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A STUDY OF NORTH AMERICAN EDRIOASTEROIDEA

A dissertation submitted to the

Division of Graduate Studies

of the University of Cincinnati

in partial fulfillment of the

requirements for the degree of

DOCTOR OF PHILOSOPHY

in the Department of Geological Sciences

of the Graduate School of Arts and Sciences

1972

by

Bruce McConnell Bell

B. S. Earlham College, 1963

M. S. University of Cincinnati, 1966

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UNIVERSITY OF CINCINNATI

May 16 19 72

I hereby recommend that the thesis prepared under my supervision by Bruce M. Bell

entitled A Study of North American Edrioasteroidea

be accepted as fulfilling this part of the requirements for the degree of Doctor of Philosophy

Approved by:

Kenneth C. Caster, Chairman

William A. Oswald

Wayne A. Hagan

Form 668—Grad. School—1M—8-67

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A B S T R A C T

Sixty-five described species, formerly grouped into the three major, commonly recognized families of the Class Edrioasteroidea Billings (1858) have been restudied. Forty of these are recognized here (thirteen only with reservations), whereas the remaining twenty-five are here synonymized. Eight new genera (Belochthus, Curvitriordo, Cryptogoleus, Edriophus, Hadrochthus, Krama, Postibulla, Rectitriordo) and six new species (Belochthus orthokolus, Cryptogoleus reticulatus, Foerstediscus solitarius, Hadrochthus commensalus, Postibulla keslingi, Rectitriordo kirkfieldensis) are described.

The forty-six edrioasteroid species here described are grouped into the following nine subdivisions of the Class. (I) Order Edrioasterida Bell, ord. nov., with a sub-globoid theca; oral frame formed by ten compound plates; hydropore penetrates two posterior oral area plates and is elongate normal to the suture line; ambulacra formed by biserial floorplates with floorplate passageways connecting the ambulacral tunnel to the thecal cavity, and biserial coverplates without intra-ambulacral or intra-thecal extensions; the margin of the oral surface is on the lower side of the theca, reflexed up toward the center of the theca, with a distal membrane which extended down to the substrate. (I-A) Family Edrioasteridae Bather (1898) with the characters of the Order. (II) Order Isorophida Bell, ord. nov., with domal discoidal or clavate theca; oral frame formed by the five proximal ambulacral floorplates and commonly by primary oral plate intra-thecal extensions; hydropore structure in or near the posterior oral area, opening between plates along sutures; ambulacra formed by uniserial

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floorplates without passageways, and by biserial or multiple series of coverplates with intra-thecal and/or intra-ambulacral extensions, with or without coverplate passageways which connect the thecal cavity to the exterior of the theca. (II-A) Suborder Lebetodiscina Bell, subord. nov., with a single alternating biseries of ambulacral coverplates with a passageway system; ambulacral floorplates imbricate; anal structure a periproct. (II-A-1) Family Lebetodiscidae Bell, fam. nov., with oral area including two pairs of lateral shared coverplates and commonly secondary orals; hydropore structure along the proximal posterior side of ambulacrum V, near the oral area; ambulacral coverplates massive, ambulacral tunnel high and narrow, coverplate passageways nearly vertical; peripheral rim plates squamose, not geniculate. (II-A-2) Family Carneyellidae Bell, fam. nov., with oral area including one large hydropore oral and no shared coverplates or secondary orals; hydropore in the right posterior part of the oral area; ambulacral coverplates of moderate thickness, ambulacral tunnel low and wide, coverplate passageways oblique; peripheral rim plates geniculate. (II-B) Suborder Isorophina Bell, subord. nov., with four large central primary orals or numerous small undifferentiated central orals; ambulacral coverplates form multiple alternating biseries or cyclic series of two to seven sets of plates; coverplate passageways absent; anal structure valvular. (II-B-1) Family Isorophidae Bell, fam. nov., with four large primary orals, two pairs of lateral shared coverplates, one large hydropore oral, and secondary orals; hydropore structure formed by few plates, integrated with the central oral rise; ambulacral coverplates form multiple

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alternating biseries of two or three sets of plates. (II-B-2) Family Agelacrinitidae Chapman (1860), with numerous oral plates, primaries commonly undifferentiated; hydropore structure commonly includes many plates which form a large separate protuberance; ambulacral cover-plates form cyclic sets of two to seven plates.

A C K N O W L E D G E M E N T S

Sincere thanks are extended to the following: Kenneth E. Caster (University of Cincinnati) who spent an exorbitant amount of time and energy as principal advisor, research associate and editor of the manuscript which constitutes my doctoral dissertation; William H. White, Jr. (Milford, Ohio) who revealed many edrioasteroid collecting sites, aided in collecting and donated numerous specimens for study; Elizabeth R. Dalvé (Cincinnati, Ohio) who draughted many of the text illustrations; Thomas E. Bolton (Geological Survey of Canada), John L. Carter (University of Illinois), May D. Dash (Peabody Museum of Natural History, Yale University), Alan S. Horowitz (Indiana University), Robert V. Kesling (University of Michigan), Porter M. Kier (Smithsonian Institution), Bernhard H. Kummel (Museum of Comparative Zoology, Harvard University), George C. McIntosh (Buffalo, New York), John Monteith (Royal Ontario Museum), Norman D. Newell (American Museum of Natural History), Eugene S. Richardson (Field Museum of Natural History), and Harrell L. Strimple (University of Iowa), for lending study specimens.

The Department of Geology, University of Cincinnati provided research facilities, financial support and Museum of Paleontology

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specimens for this study. Research and manuscript preparation costs were supported in part by grants from the Nevin M. Fenneman Fund and Walter H. Bucher Fund of the University of Cincinnati, and by the award of the Fenneman Fellowship during my terminal year of residence at the University of Cincinnati. The manuscript has been prepared during my term as the Curator of Paleontology at the New York State Museum and Science Service.

ABBREVIATIONS

Specimens are listed by catalogue numbers with the repository names abbreviated as follows:

A.M.N.H.	American Museum of Natural History, New York, New York
C.F.M.	Field Museum of Natural History, Chicago, Illinois
C.F.M. P C.F.M. PE	Field Museum Paleontology Collection
C.F.M. U.C.	University of Chicago Walker Museum deposited at the Field Museum
G.S.C.	Geological Survey of Canada, Ottawa, Ontario
I.U.P.C.	Indiana University, Department of Geology, Paleontology Collection, Bloomington, Indiana
I.S.G.S.	Illinois State Geological Survey, Urbana, Illinois
I.S.M.	Illinois State Museum, Springfield, Illinois
M.C.Z.	Museum of Comparative Zoology, at Harvard College, Cambridge, Massachusetts
N.Y.S.M.	New York State Museum, Albany, New York
R.O.M.	Royal Ontario Museum, Toronto, Ontario
S.U.I.C.	University of Iowa, Department of Geology, Paleontology Collection, Iowa City, Iowa

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U.C.M.P. Museum of Paleontology, Department of Geology, University of Cincinnati, Cincinnati, Ohio

U.C.L.A.P.C. University of California, Los Angeles, Department of Geology, Paleontology Collection, Los Angeles, California

U.I.P.C. University of Illinois, Department of Geology, Paleontology Collection, Urbana, Illinois

U.M.M.P. University of Michigan, Museum of Paleontology, Ann Arbor, Michigan

U.S.N.M. United States National Museum, Washington, District of Columbia

U.S.N.M. S United States National Museum, Springer Collection

Y.P.M. Peabody Museum of Natural History, Yale University, New Haven, Connecticut

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INTRODUCTION

Edrioasteroids are not common fossils. When an amateur paleontologist, W. H. White, Jr. revealed an exceptionally prolific occurrence of these echinoderms in the Upper Ordovician near Cincinnati, Ohio in 1964, an attempt was made to gather specimens for a population study. Preliminary attempts to classify the specimens soon demonstrated inconsistencies in the existing taxonomy, and suggested that a major review of the Class was in order. The ensuing investigation has included the type specimens of sixty-five out of the approximately one hundred fifteen described edrioasteroid species, supplemented by numerous additional undescribed specimens.

Out of the sixty-five described species that were examined, only forty are recognized here, and thirteen of these only with reservations. The remaining twenty-five species are here placed in synonymy. Six new species are described.

The original sixty-five species included types for eighteen of the approximately twenty-nine commonly recognized genera of edrioasteroids. Fourteen of these genera are recognized here, the other four are junior synonyms. Eight new genera are introduced, three based on new, and five on previously described, species.

The twenty-two genera and forty-six species of edrioasteroids described here represent most of the species which have formerly been included in three families, the Edrioasteridae, Hemicystitidae and Agelacrinitidae as defined by Bassler (1935, 1936), and Regnéll (1966). These species are here thought to represent two major group-

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ings, the Order Edrioasterida Bell, ord. nov. with one Family, the Edrioasteridae Bather (1898), and the Order Isorophida Bell, ord. nov. The first Order includes few species, whereas the Isorophida includes many. It has been subdivided into the Suborder Lebetodiscina Bell, subord. nov., with two families, the Lebetodiscidae Bell, fam. nov. and the Carneyellidae Bell, fam. nov., and the Suborder Isorophina Bell, subord. nov. with two families, the Isorophidae Bell, fam. nov. and the Agelacrinitidae Chapman (1860).

Largely for want of material a few species, mostly European, are excluded from this study although they probably belong to the Isorophida. These are Anglidiscus fistulosus Anderson (1939), Argodiscus hornyi Prokop (1965), Thresherodiscus ramosus Foerste (1914), four species assigned to Lepidodiscus Meek and Worthen (1868), seven species assigned to Agelacrinites Vanuxem (1842) and eight species assigned to Hemicystites Hall (1852).

Also omitted are four small, distinct groups of species. A family has been proposed for each of these by earlier workers. 1) The Cyathocystidae Bather (1899a) includes two genera, Cyathocystis Schmidt (1879) with the type and three other assigned species, and Cyathotheca Jaekel (1927) with the type and one other species. 2) The Stromatocystitidae Bassler (1935) includes Stromatocystites Pompeckj (1896) with the type and three assigned species, Walcottidiscus Bassler (1935) with the type and one other species, and Xenocystites carteri Bassler (1936). 3) The Pyrgocystidae Kesling (1967) includes only the type genus, Pyrgocystis Bather (1915) with the type species and twelve others, described primarily on the

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arrangement of peduncular zone plates, a feature of questionable taxonomic significance. 4) The Lispidecodidae Kesling (1967) includes only one species, Lispidecodus plinthotus Kesling (1967).

At this stage, it appears that the Cyathocystidae is a valid family grouping. The Family probably belongs to the Order Isorophida. The striking morphology of the Stromatocystidae suggests that they probably represent a new Order. The Pyrgocystitidae and Lespidocodidae have unusual thecal shapes, but both belong to the Isorophida, probably members of the Suborder Isorophina.

PREVIOUS INVESTIGATION

Numerous papers dealing with edrioasteroids are listed in the bibliography of this work, but only a handful have made major contributions. Most are brief descriptions of new taxa, commonly based on a few isolated specimens. Moreover, due to the scarcity of specimens in most collections, new descriptions have usually included little comparative data and those often based only on published descriptions. The result has been the gradual accumulation of ill-defined species, not uncommonly based on inadequate type material.

The first described edrioasteroid was found by J. J. Bigsby in 1822 (Trenton Limestone, Middle Ordovician, Ottawa, Ontario). It was described by Sowerby (1825) as a new fossil belonging to the "Class Radiata", a Cuvier subdivision of the animal kingdom embracing all animals with "radial" symmetry. Sowerby (1825, p. 319) noted that the fossil resembles the arms of an Asterias lying on an Echinus. Although he included it among the genera of the "Asteridae" due to

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"the want of ambulacra", Sowerby (1825, p. 319) suggested it might be "considered as a connecting link to be placed between the two families of Crinoidea and Blastoidea".

The second edrioasteroid to appear in the literature was a section of the "turret" or peduncular zone of what was later to be described as Pyrgocystis sulcatum (Middle Silurian, Gotland). Figured by Hisinger (1841), it was described as a fragment of a "crinoid" stem. By "crinoid" Hisinger implied only that it was a sessile echinoderm, as opposed to the mobile "Asteridae". Vanuxem (1842) applied the first binomial to an edrioasteroid, Agelacrinites hamiltonensis (Middle Devonian, New York). His specimen included six individuals, all occurring on a fragment of a large pelecypod valve. Mistaking the smooth pelecypod as a "connecting surface" between the individual edrioasteroids, he suggested (1842, p. 158) that it demonstrated a unique organization, being the only known "crinoid . . . found clustered together so as to form one system", hence the name Agelacrinites - "a herd of crinoids".

L. von Buch (1845) assigned Agelacrinites to the cystoids. The genus was reported from the Cheirurus claviger beds at Wesela, Bohemia, by Beyrich (1843, 1846). In 1848 Forbes described Agelacrinites [now Edriophus (?)] buchianus from the Caradoc beds, Denbighshire, Great Britain, based on an internal mold. He thought Agelacrinites to be a connecting link between the cystoids Pseudocrinites and Sphaeronites but not far removed from the Echini via Palaechinus. Moreover, he erroneously interpreted nearby echinoderm columnals as detached parts of his edrioasteroid, and thereby suggested relationship to the

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crinoids.

During the 1850's, several new edrioasteroids were described as cystoids, e.g., Roemer (1851), Agelacrinus [sic] cincinnatiensis, A. rhenanus; Hall (1852), Hemicystites parasiticus; Hall (1858), Agelacrinites [now Discocystis] kaskaskiensis.

E. K. Billings (1854, 1857) suggested that the edrioasteroids were not true cystoids. He pointed out that the "rays supposed to be grooves for the reception of arms are in fact true ambulacra . . . It is scarcely necessary to add that it [A. buchianus] is not a cystidea, and that in all probability neither Agelacrinites of Vanuxem, nor Hemicystites of Hall, should be placed in that Order. They are low forms of Asteriadae" (Billings, 1857, p. 293). Billings' 1857 paper also described two new species, Cyclaster bigsbyi and Agelacrinites [now Lebetodiscus] dicksoni. He noted the passage of "pores" through the ambulacral floorplates of C. bigsbyi. In 1858 Billings proposed the substitute Edrioaster for the preoccupied Cyclaster. Moreover, considering all edrioasteroids "Asteriadae", he concluded: "None of the Cystidae have ambulacra whose pores penetrate through the covering of the body, and therefore all such genera as Edrioaster, Agelacrinites, and Hemicystites belong to a very different division of the Echinodermata. When we know more of their structure, it is probable that they will be arranged as a sub-order, for which the name Edrioasteridae would be appropriate, as it would suggest their sessile condition on the one hand, and on the other their affinity to the Asteriadae" (Billings, 1858b, p. 85).

E. J. Chapman (1860) agreed with Billings' forecast for separa-

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tion of the edrioasteroids. However, he thought them closest to the cystoids, as evidenced by their "pyramidal orifice" [anal structure]. The imbricate thecal plates of some edrioasteroids suggested to Chapman relationship to the "Ophiurians", as did the ambulacral structure. However, the position of the mouth (which Chapman believed to be in the center of what is now considered the aboral side of the body) suggested they were as close to the "Echinida" as to the "Ophiurians". Chapman rejected Billings' term Edrioasteridae, because: 1) the supposed sessile or parasitic condition of the group was by no means established, and 2) the relation to the starfish implied by that name was also not certain. Thus, Chapman coined the substitute term Thyroida, which refers to the presence of the "valved aperture". The Thyroida consisted of the monotypic Agelacrinitidae with all described edrioasteroid species included in the genus Agelacrinites.

Many new edrioasteroid species were described in the last half of the Nineteenth Century. Most were brief descriptions, which covered only thecal form, ambulacral position, anal structure, and occasionally, generalized descriptions of ambulacral and oral plates. Species were commonly assigned to the "Cystidea", or merely referred to as new echinoderms. Among these are three important papers by Hall (1866, 1871, 1872) which introduced three of the more common Upper Ordovician edrioasteroids, and reviewed several other species. Barrande (1887) described a suite of seven new species from the Ordovician of Bohemia.

S. A. Miller (1877) listed the Order Agelacrinidea under the

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"Class Echinodermata", but did not define the taxon. In 1882 he modified his ordinal name to Agelacrinoidea with one Family, Agelacrinidea (derived from his arbitrary change in the spelling of Agelacrinites to Agelacrinus). He defined the Order and Family as follows (1882, p. 221):

> "Body thin, circular and parasitic upon other objects. The lower side consists of a thin, smooth, attaching membrane or plate. The upper side is more or less convex, and composed of thin, squamiform or imbricating plates, usually much smaller at the periphery than toward the center. Ambulacra constituting part of the convex surface furrowed on the interior, and composed of a double series of transverse alternating plates, sometimes having smaller, middle, intercalated ones. Two or more rows of ambulacral pores connect the exterior with the interior of each ambulacrum. The so-called ovarian or anal aperature is situated in one of the interambulacral areas, and is usually surrounded by cuneiform plates forming a depressed circular prominence. The genera belonging to this order and family are Agelacrinus, Edrioaster, and Hemicystites."

By 1889 enough additional species had been described to encourage Miller to divide his Order Agelacrinoidea into two families, Agelacrinidae and Hemicystidae. Neither family was formally defined, but it must be assumed that with the genus Hemicystites removed from the

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Agelacrinidae a new family having the attributes of the genus would be required.

Many texts and synthetic taxonomic works on paleontology appeared in the last quarter of the Nineteenth Century. Most treated the edrioasteroids quite summarily, often using their own terms for the group. Among these was Zittel's Handbuch der Palaeontologie (1879) and Grundzüge der Palaeontologie (1895) [translated and modified by Eastman (1896) as Textbook of Paleontology], in which the Family Agelacrinidae was placed with the cystoids.

Steinmann (1890) proposed the Gruppe Cystasteroidea (third group of the Class Cystoidea) for the edrioasteroids. He replaced this name by Edrioasteroidea in 1903. [Regnéll (1966) reports the term Cystostellaroidea was also proposed by Steinmann (1903) in his Einführung in die Paläontologie, but examination of this text failed to reveal that name.] Bernard (1893) gallicised Steinmann's 1890 term to "Cystoastéroides", indicating that to his mind the group represented a transition series from the "Cystides" to the "Asteroides".

Haeckel (1896a), attempting to produce a phylogenetic diagram of the echinoderms, introduced for the edrioasteroids the term Agelacystida (Order Agelacrinida) and listed it as the third "family" under the Cystoidea. He defined the Family (1896a, p. 404, here translated from German) as:

> "Cystoids with very numerous small plates, or scales, which often exhibit very different form and arrangement on the oral and aboral parts of the capsule. Five ambulacra, very elongate, and regularly divided, the

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long ambulacral groove each with two rows of cover plates. Between the central mouth and the eccentric valve-pyramid of the anus no third opening is discernible."

Haeckel's (1896b, p. 107) expanded diagnosis of the Family Agelacystida included the following additions: "Cystoid with a pentaradial, usually regular but occasionally bilateral theca . . . [thecal plates] usually have pores, . . . the theca has a vertical main axis, it is sometimes disk-shaped or semi-spheroidal, and tapered underneath into a short stem, . . . [central] pentagonal mouth, . . . [ambulacra with] pinnules". Haeckel (1896b, p. 110-111) divided the Agelacystida into two subfamilies, Subfamily Hemicystida with "theca flexible, with a flexible squamous skeleton. Plates rounded (rarely polygonal) imbricate, usually (or always?) without double pores". The genera listed with their supposed type species are: "Hemicystis (granulata), Agelacrinus (vorticellatus), Lepidodiscus (cincinnatiensis), Agelacystis (hamiltonensis)". Subfamily Asterocystida with "theca stiff, with an immovable plated skeleton. Plates polygonal, connected firmly by fibers, not imbricate; usually (or always?) with double pores". The genera listed with their supposed type species are: "Cyathocystis (plautinae), Gomphocystis (texax), Asterocystis (tuberculata), Asteroblastus (stellatus), Edriocystis (bigsbyi), Mesites (pusireffskyi)". Haeckel's summation of the morphology of the Agelacystida is confusing, due to the inclusion of four true cystoids along with the edrioasteroids, hence the description of pinnules,

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etc. His descriptions of edrioasteroid species were based largely upon interpretation of earlier publications, thus adding little new information. Moreover, he assigned different type species to described genera and altered spelling, commonly replacing generic endings with "-cytis" to reflect his phylogenetic interpretation.

Commenting upon this procedure which violated then accepted, and now formalized, rules of nomenclature, Bather (1914a, p. 115) exclaimed "Neither the nomenclatoral nor the taxonomic vagaries of Professor Haeckel won any favour, and it is needless to allude further to him or to other writers who shared his ignorance of the facts but not his imagination."

O. Jaekel (1895) introduced the term Thecoidea for the edrioasteroids. In 1899 he published a lengthy treatment of the group, the first to systematically relate thecal construction to soft part morphology and function. His discussion included analysis of the thecal shape and mode of attachment, oral area and frame, ambulacral system of coverplates and floorplates, mode of ambulacral curvature, interambulacral plating, anal structure, hydrovascular system, intestinal system, musculature system, nervous system, genital system, ontogeny, phylogeny, mode of life and geological distribution. Jaekel's work was largely a synthesis of earlier description, salted with speculation about phylogenetic and ontogenetic relationships, and functional morphology. It provided a much needed summary of the Class. Jaekel subdivided the Thecoidea into two families, summarized below.

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"Order Thecoidea

Thecoidea are Pelmatozoa, whose five radiating ambulacra have no side branches or free arms; but are fixed through their total length to the body, and are closed by differentiated thecal plates. The body is spheroidal, sack-, cup- or disc-like, free or with the underside attached to the sea floor or foreign object, without a stem. The theca is occasionally leathery with a weakly developed skeleton. The elements of the latter are irregularly arranged, interrupted by the ambulacral pentamer, and at times also equipped with respiratory grooves, but without thecal pores. The gut was turned solarly. The anus is on the upper side in interradial position, and is closed with either small, irregularly arranged plates or by larger ones that are arranged radially. The parietal pores and primary stone-canal pore may be lacking from the theca. The sex organs lie entirely within the theca.

Family Thecocystidae

Body pentagonal or spheroidal, sack- or cup-shaped, free or with a part of the undersurface coherent. Theca leathery, with small, weakly calcified to thick polygonal plates directly abutting or partly fused. Ambulacra short, and straight or spirally elongated; coverplates often little differentiated.

Genera: Stromatocystites, Cyathocystis, Thecocystis,

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Cystaster, Edrioaster, Dinocystis.

Family Agelacrinidae

Body cup-shaped or cap-shaped; upper side convex in the middle, depressed at the periphery, underside level, attached by the entire surface. Theca, apart from the coverplates of the ambulacra, composed of squamose, overlapping plates which diminish in size toward the periphery, where they are solidly fused together. Ambulacra straight or curved spirally, in doing so V and also IV can be curved contrasolarly. Anus closed by irregularly placed plates, coverplates large, finger-shaped, subambulacral plates present.

Genera: Hemicystites, Agelacrinites."

Jaekel differentiated his new Order from other Pelmatozoa on the basis of the unique combination of five traits: (1) the structure of the ambulacra, i.e., five fixed ambulacra with differentiated coverplates; (2) lack of other subvective appendages; (3) position and manner of closure of the anus; (4) the lack of a stem; (5) the lack of thecal pores. The families were differentiated on the basis of four characters: (1) thecal shape; (2) size of attachment area; (3) length and disposition of the ambulacra; (4) degree of differentiation of ambulacral coverplates. It is apparent that most of his conclusions on morphology were derived from species of the Family Agelacrinidae as defined by Bather. Jaekel doubted the presence of pores in the ambulacra of Edrioaster as described by Bather, and

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further defined the ambulacra of all edrioasteroids as having a uniseries of floorplates.

Bather (1898-1915) published a series of papers dealing with the edrioasteroids. Included were the first detailed analyses of several species, with the new taxa: Dinocystis barroisi (1898); Edrioaster levis (1914); Lebetodiscus (1908) for Agelacrinites dicksoni Billings (1857); Pyrgocystis sardesoni (1915); P. grayae (1915); and P. anstice (1915). Bather also covered Edrioaster buchianus (Forbes) (1848), Edrioaster bigsbyi (Billings) (1857). Bather's specimens included several large, well-preserved specimens of Edrioaster bigsbyi and Edrioaster [now Edriophus] levis. His extensive analysis of these two species included explanation of formerly misrepresented ambulacral structure and floorplate passageways, the oral area and underlying frame, and the hydropore opening. This information combined with analysis of internal molds of Edrioaster buchianus dictated his conclusions regarding edrioasteroid morphology and their systematic position within the echinoderms. The importance placed on the well-defined structure of the species he assigned to Edrioaster is exemplified by his misrepresentation of the coverplate passageways of Lebetodiscus dicksoni as floorplate passageways. Bather's reconstruction of the oral surface of Edrioaster (1914a, fig. 1) has been commonly reproduced in both papers and texts and used to exemplify the important morphological features of the "typical" edrioasteroid. A summary of Bather's classification of the edrioasteroids (1900) is presented below. His Family Steganoblastidae [for Astrocystites Whiteaves (1897) = Steganoblastus Whiteaves (1898)]

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and Cyclocystoides Billings and Salter (1858) need not be considered since these two genera are now placed in the Class Edrioblastoidea Fay (1962) and Cyclocystoidea Miller and Gurley (1895), respectively. Bather's classification raised the edrioasteroids to the class level, defined two new families and redefined the Agelacrinidae:

"Class Edrioasteroidea

Pelmatozoa in which the theca is composed of an indefinite number of irregular plates, some of which are variously differentiated in different genera; with no subvective skeletal appendages, but with central mouth, from which there radiate through the theca five unbranched ambulacra, composed of a double series of alternating plates (covering-plates), sometimes supported by an outer series of larger alternating plates (side-plates or flooring-plates). Pores between (not through) the ambulacral elements, or between them and the thecal plates, permitted the passage of extensions from the perradial water-vessels. Anus in posterior interradius, on oral surface, closed by valvular pyramid. Hydropore (usually, if not always, present) between mouth and anus.

Family 1. Agelacrinidae

Edrioasteroidea with a theca composed mostly of thin plates, flexible, attached temporarily or permanently by the greater part of the aboral surface; with the ambulacra confined to the oral surface.

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Genera: Stromatocystis, Cystaster (Thecocystis of Jaekel), Hemicystis, Agelacrinus, Streptaster, Lepidodiscus, Discocystis, Echinodiscus, (Haplocystis).

Family 2. Cyathocystidae

Edrioasteroidea with the theca composed on the oral surface of five deltoids surrounded by marginals, but below of a fused solid mass of stereom, with irregular longitudinal sutures; permanently attached by the aboral surface as by an encrusting root; ambulacra confined to oral surface.

Genus: Cyathocystis

Family 3. Edrioasteridae

Edrioasteroidea with flexible theca composed of thin plates; attached if at all, by a small central portion of the excavated aboral surface; ambulacra pass on to aboral surface.

Genera: Aesiocystis, Edrioaster, Dinocystis."

The publication of Jaekel's (1899) and of Bather's (1900) papers, along with Bather's subsequent publications of the detailed morphological work on which he had based his classification, marked a new era. Previously paleontologists had mostly concerned themselves with specific differentia when dealing with edrioasteroids. Only a few speculated about possible interrelationships within the group and the phylogenetic implications of the group as a whole. Due to

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the limited knowledge of the morphologic spectrum within the group, the classification and its implications remained on a rather superficial level.

In connection with description of several new species, J. M. Clarke (1901) gave a much needed review of the species belonging to Bather's 'Agelacrinidae', in order to "provide the means to unsnarl the tangle of names into which American Paleontologists with the aid of their British and German brethren have plunged these organisms." Summarizing the morphology of Agelacrinidae, Clarke (1901, p. 192-193) concluded that of the taxobases of the lower taxa of the group:

> "It appears from the foregoing that we may leave out of consideration as a generic character of the agelacrinites the variation in the direction of the rays and may consider as structures of convenient generic value 1) the character of the thecal plates, whether a) squamous, or b) mosaic, and if the latter, whether 1) polygonal and smooth, or, 2) irregular and sculptured; 2) the character of the rays, whether a) long and whiplash shaped, with narrow, arched cover plates or b) shorter and broader, with broad and long cover plates; 3) the presence and structure of a peripheral band either a) composed of few large plates with very fine ones on the outer edge or b) broad with a great number of small plates."

Although it is manifest that Clarke used several thecal features no longer considered to be of generic value, he made a great contri-

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bution by using a systematic approach to the group.

Numerous other works on the edrioasteroids appeared from 1900-1936. Among the notables of this period are Spencer (1904) who first sectioned an edrioasteroid (Carneyella pilea); Foerste (1914) presented a major summary of morphology, discussed evolutionary development and gave comparative descriptions of many species; Raymond (1915, 1921) contributed several new Middle Ordovician species; Williams (1918) reviewed Agelacrinites, including an ontogenetic series for one species; and finally, Bassler (1935, 1936) published two papers that between them listed all the known species of edrioasteroids, and attempted to group these species into a supposedly unified classification scheme.

Bassler had the great advantage over all previous workers of being able to study literally hundreds of specimens of Cincinnatian edrioasteroids in the United States National Museum collections, where there were also representatives of nearly every known genus. This sample was still too small, however, and especially the employed techniques too inadequate, to allow proper analysis of all the structural features of the group. However, Bassler did correctly evaluate as useless several of the features that had been previously used as generic traits. He listed seven features that were commonly used as generic taxobases:

Variable within a genus:

1. amount of imbrication of interambulacral plates,
2. width of peripheral border of plates,
3. number of ambulacra.

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Constant within a genus:

1. plate structure of the ambulacra,
2. plate structure of the oral area,
3. direction of the curvature of the ambulacra,
4. extent of curvature of the ambulacra.

Bassler divided the Class Edrioasteroidea into five families which included twenty-four genera and ninety-two species. Seven of these genera and thirty of the species were proposed in these two papers. A combination of the two papers results in the following summary of Bassler's classification:

Class Edrioasteroidea Billings (1858) [not 1854-58 as Bassler gave]. [no diagnosis given]

Family Stromatocystitidea Bassler (1936)

Theca with a basal layer of plates (in contrast with all other edrioasteroids with basal areas of attachment without plates).

Genera: Stromatocystites Pompeckj (1896); Walcottidiscus Bassler (1935); Xenocystites Bassler (1936).

Family Hemicystitidae Bassler (1936)

Theca composed of thin plates with an oral surface of five ambulacra separated by interambulacrals and attached by the greater part of the aboral surface permanently or temporarily to some outside object. Oral covering plates three, one large plate next to the anal area with two smaller adjacent ones.

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Genera: Cystaster Hall (1872); Cincinnatidiscus Bassler (1935); Carneyella Foerste (1917); Streptaster Hall (1872); Lebetodiscus Bather (1908); Foerstediscus Bassler (1935); Pyrgocystis Bather (1915); Hemicystites Hall (1852).

Family Agelacrinitidae Chapman (1860) [not Bassler (1935) or Clarke (1901)]

Theca as in the Hemicystitidae except that the plates covering the oral area are small, numerous, and without any definite order. A single row of ambulacral flooring plates overlapping proximally.

Genera: Thresherodiscus Foerste (1914); Agelacrinites Vanuxem (1842); Isorophus Foerste (1917); Isorophusella Bassler (1935); Lepidodiscus Meek and Worthen (1868); Discocystis Gregory (1897); Ulrichidiscus Bassler (1935); Cooperidiscus Bassler (1935).

Family Edrioasteridae Bather (1899)

Theca flexible, depressed, usually globular, attached by the small central excavated part of the aboral surface; ambulacra strongly curved and passing on to aboral surface; floor plates arranged in two series, one on each side of the ray, and alternating along the median line. [Bassler notes the only actually diagnostic feature of the family is the presence of the biseries of floor plates.]

Genera: Edrioaster Billings (1858); Dinocystis Bather (1908).

Family Cyathocystidae Bather (1899)

Edrioasteroidea in which the aboral portion consists of a

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fused solid mass of plates attached permanently to some foreign object.

Genera: Cyathocystis Schmidt (1880); Cyathotheca Jaekel (1927).

Position Uncertain:

Astrocystites Whiteaves (1897). [Now Class Edrioblastoidea Fay (1962).]

Bassler concluded his contributions to the edrioasteroids in a joint work with Moodey (1943) where they compiled the stratigraphic occurrence of the group and a bibliographic index of genera and species (in which they recognized twenty-three genera and ninety-two species). Bassler's (1935, 1936, 1943) works represent a most significant contribution. Disagreement has since arisen over many of Bassler's observations and conclusions, as is expected when new material and techniques appear, but the value of Bassler's synoptic and bibliographic work has not been diminished.

Several outstanding morphologic studies on edrioasteroids have been published in recent years. Anderson (1939) described Lepidodiscus fistulosus and gave a comparative morphological evaluation of this and other edrioasteroid species. Regnéll (1945) offered extensive redescription of species included in Stromatocystites, Cyathotheca, Pyrgocystis and (1950) gave an analysis of Agelacrinites ephraemovianus (Bogolubov) and Lepidodiscus fistulosus Anderson. Ehlers and Kesling (1958) described cyclic coverplates in Discocystis laudoni and considered their taxonomic implications. Kesling and Ehlers (1958) interpreted the cyclic coverplates and other morphologic features of Lepido-

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discus squamosus. Kesling and Mintz (1960) extensively described both internal and external morphology of Isorophus cincinnatiensis and Carneyella pilea from specimens exposing the inner and external surfaces and also from ground, serial views of two specimens. Kesling (1960) revealed hydropore structures in twenty species of edrioasteroids and most recently (1967) he described two new families; Lispidocodidae for the new Lispidocodus plinthotus, and Pyrgocystidae for Pyrgocystis.

Kesling's (1960) paper on the hydropore structures of a broad cross-section of edrioasteroid species is perhaps the most significant recent morphologic paper. This structure had been overlooked by most earlier workers except in Edrioaster bigsbyi and related species. Kesling's careful analysis of the hydropore structure in twenty species demonstrates the taxonomic significance of the structure. Moreover, his splendid reconstructions of thirteen species suggested the importance of many other thecal details commonly scantily considered. Kesling recognized six basic types of hydropore structures based on plate structure and position. Consideration of additional species has allowed refinement of Kesling's scheme, including some reorganization of his groupings. However, all of the major types of hydropore structures recognized here were reported by Kesling.

Regnéll (1966) published the only recent summary of the Edrioasteroidea. This work is largely a literature compilation due to the unfortunate unavailability of many type specimens (Regnéll, 1969, personal communication). However, Regnéll's complete review of morphology, ontogeny, evolutionary trends, ecology, and distribution is

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flavored with his own extensive knowledge of British and European edrioasteroids, adding insight to former interpretations. He accepted Bassler's five-family subdivision of the Class, although he expanded Bassler's abbreviated family diagnoses. Regnéll lists twenty-seven described genera.

M O R P H O L O G Y

TERMINOLOGY AS APPLIED TO EDRIOASTEROIDEA

aboral pole - point of intersection of the oral-aboral axis with the aboral surface of the theca; marks the center of the aboral surface.

aboral surface - morphologically related unit of the theca distal to the oral surface plates, commonly forms only part of the lower side of the individual.

adradially - direction toward the adradial suture.

adradial suture - zone of contact between the oral-ambulacral series plates and interambulacral plates; the adradial suture line marks the intersection of the adradial suture with the thecal surface.

adult stage - mature theca with fully developed structures; ephebic, sexually mature.

ambitus - theoretical line encircling the exterior of the theca which marks the greatest thecal circumference perpendicular to the oral-aboral axis; it separates the lower from the upper side of theca; commonly the greatest horizontal circumference of theca.

ambulacral bifurcation plates - see bifurcation plates.

ambulacral coverplates - plates covering the ambulacral groove which

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roof the ambulacral tunnel; may be a single or multiple biseries, or a cyclic series of plates.

ambulacral floorplates - plates underlying the ambulacral groove which floor the ambulacral tunnel; may be a uniseries, or single biseries of plates.

ambulacral radius - thecal radius defined by the midline of an ambulacrum; in curved ambulacra, the radius is defined by the midline of the proximal end of the ambulacrum, which is extended directly toward the edge of theca.

ambulacral tunnel - space enclosed between the ambulacral floorplates and overlying coverplates; the ambulacral food groove extends along the floor of this space.

ambulacrum - the morphologically and functionally unified group of structures which form each of the endothecal subjective system radii, including coverplates, floorplates, tunnel, and, in life, food groove organs. Identified by the Lovénian system, I-V, numbered clockwise, I along the left side of the posterior interambulacrum.

anal area - anal structure and the enclosed anus.

anal structure - morphologically related group of plates surrounding the anal opening.

anterior - direction toward the anterior pole of theca, along or parallel to the axial plane.

anterior oral midline - perradial line between opposing oral plates which extends anteriorly from the oral pole.

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anterior pole - intersection of the anterior-posterior axis with the anterior tip of the theca (opposite interambulacrum 5).

anterior-posterior axis - axis which extends through the center of the theca, aligned with the center of the oral area, the anterior primary ambulacral radius and the center of posterior interambulacrum; perpendicular to transverse axis.

anterior primary ambulacral radius - primary radius opposite interambulacrum 5, the anus and the hydropore region; defined by the anterior oral midline and ambulacrum III.

anus - terminal exit of digestive tract.

axial diameter - anterior-posterior thecal diameter.

axial plane - plane passing through the theca along the anterior-posterior axis, perpendicular to upper side of theca.

bifurcation plates - two large, unpaired plates, one lying at the junction of each lateral pair of ambulacra (I-II and IV-V); the perradial tip of each bifurcation plate lies at the junction of the two ambulacral perradial lines with each other and with one end of the transverse oral midline. (Bifurcation plates are classified as ambulacrals, although they could as easily be considered orals, as done by many authors.)

biseries - double row of alternating plates.

central lumen - opening which extends from the proximal ends of the ambulacral tunnels down through the oral frame into the underlying thecal cavity.

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clavate - club-shaped thecal form in which the oral surface plates form three regions: an upper gibbous "head"; a lower, constricted, pedunculate zone; and an outwardly flaring peripheral rim; the non-plated aboral surface is restricted to the area underlying (distal to) the peripheral rim and it conforms to shape of underlying substrate.

contrasolar - counterclockwise or sinistral direction of curvature.

coverplate height - elevation of a coverplate above the interambulacra, measured normal to thecal surface.

coverplate length - external dimension of a coverplate measured normal to length of the ambulacrum - i.e., distance from adradial suture to perradial line.

coverplate passageways - tubular canals which extend along lateral, sutural faces of contiguous ambulacral and oral coverplates; they connect the exterior to the interior of the theca (not in direct communication with ambulacral tunnel).

coverplate thickness - dimension from the exterior extremity of a plate to the internal extremity, perpendicular to the external surface of the plate.

coverplate width - external dimension measured parallel to length of an ambulacrum, i.e., proximal-distal dimension.

cyclic - referring to serially repeated arrangement of plates.

cyclic coverplate series - coverplates along each side of ambulacral perradial line which form serially repeated sets of plates, each set a cycle, cycles on one side of the ambulacrum a mirror image of those on the opposing side of perradial line;

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opposing cycles alternate, offset by half a cycle.

distal - relative direction or position away from the oral pole, toward the aboral pole of the theca, defined by moving along the structure to which the term is applied. E.g., for the ambulacra, the distal tip is the end furthest from the oral area. In forms with curved ambulacra the distal part is located by proceeding along the length of the ambulacrum, even though in straight-line distance the distal tip may be closer to the oral pole than another part of the same ambulacrum. See discussion under Orientation for differing definition of proximal and distal as applied to other echinoderms.

domal - thecal shape in which the oral surface is convex upward and is confined to upper side of theca; distal edge of the oral surface forms the thecal ambitus. Non-plated aboral surface forms the entire lower side of theca. Lateral view: concave-convex or plano-convex; plan view: circular or subcircular.

double biseries - two distinct sets of coverplates with each forming an alternating biseries of pairs of plates, the pairs of one set alternating with those of the other to form an integrated system.

"echinoidal" - thecal shape in which the oral surface extends past ambitus onto lower side of the theca and is divided into five areas: 1) the upper oral surface, convex upward, extending from the oral region down to the ambitus; 2) the subambital zone, constricting downward, sides sloping inward toward the oral-aboral axis; 3) the resting zone, a narrow area with plate

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exteriors parallel to the underlying substrate; 4) the incurved zone, with plates flexed upward and inward toward the thecal cavity to form a central, basal, convex upward invagination in lower side of theca; and 5) the flexible membrane, which extends from the distal edge of the incurved zone downward to the underlying substrate. The ambulacra extend past the ambitus onto the subambital zone but end or curve before reaching the resting zone; the aboral surface is restricted to a small region surrounded by the distal edge of the membrane. In lateral view: oblate spheroid, plan view: circular or sub-circular.

endotheca - ambulacra between thecal plates, in contact with both interior and exterior of theca.

exterior side of theca (external; outer side) - thecal surface in contact with the external environment, the outside of the theca; opposite of inner side.

floorplate passageways (floorplate "pores") - tubular canals which extend along lateral, sutural faces of contiguous ambulacral floorplates; they connect the ambulacral tunnel to the interior of the theca.

food groove - trough which extends along the base of the ambulacral tunnel (upper side of floorplates); proximally empties into the central lumen.

gerontic stage - old age, normally represented by unusually large theca and perhaps modification of some thecal structures.

hydropore - external opening through the theca which links the hydro-

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vascular system with the external environment, delimited by plates of the hydropore structure.

hydropore oral - unpaired oral plate in right posterior part of the oral region, commonly forming the posterior edge of the hydropore.

hydropore structure - group of plates which externally surround the hydropore.

inner side of oral surface - the side of the oral surface plates in contact with the thecal cavity, the inside of the theca, opposite the exterior side. (Commonly referred to as the aboral side of the theca by earlier authors.)

interambulacrum - sector of theca between two ambulacra, distal to oral area plates, proximal to peripheral rim; an interradius.

intra-ambulacral extension - part of an ambulacral coverplate or oral plate which is produced inward into the ambulacral tunnel.

intra-thecal extension - part of an external thecal plate which is produced inward into the interior of the theca.

juvenile stage - immature stage of growth; thecal structures incompletely formed.

lateral depression series - groups of small basin-like depressions on the exterior lateral edges of the coverplates; they flank the suture lines between contiguous ambulacral coverplates; associated with the external foramina of the coverplate passageways.

lateral shared coverplate pair - (shared coverplate) - pair of oral plates which flank the transverse oral midline, proximal to the lateral ambulacral bifurcation plate, distal to the central

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primary orals.

left-lateral primary ambulacral radius - primary ambulacral radius which extends from the oral pole out to the left ambulacral bifurcation plate along the transverse midline of theca; this radius bifurcates at the left lateral bifurcation plate and forms two lateral ambulacral radii, i.e., ambulacra I and II.

lower side of theca - the part of the theca distal to the ambitus, composed of the aboral surface of the theca and commonly the distal parts of the oral surface.

marginal area - morphologically united part of the theca which forms the distal sector of the oral surface, usually a peripheral rim.

multiple biseries - two or more sets of coverplates, each of which form an alternating biseries of pairs of plates, the pairs of each set alternate with those of the other sets to form an integrated system.

oral-aboral axis - axis which passes through the center of oral area perpendicular to the upper side of the theca.

oral area - (oral region) - morphologically related structures which surround the stomial opening, including oral covering plates, oral frame and related soft part structures.

oral frame - structure underlying the external oral area, formed by proximal ambulacral floorplates and commonly other elements; it surrounds the central lumen or stomial chamber.

oral plates - (orals, oral covering plates) - elements which form the external covering of the oral area, and roof the central lumen;

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distally continuous with the ambulacral coverplate series.

oral pole - point of intersection of the oral-aboral axis with the oral surface of the theca; marks the center of the oral region.

oral surface - the morphologically related unit of the theca that includes the oral area, ambulacra, interambulacra, anal area and marginal area; (not necessarily equal to upper side of theca); always composed of calcareous plates.

peripheral rim - quasi-regularized series of plates which form the margin of oral surface; includes several circlets of plates diminishing in size distally.

peripheral rim transition plates - plates in peripheral rim which separate plates externally elongate concentric with thecal margin from those externally elongate radially.

periproct - loosely united anal structure, composed of several circlets of plates; each circlet irregular; the structure was probably conical in life.

peristome - thecal elements surrounding mouth.

perradially - direction toward the perradial line.

perradial line - the junction between closed opposing members of coverplate pairs or series; extends approximately along the midline of each ambulacrum.

primary ambulacral radii - three radii: anterior, right lateral, and left lateral; they extend out from the center of the oral area and are marked by the anterior and transverse oral midlines. The two lateral radii bifurcate to form the two lateral pairs

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of ambulacra, I-II, IV-V, the anterior radius continues as ambulacrum III.

primary orals - large oral plates with intra-thecal extensions which participate in the formation of the underlying oral frame and have a fixed position in theca relative to ambulacra and other oral plates.

proximal - relative direction or position toward the oral pole, away from the aboral pole of the theca; defined by moving along the structure to which it is applied; opposite of distal.

right-lateral primary ambulacral radius - primary ambulacral radius which extends from the oral pole out to right ambulacral bifurcation plate along transverse midline of theca; this radius bifurcates at the right lateral bifurcation plate and forms two lateral ambulacral radii, i.e., ambulacra IV and V.

secondary orals - small to large oral plates without intra-thecal extensions, commonly with fixed position relative to primary orals; frequently only surficial elements.

shared coverplate - see lateral shared coverplate pair.

single biseries - one set of biserially arranged plates.

solar - clockwise or dextral direction of curvature of ambulacra.

stone-canal - tubular connection between the hydropore and the circumesophageal ring canal.

stone-canal passageway - opening through which stone-canal extended; leads from the hydropore to the interior of the theca; formed by the inner parts of the hydropore structure plates in combina-

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tion with additional elements, commonly the adjacent, ambulacral floorplates.

stroma canals - passageways in plates filled with stroma during life, secondarily filled with calcite, pyrite, etc. in fossil state.

sub-marginal ambulacral suture - zone of contact between the ambulacral coverplates and floorplates in the Edrioasterida.

sub-marginal suture line - intersection of the sub-marginal ambulacral suture with the thecal surface; extends along line of contact of the adradial ends of the coverplates and externally exposed parts of the floorplates in the Edrioasterida.

subvective system - organ system that gathers and transports food to the mouth; ambulacral system.

suture - the plane formed by the junction of connected plates.

suture line - surficial line on theca formed by the intersection of sutures with the thecal surface.

tessellate - plating arrangement in which sutures between contiguous elements are vertical or nearly so, adjacent plates abut one another and form a mosaic, like tiles in a floor.

test - the sum of all the mesodermal skeletal plates.

theca - enclosing body surface structures consisting of the body wall with mesodermal skeleton of discreet plates, and the non-plated body wall of the aboral surface.

thecal cavity - space surrounded by the theca, contained soft parts during life.

thecal diameter - length of a line extending through the theca in a

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plane perpendicular to the oral-aboral axis and through the ambitus.

transition plate - see peripheral rim transition plate.

transverse axis of theca - axis which extends through the oral-aboral axis perpendicular to the anterior-posterior thecal axis; location commonly expressed surficially by the position of the transverse oral midline.

transverse diameter - thecal diameter perpendicular to axial diameter.

transverse oral midline - perradial line which extends across the exterior of oral region between opposing anterior and posterior orals perpendicular to anterior primary ambulacral radius; it extends from the proximal tip of one lateral ambulacral bifurcation plate to the other.

upper side of theca - the part of the theca proximal to the ambitus - composed of plates of the oral surface, but does not necessarily contain all oral surface plates.

valvular anal structure - anal structure commonly formed by an inner and an outer circlet of large, sub-triangular plates; outer circlet elements alternate with and overlap the plates of the inner circlet along beveled, tight-fitting margins.

young adult stage - ontogenetic stage of transition from juvenile to full-sized mature adult, in which the proportional sizes of the structures are transitional from juvenile to adult forms.

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ORIENTATION

The orientation of the edrioasteroid theca is based upon thecal symmetry. Following Bather (1900a), specimens are placed in their "natural" or life position; the side of the theca containing the oral region is directed upward and the ambitus is horizontal. The interambulacrum with the anal structure is placed closest to the observer; the ambulacrum opposite the anal interambulacrum is directed away from the observer. The axial plane of bilateral symmetry is parallel to the line of observation and bisects the specimen into right and left halves, corresponding to right and left of the viewer. A plane passing through the theca at right angles to the axial plane, referred to as the transverse plane, bisects the theca into anterior and posterior halves.

The upper side of the theca lies above the ambitus, the lower side below. The upper and lower sides are not to be confused with the oral and aboral surfaces which are morphologic terms which define related groupings of thecal structures that are independent of the thecal shape. The oral surface includes the oral region, hydropore structure, ambulacra, interambulacra, anal structure, and the marginal area. The aboral surface is that part of the theca distal to the marginal area, apparently a non-plated membrane.

The oral surface of domal edrioasteroids is equal to the upper side of the theca; the distal edge of the marginal area marks the ambitus of the theca. Thus, the entire lower side of the theca is formed by the non-plated aboral surface. However, in clavate or

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"echinoidal" thecae, the oral surface extends past the ambitus onto the lower side of the theca and the lower side includes both the distal parts of the oral surface and the non-plated aboral surface.

The terms proximal and distal as applied to the edrioasteroids are used differently than in some other echinoderm groups. Proximal, as defined in standard dictionaries means toward or closest to the origin or point of attachment of a limb or organ, distal the opposite of proximal. Therefore, the term has frequently been applied to pelmatozoan echinoderms in relationship to the point of attachment of the stem. For example, the proximal parts of the ambulacra of a blastoid, as designated by Beaver (1967, p. S 347) in the Treatise on Invertebrate Paleontology, are those parts of these structures closest to the point of attachment of the stem, and thus furthest from the oral opening which lies at the summit of the calyx. In edrioasteroids, proximal is used to indicate direction toward the oral area along the course of any particular structure, distal away from the oral area. This usage was ingrained, if not originated, by Bather in his many works dealing with edrioasteroids and has been followed since by most authors. The distal parts of edrioasteroid ambulacra are those furthest from the oral region.

The directions defined by proximal and distal for a given ambulacrum are determined by following the course of the structure. The distal tip of a curved ambulacrum which extends back toward the oral area lies closer to the oral pole in straight-line distance than a more proximal part of that same ambulacrum.

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Extending the definition of proximal and distal to their most useful limits, the terms are applied to any feature of the edrioasteroid theca and always signify toward or away from the center of the oral area, along the course of the structure. For example, the distalmost point on the external thecal surface is the center of the aboral surface, i.e., the aboral pole.

MORPHOLOGY OF THE ISOROPHIDA

Text fig. 1, pl. 1-57.

Thecal shape

The Isorophida are small to moderate sized edrioasteroids, thecal diameters commonly ranging from 8 to 30 mm. A few larger species are known. The theca includes a plated oral and non-plated aboral surface, the latter presumably covered by a soft membrane.

The most common thecal shape is domal with the oral surface limited to the upper side of the theca. It is centrally convex or domed upward, the marginal peripheral rim flared outward distally parallel to the underlying substrate. Thus the distal edge of the marginal zone forms the ambitus of the theca. The oral surface appears to have been at least semi-flexible during life, capable of moderate expansion and contraction. The aboral surface forms the entire lower side of the theca, distal to the ambitus. This surface was probably covered by a soft membrane which apparently conformed to the shape of the underlying substrate.

Most "non-domal" Isorophida are clavate, with a gibbous upper area, a downwardly constricting pedunculate zone below the ambitus,

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Text Figure 1 Isorophida

A. Lebetodiscus dicksoni (Billings), 1857, G.S.C. 437, (X3), pl. 1, fig. 10.*

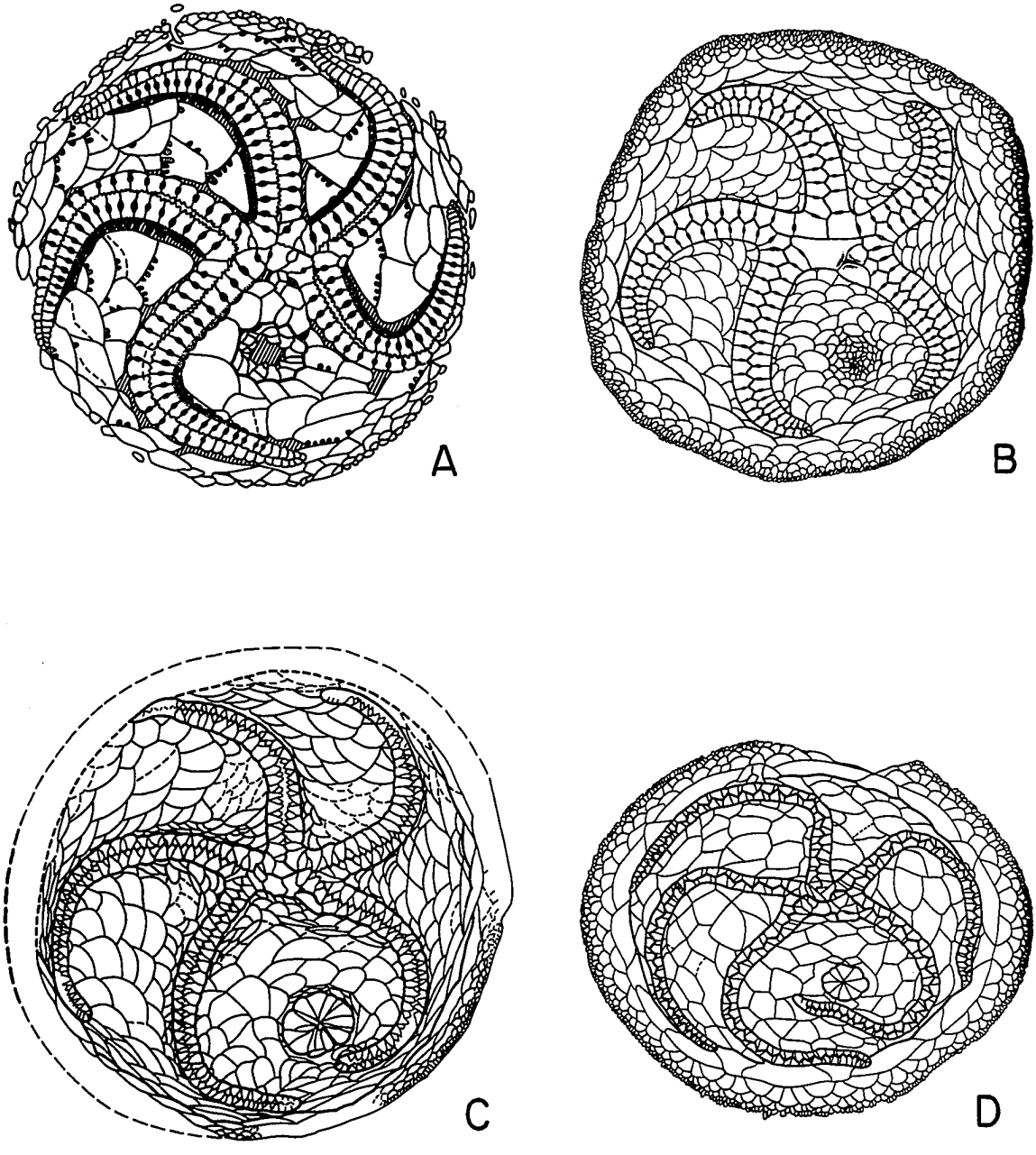
B. Carneyella pilea (Hall), 1866, U.C.M.P. 40465, (X4), pl. 17, fig. 7.

C. Isorophus cincinnatiensis (Roemer), 1851, U.C.M.P. 40470, (X3), pl. 28, fig. 8.

D. Agelacrinites hamiltonensis Vanuxem, 1842, N.Y.S.M. 362-A, (X2), pl. 40, fig. 1.

* Unless otherwise noted, all text figures are tracings of plate outlines from an enlargement of the photograph illustrated in the plate cited.

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Text Figure 1

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and a basal, marginal, peripheral rim that flares outward against the underlying substrate. Here the oral surface extends past the ambitus to form part of the lower side of the theca. The ambulacra are usually confined to the convex upper oral surface, above the ambitus. Occasionally they extend a short distance onto the lower part of the gibbous region. Clavate thecae may have been extensible in life, thus increasing and decreasing thecal height. The non-plated, aboral surface is confined to the basal section of the theca, and extends distally underneath the peripheral rim. It apparently conforms in shape to the underlying substrate.

Discoidal and cylindrical thecae occasionally occur. Individual specimens of many species may display apparently irregular or unusual, complex thecal forms. These are modifications of one of the basic thecal shapes, apparently correlated with an irregular or restricted resting surface. An extreme example of such modification is seen in a well-preserved Carneyella pilea resting upon a section of crinoid stem (pl. 17, fig. 1-4). Post-mortem thecal collapse commonly modifies original thecal shapes.

Oral area

The Isorophida oral region is composed of sets of external covering plates, or orals, which form a solid roof over the underlying oral frame structure. The oral area is elevated above the interambulacra with the highest part of this central oral rise at the oral pole.

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Oral covering plates

The external orals are classified as 1) primary orals with intrathecal extensions which participate in the formation of the oral frame; 2) secondary orals which are more surficial in nature and lack frame-forming extensions; and 3) lateral shared coverplate pairs which resemble normal ambulacral coverplates in shape, but lie proximal to the point of bifurcation of the two lateral primary radii. The two lateral ambulacral bifurcation plates are arbitrarily considered ambulacrals rather than orals for descriptive purposes. The ambulacra merge proximally with the oral region, thus no sharp boundary separates these structures and the identification of elements as orals versus ambulacrals is somewhat artificial. Most, if not all, oral elements were probably derived from ambulacral plates.

The number and arrangement of the external oral plates is variable and of taxonomic importance. Lebetodiscina have the simplest oral plate arrangement. All have three large primary oral plates, two anterior and one larger posterior element which form the center of the oral region. All three plates are in contact centrally. The suture line between the anterior two plates forms the anterior oral midline; that between the single posterior oral and the two anteriors forms the transverse oral midline. The posterior plate is the largest, often equal to the combined widths of the two anterior primary orals. Adradially the three primary orals are in contact with the adjacent interambulacral areas and form the adradial suture lines of the oral area.

In the Carneyellidae the oral plates include only the three

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primary orals plus a large, right posterior, hydropore oral. These orals are flanked distally by the proximal ambulacral coverplates and the two lateral ambulacral bifurcation plates. In the Lebetodiscidae, the three primary orals are flanked by pairs of lateral shared coverplates, one on each side of the central orals along the transverse oral midline. Additional secondary oral plates may also be present along both oral area midlines. Hydropore orals are absent in this Family. The lateral shared coverplates of the Lebetodiscidae oral region extend the transverse oral midline from the primary orals out to the bifurcation plates. The adradial ends of the shared coverplates are commonly in contact with the adjacent interambulacral areas, whereas the secondary oral plates are more commonly confined to the perradial part of the oral region, along the midlines.

The external oral plates of the Isorophina are commonly more numerous than those of the Lebetodiscina. Moreover, when externally differentiated, four large primary orals form the center of the oral region, in contrast with the three primaries of the Lebetodiscina.

In the Isorophidae, the oral area includes four central primary orals, two pairs of lateral shared coverplates, one large hydropore oral, and secondary orals. Externally the large primaries extend proximally from the interambulacra and meet centrally along the transverse and anterior oral midlines. One pair of lateral shared coverplates flanks each side of the central orals along the transverse oral midline. These are somewhat smaller than the primaries. Their distal perradial edges are commonly in contact with the proximal, perradial

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end of the two lateral bifurcation plates. Variable numbers of small secondary orals are inserted along the transverse and anterior oral midlines and lie between the four central orals and the proximal ambulacral coverplates. The large single hydropore oral abuts the right margin of the right posterior primary oral; it forms an asymmetric posterior bulge in the oral area outline. This bulge extends distally along the proximal part of the posterior side of ambulacrum V.

The oral plates of the Agelacrinitidae may be similar to those of the Isorophidae and include four large, central primary orals, several sets of secondary orals, and one or more right posterior hydropore orals. More commonly, the area is covered by numerous small orals, the primaries not being differentiated from other plates. These numerous orals commonly reflect the ambulacral coverplate pattern and thus appear to grade distally into the proximal ambulacral coverplate sequence without distinct break. Thus, it is difficult to determine the total number of orals for most of these species. Several to many specialized hydropore structure plates lie along the posterior margin and make up part of the oral area.

Oral frame and central lumen

The inner part of the oral region structure of the Isorophida is hidden under the roof of oral covering plates. It consists of a massive rim of plates which surrounds a central lumen. This rim constitutes the oral frame. It is a rigid structure composed of tightly sutured plates. The rim penetrates further into the thecal cavity than any other oral surface structure and supports the outer

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orals even after thecal collapse has occurred. This accounts for the pronounced elevation of the external oral area in most specimens.

The central lumen, bounded by the oral frame, directly underlies the center of the external oral region. It is oval in plan view, transversely elongate, and extends from the proximal ends of the ambulacral tunnels downward through the oral frame into the thecal cavity beneath. A conspicuous gap commonly occurs in the posterior side of the frame, and permits direct access from the central lumen into the thecal cavity area under interambulacrum 5. This gap may be modified by blade-like extensions that divide it into right and left halves, or into a small sub-chamber between the central lumen and the posterior part of the thecal cavity.

The transversely elongate oral frame is sub-ovate in plan view. Distally, the radial extremities are continuous with the ambulacral structures which imparts a pentagonal outline to the distal margin. The anterior part of the frame is nearly semi-circular in plan view, except for outwardly flaring lateral extremities. These form a wide zone of contact with the posterior section of the frame. The posterior unit is broadly arcuate, the flared lateral extremities being a continuation of the arc of the entire posterior side. Thus the frame is transversely elongate with the unequally curved anterior and posterior halves joining at attenuated lateral regions.

The oral frame comprises the expanded proximal floorplates of the five ambulacra, commonly combined with intra-thecal extensions from the primary oral plates. The anterior half of the frame is

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formed by the proximal floorplates of ambulacra II, III, and IV, and the intra-thecal extensions of the two anterior primary oral plates. The three floorplates are expanded proximally, both inward and laterally, each in contact with the adjacent floorplates along the innermost edges of the frame. The contact zone between the floorplate of ambulacrum III and the two adjacent lateral floorplates is small, because the intra-thecal extensions of the two anterior primary oral plates reach inward to form the interradial parts of the frame. These lie between the upper parts of the floorplates, and each wedge-shaped extension decreases in size inward to end above the base of the frame. The posterior sides of the floorplates of ambulacra II and IV flare outward to form a wide contact zone with the adjacent floorplates of ambulacra I and V.

The posterior side of the frame is composed of the proximal floorplates of ambulacra I and V, and the intra-thecal extensions of the posterior primary orals. Extensions from hydropore orals, or perhaps occasionally other plates associated with the hydropore structure may possibly be included also. The two floorplates are expanded inwardly and laterally. Their anterior edges flare outward laterally and form the wide contact zone with the expanded posterior sides of the two lateral anterior floorplates. The two posterior floorplates commonly do not make contact across the posterior interradius. Thus, this section is formed entirely by the intra-thecal extensions of the posterior primary oral (or orals), and occasionally also by hydropore plates. These intra-thecal extensions end far above the innermost edges of adjacent floorplates and thereby leave a large posterior

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interradial gap. The disposition of the intra-thecal extensions of the posterior primary oral and associated elements is variable and depends upon the family. Usually, the extensions are complex and consist of at least two inner blades on each side of the gap, one directed obliquely anterior, and one obliquely posterior. These blades delimit a shallow chamber between the central lumen and the posterior thecal cavity area. Additional blade-like extensions from the coverplates which extend down into the center of the posterior gap have been observed in some forms and these subdivide the gap into a right and left half. The intra-thecal extensions of hydropore plates and the associated plates of the stone-canal passageway may modify the right posterior region, depending upon the type of hydropore structure.

In some species of Agelacrinitidae the oral frame, although similar in shape to the above type, appears to be formed only by the five enlarged proximal floorplates, without intra-thecal extensions of the orals. This type of frame may also lack a posterior gap, the two posterior floorplates being in contact across the posterior interradius. This frame type has been observed only in agelacrinitid species in which the external oral area is formed exclusively by numerous small orals.

Hydropore structure

In the Isorophida an opening presumed to be a hydropore is located between the oral pole and the anus, commonly offset to the right of the axial thecal plane. It lies near the proximal posterior edge of ambulacrum V. It is a slit-like opening along the contact zone

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between two or more plates. Commonly the direction of elongation is either parallel to the proximal midline of ambulacrum V, or is nearly parallel to the transverse thecal axis.

Two basic types of hydropore structures occur in the Isorophida. Variations within these allow recognition of several sub-types. In one type, the structure is located within the right posterior asymmetrical bulge of the oral area and is formed by oral and ambulacral plates. The other type lies distal to the oral area, along the posterior side of ambulacrum V and is formed by ambulacral and interambulacral plates. The first of these is commoner. It is found in all Carneyellidae, Isorophidae and Agelacrinitidae. The shape and size of the structure is variable. It may be elevated above the level of adjacent oral and ambulacral plates to form a rounded, elongate, or circular protuberance, or it may be integrated into the central oral rise and thus show no separate relief. In intermediate, semi-integrated types the structure forms a small but distinct rise along the posterior part of the central oral rise.

Within this first type, considerable variation occurs in size, location and type of plates involved. The simplest condition is found in the Carneyellidae and the Isorophidae where the structure is integrated into the central oral rise; the hydropore structure is of approximately the same elevation as the proximal part of ambulacrum V. The structure is composed of the hydropore oral, commonly the adjacent edge of the right posterior primary oral, and two or three opposing proximal plates of the oral-ambulacral series.

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In the Carneyellidae the posterior edge of the opening is bounded by the anterior edge of the hydropore oral. The anterior side is commonly formed by the two proximal, posterior coverplates of ambulacrum V. However, the opening may extend proximally between the hydropore oral and the adjacent edge of the right posterior primary oral. In this case, the left anterior edge of the opening is bounded by the primary oral. In some forms in the family the opening may extend further distally along the anterior edge of the hydropore oral and the third posterior coverplate of ambulacrum V thereby forms the distal part of the anterior side of the opening.

The hydropore structure in the Isorophidae is quite similar to that of the Carneyellidae, but the plates of the anterior side differ due to the increased number of plates in the Isorophidae oral region. The anterior edge of the hydropore oral forms the entire posterior margin of the opening. The anterior side is bounded by the adradial ends of the right posterior lateral shared coverplate and the proximal posterior primary coverplate of ambulacrum V. In Isorophidae with larger openings, the right side of the right posterior primary oral forms the proximal part of the anterior edge of the opening. When the opening is distally extended the adradial margin of the second posterior primary coverplate of ambulacrum V forms its distal anterior side.

In both families the slit-like opening is commonly parallel to the proximal part of the midline of ambulacrum V. However, the large hydropore oral may extend into the adjacent proximal posterior edge of

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ambulacrum V. When this penetration is pronounced, the hydropore is elongate nearly parallel to the transverse thecal axis. The adradial ends of the plates of the oral-ambulacral series which bound the hydropore are often enlarged, their width being greater than that of adjacent orals and ambulacrals. This allows identification of these plates even in specimens in which the structure is disrupted. Moreover, the bounding edges of all plates of the hydropore structure may be thickened to form a small raised rim which surrounds the opening.

In the Carneyellidae and Isorophidae, the plates surrounding those in contact with the hydropore are frequently modified in shape and size. These are considered "peripheral" hydropore structure plates even though they are not in direct contact with the opening. The most common "peripheral" is the ambulacral coverplate adjacent to the distal end of the hydropore oral. It is commonly shortened (adradial-perradially), due to the intrusion of the hydropore oral into the edge of ambulacrum V.

The length of the opening, the number of ambulacral coverplates in contact with it, the number of "peripheral" plates and the size, shape, and orientation of the large hydropore oral are constant at either the generic or specific level within the Carneyellidae and Isorophidae.

The Agelacrinitidae have the same basic type of hydropore structure as the Carneyellidae and Isorophidae. It lies along the posterior margin of the oral area and comprises ambulacral and oral elements. However, the structure may include either several plates forming a

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small protuberance which is semi-integrated with the central oral rise, or it may contain numerous plates which form a large, elongate protuberance posterior to the oral rise. The anterior side of the protuberance is formed by plates of the oral-ambulacral series whose anterior ends may perradially reach the transverse oral midline or may lie distal to other posterior orals which form the transverse midline. The posterior margin of the structure is formed by few to many plates. These may be considered either multiple hydropore orals or modified interambulacrals that have been incorporated into the oral series. The elongate opening extends along the summit of the protuberance and lies along the contact line between the anterior and posterior plates of the structure.

The second basic type of hydropore structure found in the Isorophida is limited to the Lebetodiscidae. It lies distal to the oral area along the proximal posterior part of ambulacrum V and extends into the adjacent proximal region of interambulacrum 5. It incorporates only ambulacral coverplates and modified interambulacrals. The ambulacral components are usually the first and second proximal coverplates of the posterior side of ambulacrum V. Occasionally the third coverplate is included. The adradial edge of the proximal ambulacral coverplate is enlarged and produced outward into interambulacrum 5. The posterior adradial margin of this plate bounds the anterior edge of the hydropore. The posterior side of the opening is bounded by one or more interambulacral plates. These differ in size and shape from the adjacent, "typical", squamose interambulacral plates. At least one of

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these modified interambulacrals is large. The structure rises above the level of the adjacent interambulacral plates to form a distinct bulge along the proximal posterior side of ambulacrum V. The orientation of the slit-like opening in this type of hydropore structure is variable and ranges from nearly parallel to the midline of ambulacrum V to being parallel to the transverse axis of the theca.

"Peripheral" hydropore structure plates in the Lebetodiscidae may be ambulacral coverplates which are shortened to accomodate the intrusion of hydropore interambulacrals into the edge of the ambulacrum, or occasionally, additional modified interambulacrals. The number, arrangement, shape and size of these supplementary plates are constant at the generic or specific level.

Stone-canal passageway

The stone-canal passageway leads inward from the slit-like hydropore, into the thecal cavity. The inner end lies distal to the inner rim of the oral frame, near or adjacent to the proximal posterior side of ambulacrum V. The passageway is conical and expands inward rapidly. It ranges from sub-circular to sub-triangular in cross-section. The inner end is many times the size of the hydropore. In some forms the axis of the passageway is essentially perpendicular to the thecal surface; in others the axis is oblique, the hydropore being distal to the center of the large inner opening of the passageway.

The stone-canal passageway is formed by the intra-thecal parts of the plates of the hydropore structure, one or two underlying ambulacral floorplates, and occasionally, additional elements. The upper

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end of the passageway, immediately beneath the hydropore, is formed by the inner sections of all the plates which bound the hydropore. In those species with few hydropore structure plates, the cross-section of at least the upper part of the passageway is angular. Where many plates are involved, the passageway is nearly terete. The inner part of the passageway is formed by the posterior adradial sides of the proximal one or two floorplates of ambulacrum V, and intra-thecal extensions from one or more posterior hydropore structure plates.

The structure of the stone-canal passageway is adequately known in only a few species, due to its internal location. The details of its construction appear to be quite variable. Moreover, since the passageway is formed only in part by the hydropore structure plates, it may vary independently from the hydropore structure. Thus some species with nearly identical hydropore structures appear to have characteristically different stone-canal passageways. The stone-canal passageway structure may eventually furnish the basis for further refinement of edrioasteroid classification.

Ambulacra

The five ambulacra are commonly slightly elevated externally and form low rounded ridges above the interambulacra. Occasionally they rise more abruptly as prominent, steep-sided ridges. Proximally, the ambulacra reflect the triradiate character of the oral area, being disposed as a single anterior ambulacrum, which extends out from the anterior oral midline, and two lateral pairs, one extending from each end of the transverse oral midline. The junction of the perradial

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lines of each two lateral ambulacra with one end of the transverse oral midline occurs at the perradial tip of an unpaired lateral bifurcation plate. The two lateral bifurcation plates are usually larger than adjacent proximal ambulacral coverplates. The ambulacra may be straight, or they may curve. Direction of curvature is variable and includes all solar, all contrasolar, or various combinations of the two directions. Ambulacral disposition is a generic taxobasis. Additional variations in the shape of the ambulacra include rate of curvature, width, amount of distal taper, height of maximum elevation, and proportional length. The level of taxonomic significance of these features is variable within the Order.

Occasionally the number of ambulacra varies. One or more of the five primary ambulacra may bifurcate. These may be equally developed, or one may be a small side-shoot off the main ambulacral course. One specimen of Cystaster stellatus has four such ambulacral bifurcations; the resultant nine ambulacra are the most that have been observed. Occasionally one of the five primary ambulacra may not develop. Neither addition nor subtraction of ambulacra appear to be of taxonomic importance. They would seem to be ontogenetic "accidents". The holotype and unique specimen of Thresherodiscus ramosus Foerste (1914, Kesling, 1960) is reported to have only three primary ambulacra, one anterior and two lateral, but these split repeatedly to form nineteen distinct branches. If this species is an Isorophida, it is unique.

The ambulacra of the Isorophida are formed by a uniseries of floorplates overlain by sets of coverplates. The ambulacral tunnel is enclosed between these two sets of plates.

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Coverplates

The coverplates are disposed as alternating biseries or cyclic sets of plates along each ambulacrum. Opposing coverplates, when closed, meet centrally along the perradial line. Coverplate pattern is important taxonomically. Lebetodiscina have a single, alternating biseries of coverplates which form a zigzag perradial line. Coverplate shape, size and angle of inclination are generic or specific taxobases. The Isorophidae have alternating, multiple biseries in which individual pairs of two or more coverplate sets alternate along the ambulacrum. Double biseries, formed by two sets of plates, are the most common. The Agelacrinitidae coverplate sequence is commonly cyclic, with two to seven serially repeated sets of plates forming the cycles. Opposing cycles alternate, offset by half a cycle length, and form a prominent undulating perradial line. Other Agelacrinitidae may have complex, alternating biserial sets of coverplates or a combination of both cyclic and biserial sets. The number of sets of coverplates, the order of occurrence, and individual plate shapes are generic and specific level taxobases.

Blade-like intra-ambulacral extensions commonly extend from the inner, ambulacral tunnel, surfaces of the coverplates. They are largest under the perradial tips of the coverplates, and decrease adradially to merge with the inner sides of the coverplates before reaching the floor of the ambulacral tunnel.

In the Lebetodiscina and the Isorophidae, the inner extremities of these blades flex proximally so as to underlap the proximally ad-

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jacent coverplate. They also extend perradially under the tips of opposing plates. Thus, the intra-ambulacral extensions firmly interlock adjacent and opposing coverplates when closed. This interlocking necessitated sequential (or peristaltic) operation of the coverplates, individual plates movable only in conjunction with surrounding coverplates. Each entire half of a coverplate series was probably imbedded in continuous flesh. This would have appeared in life, like a long ribbon which extended the length of the ambulacrum. During opening, the two opposing ribbons progressively separated along the perradial line with movement initiated at the distal tip of the ambulacrum. The perradial edge of the opposing ribbons rotated slowly upward and outward, and two opposing, broad undulations swept proximally in a wave-like motion. Coverplate closure reversed the process. Coverplate intra-ambulacral extensions are thought to occur in most Agelacrinitida. However, these may not interlock adjacent or opposing elements. This being so, the coverplate movement in agelacrinitids may have differed from other Isorophida. The intra-ambulacral extensions of the coverplates in the Lebetodiscina participate in the formation of the upper parts of coverplate passageways and thus are enlarged.

Adradially, intra-thecal extensions of the coverplates commonly pass between the lateral edges of the floorplates and adjacent interambulacrals into the thecal cavity. In the Lebetodiscina, those extensions form the inner ends of the coverplate passageways. The intra-thecal extensions interlock the coverplates into the theca and may be an important part of the articulating apparatus for movement of the

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coverplates. In the Isorophidae, only coverplates of the primary set appear to develop large intra-thecal extensions which interlock the coverplates into the theca and probably also participate in the articulatory apparatus. Most, and perhaps all Agelacrinitidae lack intra-thecal extensions and the coverplates end above the lateral margins of the floorplates. Thus, the coverplates adradially abut the upper edges of the adjacent interambulacrals.

The coverplate intra-thecal extensions may have been attachment sites for muscles, used to open the coverplates. Alternatively, the upper surfaces of the extensions may merely have abutted the inner sides of the overlying interambulacrals, plate movement being due to pressure exerted on the ambulacral tunnel surfaces of the coverplates. This would have forced the perradial ends of the plates upward while the adradial ends were held in place by the extensions.

The coverplates of the Isorophida were sutured to the underlying floorplates along their zone of articulation, the adradial suture. In contrast with the common echinoderm plan, the coverplates were also sutured to one another laterally. This strengthened the coverplate series in forms with intra-ambulacral extensions that interlocked adjacent coverplates (Lebetodiscina, some Isorophidae). In those without extensions (some Isorophidae, Agelacrinitidae) the suturing alone held adjacent coverplates together. The smaller medial coverplates such as plates of the tertiary set in multiple biseries and the plates of the fourth, fifth, etc. sets in cyclic series end before they reach the adradial articulation zone. These coverplates were suspended over

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the ambulacral tunnel, held by their tight suturing to the laterally adjacent, larger coverplates which were in contact adradially with the underlying floorplates. The lateral suturing has resulted in the common preservation of the coverplate series intact, even in thecae which have collapsed during preservation. In the Isorophina, where more than one set of coverplates comprise the series, coverplates of the secondary, tertiary, etc. sets are intercalated between existing primary coverplates. These intercalates are generated by the flesh which laterally connects the primary coverplates.

Coverplate passageways

In the Lebetodiscina there is a system of ambulacral passageways along the lateral sutural faces of the serially adjacent coverplates. These extend from the exterior of the theca into the thecal cavity, one row along each side of the ambulacrum. Passageways also extend between the larger oral covering plates. Each tubular passageway is circular in cross-section and is shared subequally by two contiguous coverplates. They are formed by opposed hemicylindrical grooves in the lateral faces of the coverplates. The axis of the passageway thus parallels the exterior surface of the coverplates.

In species with thick ambulacral coverplates, oriented almost vertical to thecal surface, the axes of the passageways are also vertical (e.g., Lebetodiscus). In those with thinner coverplates, oriented almost parallel to the thecal surface, the passageway axes are almost horizontal (e.g., Cryptogoleus).

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The external foramen of each passageway opens along the external lateral suture line between the adjacent plates. The plane of the opening is nearly parallel to the outer surface of the coverplates and thus, oblique to the axis of the passageway. External openings are therefore elliptical. They are elongate normal to the ambulacral axis, and flanked by the upper, lateral edges of the two serially adjacent coverplates. The upper end of each passageway, which is visible through the external foramen, is formed entirely by the outer surface of the curved, blade-like, intra-ambulacral extension of the distal plate.

The width and shape of the external foramen are variable. In some species with large, thick coverplates which are oriented almost normal to the thecal surface, the foramina are wide, almost circular (e.g., Lebetodiscus). In other species with similar coverplates, the foramina may be very elongate. In forms with thin coverplates which externally almost parallel the thecal surface, the foramina are narrow and slit-like (e.g., Cryptogoleus).

The inner foramina of the passageways are bounded by the edges of the intra-thecal extensions of adjacent coverplates. The inner sides of these extensions are nearly parallel to the interior thecal surface, and thus are oblique to the axis of the passageways. The inner foramina are thus also elliptical and elongate normal to the ambulacral axis. These openings are shared sub-equally by serially adjacent plates.

At least two genera, Lebetodiscus and Foerstediscus, have

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accessory structures, called "lateral depression series", associated with the external foramina of the passageways. These are rows of external basin-like depressions, one along each lateral margin of the coverplate, close to the contact line between contiguous coverplates. The coverplates in genera so endowed are axially convex outward. The small basins are incised into the flanks of the axial convexity. Thus, the basins are deepest toward the axis of the coverplate. The sutural sides of the basins are confluent with the deep lateral groove formed along the suture line between the adjacent convex coverplates. There are commonly eight or nine depressions to a row. Perradially the depressions flank the external foramen of the coverplate passageway. In the opposite direction they extend almost to the adradial suture line. Depressions on contiguous coverplates do not necessarily correspond in number or position. Those on one side of the suture may lie opposite to, or alternate with, the opposing row; occasionally both conditions are found along a single suture line.

In the Lebetodiscina the coverplate passageway system appears to have housed tubular branches from the internal radial canals. These branches probably extended beyond the outer foramina and probably functioned as respiratory structures. The lateral depression series would suggest that at least in some species the external parts of the lateral branches were further branched and sent extensions into each of the depressions.

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Floorplates

The ambulacral floorplates of all Isorophida are a tightly sutured uniseries which forms a solid ambulacral floor, without passageways into the thecal cavity. Floorplates are commonly trough-shaped with concave upper sides which form the broad axial ambulacral groove. Adradially the upper margins of the floorplates are nearly planate and form articulation sites for the overlying coverplates. The inner surfaces of the floorplates vary from evenly convex inward to more angular forms with large lateral nodes. Contiguous floorplates may imbricate, their proximal margins overlapping adjacent plates along oblique sutures (e.g., Lebetodiscina and some Agelacrinitidae). In the Isorophidae and most Agelacrinitidae the floorplates are commonly quite thick and abut along vertical sutures. In the Isorophida all floorplates are completely hidden from external view by the overlying coverplates, except in disrupted or weathered specimens.

Interambulacra

The interambulacra of the Isorophida are polyplated; plates are variable in number and are distributed without apparent order. The largest elements are central and distal. Smallest plates lie along the adradial suture lines, adjacent to the ambulacra. Commonly small interambulacrals also surround the anal structure in interambulacrum 5.

Interambulacrals are commonly squamose and imbricate and form highly flexible thecal areas. The direction of imbrication is basically proximal, but near the ambulacra, the plates overlap adradially irrespective of the direction the ambulacra assume. The adanal inter-

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ambulacrals radially imbricate toward the anus.

In some Isorophida the interambulacrals are thick, polygonal and abut along vertical sutures. Such tessellate areas appear to have been little if at all flexible. Both squamose-imbricate and polygonal-tessellate interambulacrals may occur within the same genus, but are of specific significance.

Commonly, domal thecae have squamose, imbricate interambulacrals. In clavate forms the interambulacrals are polygonal and tessellate on the upper surface, but below the ambitus, where they are continuous with the pedunculate zone plates, they are in some forms squamose, proximally imbricate and irregularly arranged whereas in others they are very thin, elongate, imbricate plates which are arranged in numerous vertical columns. The transition from polygonal interambulacrals to squamose or rectangular peduncular zone plates may be abrupt or gradual. When gradational the distal interambulacrals become progressively thinner and more elongate.

The pedunculate zone of clavate forms appears to have been extensible, the imbricate plates able to telescope together. When fully contracted the theca would be more stable in turbulent water. When extended, the upper oral surface would be elevated far above the substrate, probably for feeding. Minor extensions and contractions may be related to the pumping mode of respiration believed to have been employed by these.

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Anal structure

The Isorophida anal area lies in the posterior interambulacrum, commonly near its center. Two basic anal organizations occur. In the Lebetodiscina, the anal structure is a periproct, formed by numerous plates grouped into several irregular circlets. Plate size commonly decreases toward the center and at least the more central plates are elongated toward the central anal opening. The structure may be elevated into a sub-conical mound. The periproct was merely a flexible zone around the anus.

In the Isorophina there is a radial, valvular anal structure. Commonly, it is formed by two imbricating circlets of triangular or sub-triangular plates. The plates of the outer circlet alternate with and overlap those of the inner one. Both sets are beveled along this zone of imbrication and fit snugly together. The zone of overlap is commonly wide so that all but a narrow axial strip of each inner element is hidden from external view when the structure is closed. The distal ends of the anals abut the surrounding interambulacrals; their contact zone is commonly modified by ridges, grooves or flanges on both sets of plates. Occasionally three circlets of plates appear to be included in the valvular structure, whereas a few forms appear to have only one circlet of anals.

When closed, the valvular anal structure appears to have been nearly level with the surrounding interambulacral surface or perhaps elevated into a very low, rounded mound in some. To open, the anals rotated against the surrounding interambulacrals, centrally lifting up

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and out, thus opening the central anus. The large, lateral overlap of adjacent anals would permit the structure to open widely without loss of contact of adjacent plates.

The valvular anal structure is believed to have been part of an anal pumping system involved in respiration. It is found only in the Isorophina, which lack the apparently respiratory coverplate passageways found in the Lebetodiscina.

Peripheral rim

A peripheral rim forms the margin of the oral surface in the Isorophida. It is formed by several circlets of proximally overlapping and distally diminishing plates. There are one to three proximal circlets of larger plates which are externally elongate concentric with the thecal margin. Distal circlets of varying number are formed by radially elongate elements.

The large plates of the proximal rim circlet commonly alternate proximally and distally, forming two sub-circlets. The lateral edges of plates in the distal sub-circlet overlap the lateral edges of the two adjacent proximal sub-circlet members. Thus, although plates of both sub-circlets are subequal in size, the externally exposed part of the distal ones is much larger than that of adjacent, proximal sub-circlet plates. Commonly the distal sub-circlet elements are externally squamose, the proximal plates sub-trapezoidal.

The plates of the second rim circlet are much smaller than the proximals and commonly are from five to seven times as numerous. Proximally, they overlap the distal edges of the proximal circlet.

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Second circlet plates that overlap lateral sutures between proximal elements lie in part proximal to those that overlap the centers of proximal circlet plates. This produces a scalloped line of distally convex arcs at the contact of the two circlets. In forms with proximal-distal sub-circlets, five to seven second circlet plates overlap each distal plate, whereas only three or four overlap the externally narrower plates of the proximal sub-circlet. Thus the scallops of the line adjacent to distal sub-circlet plates are much wider than, and alternate with, those adjacent to proximal sub-circlet plates. This produces a series of larger convex arcs regularly alternating with much smaller ones. The line between the second and third circlets may also be scalloped, but due to the common irregularities of the third circlet the arcs are less distinct. Outer circlets of the rim are formed by numerous small plates, in which circlet organization is less apparent.

In the center of the rim the circlets are transitional between the concentrically elongate proximal plates and the distal, radially elongate plates. In some, these are merely irregular squamose plates. In others, they are ovoid and elongate radially, but the externally exposed parts are sagittate. In such plates the exposed zone is made up of a proximally convex, semi-circular "head" which forms the anterior third of the plate. An elongate crest or shaft extends distally from the center of the straight, distal edge of the "head". The lateral margins of the distal two-thirds of the plate, which flank the shaft, are depressed and overlain by small radially elongate plates of the next distal circlet. The anterior "heads" appear to form a circlet of

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small plates elongate concentric with the thecal margin. The distal shaft also appears to be a discrete plate and to form alternate, radially elongate plates in the adjacent distal circlet. The straight distal edges of the anterior "heads" are aligned so as to form a distinct circle around the rim.

The larger plates of the peripheral rim in all Isorophina and Carneyellidae are geniculate. The upper, externally exposed parts extend down to the underlying substrate where they flex distally outward so as to form a broad basal zone parallel to the substrate. This extends distally out under the adjacent, more distal rim plates. These geniculate bases support the rim plates during thecal collapse, the upper ends of the plates remaining nearly in life position. In collapsed specimens the adjacent distal interambulacrals are depressed, and leave the upper ends of the proximal rim plates elevated far above the interambulacrals. This pronounced elevation of the rim in collapsed specimens leads many earlier workers to suggest that it was a fused structure.

Small vertical ridges of varying development may be formed on the lower sides of the bases of the rim plates. The ridges are elongate normal to the thecal margin and commonly are sharp crests which are in contact with the underlying substrate. Seven to ten ridges per plate have been observed on the large plates of the proximal circlet of the rim. These ridges appear to have been related to thecal attachment.

The rim plates of the Lebetodiscidae, and perhaps of a few other Isorophida, are squamose rather than geniculate. Thus, thecal col-

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lapse affects equally both distal interambulacral and proximal rim plates, so that the division between the two regions has no marked relief and is often difficult to locate. This difference in rim plate structure may signify a different mode of attachment for the Lebetodiscidae.

MORPHOLOGY OF THE EDRIOASTERIDA

Text fig. 2, pl. 58-63.

