the opening may extend briefly past the distal edge of the proximal ambulacral coverplate, between the hydropore oral and the second ambulacral coverplate. Kesling (1960, p. 162), who first described this structure, thought that the hydropore was straight and limited to the junction between the proximal posterior coverplate and the adjacent anterior edge of the hydropore oral plate. However, he did note that it might extend for a short distance along the suture between the left side of the hydropore oral and the adjacent right edge of the primary posterior oral, as now appears to be the case.

The two proximal posterior coverplates of ambulacrum V are short because the right side of the hydropore oral intrudes into the posterior side of the ambulacrum. In some specimens, the proximal adradial corner of the third posterior coverplate of ambulacrum V also may be reduced in length where it abuts the adjacent distal edge of the hydropore oral.

The ambulacra slowly taper distally and end in rather blunt terminations (pl. 19, 20). Commonly the ambulacra show some tendency to curve, but the curvature is always slight and the direction variable, even along the length of a single ambulacrum. Some of this apparent curvature may be due to thecal collapse. In adults, the distal tips of the ambulacra actually penetrate into the proximal circlet of rim plates and end before or upon reaching plates of the second circlet. The depth of penetration is greatest in large specimens; the ambulacra in young individuals do not reach the rim.

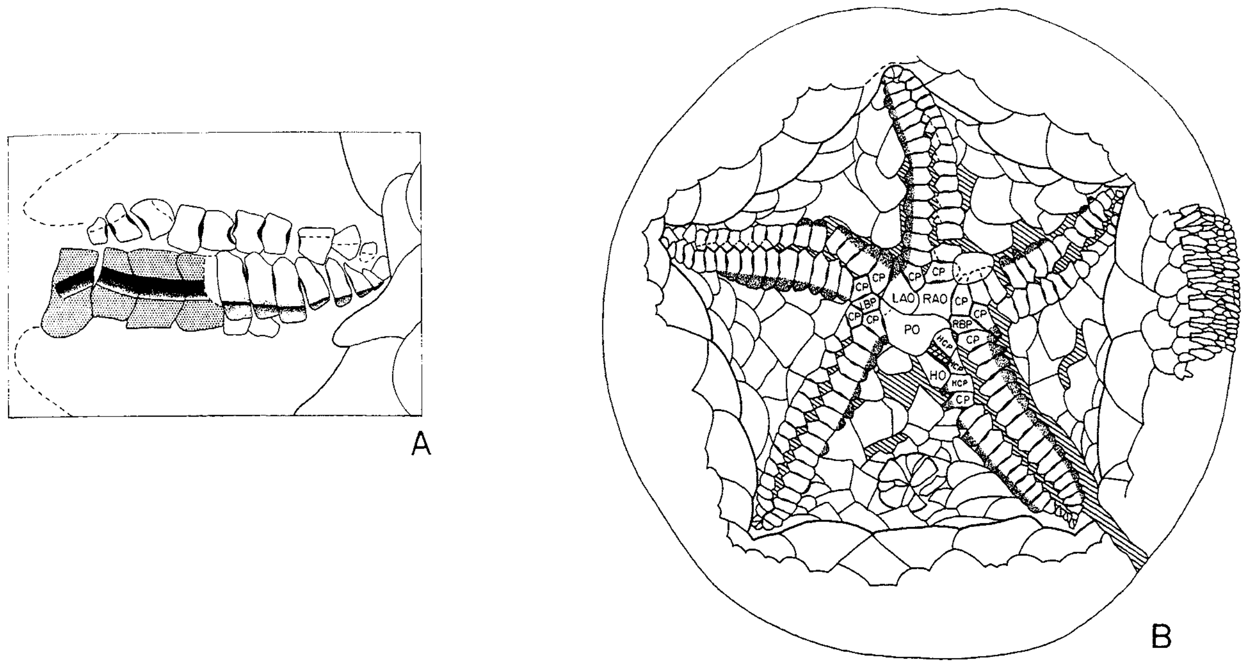
The upper surface of the intrathecal extensions of the ambulacral coverplates have been observed along the adradial edges of ambulacra where adjacent interambulacral plates had been displaced (pl. 19, fig. 1-3). The upper surface of each coverplate is abruptly depressed along the zone of overlap of the adjacent interambulacral. The ambulacral adradial suture line, when the interambulacrals and coverplates are in place, marks this line of depression and the interambulacrals rest on the lowered upper surface of the coverplate extensions. In lateral view, the upper external face of the coverplate forms a smooth, gently curved line from the perradial to the adradial suture line. At the adradial suture line the upper edge of the plate drops straight down to the lowered surface of the intrathecal part of the plate. The upper side of the lowered surface extends inward as a smooth, gently curved line. Coverplate thickness is not appreciably lessened by the depression of the adradial upper surface because, as seen in lateral view, the entire plate is slightly geniculate, with the intrathecal part of the plate angling inward and maintaining a uniform thickness.

The ambulacral floorplates are exposed in disrupted specimens which reveal the upper sides of these elements (text fig. 17A, pl. 20, fig. 8). Apparently like those of *Carneyella*, they are uniserial and trough-shaped, and the proximal edge of each one overlaps the distal edge of the adjacent floorplate along an oblique suture. The concave upper sides of these plates form the broad ambulacral trough.

The interambulacrals are large, squamose, imbricate plates. The central ones are proportionately larger than those in other species of *Cryptogoleus*, and therefore fewer in number.

The peripheral rim is formed by seven or eight circlets; it includes a circlet of transition plates that form the boundary between the large proximal rim plates, externally elongate concentric with the thecal margin, and the smaller, outer rim plates which are radially elongate. Each transition plate is oval and slightly elongate radially. However, the proximal one-third to one-half of the plate and the center of the distal half are raised far above the right and left distal sides. Only the elevated parts of the plate are visible externally when adjacent rim plates are not disrupted. The anterior edge of the proximal raised area is arcuate, but the distal side is a nearly straight edge which extends directly across the plate, concentric to the thecal margin. In nondisrupted specimens, the proximal raised area has the appearance of being a separate, small, squamose plate, elongate concentric with the thecal margin. When the entire circlet of transition plates is in place, the straight distal edges of the anterior part of the transition plates are aligned and form a distinct circle around the rim.

The raised, central posterior part of each transition plate forms a shaft which extends distally, normal to the distal straight edge of the proximal part of the plate. In nondisrupted specimens it looks like a small, narrow plate, elongate radially. The depressed lateral sides of the distal half of the plate which flank the central shaft are normally overlapped by small, radially elongate plates of the next distal circlet. These parallel the distal, raised shaft of the transition plates. Therefore, the distal shafts of the



Text figure 17. *Cryptogoleus chapmani* (Raymond), 1915

A. Ambulacrum III, ROM 28177, (x 10), pl. 20, fig. 8. Ambulacral floorplates are marked with a dotted pattern.

B. Holotype, GSC 3235-A, (x 5), pl. 19, fig. 2. Coverplate intrathecal extensions, exposed where adjacent interambulacrals are disrupted, are stippled. CP, ambulacral coverplate; HCP, hydropore ambulacral coverplate; HO, hydropore oral plate; LAO, left anterior primary oral plate; LBP, left lateral bifurcation plate; PO, posterior primary oral plate; RAO, right anterior primary oral plate; RBP, right lateral bifurcation plate.

transition plates look like discrete plates which belong to the next distal row of plates, all radially elongate.

The external surfaces of most thecal plates of *Cryptogoleus chapmani* appear smooth. However, some of the proximal rim plates in several specimens are foveolate. The original extent of the prosopon is unknown, for all traces of it can easily be removed by etching and erosion.

Description and discussion of juveniles

Two well-preserved juvenile *Cryptogoleus chapmani* and two very small individuals assigned to this species have been examined (text fig. 18A-D, pl. 20, fig. 1–5). Specimen ROM 160t-b-F, 2.9 mm axial by 3.2 mm transverse diameter, is on a small slab of Trenton Limestone with five *Isorophus inconditus*. The other three specimens are on one slab with the holotype of *Cryptogoleus chapmani* (GSC 3235). GSC 3235-C is approximately 3 mm in diameter. The two very young specimens, GSC 3235-E, F, are both approximately 0.5 mm in diameter and lie in contact with each other. These two specimens are tentatively assigned to *C. chapmani* because of their association with the holotype, although specific and generic traits are not yet fully developed. The occurrence of four other juveniles on the same slab, representing at least two different species, suggests that the two tiny individuals could belong to one of several species.

The two tiny edrioasteroids assigned to *Cryptogoleus chapmani* (text fig. 18A, B, p. 20, fig. 1) appear to represent approximately the same stage of development. The peripheral rim is the dominant thecal feature and forms nearly two-thirds of the oral surface. Smaller, outer rim plates may be missing. Proximal to the peripheral rim, both have five recognizable central plates. One of these, in specimen E, appears displaced toward the upper right.

One of the five central plates is noticeably larger than the others. Two plates oppose this largest element; they are subequal in size and are larger than the remaining two plates which are lateral in position. The three large plates are thought to be the three primary orals; the largest is the posterior primary oral, the opposing two are the anterior primaries. The two lateral plates would thus seem to be the lateral bifurcation plates. If other thecal plates are present, they are either indistinct or perhaps hidden under the proximal plates of the peripheral rim. Neither the anal structure nor the hydropore can be identified. Apparently the first ambulacral coverplates have not formed at this stage of development.

The large posterior primary oral of specimen F appears to be broken, as represented by a dashed line across the plate in text fig. 18A. If, instead, this lineation represents a suture, the left section would probably represent the posterior primary oral, and the right section probably the hydropore oral. However, this would mean that the posterior primary oral was smaller than the anterior primary orals — an unlikely situation.

These two specimens, 0.5 mm in diameter, are the smallest described edrioasteroids and represent the earliest known growth stage. Their questionable generic and specific identity does not detract from their importance, because characters of this stage are basic to the entire family. The extremely small size of individual plates makes interpretation difficult, but the close agreement in apparent plate structure between the two specimens supports the above interpretation.

The oral-ambulacral series in these two specimens forms a triradiate symmetry. The transverse oral midline extends out to the two lateral bifurcation plates and marks the right and left lateral radii. The anterior midline, between the anterior primary orals, marks the anterior radius, although this anterior radius is shorter than the lateral two.

The two larger juvenile *Cryptogoleus chapmani* (about 3 mm in diameter) are also both at approximately the same stage of development, ROM 160t-b-F (text fig. 18C) being perhaps slightly younger than GSC 3235-C (text fig. 18D). Thecal characters in these specimens differ from those in adults primarily in the relative proportions of the major structural units. Total number of plates is also reduced.

The peripheral rim is dominant and forms over half the theca. Nearly the full adult complement of rim circlets is present, although the number of plates per circlet is reduced. Moreover, the proximal rim plates appear proportionately larger than in adults. The transition plates of the rim are not clearly visible and may not be fully developed at this stage.

The central oral surface, proximal to the rim, is formed mostly by oral and ambulacral plates. The three primary orals are proportionately much larger than in adults. The hydropore oral is also relatively larger. The hydropore opening in both specimens is shorter than in adults. It is limited to only a small section of the anterior edge of the hydropore oral rather than extending along most of the length of that plate. All five ambulacra are distinct, but they occupy a relatively small part of the theca. Each ambulacrum has two to three pairs of coverplates. The coverplates are added singly at the distal tips of the ambulacra, and several ambulacra have an odd number of plates. The lateral bifurcation plates of the ambulacra are proportionately much larger than in adults and are also much larger than any of the ambulacral coverplates.

The interambulacral areas are relatively small. Individual interambulacrals are difficult to distinguish. This may be preservational, or these plates may be very thin. Additional interambulacrals may have slid under the proximal rim plates during collapse.

The anal structure is proportionately larger than in adults. Individual anals may also be larger and fewer in number but are poorly preserved in both specimens.

The transition from the 3 mm juveniles to adults includes the gradual increase in relative importance of the ambulacra and interambulacral areas at the expense of the rim, anus, and oral area. Individual plates increase in size, and the total number of plates also increases for all structures except the oral area.

Specimens

GSC 3235 (A-H). A small slab of limestone with eight edrioasteroids resting directly on the upper surface of the slab. " Cystid beds " of the *Prasopora* zone of the " Trenton Limestone," Trenton Group, Mohawkian Series, Middle Ordovician. Abandoned quarry near the entrance to Jackson Park, Peterborough, Ontario. Collected by W. A. Johnston.

GSC 3235-A. Holotype of *Cryptogoleus chapmani* (Raymond) (1915), p. 9–10, pl. 2, fig. 8, pl. 3, fig. 6). 17.3 mm axial by 17.9 mm transverse diameter.

Text fig. 17B, pl. 19, fig. 1–4.

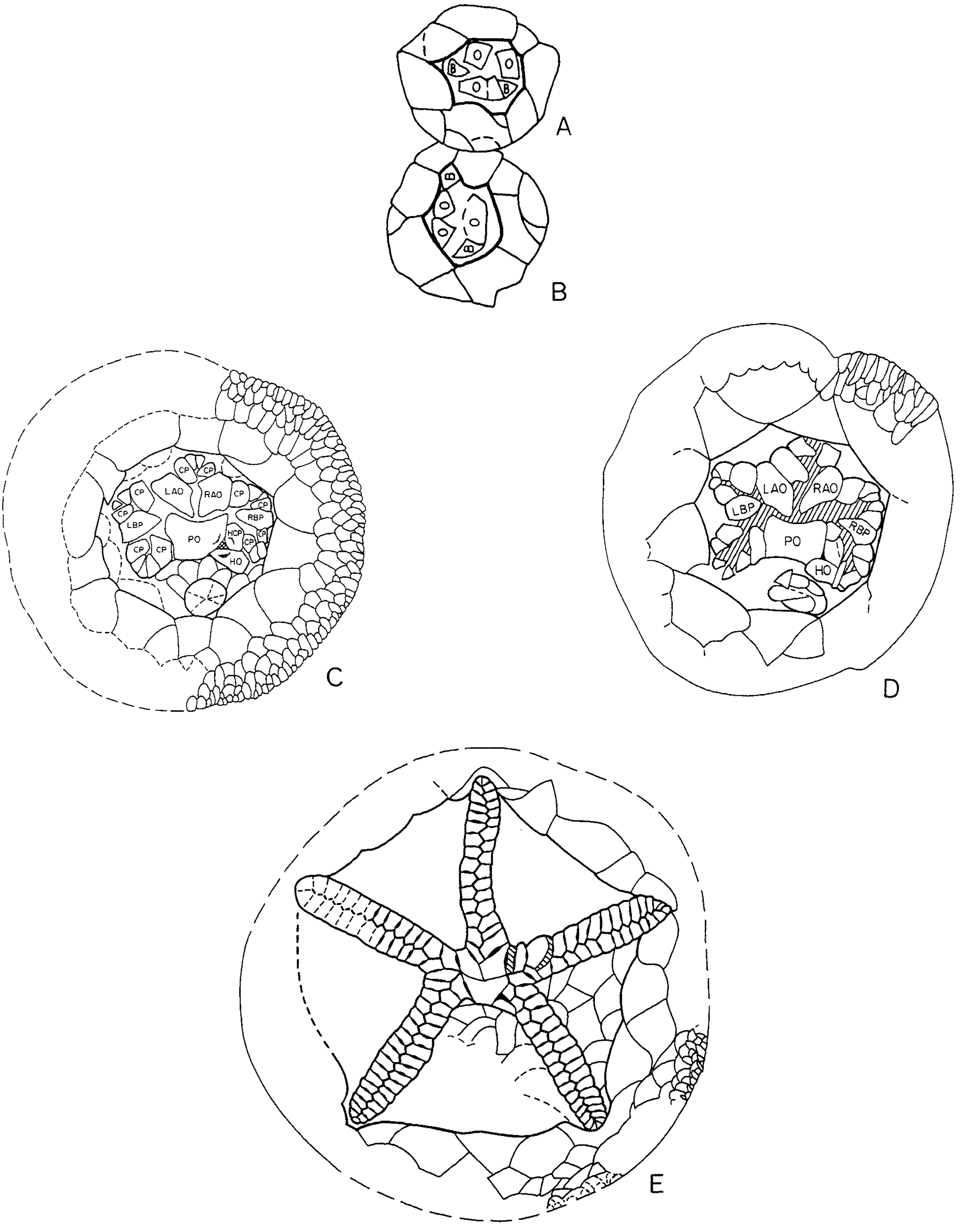
The holotype is well preserved. The theca has collapsed, but only the posterior interambulacrals and anal plates have been disrupted. The hydropore oral has been displaced somewhat posteriorly. A small part of the anterior tip of the theca and the distal tip of ambulacrum IV have

---

Text figure 18. *Cryptogoleus chapmani* **(Raymond), 1915**

A. Juvenile, GSC 3235-F, (x 50), pl. 20, fig. 1.
B. Juvenile, GSC 3235-E, (x 50), pl. 20, fig. 1. Anterior is to the left.
C. Juvenile, ROM 160t-b-F, (x 20), pl. 20, fig. 2.
D. Juvenile, GSC 3235-C, (x 20), pl. 20, fig. 5.
E. Adult, USNM S-3954, (x 5), pl. 20, fig. 10.

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



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

been crushed. The perradial edges of the three primary orals have also been slightly abraded. There is also a small separation of the plates in the right posterior part of the theca; this forms a small gap in the rim adjacent to the tip of the ambulacrum V and reveals the upper surface of the intrathecal parts of the coverplates. The specimen does not appear to be extensively etched.

GSC 3235-B. 19 mm axial by 17 mm transverse diameter. Pl. 19, fig. 5, 6.

This large individual occurs on the same slab as the holotype. The specimen is considerably disrupted, particularly the right half, which remains partially covered with tenacious matrix. All five ambulacra are visible, although all are distorted, as is the oral region. The raised rim surrounding the hydropore is intact, but the plates of that region are partially disrupted.

GSC 3235-C. 3.2 mm axial by 3.2 mm transverse diameter.

Text fig. 18D, pl. 20, fig. 4, 5.

This is one of the four known juvenile *Cryptogoleus chapmani.* The specimen has undergone little plate disruption, but the small size of the thecal plates combined with surficial etching and some recalcitrant matrix makes identification of the smaller plates difficult.

GSC 3235-E. 0.6 mm axial by 0.54 mm transverse diameter.

Text fig. 18B, pl. 20, fig. 1.

A very young edrioasteroid attributed to *Cryptogoleus chapmani* where, as in the following juvenile, the central part of the theca has collapsed to the underlying substrate. Consequently the central thecal plates are somewhat displaced. The proximal rim plates are well defined, but only a few smaller plates overlap them distally, which suggests that some of these may have been eroded away.

GSC 3235-F. 0.5 mm axial by 0.6 mm transverse diameter.

Text fig. 18A, pl. 20, fig. 1.

This is the other tiny juvenile which possibly belongs to *Cryptogoleus chapmani.*

ROM 160t-b-F. Trenton Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Peterborough, Ontario. 2.9 mm axial by 3.2 mm transverse diameter.

Text fig. 18C, pl. 20, fig. 2, 3.

This is a juvenile *Cryptogoleus chapmani* resting on a small slab of Trenton Limestone along with five *Isorophusella inconditus.* It is well preserved except for the partially disrupted anal area. The left side of the peripheral rim is mostly covered with matrix. The center of the theca has collapsed down inside the peripheral rim. The large posterior primary oral lies below the adjacent oral and ambulacral plates. The proximal rim plates of the right side of the theca are pitted.

USNM S-3954. Lectotype of *Agelacrinites rectiradiatus* Shideler (1918, p. 58, pl. 5, fig. 30, *in* Williams, 1918). Lower Whitewater Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Elk Run, east of Winchester, Ohio. 17.1 mm axial by 16.8 mm transverse diameter.

Text fig. 18E, pl. 20, fig. 10, 11.

This is an extensively eroded but otherwise typical adult *Cryptogoleus chapmani.* It rests upon a small, oblong, rounded lump of substrate of the type commonly referred to as a " clay ball." Except for the distal end of ambulacrum II, most of the ambulacral and oral plates are distinct. A few interambulacral plates are preserved in interambulacrum 4, but most others are missing. Only remnants of the peripheral rim remain on the left side of the specimen, whereas most of the rim plates are present on the right. The anal structure is missing along with the posterior interambulacrals. A few of the proximal rim plates of the right side of the theca retain remnants of large pits.

Included under the same number in the United States National Museum is a second " clay ball " with two very fragmentary individuals resting upon the surface. The larger of them, approximately 17 mm in diameter, is severely disrupted although a few of the ambulacral coverplates can be identified, and a few large proximal rim plates are pitted. This specimen is believed to be the one figured by Williams (1918, pl. 5, fig. 28), along with the lectotype, as an example of *Agelacrinites rectiradiatus.* The second specimen on the fragment is smaller, approximately 8.3 mm axial by 13.6 mm transverse diameter. It is now represented only by a pyrite film which reflects the former shape of the theca. The current location of an additional specimen mentioned by Shideler (1918) in his description of the species and figured by Williams (1918, pl. 5, fig. 29-a) is unknown.

Shideler, in describing *Agelacrinites rectiradiatus*, notes that the specimen, later designated by Bassler (1936) as the lectotype, is from the pebbly layer of the basal Whitewater Formation at Elk Run, east of Winchester, Ohio. The specimen figured by Williams (1918, pl. 5, fig. 28) is reported as from Grace's Run, Adams County, Ohio. Both specimens are now in the United States National Museum under one number, and the accompanying label lists the occurrence as Olive Branch, Harshaville, Ohio.

ROM 28177. Trenton Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Peterborough, Ontario. 14.1 mm axial by 14.3 mm transverse diameter.

Text fig. 17A, pl. 20, fig. 6–9.

This specimen is smaller than the other adult *Cryptogoleus chapmani.* Most plates proximal to the rim are disrupted, although movement of individual ones has not been great and all major thecal structures can be identified. Nearly all of the thecal plates are preserved except for some interambulacrals and a few of the proximal coverplates of the right side of ambulacrum III. The specimen exposes the proximal floorplates of ambulacrum III where coverplates are missing. The anal structure is severely disrupted, but the large, subtriangular anals are well preserved. Many of the proximal plates of the peripheral rim are pitted.

ROM 28178. Trenton Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario. Collected by J. E. Narraway. 12.5 mm axial by 12.6 mm transverse diameter.

Pl. 19, fig. 9.

This small adult *Cryptogoleus chapmani* is moderately disrupted, and the surface of the theca has been severely etched.

GSC 1414-B. Cobourg beds of the Trenton Limestone, probably the " Cystid beds " about 180 feet below the top of the Trenton Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario. 21 mm axial by 22 mm transverse diameter.

Pl. 19, fig. 7, 8.

This is the largest *Cryptogoleus chapmani* known. It rests on the surface of a small slab of Trenton Limestone near a specimen of *Lebetodiscus dicksoni.* The theca has been much disrupted and preserves only ambulacra III, IV, and V, and most of the peripheral rim. The partially disrupted ambulacral coverplates reveal their passageways, the more proximal of which are filled with secondary calcite so that they stand out as black circles in the xylene photograph, pl. 19, fig. 8.

Discussion of previous investigation

Agelacrinites chapmani Raymond (1915) was transferred to *Carneyella* by Foerste (1917) when he described that genus. Raymond (1921) republished his description and accepted Foerste's genus for his species. The original description was brief and designed to separate *Cryptogoleus chapmani* from similar Trenton species described by Raymond in the same publication, particularly *Cryptogoleus youngi.* Raymond noted that in *C. chapmani* the ambulacra are flanked by a wide border of small plates, all ambulacra are somewhat contrasolarly curved, the anal " pyramid " is composed of six triangular plates, the proximal rim plates are large and less squamose than normal, each bearing surficial pits and granules.

Shideler (1918) described *Agelacrinites rectiradiatus* based on specimens from the upper part of the Richmond Group (Upper Ordovician) (text fig. 18E, pl. 20, fig. 10, 11). He noted that these were the only individuals [known at that time] with straight ambulacra that occurred above the Trenton. The stratigraphic interval between the Richmond specimens and Trenton forms with straight ambulacra seemed sufficient to him to assure their identity as distinct species, and therefore he made no attempt to compare the forms. Many edrioasteroid species have now been shown to have very long stratigraphic ranges. Shideler's species description basically agrees with the characters of *Cryptologeus chapmani.* However, neither the lectotype nor the specimen with it in the United States National Museum preserves the anal structure, and the ambulacral floorplates are hidden in both of these. Shideler's description of these features must have been from a third specimen, which he mentioned was figured by Williams (1918, pl. 5, fig. 29, in the same issue in which Shideler's specimens were illustrated). The location of this specimen is unknown, but the illustration suggests that it may be a juvenile *Carneyella pilea.*

Bassler (1935) assigned both *Cryptogoleus chapmani* and Shideler's *Agelacrinites rectiradiatus* to the genus *Hemicystites.* In 1936 he briefly characterized each of the species and added that it was hard to distinguish between them. He suggested that when magnified to equal size, the ambulacra of *H. rectiradiatus* are slightly larger, narrower, and less tapered than those of *H. chapmani.* These differences now appear to be due to preservational factors.

Subsequent to Bassler's work, most authors followed his assignment of *Cryptogoleus chapmani* to the genus *Hemicystites.* Wilson (1946) refigured the type specimen and distinguished the species from *Cryptogoleus platys* (Raymond) by noting that *C. chapmani* is smaller in size, the peripheral rim is proportionately wider, and the ambulacra are less straight. Kesling (1960) presented a line drawing restoration of the species based on the holotype and a detailed description of the hydropore structure. Regnéll (1966) used drawings of *C. chapmani* to illustrate the features of the genus *Hemicystites.* In addition, he figured a line drawing designated *Hemicystites rectiradiatus* (Shideler) which depicts the oral region, ambulacra IV and V, and the intervening interambulacrum of what appears to be the type specimen of Shideler's species. Regnéll's drawing does not correspond to the one presented here, for it differs notably in the hydropore region.

Discussion

Cryptogoleus chapmani (Raymond) is represented here by only 10 individuals plus the two tentatively identified tiny juveniles. In spite of the small number, this is the largest group of specimens known for any one species placed in the genus *Cryptogoleus*.

The stratigraphic isolation of the Upper Richmond specimen of *Cryptogoleus chapmani* is now not as complete as indicated by the illustrated specimens. At least two have been collected from the lower Richmond and possibly a third individual from the upper part of the Maysville Group; all three are from the Cincinnati Arch area. Unfortunately, these specimens are in the hands of private collectors and could not be obtained for study.

All known *Cryptogoleus chapmani* specimens are found resting directly upon the surface of the underlying firm carbonate substrate rather than on the hard parts of organisms. The surface of the Trenton Limestone layers on which edrioasteroids are found represents a firm carbonate sea floor on which little detrital accumulation or carbonate deposition was occurring during the life of the edrioasteroids. In contrast, most edrioasteroids found in the Cincinnatian strata of the Cincinnati Arch region are resting upon the shells of other organisms which protrude above a relatively soft carbonate substrate of sands, silts, and muds. Commonly the edrioasteroid resting sites are brachiopods, pelecypods, bryozoans, and trilobites. However, all Cincinnatian *Cryptogoleus chapmani* occur on the surface of nodules ("clay balls"), which are small portions of the calcareous-argillaceous substrate that were ripped up and rolled around for short distances on the sea floor. These lumps of substrate were apparently small, firm nodules lying on, or partially imbedded in, the surrounding soft sea floor. They are the only available firm substrate other than the shells of organisms that protrude above the soft substrate. The occurrence of the nodules is sporadic and uncommon throughout the Cincinnatian Series of the Cincinnati Arch region, but usually characterizes certain layers. Possibly the rarity of *Cryptogoleus chapmani* specimens throughout the upper part of its range in the Cincinnatian corresponds to the scarcity of the nodules or hard bottoms.

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

Cryptogoleus reticulatus Bell, *sp. nov.*

Text fig. 19; plate 12

1860 [*non*] *Agelacrinites billingsi* Chapman, E. J., Canadian Jour. Industry, Sci. and Art (n.s.) 5: 358-365, text fig. 1.

1915 *Lebetodiscus billingsi* (Chapman), Raymond, P. E. [*partim*], Ottawa Naturalist 29 (5-6): 56-58.

1921 *Carneyella billingsi* (Chapman), Raymond, P. E. [*partim*], Geol. Surv. Canada, Mus. Bull. 31 (Geol. Series 38): 7-9, pl. 3, fig. 3.

1936 *Hemicystites (Agelacrinus) billingsi* (Chapman), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 12, pl. 3, fig. 2.

Diagnosis

A *Cryptogoleus* with: moderate-sized domal theca: ambulacra rectilinear, wide, nontapered, terminations blunt and impinging upon proximal rim plates; transition plates of peripheral rim externally sagittate, thecal plates with prominent coarse pits.

Description

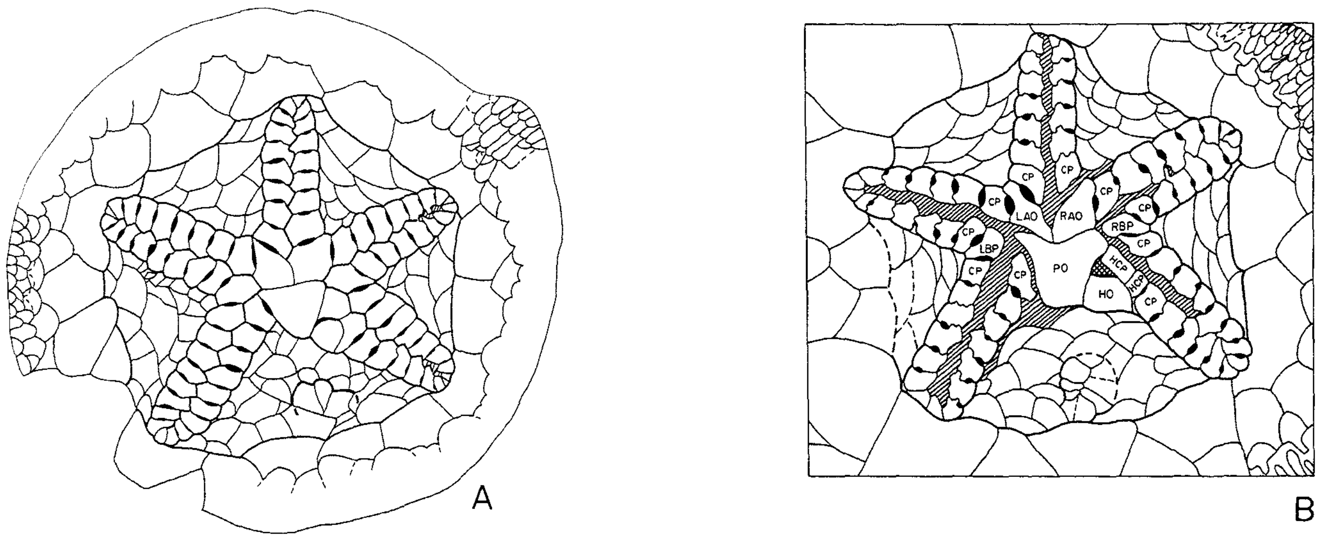
The theca of *Cryptogoleus reticulatus* averages 10 mm in adult specimens; the largest is 11 mm in diameter (pl. 21, fig. 1-11).

The oral region is comparable to that of the type species (text fig. 19). The hydropore structure is formed by the hydropore oral, the posterior primary oral, and the proximal two posterior coverplates of ambulacrum V. The slitlike hydropore is limited to the zone of contact between the anterior edge of the hydropore oral, the adradial proximal coverplate, and a small segment of the right side of the posterior primary oral. The second posterior coverplate of ambulacrum V is reduced in length and abuts the hydropore oral, but does not come in contact with the opening.

The ambulacra are straight, with no tendency to curve. Each is wide and extends to the peripheral rim without appreciable reduction in width. The distal tips are blunt and, like those of *C. chapmani*, extend into the proximal circlet of rim plates. In this species the intrusion occurs either between two large rim plates or, in several instances, into a deep recess in the proximal edge of a large rim plate.

The ambulacral coverplates of *Cryptogoleus reticulatus* are large in proportion to thecal diameter. Only seven or eight pairs of plates per ambulacrum are found in adults (text fig. 19A, B, pl. 21, fig. 1-11). Individual coverplates are externally similar to those of *C. chapmani*. The intra-ambulacral and intrathecal extensions have not been observed. The now eroded exterior surface of each coverplate appears to have been slightly convex and thereby formed a low ridge normal to the perradial line. Thus the lateral suture lines between adjacent coverplates and the external foramina of the passageway system lie in shallow troughs. The external foramina of the passageways are narrow, slitlike openings, as in *C. chapmani*.

Because of the unusual width of the ambulacra here, the interambulacral areas are proportionately reduced. The interambulacrals are squamose and imbricate, and



Text figure 19. ***Cryptogoleus reticulatus*** **Bell,** ***sp. nov.***

A. Holotype, ROM 28176, (x 7), pl. 21, fig. 2. B. Paratype, GSC 5140, (x 10), pl. 21, fig. 4.

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

smaller proportionately than in other *Cryptogoleus* of this size.

The anal structure is disrupted in all specimens, but appears to be formed by several large, subtriangular plates, in two or three irregular circlets.

The peripheral rim is formed by only five or six circlets, in contrast with the seven or eight circlets of *C. chapmani.* A circlet of transition plates with the same distinctive form as those of *C. chapmani* separates the large proximal plates elongate concentric with the thecal margin from the small, distal, radially elongate plates.

All exterior plate surfaces in *Cryptogoleus reticulatus* are coarsely pitted. The large pits are readily visible to the unaided eye, even on extensively weathered specimens. The prominent pits of *C. reticulatus* contrast with the foveolate plate surfaces of *C. chapmani,* in which etching commonly removes the prosopon which is limited to rim plates and perhaps some interambulacrals.

Specimens

ROM 28176. Holotype of *Cryptogoleus reticulatus, sp. nov.* Trenton Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario. 10.4 mm axial by 11 mm transverse diameter.

Text fig. 19A, pl. 21, fig. 1, 2.

The holotype of *Cryptogoleus reticulatus* has collapsed but is only slightly disrupted. A small section of the peripheral rim adjacent to the distal tip of ambulacrum I has been lost. The upper edges of the ambulacral and oral plates have been eroded. The remainder of the theca, with the exception of the partially disrupted anal area, is well preserved.