Thecal shape

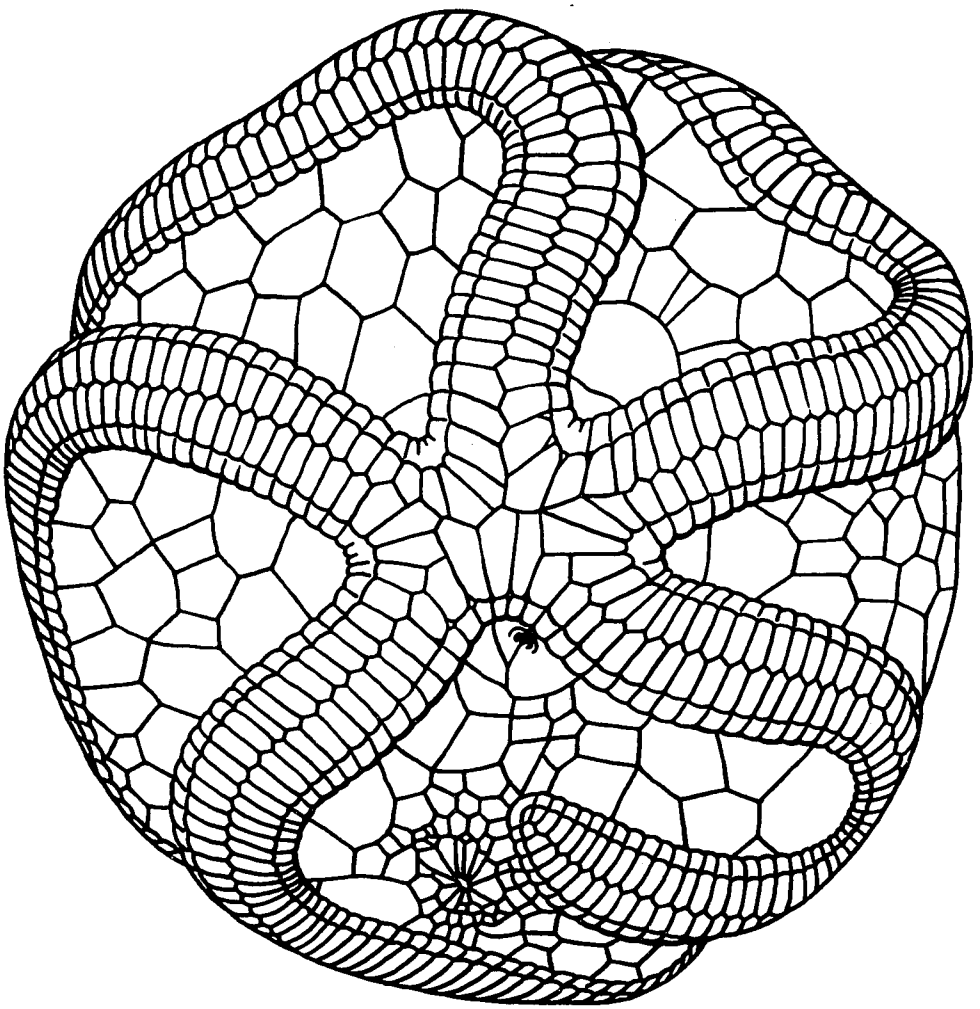
The Edrioasterida have semi-globoid thecae which resemble the test of some regular echinoids and thus are informally called "echinoidal". The upper oral surface is convex upward. Commonly the center of this area is nearly planate, the rate of curvature increasing distally. The distal margin of the upper oral surface is vertical and forms the ambitus of the theca. Below the ambitus the theca constricts gradually. This sub-ambital zone commonly forms about one-third of the total thecal height. Distal to this zone the theca constricts rapidly, the exterior parallel to the substrate, forming the resting zone. Beyond this area, the thecal plates flex upward and inward toward the center of the theca to form the incurved zone. A flexible membrane apparently extended from the distal edge of the incurved zone back down to the substrate. Numerous minute plates were imbedded in this membrane, each squamose and elongate concentric with the thecal periphery. The distal margin of this membrane was apparently attached to the substrate and surrounds a small circular (?) area comparable to the non-plated aboral surface of the Isorophida. The Edrioasterida are

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Text Figure 2 Edrioasterida

Edrioaster bigsbyi (Billings) 1857. Restoration by Kesling (1960, text fig. 1), modified from Bather (1900a, 1914).

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Text Figure 2

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commonly large edrioasteroids, adult thecal diameters ranging from 30 to over 50 mm, although a few smaller species occur.

The oral area lies in the center of the upper oral surface. The five radiating ambulacra extend past the ambitus into the sub-ambital thecal zone, but end or curve before reaching the resting zone. The hydropore structure which is associated with the posterior edge of the oral area, and the anal structure are both on the upper oral surfaces. "Echinoidal" thecae appear to have been little, if at all, flexible in life.

Oral area

The oral area includes external oral coverplates which form a solid roof over the proximal edge of the underlying oral frame and over the central lumen. Both oral covering plates and parts of the interradial frame elements are visible externally. The oral area is slightly elevated above the interambulacral areas to form a low central oral rise.

Oral covering plates

The center of the oral area is formed by seven or more oral covering plates which abut perradially along the anterior and the transverse oral midline. The proximal end of the anterior oral midline intersects the transverse midline at the central oral pole. The orals are distally continuous with the ambulacral coverplate series and there is no distinct boundary between plates of the two sets. Thus the total number of orals is not apparent in most species. Three or four

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central orals may be somewhat larger than the others. However, oral plate divisions comparable to the primaries, secondaries or lateral shared coverplates found in most Isorophida are not found in the Edrioasterida. Adradially the orals meet the exposed parts of the interradial oral frame plates along a sub-marginal suture line which is continuous with the adjacent proximal ends of the ambulacral sub-marginal suture lines.

Oral frame and central lumen

A massive oral frame, surrounding a central lumen, forms the inner part of the oral region. It lies in part under the roof of oral covering plates. The frame is formed by five large radial and five large interradial plates. All are compound. The proximal edge of the frame is sub-ovate and transversely elongate. It extends down into the thecal cavity further than any other structure. The distal margin of the frame is sub-pentagonal, the radial extremities continuous with the five ambulacra.

The central lumen lies directly under the central oral covering plates. It is transversely elongate and ovoid to sub-pentagonal in cross-section. The lumen extends from the proximal ends of the ambulacral tunnels downward through the frame and opens directly into the center of the thecal cavity below.

Each radial element of the frame is formed by the fusion of several proximal pairs of the biserial floorplates from one ambulacrum. Passageways which penetrate the frame plates mark the position of the

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fused sutures and allow determination of the number of floorplate pairs included in each compound plate. The proximal edges of the compound radials are enlarged and extend inward and laterally to form at least the five radial segments of the inner rim of the frame. In some forms these elements may extend laterally so as to meet under the interradial elements, and thereby form all of the inner edge of the frame rim. The distal ends of the radials extend out under the proximal three or four pairs of floorplates of each ambulacrum. The paired elements of two or three adoral pairs of ambulacral floorplates are separated from one another along the perradial suture. Consequently, part of the upper face of the distal part of each radial is exposed between these separated proximal floorplates.

The five compound interradial plates of the oral frame are wedged between the radials. Each is formed by two or more individual proximal floorplates from adjacent ambulacra, and the proximal interambulacral plates of the adjacent interambulacrum. Opposing pair members of two or more proximal floorplate pairs of each ambulacrum apparently have separated perradially and migrated away from each other to become incorporated into different interradial frame plates. The adjacent floorplates from each ambulacrum fuse together and also fused laterally to the proximal floorplates from the ambulacrum on the other side of that interradius, thereby forming the proximal edge of each interradial. Passageways penetrating the proximal edge of the interradial elements mark the fused sutures between the constituent ambulacral floorplates. Adradially, the ankylosed floorplates are fused to the proximal plate of the adjacent interambulacrum, and thereby incorporate this plate

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also into the oral structure. Although the interradials include fewer floorplates than the radials, the addition of the proximal interambulacral plates makes them considerably larger than the radials. The proximal margin of the interradial plates of the frame are enlarged and extend downward into the thecal cavity between the radials. In some instances the inner ends of interradials apparently extend as far inward as the radials and thus form an inner rim of alternating elements. In others, they may end before reaching the frame rim, being underlapped by the lateral edges of the radials.

The adradial ends of the oral covering plates rest on the upper surface of the fused floorplate parts of the interradial frame plates. The interradial frame plates are in part exposed externally. This exposed zone proximally includes the upper adradial ends of the fused floorplates and distally the entire upper side of the fused interambulacral constituents of the interradials. The upper ends of the fused floorplate parts of each interradial laterally abut the proximal, lateral, edge of the first normal floorplate of each adjacent ambulacrum.

Hydropore structure

The Edrioasterida opening presumed to be the hydropore is located between the oral pole and the anus, offset to the right of the axial thecal plane. It lies in the right posterior part of the oral area, adjacent to the proximal, posterior edge of ambulacrum V. The opening is a small, elliptical slit which extends across the suture between two plates. The long axis of the opening is commonly almost

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parallel to the proximal part of the midline of ambulacrum V.

The anterior end of the opening is housed in the right posterior edge of the interambulacral part of the posterior interradial plate of the oral frame. The posterior half of the slit lies in the posterior hydropore plate which is a modified proximal interambulacral that has been incorporated into the oral-ambulacral series. The left anterior edge of this plate abuts the right posterior edge of the posterior frame interradial. The right side of the posterior plate abuts, or is fused to, the adradial end of one or more proximal, posterior floorplates of ambulacrum V. Its posterior margin abuts the proximal interambulacrals. The posterior hydropore plate seems to be an element of the oral-ambulacral series because it either intrudes into the posterior side of ambulacrum V, or is fused to a proximal floorplate. Both hydropore plates have a thickened raised rim around the pore opening.

Stone-canal passageway

The stone-canal passageway leads downward from the hydropore to the thecal cavity. It penetrates both plates bounding the hydropore. Apparently the passageway is oval in cross-section and expands in diameter inward. The inner end of the passageway is apparently formed by the inner parts of the two hydropore plates. The inner opening lies adjacent to the distal edge of the right posterior margin of the oral frame rim.

Ambulacra

The five ambulacra are broad and extend past the ambitus into the

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sub-ambital zone. They are elevated above the adjacent interambulacra and form low, wide, rounded ridges on the thecal surface. Proximally, they merge with the central oral rise. The ambulacra originate as a single anterior ambulacrum, which extends from the anterior oral midline, and two lateral pairs, one pair arising from each end of the transverse oral midline. The two perradial lines of each lateral pair of ambulacra meet the transverse oral midline at the perradial tip of the lateral bifurcation plate. However, in contrast to the Isorophida, this plate is not larger than the adjacent coverplates in the Edrioasterida. It is distinguished only by its position.

The ambulacra are variously curved in all known species of the Edrioasterida; they may be all solar, all contrasolar, or I-IV contrasolar and V solar. Curvature is commonly pronounced only in the subambital zone where the ambulacra become concentric with the thecal ambitus. The ambulacra may distally curve back toward the oral area, and even extend the tips up onto the upper oral surface. Ambulacral disposition appears to be constant within each edrioasterid genus.

Edrioasterida ambulacra are formed by the two alternating biseries of coverplates and floorplates. The coverplates roof the axial ambulacral trough which is formed by the centrally depressed floorplates. The ambulacral tunnel, enclosed between the two sets of plates, is commonly large and transversely elongate in cross-section. The coverplate biseries exactly matches the floorplate with each coverplate centered over a floorplate. However, the floorplates are longer and extend adradially beyond the coverplates.

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Coverplates

The ambulacral coverplates form a single, alternating biseries of plates which meet perradially along a zigzag or sinuous line. The adradial ends of the coverplates are straight or slightly curved outward adradially. The lateral (proximal, distal) edges of each plate are straight, parallel, and normal to the ambulacral midline. Perradially the coverplates may be pointed or sinuous.

The adradial ends of the coverplates meet the externally exposed parts of the floorplates along sub-marginal suture lines. These lines extend along each side of the ambulacra, perradial to and concentric with the adradial suture lines. Adradially, the coverplates rest on the upper surfaces of the floorplates. The inner or lower adradial edges of the coverplates are beveled and fit tightly against the floorplates when closed. Except for the beveled zone, each coverplate is uniform in thickness. Neither intra-thecal nor intra-ambulacral extensions are present. Thus, in the Edrioasterida individual coverplates are not interlocked with adjacent elements as in the Isorophida. Opening and closing of the coverplates could have been random, individual plates moving independently of adjacent elements. Moreover, plate movement could have been initiated in any sector of an ambulacrum and progressed in either direction, or, all coverplates could have been moved at once. The tissue investiture of the coverplates may, of course, have imposed restrictions on the movement patterns.

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Floorplates

The ambulacral floorplates are an alternating biseries. The perradially opposing alternate floorplates slope steeply downward to form a deep, central ambulacral trough. Along the floor of the trough, the angular perradial tips of the floorplates form a medial suture line of right-angled zigs and zags.

The thick adradial ends of the floorplates abut adjacent interambulacrals along vertical or slightly oblique sutures, the latter sloping inward toward the ambulacral axis. Adjacent floorplates may vary in length and thus the adradial suture lines between the interambulacrals and the floorplates may be somewhat irregular, particularly along the proximal parts of the ambulacra. The upper surfaces of the floorplates are externally exposed between the adradial and the submarginal suture lines. These areas slope upward toward the ambulacrum and form its elevated lateral margin.

Perradial to the sub-marginal suture line, the upper surface of each floorplate forms the rather narrow articulation zone for the coverplates. This flat zone flanks the upper edge of the deep ambulacral trough and is slightly inclined toward the adjacent trough.

Floorplate passageways

A system of passageways connects the ambulacral tunnel with the thecal cavity. The passageways extend inward along the lateral sutures between adjacent floorplates, one row along each side of the ambulacral trough. The upper ends of the passageways open into small, sub-circular

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pits centered over the sutures between adjacent floorplates. The pits lie along the upper margins of the trough, along the inner edge of the articulation zone for the coverplates. The pits are thus in part roofed by the inner surfaces of the overlying coverplates. The inner ends of the passageways open as elongate depressions which extend along the inner lateral suture lines between the floorplates. Each is elongate normal to the ambulacral axis.

In at least some Edrioasterida, each floorplate pit which leads downward to a passageway, also opens perradially into a deep groove. The groove extends along the lateral floorplate suture down the slope of the ambulacral trough. The perradial end of each groove opens into a lower, sub-circular pit at the edge of the floor of the ambulacral trough. Lower pits form a single row along each side of the trough floor, but do not lead to passageways. Shallow lateral grooves may flank both sides of each deep sutural groove with a small ridge separating the grooves. The zigzag perradial suture line of the floorplate series may also be depressed and form a shallow zigzag axial groove.

The floorplate passageway system of the Edrioasterida probably housed lateral branches of the axial radial canal which lay beneath each ambulacrum. In those forms with deep sutural grooves, the branches probably extended from the passageways down the groove into the lower pits which served as podial seats. The part of the branch canal housed in the upper, lateral pits may have participated hydrostatically in coverplate opening. Expansion would have exerted pressure on the inner sides of the overlying coverplates, thereby

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opening them.

Interambulacra

The interambulacral areas of the Edrioasterida theca are formed by large, polygonal plates which abut laterally along vertical sutures. Commonly the largest plates are central, smaller ones lying along the ambulacral sutures. The tessellation of the interambulacral areas suggests relative rigidity. Distally the interambulacra extend into the sub-ambital zone between the distal parts of the ambulacra.

Anal structure

The anal structure is located in interambulacrum 5, commonly near the center of the distal edge of the upper oral surface sector. It is a periproct formed by what seems to be three, irregular circlets of plates. The central plates may be elongated toward the central anus. Distal anal elements are irregularly polygonal and much smaller than the surrounding interambulacrals. The structure appears to have acted only as a loose, flexible covering for the anal area and was capable of moderate expansion.

Margin of the oral surface

Small plates, proximally continuous with the distal large interambulacrals, form the resting and the proximal part of the incurved thecal zones. These are commonly polygonal, abutting plates, but have been reported to be squamose and imbricate in Dinocystis barroisi Bather. The resting zone is formed by plates with external surfaces

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parallel to the underlying substrate. Commonly it is very narrow, only one or two plates wide. Distal to the resting zone the thecal plates are flexed upward and inward, away from the substrate and toward the center of the thecal cavity. The plates of the most distal circlet of the incurved zone are commonly larger than the proximally adjacent plates. Their distal margin may taper to a thin edge directed toward the center of the lower surface.

A thick basal membranous ring was apparently attached to the distal edge of the incurved zone as the presence of numerous minute platelets would seem to indicate. These platelets are squamose, imbricate and elongated concentric with the thecal margin. The membrane apparently extended downward and distally attached to the underlying substrate. It surrounds a small non-plated basal area which is the aboral surface of the theca. This may have been the actual area of adhesion. The distal membrane appears to have been the only flexible part of the edrioasterid test.

P R E S E R V A T I O N

Edrioasteroid thecae have been subjected to several modifications during preservation. These affect the theca in important but often subtle ways that obscure original features and suggest erroneous alternatives.

Nearly all specimens have undergone thecal collapse in which the upper oral surface is depressed against the underlying substrate or lower surface plates. In the common domal theca, collapse accentuates the imbrication of the interambulacrals and depresses their inner faces

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against the substrate. Distal interambulacrals are commonly jumbled or pushed in under the proximal plates of the peripheral rim. The orals and ambulacral coverplates are held above the substrate by the underlying, thick oral frame and ambulacral floorplates. Thus, the apparent elevation of the oral-ambulacral structures is often greatly exaggerated by thecal collapse. The differential downward movement of interambulacrals which flank the ambulacra and oral area, tends to cause slight lateral shifting of the ambulacral coverplates and orals. Therefore, although the basic coverplate arrangement is maintained, the sporadic and irregular slippage often alters plate shapes and sutural features. The central elevation of the anal structure may be either increased or decreased during collapse. In those forms with geniculate rim plates, the upper ends of the proximal rim plates remain elevated above the substrate, nearly in life position, and the rim stands in marked relief above the adjacent, depressed interambulacrals.

Clavate edrioasteroids are commonly preserved with the lower pedunculate zone completely collapsed, the imbricate plates being telescoped together. Only slight plate disruption occurs when the upper circlets are preserved inside the lower areas, in spite of the somewhat larger diameter of the upper circlet. From this, it appears that the lower circlet plates were flexibly united laterally and that the pedunculate region was contractile in life. Occasionally, when clavate forms toppled sideways before burial, the pedunculate zone is laterally compressed but preserved in a distended condition.

In depressed clavate forms, the upper oral surface is pressed

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down onto the collapsed pedunculate zone. Collapse affects this surface as in domal forms and leaves the interambulacra depressed and the ambulacra and oral area elevation exaggerated because they are supported by inner floorplates; ambulacral coverplates and orals commonly have shifted irregularly in these forms also.

"Echinoidal" thecae are commonly depressed, the sub-ambital, resting and incurved zones flattened under the upper oral surface. These thecae appear to be more rigid than other types for the plates are commonly disrupted in an irregular manner.

Lateral compression and other stresses, perhaps related to the gradual decay of soft-parts, commonly cause complete disruption of part or all of the thecal plates. Domal forms not uncommonly preserve only the peripheral rim intact, all of the central thecal plates totally jumbled. Clavate forms may preserve a regularly collapsed pedunculate zone, with the plates telescoped together, but with the upper oral surface elements completely disrupted.

Sediment reworkers (burrowers) also disrupt individuals. Commonly edrioasteroids are preserved on the surface of a firm, calcareous layer, buried by an overlying shale. Reworker trails have been traced from overlying shales through specimens. All plates adjacent to the burrows are disarranged. This destruction most commonly is found when the burying mud is quite thin. If the overlying shale is thicker (six to eight inches or more after compression), most reworkers were not able to penetrate to the firm, calcareous layer on which the edrioasteroids lived. When the overlying shale is thin (five inches or less), most

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specimens are partially or completely disrupted by sediment reworkers.

The most subtle preservational modification of edrioasteroids is surficial etching of the thecal plates. Most of this seems to be due to etching by ground water moving along the limestone-shale interface, where the edrioasteroids occur. All exposed plate surfaces are affected, on both the inner and outer surfaces of the theca. Small plates and the thin edges of larger ones are most severely etched. The results can be quite misleading if not properly appreciated.

Etched specimens expose sub-surficial, section views of the theca. The exposed "surface" outline of plates with differing inner and outer shapes may be extensively altered by etching. The most significant alteration is to the taxonomically important coverplates. The external surfaces are removed which exposes the upper, perradial ends of intra-ambulacral extensions. This modifies the coverplate outline and may replace a simple zigzag perradial line with a complexly interdigitating one.

There may be differential etching of the skeletal stereom and the calcite filling of stroma canals. This commonly accounts for delicate pitting on etched plate surfaces.

Edrioasteroids appear to be unusually susceptible to surficial etching. Severely etched specimens are commonly associated with a variety of other calcareous fossils, including other echinoderms, which show little or no evidence of etching.

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"ATTACHMENT"

Edrioasteroids are found resting directly upon firm carbonate substrates or upon the hard parts of other invertebrates. Commonly the resting site is smooth or only slightly irregular. Occasionally individuals apparently rested on relatively small objects and the theca was contorted to maintain contact of the peripheral rim with the object (e.g., Carneyella pilea resting on a segment of crinoid stem, plate 17, fig. 1-4).

In the Isorophida the lower side of the peripheral rim is in contact with the substrate. The aboral surface of the theca , presumably a soft membrane, may also have lain on the substrate surface, surrounded by the rim. Their method of adherence to the substrate is unknown. No suggestion of calcareous cement has been found. Possibly the aboral basal membrane maintained a constant suction for fixation. In forms with geniculate rim plates (the Carneyellidae and Isorophina), small vertical ridges, which project down to the substrate surface, are often developed on the basal surfaces of the geniculate plates. These may have been sites of attachment for muscular or ligamentous tissue which distally connected to the substrate. If suction created by the basal membrane was the fixative force, these ridges may have acted as non-skid runners (Caster, personal communication, 1971).

Some Isorophida appear to have been rigidly fixed. Large clavate species are commonly attached by a very small, basal, peripheral rim. If these were not firmly fixed, the high theca would appear to have been unstable, and would have toppled sideways with only slight water agitation. Moreover, occasionally specimens with a variety of thecal

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shapes are found obliquely compressed, disrupting the upper parts of the theca, whereas the peripheral rim maintains its original position on the substrate. At least one species (Hadrochthus commensalus) lived attached to the thecae of then living cystoids. In order to cling to these bobbing cystoids, the edrioasteroids must have been firmly attached.

Some Isorophida may have been capable of very limited movement, whereas others appear to have been immobile and thus firmly anchored. Young specimens of certain species are commonly found attached to the sloping lateral margins of brachiopods, whereas large adults of these species are found centered on the upper surface of similar brachiopods. This would suggest that during growth the young edrioasteroids were able to migrate to the centers of the brachiopod valve.

Evidence suggesting some species were entirely immobile after larval settling is more convincing. Young individuals have been found with adjacent large specimens "overgrowing" part or all of the small thecae (pl. 55, fig. 15). If movement were possible, the smaller individuals would surely have moved laterally to avoid being overgrown and hence "suffocated" by the larger specimen. Thus, at least some, and perhaps all, Isorophida were incapable of movement which suggests some sort of permanent mode of attachment.

In the Edrioasterida, the "echinoidal" theca appears to have been attached by the fleshy, aboral surface membrane or perhaps by the surrounding basal edge of the distal polyplated membranous ring of the oral surface. Inadequate preservation precludes further analysis, but

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the central basal zone seems the only available site of fixation.

SYMMETRY AND PHYLOGENETIC IMPLICATIONS

Echinoderm symmetry is complex. Fundamentally, the Echinodermata are bilateral, as demonstrated by the ontogeny of extant members of the phylum (Hyman, 1955, Ubaghs, 1967, Fell, 1967, etc.). This fundamental bilateral symmetry is masked by various secondary symmetries superimposed upon the bilaterality. Although this secondary symmetry is most commonly pentamerous or pentaradiate, other types not uncommonly may be substituted, or actually superimposed upon a preceding, secondary symmetry. Thus echinoderm symmetry is best described as palimpsestic (Caster, 1967).

Adult edrioasteroid thecae commonly have prominent pentaradiate symmetry, the five ambulacra alternating with the five interambulacral regions. The adult pentaradiate symmetry is imperfect, altered by bilateral symmetry, and a subtle triradiate plan which is evident in juveniles.

Edrioasteroid symmetry is complicated by the common occurrence of ambulacral curvature which distorts the symmetry of the distal parts of the ambulacral-interambulacral regions. In species with all ambulacra curved in the same direction, the result is to add a spiral aspect. However, commonly only the more distal parts are curved so that the spiral component is irregular and apparently not homologous to the spirality of such forms as the Helicoplacoidea. Moreover, most forms

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have one or more ambulacra curved in a direction reversed from the others which destroys the spiral aspect. The ontogeny of species with curved ambulacra suggests curvature is a late development in the class since all their juveniles have straight ambulacra. Thus, the irregular spirality appears to have been superimposed on the basic bilateral, triradiate and pentaradiate symmetries. To facilitate discussion, the following description of edrioasteroid symmetry ignores ambulacral curvature. Each type described may be complicated by curvature.

The bilateral aspect of edrioasteroid symmetry is defined by the antero-posterior, or axial plane of symmetry which passes through the oral pole, the center of the posterior interambulacrum and the primary axis or midline of ambulacrum III. The plane of adult bilateral symmetry being discussed here must not be confused with the fundamental plane of bilaterality of larvae and the ancestral echinoderms, which is thought to be oriented differently. The axial plane commonly passes through the center of the anus, although occasionally this structure is offset toward one side of the posterior interambulacrum. The hydropore commonly lies to the right of the axial plane, in or near the posterior part of the oral region; it is always posterior to the midline of ambulacrum V. Thus the edrioasteroid axial plane is essentially equivalent to the crinoidal plane of Cuenot (1948), if one allows the slight offsetting of the hydropore to the right of the plane, and the occasional lateral displacement of the anal structure.

Edrioasteroid bilaterality is also reflected by the configuration of the oral region and proximal parts of the ambulacra. The oral area

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commonly has a marked, transverse elongation, symmetrically developed on each side of the axial plane except for the right lateral hydropore orals. The anterior ambulacrum, bisected by the axial plane, is distinctly set off from the four lateral ambulacra which originate as pairs from the lateral extremities of the transversely elongate oral area; I-II proximally unite at the left edge of the oral area; IV-V at the right edge. Thus, the transverse elongation of the oral region and the development of a single anterior and two lateral pairs of ambulacra are also bilaterally symmetrical with respect to the axial plane.

The five ambulacra stem from a triradiate (rather than a pentaradiate) origin as has been suggested by some earlier workers, particularly Foerste (1914, p. 412) and more recently by Caster (1967) in a general application to all pentaradiates. This triradiate pattern is reflected by the oral area midlines. An anterior midline is formed by the perradial suture line between the anterior orals. It extends along the proximal, anterior part of the axial plane of symmetry, and terminates proximally at the oral pole, perpendicular to the transverse oral midline. The transverse midline is formed by the junction between the anterior and posterior orals. It originates at the oral pole and extends laterally out to the proximal tips of the two lateral bifurcation plates. Both midlines may be serrate, a zigzag pattern imposed upon them by perradial angularity of the oral plates. However, the major direction and "averaged" position of the midlines remains constant. The midlines thus form a triradiate pattern from the oral pole, one anterior primary radius along the axial plane, two lateral primary

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radii, one right, one left, each normal to the axial plane.

The triradiate nature of the oral region is also reflected in the structure of the oral frame, although less distinctly than in the external oral area. All five ambulacral tunnels empty directly into the central lumen. However, the interambulacral (interradial) distance between the two tunnels of each lateral pair of ambulacra (I-II and IV-V) is small. The interambulacral space between the anterior member of each lateral pair (II and IV) and the anterior ambulacrum (III) is larger and distinctly separates the anterior ambulacrum from the lateral pairs. The interambulacral distance between the posterior members of the later pairs (I and V) across the posterior interradius is very large, clearly setting apart the two lateral pairs.

The pentaradiate aspect of the edrioasteroid thecal symmetry thus develops distal to the oral area. The midline of ambulacrum III, which marks the anterior ambulacral radius, is a straight-line continuation of the anterior primary radius. In contrast, the two lateral primary radii bifurcate at the edge of the oral area to form four secondary ambulacral radii, marked by the midlines of ambulacrum I and II, IV and V.

Correlations between the symmetry found in adult edrioasteroids and other echinoderms is speculative. However, because such correlations may suggest homologies and aid in interpretation of phylogenetic relationships, a few alternatives are discussed here.

Recent discussions of echinoderm symmetry are found in the Treatise on Invertebrate Paleontology, parts S and U. Ubaghs (1967)

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summarized the subject, drawing upon the ontogeny of extant classes to demonstrate that the symmetry found in adult echinoderms is secondary, superimposed upon the basic or fundamental bilaterality of the class. During ontogeny, in recent echinoderms, a secondary pentaradial symmetry is imposed upon the developing bilateral organism. Moreover, a secondary bilateral plane of symmetry is developed. This does not necessarily correlate with the primary plane of bilaterality, which cannot (or only with greatest difficulty) be identified in adult or "post-metamorphic individuals" (Ubaghs, 1967, p. S11). The adult plane of bilateral symmetry is based on features such as the anus, hydropore, madreporite, etc., and not on the features which define the bilateral symmetry of the larvae. Ubaghs concludes (1967, p. S11) that homologies based on the adult bilateral plane of symmetry are "not . . . proven". Nevertheless, although not proven, suggested correlations of adult bilateral and pentameral symmetries between echinoderm classes are important phylogenetic indicators.

Fell (1967) presents a rigorous treatment of echinoderm ontogeny and concludes, in agreement with Ubaghs, that the larvae of extant Echinodermata demonstrate the presence of a fundamental bilateral symmetry in the ancestry of the phylum, suggesting a "dipleurula"-like ancestor for the phylum. However, larval evolution has subsequently modified these stages to such great extent that extant larvae are of no help in interpreting phylogenies within the phylum beyond establishment of the "dipleurual"-like, bilateral ancestor. Fell convincingly supports his conclusion by contrasting phylogenetic inferences from the

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extant larval types with the contradictory phylogenies suggested by the morphology of post-larval echinoderms, both extant and fossil. That extant echinoderm larvae are totally irrelevant to the phylogeny of the phylum is in direct contradiction to views expressed by many notable workers, such as Hyman (1955).

Fell and Moore (1966), Moore and Fell (1966) and Fell (1967) suggest the most significant aspect of post-larval echinoderms is symmetry and related growth gradients. The "standard" pelmatozoan-eleutherozoan division of the echinoderms so forcefully promulgated by Bather (1900) is rejected by these authors because it is founded upon ecologic adaptation. A new four-part division of the phylum is proposed in the Treatise based upon symmetry and growth gradients. The subphyla, Homalozoa, Crinozoa, Asterozoa, and Echinozoa, are briefly characterized as follows:

Subphylum Homalozoa Whitehouse, 1941: asymmetrical or with some degree of bilateral symmetry

Subphylum Crinozoa Matsumoto, 1929: globose forms with partial "radiate", meridional symmetry, all with exothecal ambulacral feeding appendages of some type.

Subphylum Asterozoa Haeckel (in Zittel), 1895: commonly star-shaped forms with radially divergent axes of symmetry formed by extensions of the body.

Subphylum Echinozoa Haeckel (in Zittel), 1895: commonly globoid, cylindroid or domal forms with meridional symmetry, ambulacra con-

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fined to body surface, lacking any type of exothecal appendages like those of Crinozoa, or divergent body extensions like those of the Asterozoa.

The differing symmetry patterns exemplified by the Crinozoa, Asterozoa and Echinozoa, are discussed by Fell and Moore (1966). Homology of the symmetries for the subphyla and also within the classes assigned to the Echinozoa are given by Moore and Fell (1966). A more extensive treatment of the significance of the growth gradients in the three subphyla is presented by Fell (1967). These authors contend the four basic symmetry patterns represented by the four proposed subphyla are independent of mode of life, and represent the most significant characteristic of members of the class. Thus, the symmetry patterns are the fundamental basis for division of the Echinodermata at the subphylum level.

Acceptance of this proposed echinoderm division based upon symmetry depends upon acceptance of Moore's and Fell's interpretations of homologies of symmetry types and their related growth gradients.

A comprehensive analysis of echinoderm symmetry is beyond the scope of this paper. However, evidence provided by the Edrioasteroidea, which Moore and Fell include in the Echinozoa, appears to contradict some of their conclusions.

Basic to the four-part division of the echinoderms are the following assumptions and interpretations: (1) only two types of growth gradients exist in echinoderms, (2) the Homalozoa fit neither growth pattern and thus are far removed from other echinoderms, (3) a homologous

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primary plane of adult bilateral symmetry is found in most classes of echinoderms, (4) the ambulacra of most groups, except the Homalozoa, can be specifically identified and therefore homologized from one group to another, (5) a primary, pentameral symmetry was developed in the echinoderms immediately after the original bilaterality was lost, and only the Homalozoa lack this fundamental pentamerism.

Fell (1967, p. S83) defines two major growth gradients which are found in the development of post-metamorphic echinoderms: (1) a meridional pattern, in which the hydrocoel sends out five meridional water tubes and the entire "skeleton and nervous system thereafter differentiates under the same meridional gradients"; (2) a "radial" pattern of gradients, in which the five water tubes extend from the hydrocoel "radially outward in the horizontal plane, carrying body wall and coelom with them, and thus they produce the divergent, radiating arms. The whole skeleton and nervous system differentiates thereafter under the control of such dominant radial gradients, with the calyx alone retaining the ancient meridional system". (Fell's usage of "radial" can be confusing when used with standard terms like pentaradial, etc., which he would probably term "pentameradional" for echinoids; therefore when used in Fell's sense of radiating outward on a horizontal plane, away from the body, "radial" is placed in quotation marks.) This dual system of growth gradients is viewed by Fell as the only framework in which the larvae of extant echinoderms can be interpreted. Echinozoa (Echinoidea, Holothuroidea) follow the first pattern, while both Asterozoa and Crinoidea (the only living members of the Crinozoa) are domin-

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ated by the second type. Thus, the growth gradients of larvae which yield the symmetry of the adult members of these three subphyla, supports the phylum division as proposed by Fell and Moore (1966). Moreover, a close relationship is suggested for the Crinozoa and Asterozoa, a contention supported by fossil evidence presented by Fell in a number of works.

Fell's conclusions about growth gradients rely on two basic assumptions: (1) a pentamerous symmetry is developed in echinoderms after the fundamental bilateral symmetry of the ancestor is lost; (2) the Homalozoa, as far as can be interpreted from the fossil record, fit neither of the above growth gradient patterns, and are thus basically asymmetrical organisms with a secondary bilaterality later developed in some.

In contrast with Fell's suppositions, the carpoid Homalozoa may have a primary triradiate symmetry (Caster, 1967) which is differentially developed among the members of that group; in some carpoids, a bilateral aspect is superimposed upon the triradiate pattern. Other echinoderms, including the edrioasteroids, have a trimerous pattern and these likewise suggest that some pentameral patterns may be modified from a triradiate symmetry developed early in the evolution of at least one major segment of the echinoderms. Thus, both of Fell's basic assumptions may be questioned. Before discussing pentameral versus triradiate as the basic symmetry, the homology of the plane of bilateral symmetry found in adult echinoderms must be considered.

Moore and Fell (1966) contend that if properly identified, the

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plane of bilateral symmetry of post-larval echinoderms (not the fundamental bilateral symmetry of larvae and the ancestral stock) is homologous in most classes of echinoderms, including all Crinoidea and most other Crinozoa, Echinozoa, and probably Asterozoa. This plane is the primary anterior-posterior plane of the adult, i.e., the crinoidal plane (Cuénot, 1948) or axial plane. It extends through the anterior ambulacrum (III), the oral pole, and the posterior interambulacrum (5). Identification of the plane in Crinozoa is simple, but in other groups it is less obvious, in part due to the method of correlating Lovénian numbers with Carpenter letters. If done improperly, the anterior ambulacrum is incorrectly identified and the plane of bilaterality likewise erroneously placed.

Moore and Fell (1966) re-evaluated the methods of ambulacral identification in the Crinozoa, Asterozoa and Echinozoa to allow the consistent and accurate identification of the antero-posterior plane. Their re-evaluation produced a significant change in ray identification for the echinoids, as well as the Asterozoa. Others remain consistent with those of previous workers.

The proposed changes in ambulacral identifications are based on two features considered to be of fundamental importance: (1) modification of thecal shape; (2) the patterns of ambulacral development or distribution which indicate the location of the anterior ambulacrum. Rejected is the contention that the hydropore (or madreporite) location is of prime importance in identifying the posterior interambulacrum. Thus, according to Moore and Fell, the location of the madreporite in

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echinoids is in interambulacrum 2 which correlates to the A-E interradius of the Carpenter system and not to the C-D interradius. The madreporite of the Asterozoa is placed in the D-E interradius, on the oral side in the Ophiuroidea, the aboral side in the Asteroidea; it is not in the C-D interradius, as commonly defined. Support for the proposed changes is discussed at length by Moore and Fell (1966). Their conclusion rests not only upon a declaration that thecal shape and ambulacra disposition should be used as the primary basis of ray identification, but also upon interpretation of a variety of other thecal features previously not considered (apical system, anal migration, etc.).

Moore and Fell (1966) present a convincing argument for homology of the basic adult plane of bilaterality found in most Crinozoa, Asterozoa and Echinozoa, all of which is dependent upon acceptance of their interpretation of ray homologies. However, acceptance of their work is far from universal, as witnessed by Ubaghs' (1967, p. S11) contention in the Treatise that "the selection of any one plane as a plane of reference for orientation of all the classes [of echinoderms] is more or less arbitrary, and homologies based on such comparisons are judged as not being proven." Moreover, as noted above, the Homalozoa are excluded from consideration in the discussion of ray homology and bilateral symmetry due to their lack of an apparent five-part form, thereby deleting one of the four major subdivisions of the phylum.

An interesting observation arises when the Moore and Fell primary plane of adult bilateral symmetry is identified in the edrioasteroids. It passes through ambulacrum III, the oral pole and the anus. Thus,

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the hydropore lies in the C-D interradius (interambulacrum 5) near the bilateral plane but slightly offset to the right. In the Crinozoa and holothurians, the hydropore lies along the bilateral plane of symmetry (in the C-D interradius) although it may be slightly offset from this plane in some, as in the edrioasteroids. In contrast, the hydropore (or madreporite) does not lie in the bilateral plane in other groups, is found rather in the D-E interradius of the Asterozoa, and A-E interradius in the Echinoidea. One can accept Fell's conclusion that the hydropore should not be used to define the primary plane of bilateral symmetry because the opening has migrated in some groups. However, identical migration routes may very well be important indicators of phylogenetic relationships. Thus the location of the hydropore in the C-D interradius, either along or near the plane of bilaterality, suggests relationships between the Crinozoa and two groups included in the Echinozoa by Moore and Fell, the holothurians and the edrioasteroids. How much weight should be applied to this correlation of hydropore position is uncertain; Moore and Fell (1966, p. U125-U126) suggested the edrioasteroids respired anally, as do the holothurians, and thus the supposed hydropore ("third opening" of Regnéll, 1966) was more likely a gonopore. While anal respiration is suggested here for some of the edrioasteroids, the suggestion that the "third opening" is not a hydropore but rather a gonopore is here rejected.

The last and perhaps most important of the five assumptions noted here as inherent in the four-part division of the echinoderms found in the Treatise is the derivation of five-part symmetry. Fell and Moore

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(1966) contend that as the ancestral echinoderm stock lost its fundamental bilateral symmetry, a basic pentaradial symmetry was developed, with a more or less apparent component of bilaterality always formed as an integral part of the new radial symmetry. Fell (1967) suggests that the development of the five-part radiating symmetry apparently was related to a common unknown "globoid" progenitor of the Echinozoa, Asterozoa and Crinozoa. Thus, the Homalozoa are to be considered either early offshoots, before the radial symmetry developed, or highly degenerate.

The edrioasteroids display a marked triradiate symmetry as described above. The triradiate aspect of thecal symmetry defined by the oral area is generally accompanied by a pentaradiate pattern defined by the distal parts of the ambulacra. However, in at least one problematic genus, Thresherodiscus Foerste, only three primary ambulacra are formed. All three repeatedly bifurcate distally, and thus a five-part plan is never developed. Thresherodiscus, represented by a single specimen, may be considered a specialized offshoot rather than a representative reflecting the basic symmetry of the group. However, Foerste (1914, p. 412) concludes that Thresherodiscus "offers a striking confirmation" that a triradiate pattern is the basic edrioasteroid symmetry.

The ontogenetic development of edrioasteroid species may support the contention that triradiate symmetry is basic in the class and that the pentaradiate form is secondarily derived. In all species for which juveniles have been found, a pronounced three-part symmetry of the oral

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ambulacral structure occurs in the earliest stages. Development proceeds by the extension of three primary radii, one anterior, two transverse, radiating outward from the central oral pole. The five-part symmetry of adults is developed by the bifurcation of both lateral primary radii, thereby producing four lateral ambulacra and a single anterior ambulacrum. Thus, at least in ontogeny, the pentaradiate symmetry is a later development, superimposed upon a basic triradiate plan.

If edrioasteroids are basically triradiate, what of other groups? As noted above, Caster suggests that the carpoid Homalozoa (Stylophora, Cornuta and Soluta) which Fell and Moore (1966) dismiss as being asymmetrical, are basically triradiate. Moreover, a triradiate pattern is seen in some crinoids. Among these are the examples selected by Moore and Fell (1966) to demonstrate symmetry. Noting this obvious pattern, they suggest it correlates with the development of the trivium and bivium found in echinoids and holothurians.

However, the members of a bivium are closely associated with each other, as are the three members of the trivium, and the two groups are distinctly set apart from one another by wide interradial spaces. In contrast, the pattern of ambulacral disposition and related oral plate arrangement in the crinoids illustrated by Moore and Fell (1966) follows that described for the edrioasteroids. The anterior ambulacrum is distinctly set off from two pairs of lateral ambulacra, each two lateral ambulacra converging to form a single axis before reaching the oral pole. Thus, the two lateral ambulacra on each side of the theca are grouped as a pair, both lateral pairs distinctly set apart from the

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single anterior ambulacrum. Moreover, each lateral pair is widely set apart from the other by the very wide posterior interambulacrum. Therefore, the supposed members of the bivium as interpreted by Moore and Fell, i.e., ambulacra I and V (or D and C), have the greatest interradial distance between them of any of the five ambulacra. The triradiate nature of these crinoids hardly seems comparable to the trivium-bivium groupings of echinoids and holothurians.

Evidence of a basic triradiate symmetry in the edrioasteroids is not definitive, but certainly suggests the pentaradial pattern is secondary, superimposed upon the earlier triradiate form. Combined with the triradiate pattern seen in many crinoids, and perhaps also in the carpoid Homalozoa, this evidence casts doubt on the supposition that pentamerism is basic to all echinoderms except for the supposedly "asymmetrical" homalozoans. If one major group of echinoderms does prove to be basically triradiate, a revision of the four-part Treatise division of the phylum is suggested.

Moore and Fell (1966) conclude that a basic difference stemming from the symmetry of echinoderms is represented by the pattern of growth gradients, and this allows the distinction of three basic groups in the phylum: (1) forms with "radial" (directed outward) extensions of the body, (2) forms with exothecal ambulacral appendages, and (3) forms with meridional ambulacra, lacking any exothecal ambulacra or body extensions. A fourth group, as defined by Moore and Fell, rests largely on negative evidence, the members apparently lacking any consistent pattern of symmetry. Within this framework, the edrioasteroids, with-

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out exothecal appendages or body extensions, must be placed in the Echinozoa.

The inclusion of the Edrioasteroidea under the subphylum Echinozoa is questioned. The apparently basic triradiate symmetry of the edrioasteroids suggests closer ties to the crinoids and cystoids, some of which seem to be triradiate. Moreover, the position of the hydropore in interambulacrum 5, and the adult plane of bilateral symmetry, is comparable in most crinoids, cystoids and edrioasteroids. In contrast, the hydropore (madreporite) is found in a quite different position in the Asterozoa and the echinoids.

Thus, the phylogenetic relationships of the edrioasteroids to other echinoderms remains in question, and their placement within either the "Crinozoa" or "Echinozoa" uncertain, and the usefulness of these two supposedly systematic categories is questionable.

ORGAN SYSTEMS

DIGESTIVE TRACT

The ambulacra, central lumen and anal structure establish the location of the tissue systems involved in the ambulacral food grooves, stomial cavity and anus, respectively, in edrioasteroids. Judging from crinoids, a presumably ciliated groove extended along the floor of each ambulacral trough, conducting food to the central "mouth" or stomial cavity which lay below the roof of permanently closed oral plates. This is an organization well-suited to suspension feeding. The proximal end of the gut passed down through the central lumen of the oral

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frame into the thecal cavity. In those forms with a prominent posterior frame gap, it seems likely that the gut extended posteriorly through the gap into the thecal cavity beneath interambulacrum 5.

The anus lies in interambulacrum 5, commonly almost central. It is surrounded by a periproct in the Lebetodiscina and the Edrioasterida, by a valvular structure in the Isorophina. Little is known about the rest of the tract.

Both Jaekel (1899) and Bather (1915) reasoned that the edrioasteroid gut looped solarly around the thecal cavity, based on homology with other echinoderms. Bather (1900) suggested a specimen of Edrioaster buchianus (Forbes) implied this solar gut curvature because a slight elevation of the posterior interambulacrum to the right of the anus probably reflected the path of the rectum. Williams (1918) also thought that the presence of a coiled gut was suggested by two crushed juvenile specimens of Isorophus austini (Foerste), where he thought he saw traces of a looped internal organ impressed into the lower side of the oral surface plates. A spiral, solarly looped gut is a distinct possibility for edrioasteroids in as much as many other echinoderms show such a condition.

HYDROVASCULAR SYSTEM

The hydrovascular system in edrioasteroids is presumed to have included a hydropore, stone-canal, circumesophageal ring canal, and five radial canals which in some instances seem to have had multiple lateral branches. Such features as polian vesicles, Tiedemann's bodies or accessory organs could possibly have been part of the system without

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leaving a trace in the skeleton.

An opening through the theca, thought to be the hydropore, lies between the oral pole and the anal area, commonly offset slightly to the right of the axial plane. This is comparable to the hydropores found on many cystoids, crinoids, and other primitive pelmatozoan echinoderms. The structure is composed of orals and/or modified interambulacral plates combined with the proximal coverplates of the posterior side of ambulacrum V. Construction and exact location are taxonomically important.

As noted by Kesling (1960, p. 141), "Bather's detailed work (1900b) on Edrioaster buchianus (Forbes) leaves scarcely any room for doubt that the species had a water vascular system that opened through a hydropore". Kesling (1960) identified the location and structure of the supposed hydropore in a variety of species, ranging through all the major taxonomic groups of the class.

Regnéll (1966) maintained a neutral position concerning the hydropore, referring to it as the "third opening", in the only recent major review of the class. He notes that the opening may have been the hydropore, a genital opening or a combination of the two. The double function as both a hydropore and a gonopore is quite possible, but its primary function would seem to have been that of a hydropore.

A stone-canal presumably led from the hydropore into the thecal cavity. What is judged to be the passageway for this canal is formed by the inner parts of the plates of the hydropore structure and, commonly, also by the underlying proximal floorplates of ambulacrum V.

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The passageway is funnel-shaped, and expands inward to open along the right posterior, distal margin of the oral frame.

The stone-canal is presumed to have led to a circumesophageal ring, probably circumambient to the oral frame. However, direct evidence of this structure is lacking.

Kesling and Mintz (1960) postulated that the ring canal of Isorophus cincinnatiensis was inside the oral lumen. Noting that the inner end of the stone-canal passageway lies outside the oral frame, they reasoned that the ring canal was primarily confined to the area of the central lumen in the center of the oral frame, and presumably encircled the esophagus or anterior part of the gut. The posterior part of the canal was supposedly squeezed through the large posterior gap in the oral frame to make contact with the inner end of the stone-canal. Moreover, the radial water canal of ambulacrum V supposedly branched off this distal part of the ring canal near its connection to the stone-canal, and entered ambulacrum V through a supposed passageway between the second and third floorplate of ambulacrum V. The presence of this passageway is questionable (see I. cincinnatiensis). The remaining four radial canals presumably branched from the part of the ring canal located within the central lumen of the oral frame and extended directly into the proximal ends of ambulacra tunnels via their openings into the upper part of the central lumen.

Kesling and Mintz (1960, p. 321) reasoned that the ring canal could not have extended around the outside of the oral frame because it would have to pass under the frame twice, at ambulacrum I and V,

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and therefore "any compression of the flexible theca would pinch the ring canal between the frame and the object to which the edrioasteroid was attached". However, the inner edge of the oral frame rim extends further into the thecal cavity than any other structure, and therefore the canal could have extended around the outside of this region, free from any "pinching". Moreover, there is no indication that during life the theca would be so depressed that the base of the oral frame would come into contact with the underlying substrate. Thus the problem of pinching the ring canal or any of the other organs in the region probably never arose.

The only supposedly direct evidence of the ring canal's presence was reported by Bather (1900b, p. 198) in the type specimen of Edrioaster buchianus (Forbes), an internal mold of the theca: "The mouth was central and roughly five-lobed, widest on the posterior side, and . . . was surrounded by a stout ring of stereom, over which the food groove passed . . . The proximal or aboral pores [floorplate passageways] were connected with one another above this stereom ring, but below the outer theca [oral covering plates], so as to form a closed ring-canal (hydrocircus) around the mouth". The illustrations accompanying this description suggest a slight depression extending around the inner edge of the oral frame, the supposed location of the ring canal.

The structure of the ambulacra in the Edrioasterida and the Lebetodiscina suggest that the radial canals extend beneath the floorplates (see below). In these groups, the circumesophageal ring canal most likely encircled the oral frame. In the Isorophina, there appears to

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be no evidence as to the position of either the circumesophageal ring or the radial canals, but by analogy they too probably lay outside the lumen and beneath the floorplates respectively.

The floorplate passageways of the Edrioasterida suggest that the radial canals were under the ambulacra. Along each ambulacrum, alternate lateral branches extended from the radial canal and passed up through the two rows of floorplate passageways into the ambulacral tunnel where they entered the two lateral upper rows of pits at the upper ends of the passageways. At least in Edrioaster bigsbyi, these lateral branches appear to have extended from the pits toward the floor of the ambulacral trough along the deep grooves which follow the lateral sutures between floorplates. These open into lower basin-like depressions which perhaps housed podia. The parts of these branch canals housed in the upper pits were probably swollen, and may have aided in the opening of overlying coverplates by hydrostatic pressure. The lower, ambulacral-trough parts of the extensions, perhaps developed as podia, may have aided in food gathering or perhaps were entirely respiratory structures.

Bather (1900b, p. 196-197, 1915, p. 263) suggested a much different hydrovascular anatomy for Edrioasterida species. He thought that the radial canals extended externally along the floor of the ambulacral trough with lateral branches which extended alternately up the lateral sutural grooves to form podia in the upper pits. The floorplate passageways he thought housed tubes connecting the podia to internal ampullae. This configuration does not explain the function of the lower basin-like depressions which flank the floor of the ambulacral

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trough. Moreover, the coverplates abut the floorplates along the zone housing the upper, lateral pits and partially roof them over. This would seem to make it unlikely that they accomodated podia.

In the Lebetodiscina, coverplate passageways connect the thecal cavity with the exterior of the theca. These passageways lack direct communication with the ambulacral tunnel and therefore the radial canal for each ambulacrum must have extended axially beneath the floorplates. Alternate lateral branches extended from each side of the radial canal and passed up through the passageways to the external sides of the coverplates. The distal parts of the lateral branches apparently were respiratory structures. In Lebetodiscus and Foerstediscus, a series of lateral basin-like depressions is developed along the lateral edges of the coverplates, near and along the external foramina of the passageways. These may reflect further branching of the lateral branch canals.

Ambulacral passageways are not developed in the Isorophina. Thus radial canals, if present, may have extended either along the floor of the ambulacral trough, or more likely, may have been housed within the thecal cavity and extended along the ambulacra under the floorplates. No evidence of canals or podial structures has been observed in this group. Obviously, respiration, if that is the function of external hydrovascular podia in other edrioasteroids, must have been otherwise achieved in the Isorophina.

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RESPIRATION

As seen above, two fundamentally different methods of respiration appear to have been employed by edrioasteroids. The Edrioasterida and the Lebetodiscina are thought to have respired via external extensions of the hydrovascular system. In the Edrioasterida, this system includes lateral branches of the radial canals which lie within the ambulacral tunnels. The ends of the branches apparently formed podia which were exposed to the surrounding sea water when the ambulacral coverplates were open. As in many extant echinoderms, respiration most likely occurred by gaseous exchange through the membranous surfaces of these podia.

In the Lebetodiscina, the lateral branches of the radial canals extended through sutural passageways between the ambulacral coverplates, and thereby effected direct communication with the external environment.

In contrast to the above groups, the Isorophina appear to have respired by anal pumping, like most extant holothurians. The Isorophina lack ambulacral passageway systems. Moreover, no evidence has been found to suggest the development of any sort of hydrovascular extensions housed in the ambulacral tunnels. However, these organisms do have a valvular anal structure. It is formed by an inner and an outer circlet of large triangular plates, outer circlet ones alternating and overlapping inner plates along tight fitting, beveled edges. Due to the zone of overlap, the beveled edges of adjacent plates would remain in contact during opening and closing and thereby maintain the structural unity of the apparatus. It is suggested that this structure re-

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flects the development of a respiratory anal pumping system. The flexible theca of the Isorophina would permit expansion and contraction and thereby allow the alternate intake and expulsion of sea water into a cloacal chamber. There may have been developed some sort of anal respiratory trees analogous to that found in recent holothurians.

In support of this interpretation, it is found that the valvular anal structure of the Isorophina contrasts with the periproct of loose, irregular circlets of plates found in the Edrioasterida and Lebetodiscina. With ambulacral hydrovascular extensions capable of carrying out respiration, these forms did not rely on anal pumping. The lack of an ambulacral passageway system in all Isorophina thus appears to correlate with the development of a valvular anal structure as part of an anal respiratory apparatus.

Fell and Moore (1966, p. U 118) compared edrioasteroids to the dendrochirote holothurians and suggested that, like psolid holothurians, edrioasteroids probably had internal respiratory trees for respiration. Their conclusion thus concurs with the suggested mode of respiration proposed here for the Isorophina, but not for the Edrioasterida or Lebetodiscina. In addition, G. W. Sinclair (personal communication, 1968) has long held that the Isorophid anal structure was a valve used in thecal pumping. However, he doubts that the structure functioned as an anus. Williams (1918, p. 76) also suggested anal respiration for the edrioasteroids. He compared the edrioasteroids with Antedon, the extant crinoid, in which he reports "the rectum projects as the tubular papilla and the rectal tube is in the living animal seen to undergo

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frequent movements of contraction and dilation by means of which water is drawn into and expelled from the rectum. There is thus intestinal respiration". Citing the valvular anal structure of "Agelacrinites", Williams suggested respiration was via anal pumping, as in Antedon.

ONTOGENY

Ontogenetic development has been observed in a few edrioasteroid species. The most complete series of specimens included here is for Isorophusella incondita (Raymond), a member of the Family Isorophidae. Less complete growth series are also described for species which represent the other three families of the Isorophida. Unfortunately, juveniles are unknown among species of the Edrioasterida.

The earliest observed stage of development is found in tiny specimens, approximately .5 mm in diameter, which represent species in which average adult thecal diameters are 15 to 18 mm. The theca of these smallest forms is dominated by the peripheral rim which forms approximately two-thirds of the total oral surface area. The rim appears to be made of two or three circlets of plates, the proximal elements quite large in proportion to thecal diameter. The central third of the oral surface includes the plates of the oral-ambulacral series which form a tri-lobed structure with one anterior and two lateral radii. Primary orals form the center of the area, flanked laterally by two lateral bifurcation plates. Two anterior primary orals form an anterior hump; the anterior oral midline extends between these plates and marks the anterior primary radius. One (Lebetodiscina) or two (Isorophidae) posterior primary orals form the straight posterior side of the area

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which centrally abuts the anterior primaries along the transverse oral midline. The transverse midline extends laterally out to the tip of each lateral bifurcation plate and defines the right lateral and left lateral primary radii. The two distal bifurcation plates extend the lateral radii more than twice the distance from the center of the area than the short anterior radius.

At this stage, the central triradiate oral-ambulacral area is separated from the proximal margin of the rim by small "interambulacral" spaces, but plates have not been observed in these areas. The posterior interradius is the largest.

Proximal ambulacral floorplates may be inferred in these earliest known growth stages because the center of the oral region is arched upward in the collapsed thecae suggesting the presence of underlying floorplates. However, the inner side of the oral surface has not been observed in young specimens included in this study. Williams (1918) reported that in juvenile Isorophus austini (Foerste), 1.3 mm in diameter, only the five proximal floorplates which form the oral frame are seen. He did not describe smaller individuals.

After the earliest observed stage, development varies depending upon the family. In the Carneyellidae proximal ambulacral coverplates are the next external oral-ambulacral series plates to develop (or become manifest). In the Lebetodiscidae and Isorophina, lateral shared coverplates and/or secondary orals are formed next. They are inserted along the transverse oral midline between the primary orals and lateral bifurcation plates.

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Concurrent with the oral-ambulacral plate development, the peripheral rim slowly adds new circlets of plates and also inserts new plates into the existing circlets, thereby enlarging the circumference of the rim. Hydropore plates and anals appear suddenly in specimens approximately 1 mm in diameter. When first observed these plates are quite large in proportion to thecal diameter which suggests they were present in smaller specimens, perhaps even in those .5 mm in diameter. Perhaps these plates were hidden under the peripheral rim in the smaller collapsed specimens. Interambulacrals are also observed at approximately the same stage, usually two or three in interambulacra 1-4, but with four or five in the larger posterior interradius.

Development proceeds by the addition of new plates and the progressive increase in size of previously formed elements, although not all at the same rate.

The oral-ambulacral series adds plates along each primary radius. The two lateral radii bifurcate and form four lateral ambulacra, whereas the anterior radius continues as a single extension. The lateral bifurcations are initiated by the insertion of coverplates on both sides of each lateral bifurcation plate. After two to four coverplates have been inserted in each of the four secondary radii, the outline of the oral-ambulacral area begins to assume a five-part shape. This commonly occurs when the thecal diameter is between 2.5 and 3 mm. By the 3 to 3.5 mm stage, all five ambulacral radii are distinct. Insertion continues through the addition of coverplates at the distal tip of each ambulacrum. These are added singly at the center of the distal tip, and then shift alternately right and left to form pairs. In

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species with two or more sets of coverplates, secondary plates are inserted between primaries. The initial plate of the secondary set appears at the proximal end of the ambulacrum, adjacent to the first formed plate of the primary set, usually after four to six primaries have formed. Commonly the theca is around 3 mm in diameter at this stage. The insertion zone of the secondaries then migrates distally, but lags behind that of the primaries and remains about three to five primary plate pairs from the distal tip of the ambulacrum. Species with additional sets of coverplates continue to insert new sets as the ambulacra lengthen and the thecal diameter increases. Apparently the time of first appearance of each new set is quite variable from one species to another. Individual ambulacra of a specimen may develop at different rates, the numbers of coverplates per ambulacrum being quite variable.

The ambulacra continue to lengthen as floorplates and coverplates are added at the distal tips of the ambulacra, and by enlargement of previously formed plates. In forms with curved ambulacra, curvature is usually initiated when the thecal diameter reaches 4 or 5 mm. Prior to this, the ambulacra are straight. The distal parts of the ambulacra commonly become concentric with the thecal margin by the stage when the thecal diameter is between 5 and 7 mm. The ambulacra thus increase in proportional size rapidly and become one of the major features, in area, in the adult theca.

The oral plates continue to enlarge in size, and in those forms with shared coverplates and secondary orals, new plates are added from

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the 1 mm stage up to forms 6 to 7 mm in diameter. Commonly, most orals are present by the 5 to 6 mm stage, although some species, particularly in the Agelacrinitidae, continue to add orals for a much longer time period, perhaps throughout adulthood. Although the plates of the oral area enlarge and increase in number, the proportional size of the area decreases throughout ontogeny. In adults, this area is usually a relatively small part of the total area of the oral surface, in contrast with the youngest known juveniles where it occupies nearly a third of the total oral surface.

The interambulacra increase rapidly in areal extent as the ambulacra lengthen, and commonly form the largest part of the adult theca. New plates are apparently inserted along the proximal and lateral margins of the interradii along the adradial suture lines.

The anal structure, when first observed, is proportionally quite large and fills much of the posterior interradius. The plates are large when first observed and continue to enlarge slowly while new plates are occasionally inserted in the structure. However, the relative areal extent of the structure decreases throughout ontogeny, and the adult anal area is nearly always a relatively small part of the total oral surface.

The peripheral rim, which dominates the early growth stages, slowly adds new circlets and intercalates new plates in the existing circlets until the thecal diameter reaches approximately 5 mm. Thereafter, although new plates are inserted into the circlets which increases the circumference of the rim, only rarely are new circlets

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developed. The rim increases in size slowly, and gradually becomes proportionally smaller throughout ontogeny.

Commonly, specimens less than 5 mm in diameter are dominated by juvenile features. The ambulacra-interambulacra become the spatially dominant parts of the theca beyond this stage. In species with curved ambulacra, the direction of curvature is usually apparent by this stage. Beyond the 5 mm stage, adult thecal characters dominate. The transition from juvenile to adult is gradual, but in species of 15 to 20 mm adult diameter, the 7 to 8 mm stage appears to be almost identical in thecal proportions to the large adults. Individuals 5 to 8 mm are generally referred to as young adults.

Even in species where the average adult diameter is only 10 to 12 mm, the transition from juvenile to young adult appears to fall around the 5 mm stage. This is also the case for those with adult diameters exceeding 20 mm. Exceptions are found among the Agelacrinitidae in which species with several sets of ambulacral coverplates may continue to add new series and thus change the coverplate pattern well into, and perhaps in some instances throughout, adulthood.

What might be called gerontic edrioasteroids have been observed in only a few species. These are characterized by exceptionally large thecal diameters. In at least one species (Isorophus cincinnatiensis), geronticism is also suggested by the distal tips of the ambulacra curving back toward the oral region, whereas in average sized adults the ambulacra are merely distally concentric with the thecal margin.

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DIAGNOSTIC SUMMARY OF EDRIOASTEROID TAXA INCLUDED

Class Edrioasteroidea Billings, 1858

Polyplated, thecate, sedentary Echinodermata with:

1) anal structure in posterior interambulacrum (5);

2) triradiate or (?secondary) pentaradial symmetry;

3) endothecal ambulacral-oral system composed of two distinct sets of thecal elements,

a) coverplates,

b) floorplates,

forming five (+-) ambulacra and a central oral structure;

4) hydropore structure located in or near right posterior side of oral area;

5) accessory hydrovascular sutural passageway systems commonly present;

6) interambulacral areas polyplated; without regular order;

7) anal structure in posterior interambulacrum (5).

O-1. Order Isorophida Bell, ord. nov.

Edrioasteroidea with:

1) theca domal, discoidal or clavate, aboral surface non-plated;

2) oral frame formed by five proximal, ambulacral floorplates, (+-) intra-thecal extensions from oral covering plates;

3) hydropore structure located in or near right posterior part of oral area, adjacent to proximal, posterior edge of ambulacrum V, structure composed of ambulacral and oral or interambulacral

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elements, hydropore opening along junctions between edges of plates, elongate parallel to plate margins;

4) ambulacra composed of:

a) uniserial floorplates without sutural passageways;

b) biserial or multiple series of coverplates with intra-thecal and/or intra-ambulacral extensions, and with or without sutural passageways which extend from interior to exterior of theca;

5) margin of oral surface a peripheral rim, flaring outward parallel to substrate.

I. Suborder Lebetodiscina Bell, subord. nov.

Isorophida with:

1) Three central primary oral plates;

2) ambulacral coverplates form single, alternating biseries, with intra-ambulacral and intra-thecal extensions;

3) sutural passageways developed between coverplates, extend directly from thecal cavity to exterior of the theca;

4) ambulacral floorplates imbricate, each floorplate proximally overlapping the distal end of adjacent floorplate;

5) anal structure a periproct.

I-A. Family Lebetodiscidae Bell, fam. nov.

Lebetodiscina with:

1) Theca domal, discoidal or clavate;

2) oral area includes two pairs of lateral shared coverplates, secondary orals commonly present;

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3) hydropore structure distal to oral area, opening along adradial suture line of proximal, posterior part of ambulacrum V, composed of interambulacral plates and ambulacral coverplates;

4) ambulacra form high pronounced ridges on thecal surface;

5) ambulacral coverplates massive;

6) ambulacral tunnel high and narrow;

7) coverplate passageways commonly nearly vertical;

8) peripheral rim plates squamose, not geniculate.

I-A-a. Genus Lebetodiscus Bather, 1908

1) Theca domal, oral surface highly convex;

2) oral area includes two sizes of secondary oral plates;

3) hydropore formed by expanded adradial end of second ambulacral coverplate of posterior side of ambulacrum V, and, adjacent two or three interambulacral plates;

4) ambulacra curved, I-V contrasolar;

5) coverplate passageways large;

6) lateral depression series present;

7) interambulacral plates large, few distal to ambulacra;

8) thecal plates smooth.

A-a-aa. L. dicksoni (Billings), 1857

Type species

Characters of genus.

I-A-b. Genus Foerstediscus Bassler, 1935.

1) Theca domal, oral surface highly convex;

2) oral area commonly includes two sizes of secondary oral plates;

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3) hydropore structure like Lebetodiscus, perhaps more complex in some species;

4) ambulacra curved, I-V solar;

5) coverplate passageways large;

6) lateral depression series present;

7) few interambulacral plates distal to ambulacra;

8) thecal plates smooth or nodose.

A-b-aa. F. grandis Bassler, 1935

type species

1) Secondary oral plate arrangement unique;

2) hydropore structure includes four major plates;

3) anal structure near center of ambulacrum 5;

4) prosopon of prominent nodes covers interambulacral and marginal plates.

A-b-bb. F. splendens Bassler, 1936

1) Secondary oral plate arrangement unique;

2) hydropore structure formed by several plates;

3) anal structure near center of interambulacrum 5;

4) thecal plates smooth.

A-b-cc. F. solitarius Bell, sp. nov.

1) Secondary orals poorly known;

2) hydropore structure formed by four plates;

3) anal structure in proximal part of interambulacrum 5, near oral area;

4) thecal plates probably smooth.

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I-A-c. Genus Belochthus Bell, gen. nov.

1) Theca domal, (?) moderately convex;

2) oral area includes at least three large secondary oral plates, primary orals and bifurcation plates sagittate in external appearance;

3) hydropore structure formed by proximal two coverplates of posterior side of ambulacrum V, and at least one large interambulacral element;

4) ambulacra straight;

5) coverplate passageways somewhat oblique to thecal surface;

6) lateral depression series unknown;

7) interambulacral plates extend distal to ambulacra and form wide zone of imbricating plates proximal to the peripheral rim.

A-c-aa. B. orthokolus Bell, sp. nov.

type species

Characters of genus.

I-A-d. Genus Streptaster Hall, 1872

1) Theca domal, convex oral surface dominated by extremely high ambulacra;

2) oral area includes secondary oral plates;

3) hydropore structure composed of three plates, the second and third proximal coverplates of ambulacrum V, and one large, bulbous interambulacral;

4) ambulacra curved, I-V contrasolar;

5) coverplate passageways vertical, open externally along most of

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length of coverplates;

6) lateral depression series absent;

7) interambulacral plates few in number;

8) large spines set in basins along summit of columnar ambulacral plates; interambulacral and rim plates with large nodes.

A-d-aa. S. vorticellatus (Hall), 1866

type species

Characters of genus.

I-A-e. Genus Cystaster Hall, 1871

1) Theca discoidal to clavate;

2) secondary oral plates lacking;

3) hydropore structure formed by four plates, two proximal coverplates of posterior side of ambulacrum V, and two large interambulacrals;

4) ambulacra straight, drape down thecal surface in clavate forms;

5) coverplate passageway external foramina very elongate;

6) lateral depression series lacking;

7) interambulacral plates small, squamose, form narrow zone distal to ambulacra in discoidal forms, extensive pedunculate zone in clavate forms; large nodes on interambulacral and rim plates which commonly obscure squamose shape of plates; spines present on summit of ambulacral coverplates in some.

A-e-aa. C. granulatus Hall, 1871

type species

1) Theca clavate;

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2) external ridge on larger interambulacral hydropore plate may be larger or more prominent than in other species.

A-e-bb. C. stellatus (Hall), 1866

1) Theca discoidal;

2) external ridge on larger interambulacral hydropore plate may be smaller or less prominent than in other species.

I-B. Family Carneyellidae Bell, fam. nov.

Lebetodiscina with:

1) Theca domal;

2) oral area includes one large hydropore oral; no secondary orals or shared coverplates present;

3) hydropore structure in right posterior part of oral region, composed of orals and ambulacral coverplates;

4) ambulacra form low rounded ridges;

5) ambulacral coverplates of moderate thickness;

6) ambulacral tunnel low and wide;

7) coverplate passageways oblique;

8) peripheral rim plates geniculate.

I-B-a. Genus Carneyella Foerste, 1917

1) Ambulacra curved, I-IV contrasolar, V solar;

2) ambulacral terminations confined to interambulacral areas;

3) coverplate passageway external foramina elliptical to slit-like;

4) anal structure a periproct.

B-a-aa. C. pilea (Hall), 1866

type species

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1) Prosopon of small irregular tubercles, and small perradial coverplate ridges.

B-a-bb. C. faberi (S. A. Miller), 1894

1) Prosopon of numerous, large, clavate tubercles with distal tips rounded, commonly three or more per ambulacral coverplate; and large ambulacral coverplate ridges plus small lateral coverplate ridges.

B-a-cc. C. ulrichi Bassler and Shideler, 1936

1) Prosopon of numerous, large, clavate tubercles with distal tips acuminate, commonly one per ambulacral coverplate; and also large perradial coverplate ridges and small lateral coverplate ridges.

B-a-dd. (?) C. valcourensis Clark, 1920

Characters obscure.

I-B-b. Genus Cryptogoleus Bell, gen. nov.

1) Ambulacra straight;

2) ambulacral terminations commonly penetrate proximal circlet of peripheral rim;

3) coverplate passageway external foramina slit-like, difficult to detect;

4) anal area may be transitional from normal periproct to more complex valvular type.

B-b-aa. C. chapmani (Raymond), 1915

type species

1) Theca large;

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2) ambulacra taper moderately, terminations blunt;

3) ambulacral coverplates nearly horizontal externally;

4) interambulacral plates large;

5) thecal plates smooth to foveolate, pitting subdued, most prominent on proximal rim plates.

B-b-bb. C. reticulatus Bell, sp. nov.

1) Theca of moderate size;

2) ambulacra not tapered, terminations very blunt;

3) ambulacral coverplates moderately convex externally;

4) interambulacral plate size moderate;

5) all thecal plates covered by prominent, coarse pitting.

B-b-cc. C. multibrachiatus (Raymond), 1915

1) Theca moderate to small;

2) ambulacra taper slightly, terminations blunt;

3) ambulacral coverplates moderately convex externally;

4) interambulacral plates small, externally convex, appearing bulbous or knobby;

5) thecal plates smooth or with subdued pitting, occasional large nodes present.

B-b-dd. C. youngi (Raymond), 1915

Characters uncertain.

B-b-ee. C. platys (Raymond), 1915

Characters uncertain.

B-b-ff. C. billingsi (Chapman), 1860

Characters uncertain.

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II. Suborder Isorophina Bell, subord. nov.

Isorophida with:

1) Four large central primary orals, or numerous small undifferentiated central orals;

2) ambulacral coverplates form multiple alternating biseries or cyclic series of 2 to 7 sets of plates, coverplates with intra-ambulacral and/or intra-thecal extensions;

3) coverplate passageways absent;

4) ambulacral floorplates commonly abut along vertical sutures; rarely imbricate;

5) anal structure valvular.

II-A. Family Isorophidae Bell, fam. nov.

Isorophina with:

1) Theca domal;

2) oral area with four large, primary orals, two pairs of lateral shared coverplates, one large hydropore oral, and secondary orals;

3) hydropore structure with few plates, integrated with central oral rise;

4) ambulacral coverplates form simple, alternating, multiple biseries of two or three sets of plates;

5) interambulacrals commonly squamose and imbricate.

II-A-a. Genus Isorophus Foerste, 1917

1) Ambulacra curved, I-IV contrasolar, V solar;

2) ambulacral coverplates form double, alternating biseries;

3) ambulacra of moderate width in proportion to thecal diameter,

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with gradual distal taper;

4) interambulacra of moderate size, squamose and imbricate.

A-a-aa. I. cincinnatiensis (Roemer), 1851

type species

1) Theca moderate to large;

2) five or more secondary orals;

3) primary ambulacral coverplates distinctly larger externally than secondaries, secondaries rarely reaching adradial suture line externally.

4) interambulacrals moderate in size.

A-a-bb. I. austini (Foerste), 1914

1) Theca small;

2) five or more secondary orals;

3) proximal secondary ambulacral coverplates nearly as large externally as primaries, externally reach adradial suture line;

4) interambulacrals moderate in size.

A-a-cc. I. warrenensis (James), 1883

1) Theca small to moderate;

2) secondary orals present;

3) secondary ambulacral coverplates large, commonly reach adradial suture line externally;

4) interambulacral plates very large.

II-A-b. Genus Isorophusella Bassler, 1935

1) Ambulacra straight or slightly curved;

2) ambulacral coverplates form a regular, alternating double biseries;

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3) ambulacra of moderate to broad width with gradual distal taper;

4) interambulacrals squamose, imbricate.

A-b-aa. I. incondita (Raymond), 1915

type species

1) Theca of moderate size;

2) one right lateral secondary oral;

3) large primary ambulacral coverplates alternate regularly with small secondary coverplates;

4) thecal plates smooth.

A-b-bb. I. trentonensis (Bassler), 1936

1) Theca small;

2) one right lateral secondary oral;

3) secondary ambulacral coverplates externally nearly as large as primaries in proximal part of ambulacra;

4) thecal plates bear scattered, irregular nodes.

A-b-cc. I. pleiadae (Sinclair and Bolton), 1965

1) Theca small;

2) external oral surface not observed.

II-A-c. Genus Hemicystites Hall, 1852

1) Ambulacra straight;

2) ambulacral coverplates form double alternating biseries;

3) ambulacra wide;

4) interambulacrals squamose, imbricate.

A-c-aa. H. parasiticus Hall, 1852

type species

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1) Theca small;

2) one or more secondary orals;

3) hydropore opening on top of small protuberance formed by four or five of the six hydropore structure plates;

4) secondary ambulacral coverplates commonly large, some approaching size of primaries;

5) coverplates perradially arched, forming perradial ridge;

6) interambulacrals of moderate size;

7) valvular anal structure large.

II-A-d. Genus Rectitriordo Bell, gen. nov.

1) Ambulacra straight;

2) ambulacral coverplates forming regular triple biseries;

3) ambulacra of moderate width;

4) interambulacrals squamose, imbricate.

A-d-aa. R. kirkfieldensis Bell, sp. nov.

type species

1) Oral surface highly convex;

2) oral areas include approximately 13 secondary orals;

3) interambulacrals relatively large;

4) distal rim plates sub-triangular in external outline.

II-A-e. Genus Curvitriordo Bell, gen. nov.

1) Ambulacra curved, I-IV contrasolar, V solar;

2) ambulacral coverplates forming a triple biseries;

3) ambulacra of moderate width;

4) interambulacrals squamose, imbricate.

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A-e-aa. C. kentuckyensis (Bassler), 1936

type species

1) Triple biseries of ambulacral coverplates formed by regularly alternating pairs of three plate sets, opposing pair members in contact perradially.

A-e-bb. C. shideleri (Bassler), 1936

1) Triple biseries of ambulacral coverplates formed by alternating pairs of three plate sets, opposing pair members of primary and secondary sets separated perradially by pairs of tertiary coverplates.

II-B. Family Agelacrinitidae Chapman, 1860

Isorophina with:

1) domal or clavate theca;
2) oral plates either numerous, primaries undifferentiated, or, occasionally with four primaries flanked by numerous secondary orals;
3) hydropore structure commonly with many plates forming large, isolated or semi-integrated protuberance along posterior oral rise;
4) ambulacral coverplates form complex multiple biseries or cyclic sets;
5) interambulacrals squamose-imbricate or polygonal-tessellate.

II-B-a. Genus Agelacrinites Vanuxem, 1842

1) Theca domal;
2) 15 or more oral plates which include two or more apparently

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differentiated primary orals and one large hydropore oral;

3) hydropore structure semi-integrated, formed by few plates;

4) ambulacra curved, I-III contrasolar, IV-V solar, of moderate width;

5) ambulacral coverplates form alternating two-plate cycles;

6) interambulacrals large, sub-polygonal, slightly imbricate;

7) valvular anal structure with two circlets of alternating plates.

B-a-aa. A. hamiltonensis Vanuxem, 1842

type species

1) Theca large;

2) oral plate arrangement variable;

3) hydropore structure formed by one large hydropore oral and two to five oral-ambulacral series coverplates;

4) two sets of ambulacral coverplates forming regular to irregular two-plate cycles;

5) interambulacrals large;

6) thecal plates with prominent to subdued ridge and node prosopon.

II-B-b. Genus Krama Bell, gen. nov.

1) Theca domal;

2) 16 or more oral plates, including four large primary orals, one hydropore oral, and lateral secondary orals resembling ambulacral coverplate sequence;

3) hydropore structure semi-integrated;

4) ambulacra curved, I-III contrasolar, IV-V solar, of moderate

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width;

5) ambulacral coverplate sequence a mixture of cyclic sets and biserial pairs;

6) interambulacrals squamose, imbricate;

7) valvular anal structure formed by two circles of alternating plates.

B-b-aa. K. devonicum (Bassler), 1936

type species

1) Theca of moderate size;

2) hydropore structure formed by three or more plates;

3) ambulacral coverplate series including three-plate cycles and one late developing fourth set added as biserial pairs;

4) interambulacrals relatively large;

5) anal plates centrally elevated, forming small central protuberance.

II-B-c. Genus Postibulla Bell, gen. nov.

1) Theca domal;

2) many oral plates, primaries not differentiated, large posterior oral protuberance present;

3) hydropore structure semi-integrated;

4) ambulacra curved I-III contrasolar, IV-V solar, narrow;

5) ambulacral coverplates forming two or three-plate, irregular cycles, coverplates steeply inclined;

6) interambulacrals squamose, imbricate;

7) valvular anal structure formed by three circlets which form

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highly elevated cone.

B-c-aa. P. legrandensis (Miller and Gurley), 1894

type species

1) Theca small;

2) posterior part of posterior oral protuberance formed by three plates;

3) hydropore structure formed by four or more plates, including two posterior elements.

B-c-bb. P. keslingi Bell, sp. nov.

1) Theca of moderate size;

2) posterior part of posterior oral protuberance formed by two large plates;

3) hydropore structure formed by four plates, including one large posterior element.

B-c-cc. (?) P. jasperensis (Harker), 1953

1) Theca small;

2) posterior oral protuberance formed by two plates;

3) hydropore structure formed by two plates;

4) only one alternating set of coverplates developed.

B-c-dd. P. alpenensis (Bassler), 1936

Characters unknown.

II-B-d. Genus Discocystis Gregory, 1897

1) Theca clavate;

2) numerous small orals, primaries undifferentiated;

3) large hydropore protuberance separate from oral rise;

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4) ambulacra curved, I-IV contrasolar, V solar, long and narrow;

5) ambulacral coverplates form three- or four-plate cycles;

6) interambulacrals large, polygonal, tessellate;

7) valvular anal structure formed by two circlets.

B-d-aa. D. kaskaskiensis (Hall), 1858

type species

1) Theca large;

2) hydropore structure formed by at least three large posterior plates.

II-B-e. Genus Lepidodiscus Meek and Worthen, 1868

1) Theca highly convex domal or clavate;

2) numerous small orals, primaries undifferentiated;

3) large, elongate hydropore structure separated from central oral rise, posterior side formed by many plates;

4) ambulacra curved, I-IV contrasolar, V solar, long;

5) ambulacral coverplates form six-plate cycles;

6) interambulacrals squamose, imbricate or polygonal, tessellate;

7) valvular anal structure formed by two circlets.

B-e-aa. L. squamosus Meek and Worthen, 1868

type species

1) Theca large, highly convex, domal;

2) ambulacral coverplates smooth perradially;

3) ambulacral floorplates imbricate;

4) interambulacrals squamose, imbricate.

B-e-bb. L. laudoni (Bassler), 1936

1) Theca large, clavate, peduncular zone plates numerous, imbricate,

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sub-rectangular, very thin, and in vertical columns;

2) ambulacral coverplates perradially raised, forming small perradial ridge;

3) ambulacral floorplates abutting; each with two lower surface, lateral protuberances;

4) central interambulacrals polygonal, tessellate.

B-e-cc. L. sampsoni (S. A. Miller), 1891

1) Theca clavate or sub-clavate, peduncular zone plates squamose, imbricate, without regular order;

2) ambulacral coverplates perradially raised, forming a perradial ridge;

3) ambulacral floorplates abutting, each with four or more inner surface, lateral protuberances;

4) interambulacrals large, polygonal, tessellate.

II-B-f. Genus Ulrichidiscus Bassler, 1935

1) Theca highly convex, domal or clavate;

2) numerous oral plates, primaries undifferentiated;

3) large, elongate hydropore structure separate from central oral rise;

4) ambulacra curved, I-V contrasolar, long;

5) ambulacral coverplates form seven-plate cycles;

6) interambulacrals polygonal to squamose, tessellate to slightly imbricate;

7) valvular anal structure formed by two circlets of plates.

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B-f-aa. U. pulaskiensis (Miller and Gurley), 1894

type species

1) Theca large;

2) anterior hydropore structure orals do not reach transverse oral midline perradially;

3) thecal plates smooth or finely pustulose.

II-B-g. Genus Cooperidiscus Bassler, 1935

1) Theca clavate (?);

2) numerous orals (?);

3) hydropore structure large, separate from central oral rise (?);

4) ambulacra curved, I-V solar, long, extremely narrow;

5) ambulacral coverplate series includes two or more sets of elements;

6) interambulacrals numerous, squamose, imbricate;

7) valvular anal structure formed by two circlets of plates.

B-g-aa. C. alleganius (Clarke), 1901

type species

1) Theca large, upper oral surface convex upward, lower surface uncertain;

2) hydropore structure apparently formed by numerous plates;

3) ambulacra remain widely separated from each other distally;

4) thecal plates apparently smooth or nearly so.

II-B-h. Genus and species indeterminate:

Pennsylvanian fragments.

II-C. Family Uncertain

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II-C-a. Genus Hadrochthus Bell, gen. nov.

1) Theca domal;

2) oral area with few plates, primary orals differentiated;

3) hydropore structure semi-integrated, small;

4) ambulacra straight, wide;

5) ambulacral coverplates form a single alternating biseries;

6) interambulacrals large, thick, polygonal, tessellate;

7) valvular anal structure formed by one circlet.

C-a-aa. H. commensalus Bell, sp. nov.

1) Theca small to moderate in size;

2) fourteen oral plates including three primary orals, two pairs of lateral shared coverplates, four secondary orals, one small hydropore oral;

3) small hydropore protuberance formed by two plates;

4) ambulacral coverplates large;

5) interambulacrals large, few in number;

6) thecal plates may have large nodes.

III. Suborder and Family Uncertain

(?) Hemicystites carbonarius Bassler, 1936

Theca small, domal;

Characters not interpretable.

O-2. Order Edrioasterida Bell, ord. nov.

Edrioasteroidea with:

1) thecal shape "echinoidal", oral surface plates extending below ambitus onto lower side of theca;

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2) oral frame formed by 10 compound plates which include numerous floorplates and 5 modified proximal interambulacrals;

3) hydropore structure located in posterior part of oral area, formed by 2 plates; hydropore opening elongate perpendicular to suture line, penetrating both plates;

4) ambulacra composed of:

a. biserial floorplates with sutural passageways which extend from ambulacral tunnel into thecal cavity;

b. biserial coverplates without intra-thecal or intra-ambulacral extensions, and without sutural passageways;

5) margin of oral surface on lower side of theca, reflexed upward toward center of theca with distal membrane, imbedded with minute plates, and attached to substrate, peripheral rim not present.

I-A. Family Edrioasteridae Bather, 1898

Characters of the order.

I-A-a. Genus Edrioaster Billings, 1858

1) Ambulacra curved, I-IV contrasolar, V solar;

2) ambulacral coverplates perradially angular, forming right angle zigzag perradial lines;

3) right posterior hydropore plate abuts adradial ends of proximal posterior floorplates of ambulacrum V.

A-a-aa. E. bigsbyi (Billings), 1857

type species

1) Theca large;

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2) thecal plates with large rounded nodes;

3) ambulacra curvature initiated above ambitus.

A-a-bb. E. priscus (Miller and Gurley), 1894

1) Theca small;

2) thecal plates smooth;

3) ambulacra curvature initiated below ambitus.

I-A-b. Edriophus Bell, gen. nov.

1) Ambulacra curved, I-V solar;

2) ambulacral coverplates perradially sinuous and elevated, forming sinous perradial ridge;

3) right posterior hydropore plate fused to adradial ends of proximal, posterior floorplates of ambulacrum V.

A-b-aa. E. levis (Bather), 1914

type species

1) Theca large;

2) thecal plates smooth.

A-b-bb. (?) E. saratogensis (Ruedemann), 1912

1) Theca small;

2) thecal plates finely pustulose.

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Class Edrioasteroidea Billings, 1858

Diagnosis:

Polyplated, thecate, sedentary Echinodermata with: initially triradiate and subsequently pentaradiate symmetry; five (±) endothecal ambulacra radiate from central oral structure of covering orals and underlying oral frame; ambulacral system formed by two sets of thecal elements: coverplates and floorplates; sutural passageways present or absent, associated with ambulacra; opening judged to be hydropore in or near right posterior part of oral area, posterior to midline of ambulacrum V; interambulacra irregularly polyplated; anal structure on upper oral surface in posterior interambulacrum, periprocteal or valvular; theca domal, clavate or globose(without stalk).

Description:

Edrioasteroids are small to moderate sized echinoderms; adult thecal diameters range from 9 to approximately 50 mm, 20 mm being the average. The theca is commonly formed by a polyplated oral surface (which may extend below the ambitus) and non-plated central aboral surface, without a stem or stalk. Most thecae are domal, clavate or globose ("echinoidal").

The five (±) ambulacra are endothecal, formed by outer coverplates and underlying floorplates. Edrioasteroids lack exothecal appendages. The ambulacra radiate from a central oral area which is formed by covering orals and an underlying oral frame. The orals are distally continuous with the ambulacral coverplate series. The oral frame is formed by enlarged, proximal ambulacral floorplates and commonly, also

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by intra-thecal extensions from the overlying orals. In certain species (Edrioasterida), the oral frame includes ten large compound plates. Ambulacral coverplate passageways (Lebetodiscina) or floor-plate passageways (Edrioasterida) may be present.

The oral-ambulacral series reflects a triradiate thecal symmetry, but the five ambulacra, one anterior and two lateral pairs, impose a dominant pentaradiate form on the theca, apparently superimposed on the primary triradiate pattern.

The hydropore commonly is in the right posterior corner of the oral area, near or along the proximal, posterior margin of ambulacrum V. In certain forms (Lebetodiscidae) it is found distal to the oral area, along the proximal, posterior, adradial edge of ambulacrum V, flanked by proximal plates of interambulacrum 5. The underlying stone-canal passageway opens into the thecal cavity along the distal, right posterior margin of the oral frame.

The interambulacra are irregularly polyplated; the largest plates are in the central and distal parts of each interambulacrum.

A periproct or a valvular anal structure lies in the posterior interambulacrum.

Discussion:

The first few described edrioasteroids were commonly grouped with cystoids. In 1858, Billings first suggested the then described species be grouped together under the Suborder Edrioasteridae, placed in the Order Asteriadae of the Class Echinodermata. Chapman (1860) proposed the Order Thyroida for the edrioasteroids, equal in rank to his seven

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other major divisions of the Class Echinodermata, but closely related to the Cystidea, Asterida, and Echinida. He included one Family under the Order, the Agelacrinitidae.

S. A. Miller (1877) listed edrioasteroid species under the Order Agelacrinidea of the Class Echinodermata. In 1882 he described the new Order Agelacrinoidea with one Family, the Agelacrinidae. In 1889, Miller divided his Order Agelacrinoidea into two families, the Agelacrinidae and the Hemicystidae.

Steinmann (1890) proposed the Gruppe Cystasteroidea, for the edrioasteroids, recognized as the third group of the Class Cystoidea of the Phylum Echinodermata. Haeckel (1895) placed the edrioasteroids in his Agelacystida, the third "family" of the Cystoidea. In 1896 he included two subfamilies under this group, the Hemicystida and the Asterocystida, including both edrioasteroids and cystoids in the latter.

Jaekel (1895) introduced the term Thecoidea for the edrioasteroids, and in 1899 he published the first detailed summary of the group, subdividing his Order Thecoidea into two families the Thecocystidae and the Agelacrinidae.

Bather (1898, p. 547), in the first of a long series of articles dealing with the edrioasteroids, separated two genera (Edrioaster, Dinocystis) "from the Agelacrinidae and Cyathocystidae as the Family Edrioasteridae." In 1900 Bather (in Lankester's Treatise on Zoology) published a summary of the entire group. Resurrecting Billings' (1858) name, he recognized the Class Edrioasteroidea. He included four families, the Agelacrinidae, the Cyathocystidae, the Edrioasteridae and

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the Steganoblastidae. The latter was based on Astrocystites Whiteaves (1897) (= Steganoblastus Whiteaves, 1898) now placed in separate class of the Echinodermata.