GSC 5140. Paratype of *Cryptogoleus reticulatus, sp. nov.* Illustrated as *Carneyella billingsi* (Chapman) by Raymond (1921, p. 7-9, pl. 3, fig. 3). Trenton Limestone. Trenton Group, Mohawkian Series, Middle Ordovician. Peterborough, Ontario. 11 mm axial by 10.8 mm transverse diameter.

Text fig. 19B, pl. 21, fig. 3, 4.

The paratype of *Cryptogoleus reticulatus* has also collapsed. The anal structure and a few interambulacral plates are disrupted, but the other thecal plates remain nearly in place. The upper edges of the ambulacral and oral plates have been removed by erosion and etching to expose a subsurficial view of them. In this preservation the opposing coverplates are perradially separated and the upper ends of their passageways are large, as seen in the xylene photographs and the line drawing (text fig. 19B).

UCMP 35222 (A-D). Trenton Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario. Kopf Collection.

UCMP 35222-A. 10.3 mm axial by 10.5 transverse diameter.
Pl. 21, fig. 5.

UCMP 35222-B. 7 mm axial by 8.2 mm transverse diameter.
Pl. 21, fig. 10, 11.

UCMP 35222-C. 7.7 mm axial by 7 mm transverse diameter.
Pl. 21, fig. 8, 9.

UCMP 35222-D. 4 mm axial by 4 mm transverse diameter.
Pl. 21, fig. 6, 7.

These four *Cryptogoleus reticulatus* are smaller than the types, but agree with them in thecal construction.

Discussion

The paratype of *Cryptogoleus reticulatus* (GSC 5140) was figured by Raymond (1921) and reillustrated by Wilson (1946) as a supposed topotype of *Hemicystites billingsi* Chapman (1860). It differs from Chapman's description in two significant features: the interambulacrals of his species " grade " into the marginals with no distinct circlet of large proximal rim plates, whereas the proximal rim plates of the subsequent specimen (GSC 5140) are both large and distinct; and high magnification had failed to reveal any prosopon to Chapman, but on this new specimen all the plates have numerous, large pits which are easily seen with the unaided eye.

Specimens of *Cryptogoleus reticulatus* are distinguished from other species of the genus by the combination of: the wide, straight, nontapering, bluntly terminated ambulacra that intrude into the proximal rim plates; the small size of the interambulacra; the distinctive transition plates of the peripheral rim; and the prosopon of numerous large pits.

Cryptogoleus reticulatus is represented here by only a few specimens, but material in the hands of private collectors suggests that the species is not uncommon.

ETYMOLOGY: The trivial name *reticulatus* is Latin, alluding to the coarsely pitted surface.

RANGE AND OCCURRENCE: Trenton Group, Mohawkian Series, Middle Ordovician of Ottawa — Peterborough area, Ontario.

Cryptogoleus multibrachiatus (Raymond), 1915
Text fig. 20; plate 22

1915 *Lebetodiscus multibrachiatus* Raymond, P. E., Ottawa Naturalist 29 (5-6): 60-61, pl. 1, fig. 2.

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

1921 *Carneyella multibrachiata* (Raymond), Raymond, P. E., Geol. Surv. Canada, Mus. Bull. 31 (Geol. Series 38): 11-12, pl. 3, fig. 5.

1936 *Hemicystites (Lebetodiscus) multibrachiatus* (Raymond), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 11, pl. 4, fig. 3-4.

1943 *Hemicystites multibrachiatus* (Raymond), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 204.

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

Diagnosis

A *Cryptogoleus* with: small domal theca; ambulacra straight, slightly tapering, terminations blunt and occasionally extending into proximal rim circlet; interambulacrals small, externally convex, appearing bulbous or knobby; plate surfaces foveolate; large, irregular nodes scattered over interambulacrals and rim plates.

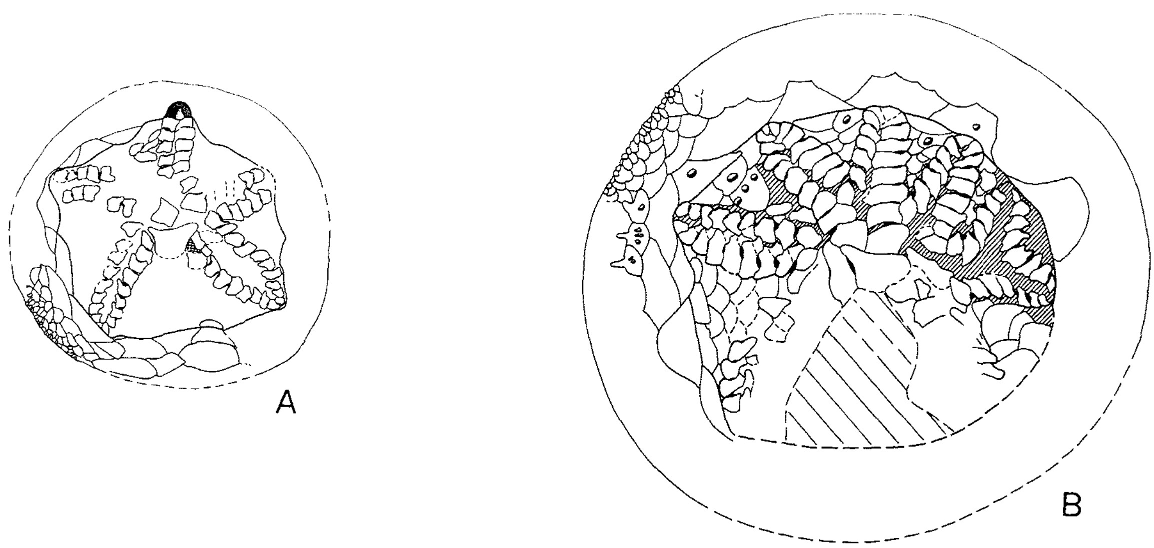
Description

Cryptogoleus multibrachiatus is based upon a specimen with probably a total of eight ambulacra (text fig. 20B, pl. 22, fig. 1-3). The individual is atypical; normal specimens with only the five primary ambulacra are included here (text fig. 20A, pl. 22, fig. 4-9).

C. multibrachiatus is slightly smaller than other species of the genus, commonly 9 to 10 mm in thecal diameter. The domal theca is found resting directly on a firm carbonate substrate in all known occurrences.

The oral area, with three primary orals and one hydropore oral, is similar to that of *C. chapmani.* The slitlike hydropore is limited to the zone between the anterior side of the hydropore oral and the adradial side of the proximal posterior coverplate of ambulacrum V. The left tip intersects the edge of the primary posterior oral, but the opening does not continue along the edge of this plate. The second proximal posterior coverplate of ambulacrum V is shortened adradially where it abuts the distal anterior edge of the hydropore oral which juts into the edge of ambulacrum V.

The straight ambulacra, normally five in number, are moderate in both length and width. They are smaller than those of *Cryptogoleus reticulatus*, the only other *Cryptogoleus* that approaches the small size of this species. As in *C. chapmani,* the ambulacra taper only slightly and the



Text figure 20. ***Cryptogoleus multibrachiatus*** (Raymond), 1915
A. GSC 7789-A, (x 5), pl. 22, fig. 7. Distal ambulacral floorplate of ambulacrum III is shaded.
B. Holotype, GSC 7789, (x 8), pl. 22, fig. 2.

terminations are blunt. The distal tips occasionally intrude into the proximal circlet of peripheral rim plates, but commonly they end adjacent to the rim, without penetration (pl. 22).

The ambulacral coverplates are moderately convex externally, as are those in *C. reticulatus*. The external foramina of the coverplate passageways are thus in shallow troughs formed by the lateral sides of the coverplates. The coverplates appear to be slightly narrower than those of the other species of the genus in proportion to thecal diameter; therefore, there are proportionately a few more plates per ambulacrum.

The interambulacral areas are moderate in size, formed by small, squamose, imbricate plates. These plates are relatively more numerous than those of the other species of *Cryptogoleus*. The exterior of each interambulacral has a large, low, central node which makes these plates appear bulbous and tessellate.

The anal structure of *Cryptogoleus multibrachiatus* includes 6 to 10 plates. These are large and subtriangular. The structure is disrupted in all known specimens but appears to be similar to that of other *Cryptogoleus*.

The peripheral rim may include five to seven circlets. The transition plates have the same characteristic form as those in *C. chapmani*, but the sagittate crests appear to be less sharply defined.

Prosopon includes a fine pitting and large, high irregular nodes (pl. 22, fig. 1, 4) which occur sporadically on the, larger peripheral rim plates and interambulacrals. Either most nodes have been removed during preservation, or they were originally very spotty in distribution. Most specimens appear to be extensively etched, so it is not unlikely that much of the prosopon has been removed.

Specimens

GSC 7789. Holotype of *Cryptogoleus multibrachiatus* (Raymond) (1915, p. 60-61, pl. 1, fig. 2). " Crinoid beds of the Hull Formation." Trenton Group, Mohawkian Series, Middle Ordovician. Lift locks 3 miles north of Kirkfield, Ontario. 9.2 mm axial by 10 mm transverse diameter.

Text fig. 20B, pl. 22, fig. 1-3.

The holotype is unusual, for it has at least eight ambulacra. The theca has collapsed and the surface has been etched. The posterior sector is missing, including all of interambulacrum 5, most of the adjacent rim, and the anal structure. It appears that parts of all the ambulacra are present.

Ambulacra I and II are formed by the normal bifurcation of the left lateral primary ambulacral axis. Ambulacrum III bifurcates distal to the first pair of coverplates and forms two nearly equal branches. The main branch extends straight outward toward the anterior edge of the theca; the secondary branch veers to the left, into the area of interambulacrum 2. Ambulacra IV and V are difficult to interpret. It appears that two primary ambulacra are formed by the normal bifurcation of the right lateral primary axis. Immediately distal to this division ambulacrum IV splits again to form two main branches — the anterior of which extends to the peripheral rim, adjacent to the right branch of ambulacrum III, which is in the region normally occupied by interambulacrum 3. The other branch of ambulacrum IV extends outward for a distance of two pairs of coverplates and then bifurcates again to form two small ambulacral branches which reach the rim. Ambulacrum V appears to be normal. It is possible to interpret ambulacrum IV as normal but displaced anteriorly; thus ambulacrum V would be the subdivided radius. Neither ambulacrum I nor V appear to have sent branches into the posterior interambulacral area, which is now missing.

The peripheral rim includes six or seven circlets of plates. The transition plates appear to be almost as distinctive as those found in *C. chapmani.*

A few large nodes are preserved on the interambulacrals and larger rim plates. The small distal plates of the peripheral rim appear to be centrally elevated and form elongate ridges parallel to the length of the plate. These ridges may be prosopon, or the result of differential etching. A fine pitting is preserved on many of the interambulacral plates.

GSC 7789-A. Specimen housed with the holotype of *Cryptogoleus multibrachiatus* (Raymond). " Crinoid beds of the Hull Formation," Trenton Group, Mohawkian Series, Middle Ordovician. Lift locks 3 miles north of Kirkfield, Ontario. 7.6 mm axial by 8.8 mm transverse diameter.

Text fig. 20A, pl. 22, fig. 6, 7.

This specimen is with the holotype in the collection of the Geological Survey of Canada and may be the second individual referred to by Raymond (1915, p. 61) in the original description as seeming " to have only six rays." This specimen has only five ambulacra, but ambulacrum V is disrupted and the opposing coverplates are spread far apart, giving the appearance of two ambulacra.

The theca has collapsed and has been deeply etched and abraded, which exposes a subsurficial view of most thecal structures. This reveals the full diameter of the coverplate passageways, clearly seen under xylene (pl. 22, fig. 7). The terminal floorplate of ambulacrum III is exposed where the coverplates are disrupted.

USNM S-3894-A. Illustrated Specimen of *Cryptogoleus multibrachiatus* (Raymond) by Bassler, (1936, pl. 4, fig. 4). Hull Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Kirkfield, Ontario. 9.3 mm axial by 9.5 mm transverse diameter.

Pl. 22, fig. 4, 5.

This is one of four specimens numbered S-3894 in the United States National Museum, and was illustrated by Bassler (1936). The specimen is a normal *Cryptogoleus multibrachiatus* with five ambulacra. The theca has been etched, but the small, numerous interambulacrals retain their bulbous appearance and many of the large plates of the rim are foveolate. Remnants of several large, high nodes are preserved on the rim and interambulacral plates. The peripheral rim appears to be formed by only four or five rows of plates, obviously fewer than in the holotype. This individual is the best preserved example of the species known.

Discussion of previous investigation

Raymond (1915) described *Lebetodiscus multibrachiatus* as similar to *Cryptogoleus chapmani, C. youngi,* and *C. billingsi,* but specifically distinct because of its more numerous ambulacra. There are eight in the holotype, and a second specimen (GSC 7789-A) was described as having six. Raymond (1921) republished the description and assigned *Lebetodiscus multibrachiatus* to *Carneyella* Foerste (1917).

Bassler (1936) reillustrated the holotype of *Hemicystites multibrachiatus* (Raymond) and also illustrated a specimen with five ambulacra. He interpreted the number of ambulacra in the holotype as extraordinary. Bassler took cognizance of the size of the ambulacra and the number of coverplates per ambulacrum, the size of the interambulacral areas, and the presence of nodes on the wide peripheral rim.

Discussion

Cryptogoleus multibrachiatus (Raymond) is slightly smaller than *C. reticulatus* in average thecal diameter. In contrast with *C. reticulatus,* which has numerous large pits on all thecal plates, *C. multibrachiatus* has a fine pitting which occurs only on the larger plates of the peripheral rim and interambulacra. Moreover, *C. multibrachiatus* has large, irregular nodes scattered over the interambulacral and rim plates; these are not found in any other species of *Cryptogoleus.* The ambulacra of *C. multibrachiatus* are somewhat narrower and shorter than in other *Cryptogoleus* species and only occasionally intrude into the rim. The interambulacra are thus larger, and the individual plates appear to be relatively smaller, than in other species. Moreover, the interambulacrals appear to be bulbous from the exterior. The ambulacral coverplates of *C. multibrachiatus* are slightly narrower than those of other *Cryptogoleus,* and are therefore proportionately more numerous per ambulacrum.

The description of *Cryptogoleus multibrachiatus* is based on only a few specimens. Private collectors indicate that the species is not rare at the type locality.

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

Cryptogoleus youngi (Raymond), 1915

Text fig. 21; plate 23, fig. 1-3

1915 *Lebetodiscus youngi* Raymond, P. E., Ottawa Naturalist 29 (5-6): 58, pl. 1, fig. 4.

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

1921 *Carneyella youngi* (Raymond), Raymond, P. E., Geol. Surv. Canada, Mus. Bull. 31 (Geol. Series 38): 9, pl. 3, fig. 4.

1935 *Hemicystites youngi* (Raymond), Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 7.

1936 *Hemicystites (Lebetodiscus) youngi* (Raymond), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 12, pl. 3, fig. 1.

1943 *Hemicystites youngi* (Raymond), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 204.

Diagnosis (tentative)

A *Cryptogoleus* with: moderate-sized theca; ambulacra straight, wide; peripheral rim transition plates apparently without characteristic form; thecal plates smooth.

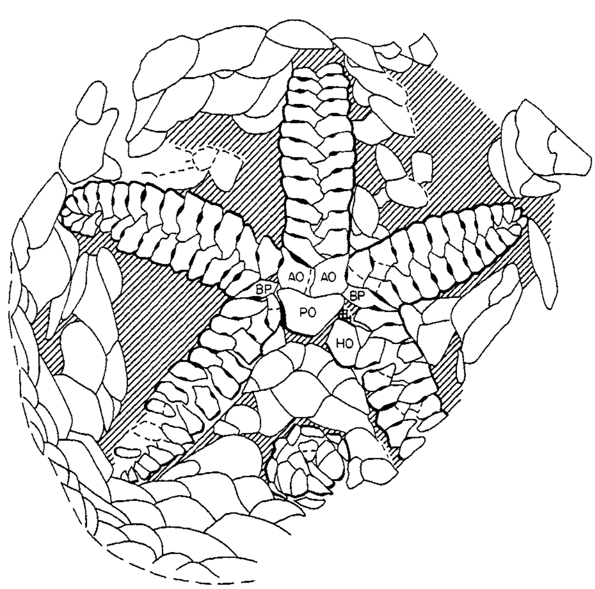
Description

Cryptogoleus youngi (Raymond) is monotypic and the holotype is a poor specimen which is partially disrupted and deeply etched (text fig. 21, pl. 23, fig. 1-3). The species is here recognized only with question.

The theca is domal, over 12 mm in diameter. The oral area appears to be similar to that of other species of *Cryptogoleus*. The hydropore structure is disrupted and the proximal coverplate of the posterior side of ambulacrum V is missing.

The ambulacra are moderately wide and long. Unlike those of *C. chapmani*, they are straight and show no tendency to curve. The ambulacra slowly taper distally, and the terminations are blunt.

The ambulacral coverplates appear almost flat externally, like those of *C. chapmani*, but they are deeply etched and could have been convex as in the other species of the genus. The partially exposed intra-ambulacral and intrathecal coverplate extensions appear similar to those of other *Cryptogoleus*.



Text figure 21. ***Cryptogoleus youngi*** **(Raymond), 1915**

Holotype, GSC 3234, (x 6), pl. 23, fig. 2. AO, anterior primary oral plate; BP, lateral bifurcation plate; HO, hydropore oral plate; PO, posterior primary oral plate.

The few preserved interambulacrals are moderate-sized, squamose, imbricate plates, proportionately about equal in size to those of *C. chapmani* or *C. reticulatus*.

This individual is the only specimen assigned to the family in which the proximal circlet of peripheral rim plates is not distinctly set off from the adjacent interambulacral plates. In light of the disrupted and weathered condition of the specimen, this feature is probably preservational. The outer plates of the peripheral rim have been lost. Transition plates are apparently squamose and without characteristic form.

The anal plates are unusually large, few in number, and loosely grouped into two circlets. As in other *Cryptogoleus*, the structure appears to be intermediate between a periproct and a valvular type.

Thecal plates are now smooth, but the deep etching of the specimen would have removed prosopon.

Specimen

GSC 3234. Holotype of *Cryptogoleus youngi* (Raymond) (1915, p. 58, pl. 1, fig. 4). Upper part of the *Prasopora* beds (Sherman Falls) of the Trenton Group, Mohawkian Series, Middle Ordovician. Lot 10, Con. 1, Eldon Township, Victoria County, Ontario. 12.5 mm axial by 12.2 mm transverse diameter.

Text fig. 21, pl. 23, fig. 1-3.

The holotype is partially collapsed, and a fragment of a brachiopod shell projects vertically up into interambulacrum 1 from the underlying limestone. The thecal diameter was several millimeters larger before loss of the outer rim plates.

Discussion

Raymond described *Lebetodiscus youngi* (1915) by contrasting it with *Cryptogoleus billingsi*. Foerste (1917) transferred the species to his new genus *Carneyella*, which Raymond (1921) accepted. Bassler (1936) reillustrated the type and assigned it to *Hemicystites*, but contributed nothing new in his brief description.

Cryptogoleus youngi is recognized here only with question because the apparently distinctive characters could be attributed to preservational alterations of the single specimen.

Cryptogoleus platys (Raymond), 1915
Text fig. 22; plate 23, fig. 4-7

1915 *Lebetodiscus platys* Raymond, P. E., Ottawa Naturalist 29 (5-6): 59-60, pl. 1, fig. 5.

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

1921 *Carneyella platys* (Raymond), Raymond, P. E., Geol. Surv. Canada, Mus. Bull. 31 (Geol. Series 38): 10-11, pl. 3, fig. 7.

1936 *Carneyella (Lebetodiscus) platys* (Raymond), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 7, pl. 7, fig. 15.

1943 *Carneyella? platys* (Raymond), Bassler, R. S., and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 198.

1946 *Carneyella? platys* (Raymond), Wilson, A. E., Geol. Surv. Canada, Bull. 4: 20.

Diagnosis (tentative)

A *Cryptogoleus* with: theca large, ambulacra long and straight; ambulacral terminations penetrating far into peripheral rim; ambulacral coverplates relatively narrower and more numerous; interambulacral plates moderate in size, relatively numerous.

Description

Cryptogoleus platys (Raymond) is based upon a single flattened and deeply etched specimen which apppears to differ from other *Cryptogoleus* species (text fig. 22A, B, pl. 23, fig. 4-7). However, these differences could be preservational, or intraspecific variation, and the species is recognized only with doubt.

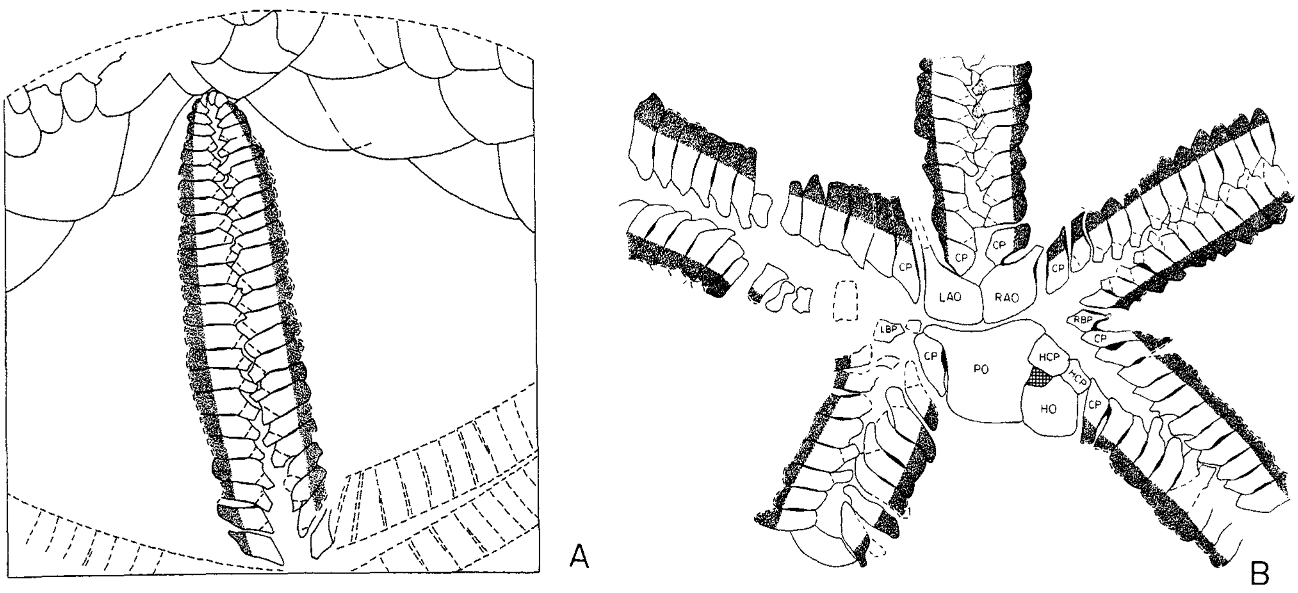
The domal theca was over 23.5 mm in diameter. The oral and hydropore structures are similar to those of other *Cryptogoleus*, although the oral plates appear proportionately larger here. This may be due to the subsurficial view of this region, which is exposed by deep etching. The external hydropore structure has been dissolved away and a sectional view of the subcircular upper part of the stone canal passageway is exposed.

The ambulacra are long, moderately wide, and straight. The slight curvature of ambulacra III and V appears to be preservational. Distally, the ambulacra extend between plates of the proximal and apparently also of the second circlet of peripheral rim plates. The depth of penetration is greater than in any other *Cryptogoleus*. It may have been accentuated by the extreme flattening of the specimen.

The deep etching of the ambulacral coverplates partially exposes the intra-ambulacral and intrathecal extensions (see shaded areas of text fig. 22). The coverplates appear somewhat narrower than in *C. chapmani*, the only other large species of *Cryptogoleus*. Therefore, they are more numerous in proportion to thecal diameter. In comparing the type specimens, *C. platys* is seen to have 0.3 more coverplates per millimeter than *C. chapmani*.

An oblique section view of one ambulacral floorplate is exposed at the broken tip of ambulacrum I. The floorplates appear to be uniserial and trough-shaped.

The interambulacrals are squamose, imbricate plates, moderate in size. These elements are relatively smaller



Text figure 22. ***Cryptogoleus platys*** **(Raymond), 1915**

Holotype, GSC 7941. Coverplate intrathecal extensions, exposed where interambulacral plates are disrupted, are stippled.

A. Ambulacrum IV, (x 7), pl. 23, fig. 7.

B. Oral region and proximal parts of ambulacra, (x 7), pl. 23, fig. 6.

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

and more numerous than the interambulacrals of *C. chapmani.*

The anal structure is missing.

The peripheral rim is poorly preserved and several outer circlets are missing.

The exteriors of all the plates are missing and thus any prosopon that might have been present is gone.

Specimen

GSC 7941. Holotype of *Cryptogoleus platys* (Raymond) (1915, p. 59-60, pl. 1, fig. 5). Cobourg beds, Trenton Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario. [Raymond, 1915, noted that the specimen was collected by T. C. Weston in 1881, probably from the "Cystid beds" at the foot of Parliament Hill, or Queens Wharf, Ottawa.] 20.5 mm axial by 23.8 mm transverse diameter.

Text fig. 22A, B, pl. 23, fig. 4-7.

The extreme flatness of the specimen suggests that the inner side of the plates have also been etched, reducing the height of the ambulacra, oral area, and proximal rim plates. The exterior surficial etching has been selective; the central parts of the plate exteriors are more deeply eroded than the edges. Each plate has a "depressed" center surrounded by a raised rim which is formed by the less etched edge. Thus the external suture lines between contiguous elements now lie along the tops of small ridges and give a very distinctive exterior appearance.

The left posterior section of the theca is missing, including the anal structure, the distal half of ambulacrum I, the tip of ambulacrum V, and the adjacent interambulacral and peripheral rim plates.

Discussion

Lebetodiscus platys Raymond (1915) was attributed by Foerste (1917) to his genus *Carneyella* and Raymond (1921) followed this assignment. Raymond believed that this species differs from *Cryptogoleus chapmani* in being larger, having longer and more slender ambulacra, a less circular theca, and ambulacra I and IV [misprint for V] curving slightly toward the anal area. Bassler (1936) also placed *Cryptogoleus platys* in the genus *Carneyella*, although "with doubt," as did Wilson (1946).

Cryptogoleus billingsi (Chapman), 1860

1860 *Agelacrinites billingsii* Chapman, E. J., Canadian Jour. Industry, Sci. and Art (n.s.) 5: 358-365, text fig. 1.

1861 *Agelacrinites billingsii* Chapman, E. J., Canadian Jour. Industry, Sci. and Art (n.s.) 6: 516, text fig. 86.

1864 *Agelacrinites billingsii* Chapman, E. J., A Popular and Practical Exposition of the Minerals and Geology of Canada, Toronto: 100, text fig. 86.

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

1901 *Agelacrinites billingsi* Chapman, Clarke, J. M., New York State Mus., Bull. 49 (2): 189, 191.

1915 *Hemicystites billingsi* (Chapman), Bassler, R. S., United States Nat. Mus. Bull. 92, 1: 606.

1915 *Lebetodiscus billingsi* (Chapman), Raymond, P. E. [*partim*], Ottawa Naturalist 29 (5-6): 56-58.

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

1918 *Agelacrinites billingsi* Chapman, Williams, S. R., Ohio Jour. Sci. 19 (1): 62.

1921 *Carneyella billingsi* (Chapman), Raymond, P. E. [*partim*], Geol. Surv. Canada, Mus. Bull. 31 (Geol. Series 38): 7-9, [*non*] pl. 3, fig. 31.

1935 *Hemicystites billingsi* (Chapman), Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 7.

1936 [*non*] *Hemicystites billingsi* (Chapman), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 12, pl. 3, fig. 2.

1943 *Hemicystites billingsi* (Chapman), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 202.

Discussion

Agelacrinites billingsi Chapman (1860) is based upon one specimen, which is now lost, from the " Trenton Limestone " (Trenton Group, Mohawkian Series, Middle Ordovician) at Peterborough, Ontario. Chapman (1860, p. 359–361) characterized the species as having: a circular theca, 0.5 inches in diameter and domal in shape, with five large orals, one separating each ambulacrum from the adjacent ray [*i.e.*, three primary orals and two lateral bifurcation plates]; five short, straight ambulacra having a single biseries of coverplates; " pores " unseen, if present; interambulacrals numerous squamose imbricate plates, without definite arrangement; marginal part of the theca a peripheral rim with small outer plates elongate normal to the thecal margin; proximal circlet of rim plates not distinctly separated from the adjacent interambulacrals, but rather, the proximal rim plates appear to grade into the interambulacral plate series; anus a " well marked pyramidal orifice " of two circlets of five plates each, the plates of one circlet alternating in position with the plates of the other; theca resting directly upon a firm carbonate substrate.

Chapman's detailed description of his species suggests that it is a *Cryptogoleus* on the basis of the thecal shape, the structure of the oral area, and the nature of the ambulacra and the interambulacra. The anus is perhaps unique if, in fact, it is a well-formed valvular type, as the description and accompanying illustration suggest. The most significant feature in Chapman's description is the apparent gradation of plates from the peripheral rim to the interambulacra. The lack of a distinct proximal circlet of rim plates was stressed by Chapman to contrast this species with other edrioasteroids. This feature would separate *C. billingsi* from all other species of *Cryptogoleus* except *C. youngi*, which has larger and far fewer interambulacrals. No specimen of *C. billingsi* (Chapman) has been seen.

Suborder Isorophina Bell, *subord. nov.*

Diagnosis

Isorophida with: center of oral area formed by four large primary orals or many small plates not differentiated from other orals; ambulacral coverplates forming multiple alternating biseries or cyclic series which include two to seven sets of plates; coverplates having intra-ambulacral extensions; intrathecal coverplate extensions found in some; contiguous ambulacral floorplates commonly abutting along vertical sutures; anal structure valvular.

Description

Species included in the Isorophina have either domal or clavate thecae.

The oral area may include externally differentiated primaries, secondaries, shared coverplate pairs, and hydropore orals. Commonly, however, the area is covered by numerous small plates which reflect the ambulacral coverplate pattern. When differentiated, four primary orals form the center of the area. These may be flanked by shared coverplates and secondary orals, or by numerous plates similar in shape and size to the proximal ambulacral coverplates. The number of orals which form the transverse oral midline greatly exceeds the number along the anterior midline. Thus the transverse elongation of the oral area outline is pronounced.

The hydropore structure lies along the posterior side of the oral region, commonly offset to the right, flanking the proximal posterior edge of ambulacrum V. The structure is formed by oral-ambulacral series plates.

The ambulacral coverplates include two or more sets of plates which form either multiple alternating biseries or cyclic series of plates. The perradial line is zigzag or serrate in forms with multiple biseries. Cyclic series coverplates commonly form sinuous, undulating perradial lines, sometimes with serrations superimposed on the major undulations. Intra-ambulacral coverplate extensions are believed to be present in all species, but intrathecal extensions are developed only in some.

The uniserial ambulacral floorplates commonly abut one another along vertical sutures. However, in at least one species the floorplates imbricate and each proximally overlaps the adjacent proximal plate. Floorplates may be relatively thin and trough-shaped, or they may be thick. Large lateral protuberances may extend into the thecal cavity from inner surfaces of the floorplates.

Interambulacral areas are covered by squamose imbricate plates, or by polygonal tessellate ones.

The valvular anal structure commonly is formed by two circlets of large triangular plates. Outer circlet plates overlap and alternate with inner circlet ones. The anals are beveled along the zone of lateral overlap and form tightly fitting, oblique sutures. Occasionally the valvular anus appears to include either only one or three circlets of plates.

The peripheral rim is formed by geniculate plates. The large plates of the proximal circlet commonly alternate to form a proximal and a distal subcirclet.

Discussion

The suborder Isorophina includes most species placed by Bassler (1935, 1936), Regnéll (1966). and others in the family Agelacrinitidae as emended by Bassler (1935).

The Isorophina are contrasted with the Lebetodiscina under the discussion of the latter. The Isorophina includes two families: the Isorophidae, which appear in the Middle Ordovician, and the Agelacrinitidae, first recorded in the Middle Devonian. The Agelacrinitidae are thought to have evolved out of the Isorophidae. This process apparently included: 1) the gradual increase in number of oral plates in conjunction with the suppression of primary oral plate differentiation; 2) an increase in the number of ambulacral coverplate sets and modification of the pattern from a multiple alternating biseries to serial cyclic coverplates; 3) derivation of clavate thecal forms and associated peduncular zone plates; 4) probably the exclusion of intrathecal oral plate extensions from the oral frame structure.

RANGE AND OCCURRENCE: Middle Ordovician to Pennsylvanian of North America (Europe, Asia).

Family ISOROPHIDAE Bell, *fam. nov.*

Type genus: *Isorophus* Foerste, 1917

Diagnosis

Isorophina with: domal theca; oral area including four primary orals, two pairs of lateral shared coverplates, one large hydropore oral, and secondary orals; hydropore structure having few plates, integrated with central oral rise; ambulacral coverplates forming alternating multiple biseries; interambulacrals squamose and imbricate.

Description

Most Isorophidae are small to moderate-sized edrioasteroids, 10 to 20 mm being common adult diameters.

The oral region arches upward as a low, rounded, central oral rise which surrounds the oral pole. Distally the oral rise merges with the equally elevated proximal ends of the ambulacra. The four large primary orals externally extend proximally from the interambulacra to meet centrally along the transverse and anterior oral midlines. The lateral shared coverplates, one pair flanking each side of the central primary orals, are somewhat smaller than the primaries. They intersect the transverse midline near the lateral bifurcation plates. A variable number of small secondary orals commonly lie along the transverse and anterior oral midlines. A large hydropore oral abuts the right margin of the right posterior primary oral and forms an asymmetrical posterior bulge in the outline of the oral area. It extends along the proximal part of the posterior side of ambulacrum V.

The oral frame, underlying the orals, is formed by the five proximal ambulacral floorplates and intrathecal extensions of at least the four primary oral plates. The frame surrounds a large, central lumen that extends downward from the proximal ends of the ambulacral tunnels and opens directly into the underlying thecal cavity. A prominent posterior gap in the frame affords direct lateral communication between the lumen and the thecal cavity beneath interambulacrum 5. The frame appears to vary in detail between species but remains inadequately known.