Most subsequent authors have recognized the Class Edrioasteroidea of the Phylum Echinodermata. In the first of the two most recent summaries of the Class, Bassler (1935, 1936) recognized five families, the Stromatocystidae, Hemicystitidae, Agelacrinitidae, Edrioasteridae, and Cyathocystidae. Regnéll (1966) followed Bassler's subdivisions. Kesling (1967) suggested further subdivision of the Class by introducing two new families, the Pyrgocystidae and the Lispidecodidae.

The present study includes most species formerly placed in three of the seven commonly recognized families of the class Edrioasteroidea, the Agelacrinitidae, Hemicystitidae and Edrioasteridae, [sensu Bassler (1935, 1936) and Regnéll (1966)]. Here two orders, two suborders, and five families are recognized (see Diagnostic Summary of Taxa Included).

Range and occurrence:

? Lower Cambrian, Lower Middle Cambrian through Upper Pennsylvanian of North America, Great Britain, Europe, Asia, Australia.

Order Isorophida Bell, ord. nov.

Diagnosis:

Edrioasteroidea with: domal or clavate theca, ambulacra commonly limited to upper oral surface; oral frame formed by five enlarged, proximal ambulacral floorplates, with or without intra-thecal extensions from primary orals, hydropore structure in or posterior to right post-

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erior margin of oral area, opening along junctions between plates, elongate parallel to plate margins; ambulacra formed by biserial or cyclic sets of coverplates, with intra-ambulacral and/or intra-thecal extensions, and uniserial floorplates, ambulacral coverplate passageways present in some; and, margin of oral surface a peripheral rim.

Description:

The domal or clavate thecae of adult Isorophida range from approximately 10 to 50 mm in diameter with domal forms 15 to 25 mm the most common.

The oral area includes external orals, distally continuous with ambulacral coverplates, and an underlying oral frame. The area is elevated above the interambulacra and forms the central oral rise which is distally continuous with the elevated ambulacral ridges.

The orals may be large specialized plates, classified as primaries, secondaries, lateral shared coverplate pairs and hydropore orals, all distinctly set apart from adjacent proximal ambulacral coverplates. In other forms, the orals are numerous small plates which resemble the ambulacral coverplate series; distally they appear to grade into the proximal ambulacral series without an obvious break. Opposing orals meet perradially along the anterior and transverse oral midlines.

The oral frame underlies the external orals and surrounds a large central lumen. The transversely elongate frame is formed by the five enlarged, proximal floorplates of the ambulacra, with or without intra-thecal extensions from the overlying orals. The proximal rim of

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the frame, which extends down into the thecal cavity, is ovate and surrounds the central lumen. Distally the frame is continuous with the floorplate series of each ambulacrum which imparts a pentagonal outline to the frame.

The hydropore structure commonly lies in the right posterior part of the oral area, adjacent to the proximal posterior edge of ambulacrum V. In some it lies immediately distal to the oral region, along the posterior side of ambulacrum V. The opening lies along junctions between plates, and thus, parallel to the plate margins. The structure is commonly formed by several plates, as many as twenty in some forms. It may be integrated into the central oral rise, semi-integrated, (i.e., forming a small but distinctly elevated area on the sloping posterior side of the rise), or it may be a separate large protuberance posterior to the oral rise.

The stone-canal passageway leads into the thecal cavity from the hydropore. The upper part of the inwardly expanding funnel-shaped passageway is formed by the plates of the hydropore structure. The inner parts may be formed by both intra-thecal extensions from the hydropore plates and also the adjacent parts of one or two proximal floorplates of ambulacrum V.

Externally, the ambulacra are commonly elevated above the interambulacra and form low, rounded ridges which radiate outward from the central oral rise. Occasionally the ambulacra form large, high ridges. They are confined to the upper oral surface in all but a few species. The ambulacra may be straight or curved. The curvature pattern is

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constant at the generic level.

Ambulacral coverplates form single alternating biseries, multiple biseries, or cyclic series which include two to seven sets of coverplates. Coverplates in most species have intra-ambulacral extensions; and in many they extend adradially past the floorplate margins into the thecal cavity as intra-thecal extensions. Coverplate passageways are sometimes developed; these extend between coverplates from the thecal cavity to the exterior of the theca.

The uniserial ambulacral floorplates are commonly trough-shaped with the upper surface centrally concave inward, forming a deep axial trough. The lateral margins of the upper surface form narrow, nearly horizontal articulation zones, one flanking each side of the trough, on which rest the adradial parts of the overlying coverplates. The inner surfaces of the floorplates are commonly convex inward. In some forms the floorplates are thick and the inner surface shape is modified. Large lateral protuberances may occur on the inner floorplate surfaces.

Contiguous floorplates may abut along vertical sutures, or they may be imbricate with the proximal end of each plate overlapping the distal margin of the adjacent proximal plate.

The interambulacra are covered by either squamose imbricate plates or by polygonal tessellate ones. Interambulacrals lack apparent order, except that the largest plates are found in the central and distal parts of the areas.

The anal structure is located in interambulacrum 5, and may be either periprocteal or valvular.

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The margin of the oral surface is a peripheral rim, formed by several circlets of plates, the plates diminishing in size distally. The large proximal plates may be grouped into alternating, proximal and distal subcirclet members. Rim plates are commonly geniculate, their basal surfaces resting on the underlying substrate. In domal thecae the distal margin of the rim forms the thecal ambitus. In clavate forms it is located at the base of the pedunculate zone.

Discussion:

The Order Isorophida embraces most of the species included in this study. Numerically, these are the common edrioasteroids. It is divided into two suborders, each with two families.

Taxonomically important structural differences between the Isorophida and Edrioasterida are summarized under the discussions of the Edrioasterida and in the Diagnostic Summary of Taxa, included in the introduction.

Range and occurrence: Middle Ordovician through Upper Pennsylvanian of North America, Europe, Asia and Australia.

Suborder Lebetodiscina Bell, subord. nov.

Diagnosis:

Isorophida with: center of oral area formed by three primary orals; ambulacral coverplates form single, alternating biseries, coverplates with both intra-ambulacral and intra-thecal extensions; ambulacral coverplate passageways present; ambulacral floorplates imbricate; anal area a periproct.

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Description:

Lebetodiscina commonly have domal thecae. In Cystaster stellatus the theca approaches a discoidal form, and in C. granulatus it is clavate.

The oral area includes three large, central primary orals. Other oral plates include either a single large hydropore oral or sets of lateral shared coverplates and secondary orals. The oral frame includes both proximal floorplates and intra-thecal extensions from at least the primary orals.

The hydropore structure lies either in the right posterior part of the oral area or distal to that area, along the posterior side of ambulacrum V. It is formed by oral-ambulacral series plates, and in some by modified posterior interambulacrals. The ambulacral coverplates form a single alternating biseries of plates, opposing plates meeting along zigzag perradial lines. The coverplates have both intra-ambulacral and intra-thecal extensions. Large sutural passageways extend from the thecal cavity to the exterior of the theca, each formed along the lateral suture between adjacent coverplates. The external foramina of the passageways vary from large, sub-circular openings to elongate slits.

The uniserial ambulacral floorplates are imbricate, the proximal margin of each overlapping the distal edge of the next proximal floorplate.

Interambulacral plates are squamose and imbricate.

The anal structure is a periproct formed by several irregular

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circlets. At least the more central elements are elongate toward the central anus. The structure commonly lies near the center of interambulacrum 5.

The peripheral rim may be formed by either geniculate or squamose plates.

Discussion:

The species within the Isorophida include most forms placed by Bassler (1935, 1936) in his Family Hemicystitidae. Regnéll (Treatise on Invertebrate Paleontology, 1966) followed Bassler's classification in the only subsequent comprehensive summary of the edrioasteroids. Kesling (1960, 1967) suggested the removal of several species included by Bassler in the Hemicystitidae, although he did not undertake a major revision of the Family. A complete discussion of Bassler's Hemicystitidae is included under the discussion of the Family Carneyellidae.

The coverplate passageway system found in all Lebetodiscina is unique and separates this Suborder from the Isorophina, the other Suborder of the Isorophida. Moreover, the Lebetodiscina have a single, alternating biseries of coverplates in contrast with the multiple biseries or cyclic sets of coverplates found in the Isorophina. Further, the Lebetodiscina anal structure is a periproct of loose, irregular circlets of plates, whereas the Isorophina have a valvular anal structure formed by large, regularly arranged, triangular plates.

The existence of a coverplate passageway system throughout the Lebetodiscina is recognized here for the first time. However, the passageways were first reported by Billings (1857). He observed that

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a series of depressions was present along the ambulacral coverplates (or "marginals") of Lebetodiscus dicksoni (Billings). Unsure whether or not they penetrated the theca, he noted their similarity to the "pores" in Edrioaster bigsbyi (Billings), which he had already demonstrated extend into the thecal cavity. However, as Billings reported, the "pores" of E. bigsbyi are formed between the ambulacral floorplates, whereas those of Lebetodiscus dicksoni are between the coverplates.

The passageways were also reported by Hall (1871) in a plate explanation of Carneyella pilea (Hall). He recorded "minute pores passing between the plates" along the perradial part of the ambulacral coverplates. Hall apparently did not know the extent or the location of the inner parts of these structures. Interestingly, this notation has been disregarded in subsequent literature.

Bather (1908) redescribed the ambulacral structure and passageways of Lebetodiscus dicksoni (Billings). He realized the passageways penetrated into the thecal cavity but thought they were homologous to the passageways which extend between the ambulacral floorplates of Edrioaster bigsbyi, and thereby misidentified coverplates as floorplates.

Raymond (1915, 1921) contradicted Bather by describing the passageways of Lebetodiscus dicksoni as located along the sutures between ambulacral coverplates. However, he attributed little importance to the passageway system and suggested that its presence was a specific or perhaps generic taxobasis. In the same work Raymond described other

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species here placed in the Lebetodiscina but failed to observe their passageway systems.

Wilson (1946) reported multiple "pores" between the ambulacral coverplates of Lepidoconia loriformis (Raymond), here recognized as a junior synonym for Lebetodiscus dicksoni. Based on a single specimen with a well-preserved lateral depression series, she reported that five "pores" lie along the lateral edges of each ambulacral coverplate. Apparently she believed the basin-like lateral depressions lead to passageways which extended into the ambulacral tunnel. It is unclear why she reported only five "pores" per coverplate edge for the specimen she described has seven to nine depressions in each lateral depression series (pl. 2, fig. 1-5). Wilson did not mention the large, elliptical, external foramen along each of these lateral suture lines of the coverplates. However, she did report the presence of a single large "pore" along the sutures between the coverplates in another specimen of Lebetodiscus dicksoni.

Regnéll (1966) summarized published reports of the passageways in Lebetodiscus dicksoni. He also reported Wilson's multiple "pore" system for Lepidoconia loriformis. Regnéll's interpretation of the functional role of the passageways was thus based in part upon erroneous data.

The Suborder Lebetodiscina includes two families which appear simultaneously in the Middle Ordovician. The nature of their prior phyletic relations is still obscure. That they are related and presumably, therefore, had a common ancestry is suggested by the occurrence

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in both of three primary orals, a single biseries of coverplates, the coverplate passageway system, the imbricate floorplates, and a periproctеal type of anal structure. The Carneyellidae appear to be the simpler forms, the oral area having only four plates and the hydropore structure integrated with the oral region. However, simplicity is not necessarily to be equated with primitiveness.

Range and occurrence: Middle Ordovician through Upper Silurian of North America, Europe, Australia.

Family Lebetodiscidae Bell, fam. nov.

Type genus: Lebetodiscus Bather, 1908

Diagnosis:

Lebetodiscina with: oral area including at least two pairs of shared coverplates, secondary orals frequently present; hydropore structure distal to oral area, opening along adradial suture line of proximal, posterior part of ambulacrum V, composed of ambulacral coverplates and interambulacral elements; ambulacra form high, pronounced ridges on thecal surface, ambulacral coverplates large, extremely thick (perpendicular to the thecal surface) and wide (perpendicular to ambulacral axis); ambulacral tunnel narrow and high; coverplate passageways nearly vertical; peripheral rim plates squamose.

Description:

Lebetodiscidae have small to moderate sized domal thecae which average 10-20 mm adult diameter. Commonly the oral surface appears to have been nearly hemispherical with the marginal plates being almost

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vertical in many specimens.

The oral area includes the three large central primary orals, two pairs of lateral shared coverplates, one on each side of the central orals along the transverse oral midline, and a variable number of secondary orals.

The hydropore structure lies distal to the oral region along the proximal posterior margin of ambulacrum V. It is formed by the adradial ends of one or two modified ambulacral coverplates and a variable number of interambulacral plates, at least one commonly enlarged.

The five ambulacra rise abruptly above the interambulacra as high ridges. This elevation results from the massiveness of the coverplates, each being extremely thick normal to the thecal surface. Moreover, these coverplates are thick perpendicular to the ambulacral axis, thereby restricting the ambulacral tunnel to a very narrow, high structure.

The coverplate passageways extend along the lateral, sutural surfaces between adjacent coverplates and are parallel to the long axis of the coverplates. Therefore, they extend normal to the thecal surface and are nearly vertical. Passageways in this family are large and open through conspicuous foramina. Series of depressions or pits may be associated with the external foramen of each passageway, one row flanking each side of the lateral suture line between adjacent coverplates. These rows of depressions are called lateral depression series.

The external appearance of the thick coverplates in the Lebetodiscidae is distinctive. Each plate is highly convex and this forms a prominent median ridge which extends from the adradial suture to the

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perradial line. Therefore, the lateral suture lines between adjacent coverplates occur at the bottom of deep troughs. The external foramen of each passageway opens between two adjacent coverplates at the perradial end of the sutural trough. The pit-like lateral depressions, when present, are incised into the lateral slope of each coverplate and open laterally into the trough.

Interambulacral plates are squamose and imbricate. They may be small and numerous, or relatively large and few in number.

The periproct, which is commonly near the center of interambulacrum 5, is formed by several irregular circlets of elongate plates, all equal to, or smaller than, surrounding interambulacrals.

The peripheral rim is formed by squamose plates. During collapse, the proximal rim plates and distal interambulacrals are equally depressed, obscuring the boundary between the two zones. This contrasts with the common high elevation of the proximal rim plates above the interambulacrals in forms with geniculate plates.

External plate surfaces are commonly smooth, but nodes and ridges are found in a few species.

Discussion:

The Family Lebetodiscidae embraces five genera and eight species. Three genera are monotypic; one genus includes two species and one has three. Except for one new genus and species, this group has been included previously in the Family Hemicystitidae Bassler (1936). This was one of five families recognized by Bassler in 1936, the first work to subdivide isorophid species into more than one family. Earlier

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workers had included all the Isorophida in a single Family, the Agelacrinitidae.

Bassler (1936) and subsequent authors included several other species in the Hemicystitidae which are excluded from the Lebetodiscidae. Most of these are included here in the Carneyellidae. An analysis of Bassler's Hemicystitidae, which is rejected here, is presented under the discussion of the Carneyellidae.

Kesling (1967) suggested that one species here considered to be a Lebetodiscidae, the clavate Cystaster granulatus Hall, be removed from Bassler's Hemicystitidae and placed in his new Family Pyrgocystidae. As described by Kesling, the primary diagnostic character of Pyrgocystis Bather (1915) is the highly elevated "turret-like" theca. Pyrgocystis was not included in this study and thus cannot be adequately discussed here. However, the Family Pyrgocystidae is tentatively recognized, but seems best restricted to the type genus. Thecal shape alone seems to be generally a poor basis for family recognition since both high and low forms occur in most families. In detailed morphology Cystaster is clearly a member of the Lebetodiscidae. However, the combination of thecal shape with other possibly distinctive features of Pyrgocystis may warrant the separation of that genus at the family level, as Kesling proposed.

Clearly there is much yet to be discovered about the evolution of the Lebetodiscidae, since three of the five genera are monotypic and all five seem to be soundly conceived. Generic taxobases include: 1) thecal shape and size; 2) number, arrangement and size of secondary

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orals; 3) hydropore construction; 4) ambulacral disposition; 5) ambulacral coverplate size and shape; and 6) structures associated with the coverplate passageways.

At least one published description of a specimen not included in this study suggests relationship to the Lebetodiscina. Phillip (1965) described the only Southern Hemisphere edrioasteroid, a small specimen from Australia, preserved only as a mold in coarse sandstone. Phillip's brief description and illustration strongly suggest that the specimen belongs to the genus Cystaster, and may even belong in the North American species C. stellatus.

Contrasting the Lebetodiscidae with the Carneyellidae, Lebetodiscidae are characterized by: 1) oral area with shared coverplates and secondary orals; 2) hydropore structure located along the right proximal posterior edge of ambulacrum V, formed by ambulacral coverplates and interambulacral elements; 3) ambulacral coverplates very thick and thereby form high ambulacral ridges, a high narrow ambulacral tunnel, and also orient the large coverplate passageways almost normal to the thecal surface; and 4) squamose peripheral rim plates. In the Carneyellidae: 1) the oral area includes only the three primary orals and one hydropore oral (no shared coverplates or secondary orals); 2) the hydropore structure is located in the right posterior part of the oral region, formed by ambulacral coverplates and orals (rather than interambulacrals); 3) ambulacral coverplates are of moderate thickness and thereby form low, rounded ambulacral ridges, low wide ambulacral tunnels, and thus the coverplate passageways are nearly parallel to the

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thecal surface; and 4) the peripheral rim plates are geniculate.

Range and occurrence: Middle Ordovician through Upper Silurian of Eastern North America and Australia.

Genus Lebetodiscus Bather, 1908

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

1857 Agelacrinites Vanuxem, Billings, E. K., Geol. Sur. Canada, Rept. Prog. 1853-1856: 294-295.

1858b Agelacrinites Vanuxem, Billings, E. K., Geol. Sur. Canada, Fig. and Descriptions of Canadian Organic Remains, dec. 3: 84, pl. 8, fig. 3-3a, 4-4a.

1881 Agelacrinites Vanuxem, Grant, J. A., Ottawa Field Naturalists' Club, Trans. 2: pl. 1, fig. 9.

1887 Agelacrinites Vanuxem, Barrande, J. [partim], Systéme Silurien du centre de la Bohéme, Prague, pt. 1, 7(1): 55, 83.

1896b Agelacrinus Vanuxem, Haeckel, E., Die Amphorideen und Cystoideen, Leipzig, 1: pl. 3, fig. 29.

1899 Agelacrinites Vanuxem, Jaekel, O. [partim], Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 50, pl. 2, fig. 2.

1901 Agelacrinites Vanuxem, Clarke, J. M., New York St. Mus. Bull. 49(2): 191, text fig. 3.

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

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1915 Lebetodiscus Bather, Raymond, P. E. [partim], Ottawa Naturalist, 29 (5-6): 53-56, pl. 1, fig. 6.

1921 Lebetodiscus Bather, Raymond, P. E. [partim], Geol. Surv. Canada, Mus. Bull. 31 (Geol. Series 38): 4-7, pl. 1, pl. 2, fig. 9, pl. 3, fig. 1-2.

1935 Lebetodiscus Bather, Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 6.

1936 Lebetodiscus Bather, Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 9, pl. 3, fig. 10.

1938 Lebetodiscus Bather, Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 122.

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

1946 Lebetodiscus Bather, Wilson, A. E., Geol. Surv. Canada Bull. 4: 19; Lepidoconia Wilson, ibid.: 21, pl. 4, fig. 2.

1966 Lebetodiscus Bather, Regnéll, G., in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U165, text fig. 127-4; Lepidoconia Wilson, idem, ibid.: U165, text fig. 127-1.

Type species: Agelacrinites dicksoni Billings, 1857.

Diagnosis:

Lebetodiscidae with: domal theca, oral surface highly convex; oral region with secondary oral plates; hydropore structure formed by enlarged adradial end of second proximal posterior coverplate of

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ambulacrum V and two or three modified interambulacrals; ambulacra curve contrasolarly; coverplate passageways large, lateral depression series present.

Description:

The genus Lebetodiscus is monotypic. Therefore, separation of generic and specific taxobases is uncertain. Features outlined in the above diagnosis are in part inferred to be of generic rank from taxobases established for related Lebetodiscidae.

Lebetodiscus dicksoni (Billings), 1857

Text fig. 3-4; plate 1-2.

1825 "A Fossil Belonging to the Class Radiaria", Sowerby, G. B., Zool. Jour., London, 2, (7 art. 37): 318-320, pl. 11, fig. 5.

1848 "A remarkable American fossil", Forbes, E., Geol. Surv. Great Britain and Mus. Practical Geology, London, Mem. 2 (2): 519-520.

1857 Agelacrinites dicksoni Billings, E. K., Geol. Surv. Canada, Rept. Prog. 1853-1856: 294-295.

1858b Agelacrinites dicksoni Billings, E. K., Geol. Sur. Canada, Fig. and Descriptions of Canadian Organic Remains, dec. 3: 84, pl. 8, fig. 3-3a, 4-4a.

1881 Agelacrinites dicksoni Billings, Grant, J. A., Ottawa Field Naturalists' Club, Trans. 2: pl. 1, fig. 9.

1887 Agelacrinites dicksoni Billings, Barrande, J., Systéme Silurien du centre de la Bohéme, Prague, pt. 1, 7 (1): 55, 83.

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1896b Agelacrinus dicksoni Billings, Haeckel, E., Die Amphorideen und Cystoideen, Leipzig, 1: pl. 3, fig. 29.

1899 Agelacrinites dicksoni Billings, Jaekel, O., Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 50, pl. 2, fig. 2.

1901 Agelacrinites dicksoni Billings, Clarke, J. M., New York St. Mus. Bull. 49 (2): 191, text fig. 3.

1908 Lebetodiscus dicksoni (Billings), Bather, F. A., Geol. Mag. (n.s.), dec. 5, 5: 543-550, pl. 25, fig. 1.

1915 Agelacrinites dicksoni Billings, Bassler, R. S., United States Nat. Mus. Bull. 92, 1: 20.

1915 Lebetodiscus dicksoni (Billings), Raymond, P. E., Ottawa Naturalist 29 (5-6): 53-56; Lebetodiscus loriformis Raymond, ibid.: 56, pl. 1, fig. 6.

1921 Lebetodiscus dicksoni (Billings), Raymond, P. E., Geol. Surv. Canada, Mus. Bull. 31 (Geol. Series 38): 4-6, pl. 1, pl. 3, fig. 1; Lebetodiscus loriformis Raymond, ibid.: 7, pl. 2, fig. 9, pl. 3, fig. 2.

1935 Lebetodiscus dicksoni (Billings), Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 6; Lebetodiscus loriformis Raymond, idem, ibid.: 6.

1936 Lebetodiscus dicksoni (Billings), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 9; Lebetodiscus loriformis Raymond, idem, ibid.: 9, pl. 3, fig. 10.

1943 Lebetodiscus dicksoni (Billings), Bassler, R. S. and Moodey, M.W.,

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Geol. Soc. America, Spec. Pap. 45: 206; Lebetodiscus loriformis Raymond, idem, ibid.: 206.

1946 Lebetodiscus dicksoni (Billings), Wilson, A. E., Geol. Surv. Canada Bull. 4: 19; Lepidoconia loriformis (Raymond), idem, ibid.: 21, pl. 4, fig. 2.

1966 Lebetodiscus dicksoni (Billings), Regnéll, G., in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U165, text fig. 127-4; Lepidoconia loriformis Raymond, idem, ibid.: U165, text fig. 127-1.

Diagnosis:

A Lebetodiscus with: oral region having four secondary oral plates which lie between perradial parts of primary orals and shared cover-plates; hydropore structure formed by second proximal posterior cover-plate of ambulacrum V and three (?two) modified interambulacral plates; interambulacral plates large, thick and bearing one or two rows of depressions along distal extremity of external part of plates.

Description:

The domal theca of Lebetodiscus dicksoni is highly convex. The rim is commonly inclined at a high angle to the substrate, and its distal edge is occasionally reflexed under the upper side of the theca. The ambulacra and central oral region are highly elevated above the interambulacra and form conspicuous ridges on the thecal surface. Adults are commonly 20 to 24 mm in diameter, 24.2 mm the greatest known diameter.

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The oral region includes three primary orals, two pairs of lateral shared coverplates and four secondary orals (text fig. 3A, pl. 1, fig. 9-11). The two anterior primary orals abut each other laterally, along the anterior oral midline. The single large, central posterior oral meets the anterior primaries along the slightly anteriorly arcuate, transverse oral midline. One pair of lateral shared coverplates flank each side of the central primary orals. These are similar in shape and size to the ambulacral coverplates.

Four small secondary oral plates lie along the transverse oral midline, inserted between the perradial ends of the primary orals and the adjacent shared coverplates. Two are anterior to the midline and lie distal to the opposing posterior secondaries. The secondary orals are surficial and end a short distance below the surface of the theca in contrast with the primary orals and shared coverplates which extend into the interior of the theca. The transverse oral midline appears finely serrate in partially etched specimens and indicates the presence of inwardly projecting extensions from the oral plates.

A large sutural passageway extends inward along both flanks of each primary oral. The external openings of the two which are along the anterior edges of the two anterior primary orals are open, as in all of the ambulacral coverplate passageways. In contrast, the other four, two flanking the lateral edges of the anterior primaries and two flanking the posterior primary oral, are obstructed by the four secondary orals. The secondary orals appear to cause each passageway to bifurcate just before it reaches the exterior of the theca and this

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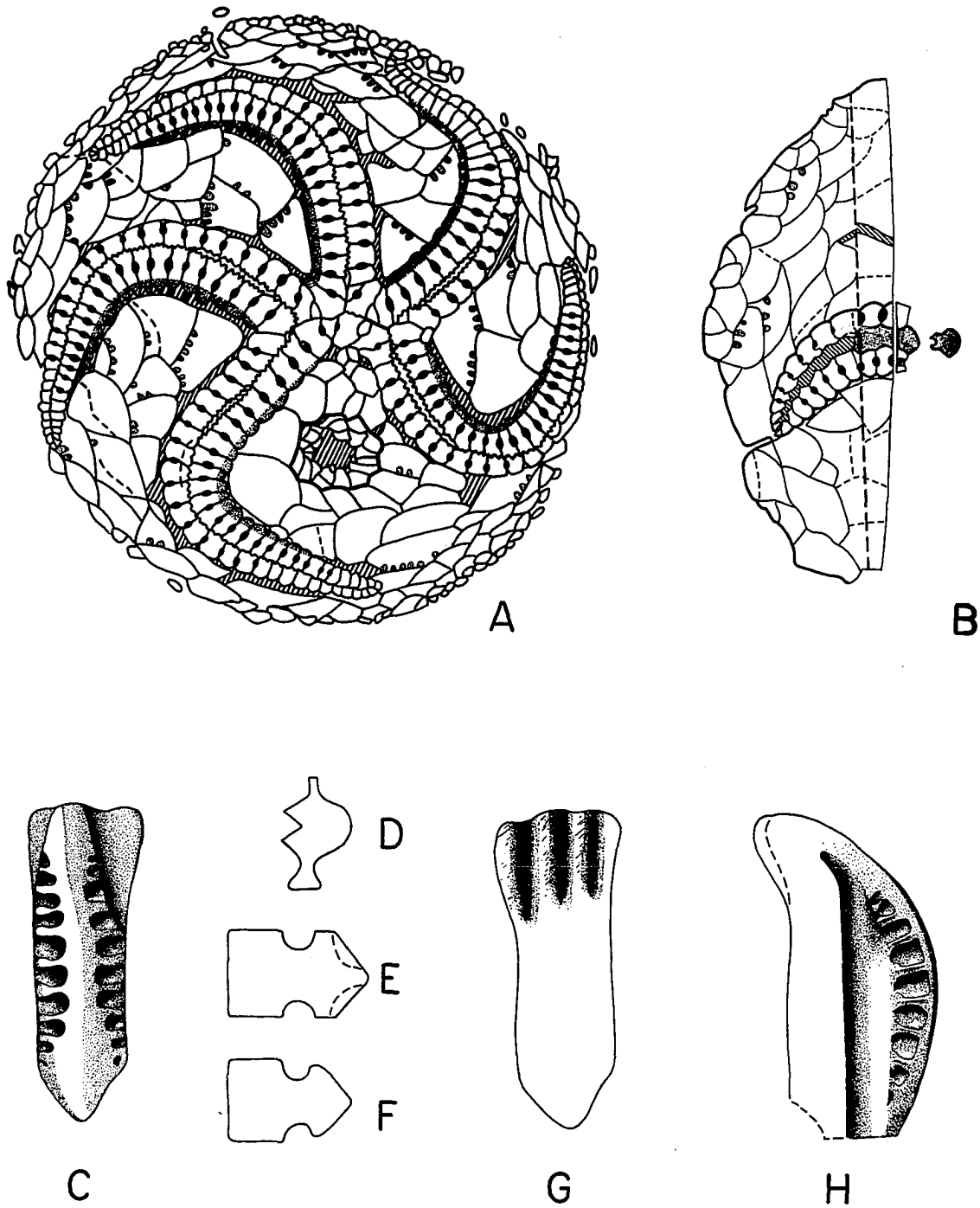
Text Figure 3 Lebetodiscus dicksoni (Billings), 1857

A. G.S.C. 437, (X4), pl. 1, fig. 10. Stippled ends of coverplates are the intrathecal extensions exposed by lateral displacement of adjacent interambulacrals.

B. Holotype, G.S.C. 1407-b, (X6), pl. 1, fig. 2. Ambulacral floorplates are shaded. A dashed line marks the left edge of the second, partial cut through the specimen. The isolated floorplate is an end view of the most proximal floorplate.

C.-H. Reconstruction of an ambulacral coverplate: C. Exterior view; D., E., F. cross-section views with exterior side to the right, ambulacral tunnel side to the left, D. the perradial end of plate, adjacent to the most perradial lateral basins, E. central section, dashed lines mark the floors of the lateral basins, F. adradial part of plate, adjacent to the most adradial basins; G. ambulacral tunnel side view; H. lateral view.

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Text Figure 3

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forms two small openings, one on either side of the secondary oral plate. In some instances one or both of the small openings appear to be completely covered by the secondary oral, so that the passageways beneath end blindly. The external closure of these passageways may have been a life condition, or it may have been effected during preservation.

The hydropore structure lies along the adradial suture line between ambulacrum V and interambulacrum 5, near the posterior edge of the oral area. It has been observed in only one specimen, G.S.C. 437, in which the area is somewhat etched, which apparently enlarged the size of the opening (text fig. 3A, pl. 1, fig. 10). The elongate, slit-like opening extends nearly parallel to the midline of the adjacent part of ambulacrum V. It appears to be bounded by four plates. The anterior or right edge of the opening is formed by the adradial end of the proximal coverplate of ambulacrum V. The proximal part of this adradial end is extended anteriorly as a broad lobe which intrudes into the distal, adradial edge of the right posterior shared coverplate. The posterior or left edge of the hydropore appears to be bounded by three interambulacral plates. Two small anterior elements form the proximal end of the opening's posterior edge. However, these may represent a single, large plate, broken during preservation. The distal part of the posterior edge of the opening is formed by the right anterior edge of an enlarged interambulacral which distally abuts the distal adradial tip of the proximal coverplate of ambulacrum V. This large interambulacral continues distally along the adradial suture line

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of ambulacrum V, and also abuts the adradial end of the second posterior coverplate.

The plates of the hydropore structure are elevated above the level of the adjacent interambulacral region. Apparently most of this relief is due to collapse of the interambulacrals whereas the hydropore plates remained elevated, supported by the plates which surround the underlying stone-canal passageway and the adjacent oral frame.

The internal structure of the oral region has not been observed. As in all known Lebetodiscidae where this area is exposed, it probably includes a large oral frame formed by the five enlarged proximal floorplates of the ambulacra, as well as the intra-thecal extensions from the three primary orals.

The five long, moderately wide ambulacra curve in a contrasolar direction. Curvature is most abrupt near the medial sectors where the ambulacra approach and become concentric with the proximal margin of the peripheral rim. The distal tips of adjacent ambulacra remain widely separated from adjacent ambulacra in both moderate-sized and some larger individuals, whereas in others they nearly touch the adjacent ambulacra. This contrasts with the closely related genus Foerstediscus in which the distal tips of the ambulacra remain widely separated from adjacent ambulacra even in quite large individuals. The ambulacra in Lebetodiscus dicksoni form high ridges above the interambulacra. This relief may be somewhat exaggerated by thecal collapse.

The ambulacral coverplates are large, extremely thick, and form a single biseries of alternating plates which meet along a serrate,

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sinuous, perradial line. In external plan view the plates are subrectangular; their perradial ends are bluntly pointed (text fig. 3 C-F). The external side of each coverplate is convex, both across the width in a proximal-distal direction, and also along the length of the plate, from the perradial line to the adradial suture (text fig. 3 C-F, H, pl. 1, fig. 5, pl. 2, fig. 4-5). The exterior arches outward and forms a rounded, sub-median ridge which extends from the adradial suture to the perradial line. Therefore, a trough is formed by the contact of the lateral edges of adjacent coverplates. The coverplate convexity is limited to the exterior due to the great thickness of these plates. The ambulacral tunnel side of each coverplate is a nearly vertical wall which extends from the upper surface of an underlying floorplate up to the central perradial part of the ambulacrum (text fig. 3 H). Thus the ambulacral tunnel is extremely narrow and exceptionally high.

Three small, intra-ambulacral ridges are formed along the perradial end of each coverplate. These extend outward perradially, normal to the ambulacral tunnel surface of the coverplate. Longest at the perradial tip of the plate, each ridge diminishes in height adradially and merges with the ambulacral tunnel side of the coverplate approximately half way down to the underlying floorplate. The middle ridge is largest, flanked by two smaller ridges which are subequal in size.

The intra-ambulacral ridges on opposing, alternate coverplates interdigitate along the perradial line when the coverplates are closed.

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The area of interlock is not great, but the ridges fit tightly together and seal the ambulacrum. In etched specimens the upper ends of these interlocking ridges are exposed and form small serrations along the perradial line.

Large, blade-like intra-ambulacral extensions are produced from the proximal edge of the ambulacral tunnel side of each coverplate (text fig. 3 D, G). They extend inward toward the ambulacral tunnel and flex proximally toward the oral region. The distal part of each extension curves upward and the distal edge of the extension abuts the inner side of the adjacent, next proximal coverplate. These intra-ambulacral extensions are thus trough-shaped (text fig. 3C, D). The perradial end of each extension is produced the furthest toward the oral region. The lower or adradial part of the extension progressively decreases in size downward and merges with the side of the coverplate approximately half way down to the floorplates. The outwardly curved proximal tip of the trough-shaped extension fits into a shallow groove on the inner surface of the next proximal coverplate. Thus the adjacent coverplates are tightly locked together when closed. Apparently this interlocking was maintained even where the coverplates were rotated open, essentially no differential movement occurring between the laterally sutured adjacent coverplates. The outer distal edge of each coverplate is slightly extended distally so as to abut the proximal outer edge of the adjacent posterior coverplate. Thus, a space is formed between this outer edge and the underlying intra-ambulacral extension of the adjacent distal coverplate. This space is

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the upper part of the sutural passageway, described below.

The basal adradial ends of the coverplates extend between adjacent interambulacrals and the underlying ambulacral floorplates into the interior of the theca and form the intra-thecal extensions of the coverplates. These are as thick as the external parts of the coverplates, in contrast with most intra-thecal extensions which are considerably thinner than the external parts of the plates.

Large passageways extend from the thecal cavity to the exterior of the theca along the lateral sutures of adjacent coverplates. Each passageway is formed subequally by the adjacent edges of two contiguous coverplates. The great thickness of the coverplates permits the passageways to extend vertically into the interior of the theca. Each coverplate has a hemicylindrical groove incised into each lateral sutural face (text fig. 3E, F, H). The two opposing grooves of adjacent coverplates unite to form a terete, tubular passageway. The inner end or inner foramen of each passageway opens into the thecal cavity. It is formed by the intra-thecal extensions of adjacent plates, each forming half of the elliptical opening. The aperture is elliptical rather than circular because the inner surfaces of the coverplate extensions lie at a slight angle to the vertical cylindrical passageway. Thus the internal foramen is elongate normal to the ambulacral axis. The external foramina are also elliptical, elongate normal to the ambulacral axis in correlation with the downward curvature of the exterior side of the coverplate. The upper end of each passageway and the external foramen are unequally shared by the two adjacent coverplates, the more

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distal plate forming a larger part than the proximal one. This disparity results from the large size of the intra-ambulacral extension on the proximal inner edge of each coverplate. The outer surface of this extension forms most of the perradial side of the upper part of the passageway and foramen, and thus restricts the participation of the proximal coverplate. The width of the proximal intra-ambulacral extension rapidly diminished inward so that shortly below the surface of the ambulacrum, the passageways are equally formed by the two adjacent coverplates, each half being formed by the hemicylindrical groove in the side of adjacent coverplates. The passageways lead from the thecal cavity to the exterior. Thus, the passageways lack direct communication with the ambulacral tunnel.

A row of obovate, basin-like depressions is incised into both external lateral edges of each coverplate so that one row flanks each side of the lateral suture line between adjacent coverplates (text fig. 3C, H, 4D, pl. 1, fig. 5, pl. 2, fig. 4-5). Perradially these depressions flank the edges of the passageway external foramina. In the opposite direction they extend down almost to the adradial suture line. Each depression of the series is sub-circular and deeply incised into the external surface of the coverplate. The floor of the basin remains at nearly the same level. Thus, due to the convexity of the external coverplate surface, each basin becomes progressively deeper toward the center of the plate. The walls of the basin are nearly vertical. Each basin opens directly into the suture line trough between adjacent coverplates through a narrow channel.

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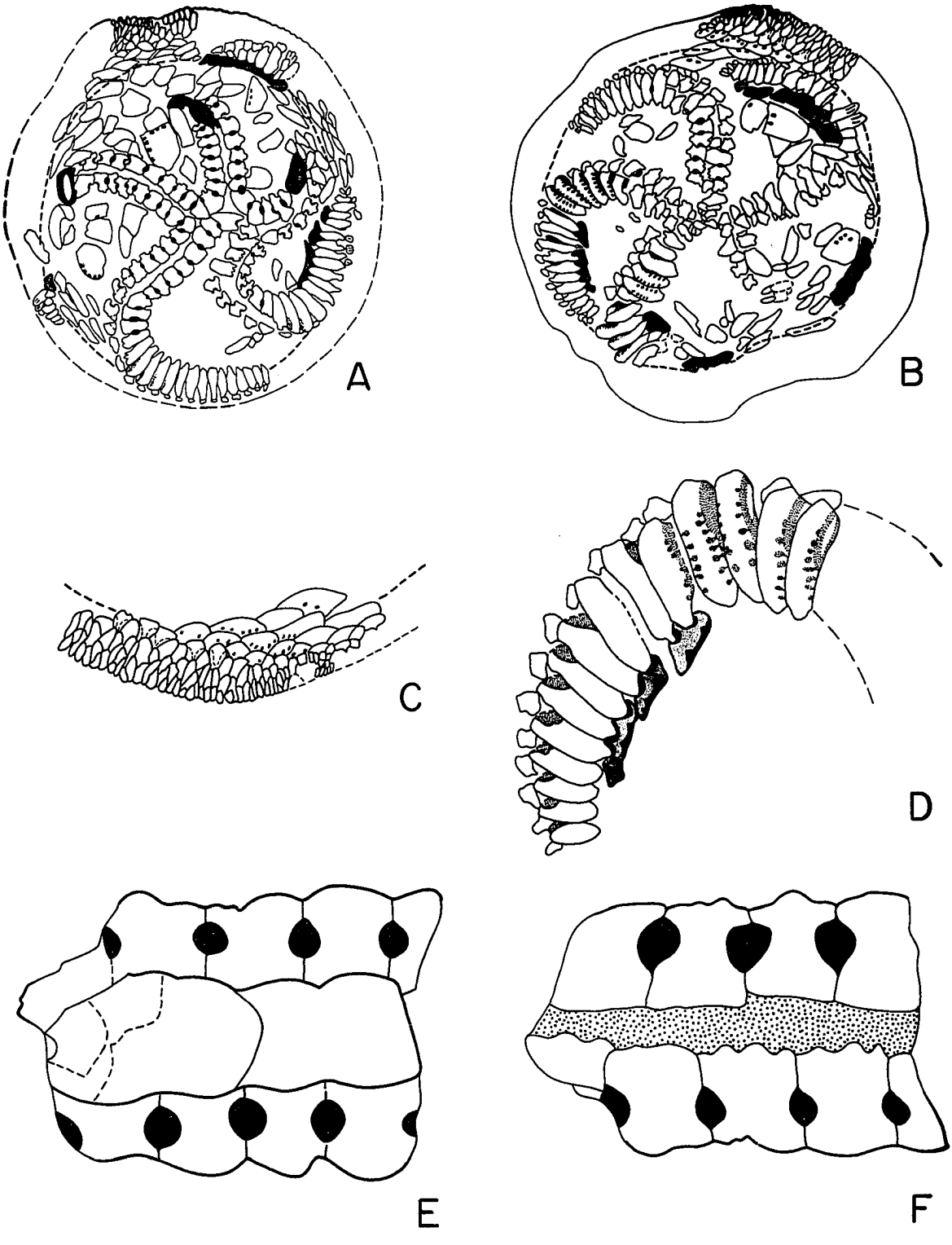
Text Figure 4 Lebetodiscus dicksoni (Billings), 1857

A. R.O.M. 160t-a, (X3), pl. 2, fig. 8. Ambulacral floorplates are shaded.

B.-D. G.S.C. 1414. B. Oral surface, (X3), pl. 2, fig. 2. Ambulacral floorplates are shaded. C. Peripheral rim segment, (X5), pl. 2, fig. 6. D. Ambulacrum II, (X11), pl. 2, fig. 4. Coverplate intra-ambulacral extensions and lateral basins are stippled; floorplates are shaded.

E.-F. Segment of ambulacrum IV, G.S.C. 1412, (X16). E. Interior side, pl. 2, fig. 12. F. Exterior side, pl. 2, fig. 13. Ambulacral tunnel zone stippled.

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Text Figure 4

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The relationship of the two opposing rows of basins along each lateral suture line appears to be random. The basins have been observed opposite one another, alternate, or even to change relationship along the length of a single sutural trough.

Commonly eight or nine basins occur in each row. Those near the center of the plate are largest and deepest, those near the adradial suture line much shallower. Basins near the perradial line are also shallow, and open broadly into the adjacent passageway foramen.

The ambulacral floorplates are uniserial and thick, sub-rectangular in plan view, the width being nearly as great as the length. Sutures between consecutive floorplates are oblique, the proximal end of each plate overlapping the distal end of the next plate. However, the degree of overlap appears to be less than in Streptaster vorticellatus or Carneyella pilea where overlap approaches half the floorplate length. The lower or inner surface of each floorplate is evenly convex inward. The upper surface is convex upward, but a small axial trough is incised into the center of each which extends the length of the floorplate. The lateral zones of the upper surface, flanking the axial trough, slope downward toward the adradial suture. Small concavities are excavated into this sloping surface, each with a small raised rim along the adradial edge. The basal part of the inner, ambulacral tunnel edge of an overlying coverplate fits into each of the excavations. Only the inner edge of the coverplate rests on the floorplate; the remaining basal part extends laterally past the floorplate margin and forms the intra-thecal extension of the coverplate.

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In the proximal parts of the ambulacra each floorplate underlies slightly more than two pairs of coverplates. Distally the floorplates decrease in proximal-distal length more rapidly than the coverplates, so the relationship between the two sets of elements approaches one to one. The ambulacral coverplates rise vertically from the edges of the narrow axial trough for most of their height. Only the uppermost part of each is flexed inward (perradially) to meet the opposing coverplate along the perradial line. The ambulacral tunnel is thus quite narrow and exceptionally high.

The interambulacrals are imbricate, sub-polygonal to squamose plates. Each is relatively large in proportion to thecal diameter compared to the interambulacral plates of most edrioasteroids. Sutures between the imbricated plates are oblique and each plate proximally overlaps the distal edge of the adjacent element. One or two rows of elongate depressions occur near the distal edge of the upper surface of each interambulacral. They are usually, in part, covered by the overlapping part of the next distal plate. Thus, the depressions falsely appear to be sutural openings into the theca.

The periprocteal anal structure lies slightly proximal to center of the posterior interambulacrum. It includes a large number of plates which form several irregular circlets. The periproct plates are elongate toward the anal orifice but become progressively smaller as it is approached. The structure appears to have been elevated to form a low conical protuberance.

The peripheral rim comprises seven or eight circlets of squamose

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plates. During collapse these are equally depressed with the adjacent distal interambulacrals which obscures the boundary between the two areas. The proximal four circlets of large plates are externally elongate concentric with the thecal margin. The following circlet is formed by a transition series of plates which are externally sagittate. The depressed distal lateral flanks of each transition plate are overlapped by radially elongate plates of the following circlet. The distal two circlets of small plates are radially elongate.

The peripheral rim appears to have been steeply inclined to the substrate in most specimens, suggesting that the proximal circlet plates did not internally intersect the underlying surface.

External plate surfaces appear to be smooth, except for a fine pitting which reflects the microstructure of the plates where stroma canals intersected the plate surface.

Specimens:

G.S.C. 1407-b Fragment of the holotype of Lebetodiscus dicksoni (Billings) (1857, p. 294-295, 1858, pl. 8, fig. 3, 3a). "Trenton Limestone", Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario. 13.1 mm long by 5.3 mm wide.

Text fig. 3B, pl. 1, fig. 1-2.

This specimen is believed to be a fragment of the holotype which apparently includes the distal tip of ambulacrum II and the adjacent parts of interambulacra 1 and 5, along with a bit of the adjacent peripheral rim. The fragment has been sawed from the holotype (sometime since the original description) by a vertical cut through the

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specimen and the matrix. A second cut was also made adjacent and nearly parallel to the first. It extends only part way through the theca and leaves both a vertical and a horizontal section visible, as seen in plate 1 and text figure 3B. Unfortunately the remainder of the holotype is apparently lost.

In the collection of the Geological Survey of Canada, this specimen had been included with the type material of Edrioaster bigsbyi. Although only a fragment, it is obvious from the structure of the ambulacra that it pertains to Lebetodiscus dicksoni. Fortunately, due to the scarcity of L. dicksoni, Raymond (1915, 1921) described in detail the holdings of the Canadian Survey. All of the specimens which he saw have been accounted for except the type, and it is therefore quite likely that this is a fragment of the missing specimen. Moreover, comparison of the fragment with Billings' (1858) original figure of the holotype shows close similarity between the specimen and the drawing. It should be noted, as Bather (1908) has previously, that Billings' illustration of the type specimen is much more complete than indicated by his written description. Bather evidently saw the type specimen before it was sawed, and indicates that the drawing was accurate. The specimen included the proximal parts of all five ambulacra, the distal part of three of these and the two intervening interambulacral areas. This contrasts with the original description which reported only one "perfect" ambulacrum and the adjacent interambulacra.

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G.S.C. 437 Illustrated Specimen of L. dicksoni by Grant (1881) and others. "Cobourg beds, Trenton Limestone", Trenton Group, Mohawkian Series, Middle Ordovician. Steamboat landing, foot of Sussex Street, Ottawa, Ontario. 23.6 mm axial by 22.5 mm transverse diameter.

Pl. 1, fig. 9-11.

The "Grant specimen" (of authors) is an extremely well-preserved individual with little plate disruption. A few peripheral rim plates are not visible. However, the surface of the theca has been deeply etched, particularly the high ambulacral and oral regions. Thus, almost all of the lateral depression series of the coverplates are missing, along with other surficial features.

G.S.C. 1414 Holotype of Lepidoconia loriformis (Raymond) (1915, p. 56). Cobourg beds of Trenton Limestone, probably the "Cystid beds", about 180 feet below the top of the Trenton, Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario. 24.2 mm axial by 22.8 mm transverse diameter.

Text fig. 4B, C, D, pl. 2, fig. 1-6.

This individual has collapsed and the interambulacra and ambulacra I, IV and V are disrupted and, in part, crushed. Only ambulacra II and III and part of the peripheral rim remain intact. Fortunately, the specimen has undergone little etching so that the rim and the two well-preserved ambulacra retain their surficial features, including the lateral depression series of the ambulacral coverplates. The partial disruption of the theca exposes lateral views of the floorplates and

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also parts of some of the coverplates that are generally hidden from external view.

The specimen was long considered an example of Lebetodiscus dicksoni, but Raymond (1915) proposed the species L. loriformis for this individual, and Wilson (1946) created the genus Lepidoconia for Raymond's species.

G.S.C. 1412 Illustrated Specimen of Lebetodiscus dicksoni by Raymond (1921, pl. 3, fig. 1). "Trenton Limestone", Trenton Group, Mohawkian Series, Middle Ordovician. Peterborough, Ontario. 21 mm axial by 23.7 mm transverse diameter.

Text fig. 4E, F, pl. 2, fig. 10-B.

This specimen (referred to by authors as the "Fitzpatric specimen") has been deeply etched. The interambulacral elements are reduced to merest films, and the thicker ambulacral and oral plates have been greatly reduced. The smaller secondary orals are lost entirely. The major thecal structures can be recognized, however. A fragment of the proximal part of ambulacrum IV was broken from the specimen at some previous time and glued back in place. This fragment was removed and is illustrated here from its outer and inner side (text fig. 4E, F, pl. 2, fig. 12, 13). Both the exterior and interior surfaces of the plates have been etched. The coverplates were disproportionately reduced by solution, thus the floorplates appear to be much larger in relationship to the coverplates than in non-etched specimens. Apparently over half the thickness of the coverplates has been removed.

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R.O.M. 161-t-a. A Lebetodiscus dicksoni described by Raymond (1915, 1921) and by Wilson (1946) as "G.S.C. 1415". "Trenton Limestone", Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario. 22.7 mm axial by 20.9 mm transverse diameter.

Text fig. 4A, pl. 2, fig. 7-9.

The specimen has collapsed, disrupting some plates, and has also been crushed after lithification. All five ambulacra are preserved, but most other thecal structures are difficult to interpret. One section of the peripheral rim is well-preserved. Sections of ambulacra II and III had been previously ground away which exposes a vertical cut through ambulacrum II and an oblique cut through III, thereby revealing sectional views of the structure of the ambulacra.

The specimen was found in the Royal Ontario Museum under the number 161-t-a. There can be little doubt about the identity of this specimen as the old G.S.C. 1415, for the specimen compares well with Raymond's 1915 description, including the ground sections through ambulacra II and III. Wilson (1946) noted that G.S.C. 1415 was missing from the Geological Survey collections and erroneously considered the specimen to be the holotype of the species, which it is clearly not, as noted by Raymond (1915). Dr. Thomas E. Bolton of the Canadian Geological Survey advises: "The loan of fossil specimens, types and non-types, was very extensive in the late 1800's and early 1900's, and it is very possible that type 1415 was included in a shipment to Parks by Billings --W. R. Billings, or even Whiteaves. Records are nil of such movements" (Personal communication, 1969).

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R.O.M. 18848-a. Trenton Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario. 17 mm axial by 20.5 mm transverse diameter.

Pl. 1, fig. 12-13.

This specimen is missing a section of the right posterior part of the theca and most of the rim plates. The specimen has been etched, leaving only remnants of the coverplate lateral depression series and enlarging the external foramina of the coverplate passageway system. Happily, the etching exposes the interdigitation across the perradial line of the inner, perradial ridges of the ambulacral coverplates, a feature clearly seen only in this specimen.

R.O.M. 18855 (a-c). Three specimens of L. dicksoni. Trenton Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Hull, Quebec.
R.O.M. 18855-a. 10.5 mm axial by 10.3 mm transverse diameter.

Pl. 1, fig. 6.

A small, poorly preserved individual that has suffered extensive etching and has collapsed into an underlying depression in the substrate.
R.O.M. 18855-b. 22.8 mm axial by 25 mm transverse diameter.

Pl. 1, fig. 3-5.

A large specimen which is centrally disrupted; a zone of less disrupted plates surrounds the jumbled central region. The distal tips of all five ambulacra are nearly intact. Fortunately, the specimen has undergone but little etching, and therefore surface detail of the plates is well-preserved. Moreover, the disrupted central plates expose views

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of all sides of the ambulacral coverplates and those normally hidden parts of these plates are revealed.

Y.P.M. 28451 (old #2361). A specimen of L. dicksoni which was one of ten specimens labeled Edrioaster. Lower Trenton, Trenton Group, Mohawkian Series, Middle Ordovician. Curd's farm, Mercer County, Kentucky. 18.6 mm axial by 15.1 mm transverse diameter.

Pl. 1, fig. 7-8.

This individual has been replaced by beekite which obscures most sutures. The main structural features of the theca are preserved, although the left anterior quarter of the specimen is missing. It is noteworthy in being the only example of the species known from outside the Ottawa, Ontario region. Moreover, ambulacrum II has a small side branch just proximal to the point at which the main extension of the ambulacrum has been broken. This is the only representative of this species in which an additional ambulacrum is known. The specimen also appears essentially uncollapsed, preserving the original convexity of the oral surface. The center of the theca is 7.7 mm above the most distal preserved part.

Three other representatives of L. dicksoni have been reported. Jaekel (1899) illustrated, but only briefly described, a specimen from the Trenton Limestone (Ottawa) from the collection of Prof. Frech at Breslau. The second individual, the first edrioasteroid ever reported, was illustrated and briefly described by Sowerby (1825), mentioned by Forbes (1848), illustrated by Billings (1858), and illustrated and

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described in detail by Bather (1908). It is from the Lower Trenton, Middle Ordovician, Table Rock at Chaudière Falls of the Ottawa River at Ottawa, Ontario, Canada. The third is a specimen listed by Ami (1905) as belonging to this species, from the collection of Sheriff Dickson, the specimen from the Trenton Limestone, at Pakenham, Ontario.

Discussion of previous investigation:

The designation of the holotype of Lebetodiscus dicksoni (Billings), (represented here by specimen G.S.C. 1407-b which is considered to be a fragment of the original specimen), requires explanation, for some earlier workers have been confused as to its identity.

The first illustration and brief description of a specimen of L. dicksoni was by Sowerby (1825), but no name was assigned to the species. This same specimen was again referred to by Forbes (1848), but remained without a binomen. In 1857 Billings proposed the name Agelacrinites dicksoni for a different specimen, then in the collection of the Canadian Geological Survey. Billings had only one specimen in his possession, but he notes he had seen others. In that his specimen was incomplete, he based part of his original description on an unspecified number of other specimens which he did not cite. The following year, Billings revised his definition of A. dicksoni, and figured two specimens, the fragmentary individual in the collections of the Geological Survey (the one specifically mentioned in the original description), and a second individual, the Bigsby specimen. It is entirely possible the Bigsby specimen played a part in the original description (i.e., one of his "other specimens" of the species), but this cannot be

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established. Thus, the fragmentary specimen specifically identified by Billings in the original description (1857) and figured by him in plate 8, fig. 3, 3a (1858) must be considered the holotype by monotypy. The Bigsby specimen is considered to be only an Illustrated Specimen. Bather (1908) evidently arrived at the same conclusion and referred to the specimen of plate 8, fig. 3, 3a as the holotype of Lebetodiscus dicksoni. G.S.C. 1407-b is believed to be a fragment of that specimen.

Billings' (1857) original description of Agelacrinites dicksoni was brief, citing thecal size and shape, the ambulacra shape and direction of curvature, and the double row of "marginals" [coverplates]. The two earlier descriptions of the Bigsby specimen (Sowerby 1825, Forbes 1848), published without a binomen, also noted only general thecal features. Billings' (1858, p. 84) redescription of the species compared "two rows of small circular indentations on each side of the rays" with the ambulacral floorplate "pores" of Edrioaster bigsbyi. However, Billings was unsure whether or not the A. dicksoni depressions actually penetrated into the theca. This paper included the first illustration of the holotype (plate 8, fig. 3-3a) and also re-illustrated the Bigsby specimen (plate 8, fig. 4-4a).

Bather (1908) redescribed A. dicksoni, and proposed the genus Lebetodiscus for it. Bather's detailed description was based on the Bigsby specimen, and differs significantly from that presented here in relation to the ambulacral structure. Bather reported the ambulacra were formed by large convex-upward, biserial floorplates [actually the coverplates] with a small, median, food groove trough roofed by tiny

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irregular covering plates. He recognized the large sutural passageways, but since he interpreted the coverplates as floorplates, he described the passageways as homologous to those in the floorplates of Edrioaster bigsbyi. Bather presented four drawings of ambulacra exteriors. Two of these (1908, text fig. 1-2) are regularized and appear as he described them. The other two (1908, text fig. 3-4) were prepared from magnifications. It appears that Bather's irregular, tiny, median "coverplates" are likely fragments of plates. This explains why he thought only a few "coverplates" are present in the specimen and that nothing could be said about them except that they were tiny and have no regular arrangement. It now appears that Bather's specimen is a typical example of L. dicksoni. Unfortunately it was not available for re-examination during this study.

Bather's misinterpretation of ambulacral coverplates in L. dicksoni as floorplates probably stemmed from his definitive work on Edrioaster bigsbyi. The plates of the latter are unusually large, and Bather studied excellently prepared specimens. This work first established the morphology of the ambulacra of E. bigsbyi, including the structure of the floorplate passageways. Bather considered E. bigsbyi to be a "typical" edrioasteroid. Thus he expected to see similar characters in Lebetodiscus dicksoni. Noting the large coverplate passageways, he assumed these to be between floorplates as in E. bigsbyi.

Raymond (1915, 1921) described all specimens of L. dicksoni in the collections of the Geological Survey of Canada. He noted that Bather had misinterpreted the ambulacral structure. Raymond also suggested

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that two of the three features Bather used to distinguish L. dicksoni from the other edrioasteroids were in fact preservational, i.e., the supposed absence of a peripheral rim and the thecal shape, which Bather described as being more convex and less sessile than that of related species. The third feature used by Bather to distinguish his new genus was the supposed biseries of ambulacral floorplates with pores. Raymond noted that Bather had misinterpreted the ambulacral coverplates as floorplates, and pointed out that the true floorplates were uniserial, hidden from view in Bather's specimen. However, Raymond did not deny the existence of the small median plates which Bather reported, but rather he ascribed them to an additional series of coverplates such as had been referred to by Foerste (1914) as median coverplates in Isorophina.

In addition to a redescription of L. dicksoni, Raymond proposed Lebetodiscus loriformis, based on one large specimen long considered to belong to L. dicksoni. Although Raymond acknowledged the close resemblance of this specimen to L. dicksoni, his diagnosis was more evolutionary than morphologic. He thought his new species "forms one of the 'connecting links' with the species of later formations" (Raymond, 1915, p. 56). The only feature actually noted by Raymond as differing from the average specimens of L. dicksoni was that the ambulacra are so long that they nearly touch one another. This supposed trait is due principally to preservation and to the large size and advanced age of the specimen. Wilson (1946) proposed the genus Lepidoconia for Raymond's "species". She admitted its similarity to

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Lebetodiscus, but distinguished her genus by the presence of a unique "pore" system consisting of five "pores" on each lateral margin of each ambulacral coverplate. She reported the "pores" on the two sides of each plate as opposite, while the "pores" of adjacent plates were alternate.

The specimen upon which Lepidoconia loriformis is based is a typical Lebetodiscus dicksoni. It has undergone little etching. Thus surficial features are well-preserved, including the lateral depression series of the ambulacral coverplates which Wilson described as a multiple "pore" system. The lateral depressions, seven to nine per row (not five), are surficial features, limited to the exterior of the plates. The only other criterion noted by Wilson for separating her new genus from Lebetodiscus was the presence of a well-developed peripheral rim. Although the peripheral rim is not well-preserved in most individuals, remnants are present in many specimens of L. dicksoni.

Wilson (1946) also briefly redescribed Lebetodiscus dicksoni. She noted the presence of "pores" in the ambulacra, but suggested that they lie between "side plates" which were larger than another set of plates "on top of the ambulacral groove". It appears that Wilson was in part using Bather's terminology and in part that of Raymond without actually attempting to reconcile their differences.

Subsequent references to Lebetodiscus dicksoni have been cursory. Bassler's brief mention of Lebetodiscus is noteworthy only because he erroneously described the interambulacral plates as mosaic (tessellate), at least in Lebetodiscus "loriformis", which is not borne out by the

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type specimen. This mistake is evidently the origin of Regnéll's (1966) erroneous statement that tessellate interambulacral plates occur in the genus Lebetodiscus.

Discussion:

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

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

The coverplate passageways in Lebetodiscus dicksoni are the largest of any yet encountered within the Lebetodiscina. It seems likely from the proximity of the external foramina of the passageways

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and the lateral depression series of the coverplates that their function may be interrelated. The most rational correlation of both would be with the water-vascular system. Apparently in this suborder, the radial water canals extended beneath the ambulacra, along the lower side of the ambulacral floorplates. Each large primary radial canal would seem to have branched laterally along its length, sending alternate branch canals to the inner foramen of each passageway. One branch radial canal would thus have entered each of the passageways through the inner foramen, extended upward through the passageway to the exterior of the theca, and made its exit through the external foramen.

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

As discussed under the introductory section on respiration, these external extensions of the hydrovascular system are thought to be respiratory structures. As in all Lebetodiscina, these extensions

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would permit respiration whether the ambulacra were open or closed.

The passageways which lie between the oral area coverplates would appear to descend into the central lumen of the oral frame, and therefore would be divorced from the radial canals. As suggested by the apparent closure of the external openings of some of these by the secondary oral plates, these oral passageways would appear to be non-functional, lacking extensions from the hydrovascular system. The oral covering plates in all edrioasteroids appear to be modified ambulacral coverplates in origin, thus the oral area passageways may be relict structures.

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

The interlocking intra-ambulacral extensions of the coverplates necessitate very little if any differential movement between adjacent

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

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

It is interesting that perradial ridges also occur on the inner surface of oral plates as well as on the ambulacral coverplates. These produce serrate oral midlines in etched specimens. Apparently there are more than three ridges on each large oral plate. If so, these ridges may indicate that the primary oral plates are compound and were

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formed by the fusion of two or more individual ambulacral coverplates. Plate compounding in edrioasteroids is otherwise known only in the formation of the oral frame elements of the Edrioasterida.

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

Range and occurrence: Trenton Limestones, Middle Ordovician, Ottawa region, Ontario (including Peterborough, Ontario), and Mercer County, Kentucky. [For those specimens from the Ottawa region with accurate

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data, the stratigraphic occurrence of all known specimens is "Cobourg beds" (= the "Cystid beds, about 180 feet below the top of the Trenton"). The Kentucky specimen is listed as Lower Trenton.]

Genus Foerstediscus Bassler, 1935

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

1936 Foerstediscus Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 9-10, pl. 2, fig. 6-7, pl. 7, fig. 13.

1938 Foerstediscus Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 12, 99.

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

1960 Foerstediscus Bassler, Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 161-162, text fig. 8, pl. 7, fig. 1-2.

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

Type species: Foerstediscus grandis Bassler, 1935.

Diagnosis:

Lebetodiscidae with: highly convex domal theca; oral area with several secondary orals; hydropore structure along adradial suture line of posterior side of ambulacrum V, formed by first three coverplates of ambulacrum V and one or more modified interambulacral plates; ambulacra

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curved, I-V solar; coverplate passageways large, external foramina elliptical; coverplate lateral depression series present.

Description:

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

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

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

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Text Figure 5 Foerstediscus grandis Bassler, 1935

A.-B. R.O.M. 543t-a.

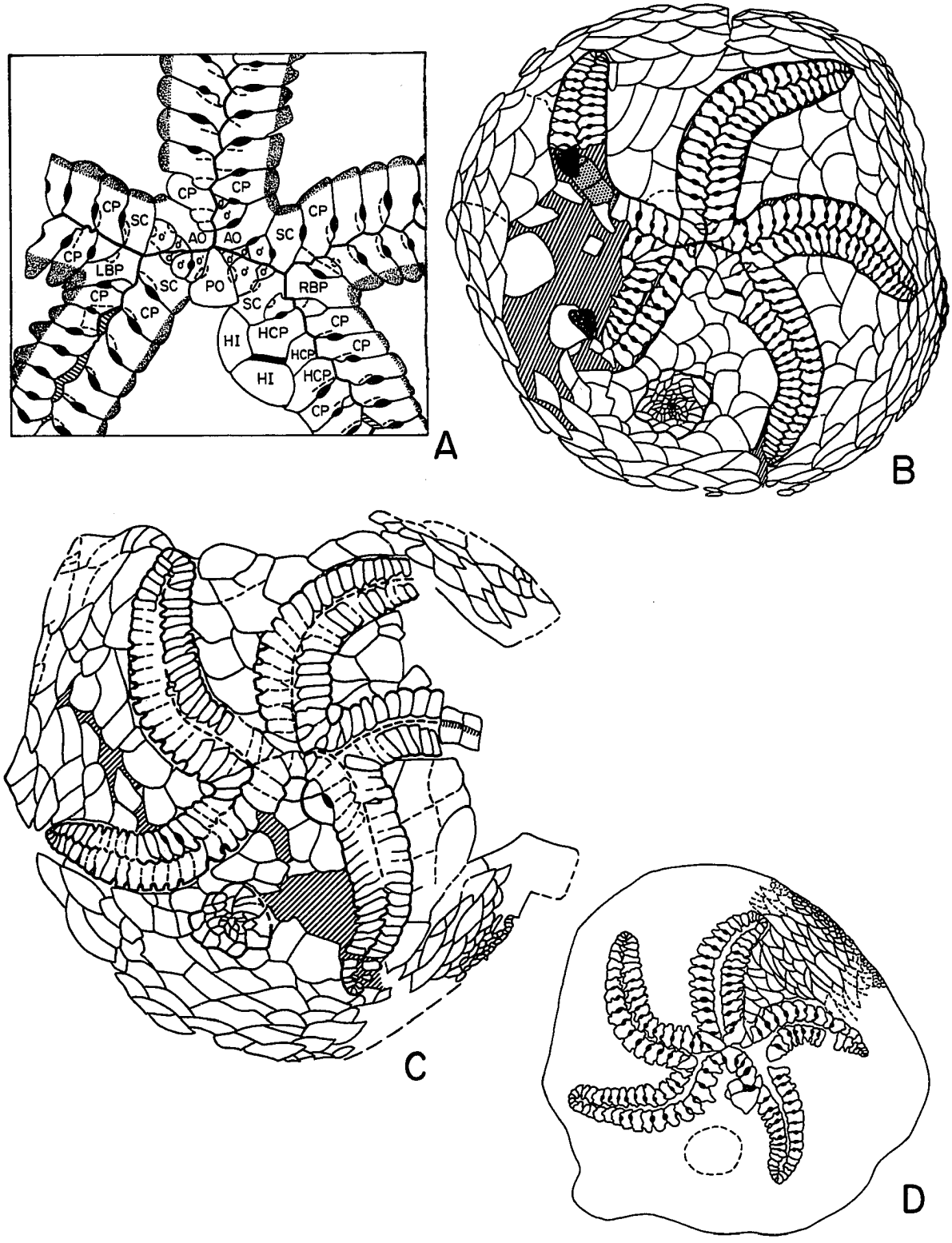
A. Oral region, (X8), pl. 3, fig. 5. Ambulacral coverplate intrathecal extensions are stippled; intra-ambulacral extensions are separated from the main body of the coverplates by dashed lines. AO. anterior primary oral plate; CP. ambulacral coverplate; HCP. hydropore ambulacral coverplate; HI. hydropore interambulacral plate; LBP. left lateral bifurcation plate; o'. secondary oral plate; PO. posterior primary oral plate; RBP. right lateral bifurcation plate; SC. lateral shared coverplate.

B. Oral surface, (X4), pl. 3, fig. 4. Ambulacral floorplates with large dots; lateral view of two disrupted ambulacral coverplates with stippled pattern, coverplate passageways blackened.

C. Holotype, U.S.N.M. S-3191, (X4), pl. 3, fig. 2.

D. U.S.N.M. S-3889-A, (X9), pl. 4, fig. 2.

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Text Figure 5

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intrudes into the edge of the ambulacrum.

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

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

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

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

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

Both smooth and pustulose species of Foerstediscus occur.

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Discussion:

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

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

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

The only known report of a specimen assigned to this genus that

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

Range and occurrence: Trenton Group, Middle Ordovician to lower Keyser Formation, Upper Silurian, of Minnesota, Kentucky, Pennsylvania and Ontario.

Foerstediscus grandis Bassler, 1935

Text fig. 5; plate 3-4

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

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

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

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

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

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Diagnosis:

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

Description:

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

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

The secondary orals are of three groupings, two lateral and one anterior. The lateral groups lie between the primary orals and shared coverplates and include an anterior and a posterior section separated by the transverse oral midline. Both anterior and posterior parts include a central secondary oral, approximately one-third the size of the

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

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

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

Most of the smaller specimens of F. grandis appear to include all

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five large secondary orals found in the larger adult (R.O.M. 543t-a), but only a few of the smaller secondaries. This may be preservation, for all the small specimens are etched, or possibly, the smaller secondaries were added late in ontogeny.

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

The hydropore structure of Foerstediscus grandis appears to be much like that found in Lebetodiscus dicksoni. However, specimens of

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both are scarce, and in most of these the hydropore structures are disrupted. Thus, the similarity may be more apparent than real.

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

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

The squamose, imbricate interambulacrals are of moderate size.

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

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and ambulacral coverplates apparently are smooth.

Specimens:

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

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

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

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

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

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

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

U.C.M.P. 40433, 40434, 40435, 40436. Four specimens of F. grandis. "Trenton Limestones", Trenton Group, Mohawkian Series, Middle Ordovician. Quarry at Kirkfield, Victoria County, Ontario (probably from near the floor of the Quarry). Kopf Collection.
U.C.M.P. 40433. 33 mm axial by 28.7 mm transverse diameter.

Pl. 4, fig. 9.

The completely collapsed theca of this specimen has been extensively etched and the right third of the specimen is missing. The peripheral rim is well-preserved in two sectors. Several lateral views of the ambulacral coverplates and their passageway structures are exposed in the disrupted distal part of ambulacrum III. The tips of the

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ambulacra remain widely separated from the nearest part of the adjacent ambulacra despite the large size of the individual. Accessory plates are seen adjacent to the bifurcation plate. This is the largest known representative of the species.

U.C.M.P. 40434. 24.6 mm axial by 26.7 mm transverse diameter.

Pl. 4, fig. 10.

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

U.C.M.P. 40435, 40436. Two poorly preserved specimens that probably belong to this species.

The above four specimens rest directly on a firm carbonate substrate which is highly irregular, with large rounded knobs separated by deep interconnected channels. This surface is quite similar to the one described by Koch and Strimple (1968) [see description p.831] and probably represents an intertidal or very shallow sub-tidal environment.

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

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

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

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

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

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

Pl. 4, fig. 3.

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

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

Pl. 4, fig. 4-5.

This is the best preserved of the six F. grandis specimens numbered U.S.N.M. 3889. The theca has collapsed, disrupting some interambulacrals, and surficial etching has removed some plate detail. However, secondary orals are seen on the left half of the oral region, and

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the hydropore plates can be recognized.

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

Pl. 4, fig. 6-7.

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

U.S.N.M. S-3889-E. Type series specimen of F. parvus Bassler (1936). 9.1 mm axial by 4.2 mm transverse diameter.

Pl. 4, fig. 8.

This is a fragmentary, severely disrupted and etched specimen.

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

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

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

Pl. 3, fig. 6.

This specimen of Foerstediscus grandis is replaced by beekite which destroys nearly all details of the plating. However, the thecal shape and morphologic structures are intact. The ambulacral cover-

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plates are distinct due to the external convexity of each. Parts of both the left and right sides of the theca are missing, along with fragments from along a break through the center which includes most of the oral area. The theca is only partially collapsed, most thecal elements little disrupted. The most significant aspect of this F. grandis specimen is its occurrence: among the other nine specimens from this collection are eight specimens of Edrioaster priscus and one Lebetodiscus dicksoni. Thus, all three species occur together, apparently in the same environment.

Discussion of previous investigation:

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

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

The types of Bassler's F. parvus are young adults of F. grandis which was based on a large adult holotype. The smaller specimens have collapsed, accentuating the interambulacral plate imbrication. Extensive etching has altered the appearance of the thecal plates,

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particularly the ambulacral coverplates, but remnants of the passageways and lateral depression series are preserved. A few of the characteristic external nodes are also preserved on several interambulacral plates.

Discussion of description:

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

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

Range and occurrence: Trenton Group, Mohawkian Series, Middle Ordovician, of Ontario and Kentucky.

Foerstediscus splendens Bassler, 1936

Text fig. 6; plate 5.

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

1943 Foerstediscus splendens Bassler, Bassler, R. S. and Moodey, M. W.,

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Geol. Soc. America, Spec. Pap. 45: 202.

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

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

Diagnosis:

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

Description:

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

The oral area includes twelve secondary oral plates in addition to the three primary orals and two pairs of lateral shared coverplates (text fig. 6). As in F. grandis, the secondary orals are in three groups, two lateral and one anterior. Two sizes of secondaries occur,

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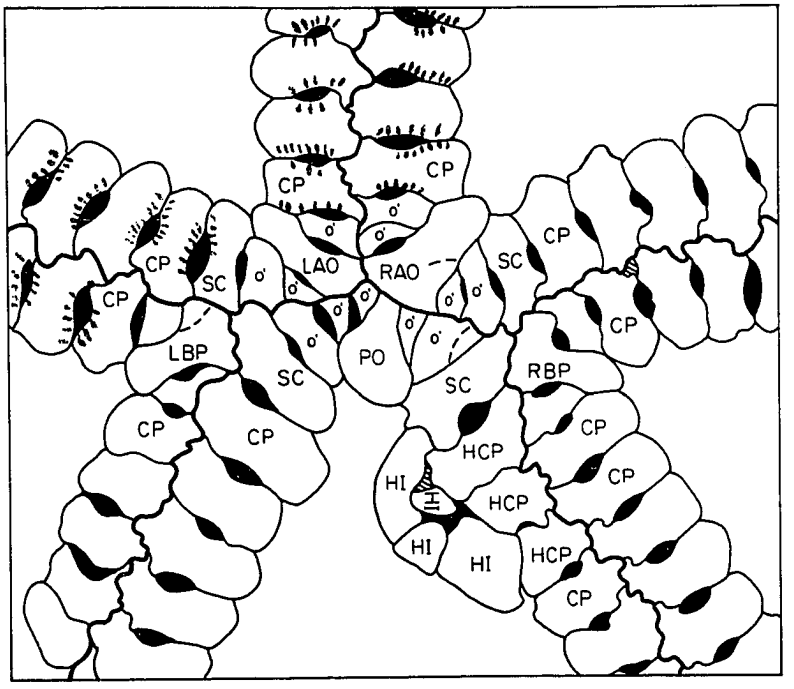
Text Figure 6 Foerstediscus splendens Bassler, 1936.

A.-B. Holotype, U.S.N.M. 4079.

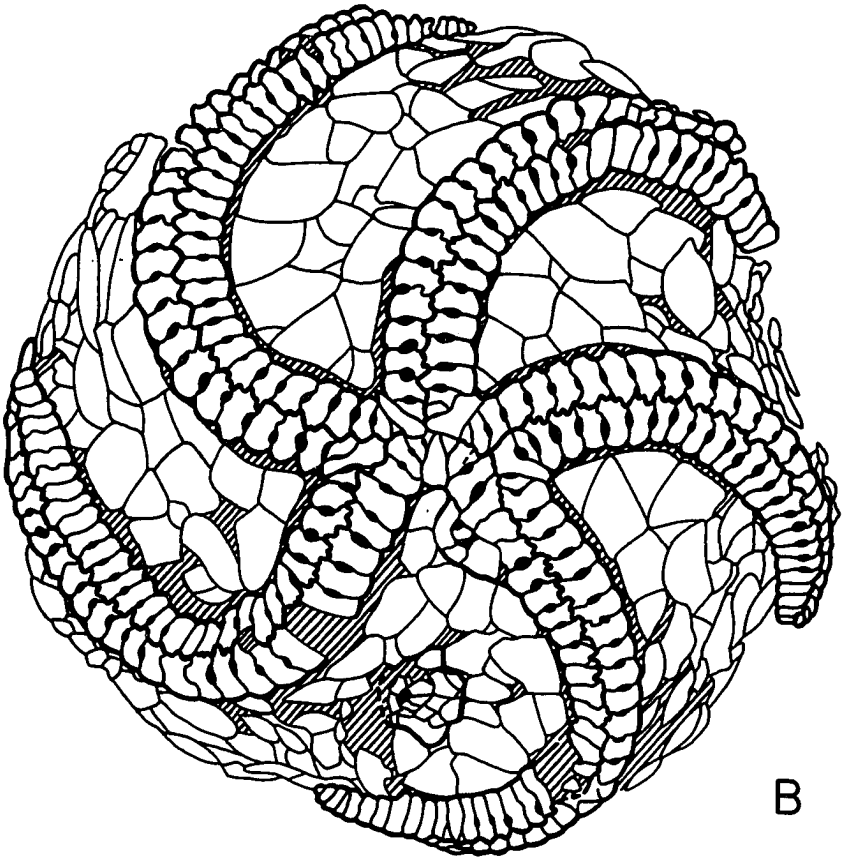
A. Oral region, (X9), pl. 5, fig. 4. Lineations thought to be fractures are dashed. CP. ambulacral coverplate; HCP. hydropore interambulacral plate; LAO. left anterior primary oral plate; LBP. left lateral bifurcation plate; o'. secondary oral plate; PO. posterior primary oral plate; RAO. right anterior primary oral plate; RBP. right lateral bifurcation plate; SC. lateral shared coverplate.

B. Oral surface, (X4), pl. 5, fig. 2.

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A



B

Text Figure 6

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the larger ones externally about one-third the size of the adjacent shared coverplates, the smaller secondaries at most half the size of the larger ones. The anterior halves of the two lateral groups, anterior to the transverse oral midline, are each formed by one large secondary and a smaller one on its proximal side. The posterior half of the left lateral grouping includes one large secondary flanked proximally by two smaller ones; the most proximal of these lies almost directly over the oral pole. The posterior half of the right lateral grouping includes one larger secondary oral and one smaller one proximal to it. (Possibly another small secondary flanks the distal margin of the larger secondary, although this supposed plate appears to be a broken fragment of the larger.)

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

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

The hydropore structure forms a low, rounded hump which extends outward from the proximal, posterior edge of ambulacrum V, distal to the oral region. Although elevated above the adjacent interambulacrals,

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

Kesling (1960) gave a different interpretation of the hydropore

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

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

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

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

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

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

The ambulacral floorplates have not been observed in this species.

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

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appears to be a typical periproct.

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

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

Specimen:

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

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

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

Discussion:

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

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being the larger, older, adult.

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

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

Foerstediscus solitarius Bell, sp. nov.

Text fig. 7; plate 6.

Diagnosis:

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

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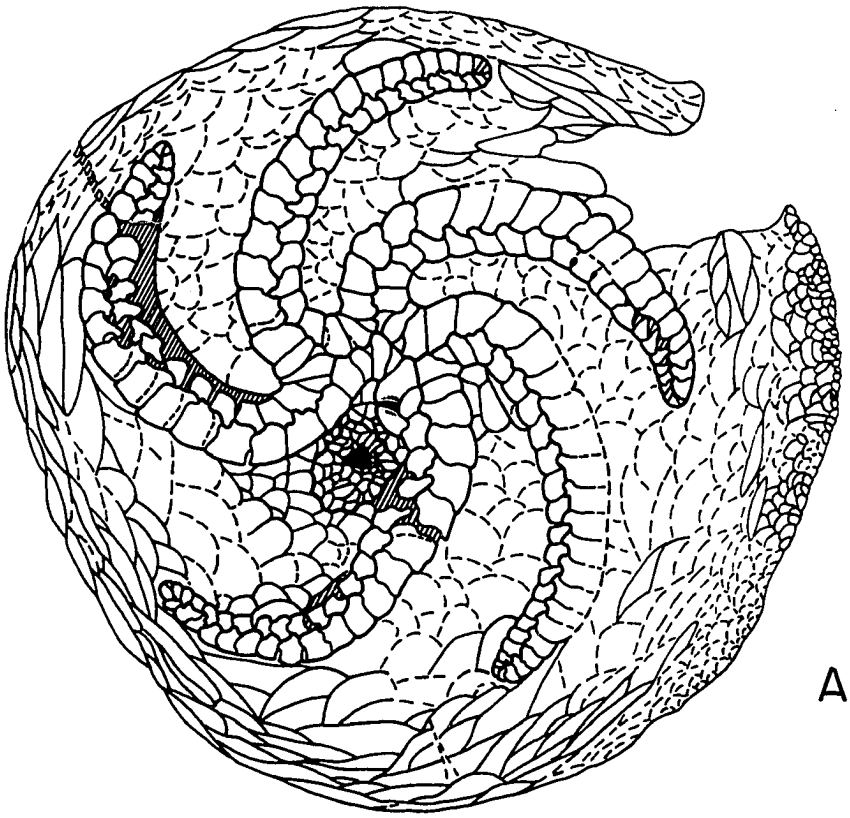
Text Figure 7 Foerstediscus solitarius Bell, sp. nov.

A.-B. Holotype, U.S.N.M. 140853.

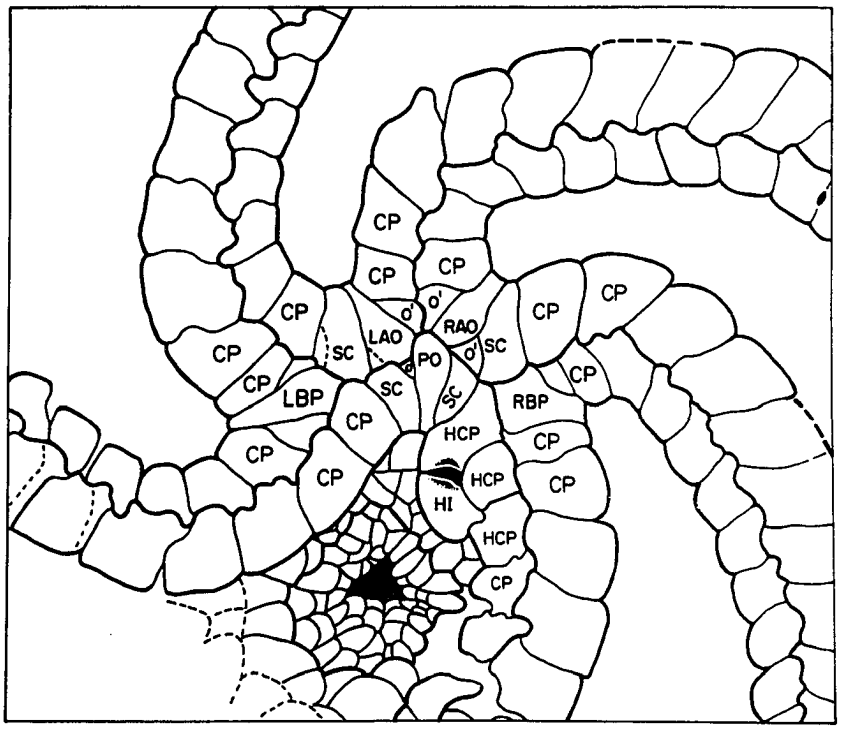
A. Oral surface, (X10), pl. 6, fig. 1.

B. Oral region, (X20), pl. 6, fig. 5. CP. ambulacral coverplate; HCP. hydropore ambulacral coverplate; HI. hydropore inter-ambulacral plate; LAO. left anterior primary oral plate; LBP. left lateral bifurcation plate; o'. secondary oral plate; PO. posterior primary oral plate; RAO. right anterior primary oral plate; RBP. right lateral bifurcation plate; SC. lateral shared coverplate.

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A


CP
CP
CP

Description:

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

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

The hydropore structure lies along the proximal posterior edge of ambulacrum V, squeezed between the central oral rise and the anal structure (pl. 6, fig. 3, 5). The area is depressed in the holotype which has partially disrupted the plates and makes interpretation tentative. It appears to be formed by four plates. A single large

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interambulacral forms the posterior, interambulacral side of the structure. Its right anterior edge bounds the posterior side of the opening. The anterior side of the hydropore is formed primarily by the adradial end of the proximal posterior coverplate of ambulacrum V. The adradial end of this plate is enlarged and juts out into interambulacrum 5. The distal part of the distended area forms the anterior side of the opening. The second and third posterior coverplates of ambulacrum V are adradially shortened and abut the right edge of the interambulacral hydropore plate which intrudes into the edge of the ambulacrum in this area. The second coverplate forms the right end of the hydropore, but the third does not make contact with the opening.

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

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

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

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

The external plate surfaces appear to have been smooth.

Specimen:

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

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

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

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Discussion:

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

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

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

Range and occurrence: Lower Keyser Formation, Upper Silurian of Pennsylvania.

Belochthus Bell, gen. nov.

Diagnosis:

Lebetodiscidae with: domal theca; oral area with at least several large secondary oral plates; large primary oral plates externally sagittate; hydropore structure includes at least two ambulacrals and one

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enlarged interambulacral plate; ambulacra straight; coverplate passageways oblique, elliptical external foramina narrow.

Description:

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

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

Range and occurrence: Trenton Group, Middle Ordovician, of Ontario.

Belochthus orthokolus Bell, sp. nov.

Text fig. 8; plate 7-8.

Diagnosis:

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

Description:

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

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Text Figure 8 Belochthus orthokolus Bell, sp. nov.

A. Juvenile, N.Y.S.M. 12774, (X40), pl. 8, fig. 1.

B. Juvenile, R. O.M. 160t-c-2, (X40), pl. 8, fig. 3.

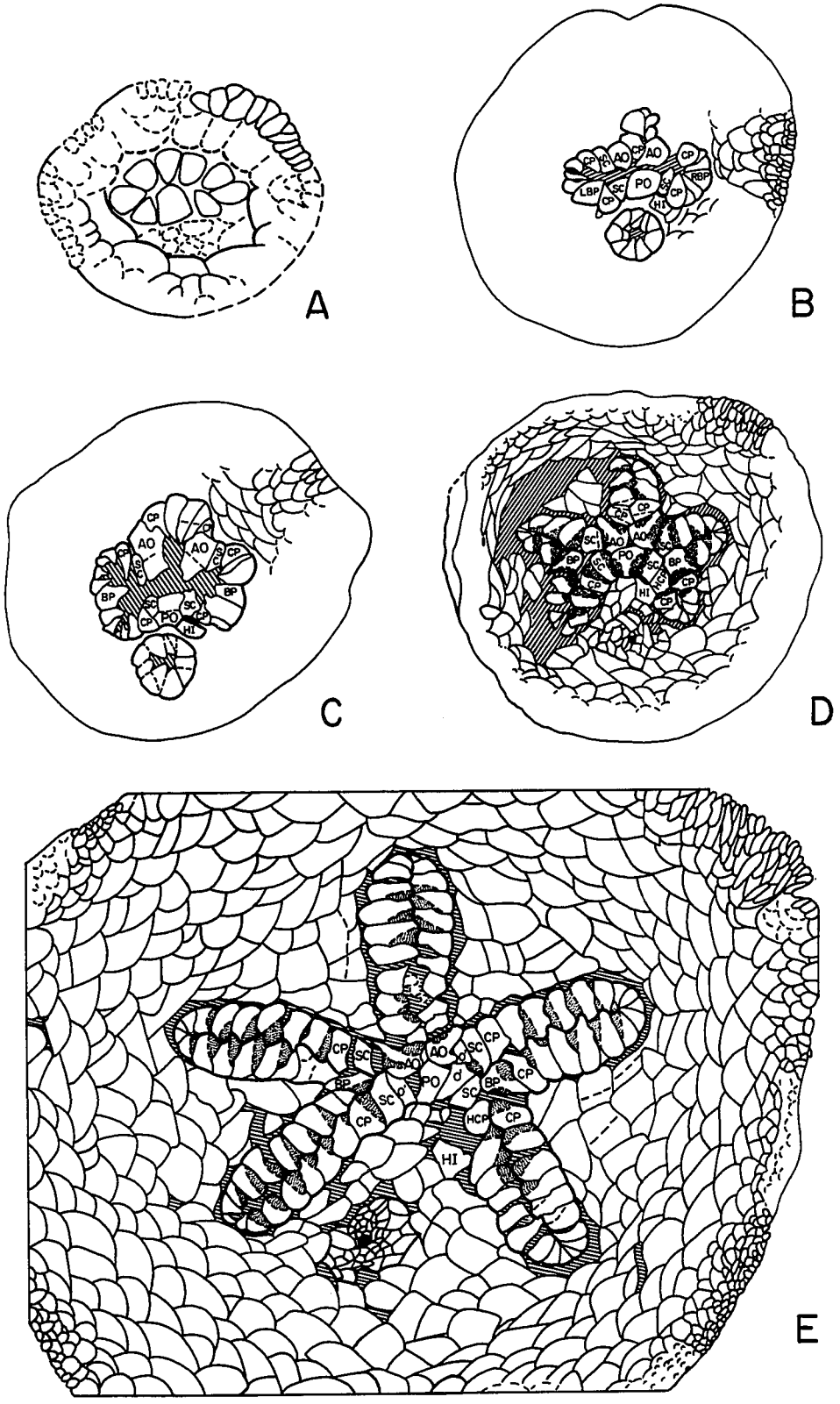
C. Juvenile, R. O.M. 160t-c-1, (X20), pl. 8, fig. 5.