The hydropore structure is in the right posterior part of the oral region, adjacent to the proximal part of the posterior side of ambulacrum V. The structure is integrated with the oral rise except for the commonly thickened edges of the hydropore plates, which form a raised rim surrounding the opening. The structure is formed by the right posterior primary oral, the hydropore oral, the right posterior shared coverplate, and a few other plates of the oral-ambulacral series. The slitlike opening usually extends along the anterior edge of the large hydropore oral and ends proximally against the right posterior primary oral. The anterior side of the opening is formed by no more than four other plates of the oral-ambulacral series.

The ambulacra are characterized externally by multiple biseries of coverplates, which are formed by two or more distinct plate sets. Most common is a double biseries, formed by alternating pairs of large primary and smaller secondary coverplates. In species with triple biseries, a third set of small tertiary coverplates is inserted along both sides of the perradial tips of the secondaries. Thus there are two pairs of tertiaries for each pair of primary or secondary coverplates.

Intra-ambulacral extensions lock the coverplates together when closed. At least the large primary coverplates have intrathecal extensions which project into the thecal cavity. They extend between the lateral margins of the floorplates and the adjacent interambulacrals.

The ambulacral floorplates are uniserial and trough-shaped. The upper surface is centrally concave and forms a trough that extends the length of the ambulacra. Laterally the upper surfaces are usually horizontal or nearly so, and form a relatively wide articulation zone on which the bases of the overlying coverplates rest. The inner sides of the floorplates are evenly convex inward. Sutures between contiguous floorplates are vertical or nearly so. Interambulacral plates vary in proportional size when compared to thecal diameter.

The valvular anal structure is formed by an inner and outer circlet of large triangular plates, alternately disposed. The anals appear to vary in number (12 to 20 or possibly more have been seen).

The proximal circlet of the peripheral rim is formed by large plates commonly subdivided into alternating proximal and distal subcirclets. The two or three proximal circlets of rim plates are externally elongate concentric with the thecal margin. These may be separated from the distal circlets of radially elongate plates by a series of transition circlet plates which have a characteristic form. All of the larger rim plates are geniculate with the bases of the inner parts parallel to the substrate. Vertical ridges are commonly formed on the basal surfaces of the geniculate plates.

Thecal plates are commonly smooth. Prosopon consisting of a fine pitting or of protuberances may occur, but is always subdued.

Discussion

The Isorophidae appear to be the older and simpler Isorophina. The domal theca varies only in the degree of convexity of the oral surface, whereas the Agelacrinitidae often have clavate thecae.

The Isorophidae oral area is formed by nine basic plates and only a few secondary orals. The hydropore structure, also composed of relatively few plates, is integrated into the central oral rise. In contrast, the Agelacrinitidae are characterized by numerous oral plates and a multiplated hydropore structure that commonly forms a separate, prominent rise posterior to the central oral rise.

The Isorophidae ambulacra are characterized by simple multiple biseries of coverplates in which pairs of each series alternate along the ambulacra. Complex cyclic coverplate series are developed only in the Agelacrinitidae. The ambulacral floorplates are plain, trough-shaped elements that lack the protuberances frequently observed on the inner sides of the floorplates of the Agelacrinitidae.

Interambulacral areas of Isorophidae are commonly covered with squamose, imbricate plates. Both squamose, imbricate interambulacrals and thick, polygonal, tessellate interambulacrals are found in the Agelacrinitidae.

Suspected structural differences between the Isorophidae and the Agelacrinitidae include the details of the oral frame and stone canal passageway structures, as well as the mode of coverplate articulation with the floorplates. Unfortunately, these areas are not adequately exposed in most specimens.

RANGE AND OCCURRENCE: Black River Group, Middle Ordovician through Clinton Group, Middle Silurian of northeastern North America.

Genus *Isorophus* Foerste, 1917

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

1851 *Agelacrinus* Vanuxem, Roemer, F. [*partim*], Decheniana 8: 370-375, pl. 8, fig. 3a-b.

1855 *Agelacrinus* Vanuxem, Roemer, F. [*partim*], *in* Lethaea Geognostica, H. G. Bronn, 3rd edition, Stuttgart, Bd. 1, pt. 2, Palaeo-Lethaea, 2: 275-278, pl. 4, fig. 6.

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

1866 *Agelacrinus* Vanuxem, Hall, J. [*partim*], New York State Mus., 20th Ann. Rept. (adv. pub.): 6-7.

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

1871 *Agelacrinus* Vanuxem, Hall, J. [*partim*], New York State Mus., 24th Ann. Rept. (adv. pub.): pl. 2, fig. 7.

1872 *Agelacrinus* Vanuxem, Hall, J. [*partim*], New York State Mus., 24th Ann. Rept.: 214, pl. 6, fig. 7.

1873 *Agelacrinites* Vanuxem, Meek, F. B. [*partim*], Geol. Surv. Ohio, v. 1, Geology and Palaeontology, pt. 2, Palaeontology, Sect. 1: 55-56, pl. 3, fig. 6a-b.

1876 *Agelacrinus* Vanuxem, Roemer, F., Lethaea Geognostica, Theil 1, Lethaea palaeozoica (Atlas), Stuttgart: pl. 3, fig. 16.

1876 *Agelacrinus* Vanuxem, Quenstedt, F. A. [*partim*], Petrefaktenkunde Deutschlands, Tübingen, 4 (12): 706-707, pl. 114, fig. 56.

1878 *Agelacrinus* Vanuxem, James, U. P., The Paleontologist, Cincinnati, 1: 2-3.

1883 *Agelacrinus* Vanuxem, James, U. P., The Paleontologist, Cincinnati, 7: 58, pl. 2, fig. 3, 3a.

1887 *Agelacrinus* Vanuxem, James, U. P., Cincinnati Soc. Nat. Hist., Jour. 10: 25-26, text fig. A, B.

1887 *Agelacrinus* Vanuxem, Barrande, J. [*partim*], Systéme Silurien du centre de la Bohéme, Prague, pt. 1, 7 (1): 56.

1889 *Agelacrinus* Vanuxem, Miller, S. A. [*partim*], North American Geology and Palaeontology, Cincinnati: 221-222, text fig. 241.

1890 *Agelacrinus* Vanuxem, Steinmann, G. and Doderlein, L. [*partim*], Elemente der Paläontologie, Leipzig: 181-182, text fig. 177.

1896b *Lepidodiscus* Meek and Worthen [*non* Hall], Haeckel, E., Die Amphorideen und Cystoideen, Leipzig, 1: 113-114, text fig. 16.

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

1900a *Lepidodiscus* Meek and Worthen, Bather, F. A. [*partim*], *in* A Treatise on Zoology, E. R. Lankester (ed.), London, pt. III, Echinoderma: 207-208, text fig. 4.

1901 *Agelacrinites* Vanuxem, Clarke, J. M. [*partim*], New York State Mus., Bull. 49 (2): 185-193, text fig. 2.

1903 *Lepidodiscus* Meek and Worthen, Delage, Y. and Herouard, E. [*partim*], Traité de Zoologie Concréte, T. 3, Echinodermes, Paris: 415, text fig. 552.

1903 *Agelacrinus* Vanuxem, Steinmann, G. [*partim*], Einführung in die Paläontologie, Leipzig: 192-193, text fig. 263.

1904 *Agelacrinus* Vanuxem, Spencer, W. K. [*partim*], Royal Soc. London, Proc. 74: 39-43, pl. 1, fig. 2.

1910 *Agelacrinus* Vanuxem, Grabau, A. W. and Shimer, H. W. [*partim*], North American Index Fossils, Invertebrates, New York, 2: 472, text fig. 1784b.

1914 *Agelacrinus* Vanuxem, Foerste, A. F. [*partim*], Denison Univ., Sci. Lab. Bull. 17 (art. 14): 399-454, pl. 1, fig. 1a-f, 4a-b, 6a-c, pl. 2, fig. 3, pl. 4, fig. 1, pl. 6, fig. 1a-c.

1915 *Agelacrinites* Vanuxem, Bassler, R. S. [*partim*], United States Nat. Mus. Bull. 92, 1: 19-21.

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

1918 *Agelacrinus* Vanuxem, Williams, S. R. [*partim*], Ohio Jour. Sci. 19 (1): 62-81, pl. 1, fig. 2, pl. 2, fig. 8-9, 11-12, pl. 3, fig. 13-18, pl. 4, fig. 20-25a, pl. 5, fig. 26-27, pl. 6, fig. 32-37, pl. 7, fig. 38-44, 46, pl. 8, fig. 50-51b, pl. 9, fig. 52, 55.

1935 *Isorophus* Foerste, Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 4-5.

1936 *Isorophus* Foerste, Bassler, R. S., Smithsonian Misc. Coll. 95, (6): 16-19, pl. 2, fig. 1, 9, pl. 5, fig. 2-3, 8-9, 11, pl. 6, fig. 1-2, 11; *Carneyella* Foerste, *idem* [*partim*], *ibid.*: pl. 2, fig. 15.

1938 *Isorophus* Foerste, Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 119.

1943 *Isorophus* Foerste, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 204-205.

1944 *Isorophus* Foerste, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 129-131, pl. 49, fig. 8.

1953 *Lepidodiscus* Meek and Worthen, Piveteau, J. [*partim*], Traité de Paléontologie, Paris, 3: 653, text fig. 4.

1960 *Isorophus* Foerste, Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 158-159, pl. 10, fig. 1-4, pl. 11, fig. 1-2, pl. 12, fig. 1-6.

1960 *Isorophus* Foerste, Kesling, R. V. and Mintz, L. W., Univ. Michigan, Contrib. Mus. Paleont. 15 (14): 315-338, pl. 1, fig. 1-2, pl. 2, fig. 1-2, pl. 3, fig. 1-9, pl. 4, fig. 1-6, pl. 9, fig. 1-2.

1966 *Isorophus* Foerste, Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U169, text fig. 121, 128-1, 129-2, 130-1.

TYPE SPECIES: *Agelacrinus cincinnatiensis* Roemer, 1851.

Diagnosis

Isorophidae with: ambulacra curved, I–IV contrasolar, V solar; ambulacral coverplates in double alternating biseries; ambulacra proportionately moderate in width with gradual distal taper; interambulacral plates squamose, imbricate.

Description

The theca of *Isorophus* is domal; adult diameters range from 10 to 25 mm.

In the oral area (text fig. 23A), the two anterior primary orals are large and subequal in size. Commonly the posterior primary oral is equal to or smaller than either anterior oral. The right posterior primary oral is largest, frequently nearly twice the size of the left posterior primary. The proximal edge of the right posterior primary oral abuts both the right and left anterior primary orals, restricting the contact of the left posterior oral to the left lateral segment of the perradial side of the left anterior oral.

One pair of lateral shared coverplates flank the primary orals on each side of the oral region. Adradially, the shared coverplates are in contact with the primary orals, but intervening secondary orals separate their perradial ends. Commonly one pair of secondary orals lie between each pair of shared coverplates and the primary orals, but occasionally additional secondary orals lie adjacent to the original pair, either singly or as an additional pair. Development of the additional secondary orals is random and their presence on one side of the oral region is independent of the opposing side. One or two secondaries may lie anterior to the anterior primary orals along the anterior oral midline. The maximum number of lateral secondary orals encountered is seven, the minimum is four.

The lateral shared coverplates are flanked distally by the proximal coverplates of the lateral ambulacra and by the proximal tips of the lateral bifurcation plates. Occasionally one of the proximal ambulacral coverplates lies far enough proximally to separate the tips of a shared coverplate and the adjacent bifurcation plate.

The hydropore oral lies adjacent to the right margin of the right posterior primary oral. It extends distally along the posterior adradial end of the right posterior shared coverplate and the proximal primary coverplate of ambulacrum V. This distal extension forms a prominent, asymmetrical, posterior bulge in the outline of the oral region.

The oral frame extends down into the thecal cavity below the adjacent ambulacral floorplates. The subovate frame is transversely elongate with attenuated lateral extremities. It is formed by the inwardly extended proximal edges of the five proximal ambulacral floorplates and the intrathecal extensions of the four primary orals. Proximally, it surrounds the ovate central lumen which opens downward into the thecal cavity. The lumen is also connected laterally to the posterior sector of the thecal cavity via a large gap in the posterior side of the frame, between ambulacra I and V. Bifurcating extensions from the proximal floorplates of these two ambulacra define a small subchamber between the central lumen and the posterior thecal cavity. Details of the frame construction are known only from *Isorophus cincinnatiensis.*

The hydropore structure basically includes five plates: the hydropore oral, the right edge of the right posterior primary oral, the right posterior shared coverplate, and the first two primary posterior coverplates of ambulacrum V (text fig. 23A). The elongate, slitlike hydropore is bounded posteriorly by the anterior edge of the hydropore oral. The anterior edge is formed mostly by the adradial edges of the right posterior shared coverplate and the proximal coverplate of ambulacrum V. In many individuals the opening appears to be limited to the region between these plates, whereas in others the extremities appear to extend further, formed by the right primary posterior oral and the second primary coverplate of ambulacrum V. Preservational distortion may account for this variability. In one species the second proximal, posterior secondary coverplate also forms part of the anterior boundary of the opening. A raised rim surrounding the opening is formed by the thickened edges of the adjacent plates.

The stone canal passageway leads from the hydropore into the thecal cavity and opens adjacent to the right posterior side of the oral frame. The passageway is a short, subconical funnel that rapidly increases in diameter inwardly. The upper sector is formed by intrathecal extensions of the plates which surround the external hydropore, *i.e.*, the hydropore oral, the right posterior primary oral, the right posterior shared coverplate, and the proximal two primary coverplates of ambulacrum V. The intrathecal extension of the hydropore oral and the right posterior primary oral extend into the theca the full length of the passageway, whereas the other upper elements are replaced inwardly by the adjacent sides of the proximal two floorplates of ambulacrum V.

The rate of ambulacral curvature (I-IV contrasolar, V solar) appears to vary intraspecifically, but is generally gradual. Curvature is initiated a short distance from the oral region and increases to a maximum as the ambulacra approach the peripheral rim. Beyond this point they are concentric with the proximal margin of the rim. The distal tips may closely approach adjacent ambulacra, or remain separated from them. The distal tips curve back toward the oral area in some large *Isorophus cincinnatiensis.* In small specimens representing young individuals, the ambulacra do not reach the rim and show only slight curvature.

Externally the ambulacra are elevated above the adjacent interambulacra as low, rounded ridges which merge proximally with the central oral rise. This elevation is due to the moderate inclination of the coverplates.

The ambulacral coverplates form a double biseries of alternating pairs of primary and secondary sets of plates. Plates of the two sets may be nearly equal in external size, and recognition of the member sets is thus difficult. In other species the primary plates are distinctly larger than the secondaries. Here the smaller secondaries are externally restricted to the medial sector of the ambulacra and separate the perradial tips of adradially contiguous large primary coverplates.

Opposing members of plate pairs of both primary and secondary sets are usually in contact along the perradial line. Occasional unpaired coverplates interrupt the regularity of the alternation of plate pairs of the two sets. Moreover, additional irregularity may occur through the separation of opposing plates of a single pair by the intercalation of a single plate of the other set.

The lateral sutures between the coverplates of adjacent primary and secondary sets are oblique; the primary plates overlap the secondaries. The plate edges of both sets are beveled to fit snugly together. In species with externally large primary and small secondary plates, the zone of overlap is extensive and the adradial ends of the secondary plates are hidden beneath the overlapping primaries.

Both primary and secondary coverplates have intrathecal extensions that lie between the adjacent interambulacrals and the underlying floorplates. Extensions of the coverplates are large, and continue beyond the lateral margins of the floorplates into the thecal cavity. Immediately past the floorplate margins, the extensions rapidly constrict to approximately one-fourth the coverplate width but may expand distally to nearly the original plate width. The extensions of the secondary coverplates end at the lateral margins of the floorplates.

Viewed from the inner surface, only the longer primary coverplate extensions are easily seen. They are separated by large, ovate gaps formed by the reduced width of the intrathecal extensions and by the apparent absence of intervening extensions of the secondary coverplates. However, these spaces are blocked at the lateral margins of the floorplates by the inner ends of the extensions of the secondary coverplates. Thus there are no openings from the thecal cavity to the ambulacral tunnels as the prominent spaces between the primary coverplate extensions might suggest.

Both primary and secondary ambulacral coverplates have small, bladelike intra-ambulacral extensions. These are limited to the more perradial part of the plates and extend obliquely inward in a proximal direction. When the coverplates are closed, each extension is in contact with the inner side of the adjacent proximal plate. The zone of underlap is small, but sufficient to wedge each element under the next coverplate. Moreover, the perradial tips of the extensions extend under the distal, perradial edge of the alternate coverplate, thereby also interlocking the coverplates across the perradial line.

The uniserial ambulacral floorplates of *Isorophus* are trough-shaped; they abut one another along nearly vertical sutures. The inner side of each is evenly convex inward, whereas the upper surface is centrally concave, but laterally the edges flare outward and form a nearly level marginal zone. The ambulacral coverplates rest upon the upper surface of these flared lateral margins (articulation zones). The ambulacral tunnel is low and broad.

The interambulacra of *Isorophus* are formed by squamose, imbricate plates, without definite arrangement. The largest plates are central and distal.

The valvular anal structure is commonly offset slightly from the center of interambulacrum V, toward the right posterior, but the location is variable. The structure includes one inner and one outer circlet of triangular plates; plates of the two circlets are alternate. Plates of the outer circlet overlap those of the inner circlet and the oblique surfaces of contact are beveled to fit tightly together. When the structure is closed, as it is most commonly preserved, only the central third of the inner circlet plates is visible externally between the overlapping edges of the outer circlet plates.

The anal structure is often surrounded by one or two rows of small plates which form irregular circlets. These are surrounded by large interambulacrals, equal in size to the central plates of the other interambulacra.

The peripheral rim includes 5 to 10 circlets; the plates diminish in size distally. Plates of the proximal two or three circlets are externally elongate concentric with the thecal margin; the more distal circlet plates are elongate radially. The central rim circlets form a transition zone between the two directions of elongation, and are made up of plates that are nearly equidimensional externally.

The large plates of the proximal circlet commonly form a proximal and distal subcirclet. The distal subcirclet elements laterally overlap the edges of the alternate proximal subcirclet plates, their lateral edges being distal to those of the adjacent proximal subcirclet plates. However, the regularity of this ordering is sometimes interrupted by a plate with one lateral edge distal to the adjacent plate, whereas its other edge is proximal to the next plate. Grouping of the more distal plates of the rim into distinct circlets is less apparent than in the proximal circlet. The gradational transition between plates elongate concentrically and plates elongate radially make distinct distal rim circlets less conspicuous.

The larger plates of the rim are geniculate. The intrathecal half of each plate is flexed distally and extends under the upper part of the adjacent distal rim plates. The lower surface of the flexed area is parallel to the substrate and forms a broad base that supports the upper end of the plate even after thecal collapse.

Prosopon may include small, rounded nodes or fine pitting, but thecal plates of most species appear to have been smooth.

Discussion of previous investigation

Foerste (1917) proposed the genus *Isorophus* for several Ordovician species previously referred to *Agelacrinites* Vanuxem (1842). These included: *Isorophus cincinnatiensis*, the type species; *Isorophus holbrooki* (here recognized as a junior synonym of *I. cincinnatiensis*); and *Isorophusella incondita*. Several earlier workers, including Meek and Worthen (1868), Clarke (1901), Bather (1898-1915), and Raymond (1915), regarded *Agelacrinites* as too broadly defined, but none had proposed generic names for the Ordovician species. Foerste's

(1914) extensive review of edrioasteroid species pointed up the need of generic revisions, but new names were not proposed because R. S. Bassler was engaged in a major taxonomic revision of the class. Apparently Bassler's delayed completion of the work (which appeared in 1935 and 1936) prompted Foerste to publish the new names in 1917.

Foerste (1917) cited the imbricate interambulacrals and the double biseries of ambulacral coverplates of the Ordovician *Isorophus* as contrasting with the tessellate interambulacrals and single biseries of coverplates [as then described] found in the Devonian *Agelacrinites*. Foerste had already noted (1914) that the ambulacra of the Ordovician forms are wider than in *Agelacrinites, ss.* He described the oral plates of *Isorophus* as similar to the primary ambulacral coverplates, and thereby contrasting with his other new Ordovician genus *Carneyella*, which has large, distinctive orals.

Bassler (1935) included as generic characters of *Isorophus*: the domal shape; ambulacral curvature, I-IV contrasolar, V solar; oral plates numerous and small; the presence of several circlets of small outer rim plates; the polygonal, slightly imbricate interambulacrals; and the triangular shape and regular arrangement of the anal plates. Bassler (1936) later noted that the interambulacrals were actually squamose, not polygonal, and more or less imbricate. Bassler's definition limited *Isorophus* to forms with curved ambulacra, I-IV contrasolar, V solar, thereby removing *Isorophusella incondita* included by Foerste and for which Bassler (1935) created the genus *Isorophusella*. Regnéll's (1966) analysis of *Isorophus* followed Bassler's description.

Isorophus cincinnatiensis, the type species of *Isorophus*, is one of the more common edrioasteroids and has been the subject of several detailed studies. Only two other species are included here under *Isorophus;* both are smaller and relatively uncommon.

RANGE AND OCCURRENCE: Trenton Group, Mohawkian Series, Middle Ordovician through Cincinnatian Series, Upper Ordovician of Cincinnati Arch region. Ohio, Kentucky, Indiana and Tennessee.

Isorophus cincinnatiensis (Roemer), 1851

Text fig. 23-25; plate 24-28

1851 *Agelacrinus cincinnatiensis* Roemer, F., Decheniana 8: 370-375, pl. 8, fig. 3a-b.

1855 *Agelacrinus cincinnatiensis* Roemer, F., *in* Lethaea Geognostica, H. G. Bronn, 3rd edition, Stuttgart, Bd. 1, pt. 2, Palaeo-Lethaea, 2: 275-278, pl. 4, fig. 6.

1857 *Agelacrinus cincinnatiensis* Roemer, Pictet, F.-J., Traité de Paléontologie ou Histoire Naturelle des Animaux Fossils, 2nd edition, Paris, 4: 305, pl. 99, fig. 25.

1866 *Agelacrinus cincinnatiensis* Roemer, Hall, J., New York State Mus., 20th Ann. Rept. (adv. pub.): 6-7.

1871 *Agelacrinus cincinnatiensis* Roemer, Hall, J., New York State Mus., 24th Ann. Rept. (adv. pub.): pl. 2, fig. 7.

1872 *Agelacrinus (Lepidodiscus) cincinnatiensis* Roemer, Hall, J., New York State Mus., 24th Ann. Rept., 214, pl. 6, fig. 7.

1873 *Agelacrinites (Lepidodiscus) cincinnatiensis* Roemer, Meek, F. B., Geol. Surv. Ohio, v. 1, Geology and Palaeontology, pt. 2, Palaeontology, sect. 1: 55-56, pl. 3, fig. 6a-b.

1876 *Agelacrinus cincinnatiensis* Roemer, F., Lethaea Geognostica, Theil 1, Lethaea palaeozoica (Atlas), Stuttgart: pl. 3, fig. 16.

1876 *Agelacrinus cincinnatiensis* Roemer, Quenstedt, F. A., Petrefaktenkunde Deutschlands, Tübingen, 4 (12): 706-707, pl 114, fig. 56.

1878 *Agelacrinus holbrooki* James, U. P., The Paleontologist, Cincinnati, 1: 2-3.

1887 *Agelacrinus holbrooki* James, U. P., Cincinnati Soc. Nat. Hist., Jour. 10: 25-26, text fig. A-B.

1887 *Agelacrinus cincinnatiensis* Roemer, Barrande, J., Systéme Silurien du centre de la Bohéme, Prague, pt. 1, 7 (1): 56.

1889 *Agelacrinus cincinnatiensis* Roemer, Miller, S. A., North American Geology and Palaeontology, Cincinnati: 222, text fig. 241.

1890 *Agelacrinus cincinnatiensis* Roemer, Steinmann, G. and Doderlein, L., Elemente der Paläontologie, Leipzig: 181-182, text fig. 177.

1896b *Lepidodiscus cincinnatiensis* (Roemer) [*non* Hall], Haeckel, E., Die Amphorideen und Cystoideen, Leipzig, 1: 113-114, text fig. 16.

1899 *Agelacrinites cincinnatiensis* Roemer, Jaeckel, O., Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 50 [*non* pl. 2, fig. 1].

1900a *Lepidodiscus cincinnatiensis* (Roemer), Bather, F. A., *in* A Treatise on Zoology, E. R. Lankester (ed.), London, pt. III, Echinoderma: 207-208, text fig. 4.

1901 *Agelacrinites cincinnatiensis* Roemer, Clarke, J. M., New York State Mus., Bull. 49 (2): 185-193; *Agelacrinites holbrooki* James, *idem, ibid.*: 185-193, text fig. 2.

1903 *Lepidodiscus cincinnatiensis* (Roemer), Delage, Y. and Herouard, E., Traité de Zoologie Concréte, T. 3, Echinodermes, Paris: 415, text fig. 552.

1903 *Agelacrinus cincinnatiensis* Roemer, Steinmann, G., Einführung in die Paläontologie, Leipzig: 192-193, text fig. 263.

1904 *Agelacrinus cincinnatiensis* Roemer, Spencer, W. K., Royal Soc. London, Proc. 74: 39-43, pl. 1, fig. 2.

1910 *Agelacrinus (Lepidodiscus) cincinnatiensis* Roemer, Grabau, A. W. and Shimer, H. W., North American Index Fossils, Invertebrates, New York, 2: 472, text fig. 1784b.

1914 *Agelacrinus cincinnatiensis* Roemer, Foerste, A. F., Denison Univ., Sci. Lab. Bull. 17 (art. 14): 399-454, pl. 1, fig. 6a-e; *Agelacrinus holbrooki* James, *idem, ibid.*: 446-448, pl. 1, fig. 1a-f, pl. 4, fig. 1; *Agelacrinus pileus* Hall, *idem* [*partim*], *ibid.*: pl. 2, fig. 3.

1915 *Agelacrinites cincinnatiensis* Roemer, Bassler, R. S., United States Nat. Mus. Bull. 92, 1: 20.

1917 *Isorophus cincinnatiensis* (Roemer), Foerste, A. F., Denison Univ., Sci. Lab. Bull. 18 (art. 4): 340-341; *Isorophus holbrooki* (James), *idem, ibid.*: 341.

1918 *Agelacrinus cincinnatiensis* Roemer, Williams, S. R., Ohio Jour. Sci. 19 (1): 62-81, pl. 1, fig. 2, pl. 2, fig. 8-9, 11, pl. 3, fig. 15, 18, pl. 7, fig. 46, pl. 8, fig. 51a-b; *Agelacrinus holbrooki* James, *idem, ibid.*: 64-81, pl. 5, fig. 26.

1935 *Isorophus cincinnatiensis* (Roemer), Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 5; *Isorophus holbrooki* (James), *idem, ibid.*: 5; *Carneyella cincinnatiensis* Bassler, R. S. [*partim*], *ibid.*: 4.

1936 *Isorophus cincinnatiensis* (Roemer), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 17, pl. 5, fig. 11; *Isorophus holbrooki* (James), *idem, ibid.*: 18, pl. 5, fig. 8, 9; *Isorophus tennesseensis* Bassler, R. S., *ibid.*: 17, pl. 2, fig. 1; *Carneyella cincinnatiensis* Bassler, *idem, ibid.*: pl. 2, fig. 15.

1938 *Isorophus cincinnatiensis* (Roemer), Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 119.

1943 *Isorophus cincinnatiensis* (Roemer), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 405; *Isorophus holbrooki* (James), *idem, ibid.*: 405; *Isorophus tennesseensis* Bassler, *idem, ibid.*: 205.

1944 *Isorophus cincinnatiensis* (Roemer), Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 129-131, pl. 49, fig. 8.

1953 *Lepidodiscus cincinnatiensis* (Roemer), Piveteau, J., Traité de Paléontologie, Paris, 3: 653, text fig. 4.

1960 *Isorophus cincinnatiensis* (Roemer), Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 158-159, pl. 10, fig. 1-4, pl. 11, fig. 1-2, pl. 12, fig. 1-6.

1960 *Isorophus cincinnatiensis* (Roemer), Kesling, R. V. and Mintz, L. W., Univ. Michigan, Contrib. Mus. Paleont. 15 (14): 315-338, pl. 1, fig. 1-2, pl. 2, fig. 1-2, pl. 3, fig. 1-9, pl. 4, fig. 1-6, pl. 9, fig. 1-2.

1966 *Isorophus cincinnatiensis* (Roemer), Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U169, text fig. 128-1, 129-2, 130-1.

Diagnosis

An *Isorophus* with: moderate to large diameter; five or more secondary orals; primary ambulacral coverplates distinctly larger externally than secondaries; secondaries rarely reaching adradial suture line externally; interambulacrals proportionately of moderate size.

Description

The domal theca of adult *Isorophus cincinnatiensis* is usually between 20 and 25 mm in diameter, but the largest recorded is nearly 40 mm (pl. 26, fig. 9, 10). The oral surface of noncollapsed specimens is almost evenly convex upward, with the oral rise and ambulacral ridges only slightly elevated above the level of the interambulacra.

The oral area is somewhat variable in number and distribution of plates (text fig. 23A). The four central primary orals, the right posterior hydropore oral, and the two pairs of lateral shared coverplates may vary somewhat from the generic description in relative size and position in response to the secondary oral plate variations. A minimum of one pair of lateral secondary orals lies along the transverse midline between the central primary orals and each of the two pairs of lateral shared coverplates. Additional secondary orals are nearly always present adjacent to these basic four secondaries, added singly or in pairs. Commonly one or more of the secondary orals are unusually large, thereby laterally displacing adjacent primary orals and shared coverplates. The greatest irregularity in the oral plate arrangement occurs in larger specimens.

One anterior secondary oral is always present in addition to the four basic lateral secondaries. It lies between the anterior primary orals and the proximal pair of ambulacrum III coverplates and is most commonly on the left side of the anterior oral midline, adjacent to the left anterior primary oral. Occasionally an additional secondary oral lies either adjacent to the standard anterior secondary, or diagonal to it, across the midline.

The oral frame of *I. cincinnatiensis* is a massive rim of plates which surrounds the ovoid central lumen (text fig. 24A, B, pl. 24, fig. 6–8, pl. 25, fig. 1–4). Except for the large posterior gap, the proximal rim of the frame extends downward far below the level of the inner surfaces of the ambulacra and is subovate in plan view. Distally the frame is continuous with the five ambulacra, and is thus subpentagonal.

The frame is transversely elongate with unequally curved anterior and posterior halves joining at attenuated lateral regions. The anterior half is nearly semicircular in plan view, except for the lateral areas which flare outward to form a wide zone of contact with the posterior unit. The posterior side is broadly arcuate, with the wide lateral extremities nearly forming a continuation of the arc of the entire posterior unit.

The frame is formed by the five proximal ambulacral floorplates and the intrathecal extensions of the four primary orals. The ambulacral floorplates dominate. The proximal end of each is greatly enlarged and produced both downward into the thecal cavity and laterally to make contact with the adjacent frame floorplates.

The semicircular anterior half of the frame is formed by the radial proximal floorplates of ambulacra II, III, and IV and the intrathecal extensions of the two anterior primary orals. These intrathecal extensions form most of the two anterior interradii on either side of ambulacrum III, but they are wedge-shaped, tapering downward, and end before reaching the innermost edge of the frame. Therefore, the adjacent floorplates achieve lateral contact near the inner edge of the frame, and alone form both the radial and interradial sections of the innermost frame rim. The posterior margins of the floorplates of ambulacra II and IV flare laterally outward to form the laterally attenuated interradial extremities of the anterior half of the frame.

The posterior half of the frame includes the enlarged proximal floorplates of ambulacra I and V and the intrathecal extensions of the two posterior primary orals. The anterior sides of both floorplates flare laterally outward and meet the flared extremities of the anterior half of the frame along a wide zone of contact. These two attenuated lateral interradii, formed only by the adjacent floorplates, accentuate the transverse elongation of the frame.

The proximal floorplates of ambulacra I and V form the radial parts of the posterior half of the frame but are not in contact with each other. Thus the posterior interradius is formed entirely by the intrathecal parts of the two posterior primary orals. These extensions are short and do not continue nearly as far into the thecal cavity as do the other frame elements and thereby leave the aforementioned conspicuous gap in the posterior side of the frame.

The posterior frame gap is modified by the intrusion of bladelike extensions from the adjacent posterior lateral edges of the two floorplates (text fig. 24B, pl. 24, fig. 8). Each plate margin bifurcates to form an anterior and a posterior blade. The anterior blades extend proximally toward the center of the frame lumen, whereas the posterior blades angle distally only slightly and extend almost straight toward the center of the posterior gap. The anterior blades are nearly twice the length of the posterior two, but both sets end before opposing blades near one another. These extensions define a small subchamber posterior to the central lumen; this is open both anteriorly and posteriorly via the gaps between the opposing blades.

The slitlike hydropore of *I. cincinnatiensis* appears to be bounded by all five hydropore structure plates (text fig. 23A-B). The raised rim surrounding the opening is prominently developed on all five plates, which suggests that the ends of the opening continued at least for a short distance along the edges of both the right posterior primary oral and the second primary coverplate of ambulacrum V.

The structure of the stone canal passageway of *I. cincinnatiensis* was described in detail by Kesling and Mintz (1960). The structure appears to be the same in all species of *Isorophus* (see generic description).

A small structure adjacent to the inner end of the stone canal passageway was described by Kesling and Mintz (1960) as an opening into the ambulacrum V for the passageway of a radial canal. The structure is a small, upwardly convex concavity, observed in one specimen (text fig. 24B, pl. 24, fig. 6-8). It lies along the axial part of the second and third floorplates of ambulacrum V, and is separated from the stone canal passageway by a low ridge. The concavity is ovate and slightly elongate normal to the ambulacral axis. It narrows rapidly upward, and the deepest part lies directly over the ambulacral midline, along the suture between the two floorplates. However, it does not appear to extend upward as a canal; the plates above the concavity are apparently tightly sutured together.

Ambulacral curvature in *I. cincinnatiensis* may be even or uneven. Distally the ambulacra may curve back toward the oral area in exceptionally large individuals (pl. 26, fig. 7-12, pl. 27, fig. 4, 5). The length of the proximally directed distal segment increases with the size of the individual. When long, the distal tip of ambulacrum V may abut the right posterior edge of the anal structure.