D. Paratype (2), young adult, N.Y.S.M. 12773, (X10), pl. 8, fig. 7.

E. Holotype, adult, R.O.M. 18874, (X11), pl. 7, fig. 2. Coverplate intra-ambulacral extensions are separated from the main body of the plates by dashed lines and are stippled.

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

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Text Figure 8

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

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

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

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rim has been observed.

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

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

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

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

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

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

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

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the progressively smaller plates of the distal two or three circlets are radially elongate.

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

Specimens:

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

Text fig. 8E, pl. 7, fig. 1-3.

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

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

Pl. 7, fig. 4-5.

The theca has collapsed; the right anterior part is disrupted and apparently crushed. Many of the ambulacral coverplates are partial-

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ly disrupted, and the upper surfaces of others have been broken off. The specimen has been moderately etched. Size indicates the specimen is a young adult.

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

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

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

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

Pl. 7, fig. 6-7.

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

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Juveniles:

N.Y.S.M. 12774. "Trenton Limestones", Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario. .8 mm axial by 1.1 mm transverse diameter.

Pl. 8, fig. 1.

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

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

R.O.M. 160t-c-1. 2.6 mm axial by 2.8 mm transverse diameter.

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

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

R.O.M. 160t-c-2. 1.3 mm axial by 1.3 mm transverse diameter.

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

This individual has collapsed, but little plate disruption has occurred. The exterior of the theca has been abraded and etched; the

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plates are distinct only when under xylene.

Ontogenetic development:

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

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

The outline of the central oral-ambulacral series group is distinctly three-part and produces a triradiate symmetry: two lateral radii and one anterior. The lateral radii are much longer than the

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anterior radius, extended by the shared coverplate pairs and bifurcation plates. The anterior radius is marked only by a small hump formed by the two large anterior primary orals.

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

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

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

The three large, thick primary orals are central, but the left

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

Distal to the left pair of shared coverplates are seven ambulacral elements. The largest of these, on the posterior side of the group, would from its size appear to be the left ambulacral bifurcation plate. If so, only one large and one tiny coverplate form ambulacrum I, whereas two pairs of coverplates form ambulacrum II. On the right side of the central orals the larger bifurcation plate lies at the distal edge of the left group; ambulacra IV and V have three coverplates each. Ambulacrum III appears to have five coverplates. Those on the left side of the midline look much larger than those on the right, no doubt due to differential etching and collapse. The hydropore may be represented by an elongate darkened area (under xylene) along the posterior, adradial edge of the right posterior shared coverplate. A large interambulacral plate bounds the posterior side of the darkened area. The right margin of this plate also abuts the adradial end of the proximal posterior coverplate of ambulacrum V, although the darkened area does not appear to extend along this zone.

The anal structure, posterior to the oral area, is formed by approximately twelve plates, irregular in size and shape, and loosely grouped into one or two circlets which form a periproct. The relative

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size of the structure is very large in comparison to adults.

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

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

One pair of lateral shared coverplates flanks each side of the central primary orals along the transverse oral midline. The plate

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immediately adjacent to the left side of the posterior primary oral would seem to be the left posterior shared coverplate. However, this could be a secondary oral plate and the next distal plate the shared coverplate. If so, ambulacrum I has only five coverplates, not six as suggested below.

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

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

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

N.Y.S.M. 12773, paratype (2), (5.4 mm axial by 5.6 mm transverse diameter, text fig. 8D, pl. 8, fig. 6-7), is considered to be a young adult. Most thecal features are identical to those seen in the larger

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adult holotype, although the proportional sizes of the structures remain in a transitional state between those found in juveniles and adults. However, the secondary orals may be lacking and the ambulacra appear to taper, whereas in the adult, the ambulacra are nearly uniform in width throughout and terminate bluntly.

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

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

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Discussion:

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

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

The external sides of the ambulacral coverplates appear to be nearly flat in adults, but are convex in small specimens, like those of most other Lebetodiscidae. This may reflect ontogenetic change or

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is perhaps preservational, the convex exteriors of adult coverplates having been removed by surficial etching as in the holotype of Foerstediscus splendens. No suggestion of a lateral depression series has been observed in B. orthokolus.

Etymology: The trivial name orthokolus is compounded from the Greek orthos - straight, and kolon - arm, denoting the straight ambulacra.

Range and occurrence: Trenton Group, Mohawkian Series, Middle Ordovician of Ontario.

Streptaster Hall, 1872

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

1966 Streptaster Hall, Regnéll, G., in Treatise Invert. Paleont., R. C.

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Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U167, text fig. 117-2, 120-3-b, 125-3, 130-2.

Type species: Agelacrinus vorticellata Hall, 1866.

Diagnosis:

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

Description:

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

Discussion:

The date of publication of the name Streptaster requires explanation. The type species of the genus Agelacrinus vorticellata was originally described by Hall in 1866. The description was published

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

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

Range and occurrence: Cincinnatian Series, Upper Ordovician, of Ohio, Indiana and Kentucky.

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Streptaster vorticellatus (Hall), 1866

Text fig. 9; plate 9-10.

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

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

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

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

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

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

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

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

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

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7a-b, pl. 4, fig. 2.

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

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

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

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

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

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

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Diagnosis:

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

Description:

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

The oral plates rise above the level of the interambulacra and form a central oral rise, but apparently its summit lies well below the tops of the proximal ambulacral ridges. Although commonly hidden, the

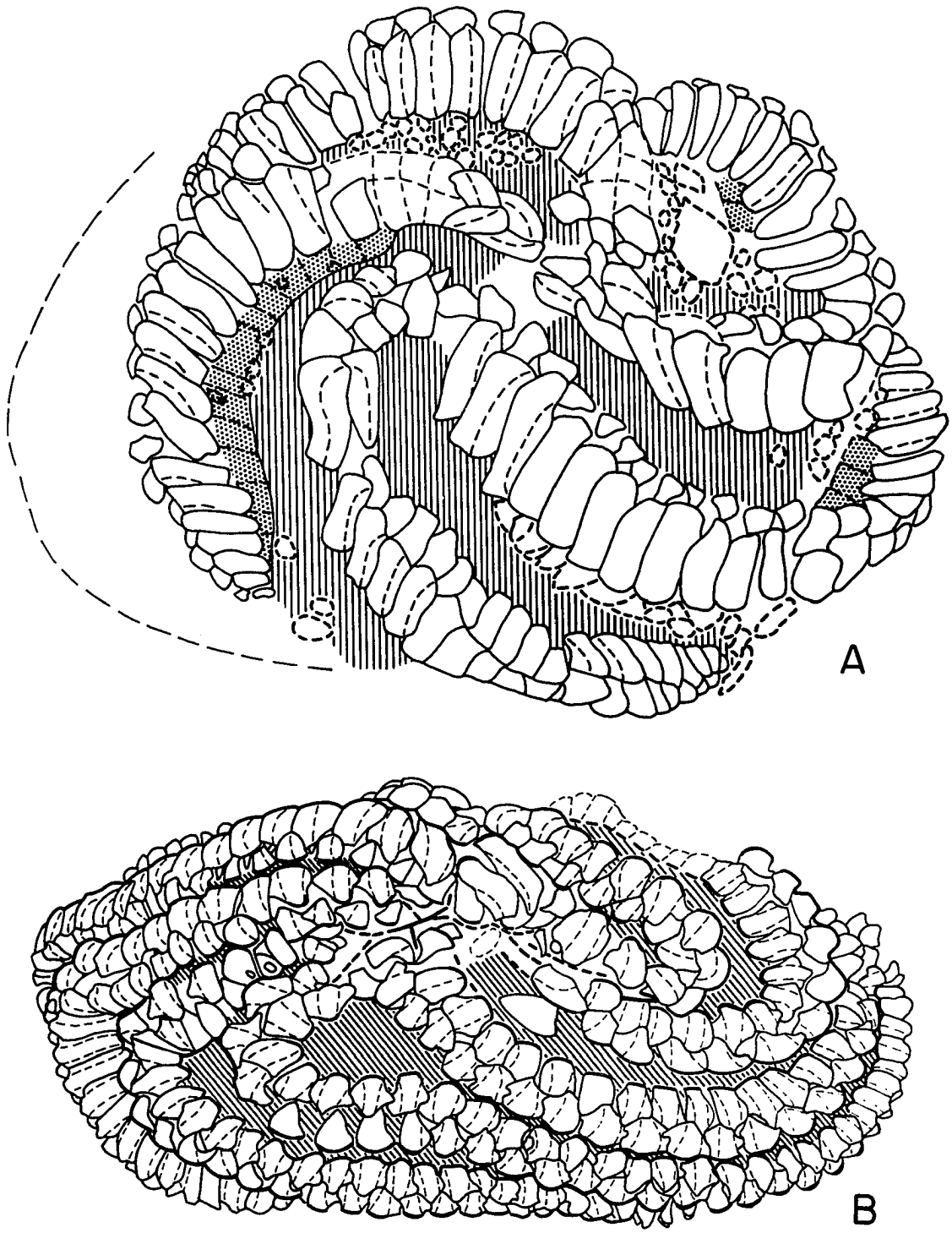
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Text Figure 9 Streptaster vorticellatus (Hall), 1866

A. M.C.Z. 520, (X9), pl. 9, fig. 3. Ambulacral floorplates are marked by the dotted pattern.

B. M.C.Z. 514, (X6), pl. 9, fig. 7-9. The anterior edge of the theca may be the left edge of the plate tracing. Dashed lines separate the main body of the ambulacral coverplates from the intra-ambulacral extensions.

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Text Figure 9

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oral area appears to include three primary oral plates, two pairs of lateral shared coverplates and several secondary oral plates. The number and position of the secondary orals is questionable, although at least seven different secondary orals have been identified tentatively in various individuals. Their diversity may be preservational, or may represent intra-specific variation.

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

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

The frame is formed by the enlarged proximal floorplates of all five ambulacra and the intra-thecal extensions of the three primary orals. The anterior half of the frame includes the floorplates of ambulacra II-III-IV. These are enlarged proximally and extend inward and laterally. The inner proximal edge of floorplate III is laterally in contact with the anterior tips of floorplates II and IV and forms the innermost edge of the interradial parts of the frame rim. However,

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large intra-thecal extensions from the right and left anterior primary orals are wedged between the upper parts of the floorplates and form all but the inner edge of the two anterior frame interradii.

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

The hydropore lies along the proximal, posterior edge of ambulacrum V. It includes at least three elements: a large interambulacral plate and the second and third coverplates of the posterior side of ambulacrum V (pl. 9, fig. 4-6, pl. 10, fig. 8-9). The enlarged adradial end of the second posterior coverplate of ambulacrum V juts out into interambulacrum 5, the proximal edge much further than the distal. The distal side of this adradial extension, oriented nearly parallel to the transverse oral midline, forms the anterior edge of the elongate, slit-like hydropore. The posterior side of the opening is formed by a large interambulacral which lies distal to the adradial extension

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of the second coverplate. This interambulacral, twice the size of any surrounding interambulacrals, is domed outward and gives the plate a bulbous appearance. The large interambulacral element has an intricate groove and ridge structure sculpted into the nearly vertical sutural face which abuts the opposing adradial edge of the second ambulacral coverplate (pl. 9, fig. 6, pl. 10, fig. 9). The groove appears to form a canal which leads from the hydropore down to the beginning of the passageway for the stone-canal. The third posterior coverplate of ambulacrum V is shorter than the others (normal to the ambulacral axis), and abuts the right margin of the large hydropore interambulacral plate which intrudes into the edge of ambulacrum V.

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

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

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in collapsed specimens only the ambulacral coverplates are visible.

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

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

The coverplate passageway system of S. vorticellatus is apparently

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

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

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The inner foramina of the passageways lie between the coverplates along this upwardly enlarging zone, above the floorplates but beneath the interambulacrals.

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

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

Mounted atop each ambulacral coverplate of S. vorticellatus is a relatively large, conical, movable spine (pl. 10, fig. 1, 3, 6-7, 11-12). Spine shapes and sizes are quite variable. Commonly the spines are broad-based and taper evenly upward to a pointed, distal extremity. The diameter of the base varies from approximately one-half to one-eighth that of the top of the coverplate on which it rests.

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Some wider-based spines are nearly two-thirds as long as the height of the underlying coverplate. Narrower-based spines may be only one-tenth the height of the coverplate. Spines also occur on the oral plates, although these appear to be much smaller than those of adjacent proximal ambulacral coverplates.

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

The interambulacra of S. vorticellatus are narrow regions squeezed between the long, wide and highly curved ambulacra. Interambulacral plates in general appear to be squamose and imbricate, although the proximal plates in many specimens may be subpolygonal and only slightly overlapping. Unfortunately, the interambulacral plates are usually hidden by the slightly disrupted columnar ambulacral coverplates. Commonly large irregular protuberances cover the external surfaces of the interambulacral plates, obscuring their definition and creating the appearance that the interambulacra are formed by granular

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plates. This prosopon ranges from rounded tubercles to irregular mounds in different parts of the same individual (pl. 10, fig. 1, 8, 10, 12). A similar prosopon extends onto the proximal plates of the peripheral rim although it diminishes rapidly outward in both size and abundance of the nodes.

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

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

Specimens:

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

Pl. 9, fig. 1-2.

The holotype is extremely poorly preserved. The collapsed theca is moderately complete and no major plate disruption has occurred, but the exterior has been deeply etched. This etching does not appear to be the typical, natural etching so commonly encountered in the edrioasteroids. The specimen may have been prepared with a caustic which

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removed most external detail. In its present state, the holotype reveals little other than gross thecal features. The specimen is resting upon a small pelecypod.

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

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

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

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

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

Pl. 9, fig. 4-6.

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

The specimen, here placed in S. vorticellatus, has reversed (solar) curvature for ambulacrum V. This allows a clear view of the plates of interambulacrum 5 which are squamose and imbricate, and bear large irregular nodes. The anal periproct is formed by one or two irregular circlets of large, sub-triangular, elongate plates. These form a conical protuberance. The ambulacral part of the hydropore structure is missing, but the large hydropore interambulacral is preserved and is much larger than any of the surrounding interambulacral elements. It rises above the surface of the interambulacrum to over half the height of adjacent ambulacral coverplates. The outer surface of the plate is convex. The adradial edge of the plate apparently was in contact with two coverplates, its proximal third with one, the distal two-thirds in contact with the next distal coverplate. The face of the interambulacral plate contacting the coverplates descends steeply toward the interior of the theca. Two upwardly convergent

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grooves are incised into this face. These intersect at a low angle at the upper edge of the plate. Where last observed near the lower covered part of this adradial face, the two grooves bend sharply inward, and are converging as they disappear from sight. These grooves apparently served as channels connecting the hydropore to the underlying stone-canal passageway. The coverplate passageways and ambulacral spines of this specimen are typical of the species.

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

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

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

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adjacent to the underlying bryozoan, and a few of the distal plates of the interambulacral areas can be seen. Both have the knobby prosopon typical of the species.

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

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

Pl. 9, fig. 10-11.

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

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are also exposed.

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

Pl. 10, fig. 1-5.

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

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

Pl. 10, fig. 6-7.

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

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

Pl. 10, fig. 13.

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

I.U.P.C. 10493. Fairmount member of the Fairview Formation, Maysville Group, Cincinnatian Series, Upper Ordovician. Specimen found in float about 10 feet stratigraphically higher than the "normal edrioasteroid

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layer" at the Forestville collecting site, Forestville, Ohio (Withamsville, Ohio-Kentucky Quadrangle, 7.5 minute topographic sheet (1953), Ohio Co-ordinate system - 397,300'; 1,474,700'). Collected by W. H. White, Jr. 9.8 mm axial by 11.2 mm transverse diameter.

Pl. 10, fig. 8-9.

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

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

Pl. 10, fig. 14.

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

U.C.M.P. 40438. Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio region. 11.7 mm axial by 13.9 mm transverse diameter.

Pl. 10, fig. 12.

This moderate-sized individual is missing a section of the poster-

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ior edge of the theca which divides ambulacrum I into two parts and creates the illusion that six rather than five ambulacra are present. Distally the peripheral rim is reflexed. Noteworthy is the small size of the ambulacral spines in relationship to the size of the underlying coverplates. The spine basins are deep.

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

Pl. 10, fig. 11.

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

U.C.M.P. 36532. Upper Waynesville Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Wash bank, North branch, Cedar Creek, near Versailles, Indiana. 6.9 mm axial by 7.6 mm transverse diameter.

Pl. 10, fig. 10.

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

In addition to the above specimens, over one hundred other S. vorticellatus have been examined in the course of this study. Unfortunately, most specimens are poorly preserved and add no information not provided by the above illustrated individuals.

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Discussion of previous investigation:

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

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

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

The stratigraphic occurrence of the seven-rayed specimen, several hundred feet above the horizon of the type of S. vorticellatus, undoubt-

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

Foerste (1914) described Streptaster reversata, based on a single fragmentary specimen which preserves only the posterior third of the theca. The specimen appears to be a typical S. vorticellatus except for the solar curvature of ambulacrum V. This curvature is considered fortuitous in this individual, as was suggested by Regnéll (1966), and does not constitute a specific difference. Ambulacral curvature direction in edrioasteroids is recognized as generically and specifically consistent, but is not a sole determinant. Other morphologic traits in conjunction with curvature constitute the taxobases. In the fragmentary holotype and sole example of S. reversata, none of the features other than the direction of curvature of the ambulacra differ from those found in typical S. vorticellatus. A similar fortuitous curvature reversal is known for one specimen of Carneyella pilea.

Williams (1918), Bassler (1935, 1936), and Regnéll (1966) all redescribed the basic features of Streptaster vorticellatus essentially

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in agreement with earlier descriptions. Williams suggested that S. septembrachiatus was merely an abnormal S. vorticellatus, although he did not indicate that S. reversata fell into the same category. On the other hand, Bassler not only accepted S. septembrachiatus as a distinct species, but even suggested that S. reversata belonged in the genus Carneyella, apparently disregarding the distinctive columnar ambulacral coverplates.

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

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

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

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these spines along most of the length of the ambulacra.

Discussion:

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

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

The limited range of possible spine movement would allow only two basic configurations of spines when the coverplates were closed, and

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

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

Streptaster vorticellatus occurs throughout the Cincinnatian Series (Upper Ordovician) in the Cincinnati Arch area. Several other species of edrioasteroids are common in this section, including Lebetodiscidae. However, S. vorticellatus, although found in the same formations as other Cincinnatian edrioasteroids, rarely is found on the

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same bedding planes. Perhaps the best illustration of this occurrence is the Forestville, Ohio site. A single bedding plane has yielded thousands of specimens of the four common Cincinnatian species, Isorophus cincinnatiensis, Carneyella pilea, Cystaster granulatus, and C. stellatus, but not a single example of Streptaster vorticellatus. However, several specimens of S. vorticellatus have been collected a few hundred feet away and not more than 10 feet stratigraphically above the densely populated layer.

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

Range and occurrence: Cincinnatian Series, Upper Ordovician of the Cincinnati Arch area, Ohio, Indiana and Kentucky.

Genus Cystaster Hall, 1871

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Type species: Hemicystites (Cystaster) granulatus Hall, 1871.

Diagnosis:

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

Description:

The thecal shape in Cystaster is singularly variable, and ranges from discoidal through most intermediates to clavate. The discoidal forms have steep short sides which rise from the substrate to a nearly flat oral surface. In plan view they are commonly sub-pentagonal, the

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distal tips of the ambulacra marking the five angles. The fully clavate forms have an upper gibbous part with the oral area at the summit, the ambulacra draping down the upper surface but ending at the ambitus. Below the ambitus the theca constricts and forms a pedunculate zone which terminates at the substrate in an outwardly flaring basal peripheral rim. Between these two extremes a nearly complete spectrum of intermediate forms has been found. The missing segment of the gradational sequence is at the discoidal end of the series, between low subclavate forms, with only a short zone of constriction below the ambitus, and the true disc-like forms.

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

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

The hydropore structure lies along the proximal part of the adradial suture line between ambulacrum V and interambulacrum 5 and is

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

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

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results in broad ambulacra which restrict the interambulacra to relatively narrow zones. Intra-ambulacral and intra-thecal extensions of the coverplates are similar to those of other Lebetodiscidae.

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

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

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

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cleaned specimens, conceals the squamose nature of the plates.

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

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

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

Discussion of previous investigation:

Hall (1871) introduced the name Cystaster as a provisional subgenus under Hemicystites in an advance printing of his 1872 paper in the 24th Annual Report of the New York State Cabinet of Natural History. It was monotypic, based on his new species Hemicystites granulatus. A footnote in the explanation accompanying plate 2 of the 1871 paper noted briefly that Cystaster was "sac-like, composed of minute plates, and surmounted by five . . . ambulacral areas, each one consisting of two series of external plates separated by a narrow groove, and beneath these a more distant series separated by a wider median groove." Hall suggested that the "granular" nature of the plates and the possible "free" condition of one individual (in which the peripheral rim is missing and the broken peduncular zone was shown

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as ending bluntly, pl. 11, fig. 1-3) were enough to provisionally separate the species as a new subgenus. Restudy of Hemicystites parasiticus, the type of that genus, has shown it is not even closely related to Cystaster granulatus. Hemicystites [with a double biseries of ambulacral coverplates, without coverplate passageways, with oral area including primary orals, shared coverplates, and a hydropore oral, and with a valvular anus] is included in the Suborder Isorophina.

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

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

Jaekel based his assessment of Hall's work on interpretation of the Hall illustrations (drawings, not the specimens) and on two additional specimens that were available to him for study. As noted by Jaekel, Hall's figure 1, plate 6 does look different from figures 2, 3, and 4. However, this is not due to morphologic differences but

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rather to the differing views and modes of preservation of the individuals portrayed. The specimens seen in figures 2, 3, and 4 are viewed from an oblique angle and preserve the pedunculate zone at least partially distended. Moreover, these individuals all display the oral and ambulacral coverplates partly open along the perradial lines. This is a common occurrence in specimens of C. granulatus, apparently related to preservational compression of high thecae. In contrast, the individual represented in figure 1 shows the ambulacral coverplates closed and interlocking along the perradial line, and the theca is depressed so as to hide the pedunculate zone.

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

Hall's original specimen of plate 6, figure 1 is M.C.Z. 515 (old 3878) in the Museum of Comparative Zoology. This specimen was erroneously listed there as the one illustrated by Hall in plate 6, figure 5, one of the types of his Hemicystites stellatus. Comparison of the specimen with the original figure and descriptions clearly shows that this is not the figure 5 specimen, whereas its size, preser-

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vation, and thecal detail appear to be identical to the one portrayed in figure 1. This specimen seems to be conspecific with the other three in the type lot, although it has collapsed vertically, flattening the oral surface. The depressed lower part of the theca, below the ambitus, is clearly constricted and forms the pedunculate region of the clavate theca. Thus, the types of Jaekel's Thecocystis sacculus are conspecific with all of Hall's types of Cystaster granulatus.

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

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

Discussion:

The two species here assigned to Cystaster are closely related and may be antipodal extremes of a gradational series. A "typical" C. granulatus is clavate and a "typical" C. stellatus is discoidal. But there is a nearly complete transition series between the two thecal expressions. These moderately convex intermediates, in all cases where the lower parts of the theca are exposed, have a short but definitely constricted pedunculate zone below the upper surface, and thus indicate that they are best attributed to C. granulatus. However, it is not unusual for the peripheral rim area of C. stellatus to be vertical or

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even slightly constricted below the upper surface of the theca, as if initiating but never actually forming a pedunculate region. Whether or not the gradation between the two forms is absolutely complete remains to be shown.

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

A possible explanation of the theca variation, suggested by Caster (personal communication, 1969) is that one form represents the paedomorphic expression of the other. The known examples of juveniles with diameters of 3 mm or less, are nearly impossible to separate specifically. The smallest known Cystaster specimens are commonly moderately convex, proportionately higher than adult C. stellatus, but lower than C. granulatus. The peripheral rim in these juveniles is almost vertical except for the distal circlets which flare outward upon contact with the substrate. Thus the theca does not clearly correlate with either adult form, and both adult shapes could be easily derived from this juvenile. Proliferation of plates above the rim could form the pedunculate zone for C. granulatus, the upper oral surface increasing in convexity. Conversely, for C. stellatus, the thecal

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diameter could be increased by addition of plates to the peripheral rim, the upper oral surface becoming nearly flat or only gently convex. It would appear that forms here called C. stellatus represent the paedomorphic form, maturing with little modification of the thecal shape except for increase in diameter. Conversely, in view of the fact that oral surface curvature in juveniles is somewhat greater than in adult C. stellatus, C. granulatus might be considered a paedomorphic form of C. stellatus. In this case, typical C. stellatus would show a slight decrease in convexity during growth, whereas the paedomorphic expression of the species, or C. granulatus, would represent the maturation and accentuation of the moderate convexity of the young C. stellatus. However, if paedomorphism is the correct explanation, it seems more likely that the form represented by the individuals referred to here as C. stellatus are the paedomorphic expressions of C. granulatus.

Range and occurrence: Trenton Group, Middle Ordovician through Richmond Group, Upper Ordovician of the Cincinnati Arch area, Indiana, Kentucky, Ohio.

Cystaster granulatus Hall, 1871

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Diagnosis:

A Cystaster with: clavate theca; ambulacra draped down upper side to ambitus; constricted lower pedunculate zone extends down to basal peripheral rim; larger hydropore interambulacral with a very prominent

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sickle-shaped ridge; interambulacral plates squamose and imbricate, but commonly appear granular due to prosopon.

Description:

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

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

The hydropore structure of Cystaster granulatus (as described for the genus) may differ from that of C. stellatus in only one respect:

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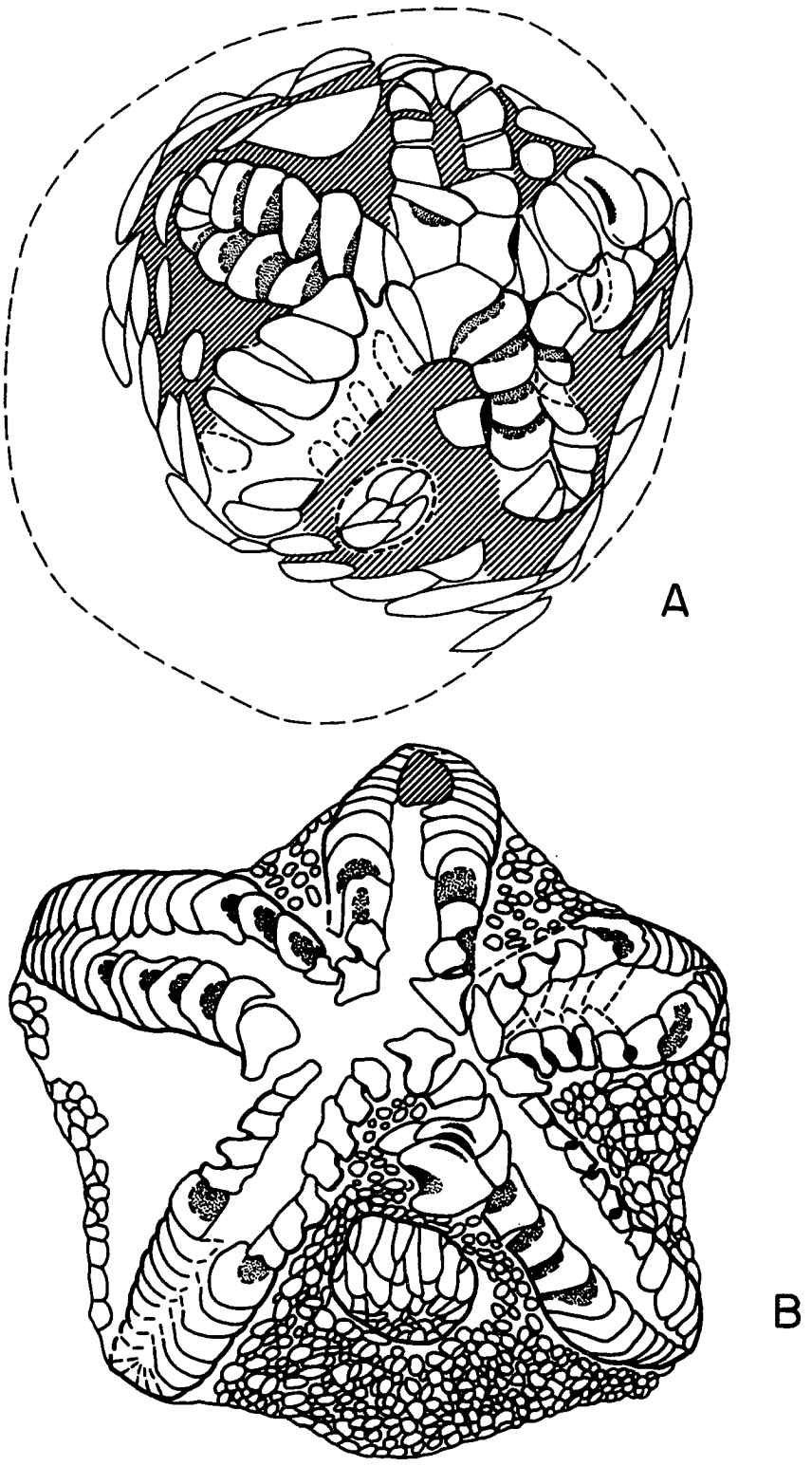
Text Figure 10 *Cystaster granulatus* Hall, 1871

A. U.S.N.M. 42138, (X25), pl. 11, fig. 11

B. U.C.M.P. 40443, (X15), pl. 12, fig. 3.

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

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Text Figure 10

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the large, sickel-shaped ridge on the exterior of the larger hydropore interambulacral may be larger in C. granulatus (text fig. 10B, pl. 12, fig. 1-3).

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

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

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occasionally it may abut the left tip of the slit. The intra-thecal part of this plate forms part of the underlying stone-canal passageway.

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

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

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

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

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quantity of material is available for C. granulatus.

Specimens:

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

M.C.Z. 521-C. Lectotype of Cystaster granulatus Hall (1871, pl. 2, fig. 4). 6.2 mm axial by 4 mm transverse diameter; maximum height 11.3 mm.

Pl. 11, fig. 1-3.

M.C.Z. 521-B. Lectoparatype of C. granulatus Hall (1871, pl. 2, fig. 3). 8.6 mm axial by 6.4 mm transverse diameter; height 5 mm.

Pl. 11, fig. 4-5.

M.C.Z. 521-A. Lectoparatype of C. granulatus Hall (1871, pl. 2, fig. 2). 6.3 mm axial by 4.3 mm transverse diameter; height 7.7 mm; maximum diameter of upper surface of theca 6.6 mm.

Pl. 11, fig. 6-8.

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

The lectotype preserves the pedunculate zone in a distended state, although it is laterally compressed. The partially disrupted

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ambulacral coverplates and adjacent orals are broken along the right side of the theca. Contrary to the impression created by Hall's 1871 illustration, the specimen was obviously attached at the base of the pedunculate zone by a peripheral rim.

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

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

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

Pl. 11, fig. 12-13.

This specimen was found in the Museum of Comparative Zoology with types of Cystaster stellatus. The accompanying label indicated that the specimen was one of Hall's original specimens supposedly

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

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

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

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

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

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of this specimen and the following ones are discussed below.

U.S.N.M. 87628 (A-C). Type specimens of Cincinnatidiscus turgida Bassler (1936, p. 6). Whitewater Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Oxford, Ohio. Three individuals on one slab.

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

Pl. 11, fig. 9.

U.S.N.M. 87628-B. 11.9 mm greatest diameter by a perpendicular of 11.1 mm.

Pl. 11, fig. 10.

U.S.N.M. 87628-C. Small fragment of a third specimen.

Specimen A is a moderately well-preserved clavate individual. Ambulacrum V, the hydropore and the anal structures are missing. The peduncular zone is completely hidden under the collapsed upper surface, but the upper surface is little disrupted.

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

Hundreds of individuals of C. granulatus were collected from a single bedding plane, all members of one population (referred to here

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as the Forestville population). A few examples are illustrated here to document morphology and variation.

U.C.M.P. 40439-40449. Fairmount member, Fairview Formation, Maysville Group, Cincinnatian Series, Upper Ordovician. North end of excavation for Beechmont Mall Shopping Center, opposite Anderson High School, Forestville, Ohio (Withamsville, Ohio-Kentucky Quadrangle), 7.5 minute topographic sheet (1953), Ohio Co-ordinate system - 397,300'; 1,474,700', equals approximate center of 200 foot by 200 foot area [now under black top].

U.C.M.P. 40439. 5.2 mm axial by 5.6 mm transverse diameter; 3.6 mm high.

Pl. 11, fig. 20-21.

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

U.C.M.P. 40440 (a, b). Two individuals on one slab, one large specimen with six ambulacra (a), and one small, normal, clavate specimen (b). (a) 7.2 mm axial by 8 mm transverse diameter; 2.5 mm high.

Pl. 11, fig. 14-15.

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

U.C.M.P. 40441. 3.8 mm axial by 4 mm transverse diameter.

Pl. 12, fig. 2.

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

U.C.M.P. 40442. Specimen broken from resting surface (brachiopod).

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6.8 mm axial by 6.4 mm transverse diameter; by 2.8 mm high.

Pl. 11, fig. 18-19.

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

U.C.M.P. 40443. 6.4 mm axial by 6.8 mm transverse diameter, 4.8 mm high.

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

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

U.C.M.P. 40444. 4 mm axial by 4.1 mm transverse diameter; 2 mm high.

Pl. 12, fig. 6.

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

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open. Wider opening would appear to have disrupted their inner ends.

U.C.M.P. 40445. 7.8 mm axial by 8 mm transverse diameter, 4 mm high.

Pl. 12, fig. 7.

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

U.C.M.P. 40446. 4.8 mm axial by 5.2 mm transverse diameter, approximately 4 mm high.

Pl. 12, fig. 5.

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

U.C.M.P. 40447. 8 mm axial by 7.9 mm transverse diameter, approximately 4 mm high.

Pl. 12, fig. 1.

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

U.C.M.P. 40448. 5.6 mm axial by 5.2 mm transverse diameter, 1.6 mm

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high.

Pl. 11, fig. 16-17.

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

U.C.M.P. 40449 (a, b, c). Three specimens: (a) C. stellatus - 6.9 mm axial by 6.4 mm transverse diameter. (b) High C. granulatus - 5.5 mm axial by 5.7 mm transverse diameter. (c) Low C. granulatus - 7.3 mm axial by 7.6 mm transverse diameter.

Pl. 12, fig. 10.

This slab includes three edrioasteroids. They have been lighted obliquely in the photograph to demonstrate thecal elevation. The left posterior member of the trio is a typical Cystaster stellatus; the

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upper oral surface is only slightly convex; the peripheral rim is vertical proximally and then flairs outwardly along the surface of the substrate. The right posterior specimen is a clavate C. granulatus, the upper surface of the theca highly convex, but the lower pedunculate zone has collapsed. The anterior specimen is another C. granulatus and represents the "intermediate" variety. The upper part of the theca is more convex than that of C. stellatus, but not nearly as high as the other C. granulatus present. The pedunculate zone is hidden beneath the collapsed upper part of the theca and a small amount of matrix.

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

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

Pl. 12, fig. 9.

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

A.M.N.H. 13263/1-g. "Lorraine group of Hudson River shale" [Maysville

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Group, Cincinnatian Series1, Upper Ordovician. 350 feet above river level, Cincinnati, Ohio. 5.2 mm axial by 5.6 mm transverse diameter, 4.8 mm high (width of upper gibbous part of theca as viewed in photograph - 6 mm).

Pl. 12, fig. 8.

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

Discussion of previous investigation:

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

Bassler (1936, p. 4-5) described Cystaster ulrichi as differing from C. granulatus in having: "a shorter, broader sac forming the basal

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portion of the theca, and in the coarser and fewer plates covering the ambulacral areas . . ." The holotype (U.S.N.M. 42138) is a juvenile, which accounts for the reduced number of ambulacral coverplates and the proportionately larger size of the individual elements. The shape of the theca is difficult to determine. The distal parts of the specimen are collapsed and the thecal plates in these areas are now highly imbricate. Since the specimen remains highly convex, it is reasonable to assume that the theca was clavate or nearly so. It is completely acceptable as a C. granulatus.

Discussion:

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

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

Range and occurrence: Eden Group through Richmond Group, Cincinnatian Series, Upper Ordovician of the Cincinnati Arch region, Indiana, Ohio,

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Kentucky.

Cystaster stellatus (Hall), 1866

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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Diagnosis:

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

Description:

Cystaster stellatus is remarkably similar to the type species of the genus. The only external difference between the two forms is the thecal shape, and in this they may intergrade. Certainly the typical C. stellatus has a discoidal theca, with a flat or slightly convex upper surface, and a peripheral rim which is proximally vertical or steeply inclined and is distally flared outward in contact with the substrate. In plan-view the theca is commonly sub-pentagonal with the distal tip of each of the five ambulacra forming a corner of the pentagon. The ambulacra are highly elevated ridges which are confined to the flat oral surface. The discoidal theca of C. stellatus is quite different from the typically clavate C. granulatus, but the latter appears to grade from highly elevated clavate forms to low individuals, which are almost discoidal and thus closely approaching C. stellatus.

The plate structure of the oral region and subjacent hydropore in C. stellatus appears nearly identical to that of C. granulatus (text fig. 11A-B). The only difference between the two is the apparently greater prominence of the sickle-shaped ridge on the larger interambulacral hydropore plate in C. granulatus. However, this region

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is commonly difficult to see in both species due to the small size of the theca and the disruption of the plates in this area. Commonly, much of the hydropore structure is obscured by the adjacent high ambulacral elements.

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

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

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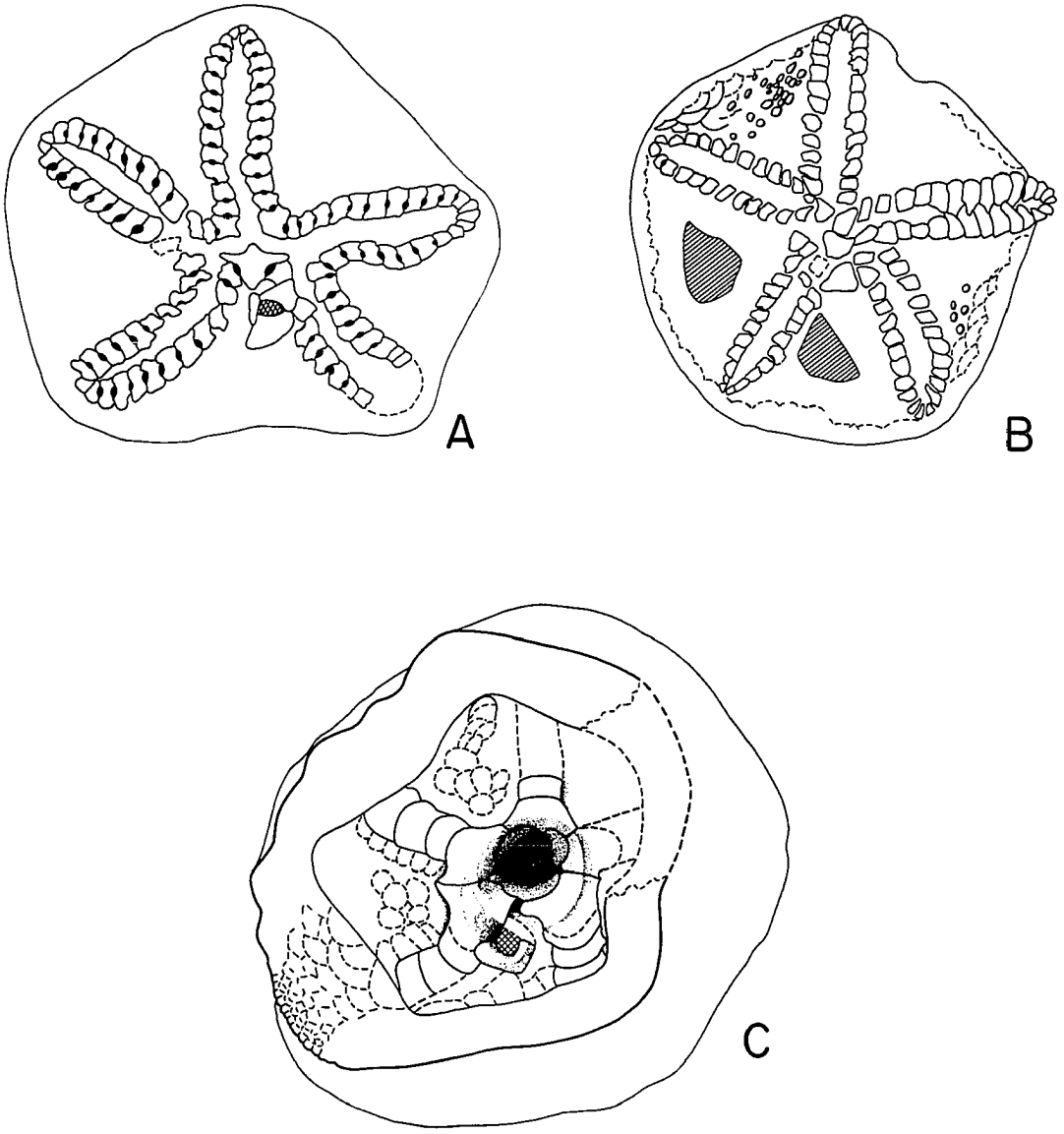
Text Figure 11 *Cystaster stellatus* (Hall), 1866

A. U.C.M.P. 40459, (X9), pl. 13, fig. 6.

B. Lectotype, M.C.Z. 523, (X6), pl. 12, fig. 12.

C. Lower side, Y.P.M. 28453, (X10), pl. 12, fig. 21.

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Text Figure 11

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extend inwards nearly as far as the adjacent floorplates. This leaves a conspicuous posterior gap in the frame that directly connects the central lumen to the thecal cavity area under interambulacrum 5.

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

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

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

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

The squamose imbricate interambulacral plates are more readily

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Text Figure 12 Cystaster stellatus (Hall), 1866

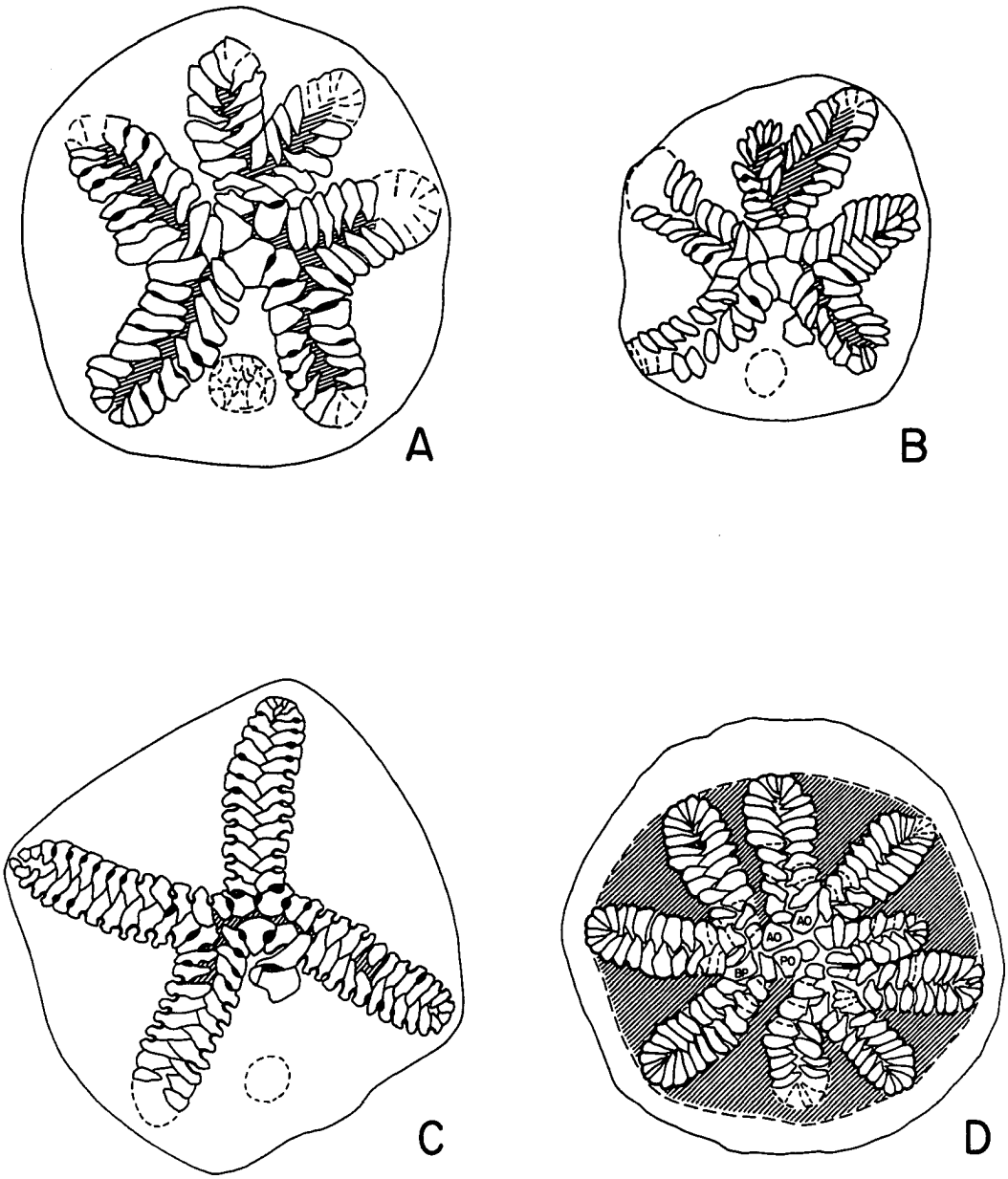
A. U.S.N.M. Acc. no. 258129-A, (X10), pl. 13, fig. 13.

B. U.S.N.M. Acc. no. 258129-B, (X10), pl. 13, fig. 16.

C. U.C.M.P. 40452, (X8), pl. 13, fig. 10.

D. U.C.M.P. 40458, (X10), pl. 13, fig. 23. AO. anterior primary oral plate; BP. left lateral bifurcation plate; PO. posterior primary oral plate.

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Text Figure 12

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observed in C. stellatus than in C. granulatus. This distinction between the two species may again be due to the effects of preservation on the different thecal forms. In some specimens, the interambulacrals of C. stellatus appear to be proportionately somewhat larger than in C. granulatus.

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

Specimens:

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

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

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

The large theca has collapsed; the peripheral rim is obscure.

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The external ends of many plates are missing, including most of the coverplates, the orals and the hydropore plates. The interambulacra are very poorly preserved, and no indication of the anal structure can be seen.

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

Pl. 12, fig. 13.

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

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

Pl. 12, fig. 14.

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

A.M.N.H. 1191-D, E.

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

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

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

Pl. 12, fig. 17-18.

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

Pl. 12, fig. 19-20.

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

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

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

Pl. 12, fig. 15.

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

Pl. 12, fig. 16.

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

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

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

U.C.M.P. 40451-A. 7.6 mm axial by 6.8 mm transverse diameter.

Pl. 13, fig. 1-2.

U.C.M.P. 40451-B. 5.7 mm axial by 5.4 mm transverse diameter.

Pl. 13, fig. 3.

These two specimens rest adjacent to each other on a brachiopod fragment and preserve the only ambulacral coverplate spines known in C. stellatus. Both are well-preserved, although the interambulacral and marginal plates are mostly vertical, disrupted during thecal

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collapse and thereby exposing the squamose, imbricate nature of these elements. The characteristic nodose prosopon of these is revealed along the edges of the specimens where the exteriors of some of the interambulacral plates are exposed. The thin, elongate and extremely delicate spines appear to rest on the flat summits of the coverplates, one per plate. The spines have been lost from the parts of the specimens in which all matrix has been removed.

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

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

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

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distinguishing between the two "species" assigned to the genus.

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

U.C.M.P. 40452-40462, 40481-40482, U.S.N.M. Acc. no. 258129 (A-B). Fairmount member, Fairview Formation, Maysville Group, Cincinnatian Series, Upper Ordovician. North end of excavation for Beechmont Mall Shopping Center, opposite Anderson High School, Route 125, Forestville, Hamilton County, Ohio (Withamsville, Ohio-Kentucky Quadrangle 7.5 minute topographic sheet (1953), Ohio Co-ordinate system: 397,300'; 1,474,700'; equals approximate center of a 200' by 200' area).

U.C.M.P. 40452. 8.4 mm axial by 8 mm transverse diameter.

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

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

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U.S.N.M. Acc. no. 258129-A. 6.4 mm axial by 6.1 mm transverse diameter.

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

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

U.S.N.M. Acc. no. 258129-B. 5.1 mm axial by 4.6 mm transverse diameter.

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

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

U.C.M.P. 40453. 8 mm axial by 8.4 mm transverse diameter.

Pl. 13, fig. 11.

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

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U.C.M.P. 40454. 4 mm axial by 4.4 mm transverse diameter.

Pl. 13, fig. 14-15.

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

U.C.M.P. 40455. 8.8 mm axial by 8.7 mm transverse diameter.

Pl. 13, fig. 17-18.

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

U.C.M.P. 40456. 7.1 mm axial by 7.2 mm transverse diameter.

Pl. 13, fig. 20-21.

This individual has seven ambulacral radii. Ambulacra I, II, and III are normal. Ambulacrum IV has two lateral, subordinate

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branches, one from each side, which arise distal to the normal bifurcation of ambulacra IV and V. The distal part of ambulacrum V appears to lie closer to ambulacrum IV (and its branches) than is normally the case. This is a rather curious development, for it would be expected that ambulacrum V would tend to be diverted away from the somewhat congested area created by the extra ambulacra.

U.C.M.P. 40457. 5.6 mm axial by 6.1 mm transverse diameter.

Pl. 13, fig. 19.

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

U.C.M.P. 40458. 6.4 mm axial by 6.3 mm transverse diameter.

Text fig. 12D, pl. 13, fig. 22-23.

This individual has nine ambulacra, eight of which extend to the rim of the theca. This is the largest number of ambulacra of any

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Isorophida included in this study. Ambulacra I, III and IV appear to be normal. Ambulacrum II bifurcates immediately distal to its normal bifurcation from ambulacrum I; the two radii formed by this bifurcation are subequal in size and both extend to the peripheral rim. Based on the relative position of these two branches, one being quite close to ambulacrum III, it appears that the anterior radius is the extra one.

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

U.C.M.P. 40481. 7.3 mm axial by 7.9 mm transverse diameter.
Pl. 13, fig. 7.

U.C.M.P. 40482. 8.2 mm axial by 8.4 mm transverse diameter.
Pl. 13, fig. 8.

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

U.C.M.P. 40459, 40462.

The upper parts of the oral surface of these two specimens have been removed by grinding to expose sub-surficial views of the

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upper theca and the coverplate passageways. The passageways are filled with secondary calcite and when the specimen is properly oriented and under xylene, these structures appear black in contrast with the white calcite of the surrounding coverplates.

U.C.M.P. 40459. 6.8 mm axial by 7.4 mm transverse diameter.

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

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

U.C.M.P. 40462. 7.8 mm axial by 6.4 mm transverse diameter.

Pl. 13, fig. 4-5.

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

Discussion of previous investigation:

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

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the anus and the biserial arrangement of the large ambulacral coverplates.

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

Bassler's (1936) redescription of Cystaster stellatus included the first accurate portrayal of the primary orals. He also noted the variation in the number of ambulacra and illustrated a specimen with six radii. In this paper Bassler also described Cincinnatidiscus edenensis based, as it now appears, on two disrupted and deeply etched

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Cystaster stellatus. The poorly preserved ambulacral coverplates led Bassler to think the ambulacra of his specimens were unique. From what is visible in the two type specimens, nothing indicates that they are not typical, but disrupted, Cystaster stellatus. Bassler was undoubtedly influenced by the occurrence of these specimens somewhat lower stratigraphically than the horizon in which the species is most common.

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

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

It is still unclear whether or not the interambulacrals of C. stellatus differ from those of C. granulatus. In forms attributed to

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the former, the nodose, granular prosopon is commonly less concealing, the outlines of the interambulacrals more clearly seen, and they seem to be relatively larger than in C. granulatus. The arcuate crest on the larger hydropore interambulacral plate seems to be more prominent in C. granulatus.

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

Range and occurrence: Trenton Group through Richmond Group, Middle and Upper Ordovician of Indiana, Kentucky, Ohio.

Family Carneyellidae Bell, fam. nov.

Type genus: Carneyella Foerste, 1917

Diagnosis:

Lebetodiscina with: domal theca; oral area with only three primary orals and one hydropore oral; hydropore in right posterior part of oral area, including oral and ambulacral plates; ambulacra form low, rounded ridges on thecal surface, coverplates of moderate thickness (perpendicular to thecal surface), ambulacral tunnel wide and low, coverplate

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passageways oblique, passageway external foramina elongate, often slit-like; peripheral rim plates geniculate.

Description:

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

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

The ambulacra form low, rounded ridges on the oral surface. The

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coverplates are of moderate thickness; their outer surface is nearly parallel to the thecal surface and slopes gradually upward from the adradial suture to the perradial line. This contrasts with the massive coverplates of the Lebetodiscidae which form high ambulacral ridges.

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

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

The peripheral rim plates are geniculate. During thecal collapse the basal parts of the rim plates support the external parts and hold them nearly in life position, whereas the adjacent interambulacrals are depressed. Thus, the proximal margin of the rim stands in high relief above the interambulacrals after collapse. This contrasts with the rim of the Lebetodiscidae in which the squamose rim plates collapse along with the interambulacrals and obscure the proximal boundary of the rim.

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

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Discussion of previous investigation:

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

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

The inclusion of lateral shared coverplates and secondary orals, and the lack of a hydropore oral plate excludes several species that have been included in Bassler's Hemicystitidae. They are here placed in a new Family, the Lebetodiscidae. Most other Hemicystitidae species are here placed in the Family Carneyellidae, with one important exception, Hemicystites parasiticus, the type species of Hemicystites. In erecting the Family Hemicystitidae, Bassler apparently did not closely examine this species and assumed that it was similar in structure to

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numerous other species that erroneously have been included in Hemicystites. Restudy of H. parasiticus has shown that it has: an oral area with four primary orals, two pairs of lateral shared coverplates, secondary orals and a hydropore oral; also, a double alternating biseries of ambulacral coverplates without coverplate passageways. Therefore, all species except the type are here removed from Hemicystites and the genus is placed in the Family Isorophidae. With the removal of Hemicystites from the group, Carneyella is selected as the type genus for the new Family Carneyellidae which includes the remainder of Bassler's Hemicystitidae species.

Discussion:

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

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

The Carneyellidae oral area is formed by only four large plates in contrast with the Lebetodiscidae where there are lateral shared

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coverplates and secondary orals in addition to the three primary orals. Moreover, the primary orals of the Lebetodiscidae are proportionally narrower than those of the Carneyellidae, and hydropore orals are absent. The large and conspicuous three primary orals in the Carneyellidae are very distinctive.

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

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

It is possible that the Lebetodiscidae evolved from the simpler Carneyellidae. This would involve the addition of lateral plates to the three primary orals of the Carneyellidae to form the more numerous orals of the Lebetodiscidae. The single large hydropore oral of the Carneyellidae may have migrated distally into the proximal part of interambulacrum 5 and in the process commonly incorporated additional interambulacrals as the structure moved distally from the oral region.

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The thin ambulacral coverplates of the Carneyellidae would have been greatly thickened to form the massive coverplates of the Lebetodiscidae. In the process the coverplate passageways and their external foramina were greatly enlarged. The "primitive" peripheral rim plates would have lost their geniculation in the reformation to achieve the highly elevated theca of the Lebetodiscidae.

Both families first appear at the same stratigraphic level and if the Carneyellidae do represent a more generalized, ancestral organization, the bifurcation in phylogeny lies considerably further back than the first records do for the two families. As a matter of fact, the present data could be employed, perhaps with equal success, to derive the Carneyellidae from the Lebetodiscidae were not the Carneyellids in most respects in better conformity with current ideas on what generalized edrioasteroids looked like.

Range and occurrence: Chazy Group, Middle Ordovician through Richmond Group, Upper Ordovician of eastern North America (and probably Europe).

Genus Carneyella Foerste, 1917

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

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

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

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

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

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

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

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

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

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

Type species: Agelacrinus pileus Hall, 1866.

Diagnosis:

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

Description:

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

The oral region is formed by three large primary orals and one large hydropore oral (text fig. 13B). Neither secondary orals nor shared coverplates are present so the proximal tips of the lateral ambulacral bifurcation plates are in contact with the lateral edges of the primary orals. The three primary orals are exceptionally large; the posterior one is nearly equal in size to the combined areas of the two anterior plates.

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The hydropore oral lies adjacent to the right margin of the primary posterior oral. Although also large, it is smaller than the adjacent posterior primary oral. The hydropore oral distorts the symmetry of the oral region by causing the right rear area to bulge outward along the posterior edge of ambulacrum V.

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

The hydropore structure, which lies in the right posterior part of the oral region, is formed by four plates: the posterior primary oral, the hydropore oral, and the two proximal posterior coverplates of ambulacrum V (text fig. 13). The two ambulacral coverplates are shortened normal to the ambulacral axis and adradially they abut the hydropore oral plate which projects into the posterior side of the ambulacrum. The slit-like hydropore is formed by three plates. The

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anterior edge of the hydropore oral forms the entire posterior side of the opening. The adradial edge of the proximal ambulacral coverplate forms most of the anterior edge of the slit, but the left end of the opening extends proximally past that plate and is formed by the right edge of the posterior primary oral. The shortened second posterior coverplate of ambulacrum V is not in contact with the opening. The thickened plate margins form a prominent raised rim which surrounds the hydropore slit.

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

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

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

The ambulacral coverplates are of moderate thickness and lie nearly parallel to the thecal surface. Each plate is elongated perpendicular to the ambulacral axis and the exterior surface is sub-rectang-

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ular, with an angular perradial tip. The plate exterior is flat or gently arched.

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

The proximal intra-ambulacral extensions are much larger than the distal ones. They extend from the perradial tip more than half-way down to the adradial suture and gradually diminish in size to merge with the inner surface of the coverplate above the level of the floor-plates. Each of these blade-like extensions arises from the proximal inner edge of the coverplate and extends proximally beneath the distal edge of the adjacent, proximal coverplate. The proximal edge of the blade is flexed up and outward, and abuts the inner, ambulacral tunnel surface of the distal, lateral edge of the next coverplate, where it fits into a shallow groove. Thus, the outer surface of the extension is convex inward, and the axis of the "trough" is parallel to the length of the coverplate. The perradial tip of the extension is widest and is also produced past the perradial tip of the coverplate, under the perradial line of the ambulacrum. It underlaps the perradial tip of the alternate coverplate on the opposite side of the ambulacrum. The

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proximal intra-ambulacral extensions thus interlock adjacent coverplates whether open or closed. Alternate opposing coverplates are locked together across the perradial line when closed, but the underlapping perradial tips of the extension slip out from under the alternate coverplates during opening.

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

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

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The tubular passageway extends into the theca between the adjacent coverplates; the inner foramina is formed by the intra-thecal extensions. The semi-circular depression in each side of each extension marks the intersection of one side of each tubular passageway with the inner side of the coverplates. The two adjacent depressions unite to form the sub-circular inner foramen.

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

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

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The interambulacrals are squamose, imbricate plates without definite order.

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

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

Discussion:

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

Carneyella has been mentioned in many papers, but most descriptions apply only to the type species, C. pilea. Bassler (1935, 1936) described several new species which he assigned to Carneyella, but his brief generic description is like that of Foerste except he excluded

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the two lateral bifurcation plates from the oral region and listed only the three primary orals.

Range and occurrence: Chazy Group, Middle Ordovician through Richmond Group, Upper Ordovician of eastern North America.

Carneyella pilea (Hall), 1866

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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pl. 5, fig. 5-7; Isorophus germanus Bassler, idem, ibid.: 18, pl. 6, fig. 3-4.

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

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

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

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

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

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

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

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

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Diagnosis:

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

Description:

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

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

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

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Text Figure 13 Carneyella pilea (Hall), 1866

A. U.C.M.P. 40464, (X3), pl. 17, fig. 8.

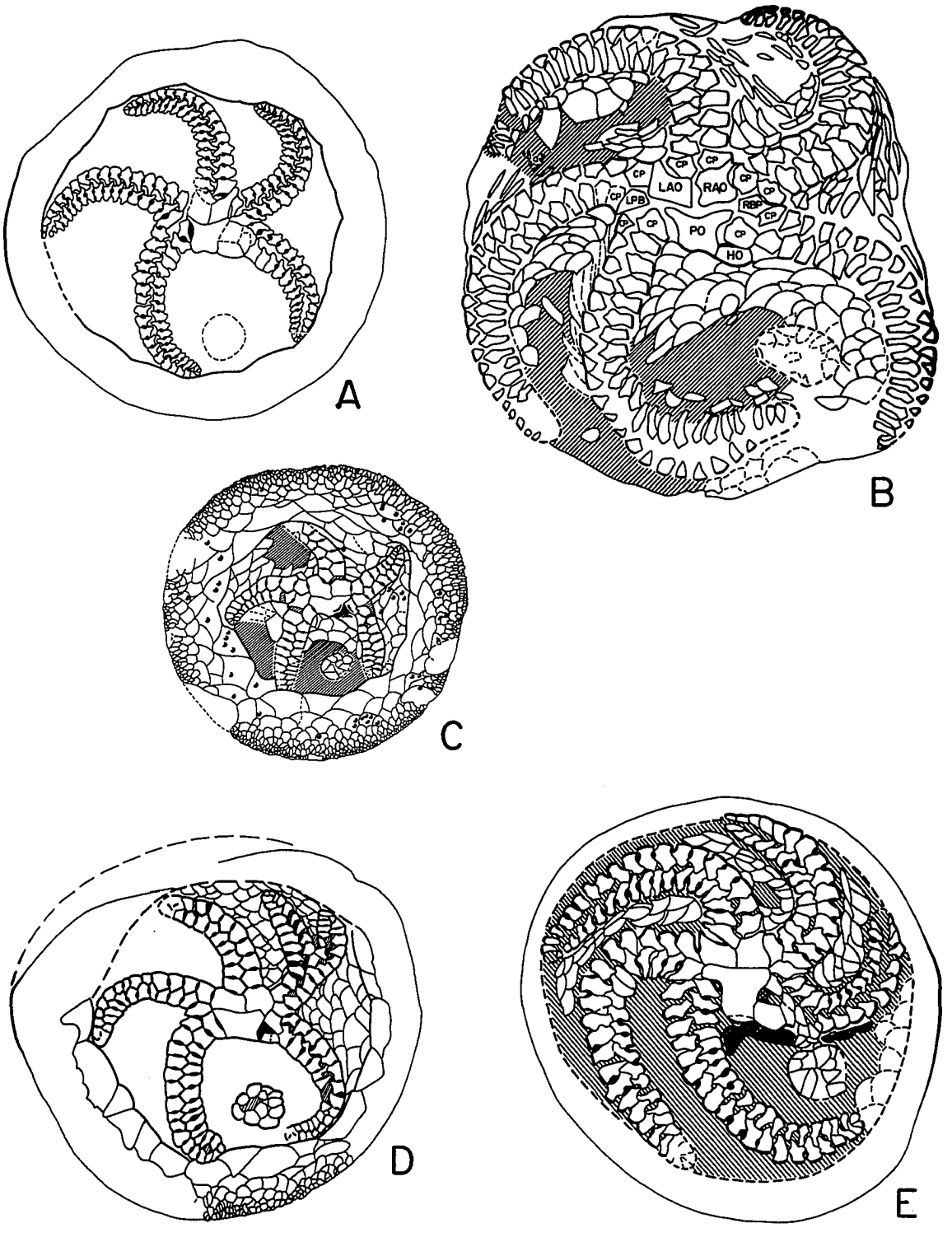
B. Lectotype, M.C.Z. 516-a, (X5), pl. 14, fig. 2. CP. ambulacral coverplate; HO. hydropore oral plate; LAO. left anterior primary oral plate; LPB. left lateral bifurcation plate; PO. posterior primary oral plate; RAO. right anterior primary oral plate; RBP. right lateral bifurcation plate.

C. C.F.M.P. 6504, (X5), pl. 16, fig. 11.

D. U.S.N.M. 40743-c, (X6), pl. 14, fig. 8.

E. U.S.N.M. 170362, (X6), pl. 15, fig. 12. Interambulacral plates along the posterior side of ambulacrum V are shaded.

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Text Figure 13

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thickened plate margins form a conspicuous raised rim around the hydropore.

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

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

The anterior half of the frame is formed by the floorplates of ambulacra II, III, and IV, and the intra-thecal extensions of the two anterior primary oral plates. The three floorplates are proximally

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

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

The posterior part of the frame includes the proximal floorplates of ambulacra I and V, and the intra-thecal extension of the large posterior primary oral. The anterior ends of the proximally enlarged floorplates flare out slightly and broadly abut the two lateral anter-

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

The passageway for the stone-canal extends downward from the

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

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

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

The peripheral rim comprises three outwardly intergradational series of plates. The proximal rim plates are elongate concentric with the thecal margin. The distal plates are small and radially elongated. Between these are transition plates which are ovate and slightly elongated radially. The shape of the transition plates is masked by a

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

The plates of Carneyella pilea bear nodes or tubercles and are pitted (pl. 14, fig. 5, 10-13, 17-18). The pitting is commonly preserved even in etched specimens. It varies from a coarse pattern visible to the unaided eye to micro-pitting that appears to be the surficial expression of the stroma canals intersecting the thecal plates surfaces.

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

Each ambulacral coverplate has a moderately large protuberance on the perradial tip of the plate (pl. 16, fig. 8-10). These elong-

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ate, ridge-like elevations extend upward from the tip of each coverplate and are highest perradially. Like the thecal nodes, these are frequently altered or removed by etching.

Specimens:

M.C.Z. 516-a. Lectotype of Carneyella pilea (Hall) (1866, p. 7). "Hudson River Group" (probably Maysville Group), Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. 16.1 mm axial by 15.5 mm transverse diameter.

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

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

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

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visible.

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

Pl. 14, fig. 3-5.

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

M.C.Z. 518-a. (?) Lectoparatype of C. pilea (Hall) (1866, p. 7). "Hudson River Group" (probably Maysville Group), Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. 13.8 mm axial by 12.5 mm trans-

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verse diameter.

Pl. 14, fig. 6-7.

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

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

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

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

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

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A.M.N.H. 1193-C. (?) Lectoparatypes of C. pilea (Hall) (1866, p. 7). "Hudson River Group" (probably Maysville Group), Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. Two individuals on one brachiopod: (1) 14.5 mm axial by 12 mm transverse diameter; (2) 12.8 mm diameter.

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

U.S.N.M. 40743 (a-d). Four specimens of C. pilea. Corryville Formation, Maysville Group, Cincinnatian Series, Upper Ordovidian. Warren County, Ohio.

U.S.N.M. 40743-a. Holotype of Carneyella cincinnatiensis Bassler (1935, p. 4, pl. 1, fig. 10). 13.1 mm axial by 13.5 mm transverse diameter.

Pl. 14, fig. 10-12.

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

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U.S.N.M. 40743-b. 10.8 mm axial by 10.5 mm transverse diameter.

Pl. 14, fig. 13.

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

U.S.N.M. 40743-c. 9.4 mm axial by 11.1 mm transverse diameter.

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

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

U.S.N.M. 40743-d. 11.4 mm axial by 11.1 mm transverse diameter.

Pl. 14, fig. 14.

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

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

Pl. 14, fig. 17-18.

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

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

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

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

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

Pl. 15, fig. 8.

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

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Text Figure 14 Carneyella pilea (Hall), 1866

A. Juvenile, U.S.N.M. 40742-a-2, (X10), pl. 15, fig. 6.

B. Lower side of the coverplates of ambulacrum I, C.F.M.-U.C. 8825, (X17), pl. 16, fig. 4.

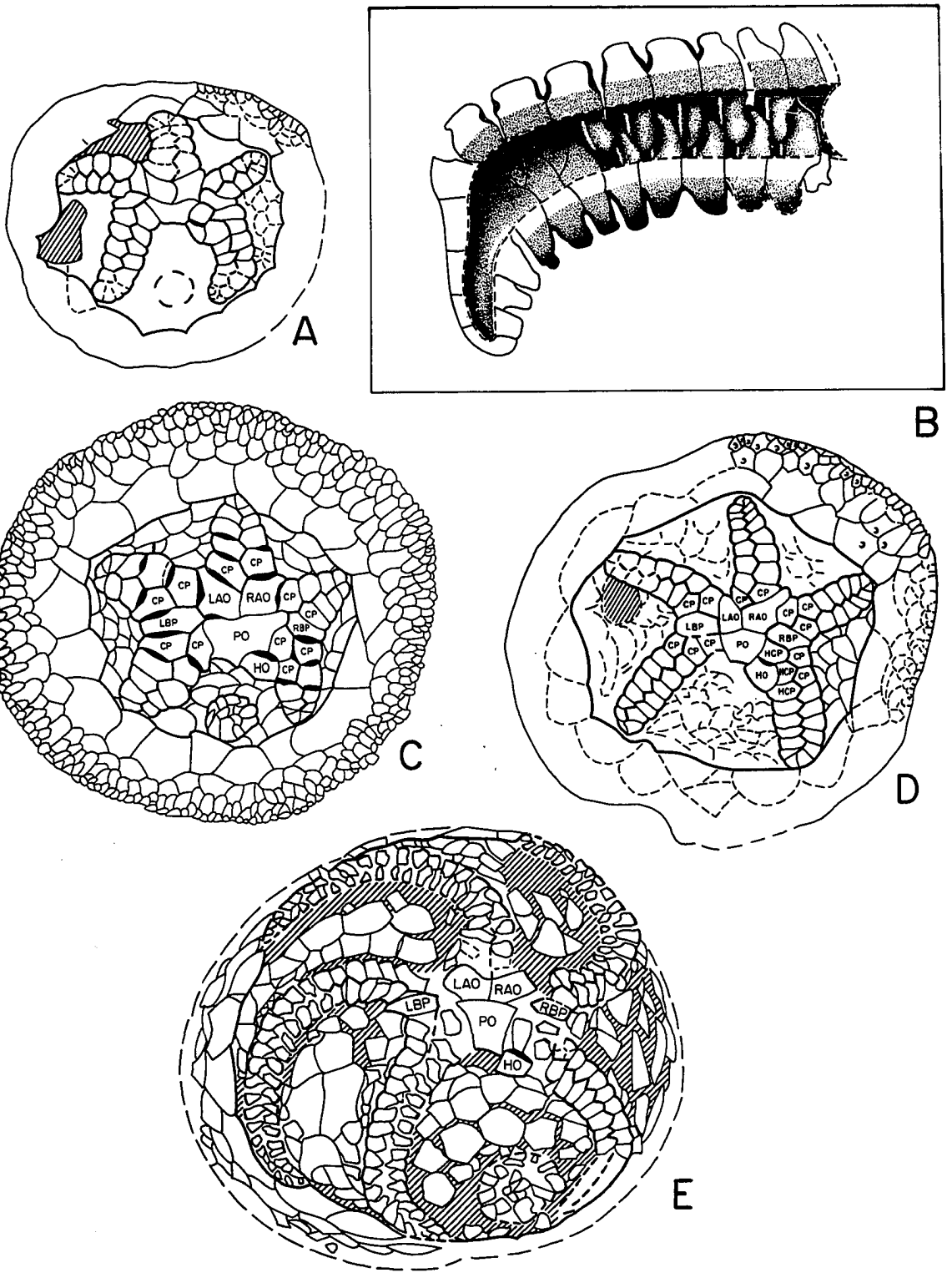
C. Juvenile, U.S.N.M. 42105, (X15), pl. 14, fig. 16.

D. Juvenile, U.S.N.M. 42111-A, (X10), pl. 15, fig. 2.

E. U.S.N.M. S-3959, (X4), pl. 15, fig. 10.

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

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Text Figure 14

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are preserved.

U.S.N.M. 42105. Holotype of Hemicystites curtus Bassler (1936, p. 12-13, pl. 4, fig. 8). Platteville Limestone, Black River Group, Middle Ordovician. Rockton, Illinois. 4.60 mm axial by 4.75 mm transverse diameter.

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

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

U.S.N.M. 68333. "Cotype" of Hemicystites richmondensis Bassler (1936, p. 13-14, pl. 5, fig. 7). Whitewater Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Adams County, Ohio. 4.9 mm axial by 5.1 mm transverse diameter.

Pl. 15, fig. 7.

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

Specimen U.S.N.M. 68333 has been crushed and etched although only the hydropore area is completely invisible. Prosopon is preserved in the depressed and protected parts of the theca and includes both nodes and pitting. In a few areas the nodes appear larger and more numerous

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than in typical C. pilea, suggesting that this individual might possibly belong to Carneyella faberi (Miller).

U.S.N.M. 40742 (A1, A2, B). Three "cotypes" of Hemicystites richmondensis Bassler (1936, p. 13-14). Waynesville Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Warren County, Ohio.

U.S.N.M. 40742-A-2. "Cotype" of Hemicystites richmondensis Bassler (1936, p. 13-14, pl. 5, fig. 5). 5 mm axial by 5.1 mm transverse diameter.

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

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

U.S.N.M. 40742-A-1. "Cotype" of H. richmondensis Bassler (not illustrated). 4.7 mm axial by 5.3 mm transverse diameter.

Pl. 15, fig. 5.

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

U.S.N.M. 40742-B. "Cotype" of H. richmondensis Bassler (not illustrated). 6.3 mm axial by 6.7 mm transverse diameter.

Pl. 15, fig. 4.

This rather poorly preserved individual is like U.S.N.M. 68333 in seeming to have somewhat larger and more abundant nodes than average Carneyella pilea which suggests that it might be a young Carneyella

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faberi.

U.S.N.M. 42111-A, B. Two "cotypes" of Hemicystites richmondensis Bassler (1936, p. 13-14). Waynesville Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Versailles, Indiana (probably the large road cut east of town on route U.S. 50).

U.S.N.M. 42111-A. (Bassler, 1936, p. 13-14, pl. 5, fig. 6). 6.7 mm axial by 6.9 mm transverse diameter.

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

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

U.S.N.M. 42111-B. 7 mm axial by 8.4 mm transverse diameter.

Pl. 15, fig. 3.

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

N.Y.S.M. 10683. Holotype of Bassleridiscus mohawkensis Fisher (1952, p. 691-693, fig. 1-2). Larrabee member, Kirkfield Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. $\frac{1}{4}$ mile east of Manny Corners, a hamlet 2 miles northeast of Amsterdam, New York. 15.5 mm axial by 15 mm transverse diameter.

Pl. 14, fig. 15.

This is a typical Carneyella pilea. It rests upon a small,

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ramose bryozoan. The peripheral rim has been flexed under the upper surface to maintain contact with the bryozoan. Thecal collapse, acting on the already distorted thecal shape, has accentuated the elevation of the ambulacra, partially disrupted the coverplates, and has preserved the distal parts of the ambulacra on the lower side of the theca.

U.S.N.M. 170362. Float block of upper 15 feet of Point Pleasant Limestone, Cynthiana Formation, Trenton Group, Mohawkian Series, Middle Ordovician. Quarry section on Bear Creek Road, 0.1 mile north of the Intersection with United States Route 52, about 3 miles east of Neville, Clairmont County, Ohio. (Moscow, Ohio-Kentucky Quadrangle 7½ minute topographic sheet, Ohio co-ordinates system: 296,275; 1,526,725'). 11.1 mm axial by 11.4 mm transverse diameter.

Text fig. 13E, pl. 15, fig. 11-13.

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

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curvature.

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

Pl. 16, fig. 5-6.

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

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

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

The specimen exposes the inner side of the oral surface. It is incomplete, missing some interambulacral plates, most rim plates and many ambulacral floorplates, including several of the proximal frame-

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forming ones. The inner, ambulacral tunnel sides of the coverplates are seen where the floorplates are missing. Especially well-preserved are the coverplates of ambulacrum I; text figure 14B shows the interlocking, intra-ambulacral extensions.

C.F.M.-U.C. 54062. Probably Maysville Group, Cincinnatian Series, Upper Ordovician of the Cincinnati Arch region. 13.5 mm axial by 14.4 mm transverse diameter.

Pl. 16, fig. 12.

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

C.F.M.-P. 6504. Maysville Group, Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio. 9.8 mm axial by 9.8 mm transverse diameter.

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

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

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

Pl. 16, fig. 7.

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

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

Pl. 16, fig. 8-10.

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

U.C.M.P. 26324. Upper part of the Corryville Member, McMillan Forma-

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

Pl. 17, fig. 1-4.

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

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

U.C.M.P. 40463-40466. 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

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Quadrangle, 7.5 minute topographic sheet (1953), Ohio Co-ordinate System: 397,300'; 1,474,700'; equals approximate center of a 200' by 200' area).

U.C.M.P. 40463. 18.5 mm axial by 18.5 mm transverse diameter.

Pl. 17, fig. 5.

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

U.C.M.P. 40464. 21.3 mm axial by 20.8 mm transverse diameter.

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

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

U.C.M.P. 40465. 16.6 mm axial by 16.4 mm transverse diameter.

Pl. 17, fig. 6-7.

Only the posterior interambulacrum of this specimen has collapsed.

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The ambulacra and the oral area form only slightly raised, rounded ridges. The specimen has been extensively etched.

In addition to the above representatives of Carneyella pilea, over five hundred other specimens were examined. These include a large number of individuals from both the Forestville and the North College Hill sites, as well as individuals from scattered localities around the Cincinnati Arch region.

Ontogeny:

Several advanced juveniles and young adult Carneyella pilea suggest that at least the later stages of ontogeny for this species are quite similar to those of Isorophusella inconditus. The advanced juveniles (U.S.N.M. 42105, 68333, 40742-A-1, A-2 and B, 42111 A) contrast with adults in the proportionately large size of the peripheral rim, oral area and periproct whereas the ambulacra and interambulacra are relatively smaller (text fig. 14A, C, D). The ambulacra are short and straight or only slightly curved. In young adults (U.S.N.M. 42111-B), the ambulacra and interambulacra become the dominant thecal structures and ambulacra curvature becomes progressively greater. Adults are characterized by the dominant ambulacra and interambulacra, whereas the peripheral rim, oral area and anal structures each form a relatively small percentage of the total oral surface area (text fig. 13A-B). Ephebic ambulacra are distally concentric with the thecal margin. A few unusually large specimens (20 mm) suggest that gerontic forms differ only in their exceptional large thecal diameter (text fig.

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14E, pl. 15, fig. 8-10).

Discussion of previous investigation:

Hall's (1866) original description of Agelacrinus pileus was unusually complete. He based the species on: shape of the theca; direction of curvature of the ambulacra; single biseries of ambulacral coverplates; three large primary orals; four lateral ambulacra which originate as "pairs"; and central location of the anal structure ("ovarian aperture") in the posterior interambulacrum. In the subsequent description of the plate (1871), Hall recorded: "Along the depression at the summit of three of the rays may be seen the minute pores passing between the plates." His "pores" are the upper ends of the coverplate passageways which extend between the partially disrupted and deeply etched coverplates of his specimen. This observation has been overlooked or ignored by subsequent workers. In that plate explanation Hall also showed and called attention to "rounded nodes" on many of the interambulacral plates.

Meek (1873) redescribed Hall's Agelacrinites pileus and emphasized the lack of a second series of ambulacral coverplates (such as those in Isorophus cincinnatiensis). He also pointed out the theca is domal (not semi-globose as described by Hall who illustrated only contorted specimens in which the peripheral rim was curved under the upper surface). Meek's specimens were etched and the nodose prosopon obscure. Thus he described the plate exteriors as smooth.

Miller and Faber (1892) described the inner surface structure

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of Carneyella pilea from specimen C.F.M.-U.C. 8825, (pl. 16, fig. 1-4, text fig. 14B) which exposes the inner side of the oral surface. In the detailed description, they reversed the terminology, i.e., ambulacral floorplates are called covering elements and coverplates are called flooring elements. In standard terminology, they described the interlocking inner sides of the ambulacral coverplates, the uniserial ambulacral floorplates, and the "subpentagonal" oral frame formed by the proximal ambulacral floorplates. Miller and Faber suggested that the innermost edge of the oral frame was flattened for attachment to the substrate. However, their specimen does not support this.

Spencer (1904) described Carneyella pilea from serial polished surfaces of a well-preserved specimen and a wax model restoration based on these. He described the ambulacral coverplates and floorplates, including "small interspaces between each covering plate" but denied the presence of passageways. He concluded that "Agelacrinites" has: (1) secondary triradiate symmetry formed by the fusion of ambulacra I-II and IV-V; (2) no regular numerical correspondence between ambulacral coverplates and floorplates; (3) orals derived from coverplates; (4) ambulacral floorplates forming the oral frame; and (5) no trace of a "madreporite" (i.e., hydropore). Spencer's assessment of the coverplate-floorplate relationship, the derivation of the orals, and the construction of the oral frame agrees with current conclusions, whereas his contention that triradiate symmetry is secondary and that no hydropore is to be found are rejected here.

Foerste (1914) gave a detailed summary of the morphology of

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Carneyella pilea, including the first account of the hydropore and stone-canal passageways (although he did not identify them as such). Most of Foerste's description agrees with that presented here except for two sets of "striations" on the articulating faces of the ambulacral coverplates (based on specimen C.F.M.-U.C. 8886, pl. 16, fig. 5-6). These areas appear to be smooth. Foerste also described small vertical ridges on the inner sides of the peripheral rim plates of Carneyella pilea. However, he based this on what has proved to be a specimen of Isorophus cincinnatiensis (A.M.N.H. 13266/1-X, pl. 25, fig. 1-2). As seen in several specimens, the rim plates of Carneyella pilea are squamose and the interior side is smooth.

Foerste (1914) also speculated on the life orientation of Carneyella pilea based on the presumed orientation of resting sites (concave-convex brachiopod shells) to current direction as related to the orientation of the edrioasteroid theca to the slope of the resting site surface. This, he contended, was indicated by the direction of thecal slump after death. He concluded that the theca was oriented to currents so as to provide maximum ease of feeding rather than for prevention of ambulacral contamination by excreta; and the direction of curvature of ambulacrum V, opposite the direction of the other four, evolved from the sloping substrate habitat of the edrioasteroids. Although Foerste's search for an ecologic and physiologic understanding was years ahead of his time, his conclusions seem to be unsupported by facts now at hand. Numerous specimens collected from a single bedding-plane from the Forestville site appear to have been randomly oriented,

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and certainly in diverse positions on many types of hard surfaces of various configuration. His second suggestion seems to depend upon a neo-Lamarkian scheme of inheritance of acquired characteristics that can no longer be accepted.

Kesling (1960) identified the hydropore structure and the underlying stone-canal passageway of Carneyella pilea that had been described but not identified as such by Foerste (1914). Kesling and Mintz (1960) summarized previous work on C. pilea and gave a detailed morphologic description based on external observations of both the inner and outer sides of the oral surface and also on serial polished surfaces of one individual. The only significant difference between their account and that given here is the identification of the cover-plate passageway system described here. Minor discrepancies between their description and this one are related to specimen A.M.N.H. 13266/1-X, (pl. 25, fig. 1-2) which exposes the inner side of the oral surface. Preparation of the individual with new techniques allowed removal of additional matrix and revealed that it is an Isorophus cincinnatiensis and not a Carneyella pilea as thought by Kesling and Mintz.

Bassler (1935, 1936) described five species which are here placed in synonymy under Carneyella pilea. The first, Carneyella cincinnatiensis Bassler (1935), was based on specimen U.S.N.M. 40743-a and three additional unfigured specimens (b, c and d) (text fig. 13D, pl. 14, fig. 8-14). Bassler listed five characters: (1) theca "thin, depressed, almost flat"; (2) theca "attached by its entire aboral

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portion"; (3) "ambulacral plates . . . less elevated" (than in C. pilea); (4) "all the plates are rather papillose"; and (5) "only three oral plates" are present (in contrast with Isorophus cincinnatiensis). He referred to his new Carneyella cincinnatiensis a specimen illustrated by Hall (1871, pl. 2, fig. 7; = 1872, pl. 6, fig. 7). Hall's illustration depicts an Isorophus cincinnatiensis, except that the oral plates shown are those typical of Carneyella pilea, i.e., three large primary orals. The oral region of Hall's specimen (A.M.N.H. 1194) is actually typical of Isorophus cincinnatiensis, formed by several plates including four primary orals. Bassler apparently examined only Hall's erroneous illustrations, and concluded from the three large orals that the specimen must belong to the genus Carneyella and not Isorophus. Bassler cited this illustration under his Carneyella cincinnatiensis as follows: "Agelacrinus (Lepidodiscus) cincinnatiensis Hall (non Roemer)". He thereby implied that the specimen belonged to the species Carneyella cincinnatiensis Bassler and not to Roemer's Agelacrinus (Lepidodiscus) cincinnatiensis (now Isorophus cincinnatiensis). This citation probably explains why Bassler selected the trivial name cincinnatiensis, in spite of the confusion it has created due to the established name Isorophus cincinnatiensis.

Carneyella nicklesi Bassler (1936) was based on a large but poorly preserved Carneyella pilea (U.S.N.M. S-3876, pl. 14, fig. 17-18). Bassler (1936, p. 7) distinguished it from all other species of Carneyella by "its long, broad, much curved ambulacra, with about 20 short, wide covering plates in each row, and by the large, slightly imbricating, plainly visible interambulacral plates not obscured by

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surface ornamentation, which in this case consists of minute papillae arising from the finely punctate surface." These are all typical features of large Carneyella pilea.

Isorophus germanus Bassler (1936) was based on two specimens (U.S.N.M. S-3959 and U.S.N.M. S-3960, text fig. 14E, pl. 15, fig. 8-10). Both are quite large and typical C. pilea. Bassler's description of his new species is brief and contrasts this form with another species of Isorophus on the basis of thecal size, shape, number of plates and anal structure. In these two types, the oral area with three large primary orals, the ambulacra with a single biseries of coverplates and sutural passageways, and the anal periproct, all bespeak Carneyella pilea and contrast with the structure of Isorophus.

Hemicystites curtus Bassler (1936) and H. richmondensis Bassler (1936) are both based on young specimens of Carneyella pilea. H. curtus was based on a single juvenile (U.S.N.M. 42105) just under 5 mm in diameter, in which ambulacral curvature had just begun and the size proportions of the major thecal structures are those of an advanced juvenile (text fig. 14C, pl. 14, fig. 16). Bassler cited the thecal proportions as distinguishing this individual from other species.

Hemicystites richmondensis Bassler (1936) was based on six specimens (U.S.N.M. 68333, 40742, 42111), five juveniles and one young adult (text fig. 14A, D, pl. 15, fig. 1-7). The features Bassler described as characteristic of his species are characters of the youthful stage of development of C. pilea. Bassler's (1936, p. 14) contention that "it is not the young of some other edrioasteroid

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because the numerous specimens discovered all maintain the same maximum size", is not supported by measurements of the six specimens of the type series. Moreover, there is a progressive development from the smallest to the largest of the six individuals although no mention is made of this in Bassler's description.

Bassleridiscus mohawkensis Fisher (1951) is also here placed in synonymy with Carneyella pilea. Fisher based his species, the type for his new genus, on a single individual (pl. 14, fig. 15) from the Middle Ordovician of New York which rests upon a fragment of a ramose bryozoan. The small, curved resting surface distorted the domal theca, and the distal parts of the ambulacra, interambulacra, and the peripheral rim are flexed under the upper side of the theca. The thecal contortion accounts for the "disco-globular" shape and long, strongly curved ambulacra that "extend onto the aboral surface" used by Fisher to differentiate the new genus and species from other forms with similar plate arrangements such as undistorted Carneyella pilea.

Discussion:

The study of over five hundred specimens of Carneyella pilea has revealed only a few features not previously described. Most important is the coverplate passageway system, noted by Hall (1871) but overlooked since. The nodose prosopon is now believed to occur in all Carneyella pilea, although it is commonly obscured by surficial etching. The recognition of the wide range of thecal contortion which results from small or unusual resting areas accounts for several seemingly unique specimens (such as the type of Bassleridiscus mohawkiensis).

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Knowledge of ontogeny necessarily broadens the taxobases.

Range and occurrence: Trenton Group, Middle Ordovician through Richmond Group, Upper Ordovician of eastern North America.

Carneyella faberi (Miller), 1894

Text fig. 15; plate 17, fig. 10-13, plate 18, fig. 1-5

1894 Agelacrinus faberi Miller, S. A., in Miller, S. A. and Faber, C. L, Cincinnati Soc. Nat. Hist., Jour. 17 (3): 156, pl. 8, fig. 24-25.