The ambulacral coverplates form a double alternating biseries of primary and secondary plates (text fig. 23B, 25D). The primary plates are externally distinctly larger than the secondaries. Viewed externally, the large primaries extend from the perradial to the adradial suture line. The smaller secondary coverplates are restricted to the medial sectors of the ambulacrum and separate the perradial tips of adradially contiguous primary coverplates. Opposing alternate members of plate pairs of both primary and secondary sets are usually in contact across the perradial line, and plate pairs of one series usually alternate with pairs of the other. However, irregularity is common in this species. Occasional unpaired plates interrupt the regularity of the plate pair alternation and may even separate the opposing alternate plates of a single pair. Moreover, the relative position of the perradial tips of members of each plate pair, one proximal to the other, frequently reverses along the length of an ambulacrum, some with the right member proximal, others with the left.

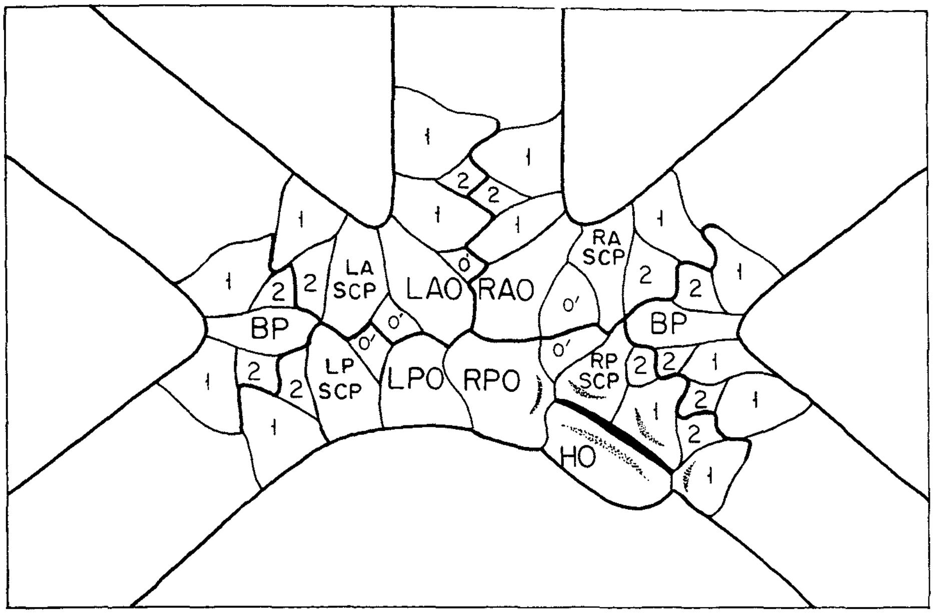
Some larger specimens of *I. cincinnatiensis* appear to have a triple biseries of ambulacral coverplates in the proximal parts of the ambulacra. This deceptive appear-

---

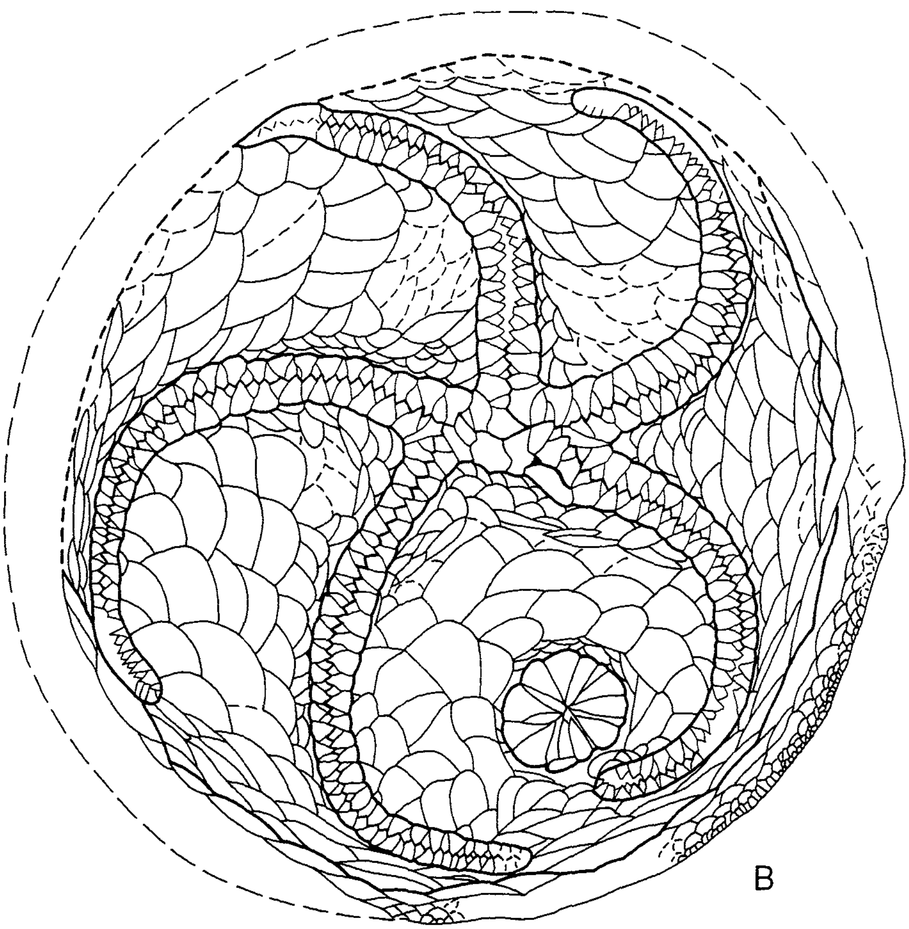
Text figure 23. ***Isorophus cincinnatiensis*** **(Roemer), 1851**

A. Reconstruction of the oral area and proximal parts of the ambulacra. BP, lateral bifurcation plate; HO, hydropore oral plate; LAO, left anterior primary oral plate; LASCP, left anterior lateral shared coverplate; LPO, left posterior primary oral plate; LPSCP, left posterior lateral shared coverplate; o', secondary oral plate; RAO, right anterior primary oral plate; RASCP, right anterior lateral shared coverplate; RPO, right posterior primary oral plate; RPSCP, right posterior lateral shared coverplate; 1, primary ambulacral coverplate; 2, secondary ambulacral coverplate.

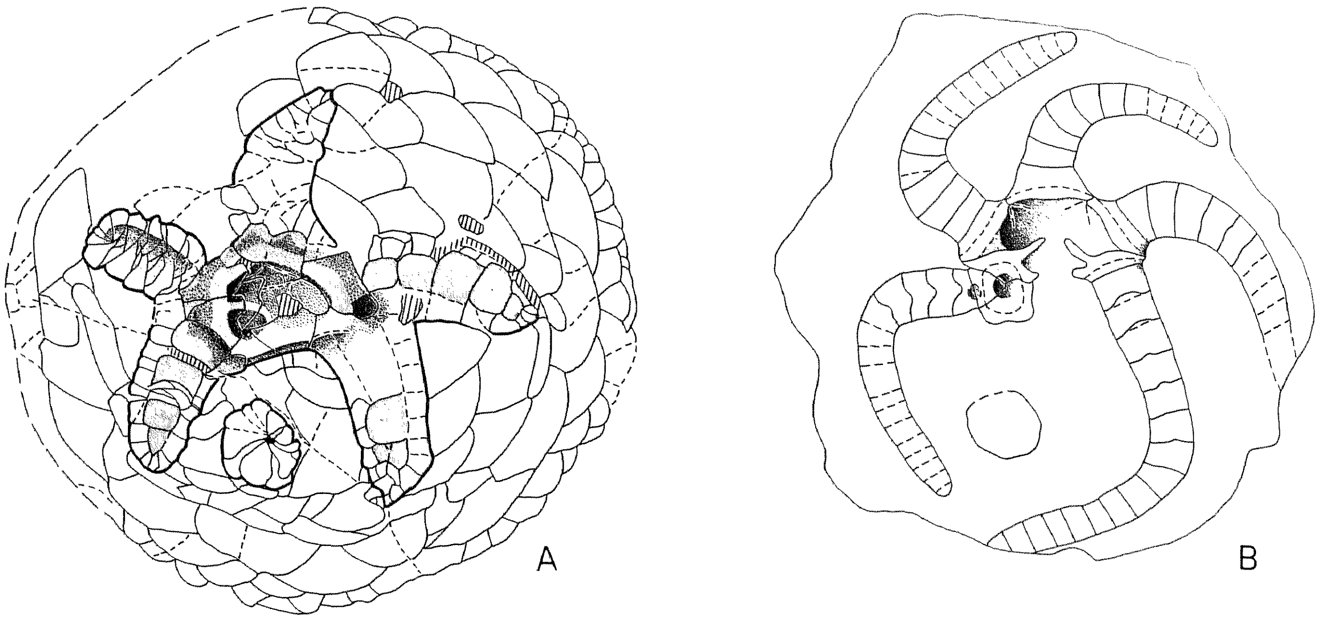
B. UCMP 40470, (x 5), pl. 28, fig. 8.


1
1
2
2
1
1
1
1
RA
SCP
LA
SCP
LAO
RAO
2
2
2
1
BP
BP
O'
O'
O'
O'
RP
SCP
LP
SCP
LPO
RPO
2
2
2
2
1
1
1
2
2
HO
1
1

A



B



A B

Text figure 24. *Isorophus cincinnatiensis* (Roemer), 1851

A. Inner side of the oral surface, CFMUC 54068, (x 14), pl. 25, fig. 3. Ambulacral floorplates are shaded.

B. Inner side of the oral surface, UCMP 26536, (x 5), pl. 24, fig. 7.

ance results from differential enlargement of adjacent primary coverplates, with every second plate being wider. The alternation of these two sizes of primary plates creates the impression of two large coverplate sets, and the small secondary coverplates thus appear to be a third set. Tracing the large plate series distally along an ambulacrum demonstrates that the apparent differentiation of two sets of larger coverplates is due only to differential enlargement of the single primary coverplate set, and not to the intercalation of new elements. The development of this condition appears to be random, for within one population some large adults develop the pseudotriple biseries appearance, whereas others of equal size do not.

The externally medial secondary coverplates extend adradially under the laterally contiguous edges of the primary coverplates and end beyond the external adradial suture line. These wedge-shaped, hidden adradial ends of the secondaries are approximately two-thirds the width of adjacent overlying primaries. Their upper edges are beveled to fit snugly against the overlapping beveled edges of the primary coverplates, as reported by Kesling and Mintz (1960).

The ambulacral coverplates are generated along the distal sectors of the ambulacra. The large primary plates are formed at the very tip of each ambulacrum. Individual plates are developed at the center of the ambulacrum tip and then shift alternately to each side, with every two successive plates moving to opposite sides to form the opposing alternate members of a single pair of primary coverplates. Unpaired primary plates appear to result from the development of two plates which consecutively shift to the same side of the ambulacrum before the normal alternate migration resumes. The secondary coverplates are generated in a different zone from the primaries, which lies approximately three to four primary coverplates from the tip of the ambulacrum. The secondaries are inserted between the adjacent primary pairs, one on each side of the midline, to form a single secondary set pair between each primary set pair. In some cases only one secondary is inserted between adjacent primary pairs, whereas in others three plates are inserted. This causes the irregularity common in the secondary coverplate series of this species.

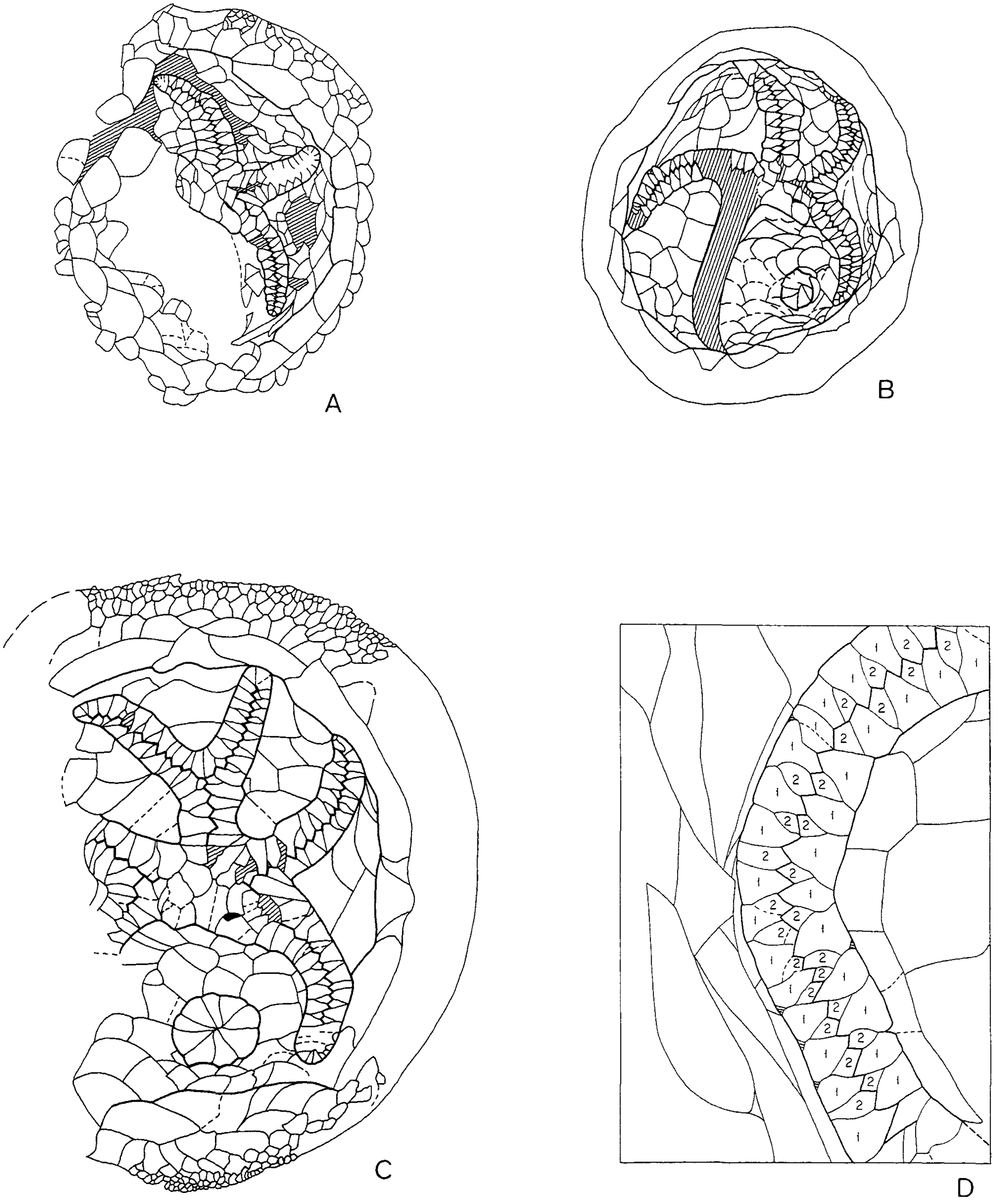
Text figure 25. *Isorophus cincinnatiensis* (Roemer), 1851

A. USNM 91839-B, (x 7), pl. 26, fig. 2.

B. USNM 91839-A, (x 7), pl. 26, fig. 4.

C. CFMPE 16328, (x 10), pl. 27, fig. 6.

D. Segment of ambulacrum I, CFMUC 1004, (x 25), pl. 26, fig. 8. 1, primary ambulacral coverplate; 2, secondary ambulacral coverplate.


A
B
C
D

The uniserial, trough-shaped ambulacral floorplates meet one another along nearly vertical sutures (text fig. 24A, B, pl. 24, fig. 6-8, pl. 25, fig. 1-4, 13, 14). However, the axial part of the inner side of each floorplate is produced proximally as a thin flange that underlaps the adjacent proximal floorplate. The flanges form rounded, proximal bulges in the inner floorplate suture lines. This gives the appearance of very oblique sutures analogous to those of the Carneyellidae. The thin flange is commonly lost during weathering, and the inner floorplate suture lines then appear straight.

Narrow, shallow grooves are present in the lateral margins of the upper surface of each floorplate, as first reported by Foerste (1914). The grooves extend parallel to the ambulacral axis and lie near the outer edges of the plate, along the articulation zone between the floorplates and the overlying coverplates. Complementary ridges or grooves may be present on the contiguous inner surfaces of the coverplates.

The squamose, imbricate interambulacrals of *Isorophus cincinnatiensis* are moderate in size in proportion to the thecal diameter. The largest plates are in the central and distal parts of the interambulacra; those adjacent to the peripheral rim are externally equal in size to the proximal rim plates. The smallest interambulacrals flank the ambulacra. This suggests that the adradial suture line is the zone of insertion of new interambulacrals. The plates apparently increase rapidly in size as they migrate away from the ambulacrum, until they reach the average interambulacral plate size. Thereafter growth is slow.

The valvular anal structure of adults is commonly composed of 16 plates (pl. 24, fig. 5, pl. 26, fig. 5, 6, 11, 12). The plates of the outer circlet are triangular, with wide distal bases that are slightly convex outward, and with acuminate proximal ends surrounding the anal opening. The inner circlet plates are subtriangular, acuminate proximally, and have enlarged, rounded, distal bases that flare laterally outward far under the overlying upper circlet plates. Inner circlet plates are commonly almost as wide as the overlapping outer circlet anals, although only the central third of each is visible from external view. Slight lateral shifting of the upper circlet plates during preservation often obscures some of the inner plates while exposing most of the normally covered upper surfaces of others. This shifting results in the common external appearance of the structure in which the alternation of inner and outer plates appears rather irregular.

The margins of the large interambulacrals that surround the anal structure are slightly concave so as to fit tightly against the arcuate distal bases of the anals. The interambulacrals are unusually thick along this junction, and the upper third of each abuts adjacent anals along a nearly vertical suture. The lower two-thirds of each interambulacral extends outward under the anals and thereby forms a ledge upon which the lower edge of the distal ends of the anals rest (pl. 26, fig. 5, 6, pl. 27, fig. 6, 7).

One or two irregular circlets of small, elongate interambulacrals may lie above the junction of the anals and adjacent large interambulacrals, hiding the contact zone. These circlets of surficial elements surround the anal structure in many large individuals, but commonly are lacking in smaller specimens.

The peripheral rim of *I. cincinnatiensis* commonly contains eight or nine circlets of plates. The geniculation of the larger plates of the rim is pronounced and forms the broad base of each plate parallel to the substrate. This base supports the external ends of the plates nearly in life position even after thecal collapse. Prominent vertical ridges extend downward from the lower surface of the bases of all but the smallest outer rim plates (pl. 25, fig. 1-9). The ridges are thickest near their inception on the plate base, and taper downward to form sharp crests directed toward the substrate. Commonly the ridges also taper distally, because the proximal end of each is both thicker and more highly elevated than the distal part. The number of ridges per plate varies from eight to nine on large plates to two or three on smaller ones. On some plates the ridges form a single row, and all are nearly equal in size, although the central ones are usually a bit larger than the others. On other plates the ridges form two rows: one of large ridges that extend across the entire base of the plate (like those found in plates with only one row of ridges), and a second row of small ridges intercalated between the larger ones, and restricted to the distal margin of the plate base.

Specimens

AMNH 1194. Illustrated Specimen of *Isorophus cincinnatiensis* (Roemer) by Hall (1866, p. 6-7; 1871, pl. 2, fig. 7; 1872, p. 214, pl. 6, fig. 7) and Bassler (1935, p. 4; 1936, pl. 2, fig. 15). Maysville Group, Cincinnatian Series. Upper Ordovician. Cincinnati, Ohio. 18.4 mm axial by 19 mm transverse diameter.

Pl. 24, fig. 1.

The specimen has been partially disrupted by thecal collapse. The distal ambulacral and interambulacral areas are now missing some plates. The oral area has been severely abraded, partially obscuring the plate boundaries. The anterior half of the peripheral rim is also partially disrupted and covered by matrix.

Despite preservational irregularities, this individual preserves the characters of *I. cincinnatiensis* (Roemer). Hall's (1871) reconstruction of the specimen misrepresents both the oral region, in which he included only three large primary orals, and the anal region, which was shown as having a prominent rim of elongated plates surrounding the triangular anals. The ambulacral coverplates in Hall's drawing have also been regularized, but both the primary and secondary sets are shown. Bassler (1935) referred Hall's picture, and ostensibly his specimen, to his species *Carneyella cincinnatiensis* Bassler and reillustrated (1936) Hall's drawing. Apparently relying entirely upon the drawing, Bassler's description corresponds to the drawing but not to the specimen.

MCZ 517 (old 3881.) Illustrated Specimen of *Isorophus cincinnatiensis* by Meek (1873, pl. 3, fig. 6a-b). Probably Bellevue Formation, Maysville Group, Cincinnatian Series, Upper Ordovician. Near the tops of the hills in Cincinnati, Ohio. 23 mm axial by 21 mm transverse diameter.

Pl. 24, fig. 4, 5.

The theca has undergone little collapse and only the central plates of interambulacrum 1 are significantly disrupted. Most of the peripheral rim is nearly vertical, and some of the plates are partially disrupted. Recalcitrant matrix obscures much of the rim structure. The anal structure is elevated above the surrounding interambulacrals as a low, rounded, conical mound.

UCMP 34539. Illustrated Specimen of *I. cincinnatiensis* by Kesling (1960, pl. 12, fig. 1, 2). Bellevue Formation, Maysville Group, Cincinnatian Series, Upper Ordovician. Then vacant lot across street from Frische's Big Boy Restaurant, Hamilton Avenue, North College Hill, Cincinnati, Ohio. 23 mm axial by 21 mm transverse diameter.

Pl. 24, fig. 2, 3.

The theca has collapsed, causing minor disruption of many of the plates. Part of the anterior and most of the left margin of the theca is missing, along with a few ambulacral and interambulacral plates. The plates of the oral and hydropore regions have been tilted upward but remain essentially in place. The thickened plate margins which form the raised rim surrounding the hydropore opening are exceptionally well preserved. The specimen was illustrated by Kesling (1960) to demonstrate the presence of the hydropore structure in this species.

UCMP 26536. Illustrated Specimen of *I. cincinnatiensis* by Kesling and Mintz (1960, pl. 1, fig. 1, 2). Corryville member, McMillan Formation, Maysville Group, Cincinnatian Series, Upper Ordovician. Layer at creek level, 100 yards south of bridge over Stone Lick Creek, 1 mile west of Newtonsville, Ohio. 15.1 mm axial by 15.4 mm transverse diameter.

Text fig. 24B, pl. 24, fig. 6-8.

This specimen is one of the few preserved with the inner side of the oral surface exposed. Most of the peripheral rim and the distal parts of the interambulacra are missing, but the remaining thecal plates are only slightly disrupted. Surficial etching has rounded the plate extremities and removed some of the more delicate features, including most of the thin, proximal flanges on the floorplates. Thus the inner surface suture lines between floorplates are nearly straight, rather than convex proximally as in non-etched specimens. The incomplete removal of some flanges has left a low, rounded protuberance on the distal end of the adjacent floorplate. The lateral, bladelike extensions of the proximal floorplates of ambulacra I and V, which define the posterior subchamber of the oral frame, have also been reduced in size by etching.

This specimen was described in detail by Kesling and Mintz (1960). It is the most complete and best preserved example of this species that exposes the inner oral surface features.

AMNH 13266/1-X. *Isorophus cincinnatiensis* illustrated as *Carneyella pilea* by Foerste (1914, pl. 2, fig. 3) and by Kesling and Mintz (1960, pl. 9, fig. 1, 2). Corryville member, McMillan Formation, Maysville Group, Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. 12.2 mm axial by 11.4 mm transverse diameter.

Pl. 25, fig. 1, 2.

This individual also exposes the inner side of the oral surface. The distal part of the peripheral rim along the left side of the theca (right side as viewed in the photographs) is missing, along with ambulacrum V, part of IV, all of interambulacrum 4, and part of 5. Most other thecal plates are nearly in place with the exception of the oral frame elements, which have been partially disrupted.

The exposed surfaces of all of the thecal plates, except some of the frame plates, have been eroded in a peculiar fashion. Some type of abrasion has removed numerous, minute cleavage rhombs. Apparently the edges of the plates were the most highly eroded and this produced prominent, jagged, central elevations on each element. This effect causes the interambulacrals to appear unusually thick and the inner sides of the floorplates to appear sharply crested. All traces of the vertical ridges on the bases of the peripheral rim plates have been obliterated.

The specimen was illustrated by both Foerste (1914) and Kesling and Mintz (1960) as an example of *Carneyella pilea*. The peculiar preservation makes the specimen appear unlike any other example of *Isorophus cincinnatiensis*. However, the specimen can be identified as pertaining to this species rather than to *C. pilea* because: the ambulacral floorplate sutures are vertical, not oblique; the ambulacral coverplates form a double biseries (the inner sides of several of these plates are exposed along the disrupted tip of ambulacrum IV); and the revealed anal structure, which was previously hidden by matrix, is valvular.

AMNH 13266/1-R. Illustrated Specimen of *Isorophus cincinnatiensis* by Foerste (1914, pl. 1, fig. 6E). "Lorraine beds," Maysville Group, Cincinnatian Series, Upper Ordovician. Cincinnati. Ohio. 18.3 mm axial by 19 mm transverse diameter.

Pl. 25, fig. 7, 8.

The specimen exposes the inner side of the oral surface. Most thecal plates are partially disrupted, but all major inner structures are recognizable, except for the anal area. The inner surfaces of the double biseries of coverplates are visible along the distal part of ambulacrum III. The larger proximal plates of the peripheral rim have been tilted; the base of each plate now faces the thecal cavity instead of downward toward the substrate. The distal ends of the large, vertical, basal ridges are preserved on most of the larger rim plates. In this individual only three or four ridges are seen on each plate, as opposed to twice that number found in other examples of this species. Foerste (1914) based his description of the rim plate ridges on this specimen.

CFMUC 1004. Illustrated Specimen of *Isorophus cincinnatiensis* figured as *Isorophus holbrooki* (James) by Foerste (1914, pl. 1, fig. 1) (perhaps one of the original type series of *I. holbrooki*). Maysville Group, Cincinnatian Series, Upper Ordovician. Lebanon, Ohio. 30 mm axial by 31 mm transverse diameter; height 16.5 mm.

Text fig. 25D, pl. 26, fig. 7, 8.

This specimen is a large, noncollapsed *Isorophus cincinnatiensis*. The highly convex oral surface of the domal theca is nearly hemispherical; the margin rim area stands almost vertically. Many of the proximal oral surface plates are now missing, including all of the orals, the hydropore structure, all of ambulacrum IV, and the proximal parts of the other ambulacra and interambulacra. Many of the distal plates of interambulacra 2, 3, and 4 have also been lost, along with the proximal half of the anal structure. The preserved thecal features agree in structure with other *I. cincinnatiensis*. These include the double biseries of ambulacral coverplates, the valvular anal structure, the squamose, imbricating interambulacrals, and the peripheral rim. The only feature not seen in smaller adults of *I. cincinnatiensis* is the pronounced distal curvature of the ambulacra, in which the tips extend proximally toward the oral region.

Foerste (1914) described this specimen in detail and suggested that it was the type of *I. holbrooki* James. However, James' (1887) illustration shows a more complete specimen than this one, at least in its present condition. Moreover, James referred to several specimens in the text of his original description. This may be a member of the original type series, but it probably is not the specimen on which the original illustration was based.

USNM 40744. Illustrated Specimen of *Isorophus cincinnatiensis* figured as *Isorophus holbrooki* (James) by Clarke (1901, fig. 2) and Bassler (1936, pl. 5, fig. 8, 9). Lower Arnheim Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Morrow, Ohio. 38.2 mm axial by 34.1 mm transverse diameter; height 18.8 mm.

Pl. 26, fig. 9-12.

The theca of this large *I. cincinnatiensis* has not collapsed; the highly convex oral surface is hemispherical and essentially in life configuration. The distal parts of the rim are slightly flexed under the upper part of the theca so as to maintain contact with the small *Pterinia* on which the specimen rests. The oral region and surrounding thecal plates have been abraded, but many of the plates in this region can still be distinguished. The thecal construction is essentially like that of average-sized adult *I. cincinnatiensis*, except for the pronounced distal curvature of the ambulacra toward the oral region and the polygonal appearance of the exteriors of the large interambulacrals. These plates are imbricate, however, and the distal interambulacrals are typically squamose. The anal structure is elevated as a low, rounded, conical mound.

A second specimen is housed under the same number. It is also a large *I. cincinnatiensis* (26.9 mm axial diameter) with distally recurved ambulacra, but the specimen is collapsed and disrupted.

USNM 91839 (A-B). Two *Isorophus cincinnatiensis*. Shaly beds in Cannon Limestone, Trenton Group, Mohawkian Series, Upper Ordovician. Fayetteville, Tennessee.

USNM 91839-A. Holotype of *Isorophus tennesseensis* Bassler (1936, pl. 2, fig. 1). 9.6 mm axial by 8.8 mm transverse diameter.

Text fig. 25B, pl. 26, fig. 3, 4.

USNM 91839-B. Specimen with holotype of *I. tennesseensis*. 9.6 mm axial by 8 mm transverse diameter.

Text fig. 25A, pl. 26, fig. 1, 2.

Specimen A is partially disrupted because of thecal collapse, especially in the distal ambulacral and interambulacral plates. The oral region is also disrupted and abraded, with many of the plates crushed and partially replaced, obscuring relationships. The anal plates have been tilted upward and the proximal tips are now centrally separated around the anal opening. The ambulacral coverplates form the typical double biseries of *I. cincinnatiensis*.

Specimen B is more disrupted, and many of the thecal plates are dislocated, broken, or missing. Ambulacra III, IV, and V, interambulacrum 3, and the adjacent section of the peripheral rim are all nearly complete. Most of the oral plates are decipherable.

USNM S-3900. An *Isorophus cincinnatiensis* from a large suite of specimens. Bellevue Formation, Maysville Group, Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. 29 mm axial(?) by 29 mm transverse(?) diameter.

Pl. 25, fig. 9.

The specimen is large and disrupted. Some of the larger geniculate proximal plates of the peripheral rim have been tilted backward away from the oral region. This has exposed the inner side of the upper part of each plate and also the proximal edge of the basal area. The proximal ends of the basal vertical ridges are visible, four or five per plate. A central flexure extends laterally across the inner side of the upper half of at least two of these rim plates.

USNM 91838. Maysville Group, Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. 20.5 mm by 20 mm diameter.

Pl. 25, fig. 5, 6.

This specimen exposes the inner side of the oral surface. Nearly all of the central thecal plates are missing or disrupted, but much of the peripheral rim remains and the basal vertical ridges of the rim plates are exceptionally well preserved. A few partially disrupted floorplates are visible adjacent to the well-preserved part of the rim.

CFMUC 54068. Whitewater Formation(?), Richmond Group, Cincinnatian Series, Upper Ordovician. Versailles, Indiana [probably from large roadcut on Highway U.S. 50, east of town]. 6 mm axial by 6.1 mm transverse diameter.

Text fig. 24A, pl. 25, fig. 3, 4.

The theca is preserved with the inner side of the oral surface exposed. This surface has been etched but most features are at least partially preserved. Interambulacrum 3 and the adjacent rim have been crushed, severely fracturing the plates. Plates of the oral frame are partially disrupted, but identifiable. The floorplates of ambulacra III and IV are missing and thereby expose the inner side of the coverplates, most clearly seen in ambulacrum IV. The basal ridges of the peripheral rim plates are in part preserved, although reduced in size by etching.

The small thecal diameter suggests that this individual was a young adult. Moreover, the ambulacra reach the rim but remain only moderately curved, with the distal tips not yet concentric with the rim.

The inner surfaces of the coverplates exposed in ambulacrum IV are well preserved. The intra-ambulacral extension of each can be seen to extend proximally under the adjacent element and also across the perradial line under the tip of the opposing plate. The alternation between primary and secondary coverplate sets is apparent because of the much larger size of the primaries. A single, small, newly added primary coverplate lies in the center of the distal tip of the ambulacrum. This is succeeded proximally by two pairs of larger primaries, followed by the first pair of intercalated secondaries. The anterior member of this most distal pair of secondaries (adjacent to interambulacrum 2) is smaller than the opposing plate and apparently is the last formed secondary present. Proximal to this pair of secondaries, the alternation between primary and secondary coverplate pairs is fairly regular. A shallow groove along the lower surface of the coverplate extensions, parallel to the ambulacral axis, may be present. However, this region has been etched. The suggested groove appears to lie beyond (adradial to) the zone of contact with the floorplates, and thus may or may not be related to the lateral groove found on the upper lateral surfaces of the floorplates in other specimens of this species.

AMNH 13269. "Lorraine beds," Maysville Group, Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. 11.6 mm axial by 11.8 transverse diameter.

Pl. 27, fig. 1–3.

This individual is a young adult. Thecal collapse has disrupted the distal parts of the ambulacral-interambulacral areas, but most of the remainder of the theca is well preserved. The ambulacra are proportionately shorter and curvature is less pronounced than in larger adults; each ambulacrum ends as it becomes concentric with the proximal margin of the peripheral rim. The oral region, and in particular the four primary orals, are larger in proportion to thecal diameter than in larger adults. The five basic secondary orals are present in the oral region, but at this stage of development no additional secondaries are seen and all of the basic five are small.

CFMPE 16328. Maysville Group, Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. 10.6 mm axial by 8.8 mm transverse diameter.

Text fig. 25C, pl. 27, fig. 6, 7.

This is a small individual with six ambulacra. The left third of the theca is missing, but the break occurs distal to the oral region and preserves the proximal parts of both ambulacra I and II. The remainder of the theca has been deeply etched, but except for a few of the orals, the plates remain distinct.

Ambulacrum III bifurcates a short distance from the oral region. The left branch extends out to the rim and curves contrasolarly. The right branch is shorter and ends as it intersects the rim without developing distinct curvature. Two large coverplates lie at the point of bifurcation; both are nearly equal in size to adjacent primary coverplates.

The anal structure has slumped downward below the level of the adjacent large interambulacrals. This has exposed the narrow ledge on the adjacent lateral sides of the interambulacrals on which the anal plates normally rest.

UCMP 40474. (?) Maysville Group, Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. 11.2 mm long by 5.5 mm wide.

Pl. 25, fig. 12–14.