1914 Agelacrinus faberi Miller, Foerste, A. F., Denison Univ., Sci. Lab. Bull. 17 (art. 14): 441-444, pl. 1, fig. 3a-c, pl. 3, fig. 4; Agelacrinus vetustus Foerste, ibid.: 439-441, pl. 3, fig. 1.

1915 Agelacrinites faberi Miller, Bassler, R. S., United States Nat. Mus. Bull. 92, 1: 20; Agelacrinites vetustus Foerste, idem, ibid.: 21.

1918 Agelacrinus faberi Miller, Williams, S. R., Ohio Jour. Sci. 19 (1): 64.

1936 Carneyella faberi (Miller), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 9; Carneyella vetustus (Foerste), idem, ibid.: 7, pl. 2, fig. 14; Carneyella foerstei Bassler and Shideler, idem, ibid.: 8, pl. 6, fig. 7-8.

1943 Carneyella faberi (Miller), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 197; Carneyella foerstei Bassler and Shideler, idem, ibid.: 197; Carneyella vetusta (Foerste), idem, ibid.: 198.

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Diagnosis:

A Carneyella with: large clavate tubercles having rounded distal extremities, numerous on interambulacral and rim plates, but only 2 to 7 per ambulacral coverplate.

Description:

Carneyella faberi is represented by only three specimens in which the domal theca ranges from 12 to 25 mm in diameter (pl. 17, fig. 10-13, pl. 18, fig. 1-5). It differs from C. pilea only in the character of the prosopon. Whereas C. pilea has small irregular nodes on the interambulacrals and rim plates, C. faberi has numerous large tubercles.

The tubercles are commonly clavate, the bulbous upper part connected to the underlying plate by a short, distinctly constricted zone (text fig. 15C-D, pl. 18, fig. 4-5). The distal tips are usually rounded, although some appear pointed. All three known specimens show evidence of etching, and thus it is not impossible that most of the nodes were originally sharply pointed like those of Carneyella ulrichi.

The number of tubercles per plate varies with the size and type of thecal plate involved. The largest plates of the interambulacra and peripheral rim average twenty-five nodes per plate, whereas smaller, average-sized plates in these areas have only twenty. The ambulacral coverplates bear from two to seven nodes per plate. The larger, proximal coverplates have six or seven. Oral plates appear to bear from ten to fifteen nodes each.

The tubercles vary greatly in size as exemplified by ambulacral coverplates which are usually dominated by two or three large nodes,

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Text Figure 15 Carneyella faberi (Miller), 1894

A.-B. Holotype, C.F.M.-U.C. 8821.

A. Sketch outlining major thecal structures, (X4).

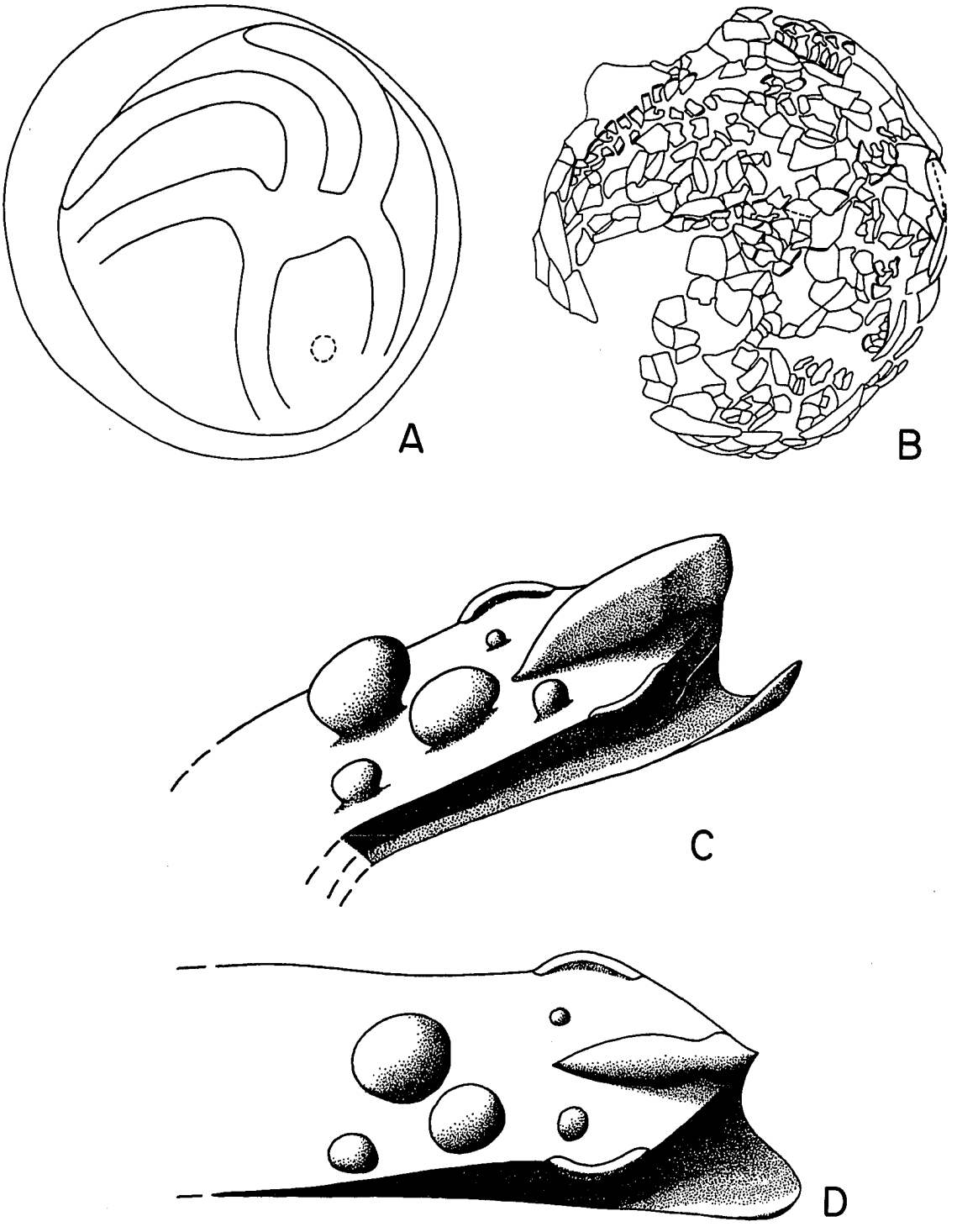
B. Oral surface, (X4), pl. 17, fig. 10.

C.-D. Reconstruction of an ambulacral coverplate;

C. Oblique lateral view.

D. Exterior surface plan view.

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Text Figure 15

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the other three or four so small that they are almost obscured by the larger tubercles (text fig. 15C-D, pl. 18, fig. 3-4).

The ambulacral coverplates, like those of Carneyella pilea, have raised perradial ridges which extend parallel to the length of the coverplate, normal to the ambulacral axis (text fig. 15C-D). These perradial ridges are more highly elevated than those of C. pilea, and appear to have a sharp lateral constriction adradial to the perradial tip of the ridge. In addition to the large central ridge, each coverplate has two smaller ridges, one along each side of the adradial end of the angular perradial margin of the plate (text fig. 15C-D). These two lateral ridges, which parallel and flank the adradial end of the large central ridge, form the most perradial point of contact between adjacent coverplates. The width of each coverplate across the lateral ridged zone is equal to the width of the coverplate along the adradial suture line. The ridged part of the plate therefore extends laterally further than the central section of the coverplate (immediately adradial to the lateral ridges) due to the constriction in external plate width along the external foramen of the coverplate passageway. The ambulacral coverplates are thus very "ornate", with large and small tubercle, a large central perradial ridge and two smaller lateral ridges at the perradial end of the external foramina of the coverplate passageway.

The external edges of all three oral plates are steeply unturned along the transverse and anterior oral midline, and form highly elevated ridges. These oral midline ridges occur in Carneyella pilea but are more subdued.

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A prominent raised rim surrounds the hydropore slit. It is formed by the upturned edges of the adjacent plates, as in C. pilea. In addition, the hydropore oral and the enlarged proximal coverplate of ambulacrum V have ridges that extend outward normal to the rim (pl. 18, fig. 5).

Small vertical ridges are also present on the distal tips of the anal plates and the outermost small plates of the peripheral rim.

Carneyella faberi can be distinguished from C. pilea solely on the basis of prosopon. Both species have external nodes and ridges, but these features in C. faberi are larger and more numerous. The surficial pitting of C. pilea appears to be less prominent than that of C. faberi, although this may be due to preservation. C. faberi is 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:

C.F.M.-U.C. 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. Half-way 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

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15A roughly delimits the location of the ambulacra, interambulacra and oral region. The prosopon is well-preserved on many of the plates.

U.S.N.M. 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 which 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.

U.S.N.M. 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 so as to disrupt some of the interambulacrals. The specimen has been etched, but most prosopon is preserved. Some of the protuberances have been lost during weathering.

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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 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 in 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

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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 due to the effects of abrasion and etching. The tubercles have been lost from various plates of all three specimens and commonly leave almost no

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trace of their original presence. The remnants of missing tubercles are small due to 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 therefore 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 and make 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

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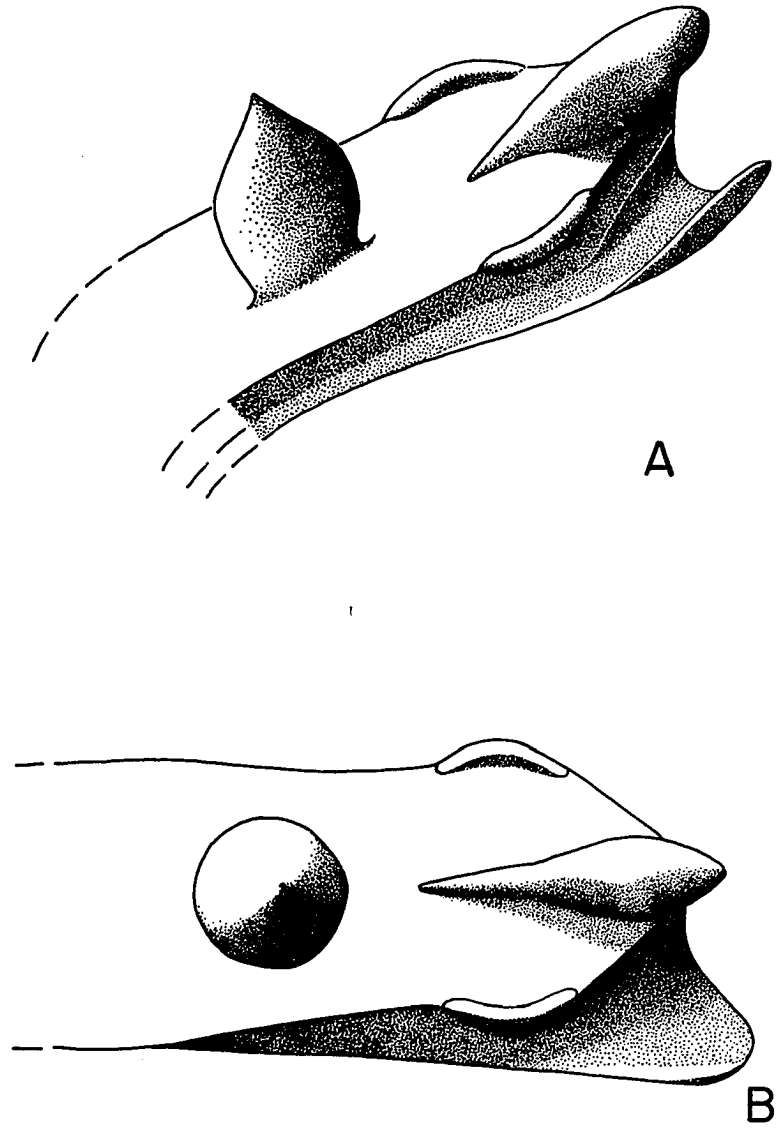
Text Figure 16 Carneyella ulrichi Bassler and Shideler, 1936

A.- B. Reconstruction of an ambulacral coverplate from the holotype U.S.N.M. S-3964.

A. Oblique lateral view.

B. Exterior surface plan view.

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Text Figure 16

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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 rounded distally, and more obviously clavate, the constricted basal neck being longer and more apparent.

As in C. faberi, the greatest numbers of tubercles in C. ulrichi occur on the largest thecal plates which are the distal interambulacrals and the proximal rim plates. Each of these have approximately twenty-five 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 are progressively larger with the largest tubercles 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

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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 vertically upward.

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 vertically upward. 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 constriction 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

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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 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 due 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 to be identical to their counterparts in C. faberi.

Specimen:

U.S.N.M. 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

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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 intra-specific variation. Additional specimens are needed to substantiate the seemingly unique character of the C. ulrichi prosopon.

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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 coverplates 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.

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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:

M.C.Z. 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 mm.

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 [nonl Agelacrinites Vanuxem, L., Nat. Hist. of New York, pt. IV, Geology 3: 158, fig. 80.

1852 [nonl Hemicystites Hall, J., Nat. Hist. of New York, pt. VI,

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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 American Geology and Palaeontology, Cincinnati: 221-222.

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

1908 [nonl 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, Rhideler, 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.

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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

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penetrate proximal peripheral rim circlet; external foramina of coverplate passageways slit-like.

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 orals and a single hydropore oral plate (text fig. 17B). These are similar in size, shape and arrangement to the oral plates of Carneyella. Secondary orals and shared coverplate pairs are lacking. 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). Like Carneyella, the slit-like 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.

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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 sub-rectangular 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 slit-like 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

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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 intra-thecal 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.

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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.

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) (1960) 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 seen it suggests an intermediate condition between the

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periproct of all other Lebetodiscina and the valvular type of the Isorophina.

In this anal structure only two to three circlets of plates are present; the anals are large and sub-triangular; 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 periprocteal 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.

Entymology: 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.

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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.

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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 taper 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 domal 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 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

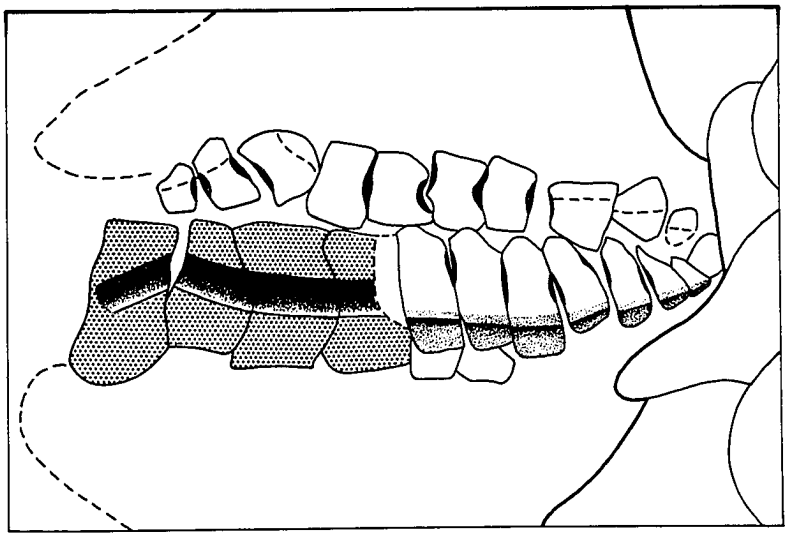
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Text Figure 17 Cryptogoleus chapmani (Raymond), 1915

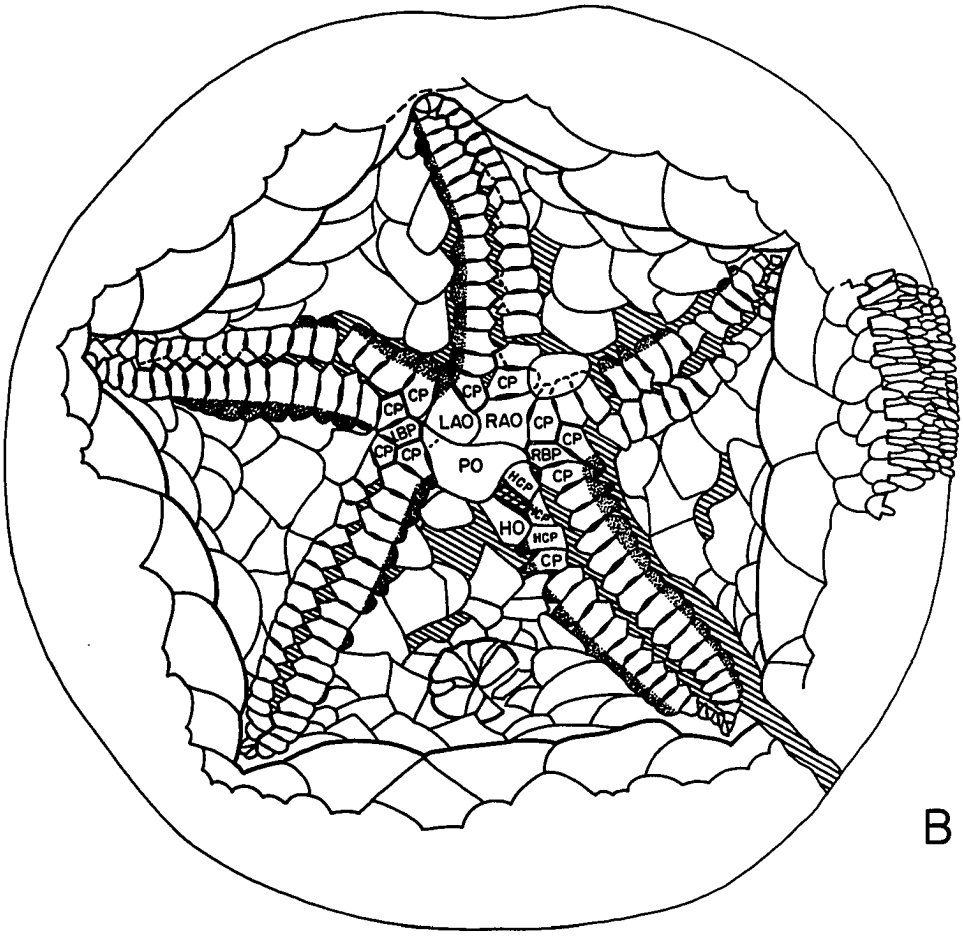
A. Ambulacrum III, R.O.M. 28177, (X18), pl. 20, fig. 8. Ambulacral floorplates are marked with a dotted pattern.

B. Holotype, G.S.C. 3235-a, (X7), 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.

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A



B

Text Figure 17

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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 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 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

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in young individuals do not reach the rim.

The upper surface of the intra-thecal 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 intra-thecal 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, the intra-thecal 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 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

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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 which 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, 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 non-disrupted 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 non-disrupted 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

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distal circlet. These parallel the distal, raised shaft of the transition plates. Therefore, the distal shafts of the 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 R.O.M. 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 (G.S.C. 3235). G.S.C. 3235-c is approximately 3 mm in diameter. The two very young specimens, G.S.C. 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 which represent at least two different species suggest that the two tiny individuals could belong to one of several species.

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Text Figure 18 Cryptogoleus chapmani (Raymond), 1915

A. Juvenile, G.S.C. 3235-f, (X50), pl. 20, fig. 1.

B. Juvenile, G.S.C. 3235-e, (X50), pl. 20, fig. 1. Anterior is to the left.

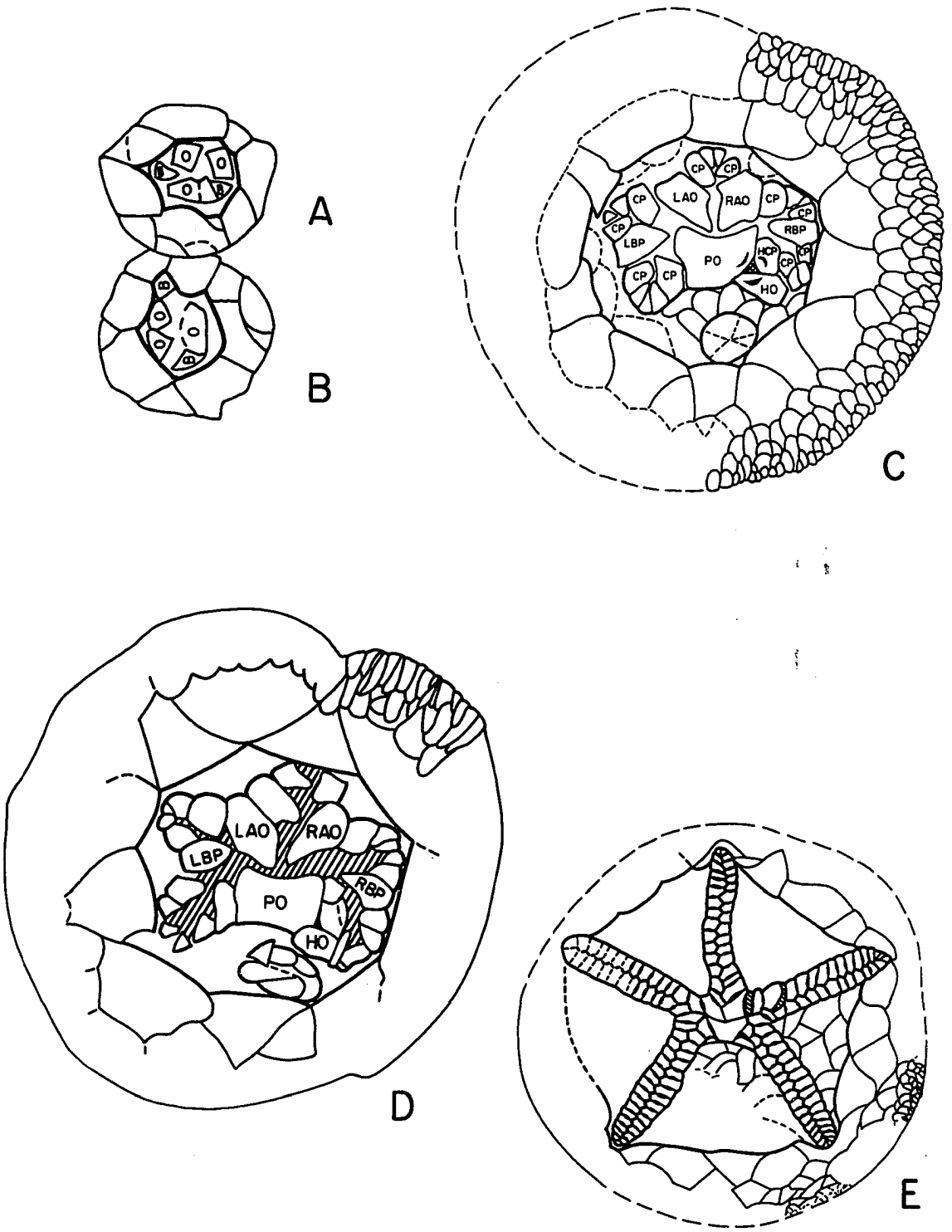
C. Juvenile, R.O.M. 160t-b-F, (X25), pl. 20, fig. 2.

D. Juvenile, G.S.C. 3235-c, (X25), pl. 20, fig. 5.

E. Adult, U.S.N.M. S-3954, (X4), 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.

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Text Figure 18

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The two tiny edrioasteroids assigned to Cryptogoleus chapmani (text fig. 18A-B, pl. 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 the text fig. 18A. If, instead, this lineation represents a suture, the left section would probably represent the posterior primary oral, the right section probably being the hydropore oral. However, this would mean that the posterior primary oral was smaller than the anterior primary orals, an unlikely situation.

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These two specimens, .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 make 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, R.O.M. 160t-b-F (text fig. 18C) being perhaps slightly younger than G.S.C. 3235-c (text fig. 18D). Thecal characters in these specimens differ from 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 one-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.

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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.

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Specimens:

G.S.C. 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, Peterboro, Ontario. Collected by W. A. Johnston.

G.S.C. 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 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 which forms a small gap in the rim adjacent to the tip of the ambulacrum V and reveals the upper surface of the intra-thecal parts of the coverplates. The specimen does not appear to be extensively etched.

G.S.C. 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

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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.

G.S.C. 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 the identification of the smaller plates difficult.

G.S.C. 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.

G.S.C. 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.

R.O.M. 160t-b-F. Trenton Limestone, Trenton Group, Mohawkian Series,

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Middle Ordovician. Peterboro, 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.

U.S.N.M. 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 16.75 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

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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 National Museum is a second "clay ball" with two very fragmentary individuals resting upon the surface. The larger, 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.

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R.O.M. 28177. Trenton Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Peterboro, 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 sub-triangular anals are well-preserved. Many of the proximal plates of the peripheral rim are pitted.

R.O.M. 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.

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

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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:

Raymond (1915) described Agelacrinites chapmani which 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, 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 slightly 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

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Richmond specimens and Trenton forms with straight ambulacra seemed sufficient to him to assure their identity as distinct species, and therefore no attempt was made 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 Cryptogoleus 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 number of the journal 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

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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, differing notably in the hydropore region.

Discussion:

Cryptogoleus chapmani (Raymond) is represented here by only ten 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

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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 which 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 characterize 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.

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Cryptogoleus reticulatus Bell, *sp. nov.*

Text fig. 19; plate 21.

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, non-tapered, terminations blunt and impinging upon proximal rim plates; transition plates of peripheral rim externally sagittate, thecal plates with prominent coarse pits.

Description:

The domal 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 slit-like hydropore is limited to the zone of contact between the anterior edge of the hydropore oral, the adradial

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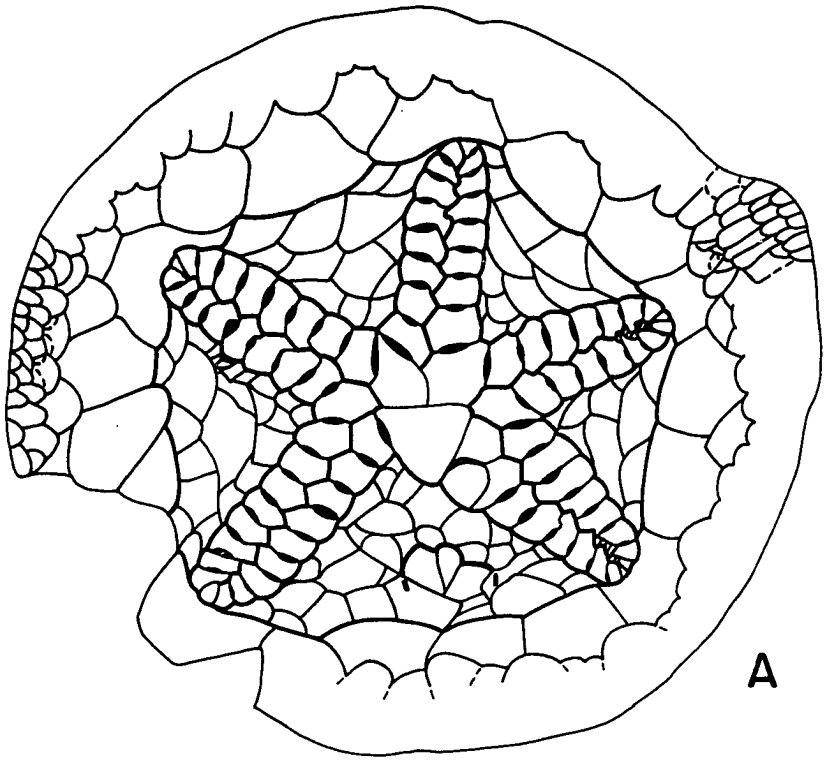
Text Figure 19 Cryptogoleus reticulatus Bell, sp. nov.

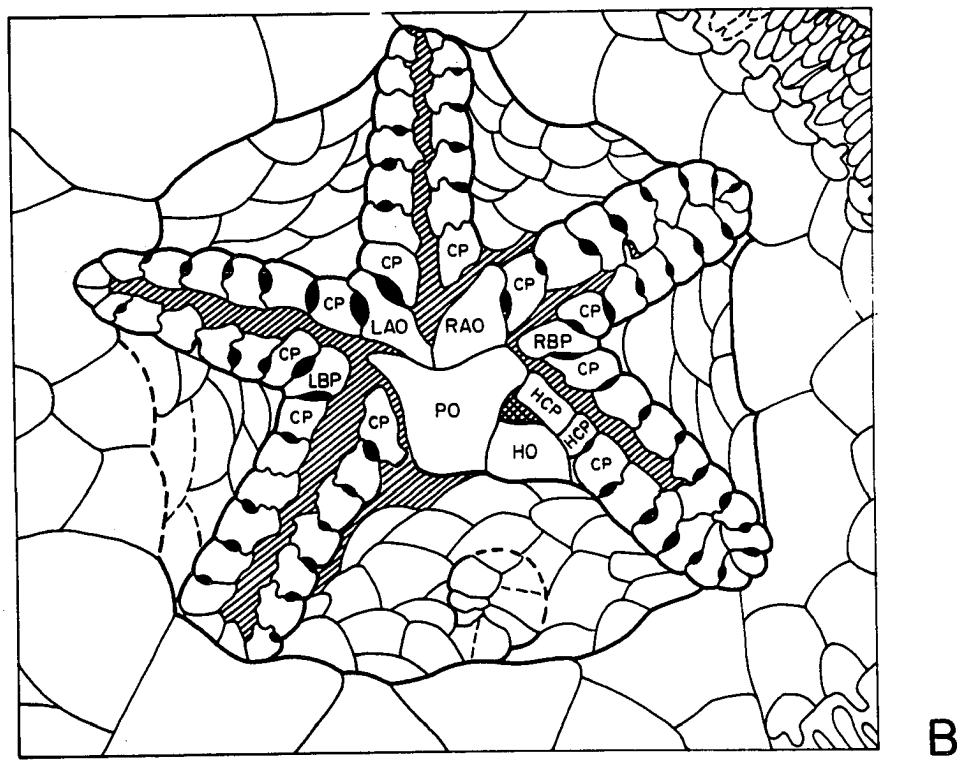
A. Holotype, R.O.M. 28176, (X10), pl. 21, fig. 2.

B. Paratype, G.S.C. 5140, (X14), 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.

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Text Figure 19

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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 intra-thecal 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, slit-like openings as in C. chapmani.

Due to the unusual width of the ambulacra here, the interambulacral areas are proportionately reduced. The interambulacrals are squamose and imbricate, and smaller proportionately than in other Cryptogoleus of this size.

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The anal structure is disrupted in all specimens, but appears to be formed by several, large sub-triangular 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 surfaces of the plates of C. chapmani in which etching commonly removes the prosopon which is limited to rim plates and perhaps some interambulacrals.

Specimens:

R.O.M. 28176. Holotype of Cryptogoleus reticulatus, sp. nov. Trenton Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. 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 little 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.

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G.S.C. 5140. Paratype of Cryptogoleus reticulatus, sp. nov. Illustrated as C. billingsi (Chapman) by Raymond (1921, p. 7-9, pl. 3, fig. 3). Trenton Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Peterboro, 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 sub-surficial 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).

U.C.M.P. 35222 (a-d). Trenton Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario. Kopf Collection.

U.C.M.P. 35222-a. 10.3 mm axial by 10.5 mm transverse diameter.

Pl. 21, fig. 5.

U.C.M.P. 35222-b. 7 mm axial by 8.2 mm transverse diameter.

Pl. 21, fig. 10-11.

U.C.M.P. 35222-c. 7.7 mm axial by 7 mm transverse diameter.

Pl. 21, fig. 8-9.

U.C.M.P. 35222-d. 4 mm axial by 4 mm transverse diameter.

Pl. 21, fig. 6-7.

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

Discussion:

The paratype of Cryptogoleus reticulatus (G.S.C. 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 (G.S.C. 5140) are both large and distinct; high magnification had failed to reveal any prosopon to Chapman, but this new specimen has numerous, large pits on all the plates 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, non-tapering, 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.

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Range and occurrence: Trenton Group, Mohawkian Series, Middle Ordovician of Ottawa — Peterboro 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 interambulacral and rim plates.

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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 slit-like 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 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).

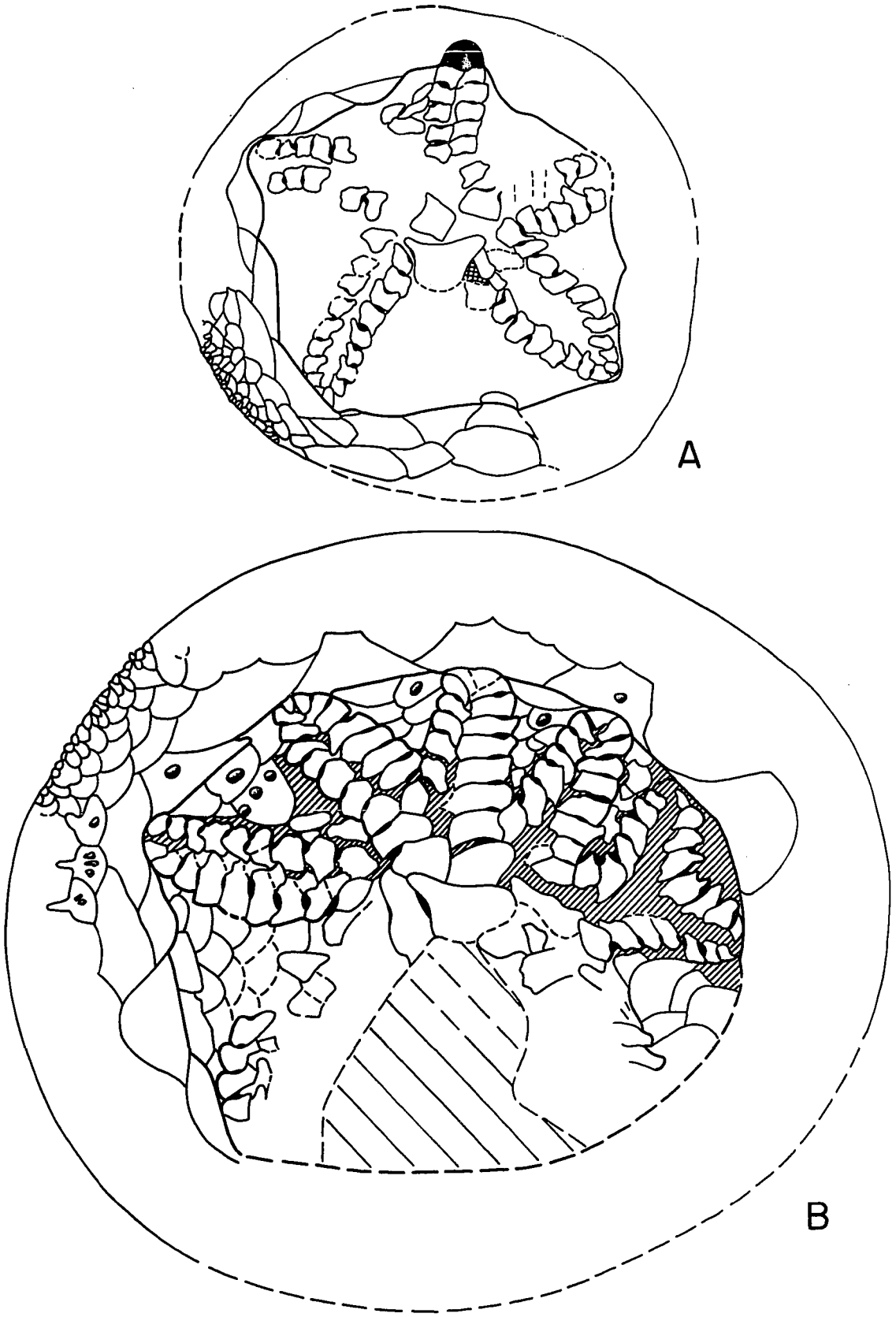
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Text Figure 20 Cryptogoleus multibrachiatus (Raymond), 1915

A. G.S.C. 7789-a, (X10), pl. 22, fig. 7. Distal ambulacral floor-plate of ambulacrum III is shaded.

B. Holotype, G.S.C. 7789, (X15), pl. 22, fig. 2.

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Text Figure 20

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The ambulacral coverplates are moderately convex externally, like 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, and therefore, proportionately there are 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 look bulbous and tessellate.

The anal structure of Cryptogoleus multibrachiatus includes six to ten plates. These are large and sub-triangular. 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 seen 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.

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Specimens:

G.S.C. 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

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to be normal. It is possible to interpret ambulacrum IV as normal, but displaced anteriorly, and 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.

G.S.C. 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

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which exposes a sub-surficial 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.

U.S.N.M. 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 with the number 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 (G.S.C. 7789-a) was described as

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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 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 look to be bulbous from the exterior. The ambulacral coverplates of C. multibrachiatus are slightly narrower than those of other Cryptogoleus, and therefore are proportionately more numerous per ambulacrum.

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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, of 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 unspecialized; thecal plates smooth.

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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 intra-thecal coverplate extensions appear similar to those of other Cryptogoleus.

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

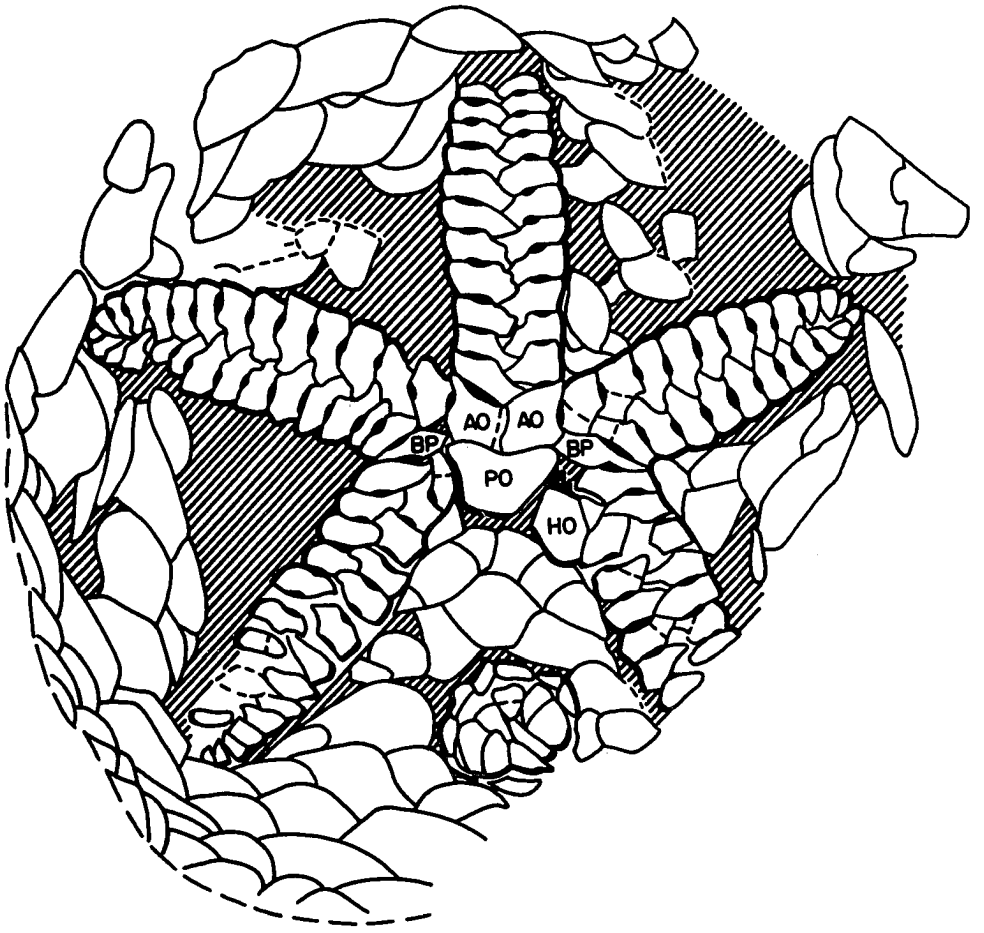
This individual is the only specimen assigned to the family in which the proximal circlet of peripheral rim plates is not distinctly set off from the adjacent interambulacral plates. In light of the disrupted and weathered condition of the specimen, this feature is probably preservational. The outer plates of the peripheral rim have

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Text Figure 21 Cryptogoleus youngi (Raymond), 1915

Holotype, G.S.C. 3234, (X10), pl. 23, fig. 2. AO. anterior primary oral plate; BP. lateral bifurcation plate. HO. hydropore oral plate; P.O. posterior primary oral plate.

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Text Figure 21

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been lost. No specialized transition plates have been observed.

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:

G.S.C. 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 the 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

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the apparently distinctive characters could be due to preservational alteration 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 more narrow and numerous; interambulacral plates moderate in size, relatively numerous.

Description:

Cryptogoleus platys (Raymond) is based upon a single, flattened

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and deeply etched specimen which appears to differ from other Cryptogoleus species (text fig. 22A-B, pl. 23, fig. 4-7). However, these differences could be preservational, or intra-specific 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 sub-surficial view of this region exposed by deep etching. The external hydropore structure has been dissolved away and a sectional view of the sub-circular 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 intra-thecal 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. Comparing the type specimens, C. platys has 0.3 more coverplates per millimeter than C. chapmani.

An oblique section-view of one ambulacral floorplate is exposed

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Text Figure 22 Cryptogoleus platys (Raymond), 1915

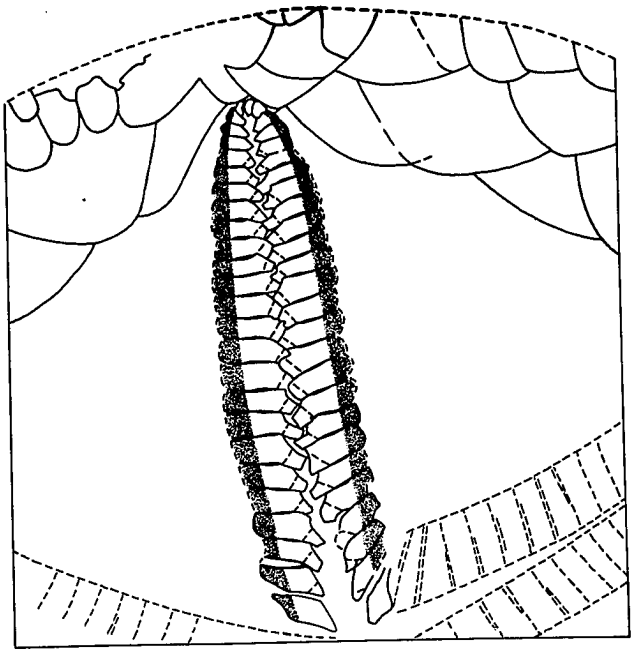
Holotype, G.S.C. 7941. Coverplate intra-thecal extensions, exposed where interambulacral plates are disrupted, are stippled.

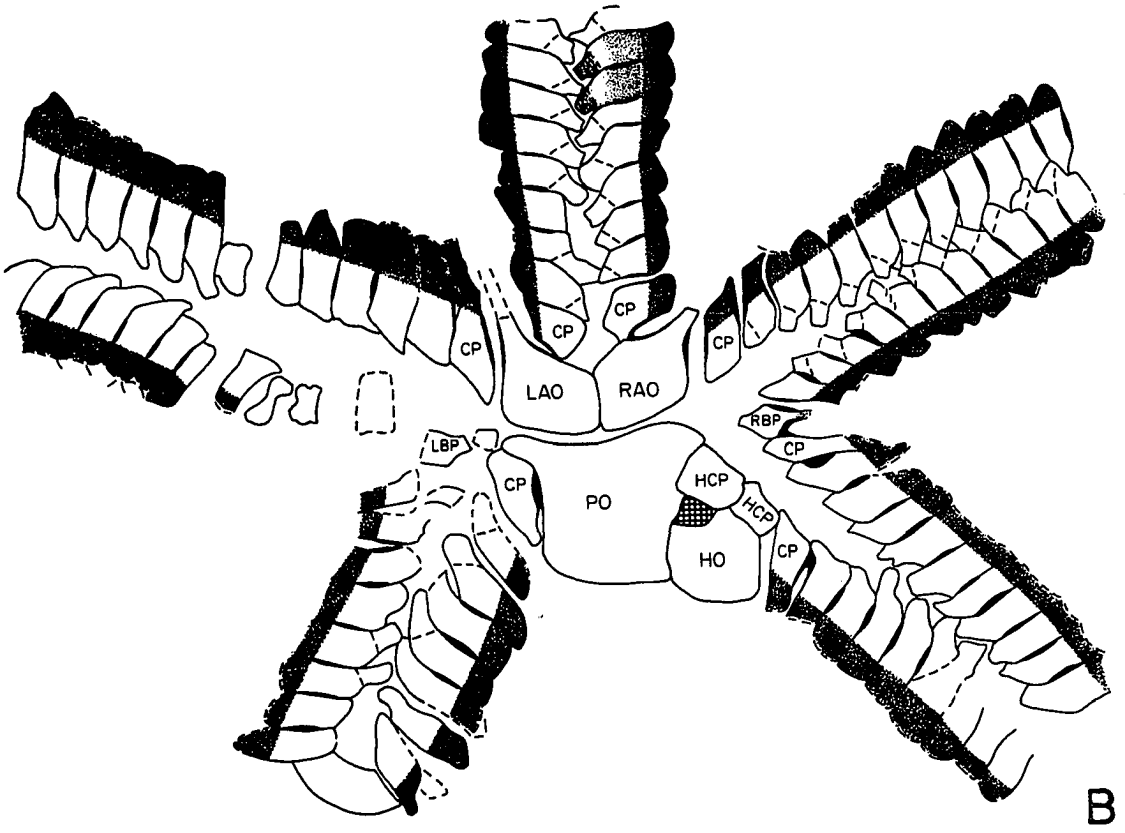
A. Ambulacrum IV, (X8), pl. 23, fig. 7.

B. Oral region and proximal parts of ambulacra, (X11), 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.

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Text Figure 22

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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 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:

G.S.C. 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 the specimen was collected by T. C. Weston in 1881, probably from the "Cystid beds" at the foot of Parliament Hill, or Queens Warf, 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

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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 VI 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: 110, text fig. 86.

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

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1901 Agelacrinites billingsi Chapman, Clarke, J. M., New York St. 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 Peterboro, Ontario. Chapman (1860, p. 359-361) characterized the species as having: a circular theca, .5 inches in diameter, and domal in shape, with five large orals, one separating each ambulacrum from the adjacent ray [i.e., three primary

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orals and two lateral bifurcation platesl; 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 many fewer interambulacrals. No specimen of C. billingsi (Chapman) has been seen.

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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 form multiple alternating biseries or cyclic series which include two to seven sets of plates; coverplates have intra-ambulacral extensions; intra-thecal coverplate extensions may be found in some; contiguous ambulacral floorplates commonly abut 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 coverplates pairs and hydropore orals. Commonly 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

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series plates.

The ambulacral coverplates include two or more plate sets which form 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 intra-thecal 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.

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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, appearing 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 intra-thecal 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,

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integrated with central oral rise; ambulacral coverplates form 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 asymmetric 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 intra-thecal extensions of at least the four primary oral plates. The frame surrounds a large central lumen which 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 inter-

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ambulacrum 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 slit-like 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, 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 intra-thecal extensions which project into the thecal cavity. They extend between the lateral margins of the floorplates and the adjacent interambulacrals.

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The ambulacral floorplates are uniserial and trough-shaped. The upper surface is centrally concave and forms a trough which 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 areas are covered with squamose, imbricate plates. These 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.

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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 multi-plated hydropore structure which 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 which 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 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.

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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. of 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 St. 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 St. Mus., 24th Ann. Rept. (adv. pub.): pl. 2, fig. 7.

1872 Agelacrinus Vanuxem, Hall, J. [partim], New York St. 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.

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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, Tubingen, 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 dentre 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 St. Mus., Bull. 49 (2): 185-193, text fig. 2.

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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-e, 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.

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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; Carnevella 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.

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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.

The oral area is formed by the four primary orals, one hydropore oral, two pairs of shared coverplates and at least four secondary orals (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

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of the additional secondary orals is random and their presence on one side of the oral region 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 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 which underlies the oral area extends down into the thecal cavity below the adjacent ambulacral floorplates. The sub-ovate 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 intra-thecal extensions of the four primary orals. Proximally, it surrounds the ovate central lumen which extends inward from the proximal ends of the ambulacral tunnels and opens downward into the thecal cavity. The lumen is also connected laterally to the posterior sector of the thecal cavity via a

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large gap in the posterior side of the frame, between ambulacral I and V. Bifurcating extensions from the proximal floorplates of these two ambulacra define a small sub-chamber between the central lumen and the posterior thecal cavity. Details of the frame construction are known only from Isorophus cincinnatiensis.

The hydropore structure forms the right posterior bulge of the central oral rise and extends along the proximal posterior side of ambulacrum V. The 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, slit-like 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 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, sub-conical funnel, rapidly

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increasing in diameter inwardly. The upper sector is formed by intra-thecal 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 intra-thecal extension of the hydropore oral and the right primary posterior 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 intra-specifically, 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 widely 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 inter-ambulacra 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

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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 intra-thecal extensions which lie between the adjacent interambulacrals and the underlying floorplates. Extensions of the primary 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 secondary

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coverplate extensions 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 intra-thecal extensions and by the apparent absence of intervening secondary coverplate extensions. However, these spaces are blocked at the lateral margins of the floorplates by the inner ends of the secondary coverplate extensions. 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 blade-like 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).

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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 closed, as 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 five to ten 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 which are nearly equa-dimensional externally.

The large plates of the proximal circlet commonly form a proximal

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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 versus those elongate radially makes distinct distal rim circlets less conspicuous.

The larger plates of the rim are geniculate. The intra-thecal 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

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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.

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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 being smaller and relatively uncommon.

Range and occurrence: Cincinnatian Series, Upper Ordovician of the Cincinnati Arch region, Ohio, Kentucky and Indiana.

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 St. Mus., 20th Ann. Rept. (adv. pub.): 6-7.

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

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

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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, Tubingen, 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, Jaekel, O., Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 50 [non pl. 2, fig. 11].

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

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1901 Agelacrinites cincinnatiensis Roemer, Clarke, J. M., New York St. 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.

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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.

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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 reach 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 non-collapsed specimens is almost evenly convex upward, 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 trans-

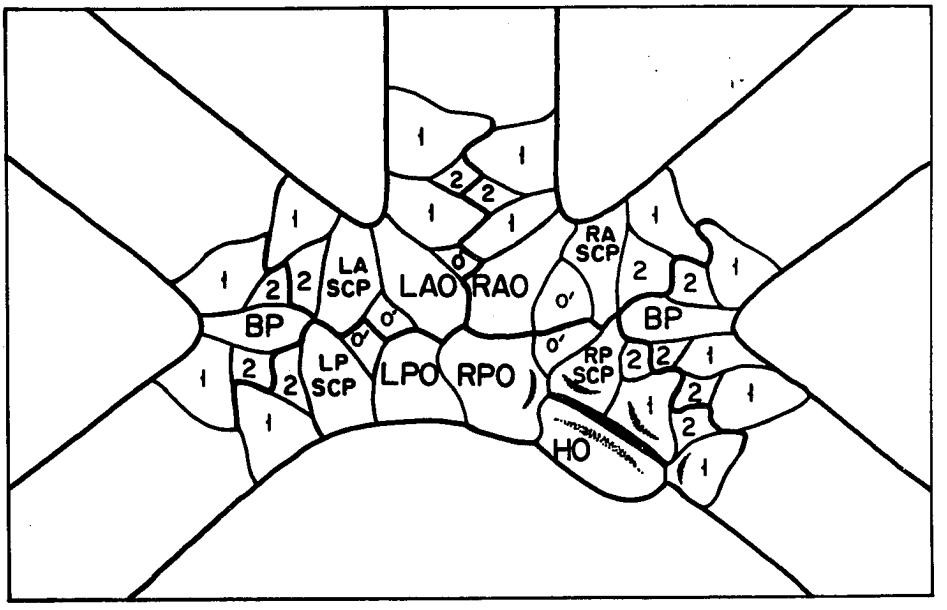
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Text Figure 23 Isorophus cincinnatiensis (Roemer), 1851

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. U.C.M.P. 40470, (X5), pl. 28, fig. 8.

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Text Figure 23

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verse 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 alternate 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). A large gap in the posterior side of the frame affords direct lateral communication between the central lumen and the thecal cavity beneath interambulacrum 5. The proximal rim of the frame extends downward far below the level of the inner surfaces of the ambulacra and is sub-ovate in plan view. Distally the frame is continuous with the five ambulacra and is thus sub-pentagonal.

The frame is transversely elongate with unequally curved anterior and posterior halves joining at attenuated lateral regions. The anterior half is nearly semi-circular in plan view, except for the

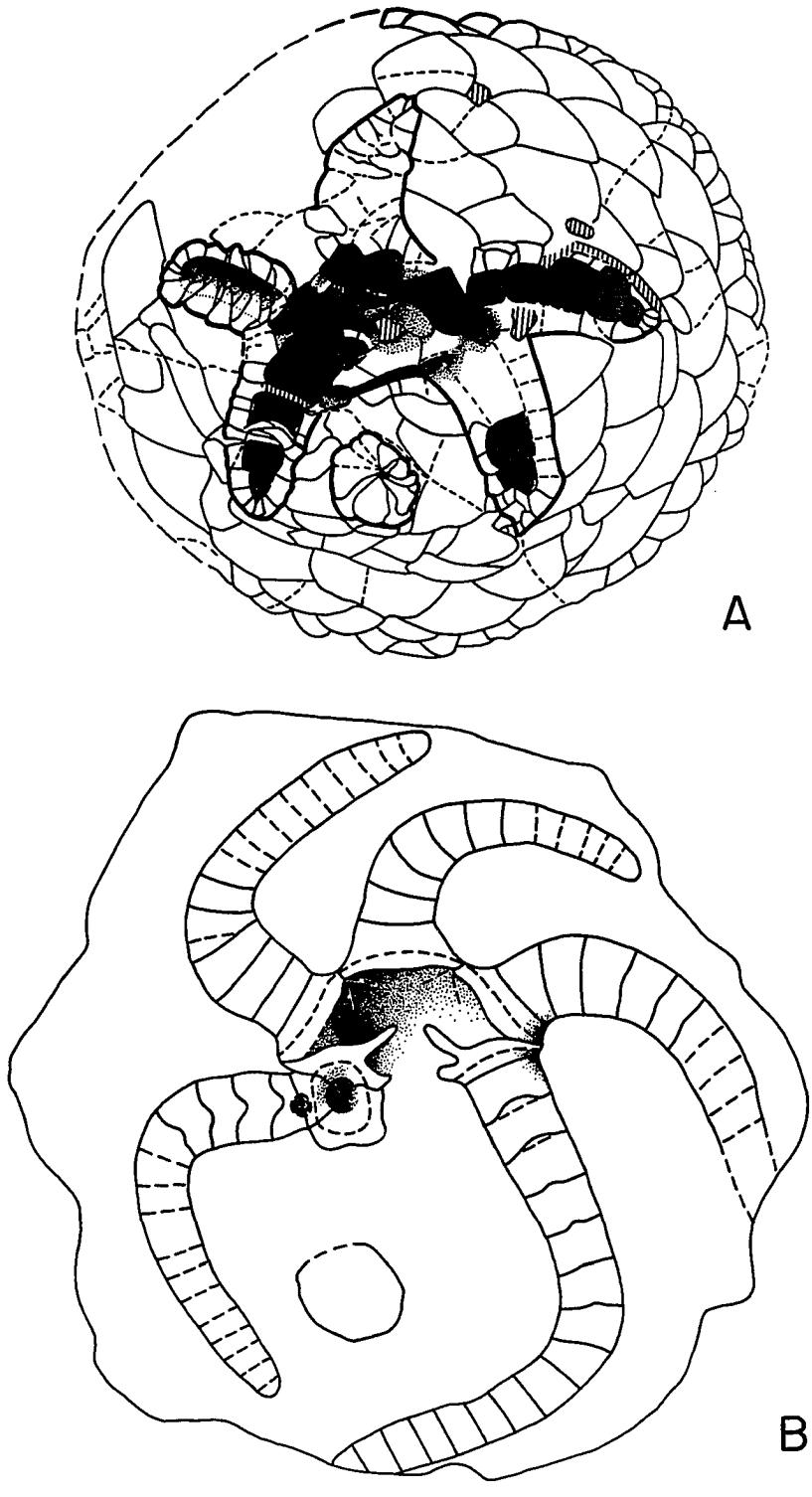
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Text Figure 24 Isorophus cincinnatiensis (Roemer), 1851

A. Inner side of the oral surface, C. F. M. U.C. 54068, (X15), pl. 25, fig. 3. Ambulacral floorplates are shaded.

B. Inner side of the oral surface, U.C.M.P. 26536, (X7), pl. 24, fig. 7.

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Text Figure 24

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lateral areas which flare outward to form a wide zone of contact with the posterior unit. The posterior side is broadly arcuate, the wide lateral extremities nearly a continuation of the arc of the entire posterior unit.

The frame is formed by the five proximal ambulacral floorplates and the intra-thecal 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 semi-circular anterior half of the frame is formed by the radial proximal floorplates of ambulacra II, III and IV and the intra-thecal extensions of the two anterior primary orals. These intra-thecal 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 interradial attenuated lateral 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 intra-thecal 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

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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 intra-thecal parts of the two posterior primary orals. These extensions are short and do not continue nearly as far into the thecal cavity as the other frame elements, thereby leaving the aforementioned conspicuous gap in the posterior side of the frame.

The posterior frame gap is modified by the intrusion of blade-like 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 sub-chamber posterior to the central lumen which is open both anteriorly and posteriorly via the gaps between the opposing blades.

The slit-like 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 suggesting that the ends of the opening continued at least for a short distance along the edges of both the right posterior primary oral and

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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 passage 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, slightly elongate normal to the ambulacral axis. It narrows rapidly upward and the deepest part lies directly over the ambulacrum 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

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Text Figure 25 Isorophus cincinnatiensis (Roemer), 1851

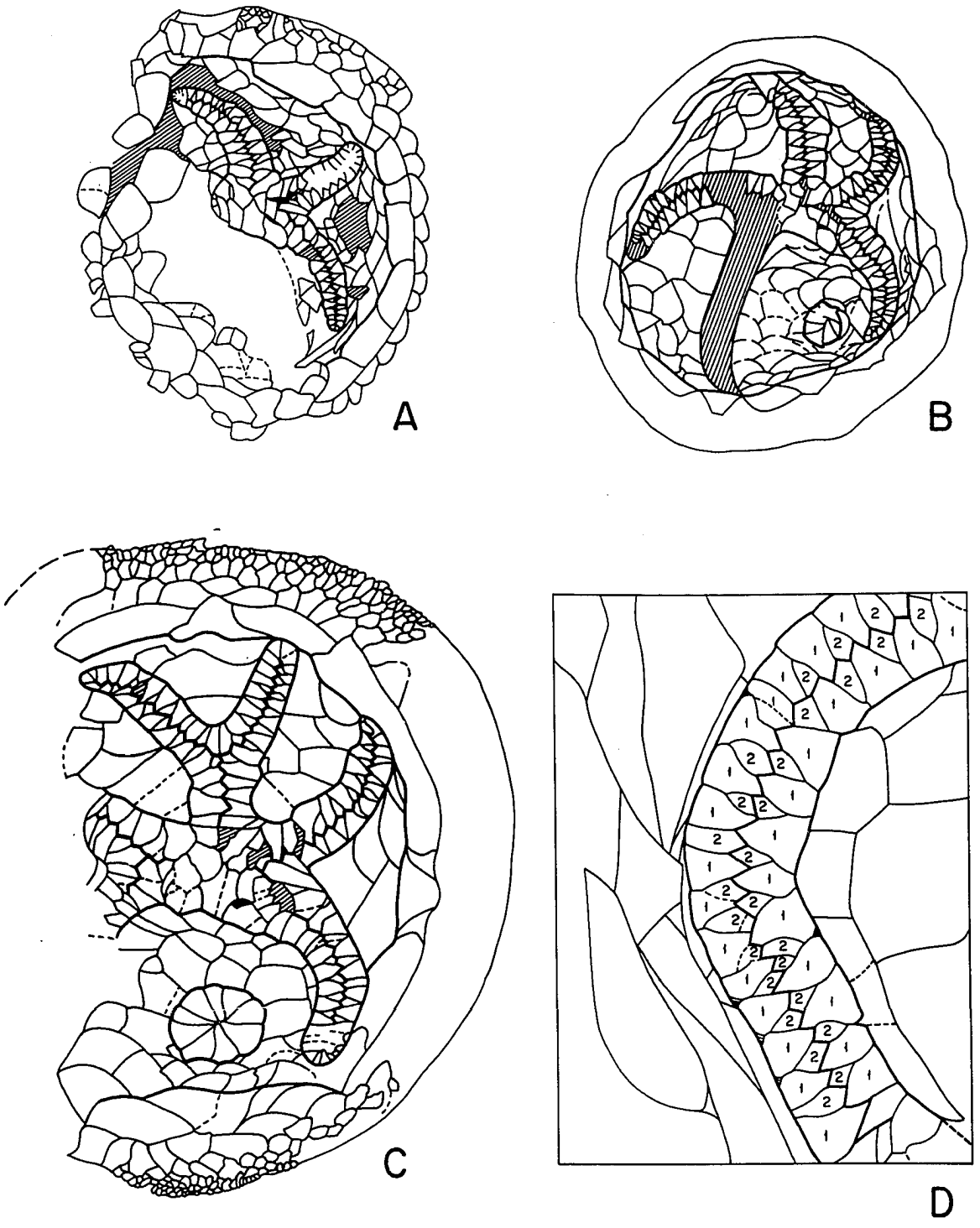
A. U.S.N.M. 91839-B, (X7), pl. 26, fig. 2.

B. U.S.N.M. 91839-A, (X7), pl. 26, fig. 4.

C. C.F.M. -P.E. 16328, (X10), pl. 27, fig. 6.

D. Segment of ambulacrum I, C.F.M.-U.C. 1004, (X25), pl. 26, fig. 8. 1. primary ambulacral coverplate; 2. secondary ambulacral coverplate.

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Text Figure 25

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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, in others 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 appearance results from differential enlargement of adjacent primary coverplates, every other plate wider. The alternation of these two sizes of primary plates creates the impression of two large coverplate sets. 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

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random, for within one population some large adults develop the pseudo-triple 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, each 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

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secondary coverplate series of this species.

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 by 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 I. 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 rapidly increase in size as they migrate away from the ambulacrum until reaching the average

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interambulacral plate size. Thereafter growth is slow.

The valvular anal structure of adults is commonly composed of sixteen plates (pl. 24, fig. 5, pl. 26, fig. 5-6, 11-12). The plates of the outer circlet are triangular with wide distal bases which are slightly convex outward, and with acuminate proximal ends surrounding the anal opening. The inner circlet plates are sub-triangular, 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 which 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 the interambulacrals extend outward under the anals and thereby form 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 interambu-

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lacrals, 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, the proximal end of each being both thicker and more highly elevated than the distal part. The number of ridges per plate varies from 8 or 9 on large plates to 2 or 3 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:

A.M.N.H. 1194. Illustrated Specimen of I. cincinnatiensis (Roemer) by Hall (1866, p. 6-7; 1871, pl. 2, fig. 7; 1872, p. 214, pl. 6,

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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 the specimen.

M.C.Z. 517 (old 3881). Illustrated Specimen of I. 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. 20.5 mm axial by 20 mm transverse diameter.

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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.

U.C.M.P. 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 Ave., 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.

U.C.M.P. 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 Ordo-

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vician. Layer at Creek level, 100 yards south of bridge over Stone Lick Creek, one 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 little 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, blade-like extensions of the proximal floorplates of ambulacra I and V which define the posterior sub-chamber 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 which exposes the inner oral surface features.

A.M.N.H. 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.

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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 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 I. cincinnatiensis. However, the specimens can be identified as pertaining to this species rather than C. pilea because: the ambulacral floorplate sutures are vertical, not oblique; the ambulacral cover-plates 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

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valvular.

A.M.N.H. 13266/1-r. Illustrated Specimen of I. cincinnatiensis by Foerste (1914, pl. 1, fig. 6-E). "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.

C.F.M.-U.C. 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.

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This specimen is a large, non-collapsed Isorophus cincinnatiensis. The highly convex oral surface of the domal theca is nearly hemispherical; the marginal 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 it was the type of I. holbrooki James. However, James' (1878) 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.

U.S.N.M. 40744. Illustrated Specimen of I. 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

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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.

U.S.N.M. 91839 (A-B). Two Isorophus cincinnatiensis. Shaly beds in Cannon Limestone, Trenton Group, Mohawkian Series, Upper Ordovician. Fayetteville, Tennesee.

U.S.N.M. 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.

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U.S.N.M. 91839-B. Specimen with holotype of I. tennesseenisis. 9.6 mm axial by 8 mm transverse diameter.

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

Specimen A is partially disrupted due to thecal collapse, especially the distal ambulacral and interambulacral plates. The oral region is also disrupted and abraded, 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.

U.S.N.M. 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, 4 or 5 per plate. A central flexure extends laterally across the inner side of

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the upper half of at least two of these rim plates.

U.S.N.M. 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.

C.F.M.-U.C. 54068. Whitewater Formation (?), Richmond Group, Cincinnatian Series, Upper Ordovician. Versailles, Indiana [probably from large road cut 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

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moderately curved, 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 due to 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.

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

Pl. 27, fig. 1-3.

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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.

C.F.M.-P.E. 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 nearly equal in size to adjacent primary coverplates.

The anal structure has slumped downward below the level of the

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adjacent large interambulacrals. This has exposed the narrow ledge on the adjacent lateral sides of the interambulacrals on which the anal plates normally rest.

U.C.M.P. 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 I. cincinnatiensis, 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.

U.S.N.M. 40746 (G, H). Two I. cincinnatiensis. Bellevue Formation,

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Maysville Group, Cincinnatian Series, Upper Ordovician. Cincinnati, Ohio.

U.S.N.M. 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 which includes two ambulacral segments and a few adjacent interambulacrals. The coverplates are missing from the center of one ambulacrum exposing 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.

U.S.N.M. 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 and 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 con-

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tiguous 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 intra-thecal 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.

I.U.P.C. 8278 (A-B). Two I. cincinnatiensis. Whitewater Formation, Richmond Group, Cincinnatian Series, Upper Ordovician. Road cut on Hwy. U. S. 50, east of Versailles, Ripley County, Indiana (CN $\frac{1}{2}$. SE $\frac{1}{4}$, Sec. 12, T. 7N, R. 11E). R. S. Nicoll, collector.

I.U.P.C. 8278-A. 10.5 mm axial by 13 mm transverse diameter.

I.U.P.C. 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.

A.M.N.H. 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

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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.

U.C.M.P. 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 I. cincinnatiensis. A cylindrical boring penetrates two of the distal plates of interambulacrum 5.

U.C.M.P. 40467-40473. The following seven specimens are representative of the Forestville population. They are normal and variant indi-

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viduals from the over four hundred I. 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 Co-ordinate System: 397,300'; 1,474,700', equals approximate center of a 200' by 200' area).

U.C.M.P. 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.

U.C.M.P. 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

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proximal posterior side of ambulacrum IV. The anal structure has shifted far to the right of its usual position to lie in the area normally occupied by the missing ambulacrum. The other thecal features appear to be typical of the species.

U.C.M.P. 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 direction of ambulacral curvature.

U.C.M.P. 40470. 24.6 mm axial by 24.8 mm transverse diameter. W. H. White, Jr., collector.

Text fig. 1-C, 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.

U.C.M.P. 40471. 21.2 mm axial by 19 mm transverse diameter.

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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.

U.C.M.P. 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.

U.C.M.P. 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 now, but they have been deeply etched, exposing a sub-surficial view of the plates. In this un-collapsed individual the junction between the

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distal interambulacral plates and the proximal rim plates is obscure.

Discussion of previous investigation:

The location of the holotype of I. 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, 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

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measurements to Roemer's description. Hall's illustration, meant 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 (A.M.N.H. 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 I. cincinnatiensis (M.C.Z. 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 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 inter-

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mediate 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 contrasolarly, V solarly, or visa-versa. Apparently he did not realize 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 intra-thecal 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

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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 underlying stone-canal passageway. The regularity of the oral plates is the only other taxonomically important structural feature 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 which figured three large primary orals like those of Carneyella. Hall's specimen (A.M.N.H. 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, non-collapsed I. cincinnatiensis (U.S.N.M. 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,

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and which are here recognized as typical of large, gerontic I. cincinnatiensis.

Bassler (1936) also described the species I. 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 (U.S.N.M. 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). Terminology aside, Kesling's description is similar to that presented here. The terminology equates as follows: his large posterocentral peristomial plate = the right posterior primary oral; the right posterior peristomial plate = the hydropore oral; the 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; the sloping spatulate plate of the peristomial region = posterior member of the right pair of secondary orals; the small wedge-like plate in larger specimens = one of the additional secondary oral plates. Kesling reported the upturned edges of the

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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 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 I. 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

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in this area in one specimen (U.C.M.P. 26536; text fig. 24B, pl. 24, fig. 6-8) ends blindly. Other specimens which 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 A.M.N.H. 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.

Isorophus cincinnatiensis as presented in Regnéll's (1966) analysis of the Edrioasteroidea summarizes the conclusions of earlier workers. Accompanying figures are reillustrations of previously published figures.

Discussion:

The description of Isorophus cincinnatiensis is based upon over 1000 specimens. Many of these were collected in-situ from two populations, which allows recognition of growth details and intra-specific variation that might otherwise have been ascribed to ecology or even to inter-specific 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

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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 and interambulacra become the areally dominant thecal feature in adults. The oral and anal structures and the rim continue to increase in absolute size by plate enlargement and 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 increased 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 I. 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; 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,

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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 (U.S.N.M. 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 sixteen to eighteen 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

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the hydropore could thus be controlled. However, the intra-thecal 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 non-collapsed specimens, the hydropore plate is almost always in place, adjacent to the other hydropore elements, and restricts the hydropore to a narrow slit-like 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 co-ordinated, wave-like motion which 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 ribbon-like strips, the opposing ribbons gradually flexing upward and away from the axis of the

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ambulacra as the broad zone of opening coverplates swept proximally. Closure of the coverplates would have been accomplished by a reversal of the process, the underlapping perradial extensions of opposing elements gradually slipping back into place as opposing plates simultaneously descended.

Kesling and Mintz suggested that the long intra-thecal extensions of the primary coverplates were for the attachment of muscles which 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 intra-thecal extensions.

An alternative method of coverplate control involves the shallow grooves which 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 complimentary 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 intra-thecal extensions of the primary coverplates would act as wedges and abut the inner surface of the adjacent interambulacrals. Coverplate

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movement could be affected by increasing the diameter of the water tube, pushing up on the coverplates. With the distal intra-thecal 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 seemingly readily account for the "peristaltic" operation of the coverplates.

The anal structure is an elevated low, rounded conical mound on several non-collapsed 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.

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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 small domal theca with an

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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 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 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

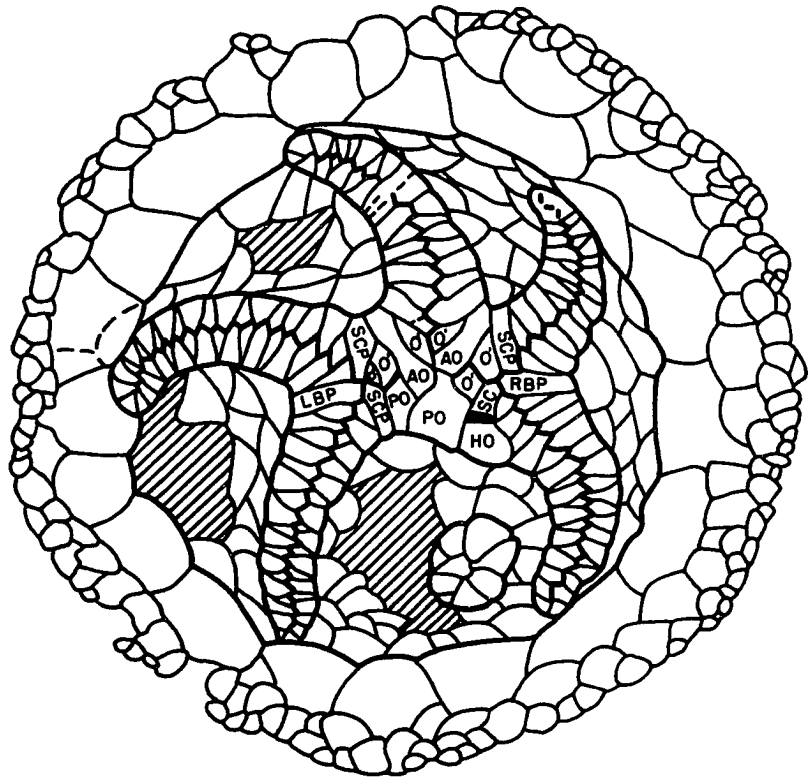
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Text Figure 26 Isorophus austini (Foerste), 1914

U.S.N.M. 70162-D, (X17), pl. 29, fig. 7.

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

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Text Figure 26

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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, like 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, like the oral frame, appears identical to that of I. 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 due to 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

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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 a little in width adradially, but occasionally they have nearly parallel sides and wide external adradial ends, equal in width to those of adjacent primaries.

The intra-ambulacral and intra-thecal 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 where 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 fewer plates are included, adults having only 12 to 14 plates each.

The peripheral rim includes approximately seven circlets of

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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 I. 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 due to the etched condition of the specimens.

Specimens:

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

U.S.N.M. 70162-A, B, C. Five type series specimens of Isorophus austini (Foerste) (1914).

U.S.N.M. 70162-C. Three specimens resting on a bryozoan fragment.

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

Pl. 29, fig. 1.

This specimen is the best-preserved individual included by Foerste

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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.

U.S.N.M. 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.

U.S.N.M. 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.

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U.S.N.M. 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.

U.S.N.M. 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.

U.S.N.M. 70162-D, E. Two I. austini accompanying the type series; topotypes.

U.S.N.M. 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.

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The surficial etching has accentuated the plate boundaries, thereby facilitating recognition of individual elements.

U.S.N.M. 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 left posterior part of the theca is missing. The ambulacral floorplates of II, III and IV show no signs of proximal flanges on the inner sides. The floorplate of ambulacrum II has been displaced anteriorly and exposes the overlying inner surfaces of the coverplates along their zone of contact with the floorplates. The intra-thecal 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.

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

U.S.N.M. 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.

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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.

U.S.N.M. 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.

U.S.N.M. 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.

U.S.N.M. 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.

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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 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 is like that of Carneyella pilea. He revised this opinion in 1917 and predicted that the oral region would be shown 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

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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

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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

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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.

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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 is a small to moderate sized species averaging 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

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Text Figure 27 Isorophus warrenensis (James), 1883

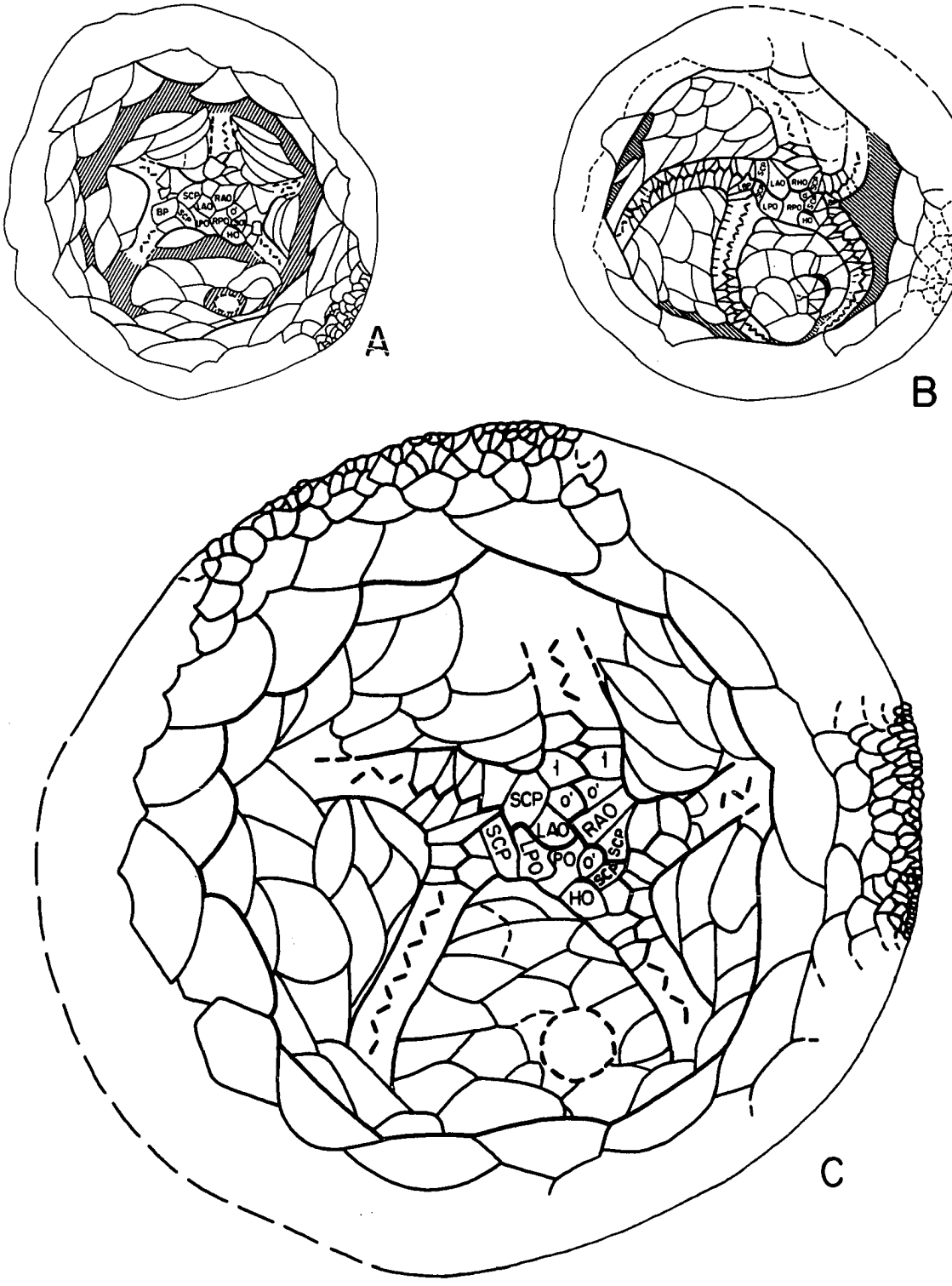
A. Lectoparatype, U.S.N.M. S-3957-C, (X5), pl. 30, fig. 8.

B. Lectoparatype, U.S.N.M. S-3957-D, (X5), pl. 30, fig. 5.

C. Lectoparatype, U.S.N.M. S-3957-E, (X10), pl. 30, fig. 6.

BP. lateral bifurcation plate; HO. hydropore oral plate; LAO. left anterior primary oral plate; LBP. left lateral bifurcation plate; LPO. left posterior primary oral plate; o'. secondary oral plate; PO. posterior primary oral plate; RAO. right anterior primary oral plate; RPO. right posterior primary oral plate; SCP. lateral shared coverplate; 1. primary ambulacral coverplate.

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Text Figure 27

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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 very 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 species 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:

U.S.N.M. S-3957 (A-G). Type series of I. 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

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Morrow", Warren County, Ohio (Foerste, 1914, p. 449). U.S.N.M. label and Bassler (1936): probably basal Arnheim Formation, Richmond Group, Cincinnatian Series, Upper Ordovician; Oregonia, Ohio.

U.S.N.M. 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 U.S.N.M. 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.

U.S.N.M. 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

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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.

U.S.N.M. 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.

U.S.N.M. 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.

U.S.N.M. 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.

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The theca has collapsed, 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.

U.S.N.M. 70165. Illustrated Specimen of I. warrenensis (James) by Bassler (1936, pl. 6, fig. 11). Basal Arheim 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 non-diagnostic. It cites only preservational characteristics and thecal features common to this and related species. Foerste (1914) noted that 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' original 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.

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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 due to 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.

Isorophusella Bassler, 1935

1852 [nonl Hemicystites Hall, J., Nat. Hist. of New York, pt. VI, Palaeontology 2: 245-246.

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

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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; ambulac-

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ral 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

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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 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

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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 intra-thecal 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 intra-thecal 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

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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 circlet of large plates is 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 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 (Lebetodiscus incondi-tus Raymond, 1915) Isorophusella as similar to Isorophus but with:

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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 said, it is very slight.

Bassler's (1936) Isorophus trentonensis and Sinclair's 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.

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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.

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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 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

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Text Figure 28 Isorophusella incondita (Raymond), 1915.

Holotype, G.S.C. 1409-A.

A. Oral area and adjacent structures, (X13), pl. 31, fig. 3.

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; U1. unpaired primary ambulacral coverplate; 1. primary ambulacral coverplate; 2. secondary ambulacral coverplate.

B. Oral surface, (X8), pl. 31, fig. 2.

Text Figure 29 Isorophusella incondita (Raymond), 1915.

A. Paratype (2), G.S.C. 1409-C, (X12), pl. 31, fig. 10. Ambulacral coverplate intra-thecal extensions, where exposed by disruption of adjacent interambulacrals, are separated from the main body of the plates by dashed lines.

B. U.C.M.P. 40475, (X5), 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, R.O.M. 18873-A, (X16), pl. 32, fig. 9.

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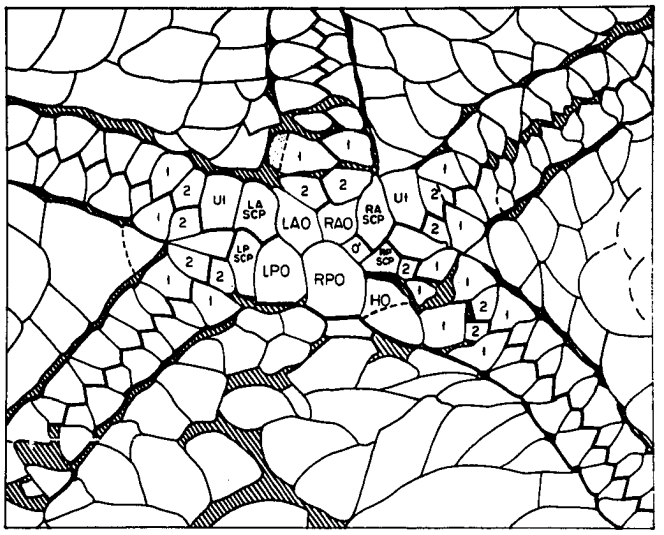
Text Figure 29 (con.) Isorophusella incondita (Raymond), 1915.

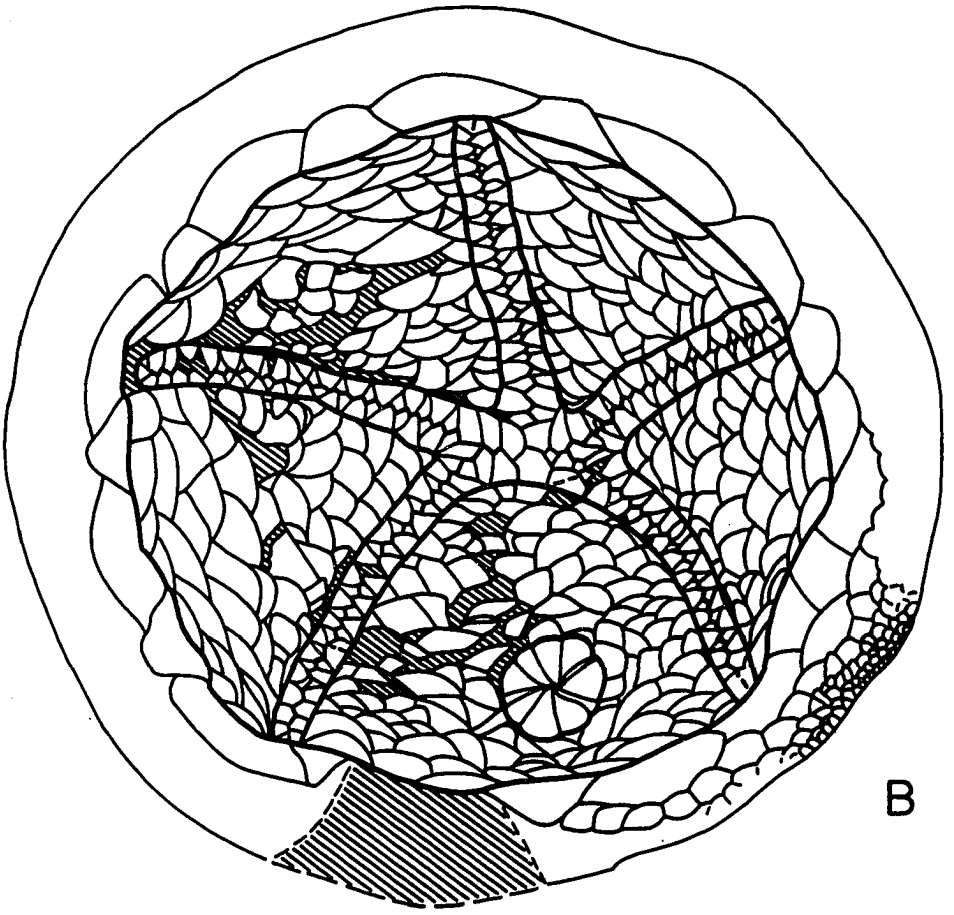
D. U.S.N.M. 42114-A-1, (X15), pl. 31, fig. 11.

E. Young adult, M.C.Z. 105, (X10), 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; Ul. unpaired primary ambulacral coverplate; 1. primary ambulacral coverplate; 2. secondary ambulacral coverplate.

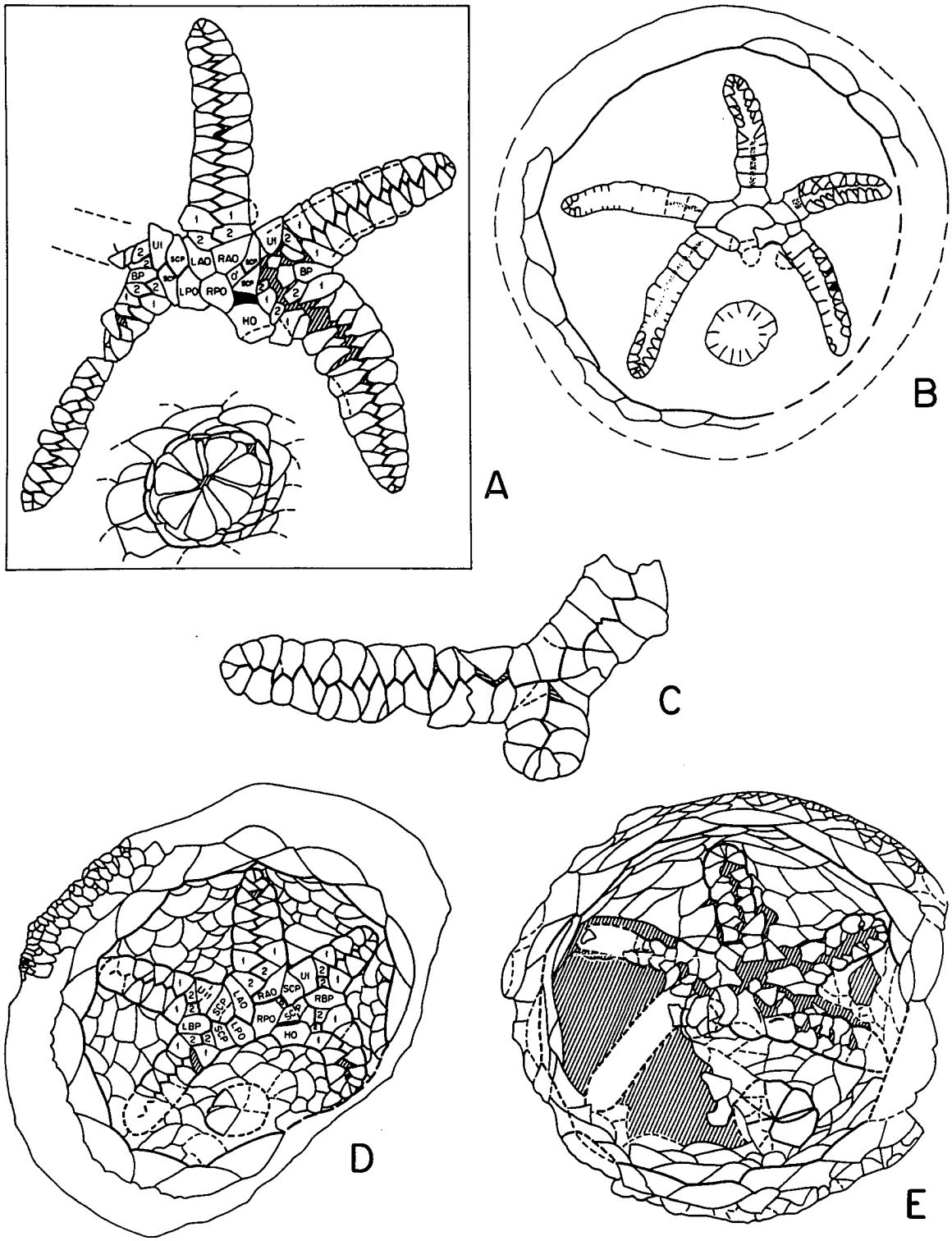
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Text Figure 28

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Text Figure 29

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oral lumen and the thecal cavity beneath interambulacrum 5. The exposed sectional view of the frame apparently lies below the inner ends of the intra-thecal extensions of the interradial oral plates. Lateral blade-like processes from the ambulacral floorplates of I and V, which form a sub-chamber 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 slit-like opening is formed by the right margin of the right posterior primary oral. The entire posterior edge is formed by the anterior margin of the hydropore oral. The proximal part of the openings anterior edge is bounded by the adradial end of the right posterior shared coverplate. Distal to this coverplate the number of plates which form the anterior edge of the opening appears to vary intra-specifically. 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 entirely absent and the unpaired primary coverplates are adjacent to the shared coverplate. Distal to the unpaired primary coverplate the hydropore

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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 thirty 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

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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 most consistent, only one exception in each out of thirty 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, blade-like 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 intra-thecal extensions of the coverplates are also generally hidden, but apparently are similar to those of Isorophus cincinnatiensis and Isorophusella plieadae.