The specimen is a fragment of one ambulacrum and a few adjacent interambulacrals of an *Isorophus cincinnatiensis*, and is almost entirely free of matrix. Both the double biseries of coverplates and the uniseries of floorplates are exposed. Their lateral relationships are visible along the outer side of the ambulacrum where the interambulacrals are missing. A cross section is seen at each end of the segment, exposing the low, broad ambulacral tunnel. The inner surfaces and proximal flanges of the floorplates are well preserved and form the convex inner suture lines between contiguous floorplates. Except for this inner, flanged area, the sutures between adjacent floorplates are vertical. The intrathecal extensions of the primary coverplates continue far into the thecal cavity; the secondaries end just beyond the edges of the floorplates. The large ovate gaps between the primary plate extensions end blindly at the lateral margins of the floorplates where the secondary coverplate extensions completely fill the gaps between them. Thus there is no direct communication between the thecal cavity and the ambulacral tunnel in this area.

USNM 40746 (G, H). Two *Isorophus cincinnatiensis*. Bellevue Formation, Maysville Group, Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio.

USNM 40746-G. 14.5 mm wide (across the ambulacra) by 14.1 mm long.

Pl. 25, fig. 10, 11.

Specimen G is a fragment of a theca that includes two ambulacral segments and a few adjacent interambulacrals. The coverplates are missing from the center of one ambulacrum which exposes the underlying structure. The upper surface of a secondary calcite filling of the ambulacral tunnel preserves the impressions of the inner surfaces of the missing coverplates. A shallow groove appears to be incised into the upper, nearly level lateral margins of each floorplate; it extends parallel to the ambulacral axis. Unfortunately, these areas have been etched, obscuring the surficial features of the grooves.

USNM 40746-H. 14.2 mm along the break by a perpendicular of 7.9 mm.

Pl. 26, fig. 5, 6.

Specimen H is also fragmentary and exposes the inner surface of the anal structure, parts of ambulacra I, II, and V, and interambulacra 4 and 5. A few proximal rim plates remain adjacent to ambulacra I and II. The anal structure is exceptionally well preserved with both the inner and outer circlet plates in place. The lateral overlapping relationship of the outer circlet plates is apparent, and the laterally expanded bases of the inner circlet plates are visible. The floorplates of ambulacra I and II are in place, but the proximal flanges have been removed by weathering, which exposes the vertical sutures between contiguous elements. The inner surface of some of the coverplates of ambulacrum V are exposed where the floorplates are missing. The tight lateral fit between the intrathecal parts of the primary and secondary coverplate sets is apparent. The primary coverplate extensions narrow abruptly as they extend into the thecal cavity beyond the secondaries. In this individual the inner ends of these extensions continue to taper and do not expand distally. The section of the lower surfaces of the coverplates normally in contact with the floorplate margins has been etched, but remnants of a groove along this zone, parallel to the ambulacral axis, appear to be present on a few of these plates.

IUPC 8278 (A, B). Two *Isorophus cincinnatiensis*. Whitewater Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Roadcut on Highway U.S. 50, east of Versailles, Ripley County, Indiana (CN½.SE¼. Sec. 12, T. 7 N, R. 11 E). R. S. Nicoll, collector.

IUPC 8278-A. 10.5 mm axial by 13 mm transverse diameter.

IUPC 8278-B. 10.5 mm axial by 14.3 mm transverse diameter.

Both specimens are incomplete; etching has removed much of the theca. These specimens document the occurrence of the species in the upper part of the Richmond Group.

AMNH 13268/1-Z. "Lorraine beds," Maysville Group, Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. 26.8 mm axial by 23.5 mm transverse diameter. Albers purchase.

Pl. 27, fig. 4, 5.

The specimen is larger than indicated by the thecal diameter because the rim is folded under the upper side. The growth of the rim was apparently restricted by the small size of the brachiopod upon which the individual rests. The specimen is well preserved except for the disruption of the posterior half of the oral area and adjacent plates of interambulacrum 5. Selective etching, combined with thecal collapse, has accentuated the external suture lines and results in the clear demarcation of the plates when photographed. The distal tips of the ambulacra tend to curve back toward the oral region, but the recurvature is less pronounced than in larger specimens.

UCMP 7781. Bellevue Formation, Maysville Group, Cincinnatian Series. Upper Ordovician. Cincinnati, Ohio. 30.6 mm axial by 28.5 mm transverse diameter.

Pl. 27, fig. 8.

The theca of this large individual has collapsed, partially disrupting many of the plates. The upper ends of the proximal rim plates have been tilted outward during collapse and expose the normally hidden, inner sides of the upper parts of these plates. The distal part of the rim is flexed under the upper thecal surface to maintain contact with the small brachiopod (*Rafinesquina*) upon which the specimen rests. The long ambulacra distally curve back toward the oral region, as in other large *Isorophus cincinnatiensis*. A cylindrical boring penetrates two of the distal plates of interambulacrum 5.

UCMP 40467–40473. The following seven specimens are representative of the Forestville population. They are normal and variant individuals from the over four hundred *Isorophus cincinnatiensis* examined from this site.

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

UCMP 40467. 19 mm axial by 20 mm transverse diameter. W. H. White, Jr., collector.

Pl. 28, fig. 1, 2.

This is one of the uncommon individuals in which only four ambulacra developed. In this example, ambulacrum III is absent. Unfortunately, the specimen has been deeply etched and abraded, obscuring many of the plate boundaries. The individual is a normal *I. cincinnatiensis* in all respects except for the missing ambulacrum.

UCMP 40468. 16.6 mm axial by 16 mm transverse diameter. J. W. Branstrator, collector.

Pl. 28, fig. 3, 4.

This is another individual with only four ambulacra, but here ambulacrum V is missing. This specimen is also deeply etched and abraded, and interambulacrum 5 has collapsed downward below the rest of the theca, losing a few plates in the process. In response to the missing ambulacrum V, the hydropore structure has developed along the proximal posterior side of ambulacrum IV. The anal structure has shifted far to the right of its usual position and lies in the area normally occupied by the missing ambulacrum. The other thecal features appear to be typical of the species.

UCMP 40469. 20.6 mm axial by 20.5 mm transverse diameter.

Pl. 28, fig. 5, 6.

This specimen is a normal *I. cincinnatiensis* except for the course of the distal part of ambulacrum V. The medial sector of the ambulacrum is curved solarly, as usual, and the more distal region becomes concentric with the peripheral rim. However, the distal end is reversed in direction, and curves outward away from the oral region to extend for a short distance along the rim in a contrasolar direction. During preservation the distal coverplates of this reversed area were shoved up over the edges of the adjacent rim plates. This is the only specimen known to exhibit a distal reversal in the direction of ambulacral curvature.

UCMP 40470. 24.6 mm axial by 24.8 mm transverse diameter. W. H. White, Jr., collector.

Text fig. 1C, 23B, pl. 28, fig. 7–9.

This specimen is a typical adult *I. cincinnatiensis*. The theca has partially collapsed, but only the proximal plates of interambulacra 1, 2, 3, and 5 have been disrupted. Nearly half the peripheral rim is covered with tenacious matrix, but the other half is well exposed.

UCMP 40471. 21.2 mm axial by 19 mm transverse diameter.

Pl. 28, fig. 12, 13.

This *I. cincinnatiensis* has been disrupted by the passage of a sediment reworker through the theca. A segment of the burrow filling is preserved between the oral and anal structures. The burrower(s) disrupted much of the central area and left only the oral and anal areas, ambulacrum III, and the distal tips of ambulacra I and V undisrupted. The burrower penetrated the rim at least three times, twice in the posterior region and once adjacent to interambulacrum 3.

UCMP 40472. 18.1 mm axial by 18.6 mm transverse diameter. W. H. White, Jr., collector.

Pl. 28, fig. 11.

This incomplete specimen is also partially disrupted by a sediment reworker. A section of the burrow filling is preserved where the animal passed through the right side of the theca.

UCMP 40473. 21 mm axial by 20 mm transverse diameter. W. H. White, Jr., collector.

Pl. 28, fig. 10.

The theca of this specimen has not collapsed, and the oral surface plates are preserved nearly in life configuration. The upper side of the oral surface is evenly convex upward; the oral and ambulacral areas are only slightly elevated above the interambulacrals. Apparently the ambulacral structures were originally slightly higher than they are now, but they have been deeply etched, exposing a subsurficial view of the plates. In this uncollapsed individual the junction between the distal interambulacral plates and the proximal rim plates is obscure.

Discussion of previous investigation

The location of the holotype of *Isorophus cincinnatiensis* Roemer (1851) is unknown. However, the original description was reasonably complete and included an excellent drawing of the specimen. Among the characters noted by Roemer were: the domal thecal shape, the ambulacral curvature (reversed in the accompanying camera lucida drawing), the double biseries of ambulacral coverplates, the lack of ambulacral " pores," and the inner and outer circlet of triangular anals (attributed by him to differential plate slippage). Roemer's text noted that the oral area of the specimen was disrupted—which explains the peculiar plate configuration found in his drawing. The geologic and geographic occurrence of Roemer's specimen, combined with his description, leaves no doubt that the holotype is conspecific with the specimens here referred to *I. cincinnatiensis.*

Roemer (1855) summarized the diagnostic characters of most described edrioasteroids and refigured his 1851 drawing of *I. cincinnatiensis.* In this paper the illustration is correctly oriented, with the image reversed from the earlier publication. The same illustration was republished by both Roemer and Quenstedt in 1876. Pictet (1857) illustrated a different *I. cincinnatiensis* in his *Traité de Paléontology.* This drawing portrayed numerous small oral area plates, but without apparent order.

Hall (1866) briefly redescribed *I. cincinnatiensis,* listed as *Agelacrinus (Lepidodiscus) cincinnatiensis*, and added diameter measurements to Roemer's description. Hall's illustration, intended to accompany the 1866 text, appeared in 1871 and again in 1872. This drawing differs from Roemer's in the oral region, where three large primary orals are shown, and in the proximal rim area, which is differentiated from the adjacent interambulacrals. The latter feature results from the collapsed condition of Hall's specimen. The oral area of this specimen (AMNH 1194) is abraded, making interpretation difficult, but it does appear to have the typical *I. cincinnatiensis* plate configuration and thereby differs from Hall's diagram.

Meek (1873) illustrated another *Isorophus cincinnatiensis* (MCZ 517) (pl. 24, fig. 4, 5) and briefly redescribed the species. Meek's drawing is quite accurate and includes most of the oral plates. Slight lateral shifting of the orals in his specimen accounts for most of the variation between Meek's drawing and the plate configuration described here. Meek also referred to another specimen of the species from Richmond, Indiana, which exposed the inner side of the oral surface. From this individual he described the uniserial ambulacral floorplates and their vertical sutures, as well as the basal ridges on the peripheral rim plates. The specimen was not illustrated and its whereabouts are unknown.

James (1878) described a large specimen of *I. cincinnatiensis* under the name *Agelacrinus holbrooki.* He distinguished the species by its large size, high convexity, polygonal shape of the interambulacrals, and the distal curvature of the ambulacra back toward the oral region. These features are all related to old age. Specimens intermediate in size between this large individual and average *I. cincinnatiensis* demonstrate the gradual gerontic acquisition of these features as they develop from normal adults. A republication by James of his species description in 1887 includes a drawing of the type specimen by J. J. G. Steddom.

Several authors referred to *I. cincinnatiensis* from 1870 through 1920, variously assigning it to *Agelacrinites* and *Lepidodiscus.* Accompanying illustrations were usually copies of Roemer's, Hall's, or Meek's drawings. Noteworthy here is Haekel's (1896) description, which allowed that the ambulacra curved, I-IV contrasolar, V solar, or vice-versa. Apparently he did not realize that the reversal seen in published figures was due to camera lucida drawings that had not been properly reversed. Another discrepancy is found in Jaekel's (1899, pl. 2, fig. 1) illustration supposedly of this species; the drawing includes the posterior third of the theca of what appears to be a *Carneyella pilea.*

Spencer (1904) published an illustration of an *Isorophus cincinnatiensis* showing the inner side of the oral surface. This confirmed the uniserial arrangement of the ambulacral floorplates described by Meek (1873). Moreover, he noted that the oral frame, with its prominent posterior gap, was formed by the proximal ambulacral floorplates. However, the intrathecal extensions of the oral covering plates, which form the frame interradii, appeared to Spencer to be separate, intermediate plates.

Foerste's (1914) extensive work on the isorophid edrioasteroids includes accurate descriptions of most of the thecal features of *I. cincinnatiensis.* In addition, he speculated on the evolutionary relationships of the species, the mode of derivation of many thecal structures, the functional morphology, possible ecological responses, and the paleoecology. One of his few significant omissions is an account of the hydropore structure and the underlying stone canal passageway. The regularity of the oral plates is the only other taxonomically important structural feature that he overlooked.

Williams (1918) redescribed many of the thecal features of *I. cincinnatiensis* and suggested that *I. holbrooki* (James) was probably a gerontic *I. cincinnatiensis.*

The name *Carneyella cincinnatiensis* was assigned by Bassler (1935) to a nodose specimen of *Carneyella pilea.* Bassler referred to Hall's (1871, 1872) illustration of *Isorophus cincinnatiensis* as a second example of his new species, and reillustrated Hall's drawing under the new name in 1936. Apparently Bassler relied entirely upon the erroneous Hall illustration that figured three large primary orals like those of *Carneyella.* Hall's specimen (AMNH 1194) is a typical *Isorophus cincinnatiensis.*

Bassler's (1936) description of new species of edrioasteroids includes several specimens of *I. cincinnatiensis.* Roemer's original drawing is refigured in his pl. 5, fig. 11. In addition, a large, noncollapsed *I. cincinnatiensis* (USNM 40744; pl. 26, fig. 9-12) is illustrated as an *I. holbrooki* in his pl. 5, fig. 8, 9. The accompanying species description cites the features described by James as typical of *I. holbrooki,* all of which are found in Bassler's specimen, and which are here recognized as typical of large, gerontic *Isorophus cincinnatiensis.*

Bassler (1936) also described the species *Isorophus tennesseensis* (a junior synonym of *I. cincinnatiensis* and cited as characteristic of the new species: the small thecal diameter; the narrow, short, much curved ambulacra; the large oral area with " an unusually large number of small plates;" and the broad rim of marginal plates. The type specimen (USNM 91839-A; text fig. 25B, pl. 26, fig. 3, 4) appears to be a typical *I. cincinnatiensis* in early adulthood. The stage of development explains the small diameter, short, moderately curved ambulacra, and the proportionately large oral area. The oral plates are poorly preserved in the holotype, but they appear to be typical of *I. cincinnatiensis.* The rim contains seven or eight plate circlets and does not appear unusually wide.

The hydropore structure of *I. cincinnatiensis* was described in detail by Kesling (1960). Except for his terminology, Kesling's description is similar to that presented here. His terminology is equated as follows: his large, posterocentral peristomial plate = the right posterior primary oral; his right posterior peristomial plate = the hydropore oral; his proximal covering plate on the left side of ambulacrum V in young specimens or the second covering plate in older individuals = the right posterior shared coverplate; his sloping spatulate plate of the peristomial region = posterior member of the right pair of secondary orals; his small, wedgelike plate in larger specimens = one of the additional secondary oral plates. Kesling reported that the upturned edges of the hydropore oral, the right posterior primary oral, and the right posterior shared coverplate form a rim around the hydropore. Additional well-preserved specimens demonstrate that the adradial ends of the proximal two primary ambulacral coverplates are also upturned. This indicates that the opening also extended distally along the junction between these plates and the adjacent distal part of the hydropore oral. Kesling noted considerable variation in the shape of several oral plates. This variability is due in part to differential enlargement of the plates during growth, as he suggested in one case; it is also in part due to lateral plate slippage during thecal collapse, which alternately exposes or covers different portions of individual elements.

Kesling and Mintz (1960) gave a detailed account of the internal and many external features in both *Isorophus cincinnatiensis* and *Carneyella pilea.* Their work included investigations of specimens which expose the inner side of the oral surface, serially ground sections of each species, and a summary of previous work on internal edrioasteroid structures. Exception is taken to only a few of their conclusions regarding *Isorophus cincinnatiensis.* The report of a possible genital duct adjacent to the anterior margin of the anal structure has not been confirmed by other specimens, and its presence in their specimen is doubted. Another supposed opening, leading from the thecal cavity into the proximal part of the ambulacral tunnel of ambulacrum V, was described as lying along the suture between the second and third proximal floorplates. They suggested that this was for the entrance of a radial canal into ambulacrum V. The convex-upward concavity found in this area in one specimen (UCMP 26536; text fig. 24B, pl. 24, fig. 6-8) ends blindly. Other specimens that expose this region show no suggestion of a comparable concavity or passageway. However, none of the other specimens is as well preserved.

The Kesling and Mintz description of the internal thecal features in *Carneyella pilea,* and the comparison of these to *Isorophus cincinnatiensis,* is clouded by their erroneous referral of specimen AMNH 13266/1-X to *Carneyella pilea.* This was no doubt due to its peculiar mode of preservation (pl. 25, fig. 1, 2), which renders the appearance most uncharacteristic. Transferring their description of this specimen to *Isorophus cincinnatiensis* resolves much of the apparent variability of the internal structures in *I. cincinnatiensis* described by them.

The diagnosis of *Isorophus cincinnatiensis* as presented in Regnéll's (1966) analysis of the Edrioasteroidea merely summarizes the conclusions of earlier workers.

Accompanying figures are reillustrations of previously published figures.

Discussion

The description of *Isorophus cincinnatiensis* is based upon over a thousand specimens. Many of these were collected *in situ* from two populations, which allows recognition of growth details and intraspecific variations that might otherwise have been ascribed to paleoecologic or even to interspecific variation.

Significant variations in thecal structures occur during growth. In juveniles with thecal diameters less than 6 mm, the peripheral rim, oral area, and anal structure dominate the external surface. The short ambulacra and relatively small interambulacra are subordinate in area. During growth the ambulacra lengthen by distal additions of new coverplates and floorplates, and the interambulacra add new elements along their zone of contact with the ambulacra. Earlier formed plates increase in size. Thus the ambulacra become the areally dominant thecal feature in adults. The oral and anal structures and the rim continue to increase in absolute size through plate enlargement and the addition of some new elements, but the rate of size increase is proportionately slow. Therefore, these areas decrease in areal extent in proportion to the ambulacral-interambulacral areas.

In addition to the changes in relative sizes of the structures, the domal theca increases in convexity, particularly in older individuals, and becomes nearly hemispherical. In the oral area, the five basic secondary orals may differentially enlarge, and sometimes become nearly as large as the shared coverplates. Additional secondary orals may be added during adulthood. This plate addition, combined with differential enlargement of existing secondary orals, causes lateral shifting and differential plate growth of the primary orals and shared coverplates. This process results in the variability of oral plate size and distribution common to adult *Isorophus cincinnatiensis*.

The ambulacra continue to lengthen throughout life by the distal addition of new plates. Initially the ambulacra extend straight out from the oral region, and curvature is initiated as they approach the rim margin. The distal ends become concentric with the rim by adulthood, and continue to lengthen along the rim margin. In older individuals, over 25 mm in diameter, the distal tips curve back toward the oral region. Maximum recurvature seen is in an individual nearly 40 mm in diameter (USNM 40744; pl. 26, fig. 9–12), where the ambulacra extend back nearly one-third the length of the interambulacra. During adulthood, the more proximal primary coverplates may differentially enlarge to form what has the appearance of being a triple biseries of coverplates.

The squamose interambulacral plates in some old individuals become nearly polygonal in external outline, although they remain imbricate at their edges.

The anal area adds new plates slowly and reaches a maximum of about 16 to 18 plates in adults of 20 to 25 mm diameter. Apparently further growth is then confined to enlargement of existing plates.

The peripheral rim early develops seven to nine irregular circlets of plates. Further increase in width is accomplished by the slow enlargement of individual plates, and new ones are added to increase the circumference.

The development of new features late in life, *i.e.*, the hemispherical thecal shape, proximal curvature of distal parts of the ambulacra, and polygonal shape of the interambulacrals, are considered to be gerontic characteristics.

Kesling (1960) and Kesling and Mintz (1960) made several possible functional interpretations of the structures of *I. cincinnatiensis*. They suggested that the large hydropore oral plate may have been moveable in life because it is frequently found somewhat posteriorly displaced, leaving the hydropore as a wide gap. They thought the size of the hydropore could thus be controlled. However, the intrathecal extension of this plate forms a major part of the underlying stone canal passageway, which appears to be a tightly sutured structure. Movement of the hydropore plate would have disrupted this passageway. A more likely explanation lies in the fact that the hydropore oral lies distal to the posterior edge of the oral frame and hence is unsupported. During thecal collapse it is pushed downward further than the anterior hydropore plates which rest on the proximal floorplates of ambulacrum V. In noncollapsed specimens, the hydropore plate is almost always in place, adjacent to the other hydropore elements, and restricts the hydropore to a narrow, slitlike opening.

The closed ambulacral coverplates of *I. cincinnatiensis* are tightly interlocked by the intra-ambulacral extensions. As suggested by Kesling and Mintz, this "zipper-like" arrangement restricts the opening of these plates. The perradial underlap of opposing, alternate coverplates necessitates simultaneous movement of both parts of the biseries, on either side of the ambulacrum. The lateral underlap of adjacent coverplates allows little differential slippage between adjacent ones, so that a large series of the adjacent coverplates must have moved at the same time. Coverplate opening must have proceeded as a coordinated, wavelike motion that originated distally and gradually swept toward the proximal end of the ambulacrum. There probably was a common integument investing each of the coverplate series halves. Thus coverplate opening would have involved two ribbonlike strips, with the opposing ribbons gradually flexing upward and away from the axis of the ambulacra as the broad zone of opening coverplates swept proximally. Closure of the coverplates would have been accomplished by a reversal of the process, with the underlapping perradial extensions of opposing elements gradually slipping back into place as opposing plates simultaneously descended.

Kesling and Mintz suggested that the long intrathecal extensions of the primary coverplates were for the attachment of muscles that operated these plates. If so, the secondaries, which end near the edges of the floorplates, must have been carried along by the primaries, their movement assured by the lateral underlap of their intrathecal extensions.

An alternative method of coverplate control involves the shallow grooves that appear to extend along the upper, nearly level, lateral margins of the ambulacral floorplates. The two grooves, one on each side of the floorplate, are just inside the lateral edges and appear to extend the length of the ambulacra (pl. 25, fig. 10, 11). The suggestion of a complementary groove and adradially adjacent ridge on the overlying inner surfaces of the coverplates has been seen in two specimens (pl. 25, fig. 3, 4, pl. 26, fig. 5, 6). The coverplate grooves may have aligned with the floorplate grooves to form a tubular passageway along the boundary between these two sets of plates. If so, the passageway might have contained an extension of the hydrovascular system related to coverplate movement. In such a scheme, the intrathecal extensions of the primary coverplates would act as wedges and abut the inner surface of the adjacent interambulacrals. Coverplate movement could be effected by increasing the diameter of the water tube, which would push up on the coverplates. With the distal intrathecal extremities secured against the interambulacrals, the net result would be an upward movement of the perradial plate tips, thereby opening the coverplates. Controlled water pressure, by injection and withdrawal, might seem to readily account for the "peristaltic" operation of the coverplates.

The anal structure is an elevated, low, rounded, conical mound on several noncollapsed specimens. This configuration was probably maintained during life when the anal plates were closed.

The small, vertical basal ridges of the geniculate peripheral rim plates found in *I. cincinnatiensis* may have been the site of muscle or ligament attachments. The primary function of these attached tissues would most likely be the anchoring of the theca to the substrate. However, the large number of ridges present suggests that some might have been related to muscles used in thecal expansion and/or contraction.

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

Isorophus austini (Foerste), 1914

Text fig. 26; plate 29, plate 30, fig. 1–2

1914 *Agelacrinus austini* Foerste, A. F., Denison Univ., Sci. Lab. Bull. 17 (art. 14): 444-445, pl. 6, fig. 1a-c.

1915 *Agelacrinites austini* Foerste, Bassler, R. S., United States Nat. Mus. Bull. 92, 1: 20.

1917 *Agelacrinus austini* Foerste, A. F., Denison Univ., Sci. Lab. Bull. 18 (art. 4): 341.

1918 *Agelacrinus austini* Foerste, Williams, S. R., Ohio Jour. Sci. 19 (1): 64-81, pl. 2, fig. 12, pl. 3, fig. 13-14, 16-17, pl. 4, fig. 20-25a, pl. 6, fig. 32-37, pl. 7, fig. 38-44, pl. 8, fig. 50-50a, pl. 9, fig. 52, 55.

1935 *Isorophus austini* (Foerste), Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 5.

1936 *Isorophus austini* (Foerste), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 17-18, pl. 2, fig. 9, pl. 6, fig. 1-2.

1943 *Isorophus austini* (Foerste), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 204-205.

1960 *Isorophus austini* (Foerste), Kesling, R. V. and Mintz, L. W., Univ. Michigan, Contrib. Mus. Paleont. 15 (14): 318-339.

1960a *Isorophus austini* (Foerste), Regnéll, G., Soc. Geol. France, Bull., serie 7, 1: 774, text fig. 1.

1966 *Isorophus austini* (Foerste), Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U155-U156, text fig. 121.

Diagnosis

An *Isorophus* with: small domal theca; five or more secondary orals; proximal secondary ambulacral coverplates nearly as large externally as primaries; interambulacrals proportionately of moderate size.

Description

Isorophus austini (Foerste) has a theca with an average diameter of around 10 mm. The largest known specimen is 14.2 mm.

The oral region includes the four primary orals, two pairs of shared coverplates, and the hydropore oral, arranged in the characteristic pattern of the genus (text fig. 26, pl. 29, fig. 6–8). Five or more secondary orals are also present. One lateral pair lies along the transverse oral midline between the two right primary orals and the right pair of shared coverplates. One anterior pair lies along the anterior oral midline between the two anterior primary orals and the proximal coverplates of ambulacrum III. One or more lateral secondary orals lie along the transverse midline of the oral region between the two left primary orals and the left pair of shared coverplates. When two left lateral secondary orals are present, both may be on the same side of the midline (text fig. 26), or they may be opposed and form a pair.

The total size of the oral region, in proportion to thecal diameter, is comparable to that found in young adult *I. cincinnatiensis* of the same size. Therefore, it is proportionately larger in adult *I. austini* than in average adult *I. cincinnatiensis*.

The oral frame of *I. austini* appears to be essentially identical to that of *I. cincinnatiensis*. However, the structure is not well preserved in those specimens examined.

The hydropore structure of *I. austini* is distinguished from that of *I. cincinnatiensis* by the direct participation of one secondary ambulacral coverplate in the formation of the opening. The right posterior primary oral, the hydropore oral, the right posterior shared coverplate, and the posterior proximal primary coverplate of ambulacrum V all have prominently thickened edges flanking the hydropore. Distal to the proximal primary coverplate, the second proximal posterior secondary coverplate of ambulacrum V abuts the hydropore oral. The adradial margin of this plate is thickened and forms part of the raised rim around the opening. The second proximal posterior primary coverplate of ambulacrum V is adradially shortened where it abuts the hydropore oral, as is the more proximal coverplate in the structure. However, this plate does not appear to have been in contact with the opening.

The passageway for the stone canal, as does the oral frame, appears identical to that of *Isorophus cincinnatiensis*.

Ambulacral curvature in *I. austini* is even, and the ambulacra end distally as they become concentric with the proximal margin of the rim. The distal tip of each remains widely separated from the adjacent ambulacrum.

The double biseries of ambulacral coverplates consists of alternating pairs of primary and secondary plates. Alternation here, as in *I. cincinnatiensis*, is frequently irregular because of the absence of one member of a plate pair, or the addition of an extra plate. The perradial tips of either the right or left member of a pair may be proximal to the other. However, the relationship of opposing coverplate tips may be more regular along a single ambulacrum than in *I. cincinnatiensis*, where it commonly reverses.

Distally, the secondary coverplates are externally much smaller than adjacent primaries, and they are externally covered by the overlapping primaries, either before or just as they reach the adradial suture line. Proximally the secondaries increase in external size more rapidly than the primaries, and become nearly as large externally as the proximal primaries. Even these proximal secondaries usually decrease slightly in width adradially, but occasionally they have nearly parallel sides and wide external adradial ends that are equal in width to those of adjacent primaries.

The intra-ambulacral and intrathecal coverplate extensions of *I. austini* apparently are similar to those of *I. cincinnatiensis*.

The uniserial, trough-shaped floorplates of *I. austini* abut one another along vertical suture lines. No trace of proximal flanges on the inner sides of these plates has been seen, although these features could have been destroyed during weathering in the few specimens in which they are exposed. The upper, lateral margins of the floorplates are nearly horizontal, as in *I. cincinnatiensis*.

The squamose, imbricate interambulacrals are of moderate size in proportion to thecal diameter; the largest are found in the central and distal parts of the areas. In external view the distal interambulacrals approach the size of the proximal rim plates, but apparently remain slightly smaller even in the largest adults.

The valvular anal structure is like that of *I. cincinnatiensis*, except that it includes fewer plates; adults have only 12 to 14 plates each.

The peripheral rim includes approximately seven circlets of plates; the regularity of the circlets decreases outward. The proximal circlet is subdivided into a proximal and distal subcirclet, but they are less regular than in *Isorophus cincinnatiensis*.

The rim occupies approximately the same percentage of the oral surface as in young adult *I. cincinnatiensis* of equal thecal size. Therefore, the rim of *I. austini* is proportionately larger than that of average adult *I. cincinnatiensis*.

The basal surfaces of the geniculate rim plates have vertical ridges comparable to those found in *I. cincinnatiensis*. The larger rim plates appear to have from five to seven ridges each.

External plate surfaces of *I. austini* occasionally bear small, rounded tubercles. The original extent of this prosopon is unknown, owing to the etched condition of the specimens.

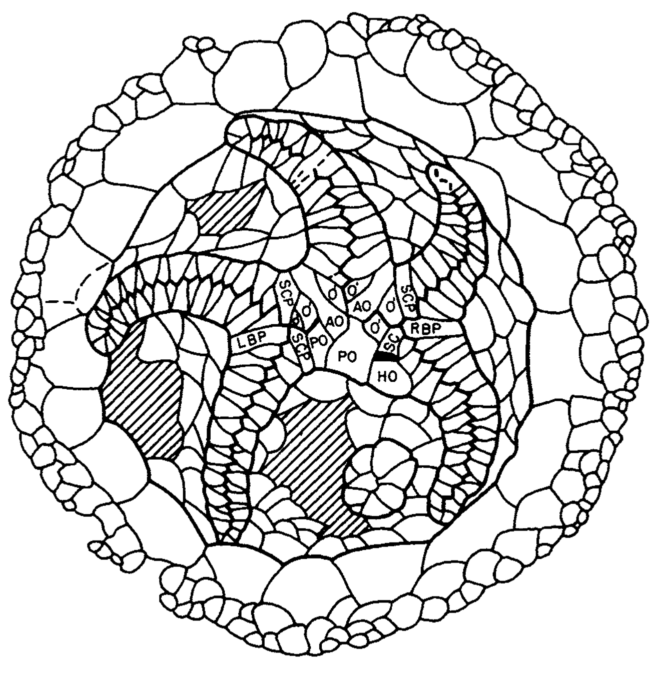
Specimens

USNM 70162. Whitewater Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Dutch Creek, south of Oakland Pike, 4½ miles northwest of Wilmington, northwestern part of Clinton County, Ohio.

USNM 70162-A, B, C. Five type series specimens of *Isorophus austini* (Foerste) (1914).

USNM 70162-C. Three specimens resting on a bryozoan fragment.

USNM 70162-C-1. Lectotype of *I. austini* Foerste (1914, pl. 6, fig. 1-c). 7.5 mm axial by 7.5 mm transverse diameter.



Text figure 26. *Isorophus austini* (Foerste), 1914

USNM 70162-D, (x 14), pl. 29, fig. 7.

AO, anterior primary oral; HO, hydropore oral plate; LBP, left lateral bifurcation; o', secondary oral plate; PO, posterior primary oral plate; RBP, right lateral bifurcation plate; SC, lateral shared coverplate; SCP, lateral shared coverplate.

Pl. 29, fig. 1.

This specimen is the best preserved individual included by Foerste in the type series and is here designated the lectotype. The theca has not collapsed; the oral surface remains convex upward. Disrupted thecal areas include most of ambulacrum III, the distal parts of ambulacra IV, V, interambulacra 4, the right distal part of interambulacrum 5, and the left edge of the anal structure. The thecal plates have been etched, and the oral region is severely abraded. However, most diagnostic features of the species are present. Remnants of nodose prosopon are preserved on a few thecal plates.

Suture lines are in part obscure in Foerste's photograph of this specimen. Apparently his illustration was retouched, making comparison with pl. 29, fig. 1, difficult.

USNM 70162-C-2. (?)*I. austini* (Foerste). 7.5 mm axial by 9.5 mm transverse diameter.

A second specimen on the same resting area with the lectotype, this individual has been so deeply etched that only the outlines of the major thecal structures are identifiable.

USNM 70162-C-3. Lectoparatype of *I. austini* (Foerste). 6.4 mm axial by 6.3 mm transverse diameter.

Pl. 29, fig. 9.

The third individual on the bryozoan is also abraded and deeply etched. Only the left side of the theca, including ambulacra I and II, is well enough preserved to allow interpretation of the features. Foerste (1914) referred to this specimen in the text of his species description, noting the small amount of ambulacral curvature.

USNM 70162-A. Lectoparatype of *I. austini* (Foerste) (1914, pl. 6, fig. 1-a). 8.4 mm axial by 8.3 mm transverse diameter.

Pl. 29, fig. 3.

This is a second specimen illustrated by Foerste in the original species description. It has been etched and partially disrupted during thecal collapse. Ambulacra I and II and the adjacent interambulacrals are disrupted, but most other thecal features are interpretable. The raised hydropore rim and the anal structure are well preserved.

USNM 70162-B. Lectoparatype of *I. austini* (Foerste) (1914, pl. 6, fig. 1-b). 8.4 mm axial by 8.3 mm transverse diameter.

Pl. 29, fig. 2.

This specimen exposes the inner side of the oral surface of the theca. The specimen is partially disrupted, particularly the posterior half of the oral frame and the adjacent stone canal passageway, along with ambulacrum II. Moreover, the exposed plate surfaces have been deeply etched, removing delicate features such as the small basal ridges of the geniculate rim plates. Most of the larger features of the inner thecal structures are preserved.

USNM 70162-D, E. Two *Isorophus austini* accompanying the type series; topotypes.

USNM 70162-D. 6 mm axial by 6.3 mm transverse diameter. Text fig. 26, pl. 29, fig. 6-8.

This specimen has been etched, but little plate disruption has occurred. Only a few of the small outer rim plates have been lost. The surficial etching has accentuated the plate boundaries, thereby facilitating recognition of individual elements.

USNM S-3961. Illustrated Specimen of *I. austini* (Foerste) by Bassler (1936, pl. 6, fig. 2). Upper Whitewater Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Dodges Creek, Oxford, Ohio. 6.8 mm axial by 10.8 mm transverse diameter.

Pl. 29, fig. 4, 5.

This individual exposes the inner side of the oral surface. The specimen is broken and the right posterior part of the theca [left as viewed] is missing. The ambulacral floorplates of II, III, and IV show no signs of proximal flanges on the inner sides. The floorplates of ambulacrum V have been displaced anteriorly and this exposes the overlying inner surfaces of the coverplates along their zone of contact with the floorplates. The intrathecal extensions of the primary coverplates extend beyond the lateral margins of the floorplates. The distal parts of these extensions appear to expand in width. The basal ridges of the geniculate floorplates are preserved on the larger rim plates.

USNM S-3963 (A-C). Three *Isorophus austini* (Foerste) on one slab. Basal Saluda Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Fallen Timbers Creek, Versailles, Indiana.

USNM S-3963-A. Illustrated Specimen of *I. austini* (Foerste) by Bassler (1936, pl. 6, fig. 1). 9.3 mm axial by 9.8 mm transverse diameter.

Pl. 30, fig. 2.

The central oral surface of the specimen is collapsed below the level of the surrounding peripheral rim, but the plates are not severely disrupted. Thecal etching has accentuated plate boundaries in some areas but obscured them in others. The specimen appears to be a typical *I. austini* with the exception of the peripheral rim. This structure appears unusually wide, although the number of plate circlets is not increased. Moreover, the exposed parts of the more distal rim plates appear unusually long. This apparent variation in the rim may be the result of thecal flattening during preservation.

USNM S-3963-B. 14.2 mm greatest diameter.

Pl. 29, fig. 10.

This is the largest representative of *I. austini.* Unfortunately, the specimen is disrupted and only the right margin of the theca allows interpretation. The typical double biseries of primary and large secondary coverplates is seen in the distal part of ambulacrum IV.

USNM S-3963-C. 6.7 mm axial by 6.6 mm transverse diameter.

Pl. 29, fig. 11.

The third individual on the slab, this small specimen is both disrupted and etched. The ambulacra are short and only slightly curved; the distal parts approach the peripheral rim.

USNM 91841. Whitewater Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Near Waynesville, Ohio. 11.3 mm axial by 11.5 mm transverse diameter.

Pl. 30, fig. 1.

This is a relatively large specimen. The theca has partially collapsed, but little plate disruption has occurred. Part of the left side of the theca is obscured by tenacious matrix. The oral region is slightly disrupted, but the characteristic oral plate arrangement is retained. The adjacent hydropore structure is well preserved, including the raised rim around the opening. The anal structure is preserved as a low, conical protuberance.

Discussion of previous investigation

Isorophus austini (Foerste) (1914) was originally placed in the genus *Agelacrinites,* although Foerste acknowledged that this and related Ordovician species required separation into a new genus. Foerste later (1917) described the genus *Isorophus* and tentatively transferred this species to it.

Foerste's (1914) original description of *I. austini* stressed the small thecal diameter. He (1914, p. 444) also referred to: the double biseries of ambulacral coverplates with the secondaries of " a relatively greater length . . . than in . . . any other species"; the moderate ambulacral curvature, less curved in smaller specimens; the anal structure with an inner and outer circlet; and the normal peripheral rim. Foerste was mistaken in thinking originally that the oral area was like that of *Carneyella pilea.* He revised this opinion in 1917 and predicted that the oral region would prove to be like that of *Isorophus.*

Williams (1918) described a growth series of upper Richmond (Whitewater Formation, Upper Ordovician) edrioasteroids from near Lawshe, Ohio. The specimens, which range in diameter from .66 mm to 17 mm, were assigned to *Isorophus austini* and informally designated " variety Lawshe." Most of the specimens are less than 10 mm in diameter and expose the inner side of the oral surface. The progressive distal addition of the ambulacral floorplate is demonstrated by these specimens, along with the general increase in numbers of interambulacral and rim plates during thecal growth. Partial disruption of most of the specimens obscures details of the oral frame, stone canal passageway, and other inner surface thecal features. The basal ridges of the rim plates are preserved in some of the specimens. If his large specimen, 17 mm in diameter, is an *I. austini,* it is the largest known representative of the species.

Bassler (1936) reillustrated the lectotype of *I. austini* along with two other specimens (pl. 29, fig. 4, 5, pl. 30, fig. 2). Curiously, Bassler (1936, p. 18) characterized the species by " the delicacy of its parts and its short, narrow, recurved rays." Ambulacral recurvature has not been found in any of the specimens assigned to this species.

Kesling and Mintz (1960) and Regnéll (1966) cited Williams' (1918) description of *Isorophus austini*, but the species was not restudied or redescribed.

Discussion

Isorophus austini (Foerste) (1914) is separated from *I. cincinnatiensis* primarily by the relatively large size of the secondary ambulacral coverplates. In the proximal ambulacra the coverplate series often resembles a single biseries because the secondaries are nearly equal in external width to the primaries. Even in the distal parts of the ambulacra the secondaries frequently reach the external adradial suture line before being hidden by the overlap of adjacent primaries. This condition is rarely found in *I. cincinnatiensis*.

The large size of the secondary coverplates dictates the distinctive plate arrangement of the hydropore structure. The secondary coverplate, which is located between the first two proximal posterior primary coverplates of ambulacrum V, forms the distal anterior edge of the hydropore opening. In *I. cincinnatiensis*, the homologous secondary coverplate is small and externally limited to the axial part of the ambulacrum. Thus it does not extend adradially far enough to intersect the hydropore opening, which is formed by the adradial ends of the two proximal primary coverplates.

The secondary oral plate arrangement of *I. austini* appears to be distinctive also. The presence of two anterior secondaries contrasts with the single secondary commonly found in *I. cincinnatiensis*. Moreover, the common occurrence of a single left lateral secondary oral contrasts with the pair usually found in *I. cincinnatiensis*. However, variation in the number and distribution of secondary orals is not uncommon in both species, and the small number of *I. austini* specimens precludes confident separation of the norm from random variation.

The size differential between *I. austini* and *I. cincinnatiensis* is apparent when average adults are compared. Curiously, in adult *I. austini* the percentage of thecal surface formed by the major thecal structures is similar to that of young adult *I. cincinnatiensis* of approximately the same thecal diameter. Thus, compared with average adult *I. cincinnatiensis*, the oral region and peripheral rim of adult *I. austini* are larger in proportion to thecal diameter, whereas the ambulacral and interambulacral areas are smaller. Only the anal structure is comparable in proportional areal extent in average adults of the two species.

RANGE AND OCCURRENCE: Whitewater Formation, Richmond Group, Cincinnatian Series, Upper Ordovician of the Cincinnati Arch Region, Indiana and Ohio.

Isorophus warrenensis (James), 1883

Text fig. 27; plate 30, fig. 3-9

1883 *Agelacrinus warrenensis* James, U. P., The Paleontologist, Cincinnati, 7: 58, pl. 2, fig. 3-3a.

1914 *Agelacrinus warrenensis* James, Foerste, A. F., Denison Univ., Sci. Lab. Bull. 17 (art. 14): 448-450, pl. 1, fig. 4a-b.

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

1918 *Agelacrinus warrenensis* James, Williams, S. R., Ohio Jour. Sci. 19 (1): 63-81, pl. 5, fig. 27.

1935 *Isorophus warrenensis* (James), Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 5.

1936 *Isorophus warrenensis* (James), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 19, pl. 5, fig. 2-3, pl. 6, fig. 11.

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

Diagnosis

An *Isorophus* with: small to moderate-sized theca; secondary ambulacral coverplates relatively large, commonly reaching the adradial suture line; interambulacral plates very large in proportion to thecal diameter.

Description

Isorophus warrenensis averages 13 mm adult thecal diameter.

The oral region and hydropore structure are inadequately known. Possible plate distributions found in three of the lectoparatypes are seen in text fig. 27A-C. The oral region appears to contain the four primary orals, the two pairs of lateral shared coverplates, and the hydropore oral typical of the genus. Secondary orals are present, but the average number and distribution of these plates have not been determined. The hydropore structure includes at least the right posterior primary oral, the hydropore oral, the right posterior shared coverplate, and two or more proximal posterior coverplates of ambulacrum V. A raised rim formed by the thickened edges of the adjacent plates probably surrounds the hydropore opening.

Ambulacral curvature is moderate; the distal tips become concentric with the proximal margin of the rim only in the larger adults. The double biseries of ambulacral coverplates appears to be similar to that of *I. austini*. The externally exposed parts of the secondaries are relatively large and often reach the adradial suture lines. In the proximal parts of the ambulacra, the adradial ends of the secondary coverplates are often one-half to three-fourths the width of adjacent primaries.

The interambulacral plates of *I. warrenensis* are quite large in proportion to thecal diameter and therefore fewer in number per interambulacrum. The relatively large size of these plates contrasts with the proportionately moderate-sized interambulacrals of the other two specimens of *Isorophus*.

The valvular anal structure of *I. warrenensis* is disrupted or hidden in all known specimens.

The peripheral rim is typical of that described for the genus. It is formed by six or seven circlets. The proximal circlet comprises large plates and is differentiated into a proximal and distal subcirclet. The alternation of these subcirclet members appears to be more regular than in either *I. cincinnatiensis* or *I. austini*.

A few widely scattered remnants of small nodes are found in some specimens of *I. warrenensis*. In others, the thecal plates appear to have been smooth.

Specimens

USNM S-3957 (A-G). Type series of *Isorophus warrenensis* (James) (1883). Reported by Foerste to be: Fairmount member, Fairview Formation, Maysville Group, Cincinnatian Series, Upper Ordovician; "short distance up a small creek entering Second Creek at the first bridge east of Morrow," Warren County, Ohio (Foerste, 1914, p. 449). USNM label and Bassler (1936): probably basal Arnheim Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Oregonia, Ohio.

USNM S-3957-A. Lectotype of *I. warrenensis* (James) (1883, pl. 2, fig. 3, 3a) and Williams (1918, pl. 5, fig. 27). 13.7 mm axial by 14.1 mm transverse diameter.

Pl. 30, fig. 3.

The lectotype is poorly preserved. The oral region is disrupted and individual plates are not identifiable. The ambulacra are disrupted and largely hidden beneath adjacent interambulacrals. The anal structure is not visible. The rim is also partly disrupted, although the right posterior part is nearly intact. However, the specimen does show the single most important species characteristic — the very large interambulacral plates. These are also in part disrupted.

This individual was the only specimen in the type series illustrated by James. It has been referred to as the "type" by Williams (1918) and as the "holotype" by Bassler (1936). It is recorded as the "holotype" in the USNM collections. The other six specimens in the type series (B-G) are lectoparatypes. James noted that there were 10 specimens in his type suite. The location of the missing three is unknown.

USNM S-3957-C. Lectoparatype of *I. warrenensis* (James). 12.2 mm axial by 11.7 mm transverse diameter.

Text fig. 27A, pl. 30, fig. 8, 9.

The central oral surface of this specimen has collapsed below the margin of the peripheral rim, obscuring the distal parts of the ambulacra and interambulacra and also the anal structure. However, the oral region and the proximal parts of the ambulacra and interambulacra are only partially disrupted. Text fig. 27A represents a possible interpretation of the plate distribution in these structures.

USNM S-3957-D. Lectoparatype of *I. warrenensis* (James) illustrated by Bassler (1936, pl. 5, fig. 2). 12.8 mm axial by 13 mm transverse diameter.

Text fig. 27B, pl. 30, fig. 4, 5.

This specimen is collapsed, partially disrupted, and partially covered by tenacious matrix. Moreover, earlier attempts at preparation have left gouges in many of the plates. The major thecal structures are visible, but plate definition is poor. Text fig. 27B represents a possible interpretation of the plate configuration.

USNM S-3957-E. Lectoparatype of *I. warrenensis* (James). 12.7 mm axial by 13 mm transverse diameter.

Text fig. 27C, pl. 30, fig. 6.

This specimen has also collapsed, but most of the major external thecal features are distinct. The distal parts of the ambulacra and interambulacra are disrupted, and the anal structure is obscured. Text fig. 27C is a tentative interpretation of the plate structure.

USNM S-3957-F-2. Lectoparatype of *I. warrenensis* (James). 10 mm greatest diameter by a perpendicular of 7.4 mm.

This specimen is the smaller of the two on a brachiopod fragment. The theca has collapsed; it is disrupted and laterally distorted. Plate boundaries are not apparent except in a small segment of the rim. This is probably the specimen James (1883) mentioned in the original description as being distorted by lateral pressure.

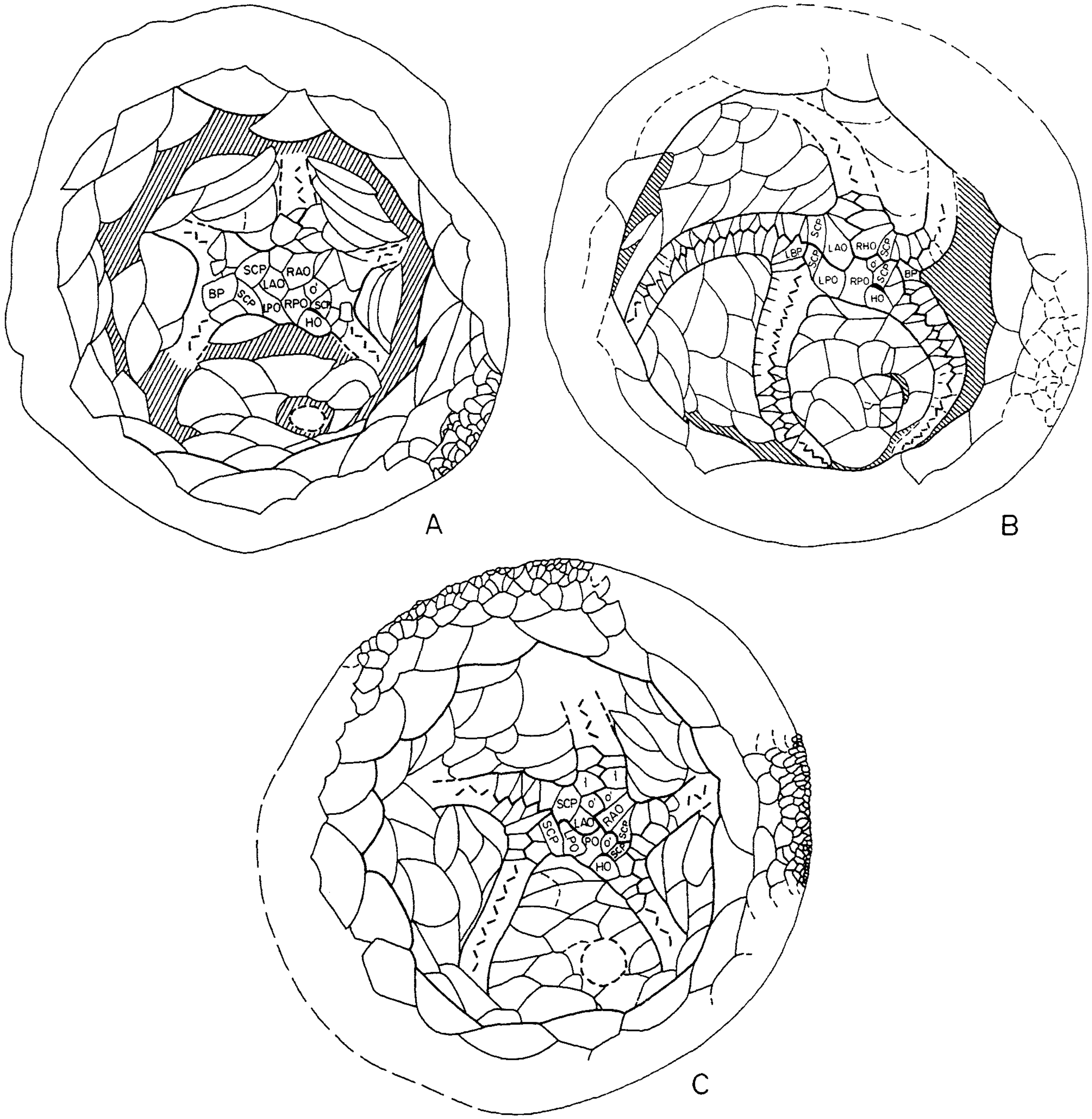
USNM 70165. Illustrated Specimen of *I. warrenensis* (James) by Bassler (1936, pl. 6, fig. 11). Basal Arnheim Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Near mouth of Second Creek of Todds Fork. Warren County, Ohio. 13.9 mm greatest diameter by a perpendicular of 12.6 mm.

Pl. 30, fig. 7.

This specimen was illustrated by Bassler to show the jumbled condition of the thecal plates. Only the large interambulacrals and some of the large rim plates are apparent.

Discussion

The original description of *Isorophus warrenensis* (James) (1883) is notably nondiagnostic. It cites only preservational characteristics and thecal features common to this and related species. Foerste (1914) noted that



Text figure 27. *Isorophus warrenensis* (James), 1883

A. Lectoparatype, USNM S-3957-C, (x 7), pl. 30, fig. 8.

B. Lectoparatype, USNM S-3957-D, (x 7), pl. 30, fig. 5.

C. Lectoparatype, USNM S-3957-E, (x 7), pl. 30, fig. 6.

BP, lateral bifurcation plate; HO, hydropore oral plate; LAC, 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; RPO, right posterior primary oral plate; SCP, lateral shared coverplate; 1, primary ambulacral coverplate.

most features described by James were preservational or common to *I. cincinnatiensis*, and he considered the specimens of the type series as young representatives of the latter species.

Williams (1918) repeated James' description and published a photograph of the lectotype. He noted Foerste's impression that the specimens were young *I. cincinnatiensis*, but did not comment on the matter himself.

Bassler (1936) redescribed the species and placed it in Foerste's genus *Isorophus*. Earlier workers had included it in the genus *Agelacrinites*. Among other features, Bassler noted both the small thecal diameter and the large size of the interambulacrals.

The very large interambulacral plates of *I. warrenensis* are its most prominent feature. During collapse these plates often slip over the ambulacra and anal area so as to hide them. The oral plates are commonly partially disrupted in this process. Hence only the interambulacrals and the peripheral rim plates are adequately defined for the species. The inner side of the oral surface has not been seen.

I. warrenensis more closely resembles *I. austini* than *I. cincinnatiensis* because of its small to moderate size and the relatively large size of the secondary ambulacral coverplates. However, the large interambulacrals serve to separate it from both *I. austini* and *I. cincinnatiensis*.

RANGE AND OCCURRENCE: (?)Fairview Formation, Maysville Group and Arnheim Formation, Richmond Group, Cincinnatian Series, Upper Ordovician of the Cincinnati Arch Region, Ohio.

Genus *Isorophusella* Bassler, 1935

1852 [*non*] *Hemicystites* Hall, J., Nat. Hist. New York, pt. VI, Palaeontology 2: 245-246.

1908 [*non*] *Lebetodiscus* Bather, F. A., Geol. Mag. (n.s.), dec. 5, 5: 543-550, pl. 25, fig. 1.

1915 *Lebetodiscus* Bather, Raymond, P. E. [*partim*], Ottawa Naturalist 29 (5-6): 61-62, pl. 1, fig. 1.

1917 *Isorophus* Foerste, A. F. [*partim*], Denison Univ., Sci. Lab. Bull. 17 (art. 14): 341.

1921 *Isorophus* Foerste, Raymond, P. E. [*partim*], Geol. Surv. Canada, Mus. Bull. 31 (Geol. Series 38): 12-13, pl. 4.

1935 *Isorophusella* Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 5, pl. 1, fig. 11.

1936 *Isorophusella* Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 19-20.

1938 *Isorophusella* Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 119.

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

1946 *Isorophus* Foerste, Wilson, A. E. [*partim*], Geol. Surv. Canada Bull. 4: 21.

1965 *Hemicystites* Hall, Sinclair, G. W. and Bolton, T. E. [*partim*], Geol. Surv. Canada Bull. 134 (3): 35-39, pl. 11, fig. 1-6.

1966 *Isorophusella* Bassler, Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U169, text fig. 128-4.

TYPE SPECIES: *Lebetodiscus inconditus* Raymond, 1915.

Diagnosis

Isorophidae with: ambulacra straight or slightly curved; ambulacral coverplates a regularly alternating double biseries; ambulacra proportionately moderate to broad in width with gradual distal taper; interambulacral plates squamose, imbricate.

Description

The theca of *Isorophusella* Bassler (1935) is domal. Average adult diameters range from 7 mm in small species to 15 mm in those of moderate size.

The oral region is formed by the four primary orals, the two pairs of shared coverplates, and the one large hydropore oral typical of the family (text fig. 28A). In addition, a single right lateral secondary oral is always present.

The two anterior primary orals are subequal in size and arranged symmetrically on either side of the anterior oral midline. The left posterior primary oral is equal to or slightly larger than the anterior primary orals. The right posterior primary oral is appreciably larger than the other primaries. Its anterior margin abuts both anterior primary orals, and its left side extends into the left half of the oral region. Therefore, the right edge of the left posterior primary oral lies to the left of center of the oral region. Anteriorly, this left primary abuts only the left posterior edge of the left anterior primary oral. The two pairs of shared coverplates flank the primary orals along the transverse oral midline. The perradial ends of the anterior members of the two pairs usually lie proximal to the perradial tips of the posterior pair members. The posterior plate of each pair is usually in contact perradially with the proximal end of the adjacent lateral ambulacral bifurcation plate.

A single posterior secondary oral plate lies along the right side of the transverse oral midline, between the perradial ends of the right posterior primary oral and the right posterior shared coverplate (text fig. 28A). The anterior margin of this plate fits between the perradial tips of the anterior primary oral and the right anterior shared coverplate. Additional secondary orals possibly are present in some species.

The hydropore structure of *Isorophusella* is formed by six or seven plates, including: the right posterior primary oral, the hydropore oral, the right posterior shared coverplate, and three or four proximal coverplates of the posterior side of ambulacrum V (text fig. 28A). The proximal two ambulacral coverplates commonly are one proximal unpaired secondary followed by one unpaired primary. However, the secondary may be restricted to the axial part of ambulacrum V, and is thus not in direct contact with the hydropore opening. In some cases this unpaired secondary is absent, in which case the unpaired primary coverplate is adjacent to the shared coverplate both adradially and perradially. Distal to the unpaired primary coverplate, the proximal posterior paired secondary coverplate forms the distal anterior edge of the hydropore opening. The adjacent posterior member of the proximal pair of primary coverplates is reduced in size along its zone of contact with the distal edge end of the hydropore oral, but does not make contact with the opening.

The ambulacra are either straight or nearly so. A very slight curvature is commonly encountered in some or all of the ambulacra of an individual, I-II-III contrasolar, IV-V solar. Ambulacrum I is most frequently curved, whereas ambulacrum IV is usually straight.

The ambulacral coverplates of *Isorophusella* form a double biseries of alternating pairs of primary and secondary plates. The primaries are larger than the secondaries, which commonly do not reach the adradial suture line in external view. As in *Isorophus*, the primary coverplates laterally overlap the adjacent secondary elements; the edges of the plates of both series are beveled to fit tightly together along the zone of overlap. The adradial reduction in width of the secondaries is due primarily to the adradially increasing width of the zone of overlap.

The primary and secondary coverplate pairs alternate regularly in *Isorophusella*. Unpaired plates are uncommon. Moreover, the proximal-distal relationship of the perradial tips of each pair is also commonly consistent along the entire length of each ambulacrum.

The intrathecal extensions of the ambulacral coverplates appear to be similar to those of *Isorophus*. The large primary plate extensions continue into the thecal cavity past the lateral edges of the floorplates. In at least one species these inner parts first narrow and then expand to nearly the full width of the coverplate, and the innermost tips of adjacent extensions are almost in contact. The intrathecal extensions of the secondary coverplates end immediately past the edges of the floorplate. Thus, marked oval hollows are left between the adjacent primary coverplate extensions.

The intra-ambulacral coverplate extensions of *Isorophusella* also appear to be similar to those of *Isorophus* but are inadequately exposed in the existing specimens.

The uniserial ambulacral floorplates of *Isorophusella* are trough-shaped, and the upper lateral margin is nearly horizontal along the zone of contact with the overlying coverplates. Sutures between contiguous floorplates are vertical.

The squamose interambulacrals are imbricate and of moderate size in proportion to thecal diameter.

The valvular anal structure is constructed like that of *Isorophus*. Average adult *Isorophusella* have 12 to 16 plates which form the inner and outer circlets.

The peripheral rim comprises five to seven circlets of plates. The proximal circlets of large plates are subdivided into proximal and distal subcirclets. Alternation of the subcirclet plates is more or less regular. The more distal rim circlets are successively less regular. Externally, the plates of the proximal two or three circlets are elongate concentric with the thecal margin, the remainder are elongate radially. Transition circlet plates with a characteristic form have not been found. The larger rim plates are geniculate, and vertical ridges may be present on their basal surfaces.

The thecal plates of *Isorophusella* are commonly smooth, but small, scattered nodes are present in at least one species.

Discussion

Bassler (1935) characterized his monotypic *Isorophusella* (*Lebetodiscus inconditus* Raymond, 1915) as similar to *Isorophus* but with: ambulacra I-II-III contrasolar, IV-V solar; and interambulacrals highly imbricating. Regnéll (1966) recognized *Isorophusella* and noted that although the ambulacral curvature is as Bassler described it, it is very slight.

Bassler's (1936) *Isorophus trentonensis* and Sinclair and Bolton's (1965) *Hemicystites pleiadae* are also assignable to *Isorophusella*. *Carneyella raymondi* Clark (1919) and *Hemicystites paulianus* Bassler (1936) are viewed as synonymous with *I. incondita* (Raymond).

Isorophusella Bassler (1935) is characterized by straight or only slightly curving ambulacra. If the ambulacra curve, the direction of each follows the pattern of I-II-III contrasolar, IV-V solar. Commonly, however, some ambulacra of one specimen are curved whereas the others are straight. Also characteristic of the genus is the regularity of the ambulacral coverplates, both with respect to the alternation of pairs of primaries and secondaries, and the relationship of the perradial tips of opposing pair members. These features contrast with the pronounced ambulacral curvature and coverplate irregularities typical of *Isorophus*. The greater number of secondary orals in *Isorophus* contrasts with the single secondary oral commonly found in *Isorophusella*.

Three species are here assigned to *Isorophusella*, although only *I. incondita*, the type species, is known in detail. But even here the inner side of the oral surface has not been observed. In *Isorophusella pleiadae* only the inner side is known. *I. trentonensis* is known only from a single, partially disrupted specimen.

RANGE AND OCCURRENCE: Black River Group, Middle Ordovician through Richmond Group, Upper Ordovician of Ontario, Quebec, New York, and Minnesota.

Isorophusella incondita (Raymond), 1915

Text fig. 28-32; plate 31-34, plate 35, fig. 1-4.

1915 *Lebetodiscus inconditus* Raymond, P. E., Ottawa Naturalist 29 (5-6): 61-62, pl. 1, fig. 1.

1917 *Isorophus inconditus* (Raymond), Foerste, A. F., Denison Univ., Sci. Lab. Bull. 18 (art. 4): 341.

1919 *Carneyella raymondi* Clark, T. H., Mus. Comparative Zoology, Bull. 63 (1): 11-12, pl. 1, fig. 18-19.

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

1921 *Isorophus inconditus* (Raymond), Raymond, P. E., Geol. Surv. Canada, Mus. Bull. 31 (Geol. Series 38): 12-13, pl. 4.

1935 *Isorophusella incondita* (Raymond), Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 5, pl. 1, fig. 11.

1936 *Isorophusella incondita* (Raymond), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 19-20; *Carneyella raymondi* Clark, *idem, ibid.*: 7; *Hemicystites paulianus* Bassler, *idem, ibid.*: 13, pl. 4, fig. 9.

1938 *Isorophusella incondita* (Raymond), Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 119.

1943 *Isorophusella incondita* (Raymond), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 206; *Carneyella raymondi* Clark, *idem, ibid.*: 198; *Hemicystites paulianus* Bassler, *idem, ibid.*: 204.

1946 *Isorophus* (?) *inconditus* (Raymond), Wilson, A. E., Geol. Surv. Canada Bull. 4: 21.

1966 *Isorophusella incondita* (Raymond), Regnéll, G., *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U169, text fig. 128-4.

Diagnosis

An *Isorophusella* with: moderate-sized theca; a single right lateral secondary oral plate; regular alternation of large primary and smaller secondary ambulacral coverplate pairs; thecal plates smooth.

Description

The domal theca of *Isorophusella incondita* (Raymond) (1915) averages 15 mm in diameter; the largest recorded specimen is 18.5 mm.

The oral plates agree in number and distribution with the generic description. The only secondary oral participating in the structure is the right lateral posterior one common to all species of the genus (text fig. 28A, 29A).

The oral frame of *Isorophusella incondita* is partially exposed in only one specimen (text fig. 29B, pl. 32, fig. 4, 5). The orals and proximal ambulacral coverplates have been removed by etching and abrasion, which exposes an oral surface view of the underlying proximal ambulacral floorplates that form the frame. The structure appears similar to that of *Isorophus cincinnatiensis*. It is transversely elongate; the nearly hemispherical anterior half meets the less curved posterior part along attenuated lateral extremities. The five proximal floorplates are laterally in contact except posteriorly, where a pronounced gap in the frame affords direct communication between the central oral lumen and the thecal cavity beneath interambulacrum 5. The exposed sectional view of the frame apparently lies below the inner ends of the intrathecal extensions of the interradial oral plates. Lateral, bladelike processes from the ambulacral floorplates of I and V, which form a subchamber in the posterior frame gap in *Isorophus*, may have been present in *Isorophusella incondita*. However, only the floorplate of ambulacrum V preserves eroded remnants of these extensions. The innermost anterior edge of the stone canal passageway is preserved along the posterior edge of the proximal floorplate of ambulacrum V.

The hydropore structure of *Isorophusella incondita* includes six or seven plates (text fig. 28A, 29A, pl. 31, fig. 3, 10). The anterior end of the slitlike opening is formed by the right margin of the right posterior primary oral. The entire posterior edge is formed by the anterior margin

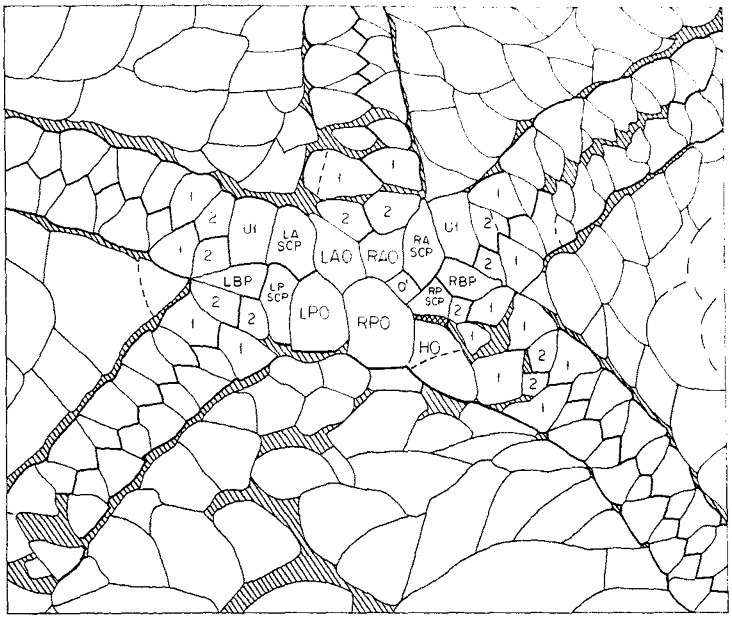
---

Text figure 28. *Isorophusella incondita* (Raymond), 1915

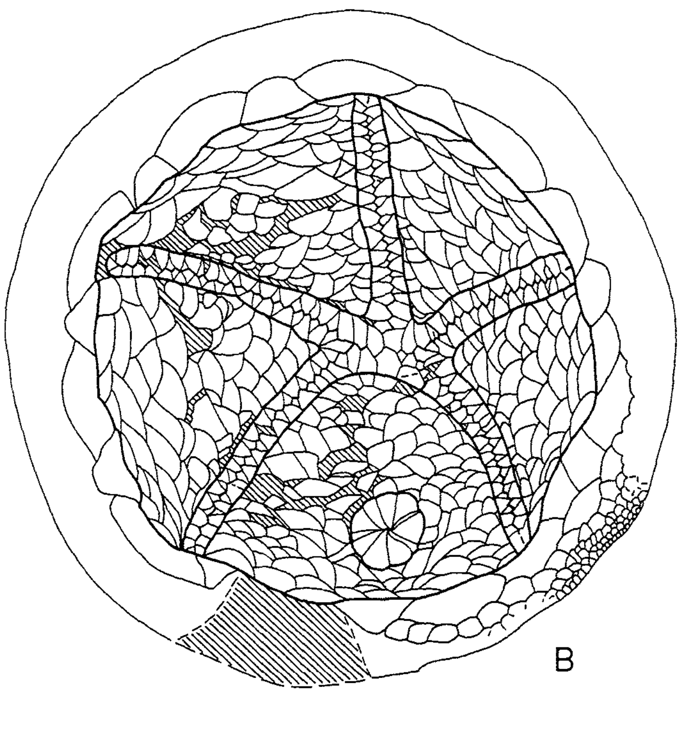
Holotype, GSC 1409-A.

A. Oral area and adjacent structures, (x 15), pl. 31, fig. 3. HO, hydropore oral plate; LAO, left anterior primary oral plate; LASCP, left anterior lateral shared coverplate; LBP, left bifurcation plate; LPO, left posterior primary oral plate; LPSCP, left posterior lateral shared coverplate; o′, secondary oral plate; RAO, right anterior primary oral plate; RASCP, right anterior lateral shared coverplate; RBP, right bifurcation plate; RPO, right posterior primary oral plate; RPSCP, right posterior lateral shared coverplate; U1, unpaired primary ambulacral coverplate; 1, primary ambulacral coverplate; 2, secondary ambulacral coverplate.