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 non-collapsed specimens.

The valvular anal structure of Isorophusella incondita comprises

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12 to 16 sub-triangular 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 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:

G.S.C. 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.

G.S.C. 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.

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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 due 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 disto-medial part of ambulacrum I and adjacent interambulacrals. The specimen preserves most of the diagnostic characters of the species.

G.S.C. 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.

G.S.C. 1409-C. Paratype (2) of Isorophusella incondita (Raymond) (1915, pl. 1, fig. 1, 1921, pl. 4). 10.6 mm axial by 10.9 mm trans-

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verse 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.

G.S.C. 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 most incomplete. 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.

U.S.N.M. 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. Phyllopora bed, Decorah Formation, Black River Group, Mohawkian Series, Middle Ordovician. St. Paul, Minnesota.

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U.S.N.M. 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 little disrupted and exhibits the typical features of Isorophusella incondita of similar size. Compare the text figure of this specimen to text fig. 32B.

U.S.N.M. 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.

U.S.N.M. 42114-B-1. 7 mm greatest diameter.

U.S.N.M. 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.

M.C.Z. 105 (old no. 3978). Isorophusella incondita (Raymond). The holotype of Carneyella raymondi Clark (1919, pl. 1, fig. 18-19). 300 feet above the base of the Trenton, Trenton Group, Mohawkian Series, Middle Ordovician. Gorge of Roaring Brook, near Martinsburg, New York.

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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 interambulacrum 1 and the left side of 5, along with most of the distal rim plates. 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.

U.S.N.M. 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.

U.C.M.P. 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

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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 intra-thecal 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.

R.O.M. 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 theca 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

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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.

R.O.M. 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.

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G.S.C. 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. 3.16 mm axial by 3.16 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 (R.O.M. 160t C-8) shown in text fig. 31C 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:

R.O.M. 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.

R.O.M. 160t. "Trenton Limestone", Trenton Group, Mohawkian Series, Middle Ordovician. Peterborough, Ontario. J. Townsend Collection.

R.O.M. 160t-a, d, e, f, g.

Five limestone slabs with eleven average specimens of Isorophusella incondita. Several are very fragmentary.

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R.O.M. 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.

R.O.M. 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.

R.O.M. 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.

C.F.M. P9635. "Trenton Limestone", Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario.

Two average adult Isorophusella incondita.

U.C.M.P. 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 sixteen specimen descriptions are arranged in order of increasing thecal development. The series begins with the

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youngest (smallest) developmental stage known and ends with a small, fully developed adult.

R.O.M. 160t. "Trenton Limestone", Trenton Group, Mohawkian Series, Middle Ordovician. Peterborough, Ontario. J. Townsend Collection.

R.O.M. 160t-b. Slab with five Isorophusella incondita.

R.O.M. 160t-c. Slab with fourteen Isorophusella incondita, 9 included in the growth series.

N.Y.S.M. 12775-12776. Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario.

Two Isorophusella incondita included in growth series on a slab with two Belochthus orthokolus (N.Y.S.M. 12773-12774).

R.O.M. 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 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

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Text Figure 30 Isorophusella incondita (Raymond), 1915, growth series.

A. Young juvenile, R.O.M. 160t-b-E, (X60), pl. 33, fig. 1.

B. Young juvenile, N.Y.S.M. 12775, (X50), pl. 33, fig. 2.

C. Young juvenile, R.O.M. 160t-c-16, (X40), pl. 33, fig. 4.

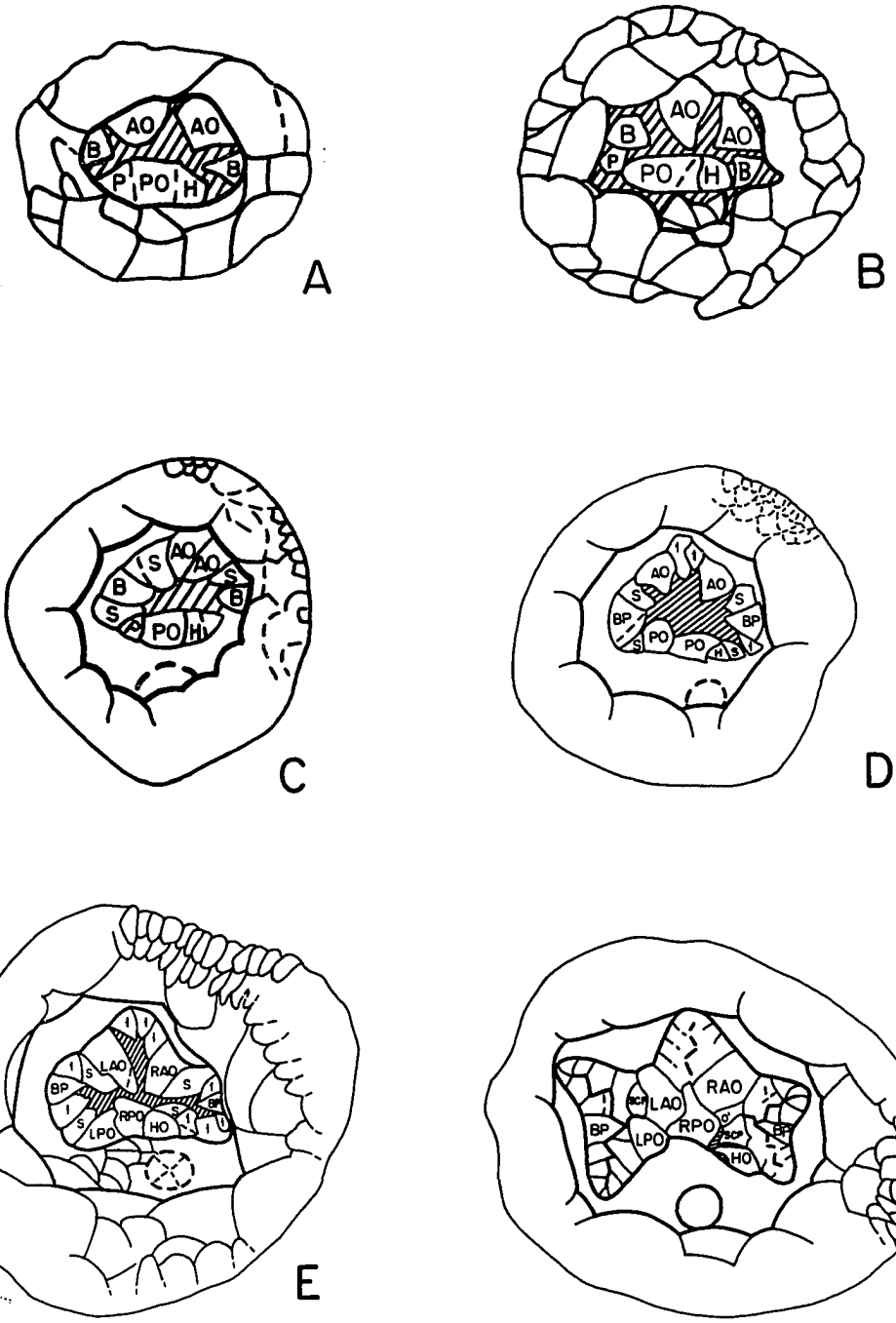
D. Juvenile, R.O.M. 160t-c-12, (X30), pl. 33, fig. 6.

E. Juvenile, R.O.M. 160t-c-3, (X25), pl. 33, fig. 7.

F. Juvenile, R.O.M. 160t-c-11, (X25), 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.

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Text Figure 30

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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 primary lateral 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.

N.Y.S.M. 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; it occupies 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

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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 sub-triangular 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.

R.O.M. 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 sixty 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 eleven plates. All are laterally in contact with adjacent plates, but centrally they are separated due to removal of the perradial parts of the plates by deep etching. The outline of this group of plates is sub-triangular; the apex is formed by the anterior primary ambulacral radius and the basal corners by the

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two primary lateral 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.

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R.O.M. 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, 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 sub-triangular shape seen in the previous specimens. Approximately fourteen 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 sub-centrally 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.

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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 due 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.

R.O.M. 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 sub-triangular 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 twenty 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

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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.

R.O.M. 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, all five ambulacra being 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.

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R.O.M. 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.

R.O.M. 160t-c-4. Juvenile. 2.4 mm axial by 2.6 mm transverse diameter.

Text fig. 31B, pl. 33, fig. 11-12.

R.O.M. 160t-c-8. Juvenile. 2.8 mm axial by 3.0 mm transverse diameter.

Text fig. 31C, pl. 33, fig. 13-14.

R.O.M. 160t-c-9. Juvenile. 3.0 mm axial by 3.28 mm transverse diameter.

Text fig. 31E, pl. 34, fig. 1-2.

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Text Figure 31 Isorophusella incondita (Raymond), 1915, growth series.

A. Juvenile, R.O.M. 160t-b-D, (X20), pl. 33, fig. 10.

B. Juvenile, R.O.M. 160t-c-4, (X20), pl. 33, fig. 12.

C. Juvenile, R.O.M. 160t-c-8, (X20), pl. 33, fig. 14.

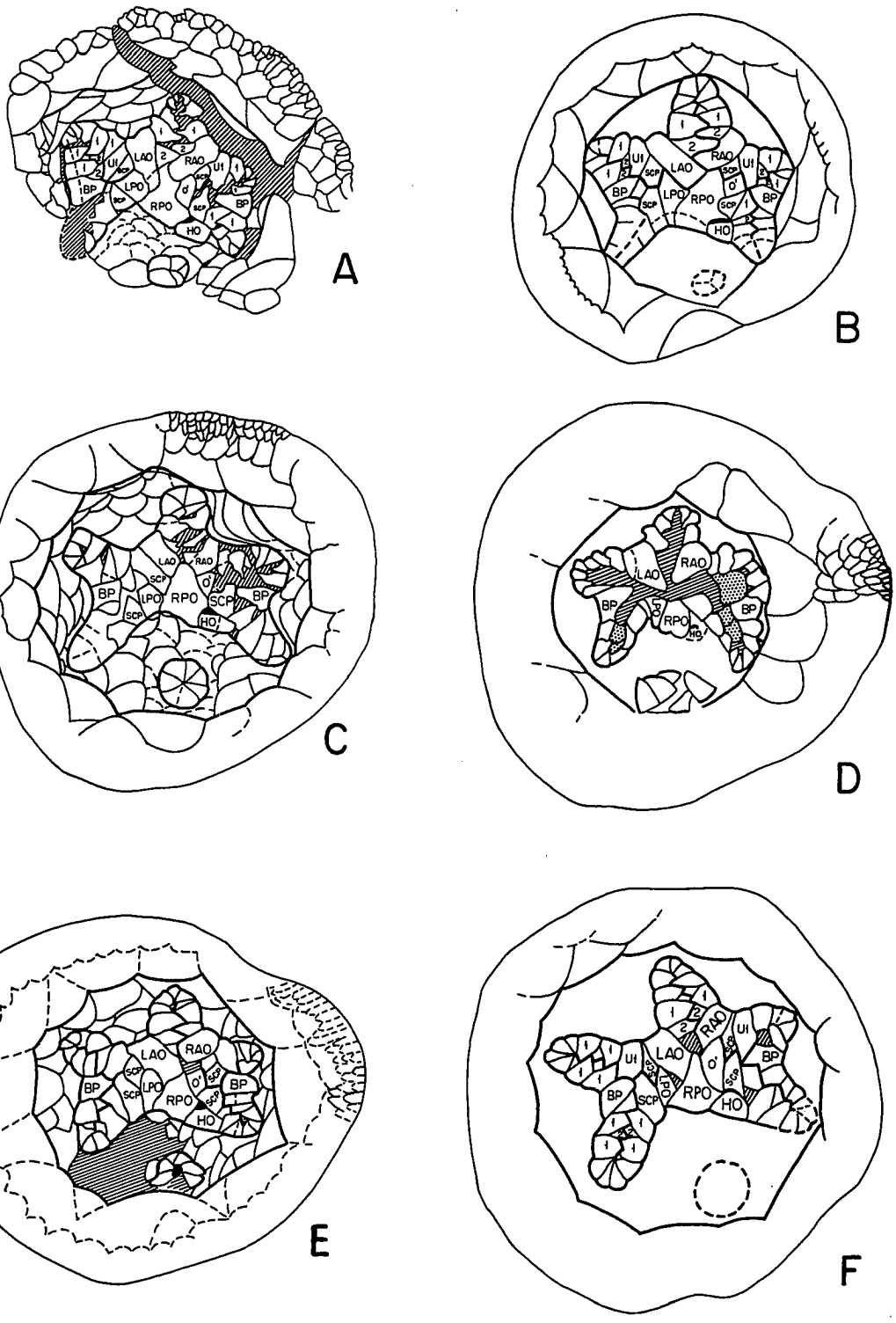
D. Juvenile, G.S.C. 3235-d, (X20), pl. 33, fig. 16. Ambulacral floorplates marked by a dotted pattern.

E. Juvenile, R.O.M. 160t-c-9, (X20), pl. 34, fig. 2.

F. Juvenile, R.O.M. 160t-c-15, (X20), 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; UL. unpaired primary ambulacral coverplate; 1. primary ambulacral coverplate; 2. secondary ambulacral coverplate.

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Text Figure 31

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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 R.O.M. 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.

R.O.M. 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 continuation of lengthening of the ambulacra and enlargement of the interambulacral areas. Ambulacrum IV is significantly shorter than the other four as in typical adults.

R.O.M. 160t-c-10. Juvenile. 3.2 mm axial by 3.2 mm transverse diameter.

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Text fig. 32A, pl. 34, fig. 5-6.

This specimen is similar in stage of development to the last. 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.

R.O.M. 160t-b-C. Advanced juvenile. 4.0 mm axial by 4.1 mm 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.

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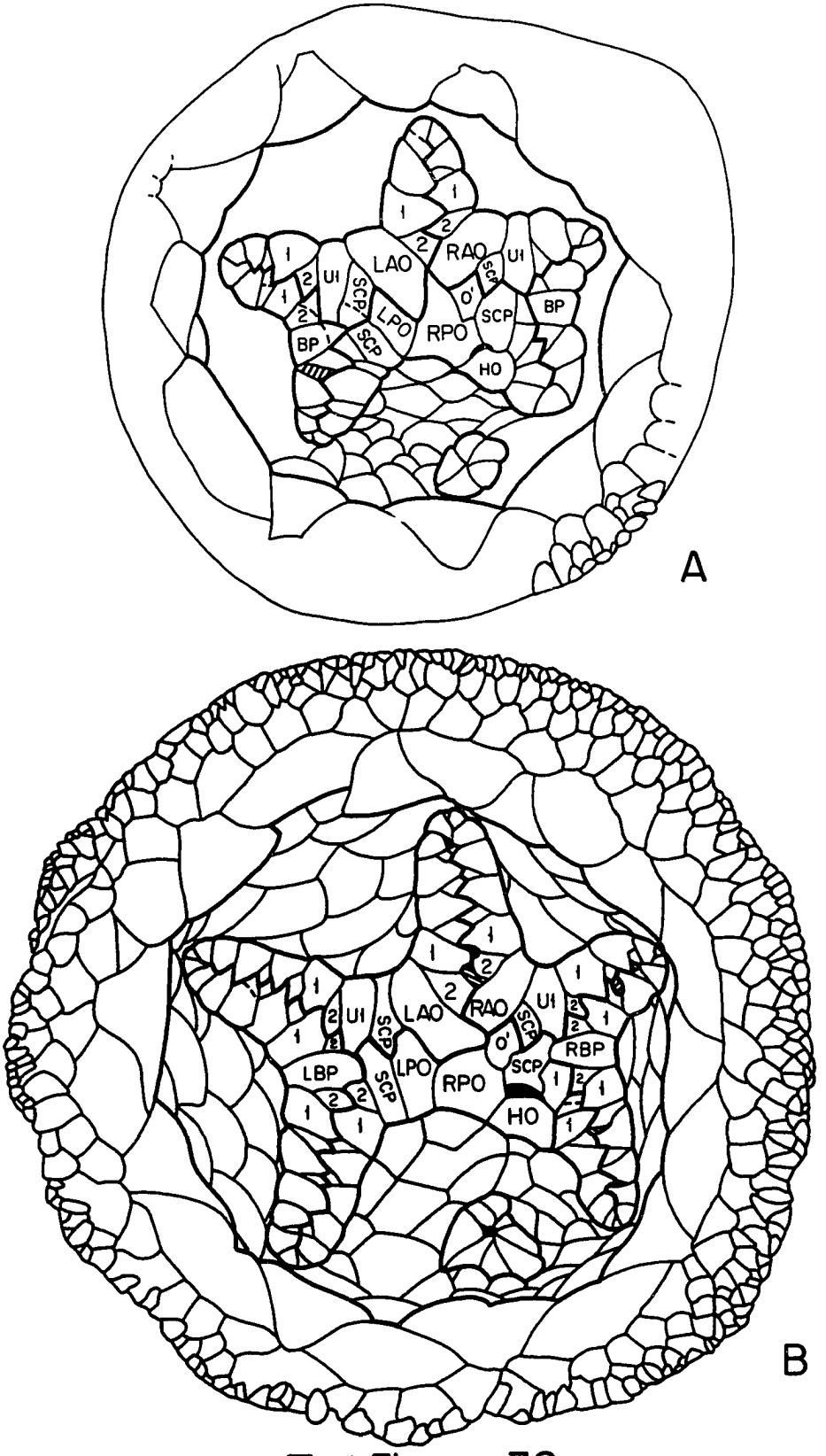
Text Figure 32 Isorophusella incondita (Raymond), 1915, growth series.

A. Juvenile, R.O.M. 160t-c-10, (X30), pl. 34, fig. 6.

B. Advanced juvenile, R.O.M. 160t-b-C, (X30), 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.

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Text Figure 32

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N.Y.S.M. 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.

R.O.M. 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 sutures. Proportional size of the major thecal structures is almost that of typical adults.

R.O.M. 160t-b-A. Adult. 8.1 mm axial by 8.2 mm transverse diameter.

Pl. 35, fig. 3-4.

The specimen is 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.

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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 manifest 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 primary lateral 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

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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, 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, the relative size of the structure decreasing in relation to thecal diameter throughout develop-

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ment.

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 Warf, 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 L. 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

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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 illustrated 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 to text fig. 32B), with which it is now identified.

Wilson (1946) did not recognize Bassler's Isorophusella, as is indicated by 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

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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 position 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: 205.

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Diagnosis:

An Isorophusella with: theca small; secondary ambulacral coverplates externally nearly as large as primaries in proximal part of ambulacra; and, thecal plates bear 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: 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.

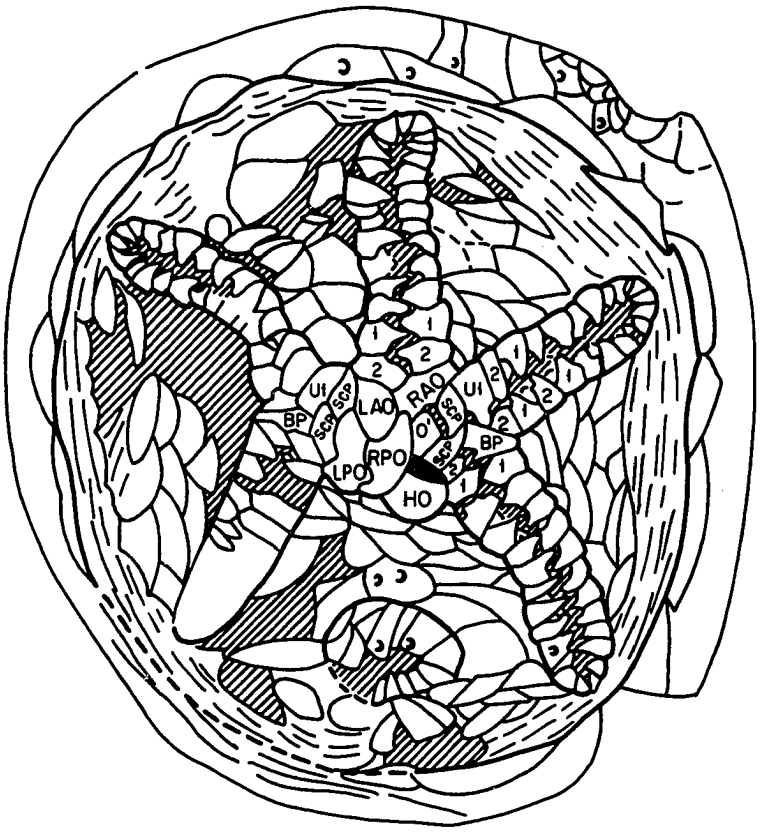
The hydropore structure includes six plates. The entire posterior margin of the opening is bounded by the anterior edge of the hydropore oral. The proximal end is formed by the right edge of the right posterior primary oral. The anterior side of the opening is formed by the right lateral secondary oral, 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

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Text Figure 33 Isorophusella trentonensis (Bassler), 1936

Holotype, U.S.N.M. 91843, (X10), 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; UL. unpaired primary ambulacral coverplate; 1. primary ambulacral coverplate; 2. secondary ambulacral coverplate.

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Text Figure 33

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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 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 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.

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Specimen:

U.S.N.M. 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 are disrupted, particularly in interambulacra 1, 2, and 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 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

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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 due 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, disregarding preservational irregularities, the ambulacra are nearly straight, as in young Isorophusella incondita.

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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:

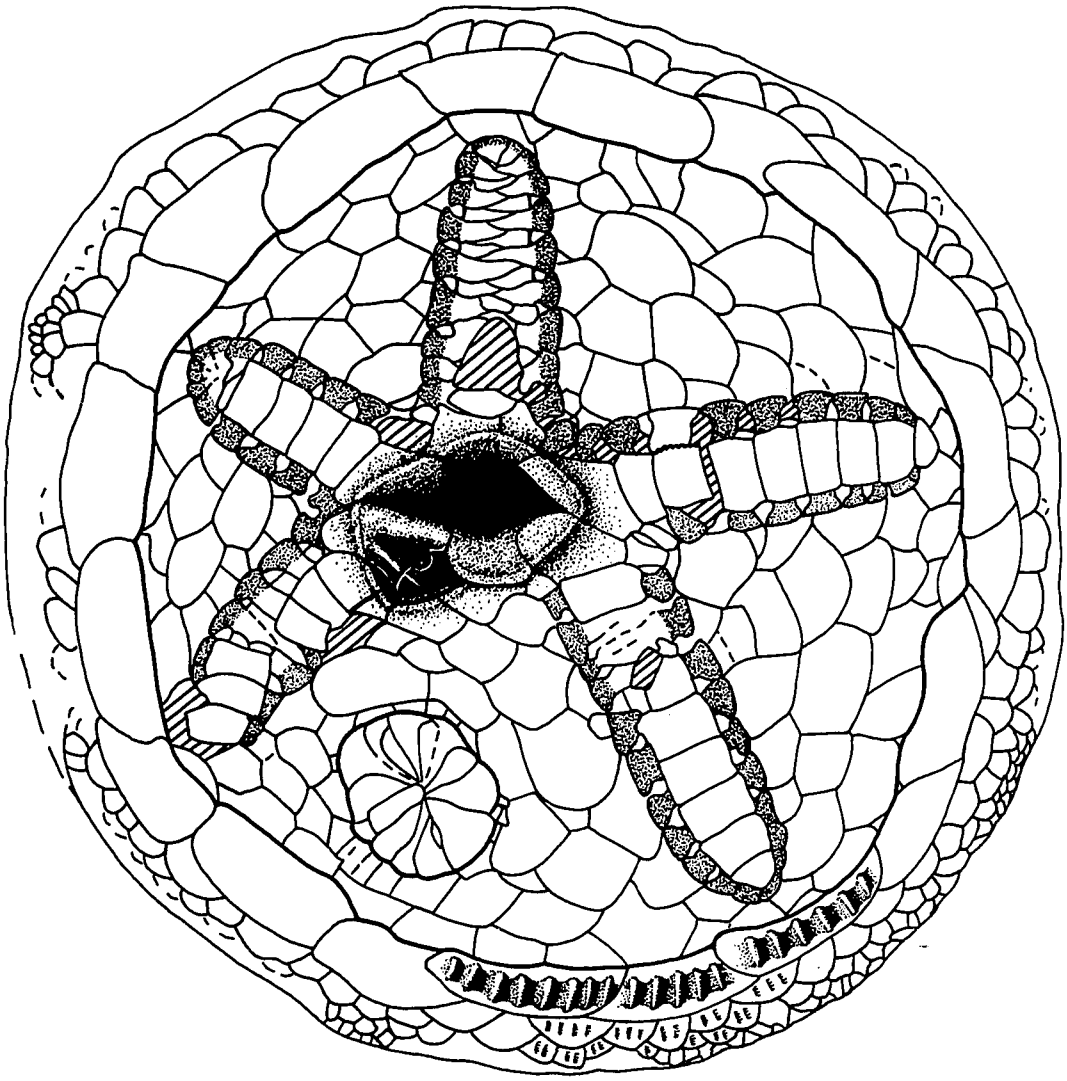
Isorophusella pleiadae (Sinclair and Bolton) (1965) is known from seven type series specimens which expose only the inner side of the oral surface (text fig. 34, pl. 36). The proportional sizes of the major thecal structures suggests that the specimens are adults. Whether this is a valid specific trait 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. Fre-

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Text Figure 34 Isorophusella pleiadae (Sinclair and Bolton), 1965

Holotype, G.S.C. 14680-1, (X20), pl. 36, fig. 1. Inner side of the oral surface. Intra-thecal extensions of the primary ambulacral coverplates are stippled.

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Text Figure 34

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quently 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.

Intra-thecal 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, 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, imparting a pentagonal shape to the distal part of the frame.

The frame is formed by the five proximal ambulacral floorplates and the intra-thecal 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

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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 intra-thecal parts of the two anterior primary orals. The intra-thecal extensions form the interradial parts of the upper frame area, but they are wedge-shaped and taper downward and end before reaching the inner-most edge of the frame. Thus, the inner rim is formed only by the three floorplates which laterally achieve contact with one another. The posterior edges of floorplates II and IV flare outward laterally to form the laterally attenuated frame margins, 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 intra-thecal 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 intra-thecal 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 intra-thecal 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

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posterior frame gap is modified into a sub-chamber by lateral blade-like 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 intra-thecal 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 blade-like 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 intra-thecal extensions of the primary coverplates continue

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past the lateral margins of the floorplates well into the thecal cavity. The inner-most 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, 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 articulation with the ambulacral coverplates. The floorplates apparently attain full size rapidly 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

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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:

G.S.C. 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. Road cut 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 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.

G.S.C. 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.

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

The holotype is well-preserved. Ambulacral floorplates have been lost from ambulacrum III which exposes the inner side of the coverplates. A few floorplates are crushed in the other ambulacra. The

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oral frame is slightly abraded but not disrupted. The anal structure lies to the right of center of interambulacrum 5 (left from the inner surface view). Etching has removed some surficial features, especially the smaller basal ridges of the distal rim plates.

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

Pl. 36, fig. 5.

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

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

Pl. 36, fig. 6.

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

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

Pl. 36, fig. 7.

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

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

Pl. 36, fig. 8.

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

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

Pl. 36, fig. 9.

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

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of the distal rim plate basal ridges.

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

Pl. 36, fig. 10.

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

Discussion:

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

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

Range and occurrence:

Richmond Group, Cincinnatian Series, Upper Ordovician of Anticosti Island, Quebec.

Hemicystites Hall, 1852

1842 Inon-1 Agelacrinites Vanuxem, L., Nat. Hist. of New York, pt. IV, Geology 3: 158, fig. 80.

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

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

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

1857 Hemicystites Hall, Pictet, F.-J., Traité de Paléontologie ou Histoire Naturelle des Animaux Fossils, 2nd edition, Paris, 4: 305-306 [non] pl. 99, fig. 251.

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

1862 Agelacrinus Vanuxem, Dujardin, F. and Hupé, H. [partim], Histoire Naturelle des Zoophytes Echinodermes, Paris: 84 [non] pl. 5, fig. 81.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Type species: Hemicystites parasiticus Hall, 1852.

Diagnosis:

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

Description:

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

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

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

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

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

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The peripheral rim is typical of the family.

Discussion:

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

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

By 1866 Hall was disposed to consider Hemicystites as a distinct genus. He also described Agelacrinus (Hemicystites) stellatus in 1866. In Hall's (1871) publication of the plate of illustrations for that work, he lists Hemicystites stellatus and also a new species, Hemicystites (s.g. Cystaster) granulatus. Detailed drawings of both species were presented. The text and plate were republished together in 1872, the two species cited as Hemicystites (s.g. Cystaster) granulatus

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and Agelacrinus (Hemicystites) stellatus. These are relatively common species and both conform to the genus Cystaster. On the other hand, Hall's (1852) illustration of Hemicystites parasiticus does not accurately portray the plating of the oral area and represents ambulacral coverplates as a single biseries rather than the actual double biseries. Specimens of H. parasiticus are rare. Unfortunately, most workers have used Cystaster stellatus or C. granulatus to represent the generic characters of Hemicystites. Meek (1873) and Miller (1877, 1889) both included the Cystaster species in Hemicystites. Haeckel (1896) even cited "Hemicystites (= Cystaster) granulatus Hall" as the type species of the genus. He characterized the genus exclusively on its sack- or disk-shape and straight ambulacra.

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

Bassler (1935, 1936) examined the holotype and several topotypes of H. parasiticus but he described Hemicystites as having an oral-ambulacral structure like that of Carneyella. The supposed presence of only three primary orals, two anterior and one large central posterior, was the prime taxobasis of Bassler's new Family Hemicystitidae. He excluded Cystaster granulatus from Hemicystites, and also Cystaster stellatus, and proposed the genus Cincinnatidiscus for the latter.

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However, he included eleven other species in Hemicystites, many of which agreed with his conception of the genus, but none of which show the structure of the type species. All are here removed from Hemicystites.

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

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

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

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

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

Range and occurrence: Clinton Group, Niagaran Series, Middle Silurian of New York.

Hemicystites parasiticus Hall, 1852

Text fig. 35; plate 37.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Diagnosis:

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

Description:

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

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

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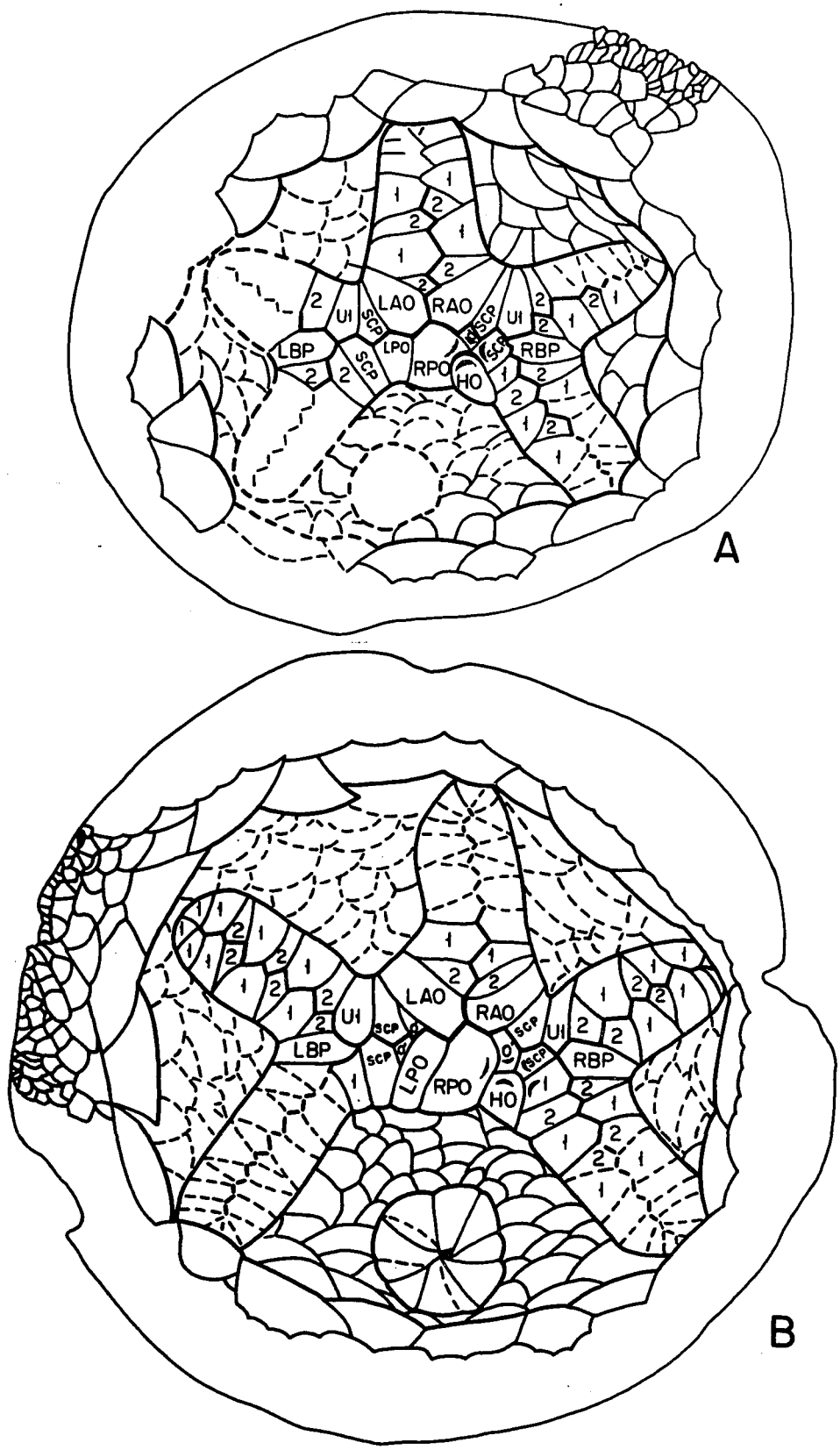
Text Figure 35 Hemicystites parasiticus Hall, 1852

A. U.S.N.M. S-3183-B, (X18), pl. 37, fig. 3.

B. U.S.N.M. S-3183-A, (X18), pl. 37, fig. 2.

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

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Text Figure 35

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each side of the central primary orals. One member of each pair is distally in contact with the perradial end of one of the two lateral bifurcation plates.

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

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

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

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

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

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

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between the proximal pair of secondary coverplates and the anterior lateral shared coverplates of the oral area.

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

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

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

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

The peripheral rim includes five or six circlets of plates. The large plates of the proximal circlet are distributed as alternating

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proximal and distal subcirclet members. The distal rim circlets are less regular. Vertical ridges may be present on the bases of the larger geniculate plates.

External plate surfaces appear to have been smooth.

Specimens:

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

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

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

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

U.S.N.M. S-3183-B. 5.3 mm axial by 6.2 mm transverse diameter.

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

This specimen is the best preserved of the topotypes. The theca has collapsed but little disruption has occurred. However, slight lateral shifting of plates has affected the oral and ambulacral areas.

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The anal structure is considerably disrupted and appears to have been abraded. Surficial etching has differentially altered some external features.

U.S.N.M. S-3183-C. 6.8 mm axial by 4.3 mm transverse diameter.

Pl. 37, fig. 4.

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

U.S.N.M. S-3183-D-1. 7.5 mm axial by 7.8 mm transverse diameter.

Pl. 37, fig. 8.

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

U.S.N.M. S-3183-D-2. 5.2 mm axial by 5 mm transverse diameter.

Pl. 37, fig. 7.

This specimen is a second which exposes the inner side of the

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oral surface. It is poorly preserved: the ambulacral floorplates are crushed and the oral frame is completely obscured; parts of the interambulacra and the rim are moderately well-preserved.

U.S.N.M. S-3183-D-3. 6.9 mm greatest diameter by 6 mm diameter.

Pl. 37, fig. 9.

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

U.S.N.M. S-3183-E. 6.7 mm axial by 6.1 mm transverse diameter.

Pl. 37, fig. 5.

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

U.S.N.M. S-3183-F. 5 mm axial by 4.8 mm transverse diameter.

Pl. 37, fig. 6.

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

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U.C.M.P. 37217. Topotype of H. parasiticus. Homocrinus beds, Rochester Shale, Clinton Group, Niagaran Series, Middle Silurian. Lecoport, New York. Kopf Collection. 7.4 mm axial by 7.2 mm transverse diameter.

Pl. 37, fig. 10-11.

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

Discussion of previous investigation:

The original description of Hemicystites parasiticus by Hall (1852) emphasized general thecal features that separate this species from other major echinoderm groups. Taxonomically important characters mentioned include: small domal theca; imbricate interambulacrals; straight ambulacra; and a valvular anal structure with an inner and outer circlet of alternating plates. In addition, Hall (1852, p. 246) described "a porous tubercle near the apex on the side opposite the ovarian orifice [anal structure], and near this the minute oral orifice, with an obscure pore below and near it . . . The oral orifice is so minute and obscure that little can be said of it more than that near the

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porous tubercle, on the side opposite the conspicuous ovarian pyramid, there is a triangular orifice and near it a circular depression or pore". Examination of an unretouched photograph of the holotype suggests that Hall's "oral orifice" is a slight separation between the raised perradial ends of the primary orals. The "triangular orifice" is the slightly disrupted and etched hydropore opening on top of the hydropore tubercle. The third opening mentioned as an "obscure pore" appears to be a preservational irregularity adjacent to the adradial end of the left posterior shared coverplate.

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

Discussion:

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

The few well-preserved topotypes establish the basic plate

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

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

Range and occurrence: Rochester Shale, Clinton Group, Niagaran Series, Middle Silurian of New York.

Rectitriordo Bell, gen. nov.

Type species: Rectitriordo kirkfieldensis Bell, sp. nov.

Diagnosis:

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

Description:

Rectitriordo is monotypic. The type species is represented by three partially disrupted specimens in which the ambulacral structure is well-preserved but the oral area and hydropore structure are

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incomplete. The genus is distinguished from other Isorophidae by the straight ambulacra with a regular triple biseries of ambulacral coverplates which includes three sets of coverplates.

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

Rectitriordo kirkfieldensis Bell, sp. nov.

Text fig. 36-37; plate 38.

Diagnosis:

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

Description:

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

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

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Text Figure 36 Rectitriordo kirkfieldensis Bell, sp. nov.

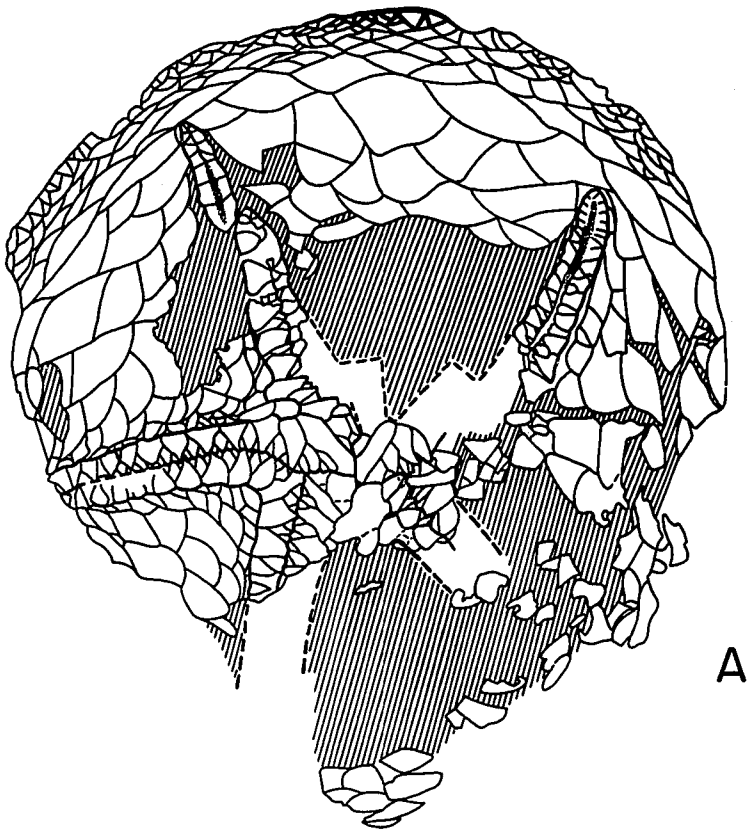
Holotype, U.C.M.P. 40476.

A. Oral surface, (X4), pl. 38, fig. 2. Ambulacral floorplate trough, exposed where coverplates are missing, is stippled.

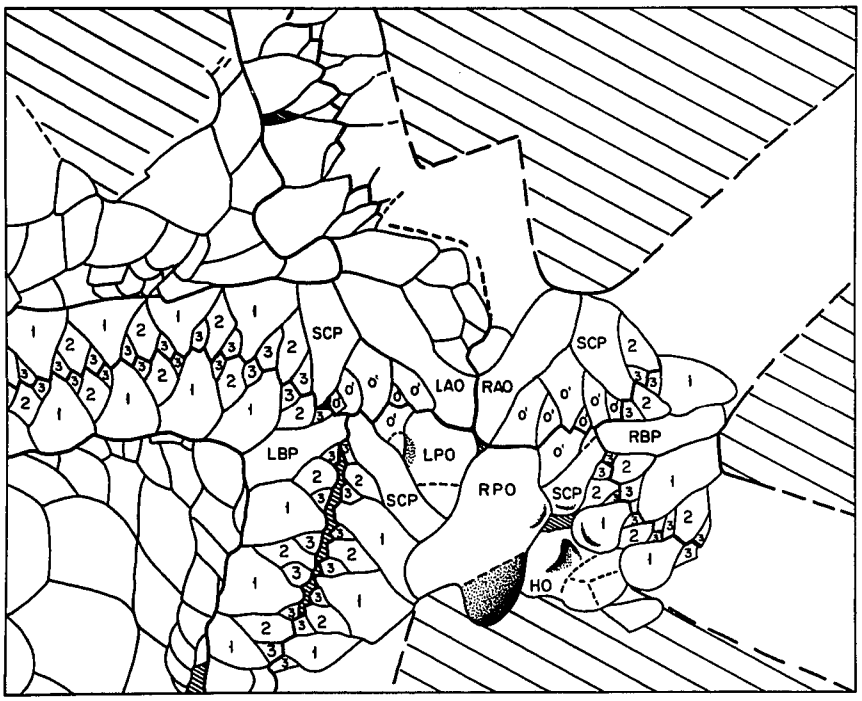
B. Oral area and adjacent structures, (X10), pl. 38, fig. 4. Adradial, intra-thecal part of the right posterior primary oral plate is stippled.

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

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A



B

Text Figure 36

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area and does not reach the adradial suture line.

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

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

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

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

The straight ambulacra taper gradually (text fig. 36A, pl. 38, fig. 1-2). The ambulacral coverplates form a triple biseries of alternating plate pairs. The primary coverplates are large and sub-triangu-

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lar in external outline. Opposing alternate members of each pair are in contact across the perradial line. Adjacent primaries are in contact adradially and restrict the external parts of the other two sets of coverplates to the medial part of the ambulacra.

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

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

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

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secondaries apparently extend past the lateral margin of the floorplates into the thecal cavity as intra-thecal extensions.

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

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

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

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

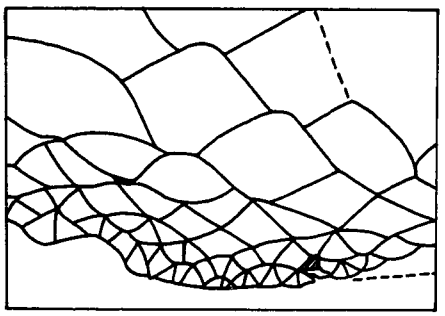
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Text Figure 37 Rectitriordo kirkfieldensis Bell, sp. nov.

A. Segment of the peripheral rim, holotype, U.C.M.P. 40476, pl. 38, fig. 3.

B. U.S.N.M. S-3889-G, (X10), pl. 38, fig. 10.

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A



B

Text Figure 37

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

Specimens:

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

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

The central part of the oral surface has collapsed inward, but the distal third of the ambulacral-interambulacral areas and the peripheral rim remain in life orientation. Large sectors of the theca are missing, including the anal structure, much of interambulacra 2, 3, 4 and 5, ambulacra IV and V, and the posterior half of the peripheral rim. Most plates of the oral area and hydropore structure appear to be present, but slight lateral shifting during collapse and later fracturing of some of these makes their identification tentative. The proximal parts of ambulacra I and II are well-preserved. The cover-plates are missing from the distal sector of ambulacrum III which exposes the upper sides of the floorplates. The proximal plates of interambulacrum 1 and the distal ones of interambulacra 2 and 3 are also well-preserved. Several segments of the anterior half of the peripheral rim are moderately well-preserved, although many of the distal circlet plates appear to be missing even from the well-preserved segments.

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U.S.N.M. S-3889-G. Paratype of Rectitriordo kirkfieldensis Bell. "Hull Limestone", Trenton Group, Mohawkian Series, Middle Ordovician. Quarry at Kirkfield, Ontario. 10.6 mm greatest diameter by 6.7 mm.

Text fig. 37B, pl. 38, fig. 9-10.

This individual is one of several housed with the type specimens of Foerstediscus parvus Bassler (U.S.N.M. S-3889) (= Foerstediscus grandis Bassler, 1935). The specimen is a disrupted fragment, but small segments of ambulacra I and V are preserved along with half of the anal structure which is completely missing in the holotype.

U.S.N.M. S-3894-D. Paratype of Rectitriordo kirkfieldensis Bell. "Hull Limestone", Trenton Group, Mohawkian Series, Middle Ordovician. Quarry at Kirkfield, Ontario. 12.4 mm axial by 12.5 mm transverse diameter.

Pl. 38, fig. 7-8.

The specimen is housed with Bassler's illustrated specimen of Cryptogoleus multibrachiatus (Raymond) (U.S.N.M. S-3894-A). The theca has collapsed and several large sectors are missing. Many of the remaining plates have been partially disrupted during collapse. However, segments of the peripheral rim, interambulacrum 2, and ambulacrum II and III are fairly well-preserved. Some of the oral plates can be identified. The plates of the peripheral rim appear to be more rounded than in the holotype and suggest the distinctive triangular shape is developed during later adult growth.

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Discussion:

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

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

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

Range and occurrence: Trenton Group, Mohawkian Series, Middle Ordovician of Kirkfield, Ontario.

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Curvitriordo Bell, gen. nov.

Type species: Isorophus kentuckyensis Bassler, 1936.

Diagnosis:

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

Description:

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

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

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

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

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Discussion:

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

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

Range and occurrence: Trenton Group, Middle Ordovician through Richmond Group, Upper Ordovician of Kentucky and Indiana.

Curvitriordo kentuckyensis (Bassler), 1936

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

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

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

Diagnosis:

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

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Description:

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

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

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

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

Three sets of ambulacral coverplates form a triple biseries (text fig. 38). The large primary coverplates are sub-triangular in external

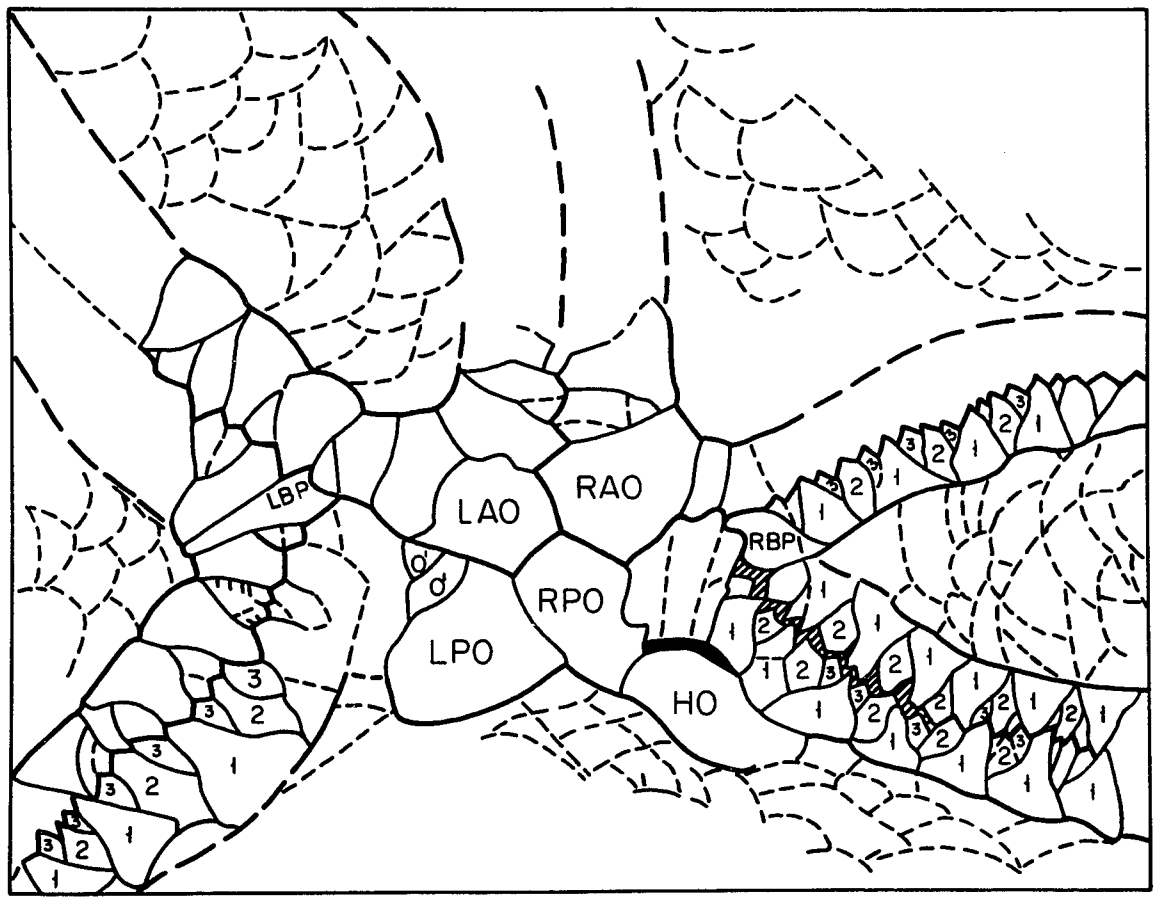
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Text Figure 38 Curvitriordo kentuckyensis (Bassler), 1936

Holotype, U.S.N.M. S-3967-A, oral area and adjacent structures, (X14), pl. 39, fig. 3.

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

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Text Figure 38

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view. Opposing alternate members of each pair are usually in contact perradially. Adjacent primaries are commonly in contact adradially and restrict the other sets to the more axial part of the ambulacra.

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

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

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

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

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

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the angular rim plates of Curvitriordo kentuckyensis appear to be directed proximally.

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

Specimens:

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

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

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

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

U.S.N.M. S-3967-B. Paratype of Curvitriordo kentuckyensis. 28.7 mm axial by 28.2 mm transverse diameter.

Pl. 39, fig. 6-7.

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

Discussion:

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

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

Some irregularity may occur in the coverplate sequence of C. kentuckyensis. Occasionally the opposing alternate members of the primary coverplate pairs appear to be separated perradially by tertiary coverplates. Observed irregularities may be preservational. The oral area and hydropore structure plate disposition may also be useful

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taxonomically at the specific level, but these areas are poorly preserved in both specimens.

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

Range and occurrence: Trenton Group, Mohawkian Series, Middle Ordovician of Kentucky.

Curvitriordo shideleri (Bassler), 1936

Text fig. 39; plate 39, fig. 8-9.

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

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

Diagnosis:

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

Description:

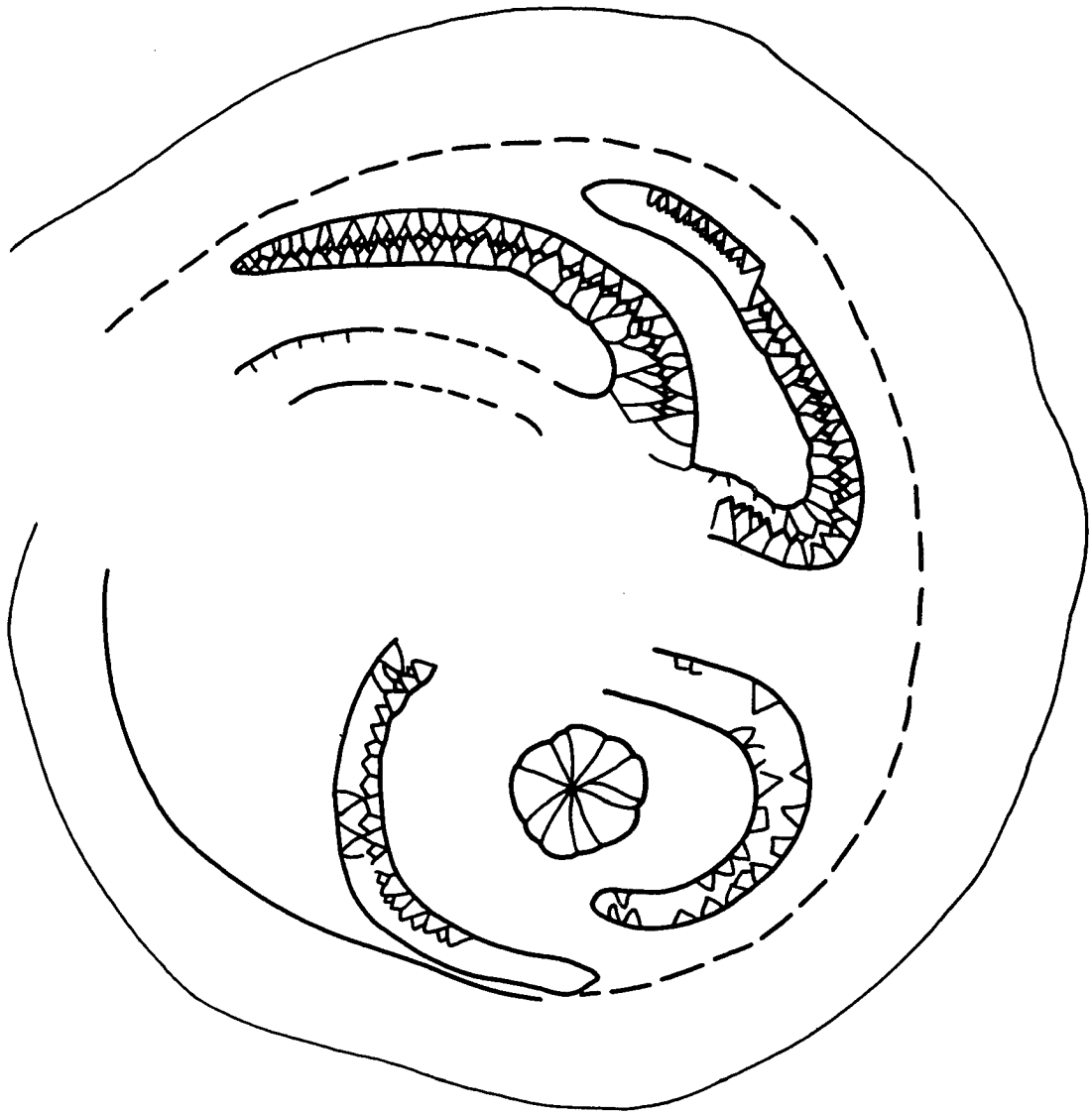
Curvitriordo shideleri (Bassler) is known only from the poorly preserved holotype in which the oral area and hydropore structure plates are completely disrupted (text fig. 39, pl. 39, fig. 8-9). The domal theca appears to have been highly convex and is 17 mm in diameter.

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Text Figure 39 Curvitriordo shideleri (Bassler), 1936.

Holotype, U.S.N.M. S-3958, (X9), pl. 39, fig. 9.

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Text Figure 39

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

The triple biseries of ambulacral coverplates consist of three sets of plates. The primary coverplates are large and sub-triangular in external outline. Adjacent primaries are usually adradially separated by the adradial ends of the alternate secondary coverplates. The opposing alternate members of each pair of primaries are separated perradially by a pair of tertiary coverplates.

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

The small tertiary coverplates are confined to the axial part of the ambulacra. Sub-rhomboidal in shape, these coverplates are the only set in which opposing alternate pair members are perradially in contact. One pair of tertiaries is inserted between the perradial tips of opposing alternate members of both the primary and secondary coverplate series. Thus, there are twice the number of pairs of tertiaries as

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primaries or secondaries. The sequence encountered along the perradial line is: primary-tertiary-secondary-tertiary-primary-etc.

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

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

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

Plate exteriors appear to have been smooth.

Specimen:

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

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

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

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is preserved in the remaining ambulacra.

Discussion:

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

Range and occurrence: Richmond Group, Cincinnatian Series, Upper Ordovician of Hamburg, Indiana.

Family Agelacrinitidae Chapman, 1860

Type genus: Agelacrinites Vanuxem, 1842

Diagnosis:

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

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Description:

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

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

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

The ambulacral coverplates commonly occur in cyclic sets composed of two to seven plates per cycle. Occasionally the coverplates are a

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mixture of cyclic and biserial sets. One species (? Postibulla jasperensis) possibly has only a single biseries of coverplates.

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

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

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

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and add an extra inner circlet of plates.

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

Discussion:

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

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

Morphologically the Agelacrinitidae is the most diverse family of edrioasteroids. Thecal shapes include both domal and clavate types.

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The oral region may include relatively few plates, with primary orals differentiated, or numerous small orals may be present and these reflect the ambulacral coverplate pattern.

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

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

The uniserial ambulacral floorplates vary from thick, axially elongate plates which abut along vertical sutures to relatively thin, imbricate, trough-shaped ones. Floorplates have been observed in only a few Agelacrinitidae species, but apparently both abutting and imbri-

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cating types occur within the same genus (Lepidodiscus). If so, this variability is in marked contrast to the Lebetodiscina in which imbricate versus abutting floorplates is a familial taxobasis.

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

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

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

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shallow sub-tidal environment for this occurrence (Koch and Strimple, 1968, p. 12-15).

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

Agelacrinites hybolopus Fraunfeller and Utgaard (1970) occurs in the Pennsylvanian Jamestown Cyclothem of Southern Illinois. The published account of this species suggests affinities to the genus Postibulla. This species, and unnamed fragmentary specimens from New Mexico (see p. 819) are the only two described edrioasteroids from the Pennsylvanian.

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

Agelacrinites Vanuxem, 1842

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Type species: Agelacrinites hamiltonensis Vanuxem, 1842.

Diagnosis:

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

Description:

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

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

The hydropore structure lies in the right posterior part of the oral area (pl. 40, fig. 1-2, 7-9). Plates surrounding the opening are raised to form a low, elongate mound, semi-integrated with the central

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oral rise. The structure involves three or more plates: the single, elongate hydropore oral forms the entire posterior side of the structure; two or more oral-ambulacral series plates form the anterior side and lateral extremities of the structure.

The ambulacra of Agelacrinites are long, moderately narrow, and I-III curve contrasolarly, IV-V solarly. Ambulacral coverplates form two-plate cyclic sets, with opposing cycles alternating along the ambulacra. The larger primary and smaller secondary plates of each set commonly unite perradially to form a single wide perradial point. The two-plate sets on each side of the perradial line are offset by half their width; the primary plates of one side lie opposite the secondaries of opposing cycles. Thus, the alternating two-plate cycles form a broadly undulating, zigzag perradial line. Occasionally anomalous coverplates may interrupt the regularity of this sequence.

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

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

The valvular anal structure is formed by an inner and outer circlet of triangular plates which alternate and are beveled to fit

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tightly together. Only the central part of the inner circlet plates are exposed between the broadly overlapping edges of the outer circlet plates.

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

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

Discussion:

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

In 1867 Hall redescribed the type species of Agelacrinites in detail. This description and Hall's contemporaneous descriptions of several other edrioasteroid species initiated the gradual restriction of the generic taxobases for Agelacrinites. Ambulacral width, length, disposition, and number, interambulacral plate morphology, thecal shape and peripheral rim development were accepted as generic criteria from 1870 through the 1920's. Using only these criteria, numerous species were placed in Agelacrinites. Bassler (1935) suggested the degree of interambulacral plate imbrication, width of the peripheral rim, and number of ambulacra vary intra-specifically in all edrioaster-

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oids. On the other hand, he thought valid generic taxobases should include ambulacral plate structure, oral area plating, and direction and degree of ambulacral curvature. Bassler's criteria have been accepted by most subsequent authors. So defined, Agelacrinites since 1935 has included all species with: domal theca; oral plates small, numerous and without definite order; ambulacra long, narrow, curved, I-III contrasolar, IV-V solar; interambulacrals squamose or polygonal, imbricating or tessellate; and peripheral rim with several rows of plates.

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

Range and occurrence: Skaneateles Formation, Hamilton Group, Erian Series, Middle Devonian of New York.

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Agelacrinites hamiltonensis Vanuxem, 1842

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Diagnosis:

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

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with prominent to subdued ridge and node prosopon.

Description:

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

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

The hydropore structure lies in the right posterior margin of the oral region (text fig. 40B, 41D) and forms a prominent distal bulge in the oral area outline. Participating plates are elevated and form a low mound, semi-integrated with the central oral rise. A single large hydropore oral extends along the proximal, posterior edge of ambulacrum V. In addition to this large hydropore oral, the structure may include two to five adjacent plates of the oral-ambulacral series. The posterior side of the elongate, slit-like opening is bounded entirely by the

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Text Figure 40 Agelacrinites hamiltonensis Vanuxem, 1842.

Lectotype, N.Y.S.M., 362-A.

A. Oral surface, (X4), pl. 40, fig. 1.

B. Oral area and adjacent structures, (X12), pl. 40, fig. 2.

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

Text Figure 41 Agelacrinites hamiltonensis Vanuxem, 1842.

A. Lectoparatype (4), juvenile, N.Y.S.M. 362-E, (X15), pl. 40, fig. 3.

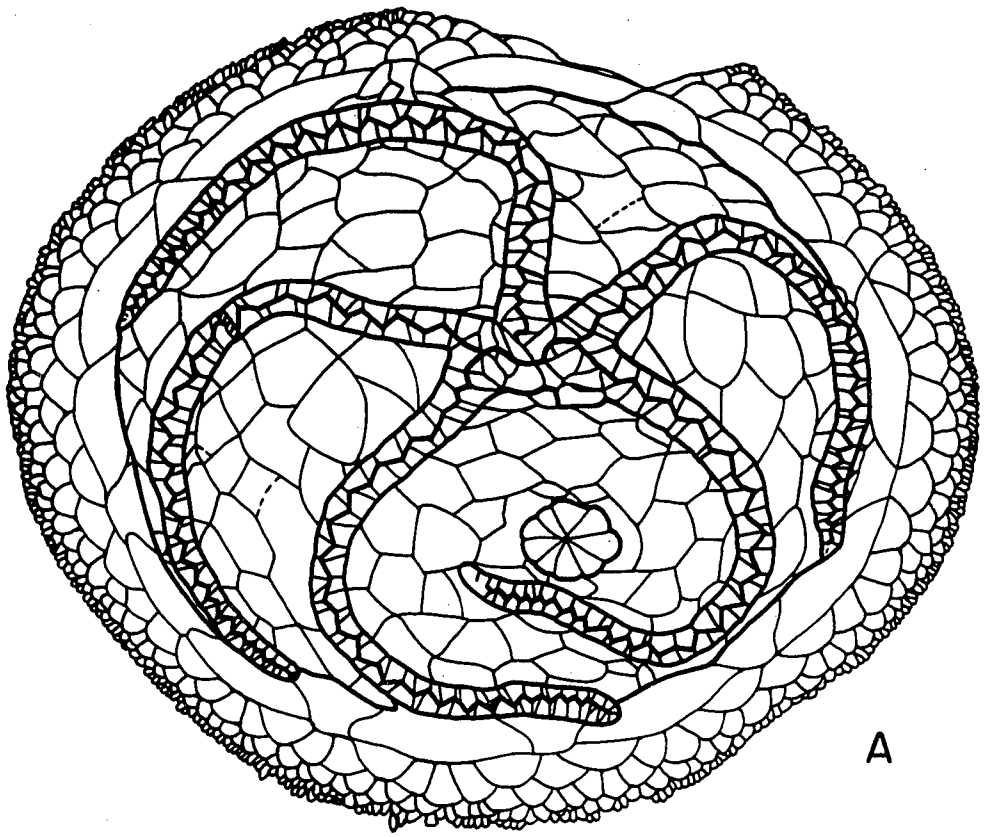
B. Lectoparatype (2), small adult, N.Y.S.M. 362-C, (X6), pl. 40, fig. 5.

C. Lectoparatype (3), juvenile, N.Y.S.M. 362-D, (X10), pl. 40, fig. 4.

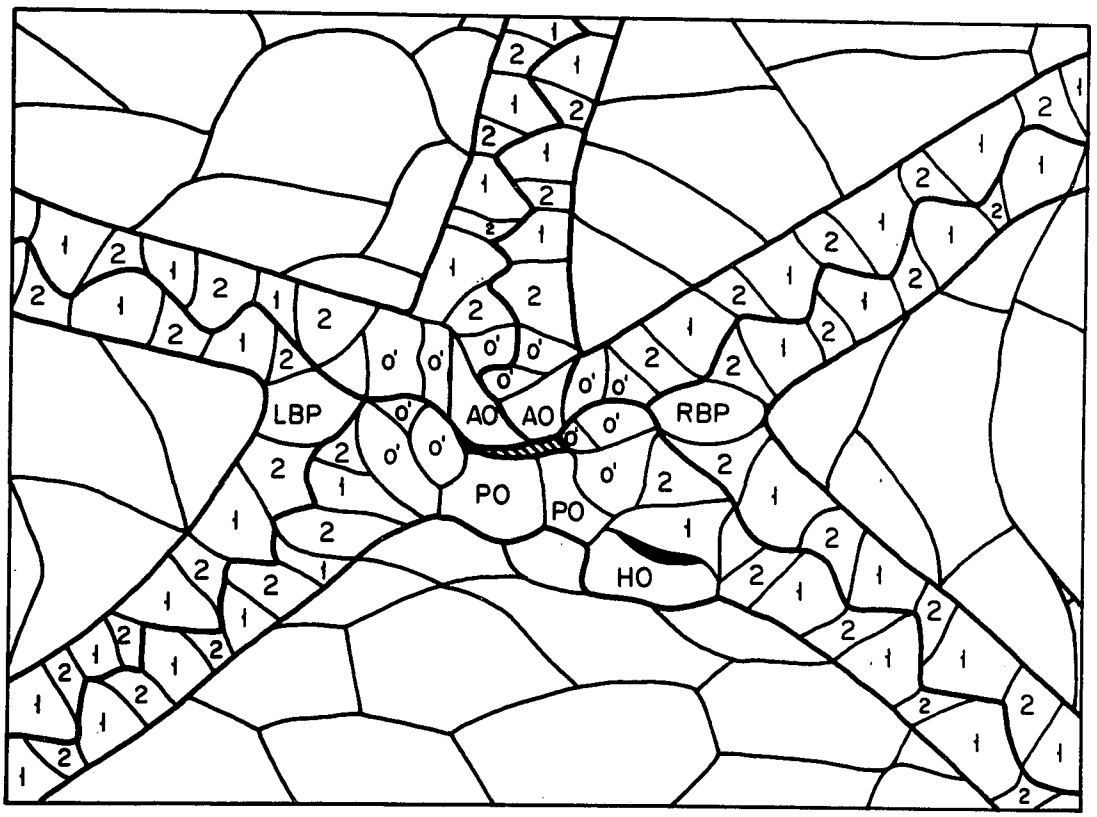
D. U.S.N.M. 85190-A, (X4), pl. 40, fig. 7.

E. Lectoparatype (1), N.Y.S.M. 362-B, (X3), pl. 40, fig. 6.

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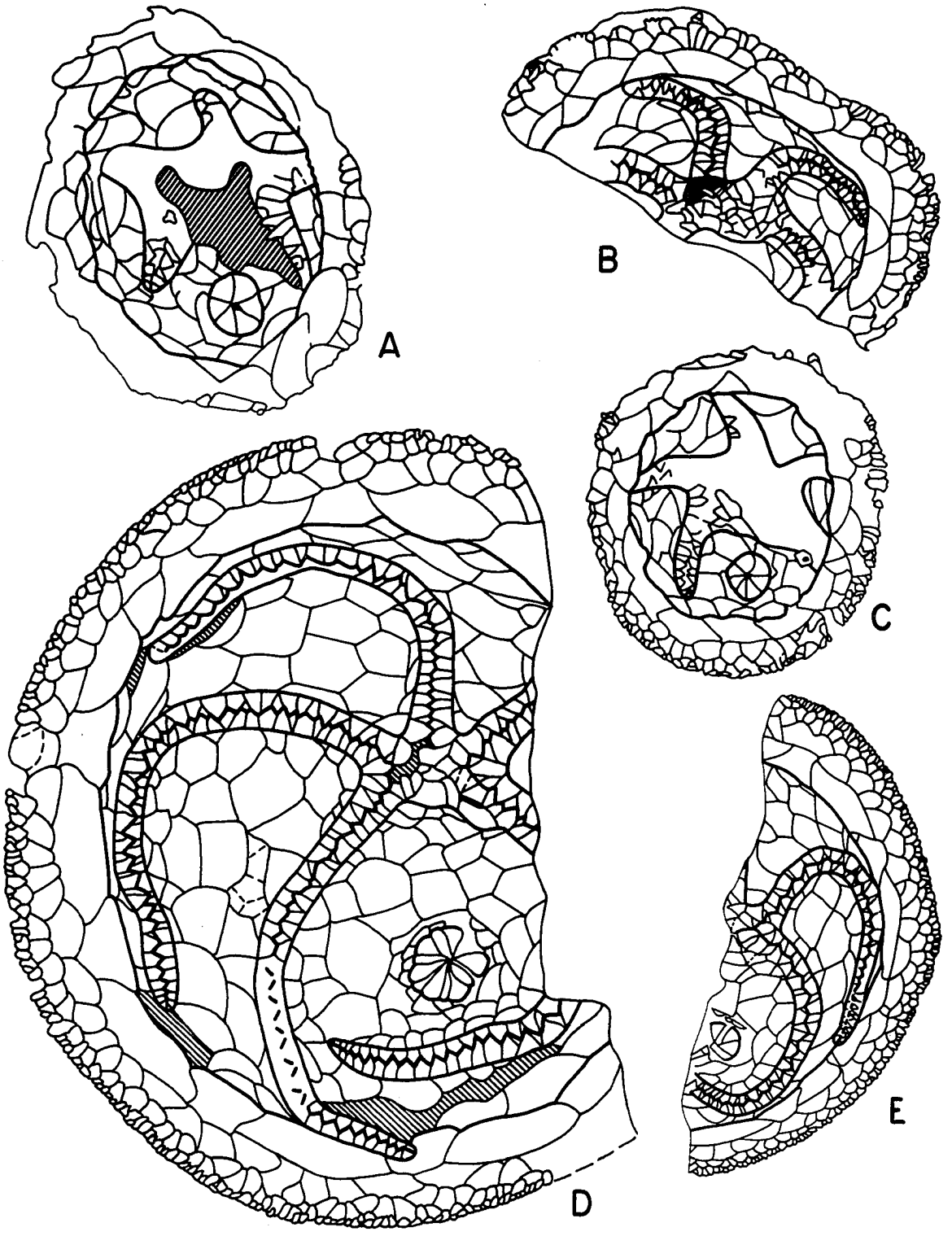
A



B

Text Figure 40

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Text Figure 41

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anterior margin of the hydropore oral. The anterior edge of the opening is formed primarily by the adradial end of the (?) proximal primary coverplate of the posterior side of ambulacrum V. The hydropore opening may be limited to the boundary between these two plates (text fig. 40B), or it may extend proximally to intersect the right margin of the large, right posterior oral plate (text fig. 41D). In both cases, the adjacent margin of this oral plate is elevated and forms part of the hydropore prominence. Specimen U.S.N.M. 85190-A suggests several other proximal coverplates of ambulacrum V are shortened adradially along their zone of contact with the hydropore oral and are thereby included in the structure. In contrast, only three plates, the right posterior oral, the hydropore oral, and the opposing large primary coverplate, appear to form the entire hydropore structure in the lectotype (text fig. 40B).

The oral frame and adjacent stone-canal passageway have been observed in one moderately well-preserved specimen and several other poorly preserved individuals (pl. 41, fig. 1-2). The transversely elongate oral frame extends into the thecal cavity below the ambulacra. The five proximal ambulacral floorplates form the radial parts of the structure; each is enlarged proximally and extends downward into the thecal cavity and also extends laterally to make contact with the adjacent floorplates of the frame. The upper extremities of the frame interradii, between ambulacra II-III and III-IV, are formed by downward tapering, wedge-shaped intra-thecal extensions from the two large anterior primary orals. Interradii between ambulacra I-II and IV-V

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are formed entirely by the enlarged proximal floorplates. The two posterior floorplates are not in contact across the posterior interradius. This sector includes only the intra-thecal extensions from two or more large posterior oral plates. These extensions are relatively short and extend downward only a short distance and thereby form a pronounced posterior gap in the frame. The central lumen, surrounded by the frame, opens downward into the thecal cavity and also laterally into the area beneath interambulacrum 5 through the posterior frame gap. Large, blade-like extensions may extend proximally into the central lumen from the two posterior floorplates or from the adjacent oral plate intra-thecal extensions.

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

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

The ambulacral coverplates form a two-plate cyclic series with opposing sets alternating along the ambulacra (text fig. 40A). The large primary coverplates are sub-rectangular, with straight adradial

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margins, parallel or moderately converging lateral sides, and an angular perradial end. Occasionally the lateral margins converge rapidly and merge with the pointed perradial end to form a sub-triangular plate outline. The smaller secondary plates lie along the proximal side of the primaries. Each is sub-rectangular to sub-triangular with a straight adradial margin and parallel or converging lateral sides. The perradial end slopes toward the adjacent, distal primary so that together, the two plates form a single wide perradial point. The perradial line is thus an undulating zigzag line, each broad point formed by both plates of each cycle.

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

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

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However, they quickly increase in size, and one or two plates proximal to their insertion zone extend to the adradial suture line.

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

A single specimen of Agelacrinites hamiltonensis exposes the inner, ambulacral tunnel side of several proximal coverplates. The latex pull seen in pl. 40, fig. 8, replicates the impressions of the inner coverplate surfaces. Although mediocre preservation obscures details, the ambulacral coverplates appear to have small, blade-like

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intra-ambulacral extensions developed on their perradial sectors. Each extension is straight, produced directly downward into the ambulacral tunnel. Thus, unlike the proximally flexed intra-ambulacral blades of the Isorophidae, the extensions of Agelacrinites hamiltonensis do not underlap the adjacent coverplates. Apparently each large coverplate has a larger central blade flanked by two smaller, lateral blades. When closed, the extensions of opposing coverplates apparently interdigitate beneath the perradial line.

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

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

The sub-polygonal interambulacral plates of Agelacrinites hamiltonensis are slightly imbricate; the oblique sutures between contiguous plates are almost vertical. The amount of overlap appears to increase in the distal parts of the interambulacra. These plates are relatively

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large in proportion to thecal diameter.

The valvular anal structure has 16 to 18 triangular plates which alternate as inner and outer circlet members. Outer circlet plates broadly overlap the inner plates along tightly fitting, beveled edges, and leave only a narrow central strip of the inner plates externally exposed. Interambulacral plates which surround the anal area are small and form an irregular bordering circlet.

The peripheral rim includes four to six circlets of plates. The proximal circlets are segregated into alternating proximal and distal sub-circlet members; the overlapping distal plates are externally much larger than the alternate proximals. Plates of the proximal two or three circlets are elongate concentric with the thecal margin. The small plates of the distal two or three circlets are radially elongate.

Prominent vertical ridges are developed on the basal surfaces of the larger geniculate rim plates (pl. 41, fig. 1, 5). Commonly, individual ridges extend across the entire basal surface, although occasionally shorter ridges are set between the distal parts of the larger ones. Each ridge is broad proximally and tapers rapidly to a thin blade which extends across the distal two-thirds of the plate base. Some ridges are nearly straight, whereas others flex distally, their course diverging from the plate centers. Each large, proximal circlet plate appears to have five to nine ridges. Smaller rim plates have fewer ridges.

Large irregular ridges and nodes lend a distinctive appearance to the thecal plates of many Agelacrinites hamiltonensis. Development is variable, pronounced in some adults but subdued in other adults and all

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juveniles. In some specimens nearly all plates bear the prosopon except for the nearly smooth proximal rim plates. In other individuals, it may be limited to interambulacrals and distal rim plates.

Specimens:

N.Y.S.M. 362 (A-E). Type series of Agelacrinites hamiltonensis Vanuxem (1842, fig. 80). Chenango Sandstone member, Skaneateles Formation, Hamilton Group, Erian Series, Middle Devonian. Colgate University Campus Quarry, Hamilton, New York.

The small sandstone slab preserves six A. hamiltonensis resting on a fragment of a smooth pelecypod valve. All are molds of the external oral surface.

N.Y.S.M. 362-A. Lectotype of Agelacrinites hamiltonensis. 27.7 mm axial by 32.3 mm transverse diameter.

Text fig. 40A-B, pl. 40, fig. 1-2.

This is the largest complete specimen in the type series and is here designated the lectotype. The theca has collapsed but little plate disruption occurred. Slight lateral shifting of plates in and around the oral region may have altered external plate shapes and locations. Latex casts of the specimen show most external features, although suture lines are somewhat obscured in the critical oral area and hydropore structure. Text fig. 40A-B depict probable plate boundaries. Each ambulacral coverplate appears to be centrally domed, so that lateral suture lines between adjacent coverplates lie in deep depressions. The perradial line between opposing coverplates is marked

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by a narrow, slightly elevated ridge which extends the length of the ambulacrum. These ridges suggest that the perradial coverplate margins were slightly elevated, although the ridges might also be preservational features. Thecal prosopon is prominently developed in this individual.

N.Y.S.M. 362-B. Lectoparatype (1) of A. hamiltonensis. 26.8 mm along break, 12.2 mm normal to break.

Text fig. 41E, pl. 40, fig. 6.

Lectoparatype (1) lies adjacent to the lectotype, the two specimens touching along a small segment of their peripheral rims. This specimen preserves only the right half of the theca, including: ambulacra IV, most of V and a small segment of III; interambulacra 4 and parts of 3 and 5; the partially disrupted right half of the oral-hydropore structure area; most of the disrupted anal structure; and the right half of the peripheral rim. Preservation is similar to that of the lectotype, although thecal collapse has caused more extensive plate disruption in this individual.

N.Y.S.M. 362-C. Lectoparatype (2) of A. hamiltonensis. 12.4 mm diameter parallel to break, 6.1 mm normal to break.

Text fig. 41B, pl. 40, fig. 5.

This lectoparatype is a small adult. The left posterior third of the theca is missing and the remainder of the specimen is partially disrupted and rather poorly preserved. Oral area plates outlined in text fig. 41B appear to be fragmented. Irregularities in the ambulacral

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coverplate pattern may be preservational.

N.Y.S.M. 362-D. Lectoparatype (3) of A. hamiltonensis. 5.5 mm axial by 5 mm transverse diameter.

Text fig. 41C, pl. 40, fig. 4.

This lectoparatype is a juvenile. The theca has collapsed but the major structural units appear to be little disrupted. Unfortunately, most individual plate boundaries are indistinct. This and the following juvenile demonstrate the relatively increased size of the oral-hydropore region, the anal structure, and the peripheral rim in young individuals. The ambulacra and interambulacral areas are proportionately small. These juvenile characteristics correspond with the growth series features observed in other edrioasterid species.

N.Y.S.M. 362-E. Lectoparatype (4) of A. hamiltonensis. 4.7 mm axial by 3.9 mm transverse diameter.

Text fig. 41A, pl. 40, fig. 3.

Lectoparatype (4) is a small juvenile. Most plate boundaries are indistinct but the outlines of major thecal structures are visible. Plates have been totally obscured in a large irregular area which includes much of the oral region and ambulacrum V. Anals, interambulacrals, some rim plates and a few ambulacral coverplates are tentatively outlined in text fig. 41A.

N.Y.S.M. 362-F. Lectoparatype (5) of A. hamiltonensis. 20.8 mm long.

This specimen is a small segment of the peripheral rim of a large adult.

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U.S.N.M. 85190. Topotypes of A. hamiltonensis. Chenango Sandstone member, Skaneateles Formation, Hamilton Group, Erian Series, Middle Devonian. Colgate University Campus Quarry, Hamilton, New York. G. A. Cooper, collector.

Ten small slabs of Chenango sandstone bearing 26 specimens of A. hamiltonensis, 8 juveniles and 18 adults, are included under this number. One specimen preserves a few weathered plates, all others are molds. Descriptions are based primarily on latex pulls of these specimens which include both external and internal oral surface casts.

U.S.N.M. 85190-A. 32.9 mm axial by 24.2 mm (broken) transverse diameter.

Text fig. 41D, pl. 40, fig. 7.

This large topotype is missing the right third of the theca and a large crack extends across the posterior rim. Collapse has partially disrupted some orals and distal interambulacrals. However, most of the ambulacral coverplates appear to be well-preserved. Proximally, the coverplate cycle in four of the ambulacra appears to include a third, irregular series of plates. Moreover, nearly all of these proximal plates form discrete, perradial points and some of the smaller plates are restricted to the axial parts of the ambulacra. Ambulacrum III is unique, for all of the proximal plates are nearly equal in size. This creates the appearance of a single alternating biseries of coverplates. The medial sectors of all the ambulacra exhibit the common two-plate cycles. Distally, the primary coverplates form a single alternating biseries, the secondary coverplates first appearing far from the distal

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tips of the ambulacra. Prosopon is subdued in this specimen, apparently developed only on the larger interambulacrals.

U.S.N.M. 85190-B. 26.5 mm axial by 29.2 mm transverse diameter.

Pl. 40, fig. 8-9.

This topotype is unique in preserving some of the original thecal plates. The specimen lies with the external oral surface toward the matrix and originally only the inner sides of the thecal plates were exposed. Loss of many plates but preservation of others provides a composite view of the individual which includes both internal and external features.

A latex pull made in 1969 (pl. 40, fig. 8) exposes the following features: the exterior oral surface of most of the peripheral rim, interambulacra 1, 2 and 5, the anal structure, the oral and hydropore area, and some of the ambulacral coverplates; also, the impressions of the ambulacral tunnel surfaces of the proximal and medial coverplates of ambulacra II-V, the inner surfaces of the plates of interambulacrum 3 and parts of 2 and 4, and the impressions of the basal surfaces of a small section of peripheral rim plates. The numerous small holes in the latex pull apparently resulted from a thin coating of glue that preserves the remaining plate calcite which is extremely soft. Although the amount of detail preserved is variable due to the weathered condition of the plate calcite, this specimen demonstrates the presence of intra-ambulacral extensions on the ambulacral tunnel surfaces of the coverplates.

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A gutta-percha squeeze of this specimen (pl. 40, fig. 9) made prior to 1941, found in the University of Cincinnati's Kopf Collection, shows that more original plate material was once present. In contrast with the 1969 pull, this squeeze preserved the impressions of the inner surfaces of the ambulacral floorplates in the proximal parts of ambulacra III and IV. The squeeze also provides a three-dimensional view of the ambulacral tunnel filling in the proximal part of ambulacrum III.

U.S.N.M. 85190-G. Small slab with four A. hamiltonensis specimens resting on a pelecypod valve.

U.S.N.M. 85190-G-1. Largest of the four specimens. 22 mm axial by 24.7 mm transverse diameter.

Pl. 41, fig. 3-4.

This large specimen is incomplete; the right posterior third of the theca is now missing. The full thecal diameter was apparently over 30 mm. Significantly, the ambulacral coverplate pattern is clearly a two-plate cyclic series with adjacent primary and secondary plates uniting to form a single perradial point. Thus, the coverplate sequence in this large adult is like that of the lectotype, but contrasts with the apparently unusual proximal sequence in specimen U.S.N.M. 85190-A. This specimen is also noteworthy for its nearly smooth plate exteriors which contrast with the pronounced development of nodes and ridges in other specimens.

U.S.N.M. 85190-G-2, G-3, G-4. Three other typical A. hamiltonensis adults.

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U.S.N.M. 85190-I. 19.5 mm axial by 19.7 mm transverse diameter.

Pl. 41, fig. 1-2.

This topotype is an impression of the inner side of the oral surface. Preservation is variable. The floorplates of ambulacra I, II and V, some of the interambulacrals, and many of the peripheral rim plates are well-preserved. The structure of the oral frame is somewhat indistinct, but better preserved here than in any other known individual examined. The stone-canal passageway is also visible but plate boundaries are difficult to identify.

U.S.N.M. 85190-J. 22.5 mm long by 11 mm wide.

Pl. 41, fig. 5.

This specimen, which exposes the inner side of the oral surface, is a fragment of the left posterior part of the theca. It includes the distal floorplates of ambulacra I, II and V, interambulacral plates, and the adjacent sector of the peripheral rim. The vertical ridges on the basal surfaces of the peripheral rim plates are well-preserved.

The remainder of the topotypes examined include:

U.S.N.M. 85190-C	Slab with 8 juveniles.
U.S.N.M. 85190-D.	One moderate sized adult.
U.S.N.M. 85190-E	Slab with three small adults.
U.S.N.M. 85190-F	Slab with 2 fragmentary specimens which expose the inner surface of the theca.
U.S.N.M. 85190-H	Slab with 4 small adults which expose the inner side of the oral surface.
Y.P.M. 28454	One adult specimen originally from the U.S.N.M. 85190 series, apparently donated to Yale.

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Discussion:

Agelacrinites hamiltonensis Vanuxem (1842) was the first formally named edrioasteroid species. It was based on the molds of six specimens, three of these fragments, which rest on the smooth surface of a large pelecypod valve. Vanuxem (1842, p. 158) interpreted the six individuals and the resting surface as "one system", and thus unique in being the only colonial "crinoidal fossil". The original description noted the shape, size, position, and prosopon of the six specimens and continued "near the center of the largest and perfect medallion [the lectotype] are five branching arms, like those of an asteria or star-fish, between two of which and those which are most expanded, is a star [anal structure] which probably was the mouth of the animal". Fortunately, Vanuxem included a woodcut (image reversed left to right) which accurately depicts many of the thecal features, although the orals and ambulacral coverplates are difficult to interpret.

A. hamiltonensis was frequently cited by early workers in subsequent descriptions of new edrioasteroid species. Recognizing the individuality of the type series specimens, most authors used Vanuxem's illustration of the lectotype as the basis for interpretation of trivial characteristics. In 1867, Hall redescribed the species in detail and in 1871 he presented a new drawing of the lectotype. The description presented here contrasts with Hall's interpretation in that he recognized: only a single alternating biseries of ambulacral coverplates; oral area with only six plates; and interambulacrals abutting. No mention was made of the hydropore structure.

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Hall's description and drawing of A. hamiltonensis have been accepted as definitive by most authors. The description presented here is the first account since Hall's based upon a restudy of the type specimens. The discovery of undescribed topotype specimens housed in the United States National Museum has substantially increased understanding of thecal structures and variations within the species.

Agelacrinites hamiltonensis is represented by relatively few specimens. All are preserved as molds and descriptions are based primarily on latex pulls prepared from them. The identification of individual suture lines is difficult in areas of small, complexly arranged plates such as the oral region, hydropore structure and, in part, the ambulacra. Thus, the apparent variability in the number and arrangement of the orals and hydropore structure plates may be, at least partially, preservational. The supposed presence of a third series of ambulacral coverplates in specimen U.S.N.M. 85190-A, and the described irregularities in the basic two-plate cyclic series of other specimens cannot be established with certainty due to the mode of preservation.

Plate boundaries are especially difficult to see in the smaller juveniles. Only the changes in areal dominance of the major thecal structures is definitely established by these specimens.

Range and occurrence: Skaneateles Formation, Hamilton Group, Erian Series, Middle Devonian of Hamilton, New York.

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Krama Bell, gen. nov.

Type species: Hemicystites devonicum Bassler, 1936

Diagnosis:

Agelacrinitidae with: domal theca; 16 or more oral plates, including 4 large primary orals, one hydropore oral, and lateral secondary orals which resemble ambulacral coverplates; hydropore structure semi-integrated; ambulacra of moderate width, curved I-III contrasolar, IV-V solar, ambulacral coverplate sequence a combination of cyclic sets and biserial pairs; interambulacrals squamose, imbricate; valvular anal structure formed by alternating inner and outer circlet plates.