B. Oral surface, (x 6), pl. 31, fig. 2.



A



B

of the hydropore oral. The proximal part of the opening's anterior edge is bounded by the adradial end of the right posterior shared coverplate. Distal to this coverplate, the number of plates that form the anterior edge of the opening appears to vary intraspecifically. In some, two unpaired ambulacral coverplates are included, first a secondary followed by a primary. Commonly both of them form part of the opening, but in others the secondary plate is externally confined to the axial part of the ambulacrum. Here, only the unpaired primary is in contact with the external opening. Occasionally the proximal unpaired secondary coverplate is absent and the unpaired primary coverplate is adjacent to the shared coverplate. Distal to the unpaired primary coverplate, the hydropore opening is formed by the posterior member of the first pair of secondary ambulacral coverplates. The opening does not appear to extend past this element. However, the next distal plate, the posterior member of the first pair of primary ambulacral V coverplates, is adradially shortened where it abuts the end of the hydropore oral. It is thus included in the hydropore structure, although not in direct contact with the opening. The plate margins adjacent to the hydropore openings are thickened and form a raised rim surrounding the opening.

The ambulacra of *Isorophusella incondita* commonly develop a very slight curvature, I-II-III contrasolar, IV-V solar. Curvature is usually greatest in ambulacrum I, followed by ambulacrum V. Ambulacrum IV is most often straight, and frequently it is also appreciably shorter than the others.

The double biseries of ambulacral coverplates in *Isorophusella incondita* is characterized by the regularity of the alternation of larger primary and smaller secondary plate pairs (text fig. 28A, B, 29A). This alternation is interrupted by irregularities in only three ambulacra out of 30 adult specimens examined.

The relative position of the perradial tips of members of each pair of coverplates, one proximal to the other, is remarkably constant along the length of each ambulacrum. Rarely is a reversal of the position encountered within an ambulacrum. Moreover, this relationship is fairly consistent for each ambulacrum in all specimens of the species. Looking distally along the ambulacrum, commonly the perradial tip of the left member of each plate pair is proximal to the right in ambulacrum I, II, III, and V, whereas the right plate perradial tip is proximal to the left in ambulacrum IV. Ambulacra II and IV are the most consistent, with only one exception in each out of 30 adult individuals investigated.

The proximal pair of ambulacral coverplates in each ambulacrum is a secondary set. In ambulacra I and III these paired secondaries are the first coverplates encountered in the proximal ambulacrum region. In ambulacrum V the unpaired primary and sometimes an unpaired secondary plate lie proximal to this first pair of secondaries. Both ambulacra II and IV have a single large, unpaired primary plate as the proximal ambulacral; these flank the distal margins of the anterior shared coverplates.

The intra-ambulacral extensions of the coverplates are large, bladelike processes. They extend proximally under the adjacent coverplates and also extend under the perradial line to underlap the opposing alternate elements. These structures are inadequately exposed in the available specimens. The intrathecal extensions of the coverplates are also generally hidden, but apparently are similar to those of *Isorophus cincinnatiensis* and *Isorophusella pleiadae*.

The interambulacrals are squamose, imbricate plates of moderate size in proportion to thecal diameter. The externally exposed parts of the distal interambulacrals are approximately equal in size to the exposed parts of the proximal plates of the rim in noncollapsed specimens.

The valvular anal structure of *Isorophusella incondita* comprises 12 to 16 subtriangular plates in two circlets. The inner circlet plates are largely hidden by the alternate, overlapping outer ones. Lateral plate margins of both sets are beveled to fit snugly together. The distal bases of the triangular plates abut large, thick interambulacrals. The inner edges of these bases flare outward slightly and apparently rest on a small ledge formed by the lower parts of the adjacent interambulacrals. Commonly one or two irregular circlets of small surficial plates cover the upper surface of the boundary between the anals and the large interambulacrals.

The margin of the oral surface is a typical peripheral rim, composed of five to seven circlets. The presence of

---

Text figure 29. ***Isorophusella incondita*** **(Raymond), 1915**

A. Paratype (2), GSC 1409-C, (x 12), pl. 31, fig. 10. Ambulacral coverplate intrathecal extensions, where exposed by disruption of adjacent interambulacrals, are separated from the main body of the plates by dashed lines.

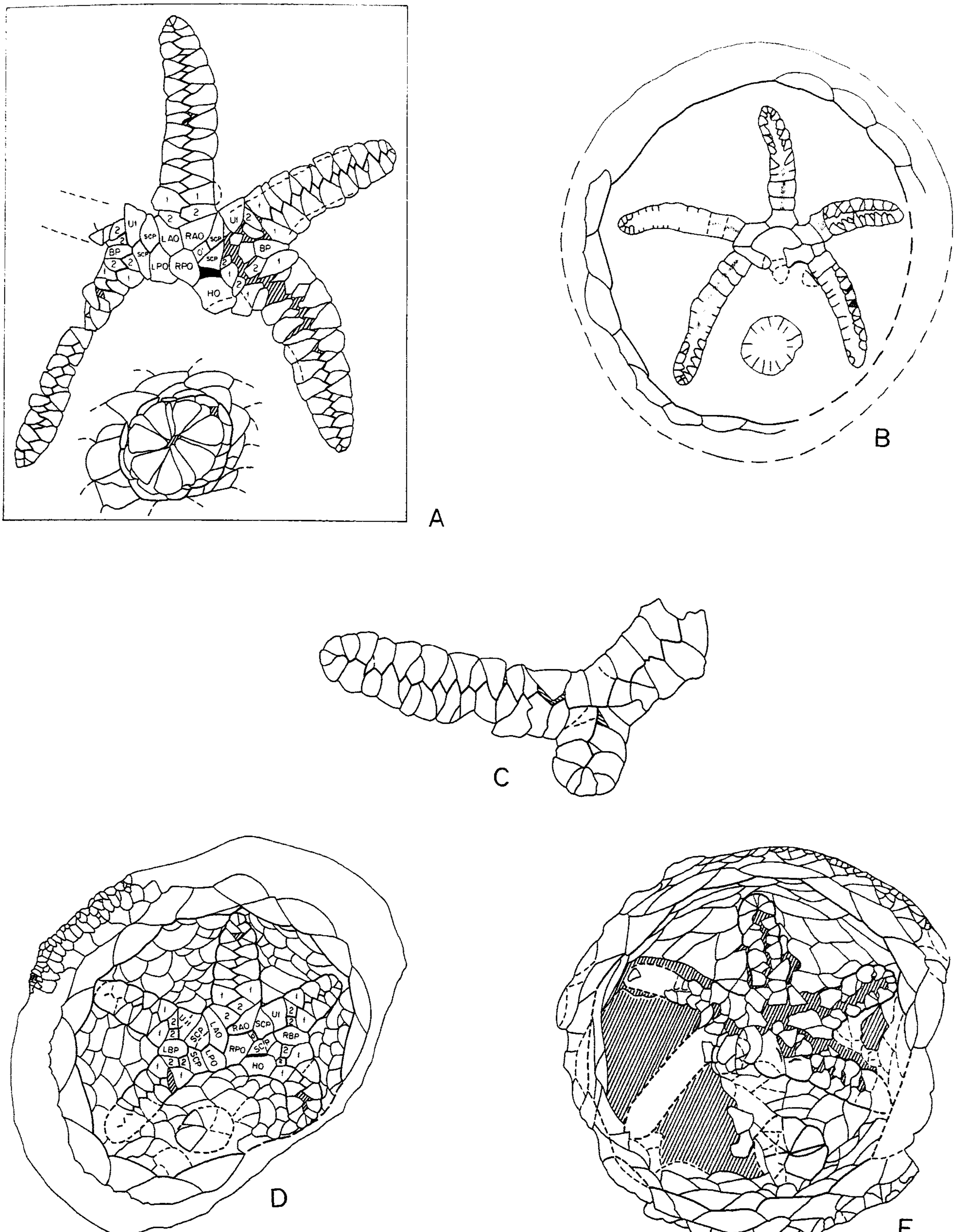
B. UCMP 40475, (x 5), pl. 32, fig. 5. View of the etched oral surface, exposing oral frame and ambulacral floorplates. The floor of the ambulacral trough is stippled.

C. Ambulacrum I, ROM 18873-A, (x 16), pl. 32, fig. 9.

D. USNM 42114-A-1, (x 15), pl. 31, fig. 11.

E. Young adult, MCZ 105, (x 10), pl. 32, fig. 1.

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; RAO, right anterior primary oral; 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.



U1
SCP
LAO
RAO
BP
LPO
RPO
HO
A
B
C
LBP
RBP
D
E

vertical ridges on the bases of the geniculate rim plates has not been confirmed.

The exteriors of the thecal plates of *Isorophusella incondita* appear to be smooth.

Specimens

GSC 1409 (A-D). Type series of *Isorophusella incondita* (Raymond) (1915). "Cystid beds of the Trenton Limestone," Trenton Group, Mohawkian Series, Middle Ordovician. Queen's Wharf, Ottawa, Ontario. T. C. Weston Collection. Wilson (1946) reports the specimens are from Cobourg beds, Trenton Group, Mohawkian Series, Middle Ordovician. Cobourg, Ontario.

GSC 1409-A. Holotype of *Isorophusella incondita* (Raymond) (1915, pl. 1, fig. 1, 1921, pl. 4). 15.2 mm axial by 15.6 mm transverse diameter.

Text fig. 28A-B, pl. 31, fig. 1-3.

The holotype is the largest of the four specimens in the type series, all of which rest directly on the surface of a small slab of Trenton Limestone. There has been a slight lateral shifting of many plates, owing to thecal collapse. This movement has altered somewhat the external shape of the orals and the plates that form the hydropore structure. The only badly disrupted thecal areas are the distal end of ambulacrum II and adjacent interambulacrals, and the small distomedial part of ambulacrum I and adjacent interambulacrals. The specimen preserves most of the diagnostic characters of the species.

GSC 1409-B. Paratype (1) of *Isorophusella incondita* (Raymond) (1915, pl. 1, fig. 1, 1921, pl. 4). 8.8 mm axial by 9 mm transverse diameter.

Pl. 31, fig. 4, 5.

This is the smallest specimen of the type series. It has collapsed and is partially disrupted. Plates are missing from interambulacrum 1 and around the anus in interambulacrum 5. The right posterior part of the theca, proximal to the rim, is depressed below the rest; the two zones are separated roughly along the perradial lines of ambulacra II and V and the transverse oral midline. Ambulacra I through IV are nearly straight, and ambulacrum V is curved toward the anus. Ambulacrum IV is much shorter than any of the others.

GSC 1409-C. Paratype (2) of *Isorophusella incondita* (Raymond) (1915, pl. 1, fig. 1, 1921, pl. 4). 10.6 mm axial by 10.9 mm transverse diameter.

Text fig. 29A, pl. 31, fig. 8-10.

The theca has collapsed, but most of the plates are in place; ambulacrum II and adjacent interambulacrals are missing. The proximal plates of ambulacra IV and V and adjacent plates of the hydropore structure have been partially fragmented and lost. Most of the other thecal plates are well preserved.

GSC 1409-D. Paratype (3) of *Isorophusella incondita* (Raymond) (1915, pl. 1, fig. 1, 1921, pl. 4). 12.1 mm axial by 11.6 mm transverse diameter.

Pl. 31, fig. 6, 7.

The largest of the three paratypes, this specimen is also the least complete. The theca has collapsed, and most of the plates proximal to the rim in the right half of the theca are missing. However, a faint impression of the missing ambulacra I and II can be seen. The oral area and the hydropore structure are poorly preserved. Ambulacra III and IV are well preserved, but V has been abraded. Most of the anal structure is present.

USNM 42114 (A, B). Two bryozoan colonies, each with two edrioasteroids. Colony A — both specimens are on the lower surface of the colony; Colony B — both specimens are on the upper surface. *Phylloporina* bed, Decorah Formation, Black River Group, Mohawkian Series, Middle Ordovician. St. Paul, Minnesota.

USNM 42114-A-1. *Isorophusella incondita* (Raymond). The holotype of *Hemicystites paulianus* Bassler (1936, pl. 4, fig. 9). 5 mm axial by 4.7 mm transverse diameter.

Text fig. 29D, pl. 31, fig. 11.

The specimen has been distorted by lateral compression which pushed the right posterior side inward. The rim plates along this zone are disrupted and partially missing. The distal tip of ambulacrum V is bent sharply toward the anal area. The remainder of the theca is only slightly disrupted and exhibits the typical features of *Isorophusella incondita* of similar size. Compare the text figure of this specimen to text fig. 32B.

USNM 42114-A-2. Approximately 3 mm diameter.

The second specimen on the lower surface of bryozoan colony A is a small individual that is poorly preserved. It is probably another *Isorophusella incondita.*

USNM 42114-B-1. 7 mm greatest diameter.
USNM 42114-B-2. 3.7 mm greatest diameter.

Two disrupted edrioasteroids on the upper surface of a bryozoan colony apparently collected with colony A. Neither is well enough preserved to permit specific identification.

MCZ 105 (old 3978). *Isorophusella incondita* (Raymond). The holotype of *Carneyella raymondi* Clark (1919, pl. 1, fig. 18, 19). Three hundred feet above the base of the Trenton Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Gorge of Roaring Brook.

near Martinsburg, New York. 7 mm axial by 7.3 mm transverse diameter.

Text fig. 29E, pl. 32, fig. 1-3.

This specimen is poorly preserved. Missing plates include all of those from interambulacrum 1 and the left side of 5, along with most of the distal plates of the rim. The plate structure of ambulacrum I is obscure. The remaining thecal plates have been deeply etched, which altered external shapes and removed most surficial features. The recognizable features of the remaining thecal structures appear to be typical of *Isorophusella incondita.*

USNM S-3871. Illustrated Specimen of *Isorophusella incondita* (Raymond) by Bassler (1935, pl. 1, fig. 11) and Regnéll (1966, fig. 128-4). "Cystid beds of the Trenton Limestone," Trenton Group, Mohawkian Series, Middle Ordovician. Island at the foot of Eddy's lumber yard, Hull, Quebec. 17.7 mm axial by 18.5 mm transverse diameter.

This specimen has collapsed, and many of the plates are disrupted or obscured by abrasion. Thecal structures appear to be typical of the species. The ambulacra are the most highly curved of any *Isorophusella incondita* examined. Curvature may have been accentuated somewhat during collapse.

UCMP 40475. An *Isorophusella incondita* (Raymond). Without data, probably Trenton Group, Mohawkian Series, Middle Ordovician of the Ottawa region, Ontario. 14.8 mm axial by 14.7 mm transverse diameter.

Text fig. 29B, pl. 32, fig. 4, 5.

This specimen is the only *Isorophusella incondita* examined that exposes any of the oral frame. The specimen is preserved with the outer side of the oral surface upward, but extreme etching has removed many of the outer thecal plates and exposed a sectional view of the oral frame and the proximal ambulacral floorplates. Sectional views of the ambulacral coverplates are seen in the distal parts of the ambulacra. Apparently the innermost part of the oral frame is exposed, because the anterior proximal ambulacral floorplates are laterally in contact with no intervening intrathecal extensions of the oral plates. A fragment of the right lateral bifurcation plate lies over the right extremity of the frame and gives the illusion of an extra plate in the structure. The innermost proximal edge of the stone canal passageway is also visible.

ROM 18873-A. "Cystid beds of the Trenton Limestone," Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario. 14.4 mm axial by 15.7 mm transverse diameter.

Text fig. 29C, pl. 32, fig. 8, 9.

The thecal of this individual has collapsed, but little plate disruption has occurred. The distal plates of interambulacra 3 and 4 have been partially removed by etching, and a few distal rim plates have been lost from the right side of the theca. The remainder of the theca is moderately well preserved. The specimen is a typical *Isorophusella incondita* except for ambulacrum I, which bifurcates a short distance from the oral area to form two branches. The posterior branch is very short and ends bluntly. The anterior branch is longer, but ends before reaching the rim and is appreciably shorter than any of the normal ambulacra of the specimen. Plate boundaries are partially obscured in the area of bifurcation. Text fig. 29C represents a possible interpretation of the plate structures in that area.

The development of additional ambulacra through bifurcation of one or more of the five normal radii occurs in many species of edrioasteroids. However, both branches of a bifurcated ambulacrum usually continue to develop. This specimen is unusual in the apparent termination of development of the posterior branch of ambulacrum I soon after it was initiated. The specimen offers no apparent cause for this cessation of growth.

A second, small *Isorophusella incondita,* 9 mm axial by 9.6 mm transverse diameter, is on the same slab near the above described specimen. Although poorly preserved, it appears to be typical of the species.

ROM 160t-h. "Trenton Limestone," Trenton Group, Mohawkian Series, Middle Ordovician. Peterborough, Ontario. J. Townsend Collection. 11.2 mm axial by 11.6 mm transverse diameter.

Pl. 32, fig. 6, 7.

This specimen is missing many plates, but the structure of the anal area is exposed. It includes six outer and six inner circlet plates, regularly alternating. The plates are partially pulled apart and expose the beveled edges of the adjacent plates. One plate on the left side of the upper circlet is displaced distally and has been moved approximately half its length.

GSC 3235-D. Juvenile *Isorophusella incondita* (Raymond). "Cystid beds, *Prasopora* zone of the Trenton Limestone," Trenton Group, Mohawkian Series, Middle Ordovician. Abandoned quarry near the entrance to Jackson Park, Peterborough, Ontario. 3.2 mm axial by 3.2 mm transverse diameter.

Text fig. 31D, pl. 33, fig. 15, 16.

This young specimen is one of eight edrioasteroids on a single slab of limestone (one is the holotype of *Cryptogoleus chapmani*). It is comparable in stage of development to the specimen (ROM 160t-c-8) shown in text fig.

31C and illustrated as part of the growth series of *Isorophusella incondita.* The theca of this specimen has been deeply etched and exposes the terminal floorplate of ambulacrum IV and parts of the floorplate series of ambulacra I and V.

Additional specimens examined but not illustrated

ROM 18873-B through I. "Cystid beds of the Trenton Limestone," Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario.

Seven slabs of "Trenton Limestone" with a total of 15 specimens of *Isorophusella incondita,* all apparently typical of the species.

ROM 160t. "Trenton Limestone," Trenton Group, Mohawkian Series, Middle Ordovician. Peterborough, Ontario. J. Townsend Collection.

ROM 160t-a, d, e, f, g.

Five limestone slabs with 11 average specimens of *Isorophusella incondita.* Several are very fragmentary.

ROM 160t-c-5, 6, 7, 13, 14.

Five juvenile *Isorophusella incondita* on the same slab as many of the specimens included in the growth series of this species.

ROM 533t-a, b. Trenton Group, Mohawkian Series, Middle Ordovician. Hull, Quebec. J. E. Narraway Collection.

Two slabs of limestone with two average adult and three fragmentary specimens of *Isorophusella incondita.*

ROM 18874. Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario. J. E. Narraway Collection.

One nearly complete and two fragmentary specimens of *Isorophusella incondita* on the slab with the holotype of *Belochthus orthokolus* Bell.

CFMP 9635. "Trenton Limestone," Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario.

Two average adult *Isorophusella incondita.*

UCMP 36115. *Prasopora* beds, Cobourg Formation, Trenton Group, Mohawkian Series, Middle Ordovician. Quarry along Lois Street, near Clairmont Street, Hull, Quebec. Kopf Collection.

One average adult and several very small specimens of *Isorophusella incondita.*

Description of growth series

The following 16 specimen descriptions are arranged in order of increasing thecal development. The series begins with the youngest (smallest) developmental stage known and ends with a small, fully developed adult.

ROM 160t. "Trenton Limestone," Trenton Group, Mohawkian Series, Middle Ordovician. Peterborough, Ontario. J. Townsend Collection.

ROM 160t-b. Slab with five *Isorophusella incondita.*

ROM 160t-c. Slab with 14 *Isorophusella incondita,* nine included in the growth series.

NYSM 12775-12776. Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario.

Two *Isorophusella incondita* included in growth series on a slab with two *Belochthus orthokolus* (NYSM 12773-12774).

ROM 160t-b-E. Very young juvenile. .56 mm axial by .66 mm transverse diameter.

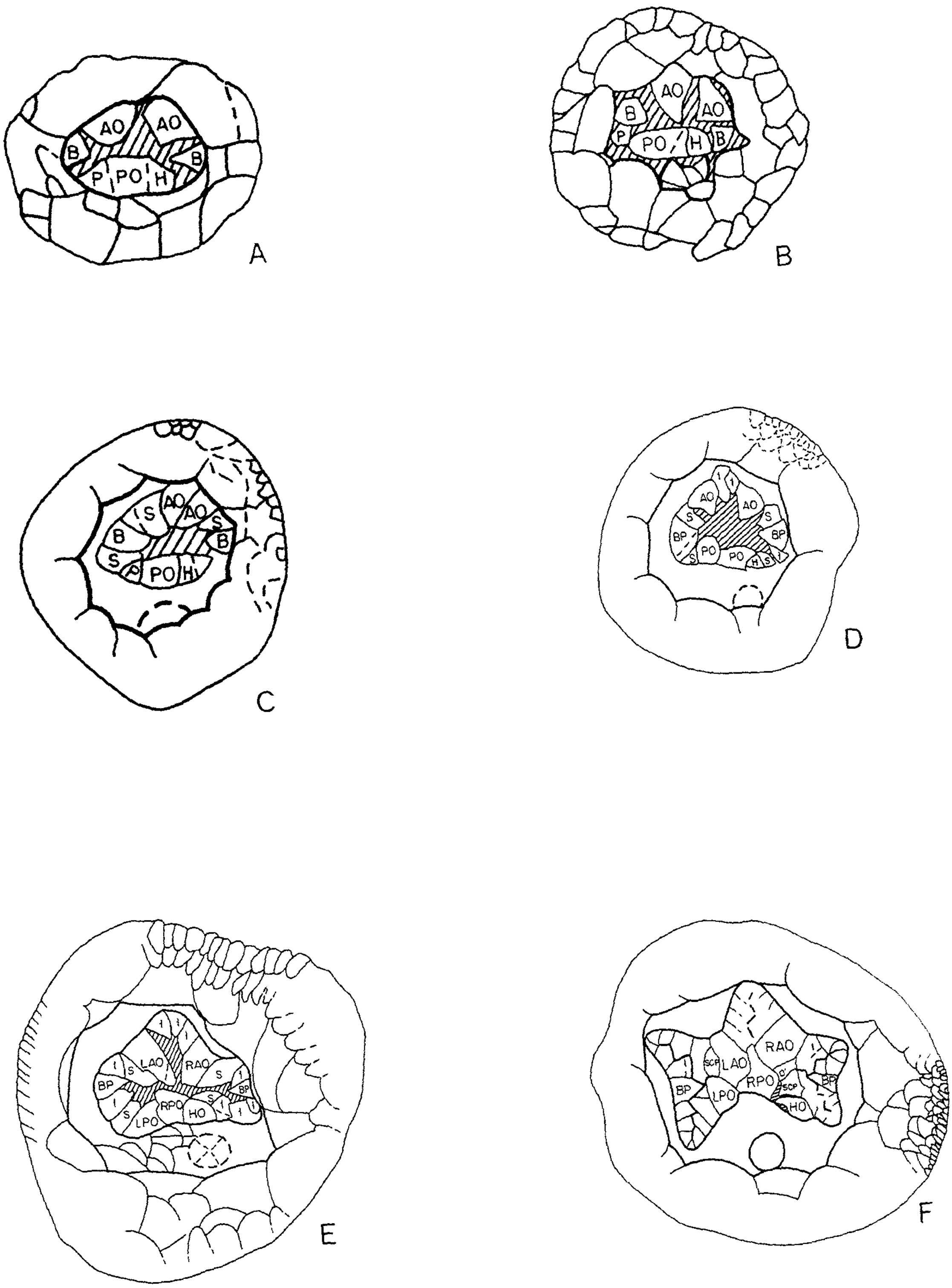
Text fig. 30A, pl. 33, fig. 1.

This specimen is in the earliest stage of development encountered. The dominant thecal feature is the peripheral rim, which forms about two-thirds of the oral surface. Apparently two irregular circlets of relatively large plates are present, although additional smaller plates may have been lost from the distal margin of the rim. The central oral surface, proximal to the rim, has collapsed inward. Seven(?) plates are exposed, but they have been centrally separated along the transverse and anterior oral midlines.

Text figure 30. *Isorophusella incondita* (Raymond), 1915, growth series.

A. Young juvenile, ROM 160t-b-E, (x 60), pl. 33, fig. 1.
B. Young juvenile, NYSM 12775, (x 50), pl. 33, fig. 2.
C. Young juvenile, ROM 160t-c-16, (x 40), pl. 33, fig. 4.
D. Juvenile, ROM 160t-c-12, (x 30), pl. 33, fig. 6.
E. Juvenile, ROM 160t-c-3, (x 25), pl. 33, fig. 7.
F. Juvenile, ROM 160t-c-11, (x 25), pl. 33, fig. 9.

AO, anterior primary oral plate; B, lateral bifurcation plate; BP, lateral bifurcation plate; H, hydropore oral plate; HO, hydropore oral plate; LAO, left anterior primary oral plate; LPO, left posterior primary oral plate; o', secondary oral plate; P, posterior primary oral plate; PO, posterior primary oral plate; RAO, right anterior primary oral plate; RPO, right posterior primary oral plate; S, lateral shared coverplate; SCP, lateral shared coverplate; 1, primary ambulacral coverplate.


AO
AO
B
B
P
PO
H
A
AO
AO
B
P
PO
H
B
B
S
AO
AO
S
B
B
S
P
PO
H
C
AO
AO
S
BP
S
BP
PO
PO
H
S
D
LAO
RAO
S
S
BP
BP
S
LPO
RPO
HO
S
E
RAO
LAO
SCP
BP
LPO
RPO
SCP
HO
BP
F

by distal displacement. Two large anterior plates appear to be the left and right anterior primary orals. The posterior side of the region appears to include three plates, although the sutures are indistinct and only tentatively identified. The right posterior primary oral is centrally located; the left posterior primary is restricted to the extreme left of the posterior margin of the area. The hydropore oral is probably adjacent to the right side of the right posterior primary oral. Two moderate-sized plates lie at the lateral extremities of the exposed central oral area. These are probably the lateral bifurcation plates of the two lateral primary ambulacral radii. Most of the thecal plates appear to have been etched, perhaps altering differentially the size and shape of individual plates. If any additional plates of the oral surface, particularly the anals and interambulacrals, are developed at this stage, they have been hidden beneath the proximal margin of the rim during collapse.

NYSM 12775. Very young juvenile. .80 mm axial by .88 mm transverse diameter.

Text. fig. 30B, pl. 33, fig. 2.

This specimen is similar to the first, although larger. The peripheral rim dominates, occupying approximately two-thirds of the oral surface. A large proximal circlet of rim plates is surrounded by a nearly complete circlet of smaller ones. In some areas a third circlet has begun to form. The central oral surface has collapsed inward, distally displacing the plates. Seven oral-ambulacral plates are tentatively identified, including: two large anterior primary orals, both laterally displaced to the right; the large right posterior primary oral, in a central position; the smaller left posterior primary oral, restricted to the far left extremity of the area; the hydropore oral plate, adjacent to the right side of the right posterior primary oral; and the two lateral bifurcation plates, the left displaced anteriorly. In addition to these, five subtriangular plates lie behind the right posterior primary oral and hydropore oral, adjacent to the posterior proximal margin of the rim. Although disrupted, these plates appear to have formed a proportionately large anal structure. Additional anals and interambulacrals are either not developed, or are hidden beneath the margin of the rim. Etching has apparently differentially altered plate sizes and shapes.

ROM 160t-c-16. Young juvenile. 1.2 mm axial by 1.04 mm transverse diameter.

Text fig. 30C, pl. 33, fig. 3, 4.

This specimen is significantly advanced in stage of development over the first two. The peripheral rim is still the single dominant thecal feature, but here it occupies only about 60 percent of the oral surface. Most of the rim plates are indistinct, but at least three circlets have developed. The very large proximal plates are surrounded by two circlets of small plates. The center of the oral surface has collapsed inward, hiding the distal parts of some of the plates beneath the proximal margin of the rim. The oral-ambulacral series includes approximately 11 plates. All are laterally in contact with adjacent plates, but centrally they are separated, owing to removal of the perradial parts of the plates by deep etching. The outline of this group of plates is subtriangular; the apex is formed by the anterior primary ambulacral radius and the basal corners by the two lateral primary ambulacral radii. Plate identifications are tentative at this stage of development, and in this instance are further complicated by the extensive differential etching. Apparently the two anterior primary orals form the apex of the series, but they are displaced to the right, which leaves the left plate nearly central in position. Three plates oppose the anterior orals. The large central plate appears to be the right posterior primary oral. The left posterior primary is unusually small and is restricted to the left edge of the area. The hydropore oral lies adjacent to the right side of the right posterior primary oral. The right end of this plate, separated by a dashed line in the text figure, may be a separate plate, perhaps the right posterior shared coverplate. Two contiguous plates lie adjacent to the right side of the right anterior primary oral. The anterior one is probably the right anterior shared coverplate, the other the right lateral bifurcation plate. Three plates lie to the left of the primary orals. The central one is probably the left lateral bifurcation plate, displaced anteriorly, and the two plates flanking it would be the left lateral shared coverplates.

The anterior third of the anal structure lies adjacent to the posterior proximal margin of the rim. The posterior part of the structure is apparently hidden beneath the rim. Individual anals are not distinct here. The zone between the central oral-ambulacral plate series and the proximal margin of the peripheral rim was probably covered with interambulacrals, but individual plates are not distinct.

ROM 160t-c-12. Juvenile. 1.4 mm axial by 1.5 mm transverse diameter.

Text fig. 30D, pl. 33, fig. 5, 6.

In this specimen the peripheral rim remains the single dominant feature in area, and forms approximately half of the oral surface. Approximately four rim circlets are present, with the plates diminishing in size outward. The central oral region has collapsed inward, which caused minor lateral plate movement. All of the central plates are highly etched, and this has removed the perradial sections of the plates and differentially altered the shape of the remainders of the plates.

The oral-ambulacral series maintains the subtriangular shape seen in the previous specimens. Approximately 14 plates are included in the series. The two large anterior primary orals are opposed by the two posterior primary orals. The right posterior oral is large and subcentrally located. The left posterior primary oral is nearly equal in size to the two anterior primary orals. The hydropore oral is small and lies adjacent to the right edge of the right posterior primary oral. Distal to the primary orals, the left side of the oral-ambulacral series includes three plates: the large left lateral bifurcation plate is central and is flanked by the two lateral shared coverplates. To the right of the primary orals, four plates are present. The large right lateral bifurcation plate is flanked anteriorly by the right anterior lateral shared coverplate. Two plates lie between the bifurcation plate and the hydropore oral; one is the right posterior shared coverplate, the other the first coverplate of ambulacrum V. The proximal pair of primary coverplates of ambulacrum III is also present; these lie along the anterior edges of the two anterior primary orals.

The anterior two-thirds of the anal structure is exposed along the right posterior proximal margin of the rim. The plate boundaries within the structure are indistinct. The entire structure appears unusually small, probably owing to the mode of preservation. Interambulacrals probably filled the gap between the oral-ambulacral series and the rim, but individual plates are not distinct in this specimen.

ROM 160t-c-3. Juvenile. 2.2 mm axial by 2.2 mm transverse diameter.

Text fig. 30E, pl. 33, fig. 7.

Here the peripheral rim still dominates, but the remainder of the oral surface has increased in proportional size. The oral-ambulacral series forms a subtriangular unit in the center of the oral surface and the four lateral ambulacra are beginning to develop. Thus the earlier triradiate plan is beginning to assume the five-part symmetry of adults.

The oral surface plates proximal to the rim have collapsed inward, but only slight lateral shifting of individual plates has occurred. Deep etching has removed the perradial parts of the plates, separating them centrally and differentially reducing individual plate sizes. The oral-ambulacral series includes approximately 20 plates, identified in text fig. 30E. The right posterior primary oral is still central in position and restricts the left posterior primary oral to the left side of the oral region. Ambulacrum III has developed three primary coverplates, ambulacrum V has two, and the others have one each. The anal structure is offset slightly toward the right side of the theca. Individual plates in this structure are not clear. Several of the interambulacrals are plainly visible for the first time and lie in the left posterior region between the ambulacrals and the rim.

ROM 160t-c-11. Juvenile. 2.2 mm axial by 2.4 mm transverse diameter.

Text fig. 30F, pl. 33, fig. 8, 9.

This specimen shows marked advancement over the latter. The rim is still large, composed of five to six circlets of plates, but the remainder of the oral surface structures now dominate the theca areally. The central oral surface has collapsed inside the rim and has shifted laterally toward the anterior edge of the theca. However, these plates appear to have moved as a unit and maintain their positions relative to one another. Plate boundaries have been partially obscured by surficial etching, but most elements have been identified in text fig. 30F. Etching has also differentially altered plate shapes and sizes.

The five-part symmetry of the adult theca is apparent in the shape of the oral-ambulacral series, with all five ambulacra now distinct. The ambulacra consist of three to four pairs of primary coverplates each. In the oral region, the right lateral secondary oral is seen for the first time. The anal structure is offset to the right of the posterior interambulacrum, but plate boundaries are obscure. Interambulacral plate boundaries are also obscure in this individual.

ROM 160t-b-D. Juvenile. 1.9 mm axial by 2.4 mm transverse diameter.

Text fig. 31A, pl. 33, fig. 10.

This specimen is incomplete; the posterior half of the rim and part of ambulacrum I are missing. A wide crack separates a large anterior segment of the rim from the rest of the theca. However, the remaining plates are distinct and only minor disruption of these has occurred during collapse. Etching has differentially altered some plate shapes, but has also accentuated plate boundaries.

The oral-ambulacral sequence continues the development of the five-part symmetry. Oral area plates are identified in text fig. 31. The ambulacra include three or four pairs of primary coverplates each. Secondary ambulacral coverplates are recognized for the first time. One pair lies at the proximal end of ambulacrum III. Ambulacrum II has one or two pairs. Apparently secondary pairs have not yet begun to develop in ambulacrum IV or V.

ROM 160t-c-4. Juvenile. 2.4 mm axial by 2.6 mm transverse diameter.

Text fig. 31B, pl. 33, fig. 11, 12.

ROM 160t-c-8. Juvenile. 2.8 mm axial by 3.0 mm transverse diameter.

Text fig. 31C, pl. 33, fig. 13, 14.

ROM 160t-c-9. Juvenile. 3.0 mm axial by 3.28 mm transverse diameter.

Text fig. 31E, pl. 34, fig. 1, 2.

These three specimens represent nearly the same stage of development. The oral surface has collapsed in each, causing minor plate disruption. Etching has differentially altered the size and shape of various plates, particularly the orals and hydropore plates, and has produced the wide range of variation seen in the figures.

The peripheral rim is still large but no longer dominant. The oral-ambulacral sequence has the five-part form of adults. The ambulacra have continued to lengthen through distal addition of primary coverplates and subsequent intercalation of secondaries. Interambulacrals are distinct in two of the three specimens. The anal structure is well preserved in ROM 160t-c-8, where it is large in proportion to the size of interambulacrum 5 and consists of an inner and outer circlet of plates. Apparently several of the inner circlet plates are completely hidden.

ROM 160t-c-15. Juvenile. 3.1 mm axial by 3.2 mm transverse diameter.

Text fig. 31F, pl. 34, fig. 3, 4.

This specimen has collapsed, but little plate disruption has occurred. Etching has differentially altered plate sizes and shapes. The specimen shows the continued lengthening of the ambulacra and enlargement of the interambulacral areas. Ambulacrum IV is significantly shorter than the other four, as is typical of adults.

ROM 160t-c-10. Juvenile. 3.2 mm axial by 3.2 mm transverse diameter.

Text fig. 32A, pl. 34, fig. 5, 6.

This specimen is similar in stage of development to the last one. The oral surface has collapsed but little plate disruption has occurred. Etching has modified some plate sizes and shapes. Interestingly, in this and the following specimen, the anterior right lateral shared coverplate is relatively small. Apparently it has enlarged less rapidly than the surrounding plates up to this stage of development. As adulthood is attained, this element must increase its growth rate relative to adjacent plates to attain its proportional size in the adult theca.

ROM 160t-b-C. Advanced juvenile. 4.0 mm axial by 4.1 transverse diameter.

Text fig. 32B, pl. 34, fig. 7, 8.

This specimen has collapsed, but only the distal interambulacrals and anal plates have been disrupted. The theca is etched, but here this has accentuated rather than obscured plate boundaries.

This individual is nearly adult. In this stage the ambulacra have begun to develop the slight curvature of the adult, and ambulacrum IV is shorter than the others. The oral region is still proportionately larger than in adults, but the ambulacra and interambulacra have continued to increase in importance toward their dominant role in the adult theca. Three or four pairs of secondary coverplates are present in each ambulacrum. The anal structure is also proportionately decreasing in size.

NYSM 12776. Advanced juvenile. 5.3 mm axial by 5.4 mm transverse diameter.

Pl. 34, fig. 9, 10.

This individual is larger than the last, but maintains nearly the same characteristics. Plates are little disrupted and only slightly etched. The ambulacra and interambulacra are slightly larger, and continue toward their dominance of the adult theca. Ambulacrum IV remains much shorter than the other ambulacra. Only the six anals of the outer circlet are visible in the anal structure.

ROM 160t-b-B. Young adult. 7.5 mm axial by 7.6 mm transverse diameter.

Pl. 35, fig. 1, 2.

This specimen has collapsed but only the distal interambulacrals are disrupted. A large crack extends through the theca and has fractured some of the plates. Etching has accentuated plate boundaries. Proportional size of the major thecal structures is almost that of typical adults.

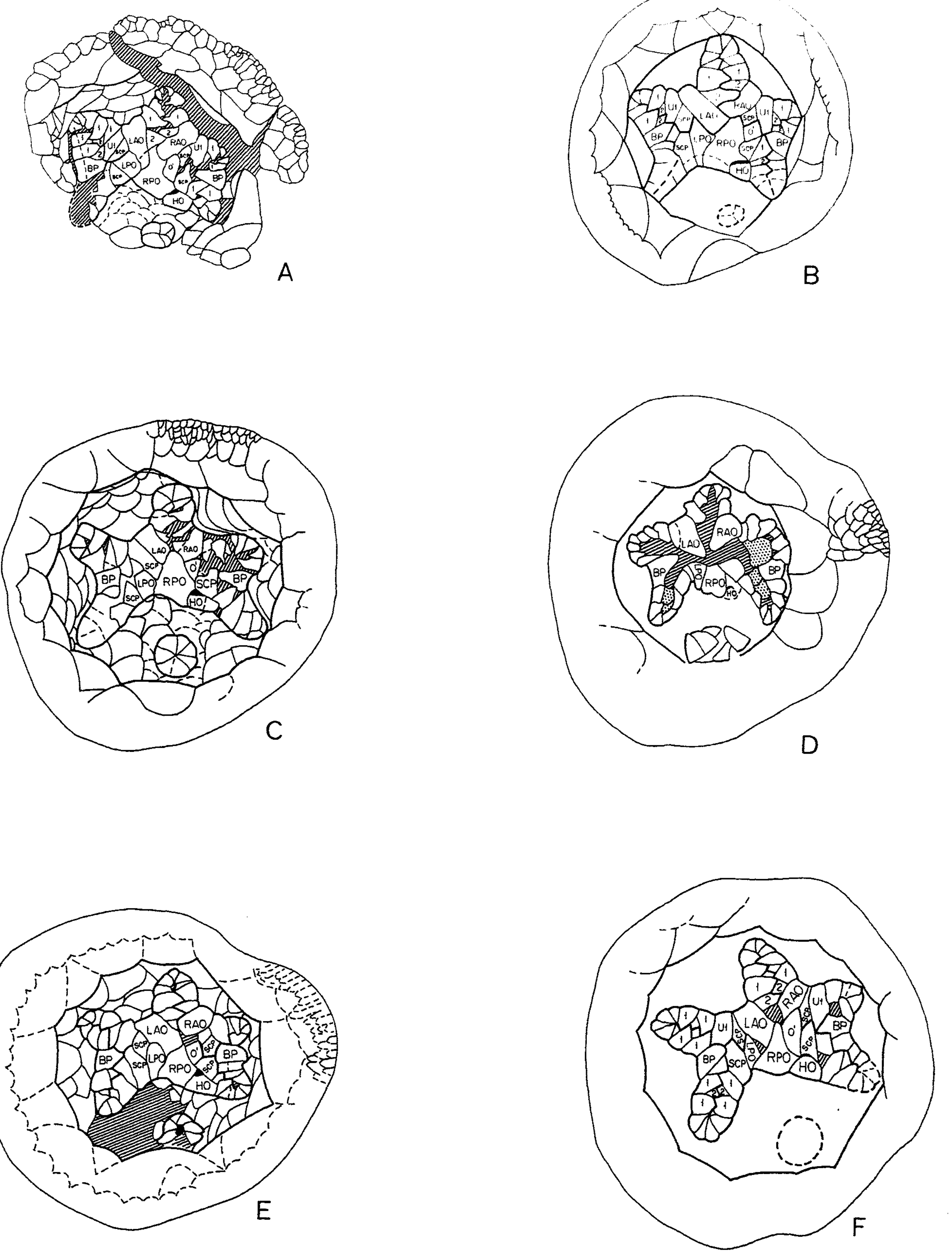
ROM 160t-b-A. Adult. 8.1 mm axial by 8.2 mm transverse diameter.

Pl. 35, fig. 3, 4.

Text figure 31. ***Isorophusella incondita*** **(Raymond), 1915, growth series.**

A. Juvenile, ROM 160t-b-D, (x 20), pl. 33, fig. 10.
B. Juvenile, ROM 160t-c-4, (x 20), pl. 33, fig. 12.
C. Juvenile, ROM 160t-c-8, (x 20), pl. 33, fig. 14.
D. Juvenile, GSC 3235-D, (x 20), pl. 33, fig. 16. Ambulacral floorplates marked by a dotted pattern.
E. Juvenile, ROM 160t-c-9, (x 20), pl. 34, fig. 2.
F. Juvenile, ROM 160t-c-15, (x 20), pl. 34, fig. 4.

BP, lateral bifurcation plate; HO, hydropore oral plate; LAO, left anterior primary oral plate; LPO, left posterior primary oral plate; o', secondary oral plate; RAO, right anterior primary oral; RPO, right posterior primary oral plate; SCP, lateral shared coverplate; U1, unpaired primary ambulacral coverplate; 1, primary ambulacral coverplate; 2, secondary ambulacral coverplate.


A
LAO RAO LPO RPO SCP BP U1 O' HO 1 2
B
LAO RAO LPO RPO SCP BP U1 O' HO 1 2
C
LAO RAO LPO RPO SCP BP O' HO
D
LAO RAO LPO RPO BP HO
E
LAO RAO LPO RPO SCP BP O' HO
F
LAO RAO LPO RPO SCP BP U1 O' HO 1 2

The specimen has partially collapsed, disrupting the distal interambulacrals. Thecal plates are well preserved except for the anals. Etching has accentuated plate boundaries. Although still a small individual, this specimen exhibits all of the typical ephebic traits common to the species.

Summary of the growth process

In the youngest individuals known, about 0.6 mm in diameter, the theca is dominated by the peripheral rim, which occupies approximately two-thirds of the oral surface. The structure includes a proximal circlet of large plates and one or two irregular distal circlets of small plates. The remainder of the theca includes the four primary orals, the hydropore oral, and the two lateral ambulacral bifurcation plates. If interambulacrals surround the oral structure, they are too small or thin to be observed. The anal structure is probably present at this stage, but is hidden under the proximal margin of the rim during collapse. When it is first observed in a slightly larger specimen, it is large and formed by several large triangular plates.

The development of the oral-ambulacral series proceeds from this stage by the addition of the four lateral shared coverplates, followed by the formation of primary ambulacral coverplates. In early stages the oral-ambulacral series has a three-part symmetry manifested by one anterior and two lateral radii. As the first few pairs of primary coverplates are added to each ambulacrum, this form gradually changes to the five-part symmetry of adults through the bifurcation of the two lateral primary radii to form the four lateral ambulacra. Thecal diameter is approximately 2.25 mm when the five-part symmetry initially becomes apparent. Correlated with this development is the appearance of the right lateral secondary oral plate. The secondary ambulacral coverplates begin to be intercalated after three or four pairs of primaries have been formed. Apparently individual ambulacra develop at different rates, the secondaries first appearing randomly in any ambulacrum.

The development of the oral-ambulacral series continues by gradual lengthening of the ambulacra through the addition of new coverplates (and floorplates) and the enlargement of the existing elements. The oral area plates continue to increase in absolute size, but as the ambulacra develop, the oral area forms a progressively smaller percentage of the oral surface and thus continuously decreases in size in proportion to thecal diameter. The slight curvature of adult ambulacra is not developed until individuals are young adults, approximately 5 to 7 mm in diameter. Ambulacrum IV is consistently shorter than the others in specimens 3 mm in diameter and over.

The interambulacral plates are difficult to distinguish in the young juveniles. When first distinct, these plates are already numerous, the component elements being of proportionately moderate size, as in adults. The interambulacral areas progressively increase in importance along with the ambulacra, by proliferation of new plates and slow enlargement of existing ones.

The anal structure is often partially hidden beneath the margin of the peripheral rim or severely disrupted during thecal collapse. It appears to be proportionately quite large in young specimens, being composed of six to eight plates. Additional elements are added slowly until the normal adult complement of 12 to 16 is attained. Growth of existing plates is continuous but slow, with the relative size of the structure decreasing in relation to thecal diameter throughout development.

The peripheral rim adds new circlets of plates until in the average adult there are five to seven circlets. This stage is usually reached when the specimen is approximately 3.5 to 4 mm in diameter. Additional plates are intercalated in existing circlets, and all rim plates continue to enlarge. The initial dominance of the rim gradually decreases. In specimens about 2.5 mm in diameter the rim forms less than half the total thecal surface, and it continues to slowly decrease in proportional size until adulthood is reached.

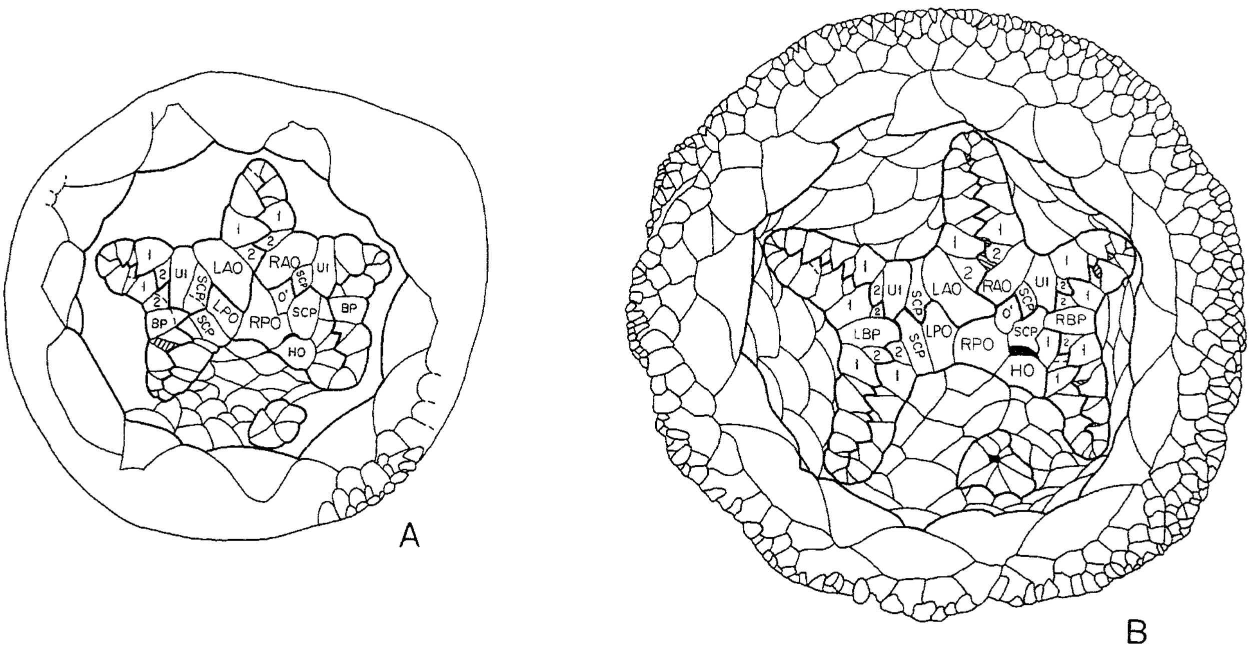
Discussion of previous investigation

Raymond (1915, p. 6) proposed the name *Lebetodiscus inconditus* for "the form which is so common in the 'Cystid bed' below Parliament Hill and Queen's Wharf, Ottawa (Ontario), and which has always been identified as *Agelacrinites billingsi*." His description included most of the features common to the species, but he was of the opinion that: ambulacrum IV curves slightly either solarly or contrasolarly; that a single biseries of ambulacral coverplates is present; and that the oral area includes numerous small plates with interambulacrals "mixed in with ray and supra-oral series."

Foerste (1917) referred *Lebetodiscus inconditus* to his new genus *Isorophus*. Raymond (1921) accepted Foerste's generic assignment.

In describing *Carneyella raymondi* Clark (1919), the author noted the poor preservation of the single specimen and reported six ambulacra. Apparently the ambulacral number was thought to be the most significant characteristic of the species. The specimen actually has only five ambulacra and those features well enough preserved to allow interpretation are all typical of *Isorophusella incondita*.

Bassler (1935) proposed the genus *Isorophusella* based on *Isorophus inconditus* (Raymond). The specimen illus-



Text figure 32. ***Isorophusella incondita*** **(Raymond), 1915, growth series.**

A. Juvenile, ROM 160t-c-10, (x 20), pl. 34, fig. 6.

B. Advanced juvenile, ROM 160t-b-C, (x 20), pl. 34, fig. 7.

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; 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.

trated by Bassler is collapsed and rather disrupted. He called attention to the double biseries of ambulacral coverplates, but their regularity was not apparent in his specimen. He emphasized the ambulacral curvature, which is more marked in his specimen than in any other yet encountered.

In 1936 Bassler described the species *Hemicystites paulianus* (text fig. 29D). The holotype of this species is a juvenile, and is comparable to specimens of equal development included here in the growth series of *Isorophusella incondita* (compare with text fig. 32B), with which it is now identified.

Wilson (1946) did not recognize Bassler's *Isorophusella,* as is indicated by her citation of this species as *Isorophus ? inconditus.* Her brief species description noted some of the differences between this species and *Isorophus cincinnatiensis,* but concluded that without other species to confirm the validity of the generic traits, it should be retained in *Isorophus* with question.

Discussion

Isorophusella incondita (Raymond) is reported by Raymond (1915, p. 62) to be " common in the ' Cystid bed ' of the 'Prasopora zone' " of the Trenton on " both the Ottawa and Hull sides of the Ottawa River." The large suite of specimens available unfortunately lacks more specific locality data.

The external characters of *Isorophusella incondita* are well established by the existing specimens. However, little is known of the inner side of the oral surface. Specimens are nearly always found resting in life positions directly on the surface of limestone slabs. The unusually well preserved juveniles provide an extraordinarily complete growth series.

The characteristic regularity of ambulacral coverplates in *Isorophusella incondita* contrasts with the irregularity found in *Isorophus cincinnatiensis.* The functional significance of this contrast is not apparent. The mode of secondary coverplate formation appears to be similar in both species; they are inserted between pairs of primaries at a point three to four primary pairs from the distal tip of the ambulacra. Perhaps related to the coverplate regularity is the consistently shorter length of ambulacrum IV in *Isorophusella incondita*, which also has no apparent functional explanation.

RANGE AND OCCURRENCE: Black River and Trenton Groups, Middle Ordovician of the Ottawa — Peterborough region of Canada, New York, and Minnesota.

Isorophusella trentonensis (Bassler), 1936
Text fig. 33; plate 35, fig. 5, 6.

1936 *Isorophus trentonensis* Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 17, pl. 5, fig. 1.

1943 *Isorophus trentonensis* Bassler, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 250.

Diagnosis

An *Isorophusella* with: theca small; secondary ambulacral coverplates externally nearly as large as primaries in proximal part of ambulacra; thecal plates bearing scattered, irregular nodes.

Description

The maximum diameter of the domal theca is 11 mm in the only known specimen (text fig. 33, pl. 35, fig. 5, 6).

The oral region appears to be typical of the genus, with four primary orals, one hydropore oral, two pairs of lateral shared coverplates, and a single right lateral secondary oral (text fig. 33, pl. 35, fig. 5, 6). As in *Isorophusella incondita,* the right posterior primary oral is the largest of the primaries and is nearly central; it restricts the left posterior primary oral to the far left side of the oral area. The anterior orals are symmetrical on either side of the anterior oral midline. The perradial tips of the two posterior lateral shared coverplates are distal to the tips of the anterior members of the two pairs and are distally in contact with the lateral bifurcation plates.

The hydropore structure includes six plates. The entire posterior margin of the opening is bounded by the anterior edge of the hydropore oral. The proximal end is formed by the right edge of the right posterior primary oral. The anterior side of the opening is formed by the right lateral secondary oral, the right posterior shared coverplate, and a proximal, posterior, unpaired coverplate of ambulacrum V. The posterior member of the proximal pair of primary coverplates of ambulacrum V lies adjacent to the distal edge of the unpaired coverplate. It is indented along its proximal adradial edge where it meets the hydropore oral. However, the hydropore opening probably ends just proximal to this plate, so that it is not in direct contact with the opening.

The ambulacra of *Isorophusella trentonensis* are nearly straight in the only known specimen, although ambulacrum V is curved slightly in a contrasolar direction. The slight medial solar curvature of ambulacrum II, and the distal contrasolar curvature of III appear to be preservational.

The double biseries of ambulacral coverplates appears to alternate regularly where best preserved. Externally, the distal secondary coverplates are conspicuously smaller than the primaries, but proximally they increase in size and are commonly nearly as large as adjacent primaries. The secondaries externally reach the adradial suture line along most of the length of the ambulacra. As in *Isorophusella incondita*, a large unpaired primary coverplate is present on the anterior side of the proximal ends of ambulacra II and IV.

Interambulacrals are squamose, imbricate plates, of moderate size in proportion to thecal diameter.

The valvular anal structure and the peripheral rim are probably similar to those of *Isorophusella incondita,* although they are not well shown.

Rounded, irregular nodes are preserved on some of the thecal plates, including rim plates, interambulacrals, anals, and ambulacral coverplates. The nodes are extensively etched, hence their original shape and abundance remain to be demonstrated.

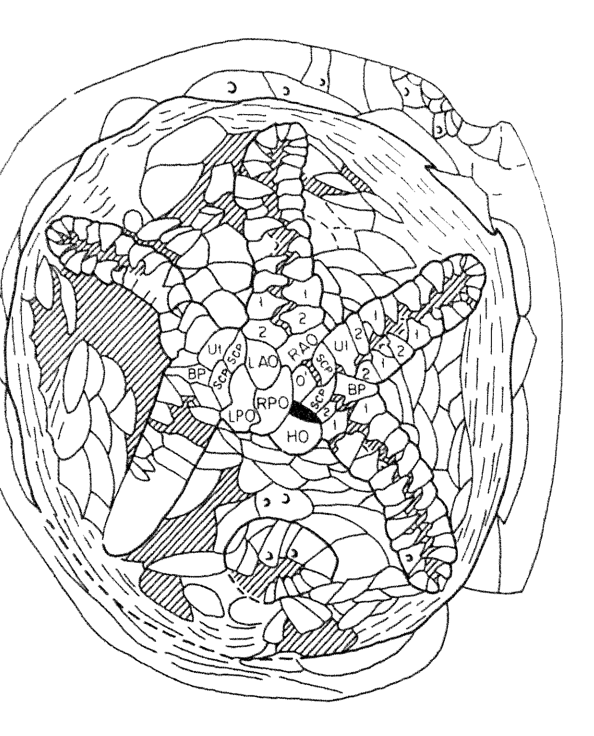
Specimen

USNM 91843. Holotype of *Isorophusella trentonensis* (Bassler) (1936, pl. 5, fig. 1). Upper part of the *Deltoidea* Zone, Cobourg beds, Trenton Group, Mohawkian Series, Middle Ordovician. In rock pile just north of the east end of the railroad bridge, Trenton Falls, New York. 11 mm axial by 10.2 mm transverse diameter.

Text fig. 33, pl. 35, fig. 5, 6.

The specimen is collapsed and partially disrupted. Many of the oral and ambulacral plates are separated from adjacent plates. Distal to the central oral rise the ambulacra and interambulacra are extremely depressed and disrupted, particularly in interambulacra 1, 2, 5, and ambulacrum I. Differential etching has modified external plate shapes and removed most surficial features, including most of the nodose prosopon.

The medial part of ambulacrum II and the distal tip of ambulacrum III appear to have been displaced to the right, creating the impression of ambulacral curvature — contrasolar for ambulacrum II, solar for III. The anal structure has been disrupted and several of the anals appear to have been fractured. The peripheral rim is



Text figure 33. *Isorophusella trentonensis* (Bassler), 1936

Holotype, USNM 91843, (x 8), pl. 35, fig. 6.

BP, lateral bifurcation plate; HO, hydropore oral plate; LAO, left anterior primary oral plate; LPO, left posterior primary oral plate; o', secondary oral plate; RAO, right anterior oral plate; RPO, right posterior primary oral plate; SCP, lateral shared coverplate; U1, unpaired primary ambulacral coverplate; 1, primary ambulacral coverplate; 2, secondary ambulacral coverplate.

---

partially disrupted and appears to be missing most of the smaller distal plates. A small wedge of the rim is missing adjacent to the tip of ambulacrum V.

Discussion

Bassler's (1936, p. 17) original description denotes only the features interpreted by him to separate the species from *Isorophus tennesseensis* Bassler (1936) (= *Isorophus cincinnatiensis*). The oral area was described as broad, formed of larger plates than in *Isorophus tennesseensis,* but the arrangement of these plates was not mentioned. The ambulacra were characterized only as " broad, almost straight, bluntly terminating." The ambulacral disposition and the plate structure of the oral area and hydropore region clearly places this species in the genus *Isorophusella.*

Isorophusella trentonensis (Bassler) is known only from the rather poorly preserved holotype. It differs from *Isorophusella incondita* in the relatively larger size of the secondary ambulacral coverplates, particularly the more proximal ones, and in the presence of a nodose prosopon. The poor preservation prevents assessment of the regularity of coverplates. Moreover, the original extent of the nodose prosopon is unknown owing to the etched condition of the holotype.

The hydropore structure of *Isorophusella trentonensis* includes only one relatively small, unpaired ambulacral coverplate, apparently a plate of the secondary series. This contrasts with the common occurrence of two unpaired coverplates, a secondary and a primary, in *Isorophusella incondita.* Moreover, where *Isorophusella incondita* bears only a single unpaired coverplate, it is a plate of the primary series.

The size of the oral area in the holotype of *Isorophusella trentonensis* appears to be relatively greater than in the larger, average adults of *Isorophusella incondita.* This suggests that fully developed *Isorophusella trentonensis* will prove to be larger than the holotype. Moreover, aside from preservational irregularities, the ambulacra are nearly straight, as in young *Isorophusella incondita.* This, too, suggests that the holotype of *Isorophusella trentonensis* is immature.

Neither the anal structure nor the peripheral rim is well enough preserved to allow adequate description.

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

Isorophusella pleiadae (Sinclair and Bolton), 1965
Text fig. 34; plate 36

1965 *Hemicystites pleiadae* Sinclair, G. W. and Bolton, T. E., Geol. Surv. Canada Bull. 134 (3): 35-39, pl. 11, fig. 1-6.

Diagnosis (tentative)

An *Isorophusella* with: small, domal theca.

Description

Isorophusella pleiadae (Sinclair and Bolton) (1965) is known from seven type series specimens, which expose only the inner side of the oral surface (text fig. 34, pl. 36). The proportional size of the major thecal structures suggests that the specimens are adults. Whether this is a valid specific trait is questionable. Other external thecal features, not yet revealed, will be the determinants. They await exposure on the type material. Unfortunately, permission to remove one of the seven types from the matrix and expose the upper oral surface was denied. A suggested alternative, that topotypes must be found to determine external thecal features, is not acceptable. Frequently several species of edrioasteroids are found together and topotypes could not be assumed to be conspecific with these original specimens. Only one of the type series seven will suffice.

The domal theca of *Isorophusella pleiadae* ranges from 5.5 mm to 8.8 mm in the type series.

Intrathecal extensions and inner plate surfaces suggest that at least four primary orals and one hydropore oral are included in the oral area.

The oral frame is a massive rim of plates which surrounds the ovoid central lumen (text fig. 34, pl. 36). The lumen extends downward from the ambulacral tunnels and opens into the thecal cavity below. A large gap in the posterior side of the frame forms direct lateral passage from the lumen into the thecal cavity beneath interambulacrum 5.

The proximal margin of the oral frame extends downward into the thecal cavity below the level of the inner surface of the ambulacral structures. This rim is subovate in plan view, and transversely elongate. The more highly arcuate anterior half meets the posterior side along attenuated lateral regions. Distally the frame grades outward into the five ambulacra, which imparts a pentagonal shape to the distal part of the frame.

The frame is formed by the five proximal ambulacral floorplates and the intrathecal extensions of the four primary orals. The radial ambulacral floorplates dominate the structure. Each is enlarged proximally and extends both downward into the thecal cavity and laterally to make contact with the adjacent floorplates.

The anterior half of the frame is formed by the proximal floorplates of ambulacra II, III, and IV, and the intrathecal parts of the two anterior primary orals. The intrathecal extensions form the interradial parts of the upper frame area, but they are wedge-shaped and taper downward and end before reaching the innermost edge of the frame. Thus the inner rim is formed only by the three floorplates that laterally achieve contact with one another. The posterior edges of floorplates II and IV flare outward laterally to form the laterally attenuated frame margins; they are broadly in contact with the posterior half of the frame.

The posterior unit of the frame is formed by the enlarged proximal floorplates of ambulacra I and V and the intrathecal parts of the two posterior primary orals. The anterior margins of the floorplates are flared outward laterally and meet the flared extremities of the anterior half of the frame. The two posterior floorplates are not in contact across the center of the posterior side of the frame. This area is formed by the intrathecal parts of the posterior primary orals. They do not extend downward nearly as far as the adjacent floorplates, and thereby create the conspicuous posterior gap in the frame.

The inner, proximal sides of the intrathecal extensions of the posterior primary orals form a low ridge crossing the posterior gap in the frame. This ridge extends between the rounded, lateral, posterior edges of the two floorplates. Thus the oral frame of *Isorophusella pleiadae* contrasts with that of *Isorophus cincinnatiensis* in which the posterior frame gap is modified into a subchamber by lateral bladelike extensions from the ambulacral floorplates.

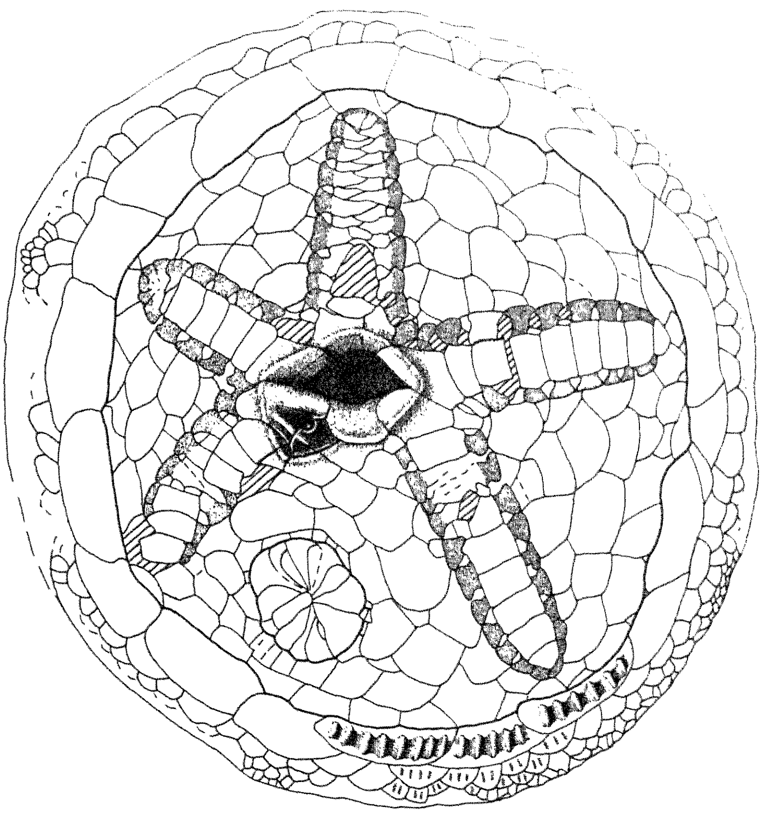
The stone canal passageway opens into the thecal cavity along the proximal posterior margin of ambulacrum V (text fig. 34). It is a funnel-shaped opening which expands rapidly in diameter downward. The inner end of the passageway is formed by the proximal two floorplates of ambulacrum V and the intrathecal parts of the hydropore oral and the right posterior primary oral. These plates extend inward to form a low rim, which defines the inner end of the passageway. A subtle ridge formed by the proximal floorplate and the hydropore oral appears to partially isolate the posterior third of the passageway funnel from the anterior two-thirds (text fig. 34).

The ambulacra are straight or slightly curved — I, II, III contrasolar; IV, V solar. Ambulacrum IV is most often straight and is conspicuously shorter than the others. The ambulacral coverplates form a double biseries of apparently regularly alternating large primaries and smaller secondary coverplate pairs.

The intra-ambulacral extensions of the coverplates appear to be bladelike processes which extend proximally from the inner, proximal edges of the coverplates. They underlap adjacent coverplates and also extend under the perradial line to underlap the tips of opposing alternate coverplates. Thus the ambulacral coverplate series of *Isorophusella pleiadae* is tightly interlocked in the same manner as described for *Isorophus cincinnatiensis*.

The intrathecal extensions of the primary coverplates continue past the lateral margins of the floorplates well into the thecal cavity. The innermost ends of these extensions are greatly expanded so that adjacent extensions are often in contact, or nearly so. The smaller secondary coverplate extensions end adjacent to the edges of the floorplates. They completely fill the spaces between the primary extensions along the lateral margins of the floorplates and prevent direct communication between the thecal cavity and the ambulacral tunnels. Thus the ovate hollows formed between the primary plate extensions, adjacent to the floorplates, end blindly, for they are plugged by the secondary coverplate extensions.

The uniserial, trough-shaped floorplates meet along vertical sutures. Each is rectangular in plan view, elongate normal to the ambulacral axis. The inner surface is evenly convex inward, the upper surface concave downward, but with lateral margins nearly horizontal along the zone of



Text fig. 34. ***Isorophusella pleiadae*** **(Sinclair and Bolton), 1965**

Holotype, GSC 14680-1, (x 15), pl. 36, fig. 1. Inner side of the oral surface. Intrathecal extensions of the primary ambulacral coverplates are stippled.

articulation with the ambulacral coverplates. The floorplates apparently attain full size soon after their formation, for only the distal two plates are smaller than the others. The terminal plate is bluntly rounded distally.

Interambulacrals are squamose, imbricate plates, apparently of moderate size in proportion to thecal diameter.

The valvular anal structure is composed of approximately 16 plates, regularly alternating as inner and outer circlet members. The structure appears similar to that of other species of *Isorophusella*. It is consistently offset toward the right side of interambulacrum 5.

The peripheral rim appears to include four to six circlets. The proximal circlet may be divided into a proximal and distal subcirclet by alternation of the plates. The basal surfaces of the geniculate rim plates have prominent vertical ridges like those found in *Isorophus cincinnatiensis*. Larger proximal plates have up to eight ridges, which form a single row across the plate bases.

Specimens

GSC 14680 (1-7). Type series of *Isorophusella pleiadae* (Sinclair and Bolton) (1965). Vaureal Formation, Richmond Group (210 feet below base of Ellis Bay Formation), Cincinnatian Series, Upper Ordovician. Roadcut in escarpment of south end of Princeton Lake, 9 miles northeast of Port Menier where highway abruptly turns east. Anticosti Island, Quebec.

The seven specimens expose only the inner side of the oral surface. It appears that they were resting on the inside surface of the siphuncular sheath of an endoceroid endocone (cephalopod), not the conch as reported by Sinclair and Bolton. It was later filled with sediment, followed by solution of the siphuncle, which exposed the edrioasteroids.

GSC 14680-1. Holotype of *Isorophusella pleiadae* (Sinclair and Bolton) (1965, pl. 11, fig. 1, 2, 3, 5, 6). 7.3 mm axial by 7.2 mm transverse diameter.