Description:

The genus Krama is monotypic and therefore separation of generic and specific taxobases is uncertain. Features outlined in the above diagnosis are inferred to be of generic rank from taxobases for related Agelacrinitidae genera.

Etymology: Krama is Greek meaning mixture, and refers to the mixture of cyclic and biserial sets of coverplates.

Range and occurrence: Traverse-Hamilton Groups, Erian Series, Middle Devonian of eastern Michigan and western Ontario.

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Krama devonicum (Bassler), 1936

Text fig. 42-45; plate 41, fig. 6-8, plate 42-43.

1936 Hemicystites devonicus Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 14, pl. 7, fig. 1; Agelacrinites southworthi Bassler, idem, ibid.: 16, pl. 4, fig. 12.

1943 Hemicystites devonicus Bassler, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 203; Agelacrinites southworthi Bassler, idem, ibid.: 196.

1944 Hemicystites devonicus Bassler, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, pl. 49, fig. 23.

1958b Agelacrinites southworthi Bassler, Ehlers, G. M. and Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 14 (15): 271-272.

1960 Hemicystites devonicus Bassler, Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 159-160, pl. 10, fig. 5-7; Agelacrinites sp. B, idem, ibid.: 149-150, text fig. 2, pl. 5, fig. 1-2; Agelacrinites southworthi Bassler, idem, ibid.: 150-151, pl. 5, fig. 3-4.

1966 Agelacrinites sp. B. Kesling, Regnéll, G., in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: text fig. 120-4.

Diagnosis:

A Krama with: moderate sized domal theca; oral plates include two anterior and two posterior primaries; semi-integrated hydropore structure formed by three or more plates; ambulacral coverplate series

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includes alternate cyclic series of three plate sets and one late, fourth set added as biserial pairs; squamose, imbricate interambulacrals relatively large in proportion to thecal diameter; large triangular anals arranged as alternate inner and outer circlet members, with elevated acuminate tips forming central anal protuberance.

Description:

The domal theca of Krama devonicum (Bassler) is moderate in size; the maximum known diameter approaches 18 mm.

The oral area is composed of approximately 20 plates in large adults (text fig. 42). Oral plate number and disposition change during ontogeny. In small specimens four primary orals, two anterior and two posterior, form the center of the oral area (text fig. 44A-B). All four are adradially in contact with adjacent interambulacra and extend proximally to the central transverse oral midline. The two sub-equal anteriors are symmetrically disposed on either side of the anterior oral midline. The right posterior is larger than the other primaries and perradially abuts both anterior primary orals. The left posterior is the smallest primary and perradially abuts only the left side of the left anterior primary. A single, moderate-sized hydropore oral lies adjacent to the right posterior edge of the right posterior primary oral and forms a distal bulge in the oral area outline which extends along the posterior proximal part of ambulacrum V. Secondary orals distally flank the central primaries, four or more on each side along the transverse oral midline, and two along the anterior oral midline. Thus, oral plates total fifteen or sixteen in the smaller specimens.

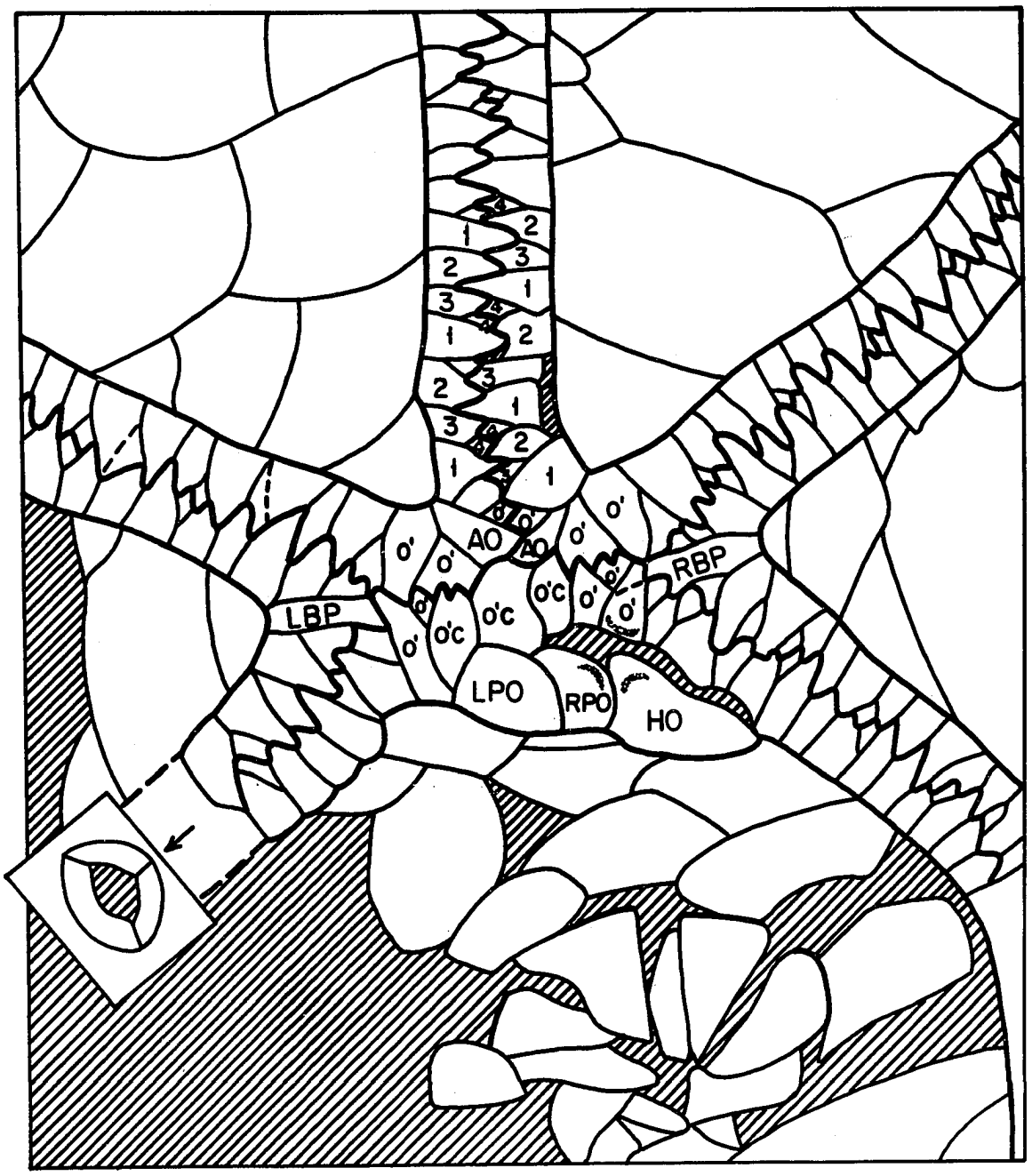
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Text Figure 42 Krama devonicum (Bassler), 1936

Oral area and adjacent structures, U.S.N.M. S-3478, (X20), pl. 43, fig. 11. Inset at the broken end of ambulacrum I is a vertical cross-section view of the most distal, preserved plates of ambulacrum I.

AO. anterior primary oral plate; HO. hydropore oral plate; LBP. left lateral bifurcation plate; LPO. left posterior primary oral plate; o'. secondary oral plate; o'c. central secondary oral plate; RBP. right lateral bifurcation plate; RPO. right posterior primary oral plate; 1. primary set ambulacral coverplate; 2. secondary set ambulacral coverplate; 3. tertiary set ambulacral coverplate; 4. quaternary set ambulacral coverplate.

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Text Figure 42

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In the largest adult specimen (U.S.N.M. S-3478, text fig. 42), the oral area includes twenty or more plates. The two anterior primary orals remain distinct and are located in the same position as in younger specimens. However, some of the lateral secondary orals are larger than either anterior primary. The two large posterior primary orals have apparently shifted position and no longer meet the anterior primaries perradially. Three moderately large "central secondary orals" lie between the anterior margins of the posterior primaries and the transverse oral midline. The middle "central secondary" is largest. Perradially, it abuts both anterior primaries and forms the center of the transverse oral midline. The posterior margin of this plate meets the anterior edge of both posterior primaries. The right "central secondary" perradially abuts the right anterior primary oral and, before thecal collapse, apparently also abutted the right posterior primary oral. The left "central secondary" posteriorly meets the left posterior primary oral but perradially it is in contact with an anterior lateral secondary oral. The large hydropore oral lies adjacent to the right margin of the right posterior primary oral and extends distally along the proximal, posterior margin of ambulacrum V. Additional secondary orals flank the central oral plates, two along the anterior oral midline and four or more on each side along the transverse oral midline. The lateral secondaries in part reflect the pattern of the ambulacral coverplate series and appear to grade distally into the proximal coverplate series without a distinct break. Therefore, the distinction between distal orals and proximal coverplates is obscure,

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and the exact number of lateral secondary orals indeterminate.

An intermediate sized adult (U.M.M.P. 57679, 8 mm diameter, text fig. 45B) suggests the central separation of the anterior and posterior primary orals is accomplished late in ontogeny by proximal migration of lateral secondary orals. In this individual the two anterior primaries are larger than adjacent secondaries, one disposed on each side of the anterior oral midline. Meeting perradially, they form the anterior edge of the central transverse oral midline. The two large posterior primaries form most of the central posterior oral area. Adradially they form the posterior margin of the oral area, but perradially they are separated from the anterior orals. Centrally, the separation is an open gap between the primaries, perhaps accentuated somewhat during thecal collapse. But laterally, two secondary orals, which formerly flanked the right and left posterior orals, have apparently migrated both anteriorly and proximally. The right secondary, apparently ahead of the left, completely separates the right anterior and posterior primaries. The left plate separated only the distal parts of the two left primary orals. Continued posterior movement of the two posterior primaries coupled with continued proximal migration of the lateral secondaries would produce the oral plate arrangement seen in the larger adult (text fig. 42).

The hydropore structure of Krama devonicum lies in the right posterior, distal bulge of the oral region. It is semi-integrated with the central oral rise; the adjacent margins of plates surrounding the opening are elevated to form a low mound-like protuberance along the

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distal edge of the oral rise. At least three plates participate directly in its formation. The posterior side includes the proximal part of the hydropore oral and the right margin of the right posterior primary oral. The anterior side of the mound is formed primarily by the adradial end of one elongate plate of the oral-ambulacral series which opposes the junction between the hydropore oral and the right posterior primary. This anterior plate is either a posterior right lateral secondary oral, or the proximal primary coverplate of the posterior side of ambulacrum V. One or two oral-ambulacral series plates which flank this central anterior one may be adradially elevated and thereby also participate directly in the structure. In addition, one or more of the proximal coverplates of the posterior side of ambulacrum V may be adradially shortened where they meet the adjacent right anterior edge of the hydropore oral plate, and thus are indirectly included in the hydropore complex.

In young individuals the hydropore protuberance is formed entirely by the hydropore oral, right posterior primary oral and the opposing oral-ambulacral series plate. The hydropore is a small triangular gap between these three plates at the summit of the prominence. In larger specimens both the opening and the elevated protuberance appear to be elongated parallel to the axis of ambulacrum V and may include additional plates of the oral-ambulacral series which are adjacent to the initial anterior element.

The ambulacra are curved, I-III contrasolarly, IV-V solarly. In young adults the ambulacra curve gradually, whereas in larger speci-

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mens the proximal parts are nearly straight. The distal tip of each ambulacrum remains separated from the adjacent ray by several interambulacrals. Distally, ambulacrum V may curve proximally toward the anal structure in large individuals.

The ambulacral coverplate series, when fully developed (text fig. 43H, 44C), contains four sets of plates. The initial three sets are disposed in alternating cyclic series; the final set forms biserial pairs which are inserted into the cyclic series. In mature segments of the ambulacra the primary plates are largest and triangular in outline, with wide adradial bases and pointed perradial tips. The plates of the second set are the next largest, often two-thirds the size of the primaries. They vary from broad-based triangular plates to elongate sub-triangular ones with straight adradial margins, nearly parallel sides, and a pointed perradial end. These plates lie adjacent to the proximal margins of the primary plates of the next distal cycle. The tertiary plates are somewhat smaller than the secondaries, but usually not less than half the size of the primaries. They range from sub-triangular plates which broadly abut the adradial suture line, to sub-rhombic forms angular both perradially and adradially. The latter may extend to the adradial suture line or end before intersecting it. The tertiaries lie between the primary and secondary plates of each cycle.

These first three sets of coverplates complete the cyclic part of the mature coverplate series. Cycles on opposite sides of the perradial line alternate, offset by half a cycle width. Thus, the pointed perradial tips of the primary plates fit between the pointed tips of

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Text Figure 43 Krama devonicum (Bassler), 1936.

Schematic reconstruction of ambulacral coverplate development. The proximal end of each ambulacral segment is the bottom of the illustration. A through E depicts the development of the cyclic primary (Roman numerals), secondary (capital letters) and tertiary (Arabic numbers) set ambulacral coverplates. F is a regularized drawing of actual plate shapes seen at this stage of development. G shows the addition of the quaternary (small letters) set as pairs of coverplates. H is a regularized drawing of actual plate shapes where all four sets of coverplates have developed.

Text Figure 44 Krama devonicum (Bassler), 1936.

A. Juvenile, U.M.M.P. 35390, (X25), pl. 41, fig. 7.

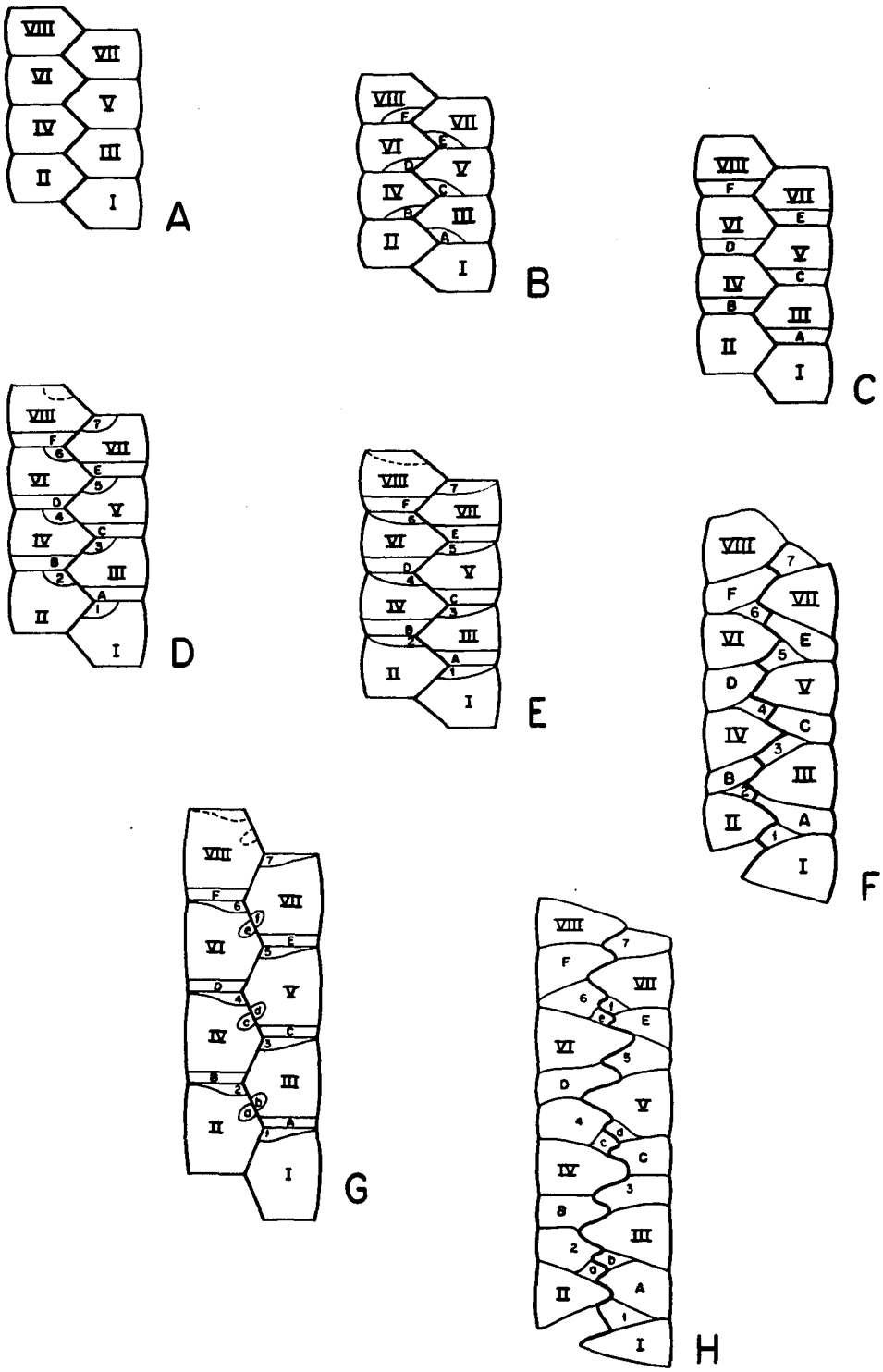
B. Juvenile, U.M.M.P. 21123, (X16), pl. 42, fig. 1.

C. Ambulacrum III, U.S.N.M. S-3478, (X21), pl. 43, fig. 9.

D. Holotype, U.M.M.P. 17295, (X10), pl. 41, fig. 6.

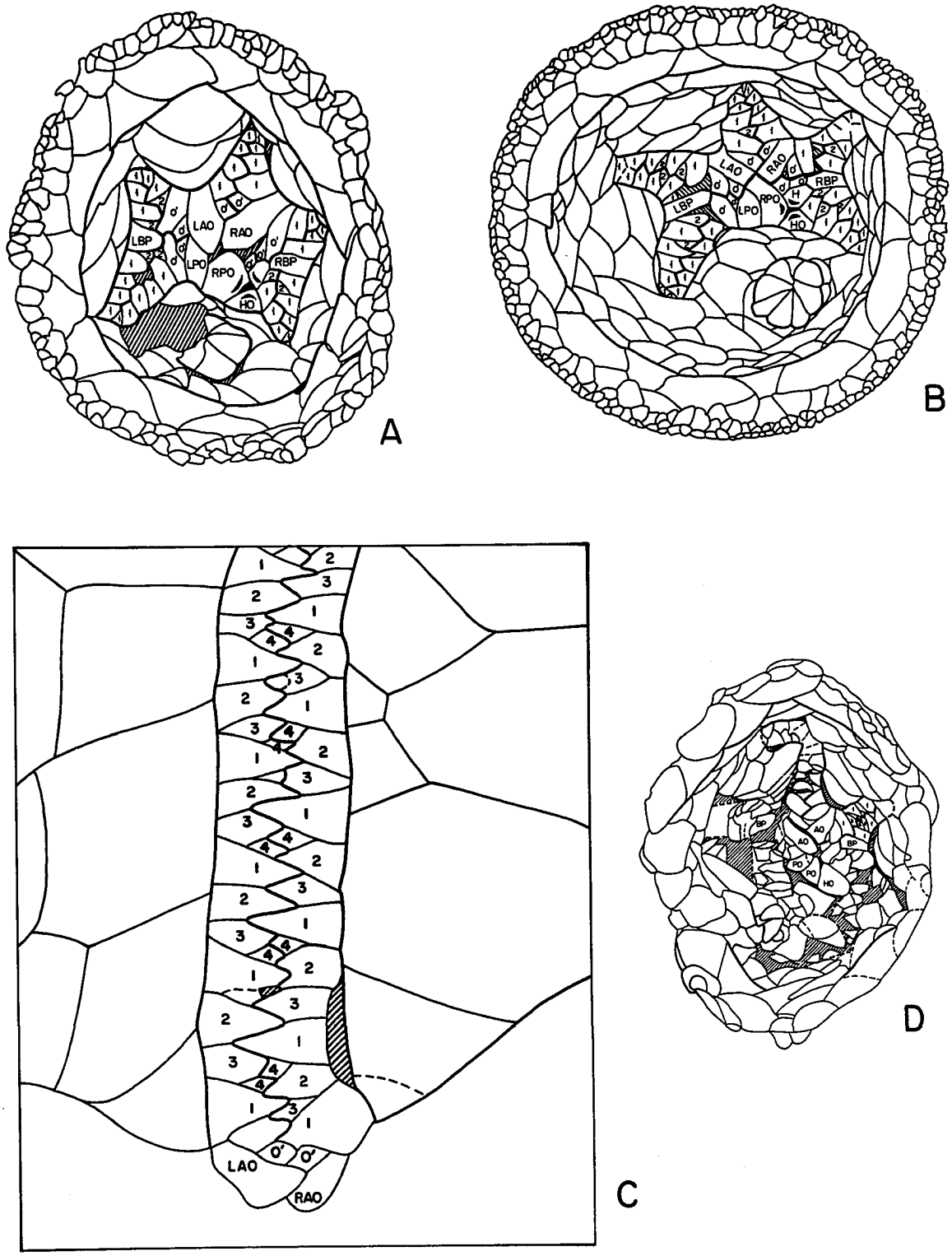
AO. anterior primary oral plate; BP. lateral bifurcation plate; HO. hydropore oral plate; LAO. left anterior primary oral plate; LBP. left lateral bifurcation plate; LPO. left posterior primary oral plate; o'. secondary oral plate; PO. posterior primary oral plate; RAO. right anterior primary oral plate; RBP. right lateral bifurcation plate; RPO. right posterior primary oral plate; 1. primary set ambulacral coverplate; 2. secondary set ambulacral coverplate; 3. tertiary set ambulacral coverplate; 4. quaternary set ambulacral coverplate.

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Text Figure 43

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Text Figure 44

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contiguous tertiary and secondary plates of opposing cycles (text fig. 44C). The offset three-plate cycles yield a broadly undulating perradial line, but the large, discrete, angular tips of each cycle plate form sharp perradial serrations which partially mask the broader undulations.

The quaternary plates are small and are restricted to the axial part of the ambulacra. Each is rhombic, and pointed both perradially and adradially (text fig. 44C). The quaternaries are added as biserial pairs, inserted into the fully formed three-plate cycles. Opposing pair members are perradially in contact and thus lie in different parts of the offset, opposing cycles. Looking distally along the ambulacra, the adradial end of each right quaternary is inserted between the pointed perradial tip of each right tertiary plate and the tip of the adjacent right primary plate of the following, distal cycle (text fig. 44C). The adradial end of the left member of the quaternary pair is inserted between the tips of the primary and the adjacent tertiary plate of each left cycle. The pointed perradial tip of the left member of the quaternary pair lies adjacent and proximal to the tip of the right plate.

The ontogenetic development of the coverplate sequence is schematically depicted in text fig. 43A-H. Primary coverplates are developed singly at the distal tip of the ambulacra and shift alternately left and right to form an alternating biserial pattern (text fig. 43A, U.M.M.P. 57677). Apparently specimens less than 2 mm in diameter include only primary coverplates.

Formation of secondary coverplates begins after four or five primary plates are present on each side of the perradial line. The

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first secondary plate is introduced adjacent to the distal margin of the proximal primary coverplate. At approximately the same time, a new primary plate is added at the distal tip of the ambulacrum. Thus, the zone of secondary coverplate insertion is perpetually four or five primary plates from the distal tip of the ambulacrum. The secondaries are added alternately along the ambulacra, one adjacent to the distal edge of each primary. When first developed, each secondary is a small rhombic element, restricted to the medial part of the ambulacrum. Rapidly increasing in size, they become sub-triangular in outline as their bases widen after reaching the adradial suture line (text fig. 43B-C).

Development of the tertiary coverplates parallels that of the secondaries (text fig. 44D-F). Their formation begins in the proximal part of the ambulacra after four or five alternate sets of secondaries have been developed. Corresponding insertions of new secondaries maintain the zone of tertiary coverplate implacement four or five secondary plates proximal to the zone of secondary plate formation. Each tertiary is inserted along the distal margin of each primary and thereby separates the primary and secondary coverplates of each cycle. Initially the small rhombic tertiaries are limited to the axial part of the ambulacra. They gradually increase in size and extend toward the adradial suture line. The tertiaries commonly maintain the rhombic shape and end before reaching the adradial suture line in all but very large adults. Text fig. 43F represents actual plate shapes in the proximal part of the ambulacra of specimen U.M.M.P. 57679, approximate-

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ly 8 mm in diameter, and shows the typical three-plate cyclic pattern in moderate sized adults. The holotype is in the same stage of ambulacral coverplate development.(text fig. 44D).

Quaternary plate development which begins proximally, is initiated late in adult development, after numerous three-plate cycles are complete (text fig. 43G). The rate of quaternary plate pair insertion is apparently more rapid than development of the cyclic plates. Thus the zone of quaternary plate insertion gradually migrates closer to the zone of tertiary plate insertion. For example, the ambulacral sequence in specimen U.M.M.P. 4796, 14.5 mm in diameter (text fig. 45 C-D), contains only numerous three-plate cycles throughout the long ambulacra. In contrast, the entire proximal halves of the ambulacra in specimen U.S.N.M. S-3478, 17.5 mm in diameter (text fig. 42, 44C), have quaternary plate pairs.

Individual cyclic coverplates continue to increase in size as the quaternary pairs are added. The secondaries expand adradially and become nearly triangular in outline. The once rhombic tertiaries commonly become sub-triangular as their adradial bases intersect the adradial suture line and widen. In contrast, the quaternaries apparently remain small, rhombic plates, always confined to the axial parts of the ambulacra (text fig. 42, 43H).

Modifications of the ambulacral coverplate pattern are encountered occasionally. Looking distally along the ambulacra, the proximal primary coverplate may be on the left side of the perradial line rather than on the right, its usual position. The relative proximal-

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Text Figure 45 Krama devonicum (Bassler), 1936

A. U.M.M.P. 21203, (X9), pl. 42, fig. 7.

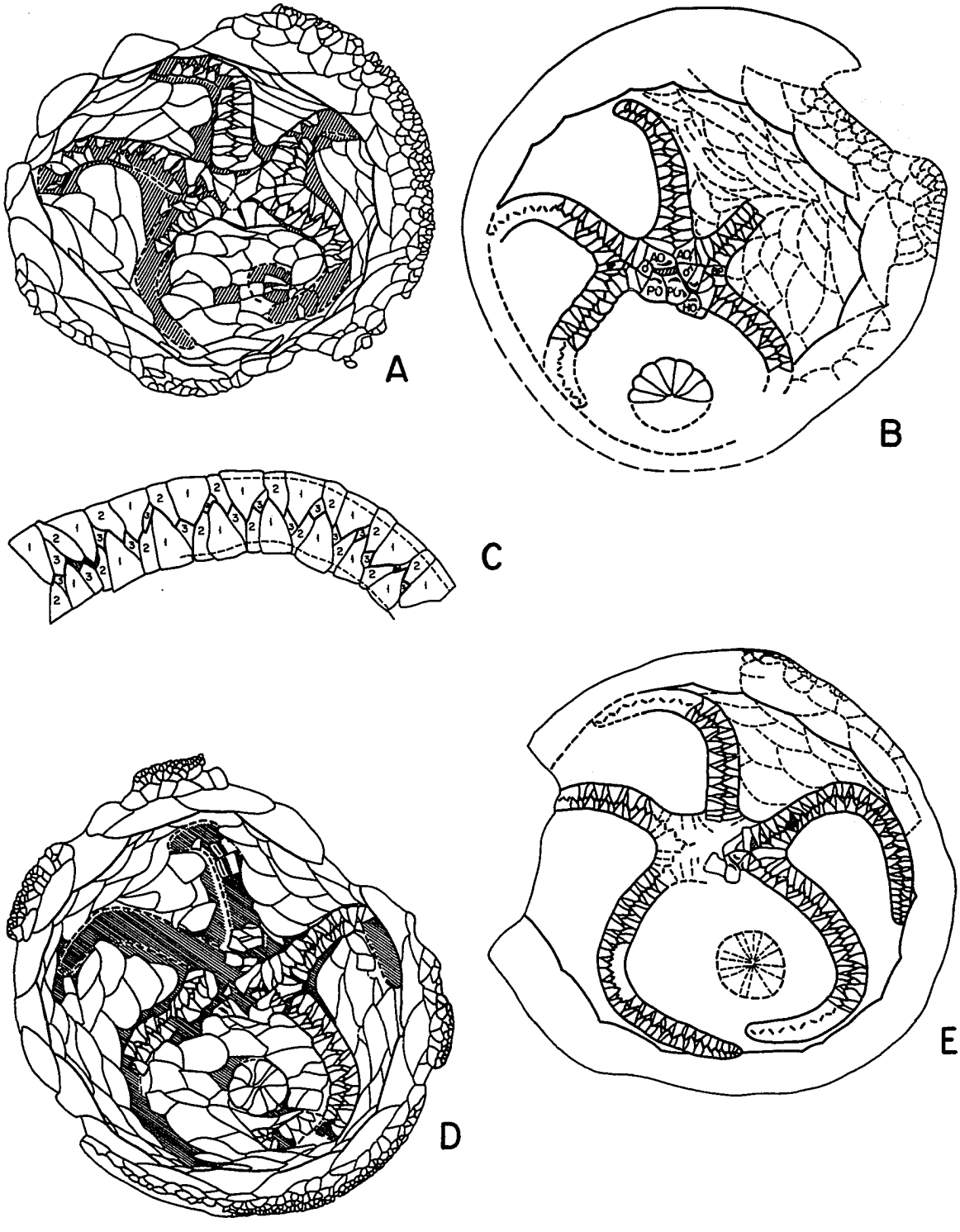
B. U.M.M.P. 57679, (X9), pl. 42, fig. 9. AO. anterior primary oral plate; HO. hydropore oral plate; BP. lateral bifurcation plate; o'. secondary oral plate; PO. posterior primary oral plate.

C. Ambulacrum V, U.M.M.P. 4796, (X15), pl. 43, fig. 3. Proximal end is to the left. 1. primary set ambulacral coverplate; 2. secondary set ambulacral coverplate; 3. tertiary set ambulacral coverplate.

D. U.M.M.P. 4796, (X5), pl. 43, fig. 1.

E. U.M.M.P. 57677-A, (X6), pl. 43, fig. 5.

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Text Figure 45

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distal location of the opposing, interdigitating, pointed perradial tips of the coverplates is thus reversed, the perradial tip of the right, rather than the left member of the quaternary pair of plates lying proximal to the opposing quaternary plate, and so on (ambulacrum II, text fig. 42). In addition to plate reversals, the secondary and tertiary plates occasionally become unusually large and approach the size of adjacent primary coverplates. Small extraneous plates occasionally appear in the coverplate sequence, although these supposed plates may be fragments of adjacent coverplates, broken during preservation (text fig. 44C).

The primary coverplates laterally overlap adjacent secondary and tertiary ones and the contiguous margins of these plates are beveled to fit tightly together. In fully developed adults, all three plates of the cyclic series commonly reach the adradial suture externally, and their bases rest upon the lateral margins of the underlying floorplates. In smaller adults the tertiaries may end externally before reaching the adradial suture line, but apparently they extend under the adjacent, overlapping coverplates and internally make contact with the inner edge of the lateral floorplate margin. Only small, newly formed secondary and tertiary plates are confined to the axial part of the ambulacra, both externally and internally. In contrast, all quaternary coverplates are limited to the axial ambulacral area, both externally and internally.

The inner surfaces of the coverplates are inadequately known. Intra-ambulacral extensions apparently are developed on the primary, secondary and perhaps tertiary coverplates, but their shape and size

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has not been determined. Adradially, the coverplates end adjacent to the edges of the underlying floorplates and apparently lack intrathecal extensions. The adradial ends of the coverplates are overlapped by the upper edges of adjacent interambulacral plates whereas the lower parts of these interambulacrals abut the adradial faces of the coverplates. A pronounced groove is incised into the abutted adradial face of each coverplate, apparently facilitating articulation between the coverplates and the lower, abutting part of the adjacent interambulacral plates.

The ambulacral floorplates, seen only in disrupted specimens, are uniserial, trough-shaped and meet one another along vertical sutures. The inner surfaces are evenly convex inward. The upper surfaces are concave downward except for the lateral adradial margins which slope gently and form a moderately wide articulation zone upon which the bases of the overlying coverplates rest (insert, text fig. 42). These lateral margins slope toward the ambulacral trough in specimen U.M.M.P. 4796 (pl. 43, fig. 1-2) but appear to slope away from the trough in U.S.N.M. S-3478 (insert, text fig. 42).

The squamose interambulacral plates are imbricate and moderately large in proportion to thecal diameter.

The valvular anal structure of Krama devonicum includes approximately sixteen triangular plates, alternating as inner and outer circlet members. Outer circlet plates broadly overlap inner ones and leave only a narrow central strip of each inner plate exposed externally. The central, pointed tips of the anals are flexed upward to form

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a small, conical protuberance in the center of the anal structure. The basal ends of the anal plates are grooved, like the adradial ends of the ambulacral coverplates, and apparently aid in articulation of the anals with the adjacent, abutting interambulacrals (pl. 43, fig. 1-3).

The peripheral rim is formed by four to six circlets. The large proximal circlet plates regularly alternate as proximal and distal subcirclet members. Plates of this and the following circlet are elongate concentric with the thecal margin, whereas the distal two to four circlets are formed by radially elongate plates.

External plate surfaces are smooth except for the extremely fine pustulation reflecting the microstructure of the plates.

Specimens:

U.M.M.P. 17295, U.M.M.P. 35390, U.M.M.P. 21123, U.M.M.P. 21203, U.C.M.P. 36118, U.M.M.P. 57078, U.M.M.P. 4796, U.M.M.P. 57679.

Holotype and seven topotypes of Krama devonicum (Bassler). Ferron Point Formation (Long Lake Beds), Traverse Group, Erian Series, Middle Devonian. Abandoned shale pit of the Alpena Portland Cement Company, SE $\frac{1}{4}$, Sec. 18, T. 32 N., R. 9 E., Alpena County, about 7 miles north of Alpena, Michigan.

U.M.M.P. 17295. Holotype of Krama devonicum (Bassler) (1936, p. 14, pl. 7, fig. 1, as Hemicystites devonicus). H. H. Hindshaw, collector. 6.6 mm axial by 4.8 mm transverse diameter.

Text fig. 44D, pl. 41, fig. 6.

The holotype is a small, poorly preserved specimen. Thecal

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collapse and lateral compression have disrupted most of the plates. Many outer rim plates have been eroded away, and the oral region plates are centrally abraded. The ambulacral curvature pattern is discernible and the three-plate cyclic coverplate pattern is preserved in the proximal part of ambulacrum IV. The quaternary coverplates are not present in this young adult. The four primary orals, hydropore oral and some of the secondary orals are outlined in text fig. 44D.

U.M.M.P. 35390. Topotype of Krama devonicum, illustrated by Kesling (1960, pl. 10, fig. 7, as a juvenile Hemicystites devonicus). 2.8 mm axial by 2.5 mm transverse diameter.

Text fig. 44A, pl. 41, fig. 7-8.

This well-preserved topotype is a young juvenile. The theca has collapsed, but little plate disruption has occurred. All five ambulacra are distinct, but curvature has not yet been initiated. Each ambulacrum includes four or five sets of primary coverplates. Proximal secondary coverplates are present in ambulacra I, II and V, but have not yet appeared in ambulacra III and IV. The oral area is formed by the four primary orals, the right posterior hydropore oral, two anterior secondary orals, and four or five lateral secondaries on each side of the central primaries. Three plates form the hydropore protuberance: the right posterior primary oral, the hydropore oral and the single opposing oral-ambulacral series plate. Interambulacrals are few in number, each relatively large in proportion to thecal diameter. The partially disrupted anal structure includes approximately eight plates. The peripheral rim is formed by the proximal circlet of large plates

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and two or three poorly ordered distal circlets.

U.M.M.P. 21123. Topotype of Krama devonicum illustrated by Kesling (1960, pl. 10, fig. 6, as a juvenile Hemicystites devonicus). 4.4 mm axial by 4.6 mm transverse diameter.

Text fig. 44B, pl. 42, fig. 1-2.

Although nearly twice the size, this juvenile is about equal in development to the above specimen. Thecal collapse has shifted the oral-ambulacral series toward the right anterior edge of the rim. Apparently it moved as a unit and only the distal interambulacrals are disrupted. Ambulacra I, II and III show slight curvature. Each ambulacrum includes four to six primary coverplate sets and one to three proximal secondary coverplates. The plating of the oral area and hydropore structure is identical to that of specimen U.M.M.P. 35390. However, interambulacral plates are more numerous in this specimen than in the last. The anus includes eight plates, and the peripheral rim three or four circlets. The pointed tips of the anals are flexed upward and form a small conical mound in the center of the anal structure. Minute external plate pustulation is seen in enlarged photographs.

U.M.M.P. 57678. Topotype of Krama devonicum. G. C. McIntosh, collector (May, 1967). 6.8 mm axial by 6.7 mm transverse diameter.

Pl. 42, fig. 4.

In this partially disrupted specimen, the theca has collapsed and most of the left-half plates proximal to the rim are disrupted. The right side of the oral region, the hydropore structure, ambulacra

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IV and V, most of the anal structure, and the anterior half of the peripheral rim are well-preserved. All ambulacra curve, but the degree is less pronounced than in larger individuals. All three sets of cyclic coverplates have formed in the proximal parts of the ambulacra, but the tertiary plates are small and are restricted to the axial part of the ambulacra. A short distance from the oral region only the primary coverplates reach the adradial suture line externally, with the secondaries also restricted to the axial region. The anal structure appears to include fourteen plates, their pointed tips forming a small central protuberance. The rim is formed by four circlets of plates.

U.C.M.P. 36118. Topotype of Krama devonicum. Kopf Collection. 4.4 mm axial by 6 mm transverse diameter.

Pl. 42, fig. 5-6.

Large sections of the anterior and posterior parts of the theca are missing. The complete specimen appears to have been over 6 mm in diameter. Plates in the posterior third of the specimen are depressed below the level of the anterior elements. Ambulacral curvature is slight. Proximally, the coverplate series includes primary, secondary, and tertiary plates, but only the primaries reach the adradial suture line regularly. The distal halves of the ambulacra appear to include only primary coverplates. Ten triangular anals form the anal structure, their pointed tips raised to form a small, central, conical prominence.

U.M.M.P. 21203. Topotype of Krama devonicum illustrated by Kesling (1960, pl. 5, fig. 2, as Agelacrinites sp. B). 7.2 mm axial by 7.6 mm

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transverse diameter.

Text fig. 45A, pl. 42, fig. 7-8.

This small adult is partially disrupted. Some of the interambulacrals and rim plates have been lost and the plates of interambulacra 1, 2 and 5, the anal structure, and the distal parts of all the ambulacra are disrupted. However, the three-element coverplate cycles are well-preserved in the proximal parts of ambulacra III, IV and V. The specimen appears to include all typical adult features, with the exception of the quaternary coverplates and the perradial separation of the primary orals.

U.M.M.P. 57679. Topotype of Krama devonicum. G. C. McIntosh, collector (May, 1967). 7.8 mm axial by 8.5 mm transverse diameter.

Text fig. 45B, pl. 42, fig. 9-11.

This topotype has collapsed, disrupting many of the distal parts of the theca. However, the oral region, hydropore structure, proximal two-thirds of the ambulacra, interambulacrum 4, and a segment of the peripheral rim are well-preserved. Distal displacement of the two posterior primary orals has begun here, with concurrent proximal migration of lateral secondary orals. The coverplate sequence includes all three cyclic series elements, but the tertiary plates, and distally the secondaries, are confined to the axial part of the ambulacra. The anal structure apparently includes fourteen plates. Four circlets of rim plates are present.

U.M.M.P. 4796. Topotype of Krama devonicum illustrated by Kesling

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(1960, pl. 5, fig. 1, as Agelacrinites sp. B). 14.6 mm axial by 14.5 mm transverse diameter.

Text fig. 45C-D, pl. 43, fig. 1-3.

This specimen is a moderately large adult. The coverplates of ambulacra II and III, and the distal parts of I and IV are disrupted, as are most oral plates. Several sections of the distal rim circlets are missing. However, the three-element cyclic series of coverplates is well-preserved in parts of ambulacra I and IV, and most of V (text fig. 45D). Quaternary coverplates have still not begun to develop. Lateral displacement of adjacent interambulacrals has exposed the grooved, adradial ends of most of the ambulacral coverplates and the grooved basal edges of the anals. The upper surfaces of two floorplates are exposed in ambulacrum III where the coverplates have been lost. Secondary orals may separate the anterior and posterior primary orals, although disruption of this area partially obscures the oral plate relationships. Approximately twelve triangular plates form the anal structure; each is centrally elevated to form a conical mound. The rim includes five plate circlets. Minute surficial plate pustulation is apparent in the enlarged photographs (pl. 43, fig. 3).

U.M.M.P. 57677. Three specimens of Krama devonicum resting on a convex brachiopod valve previously encrusted with bryozoa. Arkona Shale, about 25 feet below the contact with the Hungry Hollow Formation, Hamilton Group, Erian Series, Middle Devonian. Lot no. 8, northwest bank of Ausable River, 3 miles north-northeast of Arkona, Middlesex County, Ontario.

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U.M.M.P. 57677-A. Largest of three. 13.5 mm axial by 12.6 mm transverse diameter.

Text fig. 45E, pl. 43, fig. 4-5.

The specimen is a moderately large adult. The theca has collapsed but the plates are well-preserved except for the partially disrupted oral area and a small missing segment of the left thecal margin. This individual is essentially equal in stage of development to the last. In this specimen the distal parts of ambulacra I and IV are well-preserved and demonstrate the mode of coverplate addition. The distal tips include only primary coverplates, six to eight on each side of the perradial line. Secondary plates are developed in the next sector, inserted alternately along the perradial line, adjacent to the distal edge of each primary. Tertiary plates first appear after four (ambulacrum I) to six (ambulacrum II) secondary sets are present. Thus, the zone of tertiary plate insertion is separated from the distal tip of the ambulacrum by approximately twelve sets of primary coverplates. The anal structure appears to include fifteen plates in this specimen.

U.M.M.P. 57677-B. 8 mm axial by 8.6 mm transverse diameter.

This individual is a small adult. The theca is poorly preserved except for the three-plate cyclic sets of ambulacral coverplates in II, IV and V. The grooved adradial ends of the coverplates are exposed in the distal part of ambulacrum V.

U.S.N.M. S-3478. Large adult Krama devonicum (Bassler). The holotype

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of Agelacrinites southworthi Bassler (1936, p. 16, pl. 4, fig. 12) and illustrated by Kesling (1960, pl. 5, fig. 3). Arkona Shale, 20 to 30 feet below the Encrinal Limestone (Hungry Hollow Formation) Hamilton Group, Erian Series, Middle Devonian. Marsh's Mills, Arkona, Ontario. 17.5 mm axial by 17.8 mm transverse diameter.

Text fig. 42, 44C, pl. 43, fig. 6-11.

The largest known specimen of Krama devonicum, this individual is the only representative in which the final, quaternary set of ambulacral coverplates has developed. The specimen is well-preserved. Only partial thecal collapse has occurred, which caused slight disruption of the interambulacrals. The medial part of ambulacrum I is missing, along with the adjacent plates of interambulacra 1 and 5. The anal structure is also disrupted. The remainder of the oral and ambulacral plates appear essentially undisturbed except for the right posterior primary oral and adjacent hydropore oral plates. These elements have slipped toward the left posterior margin of the theca, and thus the left margin of the right posterior primary oral has slipped beneath the right edge of the left posterior primary oral. This movement has opened a small gap along the anterior margins of both the hydropore oral and right posterior primary oral plate. The broken end of ambulacrum I reveals an oblique cross-section of both the coverplates and a floorplate (insert, text fig. 42). Quaternary ambulacral coverplates are present in the proximal one-half to two-thirds of all the ambulacra. Distal to the quaternary plates, the three-plate cyclic series of coverplates is like that of smaller adults. Distally, first

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the tertiary, and then the secondary coverplates are lost, the distal tips formed by four or five sets of primary plates. In the well-preserved oral region, the anterior and posterior primary orals are separated by three, intervening secondary orals. Some of the lateral secondary orals are quite large and form multiple perradial points, perhaps suggesting they were formed by the fusion of two or more adjacent secondary orals.

U.S.N.M. 94643. Juvenile Krama devonicum illustrated by Kesling (1960, pl. 5, fig. 4, as a young Agelacrinites southworthi). Labeled "Widder" at Thedford, Ontario. "G. A. Cooper is uncertain about the history of this edrioasteroid [probably collected by Mr. Southworth] but states that the matrix resembles the Arkona Shale instead of the younger Middle Devonian Widder formation" (Kesling, 1960, p. 151). 5 mm axial by 5.2 mm transverse diameter.

Pl. 42, fig. 3.

This well-preserved small specimen has collapsed, but plate disruption is confined to slight separation of a few of the proximal elements. Surficial abrasion has smoothed many of the plates, particularly in the hydropore region. The specimen is similar to the other two described juveniles, U.M.M.P. 35390 and U.M.M.P. 21123. The oral area includes four abutting primary orals, one right posterior hydropore oral, two anterior secondary orals and four or five lateral secondary orals on each side of the central primaries. The hydropore structure is formed by the right posterior primary oral, the hydropore oral, and the one oral-ambulacral series plate which opposes the

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junction between the hydropore oral and right posterior primary. The adjacent plate margins appear to have been elevated to form a small hydropore protuberance, but abrasion has obscured its original height. The anal structure includes nine or ten plates, and the rim has four circlets of plates.

Discussion of previous investigation:

Bassler (1936, p. 14) described Hemicystites devonicus as a small edrioasteroid with: rather large interambulacrals and orals; exceptionally short, straight, rapidly tapering ambulacra with broad oral extremities, only four or five coverplates per row; and other thecal features as in Hemicystites [i.e., three primary and no secondary orals, coverplates in a single alternating biseries, interambulacrals squamose and imbricating]. He illustrated only the holotype. In contrast with Bassler's description, a plate-tracing of that specimen, text fig. 44D, shows: the oral region has many plates and an adjacent semi-integrated hydropore structure; and, the ambulacra are curved, with coverplates forming a three-plate cyclic series.

In the same paper, Bassler (1936, p. 16) described Agelacrinites southworthi [= Krama devonicum (Bassler)], based on one specimen, U.S.N.M. S-3478. Bassler characterized the species as like Agelacrinites hamiltonensis but with large, squamose and smooth interambulacrals, and ambulacra shorter but similar to A. hamiltonensis [i.e., curved, I-III contrasolar, IV-V solar, and, apparently following Hall's description, with a single, alternating biseries of coverplates]. As seen in text fig. 42, a plate-tracing of that specimen, Bassler apparently over-

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looked the complex plating of the oral-hydropore area and the intricate mixture of cyclic and biserial ambulacral coverplates.

Kesling (1960) described the hydropore structures of Hemicystites devonicus, Agelacrinites southworthi, and a species referred to as Agelacrinites sp. B. All seven specimens included by Kesling in these three species are here recognized as Krama devonicum (Bassler). The hydropore of Hemicystites devonicus was described from three specimens, including the partially disrupted holotype which is a young adult, and two juvenile topotypes (U.M.M.P. 21123 and U.M.M.P. 35390). Kesling included the hydropore oral and one to three opposing plates of the oral-ambulacral series in the structure, but apparently excluded the right posterior primary oral, included here. No mention was made of the elevation of the hydropore plates into a small protuberance, although it is pronounced in both juveniles. As interpreted here, only three plates actually contact the hydropore opening in these two young Krama devonicum specimens: the hydropore oral, the right posterior primary oral, and the one plate of the oral-ambulacral series directly opposite the junction between them.

Kesling's interpretation of the oral plates and hydropore structure of Agelacrinites southworthi, based on the holotype and one small specimen which he assigned to that species, differs significantly from that presented here. He described the right posterior primary oral as sub-triangular, abutting the left posterior primary along a prominent straight suture line, and elevated to form a "vaulted structure". As seen in pl. 43, fig. 10 , the right posterior primary has

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apparently slipped under the left primary, and thus Kesling's "vaulting" is preservational. "The right plate [here the hydropore oral], subtriangular and transversely elongate, has its right anterior border indented parallel to the convex end of the adjacent ambulacral [V] plate. The hydropore seems to be between the indentation in the right posterior peristomial plate [the hydropore oral] and the adjacent part of ambulacrum V", (Kesling, 1960, p. 151). As seen in pl. , fig. both the right posterior primary oral and adjacent hydropore oral are distally displaced which leaves a gap between them and the opposing ambulacrals that obscures the hydropore location. The hydropore structure is here thought to lie between the elevated proximal, or "left", anterior edge of the hydropore oral, the adjacent elevated right anterior edge of the right posterior primary oral, and the elevated adradial margin of the oral-ambulacral series plate opposite the junction between these two (text fig. 42, pl. 43, fig. 10-11). Prior to preservational plate slippage, the elevated margins of these three plates appear to have formed a small protuberance with the hydropore opening along the summit, as described here for other specimens of Krama devonicum as well. The following one or two ambulacral cover-plates distal to the elongate plate of the oral-ambulacral series may have been slightly elevated also which suggests the opening continued distally between these elements and the opposing anterior edge of the hydropore oral.

Kesling's other specimen of Agelacrinites southworthi (U.S.N.M. 94643, pl. 42, fig. 3) has a relatively small hydropore oral which

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lies adjacent to the right posterior edge of the right posterior primary oral. The hydropore opening is formed by these two plates and the adradial end of the elongate, oral-ambulacral series plate which opposes their junction. The adjacent corners of the two orals and the adradial margin of the opposing plate appear to have been elevated to form a protuberance with the opening at the summit, but erosion has partially leveled the area. Kesling, overlooking or disregarding the smaller hydropore oral, recognized only two posterior orals. He suggested the right plate was the"homologue" of the combined right posterior oral and hydropore oral plates of the adult (U.S.N.M. S-3478). He thought the opening was along the edge of this plate, apparently referring to the perradial edge, where a small preservational gap separates it from the anterior primary orals. The junction between the two posterior primary orals is slightly elevated. This is interpreted here as preservational tilting of the plates, whereas Kesling identified this as a "vaulted structure" like the one he described in specimen U.S.N.M. S-3478. Kesling's location of the hydropore in the juvenile U.S.N.M. 94643 lies "slightly ahead" of the suture line between the two posterior primary orals, whereas his placement of the opening in the adult U.S.N.M. S-3478 is posterior to or "behind" this suture line. Thus, he suggested the opening migrated distally during ontogeny. Relative to the oral pole, the hydropore does shift somewhat distally during growth due to the increase in size and number of the secondary orals. However, the same three plates, the hydropore oral, the right posterior primary oral, and the opposing oral-ambulacral series plate

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always surround the opening. It is possible, however, that the opening may actually lengthen distally somewhat during growth, and extend farther along the anterior edge of the hydropore oral in large adults to include the next one or two ambulacral series plates as well.

Two additional specimens of Krama devonicum (U.M.M.P. 4796: text fig. 45C-D, pl. 43, fig. 1-3; and U.M.M.P. 21203: text fig. 45A, pl. 42, fig. 7-8) were included in Kesling's hydropore study under the label Agelacrinites sp. B. As seen in the text figures, the disrupted oral area and hydropore region are difficult to interpret in both, although apparently they are consistent with the structure found in better preserved specimens of Krama devonicum (text fig. 42, 45B). In both, the two posterior orals and the right posterior hydropore oral plate are tentatively recognized. In the smaller (U.M.M.P. 21203), the anterior and posterior primary orals apparently were perradially in contact, whereas in the larger (U.M.M.P. 4796) lateral secondary orals had probably migrated between the primaries, as in specimen U.S.N.M. S-3478. Kesling's reconstruction of Agelacrinites sp. B deviates from the description presented here in: (1) the oral plating, in which the two anterior primary orals are not distinct but a large central anterior oral is shown meeting the proximal coverplates of both sides of ambulacrum III; (2) the elongate shapes of the posterior oral plates; (3) the indication of a posterior oral ridge formed by the supposedly upturned contiguous edges of the two posterior orals; (4) the hydropore structure, shown as formed by only the right anterior edge of the hydropore oral and one large, opposing plate of the oral-ambulacral

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series [thereby deleting the right edge of the right posterior primary oral which actually extends laterally to meet the opposing oral-ambulacral series plate]; and (5) the inclusion of a border of extremely narrow, elongate plates which flank the ambulacra and surround the anal structure [which actually represent the exposed, grooved, adradial faces of the coverplates and anals]. In spite of the somewhat fragmentary condition of both specimens, Kesling accurately portrays the complex three-element cyclic pattern of the ambulacral coverplates, including the distal absence of the tertiary and secondary plates. However, both sets are shown ending at approximately the same point. Kesling considered Agelacrinites sp. B as closely allied to Agelacrinites southworthi and separated the two on the supposed presence of the narrow bordering plates of the ambulacra [i.e., the exposed adradial edges of the coverplates] and the wider ambulacra of A. sp. B. The later difference results from the differing sizes of the specimens, the interambulacra increasing in width more rapidly than the ambulacra during growth.

Other references to specimens of Krama devonicum include: a reillustration of the holotype and summary of Bassler's original description by Shimer and Shrock (1944); mention of the squamose interambulacrals of Agelacrinites southworthi by Ehlers and Kesling (1958); and a reillustration of Kesling's 1960 reconstruction of Agelacrinites sp. B by Regnéll (1966) included with his summary of Kesling's hydropore structure study.

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Discussion:

The twelve described specimens of Krama devonicum (Bassler) represent a moderately complete growth series which includes three juveniles (2.5 to 5 mm diameter) and nine adults, ranging from small to large individuals (6 to 17.8 mm in diameter). Earliest ontogenetic stages are unknown. In the smallest juvenile (2.5 mm diameter), all major structural units of the theca are distinct. The oral-hydropore area, anal structure and rim are proportionately large, whereas the ambulacral-interambulacral sector of the theca is relatively small, compared to adults. As the ambulacra lengthen and interambulacra increase in area, the oral-hydropore area, anal area and rim become proportionately smaller, although still increasing in absolute size. Interambulacra increase in width relatively faster than the ambulacra widen, so that proportionately, the ambulacra decrease in width during growth.

The oral region, when first observed, includes: four very large primary orals, two anterior and two posterior, perradially in contact; one small right posterior hydropore oral; and ten to twelve secondary orals, two anterior and four or five laterals on each side of the central primaries. During growth the primaries decrease somewhat in relative size, whereas the hydropore oral increases greatly. Secondary orals increase slowly in total number, and some increase in size relative to the primaries. The exact number of secondaries is difficult to determine because the lateral secondaries reflect the ambulacral coverplate pattern which obscures the break between the lateral orals and proximal ambulacral coverplates. Apparently large adults include

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a minimum of fifteen secondaries versus the ten to twelve of the youngest known juveniles. During the continuing growth of adults, apparently when the theca reaches 8 to 10 mm in diameter, lateral secondary orals, which originally flank the posterior primaries, migrate anteriorly and proximally as the posterior orals migrate posteriorly. When migration is complete, two or three secondary orals lie between the perradial edges of the anterior and posterior primaries.

In the youngest known specimen the posterior side of the hydropore protuberance is formed by the contiguous corners of the hydropore oral and right posterior primary oral. The anterior side includes only the adradial margin of an elongate plate of the oral-ambulacral series which lies opposite the junction between the two posterior plates. During growth, the hydropore structure appears to shift slightly in a distal direction along the posterior side of ambulacrum V due to the increasing size and number of oral plates. Although the same three plates continue to participate in the structure throughout adult development, possibly one or two proximal posterior coverplates of ambulacrum V, distal to the original single anterior plate, may also flank the anterior side of the opening and thereby lengthen it distally.

The ambulacra are short, broad and straight in the youngest known juvenile. Four to six sets of primary coverplates are included in each ambulacrum of specimens 2.5 to 4 mm in diameter. Secondary coverplates are first inserted near the oral area after four to six primary sets are present, apparently when the theca is approximately 2 mm in diameter. Ambulacral curvature appears to be initiated as the

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theca approaches 4 mm in diameter. Tertiary coverplates first appear after four to six secondary sets have formed, the theca somewhere between 4 and 6 mm in diameter. These three sets of cyclic coverplates continue to develop and ambulacral curvature continues to increase without change until very late in adult development. When the theca is approximately 15 mm in diameter, quaternary plate pair development is initiated. Addition of quaternaries apparently proceeds rapidly and fills the entire proximal half to two-thirds of each ambulacrum by the time the theca reaches 17.8 mm in diameter.

The interambulacrals are proportionately large even in the juveniles. Numbers increase continuously throughout growth by the proliferation of new plates along the ambulacral adradial suture lines.

The anal structure grows from eight plates when first observed in the juveniles, to approximately sixteen in large adults. Development of new plates seems to be erratic, without apparent correlation to thecal diameter. Peripheral rim development proceeds by the addition of new circlets, from three in the youngest known specimens to five or six in adults.

In contrast to the moderately complete understanding of external thecal features of Krama devonicum, most inner surface features are unknown. Ambulacral floorplates are seen only in two specimens which expose partial views of a few plates. The oral frame, stone-canal passageway and inner surface features of other thecal structures have not been observed.

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Krama devonicum is the only edrioasteroid in which secondary oral plate migration during adult development results in the perradial separation of anterior and posterior primary orals. The addition of a new set of coverplates late in adult development is also uncommon. Moreover, the biserial pair arrangement of these late coverplates contrasts to the cyclic arrangement of the earlier coverplate series and produces a unique mixture of coverplate patterns.

Range and occurrence: Traverse-Hamilton Groups, Erian Series, Middle Devonian of eastern Michigan and western Ontario.

Postibulla Bell, gen. nov.

Type species: Agelacrinus legrandensis Miller and Gurley, 1894

Diagnosis:

Agelacrinitidae with: domal theca; oral area with many plates, primaries not differentiated; large, elevated, posterior oral protuberance present; hydropore protuberance semi-integrated, including three or more plates; ambulacra narrow, curved, I-III contrasolar, IV-V solar, coverplates steeply inclined to thecal surface, two or three sets forming irregular cycles; interambulacrals squamose, imbricate; anal structure highly elevated and conical, with three circlets of plates.

Description:

Postibulla includes small to moderate sized, domal edrioasteroids. The oral area is formed by many plates. Most of the oral plates are variable in size and shape, and their arrangement appears to be

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variable intra-specifically. Lateral and anterior orals reflect the pattern of the ambulacral coverplate series, and thus appear to grade into the coverplate series. Therefore, separation of distal orals from proximal ambulacrals and determination of the total oral plate number is impossible. Differentiation of primary orals is not apparent in adults. Along the posterior margin of the region four or more plates are flexed upward to form a prominent, protruding, axially elongate ridge, the posterior oral protuberance. Equal in elevation to the center of the oral rise, the protuberance extends distally into the proximal part of interambulacrum 5. It lies along the axial midline of the theca and the central suture line of the protuberance, in effect, extends the anterior oral midline directly across the posterior half of the oral region. The structure is distinct even in juveniles. Two of the posterior plates which form the protuberance are consistently larger than any other orals.

The hydropore structure lies in the right posterior part of the oral region between the posterior oral protuberance and the proximal posterior edge of ambulacrum V. Plate margins surrounding the opening are flexed upward to form a conical or ovate prominence which rises above the distal part of the central oral rise. The hydropore, varying from a sub-triangular gap to an elongate arcuate slit, lies at the summit of the prominence. In younger individuals the hydropore structure involves three or four plates, whereas four or five are commonly included in larger adults.

The ambulacra are curved, I-III contrasolarly, IV-V solarly.

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Each is a narrow, highly elevated ridge which rises above the adjacent interambulacra. Perhaps accentuated during collapse, the ambulacral elevation results primarily from the high angle inclination of the coverplates to the adjacent thecal surface.

The ambulacral coverplate pattern appears to be an irregular cyclic series of two sets of plates. A third series may be included in large adults. Large primary coverplates laterally overlap alternate secondary coverplates and form a two-plate cyclic sequence along each side of the ambulacrum. In mature parts of the ambulacra, the secondary coverplates are commonly almost as large as primaries (externally), and thus mask their identity. Each coverplate forms a discrete perradial point. Cycles on opposite sides of the perradial line alternate, offset by half a cycle width.

The broad interambulacra are covered by numerous, squamose, imbricate plates.

The anal structure is a highly elevated, conical mound formed by three somewhat irregular circlets of plates. The triangular to subtriangular anals are steeply inclined to the surrounding thecal surface, like the ambulacral coverplates. Outer circlet plates overlap the more or less regularly alternating plates of the second circlet along beveled margins. The pointed tips of a third innermost circlet of anals are commonly exposed in the center of the anal structure. Lateral slippage of the highly inclined anals commonly obscures the original plate arrangement.

The peripheral rim includes five or six circlets. The large

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plates of the proximal circlet regularly alternate as proximal and distal sub-circlet members in some species, but not in others.

Thecal plates have smooth exteriors in all known species.

Discussion:

Postibulla embraces several species previously placed in Agelacrinites. Species of both genera have domal thecae, numerous oral plates, ambulacra curved I-III contrasolarly, IV-V solarly, cyclic ambulacral coverplates, and imbricating interambulacrals. But in contrast with Agelacrinites, species of Postibulla: (1) develop a unique, prominent, posterior oral protuberance; (2) have steeply inclined coverplates which form externally narrow and high ambulacra; and, (3) have three circlets of anal plates which form a highly elevated conical protuberance. These three features also separate Postibulla species from Krama devonicum which exhibits similar thecal form and ambulacral disposition. Moreover, the mixture of cyclic sets and biserial pairs of coverplates is unique to Krama devonicum.

Limited irregularities in the ambulacral coverplate pattern are not uncommon throughout the Agelacrinitidae, but in Postibulla they seem to dominate. Perhaps much of this apparent irregularity is preservational. The steep inclination of the coverplates may dictate instability during thecal collapse, and thereby facilitate random lateral slippage of individual plates, disrupting the original order. Moreover, the relatively large size of the secondary coverplates obscures recognition of coverplate patterns. The anal structure of Postibulla more resembles the loose, irregular periproct found in the

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Lebetodiscina than the valvular structure of other Agelacrinitidae. Like the ambulacral coverplates, the steeply inclined anals may be unstable during collapse and promote preservational disruption of the structure. In the least disrupted specimens, the outer circlet plates appear to overlap the alternate second circlet ones along tightly fitting, beveled margins, and thus form a well-ordered valvular structure. However, the inclusion of a third, inner circlet of plates commands the recognition of this structure as unique among the Agelacrinitidae.

Etymology: Postibulla is compounded from the Latin post, behind, and bulla, knob or swelling, referring to the posterior oral protuberance.

Range and occurrence: Erian Series, Middle Devonian to Kinderhookian Series, Mississippian of Michigan, Alberta and Iowa.

Postibulla legrandensis (Miller and Gurley), 1894

Text fig. 46; plate 44.

1894 Agelacrinus legrandensis Miller, S. A. and Gurley, F. E., Illinois St. Mus. Bull. 5: 15-16, pl. 3, fig. 13-14.

1897 Agelacrinus legrandensis Miller and Gurley, Miller, S. A., Second Appendix to North American Geology and Palaeontology, Cincinnati: 733.

1901 Agelacrinites legrandensis Miller and Gurley, Clarke, J. M., New York St. Mus., Bull. 49 (2): 182-198.

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1936 Agelacrinites legrandensis Miller and Gurley, Bassler, R. S., Smithsonian Misc. Coll. 95 (6): pl. 4, fig. 16.

1943 Agelacrinites legrandensis Miller and Gurley, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 196.

Diagnosis:

A Postibulla with: small domal theca; posterior part of posterior oral protuberance formed by three plates; hydropore structure formed by four or more plates, including two posterior ones.

Description:

The domal theca of adult Postibulla legrandensis (Miller and Gurley) averages 8 or 9 mm in diameter, the largest recorded specimen approximately 10 mm (pl. 44).

The oral area includes many plates equal to or smaller than the proximal ambulacral coverplates (text fig. 46B). Oral plate arrangement appears variable. Plate shapes are similar to the ambulacral coverplates and thus the boundary between the distal orals and proximal ambulacrals is indistinct.

The posterior oral protuberance is formed by three or more average-sized orals and two large plates (text fig. 46B, pl. 44, fig. 11). All are flexed upward to form the high, nearly vertical sides of the elongate prominence. Opposing protuberance plates meet centrally to form a nearly straight central suture line along the summit. It extends from the transverse oral midline directly across the posterior half of the oral area, along the axial midline of the theca. Commonly, abrasion

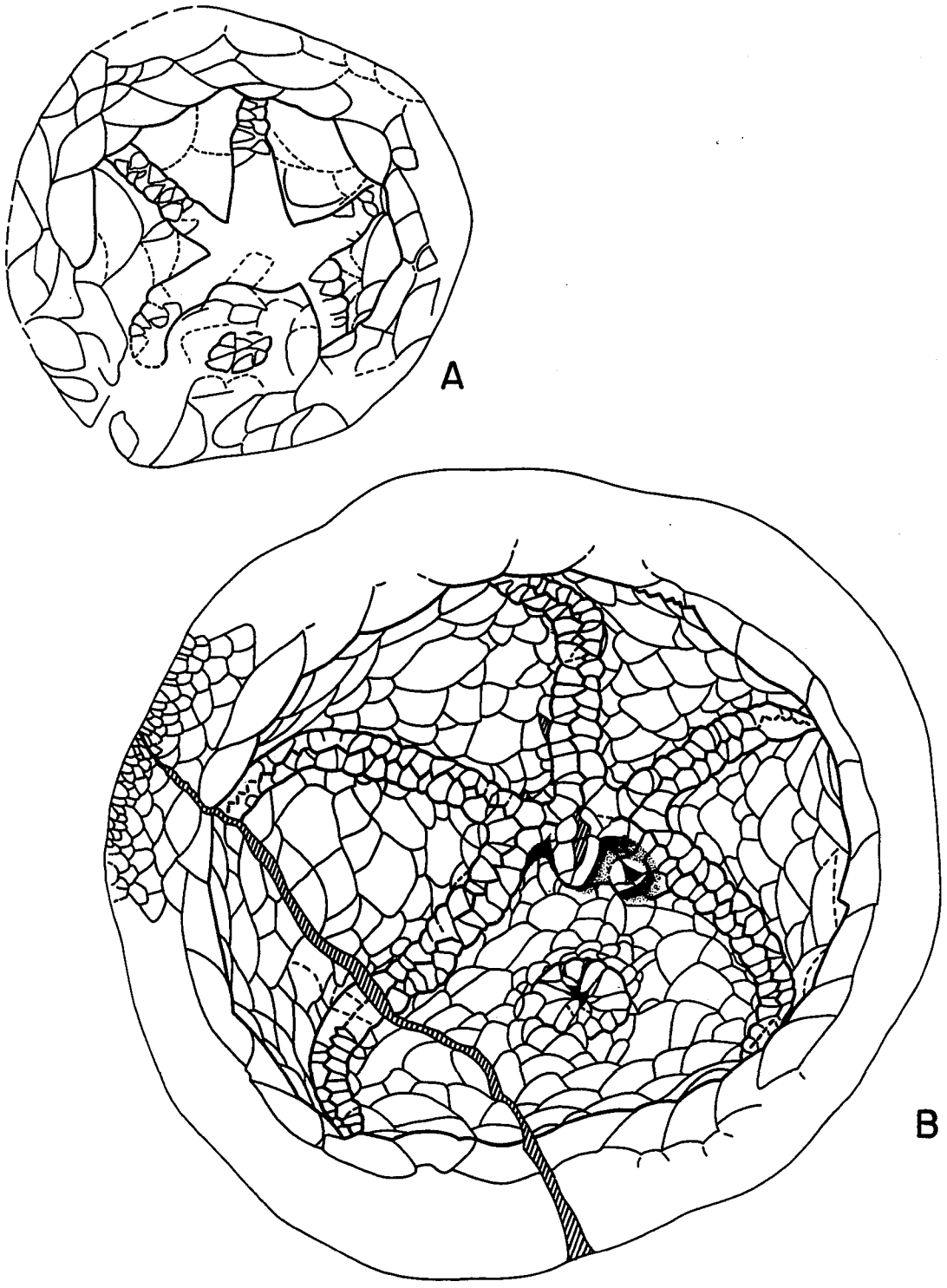
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Text Figure 46 Postibulla legrandensis (Miller and Gurley), 1894

A. Lectoparatype, juvenile, C.F.M.-U.C. 6495-B, (X20), pl. 44 fig. 2.

B. G.S.C. 25143, (X20), pl. 44, fig. 9.

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Text Figure 46

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has leveled off the summit of the protuberance which leaves a flattened, nearly horizontal summit with a central gap that separates opposing plates.

The arrangement of the protuberance plates varies among observed specimens. Commonly, a single very large oral forms the posterior two-thirds of the right side (text fig. 46B). Two opposing plates form the left posterior side, a proximal large plate and a small distal one. The anterior third of the protuberance is formed by two or four opposing, average-sized orals. Their posterior margins lie adjacent to the large posterior plates, their anterior edges form the center of the transverse oral midline.

The hydropore structure is a small, conical prominence which rises from the right posterior part of the oral region; it is formed by four or five plates (text fig. 46B, pl. 44, fig. 10). The posterior half includes two, moderate-sized plates; apparently one hydropore oral and one modified interambulacral. The left side of the elevation is formed by the pointed right margin of the large, right plate of the posterior oral protuberance. The right anterior side includes one large, adradially expanded plate of the oral-ambulacral series, and perhaps one (? or more) plate of the oral-ambulacral series which flanks the distal side of the expanded plate. The contiguous margins of the hydropore plates are upturned and form the conical elevation. (Thus, the large, right posterior plate of the oral protuberance is saddle-shaped; it is elevated along both its elongate left and pointed right side, and the center of the plate forms a deep trough which separates

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the oral protuberance from the hydropore mound.) The hydropore was apparently an arcuate slit lying at the summit of the hydropore structure. Commonly abrasion has enlarged the opening into a sub-triangular gap between the opposing plates.

The curvature of the narrow ambulacra is variable. It may be even throughout from near the proximal ends; or it may be uneven, with long, nearly straight proximal sectors followed by pronounced curvature as the ambulacra approach the peripheral rim. The distal tip of each ambulacrum remains widely separated from the other ambulacra, even in large adults.

The ambulacral coverplate series appears to be cyclic, and includes two or three sets of coverplates. Large primary coverplates are sub-triangular to sub-rectangular in outline, perradially angular. Somewhat smaller secondary plates flank the primaries. Commonly almost as large as the primaries, the secondary plates are sub-triangular to sub-rectangular. Each may form a discrete perradial point, or its perradial margin may slope toward the adjacent primary, the two plates uniting to form a single, broad perradial point. Commonly two plates, nearly identical in size and shape, lie between successive primary coverplates. Both have the appearance of secondaries. In other cases only one secondary separates successive primaries. Thus, two types of cycles are present, one with two plates, one primary and one secondary, the other with three plates, one primary and two secondaries. The occurrence of these two types of cycles appears to be random along the ambulacra.

In mature sectors of the ambulacra, occasionally, small rhombic

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coverplates are also present. Lacking any apparent regularity, these plates may represent atypical secondaries or perhaps a new, third, set of coverplates, inserted late in ambulacral development. The degree to which lateral plate-slippage during thecal collapse has contributed to the apparent irregularity of the coverplate sequence is uncertain, but appears to be great.

The ambulacral floorplates have been observed in one disrupted specimen tentatively identified as a Postibulla legrandensis (pl. 44, fig. 5). The floorplates are uniserial and abut along vertical sutures. Each is rectangular in outline, elongate normal to the ambulacral axis. The upper surface of the trough-shaped plate is concave downward, except for the nearly horizontal lateral margins which slope slightly toward the ambulacral axis. These margins apparently form a broad surface of articulation upon which rested the bases of the overlying coverplates. The convex-inward, inner sides of the floorplates appear to bear small lateral nodes which extend into the thecal cavity, at least one on each side of each plate.

The numerous, squamose, imbricate interambulacrals are relatively small in proportion to thecal diameter.

The anal structure is formed by at least twenty plates in large adults. Outer circlet elements appear to alternate regularly with second circlet plates, whereas plates of the third or innermost circlet are fewer in number than each of the two outer circlets and they appear to occur sporadically.

The peripheral rim is formed by five or six circlets of plates.

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The large plates of the proximal circlet occasionally alternate as proximal and distal sub-circlet members. More commonly, one lateral margin of each plate lies proximal to the adjacent rim plate, whereas the other is distal to its neighbor. Thus, subdivision of the proximal circlet plates into two sub-circlets is incomplete.

Specimens:

C.F.M.-U.C. 6495. Type series of Postibulla legrandensis (Miller and Gurley) (1894, p. 15-16, pl. 3, fig. 13-14, as Agelacrinus legrandensis). LeGrand beds, Hampton Formation, Easley Group, Kinderhookian Series, Mississippian. LeGrand, Marshall County, Iowa.

C.F.M.-U.C. 6495-A. Lectotype of Postibulla legrandensis. 7.3 mm axial by 7.2 mm transverse diameter.

Pl. 44, fig. 1.

The lectotype is poorly preserved. The theca has collapsed, and many of the plates are disrupted; the right half of the theca has been severely crushed. A small fracture separates the posterior edge of the theca from the remainder. Plate structure can be interpreted in parts of ambulacra I and II, interambulacra 1, 2, and part of 5, and in the left anterior half of the rim. Only the original outline of ambulacra III-V is visible. The specimen does have five ambulacra, although V is particularly difficult to locate, thereby explaining Miller's and Gurley's original description of only four ambulacra. The anal structure is not visible.

C.F.M.-U.C. 6495-B. Lectoparatype of Postibulla legrandensis. 3.8 mm

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axial by 3.6 mm transverse diameter.

Text fig. 46A, pl. 44, fig. 2.

The second specimen of the type series is a juvenile and lies near the lectotype on the same small piece of limestone. The theca has collapsed, causing partial disruption of many plates. All five ambulacra are visible; II and III are nearly straight whereas I, IV and V show slight curvature. Each ambulacrum includes approximately eight to ten sets of coverplates. Most of the coverplates are primaries, but a few secondaries may be included proximally. The orals, anals and interambulacrals are disrupted. The anterior half of the rim is well-preserved and is composed of three or four circlets of plates.

G.S.C. 25143 (old 9011, S-3881). Topotype. LeGrand Beds, Hampton Formation, Easley Group, Kinderhookian Series, Mississippian. LeGrand, Marshall County, Iowa. 5.9 mm axial by 6.4 mm transverse diameter.

Text fig. 46B, pl. 44, fig. 9-10.

This topotype is a moderate-sized adult. The theca has collapsed, but only the distal interambulacrals and tips of ambulacra III-V have been extensively disrupted and have slipped beneath the proximal edge of the rim plates. A crack extends through the left posterior part of the theca. The plates of the oral-ambulacral series and the anals appear to be partially disturbed due to random lateral slippage. The upper parts of the plates of the posterior oral protuberance have been abraded, leveling the summit of that structure. Plate boundaries in the anterior half of the hydropore structure are obscure. One of the older numbers assigned to this specimen (S-3881) corresponds to the United

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States National Museum number for other topotypes, and suggests that the specimen was originally included in that collection.

U.S.N.M. S-3881. Topotypes of Postibulla legrandensis (Miller and Gurley), five slabs, eight specimens. LeGrand beds, Hampton Formation, Easley Group, Kinderhookian Series, Mississippian. LeGrand, Marshall County, Iowa.

U.S.N.M. S-3881-A-1. Illustrated Specimen of P. legrandensis by Bassler (1936, pl. 4, fig. 13, as Agelacrinites legrandensis). 9.5 mm axial by 8.6 mm transverse diameter.

Pl. 44, fig. 14.

The theca of this large adult has collapsed and the distal interambulacrals and ambulacrals have slipped under the proximal rim plates. Orals and many ambulacrals have been abraded, partially obscuring the plate boundaries. The abraded posterior oral protuberance appears to include five plates, three posterior and two anterior. The hydropore opening is unusually large due to erosion of the upper ends of the four or five plates which form the tubercle. The ambulacral coverplate pattern is visible in many sectors of the ambulacra. The anal structure is partially disrupted.

U.S.N.M. S-3881-A-2. Topotype. 8.5 mm axial by 8.3 mm transverse diameter.

Pl. 44, fig. 4.

This small adult is on the slab with A-1. Collapse has accentuated the interambulacral plate imbrication. The posterior part of the

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theca is deeply depressed, and the left posterior sector of the rim is missing. The posterior oral protuberance is well-preserved, except for abrasion of the upper surface. The cyclic sequence of ambulacral coverplates is preserved in ambulacra III-V. The anal structure shows the outer circlet plates overlapping alternately the second circlet ones. The tips of four or five anals of the inner third circlet are exposed centrally.

U.S.N.M. S-3881-B-1. Topotype. 8.1 mm axial by 8.1 mm transverse diameter.

Pl. 44, fig. 6-7.

This topotype is another moderately well-preserved adult with a collapsed theca. Interambulacra 2 and 4 are disrupted distally. The posterior oral protuberance and the hydropore structure are well-preserved except for erosion of the upper ends of the plates which centrally separate the opposing plates. The ambulacral coverplate sequence is preserved, although distally the opposing coverplates are separated perradially.

U.S.N.M. S-3881-B-2. Topotype. 5.6 mm axial by 5.8 mm transverse diameter.

Pl. 44, fig. 3.

This small adult has collapsed, but only distal interambulacrals and ambulacrals are disrupted. Ambulacral curvature is less pronounced than in larger adults. Erosion has leveled the tops of the hydropore and posterior oral protuberances.

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U.S.N.M. S-3881-C-1. Topotype. 7.1 mm axial by 7.9 mm transverse diameter.

Pl. 44, fig. 8.

This collapsed adult is missing the right anterior sector of the rim. Abrasion has leveled the upper ends of the oral and ambulacral series plates. The anals are in part laterally separated due to thecal collapse.

U.S.N.M. S-3881-E. Topotype. 9 mm greatest diameter by a perpendicular of 6 mm.

Pl. 44, fig. 5.

This fragment of a large adult is tentatively identified as Postibulla legrandensis. Only the right half of the theca is preserved, and here etching and abrasion have removed all oral-ambulacral series covering plates. The upper sides of the floorplates are partially exposed. Secondary calcite fills the ambulacral trough and preserves the impressions of the inner surfaces of the coverplates.

N.Y.S.M. 12777. Topotype. LeGrand beds, Hampton Formation, Easley Group, Kinderhookian Series, Mississippian. LeGrand, Marshall County, Iowa. 10.2 mm axial by 10.9 mm transverse diameter.

Pl. 44, fig. 11-13.

This large adult is collapsed, partially disrupting the interambulacral plates. Plates of the oral-ambulacral and anal series are well-preserved, although the upper surfaces of the plates of the posterior oral protuberance have been eroded and form a large central gap

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between opposing plates. The hydropore tubercle is well-preserved and apparently little abraded.

Discussion:

Miller and Gurley (1894) differentiated Agelacrinus legrandensis from other Agelacrinites by the small thecal size and occurrence of only four ambulacra, three contrasolar, one solar. Based on two specimens (C.F.M.-U.C. 6495-A-B), one adult and one juvenile, they also recorded the domal thecal shape; the squamose, imbricate interambulacral and rim plates; the narrow, ridge-like ambulacra; the numerous small orals; and, the disrupted anal structure. The larger specimen (C.F.M.-U.C. 6495-A), here designated the lectotype, is poorly preserved, but five ambulacra are present, I-III contrasolar, IV-V solar (pl. 44, fig. 1). The five ambulacra are more easily observed in the smaller lectoparatype (pl. 44, fig. 2). The taxonomically important ambulacral coverplate pattern is preserved in part of ambulacrum III of the lectotype. The equally important structure of the oral region, the posterior oral protuberance, the hydropore and anal area are not recognizable in the type specimens.

Bassler (1936, p. 16, pl. 4, fig. 13) illustrated a moderately well-preserved topotype of Agelacrinites legrandensis. He noted the presence of five ambulacra as "normal", but made no mention of the posterior oral protuberance, hydropore structure, ambulacral coverplate pattern, or the anal area construction.

In Postibulla legrandensis (Miller and Gurley) the external thecal plating appears to vary intra-specifically in several taxonomically

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important structures. Oral plates are small, numerous, and lack apparent regularity. The posterior oral protuberance includes seven or nine plates with the anterior third being formed either by two or four plates. Plates participating in the hydropore structure vary from four to five, or (?) six. The ambulacral coverplate sequence includes primary and secondary coverplates variably arranged in two- or three-plate cycles. Distribution of the differing cycles appears to be random along the ambulacra. In large adults a third set of coverplates may occur sporadically in the proximal parts of the ambulacra. Preservational distortion of these steeply inclined plates of the oral-ambulacral series can account only for part of this variation. Thus, plating variability appears to be basic to the species. Other distinguishing features include the small adult thecal size and the proportionately small size of the numerous interambulacrals.

Range and occurrence: Hampton Formation, Easley Group, Kinderhookian Series, Mississippian of LeGrand, Iowa.

Postibulla keslingi Bell, sp. nov.

Text fig. 47; plate 45, fig. 1-10.

1960 Agelacrinites sp. A. Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 148-149, pl. 4, fig. 1-5.

Diagnosis:

A Postibulla with: moderate sized theca; posterior part of posterior oral protuberance formed by two large plates; hydropore structure

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formed by four plates, including one large posterior plate.

Description:

The domal theca of Postibulla keslingi Bell is of moderate size; recorded adult diameters reach 13 mm.

The oral area in all adult specimens examined is partially disrupted, but it appears to be formed by numerous small plates (text fig. 47A-C). These small orals reflect the pattern of the ambulacral cover-plate series in size and shape. Thus, the orals appear to grade into the ambulacrals without apparent break. Only the four to six plates which form the posterior oral protuberance are constant in position. The contiguous parts of these plates are upturned and form the highly elevated, elongate protuberance. The posterior two-thirds of the protuberance is formed by two large opposing plates, one right, the other left. They meet centrally along a straight to moderately sinuous suture line which approximates the position of the axial midline of the theca. The anterior third of the structure is commonly formed by two small opposing plates. Their posterior margins abut the two large posterior protuberance plates, and their anterior margins form the central section of the transverse oral midline (text fig. 47A-B). Occasionally an additional pair of small plates may lie between the anterior and posterior pairs and raise the total to six protuberance plates (text fig. 47C, pl. 45, fig.). The suture line between opposing plates of the protuberance extends to the central oral pole where it intersects the transverse oral midline and aligns with the posterior end of the anterior oral midline.

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Text Figure 47 Postibulla keslingi Bell, sp. nov.

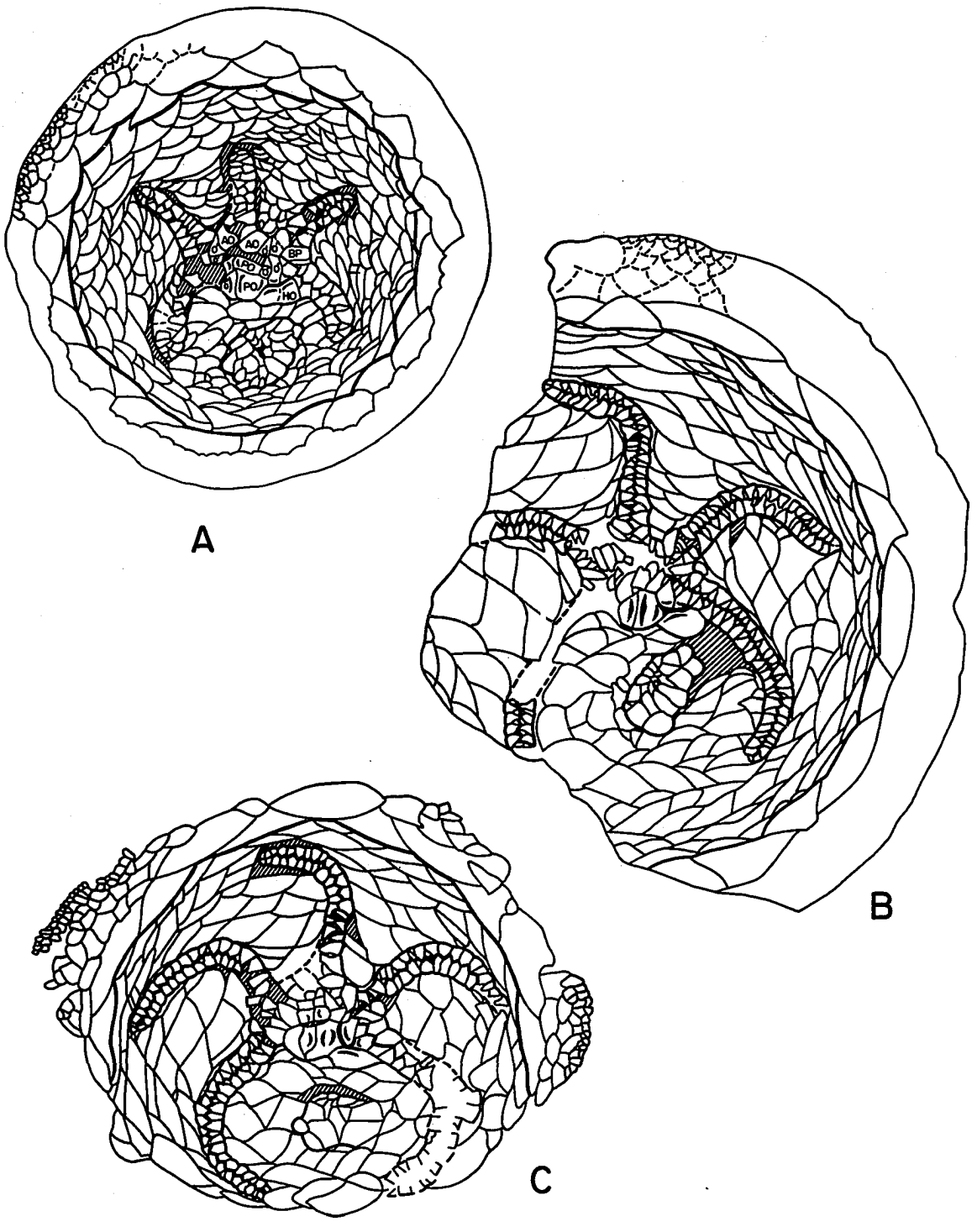
A. Paratype (3), U.M.M.P. 35379, (X15), pl. 45, fig. 3.

AO. anterior primary oral plate; BP. lateral bifurcation plate; HO. hydropore oral plate; o'. secondary oral plate; PO. posterior primary oral plate.

B. Holotype, U.M.M.P. 35387, (X9), pl. 45, fig. 1.

C. Paratype (1), U.S.N.M. 111225, (X10), pl. 45, fig. 7.

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Text Figure 47

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In juveniles, the oral area is formed by fewer plates than in adults. Moreover, two large anterior primary orals are distinct (text fig. 47A, pl. 45, fig. 9). The posterior oral protuberance is proportionately larger in younger specimens where it is formed by only one pair of small anterior plates and two very large posterior plates.

Four or more plates form the hydropore tubercle in the right posterior part of the oral region (text fig. 47A-C). A single large hydropore oral forms the entire posterior side of the structure. The right side of the large, right plate of the posterior oral protuberance forms the left side of the hydropore tubercle. The adradial ends of two moderate-sized plates of the right posterior oral-ambulacral series complete the structure; they lie opposite the anterior edge of the large hydropore oral plate. The contiguous margins of the hydropore plates are upturned and form the oblong elevated tubercle with the slit-like hydropore opening along the summit. Probably due to preservational disruption, the orientation of the tubercle (and the opening) appears to vary, either paralleling the axis of ambulacrum V, or being nearly normal to that axis (text fig. 47A-C). As in P. legrandensis, both the right and left margins of the large, right plate of the posterior oral protuberance are upturned, the plate participating in both the hydropore structure and the posterior oral protuberance. Thus, the central part of this saddle-shaped plate forms a deep trough separating the two structures.

Ambulacral curvature is even, and is initiated near the oral region. Distally the ambulacra remain separated from one another by

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many interambulacrals, and commonly they are also separated from the proximal margin of the peripheral rim by an unusually large number of interambulacrals, even in larger adults.

The ambulacral coverplates form an irregular series of alternating large and small plates (text fig. 47A-C, pl. 45, fig. 1-10). They are apparently grouped into irregular, alternating cycles, but no consistent pattern of plate disposition is apparent. On each side of the perradial line, in the proximal parts of the ambulacra, large sub-triangular plates alternate with smaller, sub-rhombic plates. The latter do not reach the adradial suture line externally. One moderate sized sub-rhombic plate lies adjacent to each large sub-triangular plate. A third smaller rhombic plate is occasionally also present. Thus, proximally, there appear to be large primary coverplates and smaller secondary coverplates which form both two- and three-plate cycles, but without apparent regularity.

The small rhombic and moderate-sized sub-rhombic plates (? secondaries) occur only in the proximal one-half to two-thirds of the ambulacra. Distally, all plates are large and sub-triangular and broadly intersect the adradial suture line. However, two slightly different sizes of plates are sometimes present, with larger plates more or less regularly alternating with smaller ones. These perhaps represent two different sets of coverplates. If so, the slightly smaller plates may be a secondary set inserted between the larger primaries very near the distal tips of the ambulacra. Proximally all these coverplates are nearly equal in size and thus not readily distinguished as different

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sets. If two sets are present distally, the small rhombic and sub-rhombic proximal coverplates represent a tertiary set, and each coverplate cycle would contain: one primary followed by one or two tertiaries, followed by one secondary, and then, one or two more tertiaries, thereby totaling four to six plates per cycle. All coverplates form discrete perradial points and thus obscure any cyclic pattern in the course of the perradial line.

The large sub-triangular coverplates laterally overlap adjacent smaller ones. Apparently all but the small rhombic plates extend under adjacent larger plates and internally meet the adradial suture. Adjacent interambulacrals overlap the adradial ends of the large ambulacral coverplates. The coverplates appear to end near the lateral margins of the underlying ambulacral floorplates, without forming large intrathecal extensions. Intra-ambulacral extensions, developed on the ambulacral tunnel surfaces of the coverplates, are suspected but have not been clearly observed.

The ambulacral floorplates are uniserial and trough-shaped, and have been observed only in cross-section in one broken specimen (pl. 45, fig. 1).

The numerous interambulacral plates are squamose and imbricate. Rather small in younger specimens, they appear to increase rapidly in size during ontogeny and become moderate-sized in proportion to thecal diameter in larger adults.

The anal structure, disrupted in all known specimens, appears to include three circlets of plates. The outer circlet ones are large,

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very wide-based, triangular plates, and overlap and apparently alternate with the second circlet anals. Only the tips of a few plates which form a third, innermost irregular circlet have been observed (pl. 45, fig. 1, 5).

Five or six circlets comprise the peripheral rim. The large plates of the proximal circlet alternate in position to form proximal and distal sub-circlets.

External plate surfaces are smooth except for the minute pustulation seen in enlarged photographs, related to the microstructure of the plates.

Specimens:

U.M.M.P. 35387, U.S.N.M. 111225, U.M.M.P. 35377, U.M.M.P. 35379, U.M.M.P. 35389. Upper part of the Ferron Point Formation, Traverse Group, Erian Series, Middle Devonian. Abandoned shale pit of the Alpena Portland Cement Company, S.E. $\frac{1}{4}$, Sec. 18, T. 32N., R. 9E., Alpena County, about 7 miles north of Alpena, Michigan.

U.M.M.P. 35387. Holotype of Postibulla keslingi Bell, sp. nov., illustrated by Kesling (1960, pl. 4, fig. 1-2, as Agelacrinites sp. A). 12.2 mm axial by 9.5 mm transverse diameter.

Text fig. 47B, pl. 45, fig. 1-2.

The left side of the holotype is missing, including part of ambulacra I, II, interambulacra 1, 2, 5, and the entire left half of the peripheral rim. The missing thecal area has left a faint trace of its outline on the underlying brachiopod (Kesling, 1960, pl. 4, fig. 1-

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2). Collapse has disrupted distal interambulacrals, some oral plates and most of the proximal coverplates of ambulacrum I. However, the remaining ambulacra preserve the coverplate pattern. The posterior oral protuberance and the hydropore structure are well-preserved. The anal structure is deeply depressed, the plates partially disrupted. In spite of preservational distortion, the specimen records the taxonomically critical structures. It is the largest known representative of the species.

U.S.N.M. 111225. Paratype (1) of Postibulla keslingi. 7.6 mm axial by 8.9 mm transverse diameter.

Text fig. 47C, pl. 45, fig. 7-9.

The theca of this adult has collapsed, accentuating the imbrication of the interambulacrals and causing some lateral shifting of the oral and ambulacral plates. Most of the plates of the distal circlets of the peripheral rim have been lost, along with some of the posterior, proximal plates of the rim. Surficial etching may have accentuated the minute pustulation which reflects the microstructure of the plates. This minute surficial irregularity includes elongate grooves and channels on many of the ambulacral coverplates. The anal structure and surrounding interambulacrals are much depressed, thus disrupting the anal plate arrangement. The ambulacral coverplate pattern, the arrangement of the plates of the posterior oral protuberance, and the hydropore structure are moderately well-preserved.

U.M.M.P. 35377. Paratype (2) of Postibulla keslingi Bell, illustrated

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by Kesling (1960, pl. 4, fig. 3, as Agelacrinites sp. A). 8.8 mm axial by 9.2 mm transverse diameter.

Pl. 45, fig. 5-6.

The specimen is nearly complete, but much of the collapsed theca is covered by a thin layer of tenacious matrix which obscures plate boundaries. Only the larger ambulacral coverplates are distinct. The posterior oral protuberance appears to include six plates, two large posterior ones and two pairs of small anterior plates. However, the right anterior part of the protuberance is crushed. Thus, the supposed left central plate could be the anterior end of the broken large left posterior plate. Ambulacral curvature is less pronounced in this adult; I and III are nearly straight. The anal plate arrangement is obscure.

U.M.M.P. 35379. Paratype (3) of Postibulla keslingi Bell, illustrated by Kesling (1960, pl. 4, fig. 4, as Agelacrinites sp. A). 5.3 mm axial by 5.1 mm transverse diameter.

Text fig. 47A, pl. 45, fig. 3-4.

The specimen is a young adult or an advanced juvenile. Thecal collapse has accentuated interambulacral plate imbrication, and caused some oral-ambulacral plate disruption, particularly in the hydropore structure and left side of the oral region. Two large anterior primary orals form the center of the anterior side of the oral region. The posterior oral protuberance includes only four plates; the two posterior plates are proportionately larger than in a large adult. The hydropore oral plate also appears exceptionally large.

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The ambulacra are short, and extend only halfway to the proximal margin of the rim. Two sets of coverplates form an irregular alternating two-plate cyclic series, primary plates only slightly larger than the secondaries. The anal plates apparently form three circlets.

In contrast to most other young edrioasteroids, the interambulacral areas are relatively large in proportion to thecal diameter. They extend distal to the ambulacra and form a broad zone which separates the ambulacra from the rim. The peripheral rim is formed by approximately four circlets of plates.

U.M.M.P. 35389. Topotype of Postibulla keslingi Bell, illustrated by Kesling (1960, pl. 4, fig. 5, as Agelacrinites sp. A). 2.9 mm axial by 2.7 mm transverse diameter.

Pl. 45, fig. 10.

This individual is a poorly preserved juvenile, probably belonging to Postibulla keslingi. Collapsed, partially obscured by matrix, and somewhat abraded, many thecal plates are difficult to identify. The peripheral rim dominates. The oral area is proportionately larger than in adults. The posterior oral protuberance may include only the two large posterior plates. The ambulacra are short and straight, only four to six pairs of coverplates per ambulacrum. Interambulacral plates are indistinct, and the anal structure is disrupted. Only three or four circlets of plates form the peripheral rim.

Discussion:

Specimens here designated Postibulla keslingi Bell, sp. nov. were

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first described by Kesling (1960) as Agelacrinites sp. A. Primarily interested in hydropore structures, Kesling concentrated on that feature. He included both juveniles (U.M.M.P. 35389, 35379) and an adult (U.M.M.P. 35387) and suggested that the hydropore structure migrated distally along the posterior side of ambulacrum V during ontogeny, involving different plates in adults than in juveniles. Admittedly additional plates are present between the hydropore tubercle and the center of the oral region in larger adults than in juveniles, but these may be new elements rather than modified hydropore plates. Moreover, distinguishing between distal orals and proximal coverplates is difficult in this species due to the similarity in shapes and sizes of the two series. Thus, identification of homologous ambulacral coverplates in individuals of differing size is tentative. Added to the partially disrupted condition of all of the available specimens, these factors make Kesling's proposed hydropore migration highly speculative.

Kesling (1960, p. 149) further supposed that the posterior oral protuberance, or "vaulted structure" as first described by him, "may have operated like a hinge, with the larger plate [right posterior saddle-shaped element] lifting to admit water through the hydropore along its right edge." The posterior oral protuberance includes not only the two large posterior plates described by Kesling, but also one or two pairs of anterior plates which extend the structure to the center of the oral region. Thus it appears to be functionally integrated with the central oral region, or underlying oral frame and oral lumen. Movement of the large right posterior plate seems improbable, although not

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impossible. The function of the posterior oral protuberance remains uncertain.

Postibulla keslingi resembles P. legrandensis but differs in the plate structure of the posterior oral protuberance, the hydropore structure and the ambulacral coverplate pattern. Perhaps also significant is the relatively wide separation of the ambulacra from the proximal margin of the peripheral rim, the great width of the bases of the outermost anal plates, and the increase in proportional size of the interambulacrals in larger adults.

Etymology: The species is named in honor of R. V. Kesling for his outstanding work with edrioasteroids.

Range and occurrence: Ferron Point Formation, Traverse Group, Erian Series, Middle Devonian of the Alpena area, Michigan.

(?) Postibulla jasperensis (Harker), 1953

Text fig. 48; plate 45, fig. 12-14.

1953 Agelacrinites jasperensis Harker, P., Jour. Paleont. 27 (2): 288-289, text fig. 1.

Description:

Postibulla jasperensis (Harker) is represented by one small specimen, 7.6 mm in diameter, probably a young adult or an advanced juvenile in which plate development is incomplete.

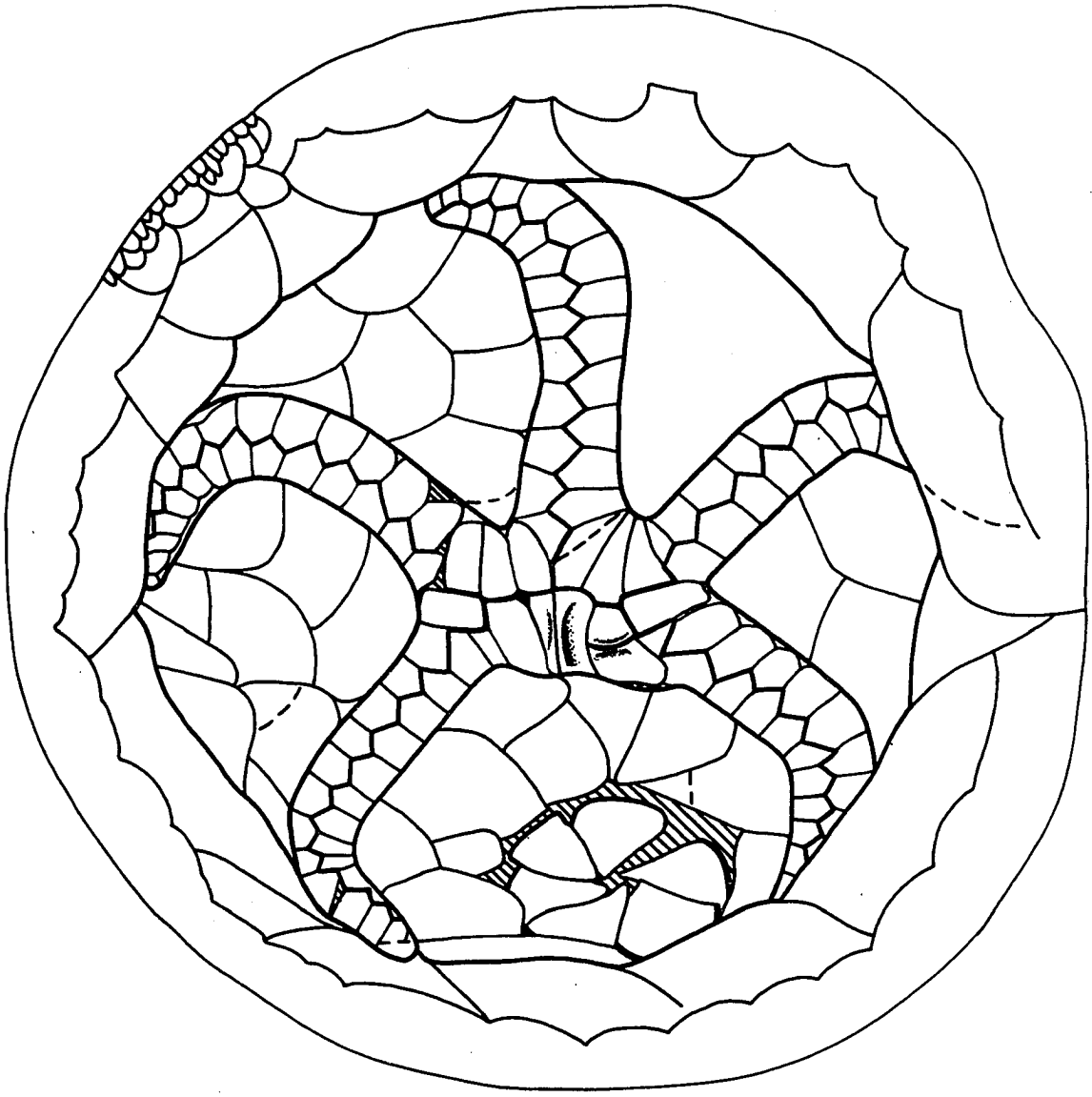
The oral region includes four elongate plates which meet centrally; these are perhaps primary orals (text fig. 48, pl. 45, fig. 14);

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Text Figure 48 Postibulla jasperensis (Harker), 1953.

Holotype, G.S.C. 10051, (X20), pl. 45, fig. 13.

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Text Figure 48

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three or four additional elongate orals flank the central four on each side, along the transverse oral midline. A single small anterior oral lies along the anterior oral midline, distal to the two large anterior central orals. The two central posterior orals meet along upturned lateral margins and form a small posterior oral protuberance. Its straight central suture line parallels the axial midline of the theca and aligns with the posterior end of the anterior oral midline.

The arcuate, slit-like hydropore is believed to lie along the junction between two plates in the right posterior corner of the oral region. The posterior plate (? hydropore oral) lies between the distal right margin of the right posterior central oral and the adradial ends of the proximal two posterior coverplates of ambulacrum V. The opposing anterior hydropore plate is a moderate-sized, posterior, right lateral secondary oral. The margins of the two plates bounding the supposed hydropore are thickened and form a low, transversely elongate mound.

The ambulacra are moderate in width, and curve I-III contrasolar, IV-V solar. The coverplates appear to form a single alternating biseries of sub-rectangular plates with wide, pointed, perradial ends. Each coverplate is inclined to the adjacent interambulacral surface and angles vary from 30 to 45 degrees. Thus, the coverplates form high ambulacral ridges.

The interambulacral plates are very large in proportion to thecal diameter and few in number. They are subpolygonal to squamose, and abut or slightly overlap adjacent interambulacrals.

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The large anal structure is formed by six or more large, triangular plates, grouped into a (?) single circlet.

The relatively wide peripheral rim includes approximately four circlets of plates. Plates of the proximal circlet are very large and alternate, more or less regularly, as proximal and distal sub-circlet members.

External plate surfaces are smooth.

Specimen:

G.S.C. 10051. Holotype of Postibulla jasperensis (Harker) (1953, p. 288-289, fig. 1, as Agelacrinites jasperensis). Upper Banff Formation, 135 feet below the Banff-Rundle contact, Kinderhookian Series, Mississippian. Morro Creek, just south of Jasper-Edmonton highway, about 10 miles north of Jasper, Alberta. 7.6 mm axial by 7.6 mm transverse diameter.

Text fig. 48, pl. 45, fig. 12-14.

The specimen has collapsed; the distal interambulacrals and ambulacrals have slipped under the proximal plates of the rim. The oral and anal plates are partially disrupted, but other thecal elements appear to be little disturbed. A few rim plates are missing from the right side of the theca.

Discussion:

The relative sizes of the thecal structures in the holotype of Postibulla jasperensis suggest the specimen is not fully developed. The oral area, anal structure and peripheral rim are proportionately larger than is common in adult edrioasteroids. However, the combined

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ambulacral-interambulacral areas dominate the theca, and ambulacral curvature has developed which suggests the specimen is at least a young adult.

The presence of a small posterior oral protuberance seems to link the specimen to species of Postibulla. However, the single biseries of ambulacral coverplates and the relatively few oral and hydropore structure plates contrast with both the generic and even the familial and subordinal taxobases. Thus, the specimen could represent a young individual of a very large species in which additional sets of coverplates and more oral-hydropore series plates would have appeared later in ontogeny. More likely is the interpretation that this form represents a specialized genus in which all but the primary ambulacral coverplates have been suppressed along with a corresponding reduction in number of orals and hydropore plates.

Range and occurrence: Banff Formation, Kinderhookian Series, Mississippian, of the Jasper area, Alberta.

(?) Postibulla alpenensis (Bassler), 1936

Plate 45, fig. 11.

1936 Lepidodiscus alpenensis Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 20, pl. 3, fig. 3.

1943 Lepidodiscus alpenensis Bassler, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 206.

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Specimen:

U.M.M.P. 17296. Holotype of Postibulla alpenensis (Bassler) (1936, p. 20, pl. 3, fig. 3, as Lepidodiscus alpenensis). Presque Island division of the Long Lake Formation (Ferron Point Formation), Traverse Group, Erian Series, Middle Devonian. Quarry of the Alpena Portland Cement Company, Alpena, Michigan. 8.6 mm axial by 6.8 mm transverse diameter.

Description and discussion:

The species is based on a single, poorly-preserved specimen (pl. 45, fig. 11). The domal theca has collapsed and is laterally compressed. Most of the oral, hydropore and ambulacral coverplates are jumbled, along with many interambulacrals and the anal plates. The five narrow ambulacra are curved, I-III contrasolar, IV-V solar. The distal part of a prominent posterior oral protuberance is preserved and is formed by two very large opposing plates, similar to those of Postibulla keslingi. The squamose imbricating plates of interambulacrum 2 are less disrupted than others. The anal plates are centrally separated and form a gaping opening in the center of the anal area. Approximately four or five circlets of plates form the peripheral rim.

Bassler (1936, p. 20) reported that the specimen "shows clearly four ambulacra curved to the left and the fifth, the right posterior, to the right, as well as the strongly imbricating plates of typical Lepidodiscus." The small thecal size was cited as diagnostic at the species level. However, ambulacrum IV, which is very poorly preserved, appears to curve solarly, not contrasolarly. Thus the ambulacral curva-

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ture and other interpretable thecal features, particularly the posterior oral protuberance, suggest this specimen belongs to Postibulla. Unfortunately, the critical ambulacral coverplate pattern, the hydropore structure and the oral area plating are too poorly preserved to allow definition of specific characters.

Discocystis Gregory, 1897

1842 [nonl Agelacrinites Vanuxem, L., Nat. Hist. of New York, pt. IV, Geology, 3: 158.

1858 Agelacrinus Vanuxem, Hall, J., Iowa Geol. Surv. Rept., 1855-1857, v. 1, pt. 2, Palaeontology: 696, pl. 25, fig. 18.

1883 Echinodiscus Worthen, A. H. and Miller, S. A., Geol. Surv. Illinois, v. 7, Geology and Palaeontology, sect. 2, Palaeontology of Illinois: 335.

1889 Echinodiscus Worthen and Miller, Miller, S. A. [partim], North American Geology and Palaeontology, Cincinnati: 241.

1897 (Feb.) Discocystis Gregory, J. W., Geol. Soc. London, Quart. Jour. 53: 131.

1897 (Oct.) Ageladiscus Miller, S. A. [partim], Second Appendix to North American Geology and Palaeontology, Cincinnati: 734.

1901 Discocystis Gregory, Clarke, J. M. [partim], New York St. Mus., Bull. 49 (2): 182-198.

1904 Discocystis Gregory, Klem, M. J. [partim], St. Louis Acad. Sci., Trans. 14: 73; Echinodiscus Worthen and Miller, idem, ibid.: 73.

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1935 Discocystis Gregory, Bassler, R. S. [partim], Smithsonian Misc. Coll. 93 (8): 8.

1936 Discocystis Gregory, Bassler, R. S. [partim], Smithsonian Misc. Coll. 95 (6): 21.

1938 Discocystis Gregory, Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 88.

1943 Discocystis Gregory, Bassler, R. S. and Moodey, M. W. [partim], Geol. Soc. America, Spec. Pap. 45: 200.

1944 Discocystis Gregory, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, pl. 49, fig. 19-20.

1958b Discocystis Gregory, Ehlers, G. M. and Kesling, R. V. [partim], Univ. Michigan, Contrib. Mus. Paleont. 14 (15): 271.

1966 Discocystis Gregory, Regnéll, G. [partim], in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U169, text fig. 113-3 (?), 128-3 (?).

Type species: Echinodiscus optatus Worthen and Miller, 1883 = Agelacrinus kaskaskiensis Hall, 1858.

Diagnosis:

Agelacrinitidae with: clavate theca; numerous oral plates; large hydropore protuberance separated from central oral rise; ambulacra long, narrow, curved, I-IV contrasolar, V solar, coverplates in three- or four-plate cyclic series; interambulacrals large, polygonal, tessellate; valvular anal structure with two circlets of plates.

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Description:

The genus Discocystis, as recognized here, is monotypic. Therefore, separation of generic and specific taxobases is uncertain. Features outlined in the above diagnosis are in part inferred to be of generic rank from taxobases established for related Agelacrinitidae genera.

Discussion of previous investigation:

The status of the name Discocystis is problematic. Clarke (1901) recorded most of the relevant information. Hall (1858) described and illustrated Agelacrinus kaskaskiensis based upon a single specimen from the Chester Group, Mississippian, Kaskaskia, Illinois. The holotype (pl. 46, fig. 1-7) preserves the upper side of the oral surface, including the oral region, hydropore structure, five ambulacra (I-IV contrasolar, V solar), cyclic ambulacral coverplates, and large, polygonal, tessellate interambulacrals. As noted by Meek and Worthen (1868), only five ambulacra are present, not six as described by Hall.

> "In 1883 Worthen and Miller introduced the generic term, Echinodiscus, with a single species, E. optatus, from the Chester limestone of Illinois. [The specimen illustrated is fragmentary, and exposes only part of the lower, peduncular zone, and one section of the ambitus of a clavate theca.] Of itself it serves to define nothing, affording no clue either to generic or specific structures. As establishing either species or genus it is practically worthless. Notwithstanding this fact, the definition given of both species and genus is full

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and clear, describing all the main features of the theca and ambulacra. One cannot fail of conviction, nor therein be far from the truth, that in the preparation of this account the authors were relying mainly on the original specimen of Agel. kaskaskiensis Hall, which belonged to the Worthen collection. That Ech. optatus W. and M. is not the same thing as A. kaskaskiensis has not been proven, and every indication favors the presumption that it is. Sidelight is thrown on this proposition by two facts, viz, that in the description of Echinodiscus and E. optatus, the remotest reference to A. kaskaskiensis is avoided, and also that in the edition of Miller's North American Geology and Paleontology (1889) next succeeding the date of Worthen and Miller's publication, A. kaskaskiensis is referred to Echinodiscus." (Clarke, 1901, p. 185-186).

Gregory (Feb. 1897) proposed Discocystis as a substitute term for Echinodiscus which had been used twice before for other echinoderms (Leske, 1778, and d'Orbigny, 1854). Miller (1897) also noted this circumstance, and proposed the name Ageladiscus, but his work did not appear until October, 1897 (Clarke, 1901, p. 187). Thus, Discocystis has priority.

Subsequent to, and in agreement with, Clarke's 1901 analysis, Discocystis optatus (Worthen and Miller) has been recognized as a junior synonym for Discocystis kaskaskiensis. The occurrence of the type specimens of these two taxa lends support to Clarke's thesis; both

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specimens are from Chester Group limestones of southern Illinois. However, the etched and abraded holotype of D. optatus exposes only part of the lower peduncular zone of the theca and one, extremely etched, ambulacral segment. The rather vague cyclic coverplate pattern appears to contain three plates like D. kaskaskiensis, but this is still uncertain (pl. 47, fig. 6-8). There now seems no compelling reason to consider it different from D. kaskaskiensis.

Previous accounts of Discocystis have been based upon specimens of D. kaskaskiensis, including the original diagnosis of Echinodiscus, and the type species is D. kaskaskiensis, of which D. optatus is a junior synonym.

The alternative approach would be to recognize D. optatus as a valid species, represented only by the fragmentary holotype. Thus, Discocystis would become a problematic genus represented only by its type species, D. optatus. This approach would require the proposal of yet another generic name for D. kaskaskiensis. Such proliferation of generic names, combined with restriction of Discocystis to an essentially meaningless species, would seem only to increase confusion.

Range and occurrence: Chester Group, Mississippian of southern Illinois.

Discocystis kaskaskiensis (Hall), 1858

Text fig. 49-50; plate 46, plate 47, fig. 1-8.

1858 Agelacrinus kaskaskiensis Hall, J., Iowa Geol. Surv. Rept., 1855-1857, v. 1, pt. 2, Palaeontology: 696, pl. 25, fig. 18.

1860 Agelacrinites kaskaskiensis Hall, Chapman, E. J., Canadian Jour.

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Industry, Sci. and Art (n.s.), 5: 360-365.

1868 Agelacrinites kaskaskiensis Hall, Meek, F. B. and Worthen, A. H., Philadelphia Acad. Nat. Sci., Proc. 5: 357.

1873 Agelacrinites kaskaskiensis Hall, Meek, F. B. and Worthen, A. H., Geol. Surv. Illinois, v. 5, Geology and Palaeontology, pt. 2, Palaeontology of Illinois: 514-515.

1876 Agelacrinus kaskaskiensis Hall, Quenstedt, F. A., Petrefaktenkunde Deutschlands, Tubingen, 4 (12): 708.

1879 Agelacrinites kaskaskiensis Hall, Sladen, W. P., Geol. Soc. London, Quart. Jour. 35: 748-750.

1883 Echinodiscus optatus Worthen, A. H. and Miller, S. A., Geol. Surv. Illinois, v. 7, Geology and Palaeontology, sect. 2, Palaeontology of Illinois: 336-337, pl. 31, fig. 9.

1889 Echinodiscus kaskaskiensis (Hall), Miller, S. A., North American Geology and Palaeontology, Cincinnati: 241.

1894 Echinodiscus kaskaskiensis (Hall), Keyes, C. R., Missouri Geol. Surv. 4 (1): 133, pl. 18, fig. 3.

1901 Discocystis kaskaskiensis (Hall), Clarke, J. M., New York St. Mus., Bull. 49 (2): 182-198, text fig. 1.

1904 Echinodiscus kaskaskiensis (Hall), Klem, M. J., St. Louis Acad. Sci., Trans. 14: 73.

1910 Agelacrinus (Discocystis) kaskaskiensis Hall, Grabau, A. W. and Shimer, H. W., North American Index Fossils, Invertebrates, New York, 2: 473.

1936 Discocystis kaskaskiensis (Hall), Bassler, R. S., Smithsonian

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Misc. Coll. 95 (6): 21-22, pl. 1, fig. 4, pl. 1, fig. 5 (?), pl. 3, fig. 4-5 (?), Inon 61, pl. 7, fig. 11 (?).

1938 Discocystis kaskaskiensis (Hall), Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 88.

1943 Discocystis kaskaskiensis (Hall), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 200-201.

1944 Discocystis kaskaskiensis (Hall), Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, (?) pl. 49, fig. 19-20.

1958b Discocystis kaskaskiensis (Hall), Ehlers, G. M. and Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 14 (15): 271.

1966 Discocystis kaskaskiensis (Hall), Regnéll, G., in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U169, text fig. 113-3 (?), 128-3 (?).

Diagnosis:

A Discocystis with: large, clavate theca; numerous small oral plates, primary orals undifferentiated; large hydropore protuberance formed by several plates including at least three, large, posterior plates.

Description:

The clavate theca of Discocystis kaskaskiensis is large, diameters of the gibbous upper oral surface reaching 50 mm.

The numerous oral plates, seen only in the crushed oral area of the holotype (text fig. 49A, pl. 46, fig. 3) are similar in size to the

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Text Figure 49 Discocystis kaskaskiensis (Hall), 1858

A-B. Holotype, I.S.M. 10037.

A. Oral area and adjacent structures, (X10), pl. 46, fig. 3. Plates in the left anterior oral area and proximal part of ambulacrum II, which have been depressed below the level of the surrounding elements, are marked by a dotted pattern.

B. Anal area and adjacent structures, (X10), pl. 49, fig. 7.

C. Reconstruction of a primary set ambulacral coverplate, oblique lateral view.

Text Figure 50 Discocystis kaskaskiensis (Hall), 1858

A. Segment of ambulacrum, U.S.N.M. S-3885, (X10), pl. 47, fig. 3. Proximal end of segment is to the left.

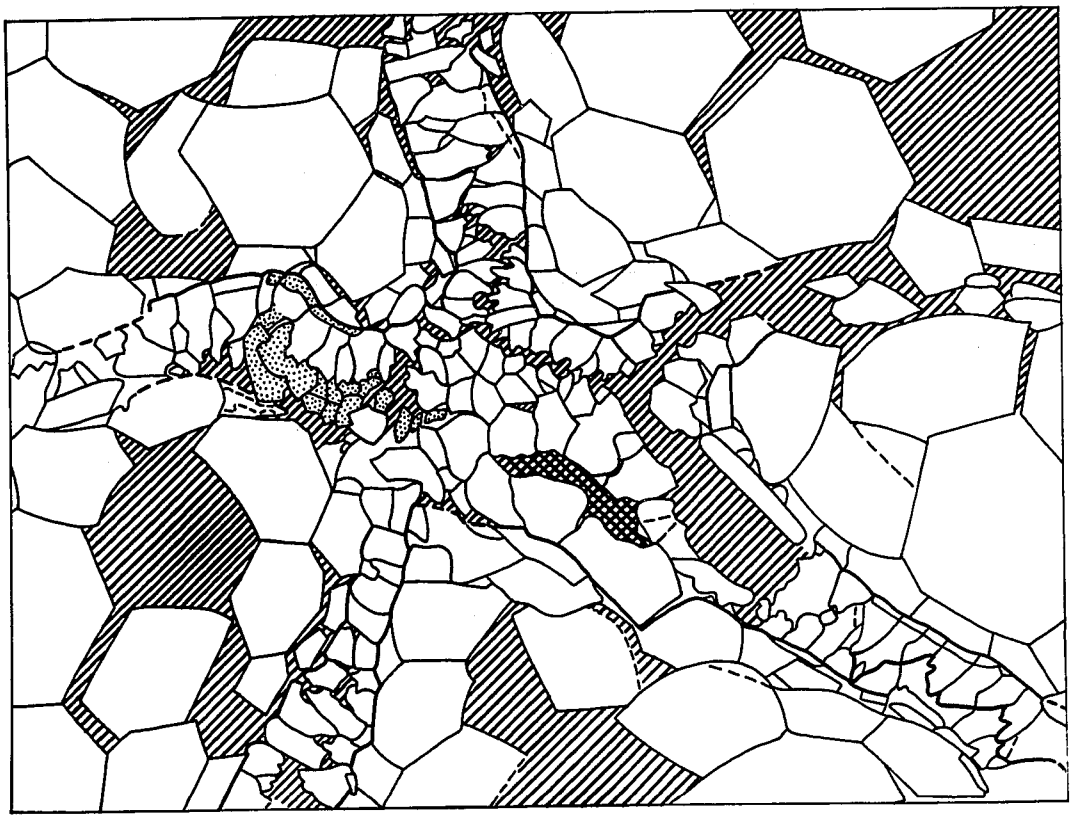
B-C. Holotype, I.S.M. 10037.

B. Segment of ambulacrum III, (X20), pl. 46, fig. 4. Proximal end of segment is to the left.

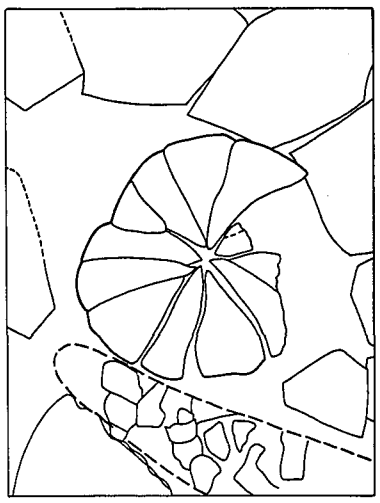
C. Segment of ambulacrum V, (X20), pl. 46, fig. 6. Proximal end of segment is to the left.

1. primary set ambulacral coverplate; 2. secondary set ambulacral coverplate; 3. tertiary set ambulacral coverplate; 4. ? quaternary set ambulacral coverplate.

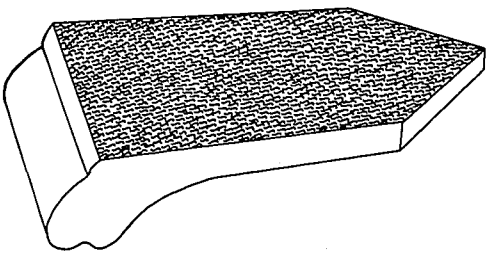
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A



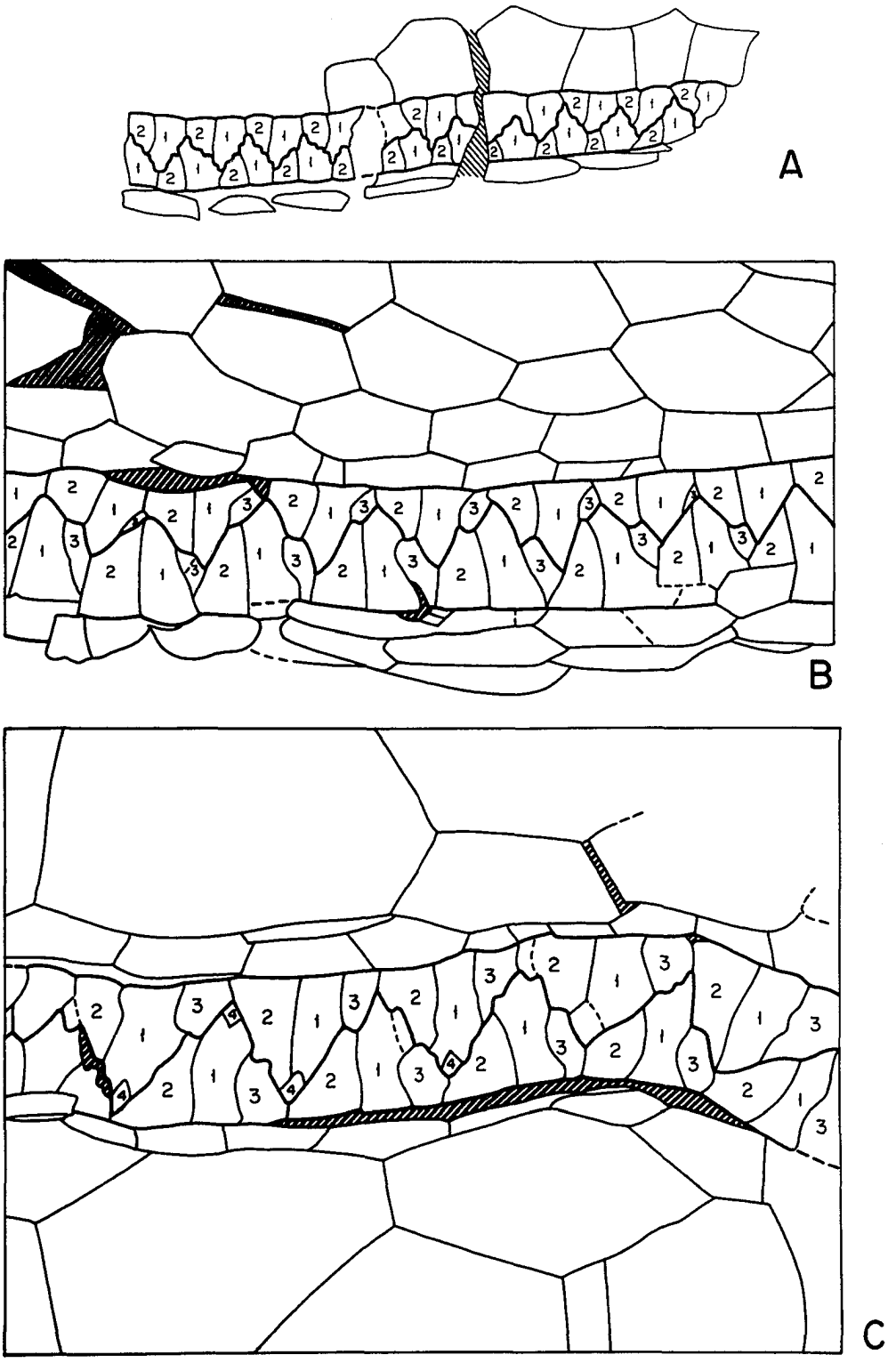
B



C

Text Figure 49

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Text Figure 50

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proximal ambulacral coverplates and appear to reflect the ambulacral coverplate pattern. Thus the oral series appears to grade distally into the proximal ambulacral series without apparent break and obscures the total number of orals present. The regularity of the oral plate arrangement has not been determined. Primary orals are not differentiated externally.

The hydropore structure lies distal to the central oral rise and extends from the axial midline of the theca postero-laterally along the proximal, posterior side of ambulacrum V (text fig. 49A). The structure has been observed only in the holotype where it is partially disrupted and the upper ends of the plates have been extensively crushed (pl. 46, fig. 3). Apparently the ten (or more) plates which form the structure extend upward and produce a highly elevated, large, elongate elevation. The elongate slit-like hydropore extends along the summit. The posterior side is formed by three or four large plates, apparently modified interambulacrals or multiple hydropore orals. The distal part of the anterior side of the structure is formed by the adradial ends of several proximal, posterior coverplates of ambulacrum V. The proximal anterior part appears to be formed by several orals, but these apparently do not extend perradially to the transverse oral midline. The proximal or left end of the prominence is separated from the central oral rise by a deep groove. The right end of the structure appears to merge with the proximal part of ambulacrum V, although a shallow but distinct trough separates the two equally elevated zones.

The ambulacra are long, narrow and curve, I-IV contrasolar, V

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solar (pl. 46, fig. 1-2). Curvature is variable, initiated near the proximal ends in some, whereas in others, long proximal sectors are straight. Distally the long ambulacra become concentric with the ambitus of the upper oral surface. Each extends along the distal edge of the adjacent ambulacrum, separated from it by only a few interambulacrals. The distal tip of ambulacrum V curves proximally, away from the ambitus, and extends into interambulacrum 5 where it ends near the left posterior side of the anal structure.

The ambulacral coverplate series is cyclic (text fig. 50A-C). Cycles on opposite sides of the perradial line alternate, offset by half a cycle length. The plates in each cycle form a single, wide perradial point, yielding a broadly undulating, zigzag, perradial line. Small points formed along the perradial edges of the cycle plates superimpose fine serrations on the broad, perradial undulations.

Along most of the length of the ambulacra each cycle includes three plates (text fig. 50B). Large primary plates are central. Each has a wide adradial base and an angular perradial tip which extends across the midline of the ambulacrum to form the center of the cycle point. Secondary set plates lie adjacent to the proximal side of the primaries and their perradial margins slope toward the adjacent, distal primary plate of the cycle. Smaller than the primaries along most of the length of the ambulacra, proximally these secondaries become nearly equal in size to the primaries. The tertiary coverplates flank the distal sides of the primaries and perradially slope proximally toward the adjacent primary plate of the cycle. The tertiaries are consist-

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ently smaller than the secondaries.

Proximally, small, rhombic "quaternary" plates may be added to the cycles (text fig. 50A). They are inserted at the tips of the broad perradial point of a cycle and lie either between the tips of the adjacent primary and secondary set plates, or are inserted into a small notch formed in the center of the perradial tip of the primaries. Observed in only one ambulacrum of the holotype, their occurrence appears to be erratic.

Primary coverplates are developed at the distal tip of each ambulacrum. The zone of insertion of the plates of the secondary set is separated from the ambulacrum tip by only two or three sets of primary plates. Each secondary is inserted along the proximal, perradial margin of a primary. The tertiary coverplates are inserted along the distal, perradial margins of the primaries and do not appear until numerous sets of primaries and secondaries have formed. Thus, the zone of tertiary plate insertion lies far from the distal tip of the ambulacra. Apparently it commonly lies in the most highly curved part where the ambulacra become concentric with the ambitus of the upper oral surface. The supposedly quaternary plates are formed only in the proximal parts of the ambulacra and developed late in adult ontogeny.

The adradial ends of the coverplates are overlapped by the adjacent interambulacrals. The upper adradial edge of each coverplate is depressed along the zone of overlap; a nearly vertical cliff separates the upper external plate surface from the rounded, sloping, adradial end. Text fig. 49C depicts an oblique view of a large cover-

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plate and shows the rounded margin, increased thickness, and slightly concave base of the adradial part of the plate.

The trough-shaped ambulacral floorplates are axially elongate and rectangular in plan view (pl. 46, fig. 8-9). Their upper sides are centrally concave downward and form a deep, central, axial trough. The lateral margins of this upper surface slope slightly toward the trough to form a narrow articulation zone upon which rest the bases of the overlying coverplates. The inwardly convex lower sides of the floorplates bear large lateral nodes which project obliquely downward into the thecal cavity. Each plate develops at least one node on each lateral margin. Additional smaller prominences may also be developed occasionally. Contiguous floorplates meet along vertical sutures.

The interambulacrals on the upper surface of the theca are large, thick, polygonal plates and abut one another along vertical sutures (pl. 46, fig. 1-3, 8-9). Distal to the ambulacra, below the ambitus of the upper oral surface, the interambulacrals become progressively thinner and more elongate concentric with the ambitus (pl. 47, fig. 1-2, 7-8). In a zone beginning approximately seven to ten plates below the ambitus, the plates are sub-rectangular, extremely thin, elongate, and imbricate; these form vertical columns that include tens to hundreds of plates. The plate columns form the long, extensible, pedunculate zone. Presumably a small peripheral rim was developed at the base of the pedunculate zone and flared outward against the substrate.

The valvular anal structure lies proximal to the center of interambulacrum 5 (text fig. 49B, pl. 46, fig. 7). The outer circlet plates

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overlap the alternate, inner circlet ones along tightly fitting, beveled margins. However, the zone of overlap is rather narrow and most of the width of the inner circlet plates is visible externally. A total of twelve to fourteen triangular plates are included in the adult anal structure.

External plate surfaces are smooth, except for a minute pustulation reflecting the microstructure of the plates.

Specimens:

I.S.M. 10037. Holotype of Discocystis kaskaskiensis (Hall) (1858, p. 696, pl. 25, fig. 18, as Agelacrinus kaskaskiensis). Kaskaskia Formation, Chester Group, Mississippian. Near Kaskaskia, Randolph County, Illinois. A. H. Worthen Collection, no. X-129. 31 mm axial by 31.5 mm transverse diameter.

Text fig. 49A-B, 50B-C, pl. 46, fig. 1-7.

The holotype is a partially disrupted specimen which exposes only the upper side of the oral surface, above the ambitus. The oral region and hydropore structure are partially disrupted. Extensive crushing has removed the upper parts of these plates. All five ambulacra are visible, but the coverplates are well-preserved only in isolated sectors of each. The medial sector of ambulacrum IV is completely obliterated. Upper surface interambulacrals are mostly disrupted, the best preserved are found in interambulacrum 1. The anal structure is missing the distal parts of several posterior plates. Thecal plates below the ambitus are apparently missing, unseen even in areas where the upper surface plates have been lost.

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U.S.N.M. S-3885. D. kaskaskiensis. Chester Group, Mississippian. Carter's Glade, Crittenden County, Kentucky. 44.9 mm greatest length.

Text fig. 50A, pl. 47, fig. 1-5.

The specimen is a fragment of a large individual, originally at least 50 mm in diameter. It preserves the external surface of a narrow zone of upper oral surface plates which includes the distal parts of two ambulacra and a few adjacent interambulacrals. The upper oral surface plates originally proximal to this marginal strip are missing and this exposes the inner sides of the plates which form the lower thecal zone, below the ambitus. This part of the specimen includes both the larger thick plates immediately below the ambitus which form the transition zone, and the proximal part of about nine columns of thin elongate, imbricate plates of the peduncular zone.

The proximal part of the longer ambulacral segment preserves three-plate cycles of coverplates, whereas the long distal part of this ambulacrum, concentric with the ambitus, includes only two plates per cycle, the primary and secondary set plates. The distal tip of this ambulacrum is not exposed. A few ambulacral floorplates are exposed in the second fragmentary ambulacrum. Each has the deep central trough and less steeply sloping upper lateral margins or articulation surfaces. The upper sides of the large, inner surface nodes of the floorplates extend laterally beyond the plate margins. In the central sector of the larger ambulacral segment, where adjacent interambulacrals are missing, these nodes appear to be enlarged distally to form a broad support for the overlying inner sides of the interambulacrals.

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U.S.N.M. S-3883. D. kaskaskiensis ?. Stratigraphic and geographic occurrence unknown. (Label with specimen suggests it may be from the St. Genevieve Limestone, Chester Group, Mississippian, near Huntsville, Alabama, but the matrix resembles that of the holotype from Kaskaskia, Illinois.) 44.2 mm axial by 26.4 mm transverse diameter.

Pl. 46, fig. 8-9.

This fragmentary specimen exposes part of the inner side of the upper oral surface of a large individual. Preserved structures include: the oral frame and stone-canal passageway; the proximal parts of ambulacra IV and V , and about half of ambulacra I, II and III; the proximal parts of the interambulacra, 2 and 5 the most complete; and, most of the anal structure. The anterior tip of the specimen preserves the external surface of a few plates distal to the ambulacra. These hide the distal end of ambulacrum III. Siliceous beekite appears to have sporadically replaced some thecal plates.

This specimen is tentatively assigned to D. kaskaskiensis, although the ambulacral coverplates and other external oral surface features necessary for confirmation are not exposed. The inner surface structures of all of the clavate Agelacrinitidae are inadequately known, and thus cannot be used for specific identifications. The inner oral-ambulacral series structures of this specimen closely resemble those found in Lepidodiscus laudoni. But in contrast with that species, here the polygonal interambulacrals appear to be thicker, and the anal structure suggests that wide central sections of the inner circlet plates are exposed on the external oral surface. Both these features

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agree with the holotype of Discocystis kaskaskiensis and suggest the specimens are conspecific. The following description of the inner surface features seen in this specimen is presented here rather than in the species description due to the possible misidentification of the specimen.

The oral frame and stone-canal passageway structures are somewhat obscure, and thus their description is tentative. The large, transversely elongate, ovate oral frame underlies the oral area. It surrounds the large oral central lumen which extends from the proximal ends of the ambulacral tunnels directly downward, opening into the thecal cavity below. The frame is formed by the proximal floorplate of each ambulacrum, expanded both inwardly and laterally. The frame may also include intra-thecal extensions of some oral area covering plates. The anterior half of the frame is semicircular, with laterally attenuated extremities. It is formed by the enlarged proximal floorplates of ambulacra II, III and IV. If intra-thecal extensions from the overlying oral plates participate in the formation of the two anterior interradii, they are obscure in this specimen. The arcuate posterior side of the frame is formed by the proximal floorplates of ambulacra I and V and perhaps intra-thecal parts of overlying posterior oral plates. The anterior edges of the two posterior floorplates are wide and meet the two lateral, anterior floorplates of the frame along a wide zone of contact. This wide lateral contact zone produces the lateral attenuations of the frame. Intra-thecal extensions do not participate in the formation of these two lateral frame interradii.

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The two posterior floorplates apparently are not in contact across the posterior side of the frame and leave a large gap which laterally connects the central oral lumen to the thecal cavity beneath interambulacrum 5. The gap appears to be offset toward the right side of the frame (left side seen from below) and it distally intersects the inner end of the stone-canal passageway. This gap exposes the inner ends of the posterior oral covering plates which thus appear to form the upper part of the posterior side of the frame, above the posterior gap. It is not impossible that this posterior frame gap is preservational and that the posterior floorplates originally extended straight across the posterior side.

The stone-canal passageway extends into the thecal cavity along the right posterior margin of the oral frame (left as viewed from below). The inner end of the passageway appears to intersect the distal end of the supposed posterior frame gap. The diameter of the entire passageway appears to be large, only slightly increasing inwardly. The structure is formed by eight or nine elements, apparently intrathecal parts of the hydropore structure plates and parts of the adjacent ambulacral floorplates.

I.S.G.S. (I.S.M.) 2478. Discocystis kaskaskiensis; the holotype of Echinodiscus optatus Worthen and Miller (1883, p. 336-337, pl. 31, fig. 9). Chester Group, Mississippian. Pope County, Illinois. A. H. Worthen Collection. 24 mm greatest length by 21.2 mm wide.

Pl. 47, fig. 6-8.

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This fragmentary specimen, imbedded in matrix, exposes about half of the lower pedunculate zone plates and a few interambulacrals of the transition zone below the ambitus. Along the ambital edge of the specimen, one segment of an ambulacrum is exposed. The entire specimen is deeply etched and abraded which obscures the exact location of many of the plate boundaries. The coverplates of the small ambulacral segment appear to be a three-plate cyclic series.

Discussion of previous investigation:

Hall (1858, p. 696) described Agelacrinus kaskaskiensis as: discoidal; ambulacra six, radiating from a plated oral area; ambulacral coverplates subcuniform, perradially "crenulate or poriferous", interlocking and forming a single alternating biseries, or, with smaller intermediate plates; interambulacrals polygonal, flat. The accompanying drawing depicts six ambulacra all curved contrasolarly, and tessellate interambulacrals.

Meek and Worthen (1969, p. 357), after restudying the holotype, noted that Hall's anomalous sixth ambulacrum "is the incurved extremity of the dextral Isolarl right posterior ray." They cited the large polygonal, tessellate interambulacrals as the "important character" separating Agelacrinites kaskaskiensis from their new Mississippian species, Agelacrinites (Lepidodiscus) squamosus, which has squamose, imbricate interambulacrals.

Worthen and Miller (1883) expanded and emended earlier descriptions of Discocystis kaskaskiensis under the name Echinodiscus optatus. The upper oral surface features were apparently described from Hall's

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holotype, and the features of the peduncular zone of the lower surface from the fragmentary holotype of Echinodiscus optatus (= Discocystis kaskaskiensis; see generic discussion). Worthen and Miller (1883, p. 335) termed the thecal shape discoid, but also noted the "border . . . of narrow rim plates elongated in the direction of the circumference, and passing around upon the underside, forming a cylindrical nonsessile rim" [i.e., the peduncular zone of the theca, the basal peripheral rim being missing]. They also reported: the ambulacra arise in three radii, one anterior and two lateral, each lateral radius bifurcating a short distance from the oral pole; ambulacral coverplates "composed on each side [of the perradial line] of alternately longer [primary] and shorter [secondary and tertiary] plates which interlock at the angular arch [perradial line], with each other and with smaller intercalated plates" [? irregular quaternaries, or tertiaries]; and, "mouth" [oral area] central or subcentral, covered by numerous "larger and smaller" plates, supported internally by other elements [oral frame plates].

Miller (1889) listed Hall's Agelacrinites kaskaskiensis as a second species of Echinodiscus, along with E. optatus. The pre-empted name Echinodiscus was replaced by Discocystis Gregory (1897). Most subsequent works have referred to the species as Discocystis kaskaskiensis (Hall).

Although commonly cited in later works, only two papers added new data about D. kaskaskiensis. The first is Clarke's (1901) interpretation of the confused taxonomy in earlier works (see generic discussion).

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In the second paper, Bassler (1936) "corrected" Hall's (1858) drawing of the D. kaskaskiensis holotype and showed ambulacrum V curved solarly, the distal tip extending back toward the oral area. He also refigured the original drawing of Echinodiscus optatus and described the specimen as conspecific with Discocystis kaskaskiensis. Moreover, Bassler figured four new specimens listed as D. kaskaskiensis: (1) (1936, pl. 3, fig. 4) an adult edrioasteroid, present location unknown, which exposes oral surface features similar to D. kaskaskiensis; however, the coverplate pattern cannot be determined from the illustration, and thus, identification is questionable; (2) (1936, pl. 3, fig. 5) a broken specimen with only four ambulacra, present location unknown; the illustration suggests the individual may be a Lepidodiscus laudoni (Bassler) (1936); (3) (1936, pl. 3, fig. 6; U.S.N.M. S-3884) a Lepidodiscus laudoni [see pl. 49, fig. 7-12]; (4) (1936, pl. 7, fig. 11) the collapsed peduncular zone of a clavate edrioasteroid, perhaps a D. kaskaskiensis, present location unknown. Bassler correctly described the ambulacral floorplates as uniserial, although his conclusion was based upon a specimen (U.S.N.M. S-3884) which is a representative of Lepidodiscus laudoni.

Discussion:

Discocystis kaskaskiensis is here described from four specimens, only two of which are identified with certainty. Externally, the plating of the oral area and hydropore structure remain inadequately described. Moreover, the cyclic ambulacral coverplate sequence commonly includes three plates, but a fourth proximal set, seen only in one

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ambulacrum of the holotype, suggests development may be incomplete in this specimen. The holotype, about 31 mm in diameter, is significantly smaller than the projected 50 mm diameter of specimen U.S.N.M. S-3885. Unfortunately only the distal parts of the ambulacra are preserved in the larger specimen.

The internal structures of D. kaskaskiensis are also inadequately represented in available specimens. The single individual which exposes the oral frame, stone-canal passageway and the inner surfaces of ambulacral floorplates eludes positive identification. Moreover, the inner surface of the ambulacral coverplates has not been observed. However, the fine serrations developed along the perradial ends of the coverplates may indicate the presence of multiple intra-ambulacral extensions on the ambulacral tunnel surfaces of the coverplates.

Range and occurrence: Chester Group, Mississippian of Illinois and Kentucky.

Lepidodiscus Meek and Worthen, 1868

1842 [non] Agelacrinites Vanuxem, L., Nat. Hist. of New York, pt. IV, Geology 3: 158.

1868 Lepidodiscus Meek, F. B. and Worthen, A. H., Philadelphia Acad. Nat. Sci., Proc. 5: 357-358.

1873 Lepidodiscus Meek, F. B. and Worthen, A. H., Geol. Surv. Illinois, v. 5, Geology and Palaeontology, pt. 2, Palaeontology of Illinois: 513-515, pl. 16, fig. 1.

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1879 Lepidodiscus Meek and Worthen, Sladen, W. P. [partim], Geol. Soc. London, Quart. Jour. 35: 749-750.

1883 [non] Echinodiscus Worthen, A. H. and Miller, S. A., Geol. Surv. Illinois, v. 7, Geology and Palaeontology, sect. 2, Palaeontology of Illinois: 335.

1891 Echinodiscus Worthen and Miller, Miller, S. A. [partim], Geol. Surv. Indiana, 17th Ann. Rept. (adv. pub.): 76, pl. 12, fig. 16.

1892b Echinodiscus Worthen and Miller, Miller, S. A., Geol. Surv. Indiana, 17th Ann. Rept.: 686, pl. 12, fig. 16.

1896b [non] "Lepidodiscus Hall", Haeckel, E., Die Amphorideen und Cystoideen, Leipzig, 1: 113-114.

1897 (Feb.) [non] Discocystis Gregory, J. W., Geol. Surv. London, Quart. Jour. 53: 131.

1897 (Oct.) Ageladiscus Miller, S. A. [partim], Second Appendix to North American Geology and Palaeontology, Cincinnati: 734.

1901 Lepidodiscus Meek and Worthen, Clarke, J. M. [partim], New York St. Mus., Bull. 49 (2): 182-198; Discocystis Gregory, idem [partim], ibid.: 182-198; Agelacrinites Vanuxem, idem [partim], ibid.: 195-196, fig. 4-6.

1904 Echinodiscus Worthen and Miller, Klem, M. J., [partim], St. Louis Acad. Sci., Trans. 14: 73-74.

1935 Lepidodiscus Meek and Worthen, Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 8.

1936 Lepidodiscus Meek and Worthen, Bassler, R. S. [partim], Smithsonian Misc. Coll. 95 (6): 20, pl. 1, fig. 17; Discocystis Gregory,

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idem [partim], ibid.: 21, pl. 3, fig. 7-8.

1938 Lepidodiscus Meek and Worthen, Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 123.

1943 Lepidodiscus Meek and Worthen, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 206; Discocystis Gregory, idem [partim], ibid.: 201.

1944 Lepidodiscus Meek and Worthen, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, pl. 49, fig. 21.

1958b Lepidodiscus Meek and Worthen, Ehlers, G. M. and Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 14 (15): 265-276; Discocystis Gregory, idem [partim], ibid.: 265-276, pl. 1, fig. 1-4, pl. 2, fig. 1-2, pl. 3.

1958 Lepidodiscus Meek and Worthen, Kesling, R. V. and Ehlers, G. M. [partim], Jour. Paleont. 32 (5): 923-932, text fig. 1, pl. 119, fig. 1-3, pl. 120, fig. 1-6.

1960 Discocystis Gregory, Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 155, text fig. 4, pl. 3, fig. 1-3; Lepidodiscus Meek and Worthen, idem, ibid.: 155-157, text fig. 5, pl. 2, fig. 1-2.

1966 Lepidodiscus Meek and Worthen, Regnell, G. [partim], in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U169, text fig. 120-6a, 130-4; Discocystis Gregory, idem [partim], ibid.: U169, text fig. 120-6a, 129-3, 130-5.

1968 Discocystis Gregory, Strimple, H. L. [partim], Iowa Acad. Sci., Proc. 73: 260-262, text fig. 1-4.

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Type species: Agelacrinites (Lepidodiscus) squamosus Meek and Worthen, 1868.

Diagnosis:

Agelacrinitidae with: theca highly convex and domal, or clavate; oral plates numerous, reflect proximal ambulacral coverplate pattern, primary orals undifferentiated; large, elongate hydropore protuberance separated from central oral rise, posterior side formed by many plates, anterior side formed by adradial ends of elongate orals; long ambulacra curved, I-IV contrasolar, V solar, coverplates form alternating six-plate cycles; interambulacrals squamose, imbricate, or, polygonal, tessellate; valvular anal structure plates alternate as inner and overlapping outer circlet members.

Description:

Lepidodiscus Meek and Worthen is represented by species of large size with either a clavate or a highly convex domal theca. Species with a clavate theca include an elongate, downward constricting, pedunculate zone (below the ambitus of the upper gibbous region) formed by numerous columns of numerous, thin, elongate, sub-rectangular, imbricate plates. Both domal and clavate species develop a peripheral rim composed of several circlets of geniculate plates. The rim forms the margin of the upper oral surface in domal forms, whereas it is located at the base of the pedunculate zone in clavate species.

The transversely elongate oral region includes numerous plates. These imperfectly mimic the cyclic ambulacral coverplates in shape,

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size, and distribution. Thus, distally, they appear to grade into the proximal ambulacrals without distinct break and thereby obscure the total number of orals present. Primary orals are not differentiated externally. Lateral orals greatly exceed the anteriors in number and produce the transversely elongate oral area outline.

The large, transversely elongate, hydropore structure lies along the right posterior margin of the oral area. Participating plates are upturned to form the steep-sided, highly elevated protuberance which rises abruptly from the posterior edge of the central oral rise. Numerous plates, probably modified interambulacrals, form the posterior side of the elevation. The proximal part of the anterior side of the protuberance is formed by the adradial ends of elongate orals. These perradially extend to the transverse oral midline. The distal part of the anterior side of the prominence includes the adradial ends of several proximal, posterior coverplates of ambulacrum V. The elongate, slit-like hydropore opens along the junction between the anterior and posterior plates and extends along the summit of the protuberance.

The long, moderately narrow ambulacra curve, I-IV contrasolarly, V solarly. Distally, they become concentric with the margin of the theca, and commonly, each distally extends along the distal edge of the adjacent ambulacrum, separated from it by only a few interambulacrals. However, the distal part of ambulacrum V lies proximal to the distal part of I with the tip curved proximally and ending near the posterior edge of the anal structure.

The ambulacral coverplates form six-plate cycles. Cycles on

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opposite sides of the perradial line alternate, offset by half the width of a cycle and thereby produce a broadly undulating, zigzag, perradial line. Individual cycle plates form small discrete perradial points, and these superimpose a fine serration upon the broad perradial line undulations.

The uniserial ambulacral floorplates are trough-shaped; the convex inward inner surfaces bear large lateral nodes. The concave downward central part of the upper sides of these floorplates is flanked by gently sloping lateral margins; these are the articulation zones upon which the bases of the overlying coverplates rest. Contiguous floorplates abut one another along vertical sutures in some species. In others the sutures are oblique, the proximal end of each floorplate broadly overlapping the distal margin of the next.

Interambulacral plates are squamose and imbricate in domal species, polygonal and tessellate to slightly imbricate in clavate forms.

The valvular anal structure includes an inner and an outer circlet of triangular to sub-triangular plates. Outer circlet plates laterally overlap alternate inner circlet ones along tightly fitting, beveled edges.

The prominent peripheral rim is formed by six to eight circlets. Proximal circlet plates are largest, distal circlet plates gradually diminishing in size outward. The proximal two to four circlets are formed by plates externally elongate concentric with the thecal margin; the distal circlet plates are elongate radially. All but the tiny outer elements are geniculate.

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External plate surfaces are smooth in all known species except for the fine pustulation reflecting the plate microstructure.

Discussion of previous investigation:

Meek and Worthen (1868) introduced Lepidodiscus as a subgeneric term for Agelacrinites (Lepidodiscus) squamosus. In describing the major thecal features of the species, they cited its squamose interambulacrals and the direction of ambulacral curvature as contrasting with the polygonal, tessellate interambulacrals and differing ambulacral curvature of the type species of Agelacrinites, A. hamiltonensis, (as described by Hall). "It therefore certainly seems to us doubtful whether species differing in two such important characters as these are strictly congeneric. If they are not, then a new generic name should be applied to our species, . . . Lepidodiscus . . . At least we should think they ought to be separated subgenerically" (Meek and Worthen, 1868, p. 358). Their 1868 paper was republished in 1873 with the addition of a detailed line drawing of the holotype of L. squamosus.

Lepidodiscus was occasionally used as a subgenus (Hall, 1872; Miller, 1889; Grabau and Shimer, 1910), but most authors have used it at the generic level. Hall (1871, 1872) and many other authors transferred Ordovician species, including Isorophus cincinnatiensis (Roemer) and Carneyella pilea (Hall), from Agelacrinites to Lepidodiscus and thereby introduced strikingly different morphologic characters into the generic descriptions. Foerste (1914, 1917) ended this practice by noting the obvious differences between the Ordovician forms and the Mississippian type species of Lepidodiscus and by describing new

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genera for the Ordovician species.

New species have been occasionally assigned to Lepidodiscus (e.g., L. alleganius Clarke, 1901, L. alpenensis Bassler, 1936). However, Meek's and Worthen's (1868) diagnosis (ambulacra I-IV contrasolar, V solar, interambulacrals squamose, imbricate) was used without modification until Kesling and Ehlers (1958) published a detailed account of the holotype of Lepidodiscus squamosus which included description of the oral area plating, hydropore structure, and the complex ambulacral coverplate cycles. Ehlers and Kesling (1958) redescribed the type specimens of Discocystis laudoni and reported that they differed from Lepidodiscus squamosus only in the nature of the interambulacral plates. Judging ambulacral coverplate pattern to be of major taxonomic importance, they questioned the use of squamose-imbricate versus polygonal-tessellate interambulacrals as a generic taxobasis for Lepidodiscus.

In agreement with Ehlers and Kesling (1958), Discocystis laudoni is here included in Lepidodiscus. The generic description has been modified to include (a) both clavate and domal thecae, and (b) both squamose-imbricate and polygonal-tessellate interambulacrals. The structure of the oral area and hydropore and the disposition of the ambulacral coverplates are now considered generic taxobases.

Several species other than those recognized here have been referred to Lepidodiscus as defined by Meek and Worthen. Among these are the following European species excluded from this investigation: Lepidodiscus lebouri Sladen (1879), Lepidodiscus ephraemovianus

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(Bogolubov) (1926) I = Agelacrinites ephraemovianus 1, Lepidodiscus fistulosus Anderson (1939) I = Anglidiscus fistulosus (Anderson) according to Regnéll, 1950 1, Lepidodiscus milleri Sharman and Newton (1892). Published accounts of these species suggest that most (probably all) of them do not comply with the restricted generic diagnosis for Lepidodiscus presented here.

Discussion:

Lepidodiscus includes species showing variability in three important characters which are constant in related genera. Most obvious is the inclusion of both domal and clavate thecae. Each form develops a distal peripheral rim, but the clavate theca includes an elongate, downwardly constricting zone below the ambitus. The numerous, thin, sub-rectangular plates which form the peduncular zone appear to have no homologue in domal species. The second important variable is the occurrence of squamose, imbricate interambulacrals in domal forms, in contrast with the polygonal, tessellate interambulacrals of the upper oral surface of clavate types. Finally, the uniserial ambulacral floorplates are believed to be imbricate in domal forms, whereas they abut one another along vertical sutures in clavate species. Imbricate versus abutting floorplates is a familial taxobasis in the Lebetodiscina. Floorplate disposition is inadequately known throughout the Agelacrinitidae, but in all other species where observed, the floorplates abut along vertical sutures. Thus, floorplate structure may have more taxonomic importance than it has received in this analysis of Lepidodiscus, suggesting further subdivision of the species here included in

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Lebetodiscus, or even eventual room for new genera.

Range and occurrence: Mississippian of Indiana, Kentucky, Pennsylvania, Iowa, Missouri, and Alabama.

Lepidodiscus squamosus Meek and Worthen, 1868

Text fig. 51; plate 47, fig. 9-10, plate 48.

1868 Agelacrinites (Lepidodiscus) squamosus Meek, F. B. and Worthen, A. H., Philadelphia Acad. Nat. Sci., Proc. 5: 357-358.

1873 Agelacrinites (Lepidodiscus) squamosus Meek, F. B. and Worthen, A. H., Geol. Surv. Illinois, v. 5, Geology and Palaeontology, pt. 2, Palaeontology of Illinois: 513-515, pl. 16, fig. 1.

1879 Lepidodiscus squamosus Meek and Worthen, Sladen, W. P., Geol. Soc. London, Quart. Jour. 35: 749-750.

1889 Agelacrinus squamosus Meek and Worthen, Miller, S. A., North American Geology and Palaeontology, Cincinnati: 222.

1899 Agelacrinites squamosus Meek and Worthen, Jaekel, O., Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 51.

1901 Lepidodiscus squamosus Meek and Worthen, Clarke, J. M., New York St. Mus., Bull. 49 (2): 182-198; Agelacrinites beecheri Clarke, J. M., ibid.: 195-196, text fig. 4-6.

1910 Agelacrinus (Lepidodiscus) squamosus Meek and Worthen, Grabau, A. W. and Shimer, H. W., North American Index Fossils, Invertebrates, New York, 2: 473.

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1914 Agelacrinites beecheri Clarke, Foerste, A. F., Denison Univ., Sci. Lab. Bull. 17 (art. 14): 417, pl. 1, fig. 2.

1936 Lepidodiscus squamosus Meek and Worthen, Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 20, pl. 1, fig. 17.

1938 Lepidodiscus squamosus Meek and Worthen, Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 123.

1943 Lepidodiscus squamosus Meek and Worthen, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 207; Lepidodiscus beecheri (Clarke), idem, ibid.: 206-207.

1944 Lepidodiscus squamosus Meek and Worthen, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, pl. 49, fig. 21.

1958b Lepidodiscus squamosus Meek and Worthen, Ehlers, G. M. and Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 14 (15): 265-276.

1958 Lepidodiscus squamosus Meek and Worthen, Kesling, R. V. and Ehlers, G. M., Jour. Paleont. 32 (5): 923-932, text fig. 1, pl. 119, fig. 1-3, pl. 120, fig. 1-6.

1960 Lepidodiscus squamosus Meek and Worthen, Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 155-157, text fig. 5, pl. 2, fig. 1-2.

1966 Lepidodiscus squamosus Meek and Worthen, Regnéll, G., in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U169, text fig. 130-4, 120-6a'.

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Diagnosis:

A Lepidodiscus with: large, highly elevated, domal theca; ambulacral floorplates imbricate; and, interambulacrals squamose, imbricate.

Description:

The large domal theca of Lepidodiscus squamosus Meek and Worthen reaches at least 45 mm in diameter and was highly convex, the oral surface nearly hemispherical before thecal collapse.

The oral area is formed by numerous plates. Text fig. 51B presents a tentative interpretation of oral area plating in the holotype, differentiating between plate boundaries (solid lines) and secondary fractures (dashed lines). Primary orals are not differentiated externally from other orals. Distally the oral plates reflect the pattern of the proximal, cyclic, ambulacral coverplate series and the orals appear to grade distally into the ambulacral sequence without distinct break. Oral plate sizes and shapes are similar to the ambulacral coverplates and include large, intermediate, and small elements. Approximately thirty lateral orals and seven or eight anteriors are included. The relatively numerous lateral orals which lie proximal to the lateral bifurcation plates produce the pronounced transverse elongation of the area.

The hydropore structure is a large, transversely elongate, elevated mound which arises from the right posterior margin of the oral region (text fig. 51B, pl. 48, fig. 1). It extends along the right posterior half of the oral region and the proximal posterior margin of ambulacrum V. Participating plates are flexed upward and form the

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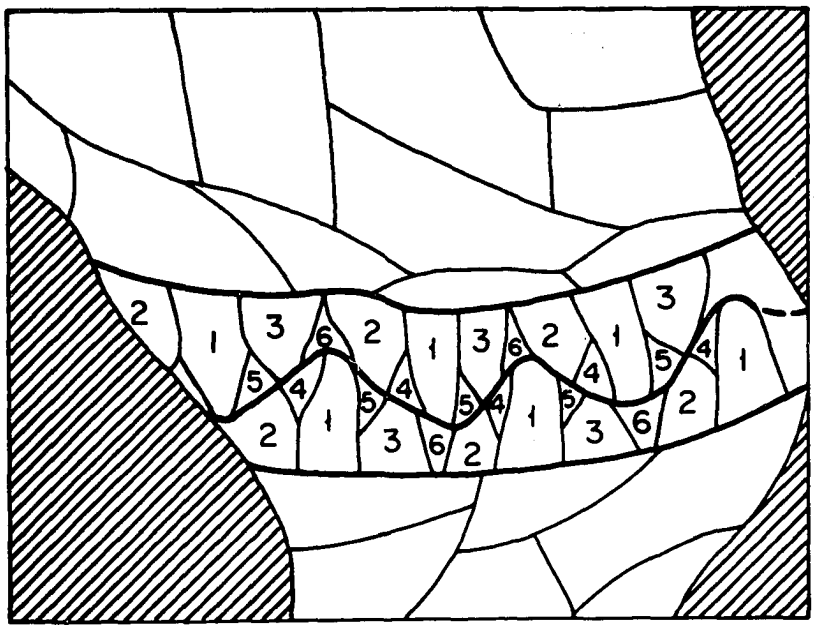
Text Figure 51 Lepidodiscus squamosus Meek and Worthen, 1868.

A. Proximal segment of ambulacrum III, Y.P.M. 24804-b, (X22), pl. 48, fig. 6.

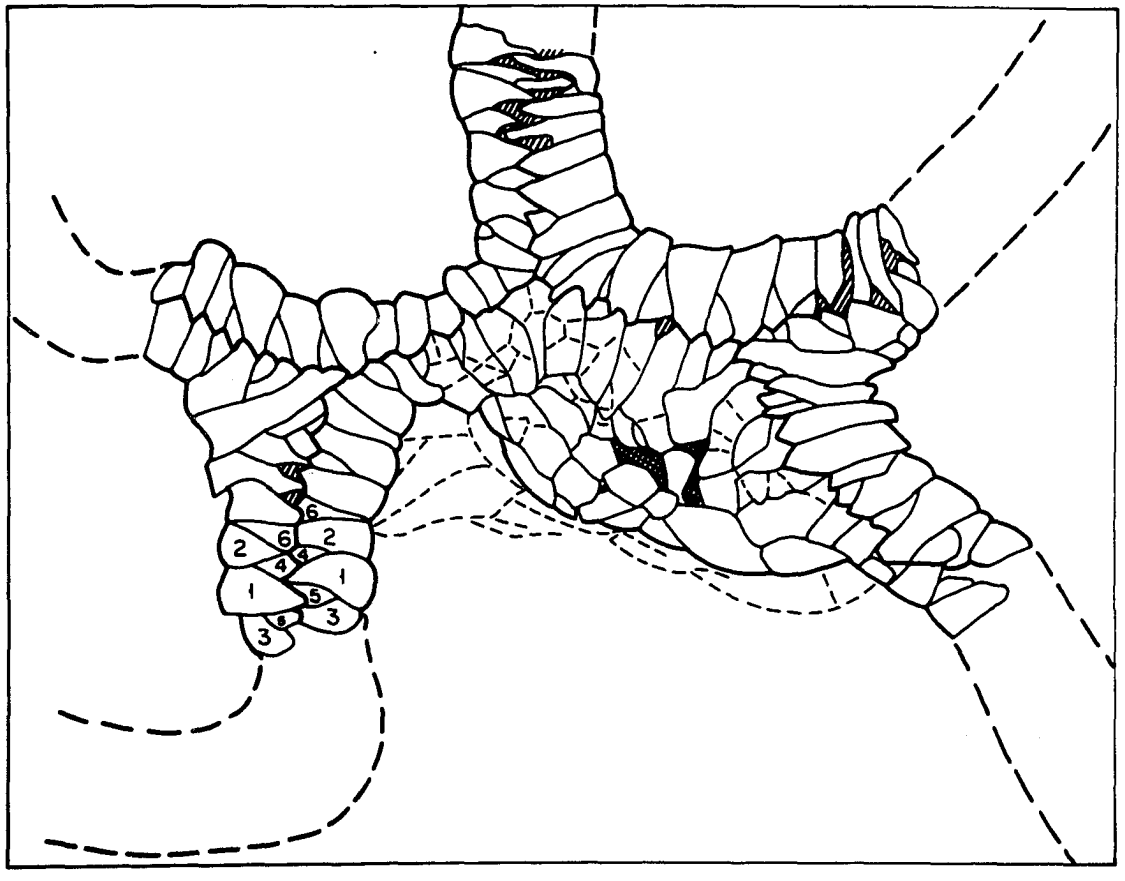
B. Holotype, oral area and adjacent structures, U.M.M.P. 5420, (X1^2), pl. 48, fig. 1.

1. through 6. are the first through sixth sets of ambulacral cover-plates, respectively.

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A



B

Text Figure 51

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steep, nearly vertical sides of the protuberance. The posterior side of the structure is formed by six or more plates. These may be interpreted as multiple hydropore orals which correspond to the single large hydropore oral found in some edrioasteroid species, or as modified interambulacrals that have been incorporated into the oral sequence. The proximal part of the anterior side of the structure is formed by the adradial ends of elongate oral plates. These perradially reach the transverse oral midline. The distal part of the anterior side is formed by the adradial ends of proximal, posterior coverplates of ambulacrum V. All of the anterior side plates of the oral-ambulacral series are centrally depressed and form a trough between the hydropore protuberance and the elevated oral area and ambulacrum V. The hydropore opening appears to have been an arcuate slit which extends along the summit of the protuberance.

Distally, ambulacral curvature is consistent with the generic description, I-IV contrasolar, V solar. However, in the holotype, ambulacra I, II, III and IV proximally flex solarly before initiating the dominant contrasolar curvature. Proximally, ambulacrum V curves solarly, then slightly contrasolarly, before beginning the final distal solar curvature. Preservational distortion may account for some of these proximal sinuations in the holotype. In two other specimens, the proximal parts of the ambulacra appear to be essentially straight.

The ambulacral coverplate pattern is cyclic (text fig. 51A-B, pl. 48, fig. 1-2, 6). The six-plate cycles on opposite sides of the perradial line alternate, offset by half a cycle length and thereby

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produce the broadly undulating, zigzag, perradial line.

As first described by Kesling and Ehlers [adjacent plates numbered consecutively]:

> "the first [cycle plate] is short and subquadrate; the second is intermediate in length and irregularly hexagonal, its outer part subquadrate and its inner part acuminate; the fourth plate, the longest in the cycle, is subquadrate except that the inner corners are beveled; and the sixth plate is a mirror image of the second. The third plate is subrhombic, inserted between the second and fourth plates, with its inner apex forming a serration on the central line of the ambulacrum. The fifth plate is a mirror image of the third, lying on the opposite side of the long fourth plate. In most cycles the subrhombic third and fifth plates do not extend to the outside edge of the ambulacrum, but terminate along the side of the fourth plate" (Kesling and Ehlers, 1958, p. 927-928).

In the proximal parts of the ambulacra the cyclic pattern is partially obscured by the differential enlargement of the cycle plates, and perhaps also occasionally by the insertion of irregular additional plates. Extraneous plates may also occur occasionally in the highly curved, medial ambulacral zones.

The distal tips of the ambulacra are too poorly preserved in specimens of L. squamosus to determine the sequence of coverplate insertions with certainty. It is probably similar to that of L. laudoni

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which has a six-plate cycle nearly identical to that of L. squamosus. It appears that the Kesling's and Ehler's consecutive plate numbering corresponds to the sets of cyclic plates as follows: primary set plate = their fourth plate; secondary = their second; tertiary = their sixth; quaternary = their third; quintary = their fifth; and the sixth set plate = their first plate.

The intra-ambulacral surfaces of the coverplates have not been directly observed in L. squamosus. However, in extremely eroded sections of the holotype, the centers of the perradial ends of the coverplates appear to be thicker than the lateral edges and suggest the presence of blade-like intra-ambulacral extensions. Adradially, the coverplates appear to end adjacent to the lateral margins of the underlying floorplates, without development of intra-thecal extensions.

The coverplates which form each cycle appear to be tightly sutured together laterally. It is unclear whether these sutures are vertical or oblique. Thus, smaller plates of the cycle which externally end before reaching the adradial suture line, could reach the adradial suture internally.

Ambulacral floorplates have been observed in two specimens assigned to L. squamosus (pl. 48, fig. 3-4, 7-11), but only a partial cross-section of one floorplate is exposed in the holotype. Floorplates appear to be uniserial and trough-shaped. The upper surface is centrally concave downward; the upper lateral margins slope only slightly toward the ambulacrum axis and form the nearly horizontal lateral articulation zones on which the bases of the overlying coverplates rest.

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The lower sides of the floorplates are convex downward. Large nodes are developed along the lateral margins of these inner surfaces, one on each side. They arise near the center of the upper edge of the inner surface of the floorplate and extend laterally outward into the thecal cavity. Sutures between contiguous floorplates are oblique and the proximal margin of each overlaps almost the entire distal half of the next (pl. 48, fig. 11).

Interambulacrals are squamose, imbricate plates.

The valvular anal structure is offset toward the left side of interambulacrum 5. In the holotype it appears to be only a few plates away from ambulacrum I. However, at least part of this left lateral position appears to be preservational. In specimen Y.M.P. 24803, the anus lies much nearer the center of interambulacrum 5. The structure is formed by 14 large, triangular plates in the holotype, regularly alternating as inner and overlapping outer circlet members. The zone of overlap is of moderate width and exposes most of the upper surface of the inner plates. Several small triangular plates appear to be wedged between the larger anals in the holotype and perhaps represent new, incompletely formed anals.

The peripheral rim includes six to eight circlets of plates. The large plates of the proximal circlet may alternate as proximal and distal sub-circlets. Plates of the proximal three circlets are elongate concentric with the thecal margin, whereas the plates of the distal circlets are radially elongate. Small vertical ridges are present on the basal surfaces of at least the large, proximal, geniculate rim

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plates.

External thecal plate surfaces are smooth except for fine pustulation reflecting the plate microstructure.

Specimens:

U.M.M.P. 5420. Holotype of Lepidodiscus squamosus Meek and Worthen (1868, p. 357-358; 1873, p. 513-515, pl. 16, fig. 1). Edwardsville Formation, Osagean Series, Mississippian. Crawfordsville, Indiana. 45.2 mm axial by 33 mm transverse diameter.

Text fig. 51B, pl. 47, fig. 9-10, pl. 48, fig. 1-2.

The holotype is laterally compressed; at least some of this compression appears to be preservational. Originally highly domed, the theca has collapsed, disrupting interambulacrals and rim plates, and, to a lesser extent, the ambulacra. A small part of the right anterior edge of the theca is missing, including a section of ambulacrum IV and the adjacent peripheral rim. The central oral region and hydropore structure has been extensively crushed, removing the upper parts of the plates and commonly fragmenting the remaining lower parts. The central segments of the ambulacra preserve the cyclic ambulacral coverplate pattern. Neither the proximal nor distal parts of the ambulacra are well enough preserved to allow detailed analysis of the coverplate pattern.

A complete description of the specimen and its status as the holotype is given by Kesling and Ehlers (1958).

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Y.P.M. 24803-24804. Two specimens of Lepidodiscus squamosus; the type specimens of Agelacrinites beecheri Clarke (1901, p. 195-196, fig. 4-6). Labeled "Lower Carbonic below the horizon of the Olean Conglomerate, Waverly." K. E. Caster suggests the matrix and associated fauna is typical of the lowermost Mississippian Syringothyris zone, probably Cuyahoga Group, Kinderhookian-Osagean Series, Mississippian. "They probably came from the Yankee Bush Hill site, just north of Warren, Pennsylvania, where Charles Beecher and his friends collected so many of the perishoechinoids described by R. T. Jackson" (personal communication, 1971). Warren, Pennsylvania. C. E. Beecher, collector.

Y.P.M. 24803. (a) internal and (b) external mold of the specimen. (a) 27.4 mm axial by 23 mm transverse diameter. (b) 27.6 mm axial by 23.5 mm transverse diameter.

Pl. 48, fig. 7-13.

The specimen was only partially collapsed during preservation, and the upper oral surface remains convex upward. A large central part of the theca is not preserved, and leaves only the distal halves of the ambulacra-interambulacra, along with the anal structure and the peripheral rim.

The internal mold, and latex pulls prepared from it, reveal the imbricate floorplates which bear large lateral nodes. Vertical ridges are seen on the bases of the large, geniculate, proximal rim plates, usually two or three near the center of each plate base. Distal rim plates appear to lack the basal ridges.

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The cyclic ambulacral coverplate pattern is preserved by the external mold of the specimen. Smaller plates are difficult to identify along most of the preserved parts of the ambulacra, but are clear in a few segments (pl. 48, fig. 12-13). The broadly undulating perradial line is commonly apparent, and in some areas the perradial tips of the coverplates appear to have been flexed upward to form a small central ridge along the perradial line. The anal structure is preserved as a low, rounded, conical elevation near the center of interambulacrum 5.

Y.P.M. 24804. (a) internal and (b) external mold of a fragment of one specimen. (a) 20.5 mm long by 12 mm wide. (b) 18.8 mm long by 12. mm wide.

Text fig. 51A, pl. 48, fig. 3-6.

This specimen is a fragment of a large individual that includes the hydropore structure, the proximal parts of ambulacra III, IV and V, interambulacra 3 and 4, and a small segment of the peripheral rim. Most of the details of the thecal plates have been obscured during preservation. The internal mold is very poorly preserved. The imbrication of the ambulacral floorplates can be seen only in ambulacrum V. Other features, including the basal ridges of the geniculate rim plates, are difficult to identify. The external mold preserves the shape of the hydropore protuberance, but individual plate boundaries are obscure. The cyclic ambulacral coverplate pattern is well-preserved in a short segment of the central part of ambulacrum III (text fig. 51A). The coverplates appear to be perradially elevated in this individual also, and form a small, distinct perradial ridge.

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Discussion of previous investigation:

Meek and Worthen (1868, p. 357) described Agelacrinites (Lepidodiscus) squamosus as: domal; ambulacra long, narrow, curved, I-IV contrasolar, V solar, coverplates in "two zigzag rows of very small pieces, with some irregular ones apparently not belonging properly to either row"; interambulacrals squamose, imbricate; anal structure near the left side of interambulacrum 5, including ten laterally overlapping plates which form a "depressed cone"; "surface minutely granular". Citing the crushed and disrupted condition of the specimen, with question they suggested that the ambulacral coverplates closed over the ambulacra, the plates "interlocking" and with "pores arranged along them in a zigzag row between the pieces". A drawing of the holotype published by Meek and Worthen (1873) illustrates the dominant thecal structures and includes the varied ambulacral coverplates which in some parts of the drawing closely resemble the individual cycle plates. The undulating perradial line is accurately depicted in all of the ambulacra.

Meek's and Worthen's description of Lepidodiscus squamosus was accepted without modification until Kesling and Ehlers (1958) presented a detailed redescription of the holotype. Included in this work was the first accurate account of the oral area, hydropore structure and the recognition of the complex six-plate cyclic ambulacral coverplate pattern. In contrast to the original description, Kesling and Ehlers reported that the coverplates were not interlocking across the perradial line, and that the holotype shows no evidence of ambulacral "pores".

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Agelacrinites beecheri Clarke (1901) was based upon two specimens (Y.P.M. 24803-24804) which preserve both internal and external molds of the two individuals. The original description notes thecal shape and size, ambulacral curvature and plating, and, interambulacral and rim plating. Ambulacral coverplates were described as "triangular and interlocking along the median [perradial] line"(Clarke, 1901, p. 195). The imbrication of the ambulacral floorplates was cited as the important feature of the specimen as those plates had been only rarely observed in other edrioasteroids. Clarke did not contrast his new species to other edrioasteroid species.

Occasional references to Agelacrinites beecheri include Foerste's (1914) acceptance of the imbricate nature of the ambulacral floorplates, accompanied by a republication of Clarke's (1901) drawing of them. Bassler (1935, 1936) and Bassler and Moodey (1943) referred the species to Lepidodiscus without explanation.

Discussion:

The redescription of Lepidodiscus squamosus Meek and Worthen presented here is based upon the holotype and the two type specimens of Clarke's Agelacrinites beecheri. Restudy of the Clarke specimens revealed an ambulacral coverplate pattern identical to that of the holotype of Lepidodiscus squamosus. Other thecal structures, although incompletely preserved in the two specimens, also appear to be in complete agreement with L. squamosus.

Kesling's and Ehlers' detailed description of the holotype of L. squamosus included most thecal structures found in this species.

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The above redescription varies only in two significant aspects: the identification of the individual sets of ambulacral coverplates which form each cycle; and the description of the imbricate ambulacral floorplates, based on the specimens formerly called Agelacrinites beecheri. The occurrence of imbricate ambulacral floorplates in the Agelacrinitidae is known only from these two specimens.

Range and occurrence: Lower Mississippian of Indiana and Pennsylvania.

Lepidodiscus laudoni (Bassler), 1936

Text fig. 52-54; plate 49-50, plate 51, fig. 1-10.

1936 Discocystis laudoni Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 21, pl. 3, fig. 7-8.

1943 Discocystis laudoni Bassler, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 201.

1958b Discocystis laudoni Bassler, Ehlers, G. M. and Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 14 (15): 265-276, pl. 1, fig. 1-4, pl. 2, fig. 1-2, pl. 3.

1960 Discocystis laudoni Bassler, Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 155, text fig. 4, pl. 3, fig. 1-3.

1966 Discocystis laudoni Bassler, Regnéll, G., in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U169, text fig. 120-6a, 129-3, 130-5.

1968 Discocystis priesti Strimple, H. L, Iowa Acad. Sci., Proc. 73: 260-262, text fig. 1-4.

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Diagnosis:

A Lepidodiscus with: large clavate theca, peduncular zone plates numerous, imbricate, thin and elongate, in vertical columns; cyclic ambulacral coverplates perradially raised, forming small, distinct perradial ridge; ambulacral floorplates abut, each with two lower surface, lateral nodes; central interambulacrals polygonal, tessellate.

Description:

The large clavate theca of Lepidodiscus laudoni (Bassler) includes a broad, gibbous upper oral surface, 30 to 40 mm in diameter, and an elongate, lower, peduncular zone (pl. 51, fig. 9-10). The length of the extended peduncular zone is apparently equal to or greater than the diameter of the upper oral surface. Total thecal height in specimens approximately 35 mm in upper oral surface diameter appears to have been approximately 50 mm in laterally compressed specimens which preserve the lower zone in an extended state.

The oral area is formed by numerous plates (pl. 49, fig. 6, pl. 50, fig. 2, pl. 51, fig. 2). Primary orals are not externally differentiated from other orals in adults. The various sized oral plates imperfectly mimic the proximal ambulacral coverplates in size, shape and cyclic pattern. Thus, distally, they appear to grade into the coverplate sequence without distinct break. Thirty or more lateral orals form the elongate transverse oral midline, proximal to the lateral bifurcation plates, whereas only about ten anterior orals are present. Thus the oral area outline is transversely elongate, the two lateral primary radii bifurcating far from the central oral pole.

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Total number, shapes, sizes and arrangement of the oral plates appear to vary intra-specifically.

The large oral frame surrounds a transversely elongate, ovate, central lumen (pl. 50, fig. 12, pl. 51, fig. 3-4). The lumen extends from the proximal ends of the ambulacral tunnels directly downward, and opens into the thecal cavity below. The frame, also transversely elongate, is ovoid proximally, but sub-pentagonal distally where it is confluent with the five radiating ambulacra. Plating of the oral frame is inadequately known. Apparently the frame is formed by the enlarged proximal floorplate of each ambulacrum, expanded inwardly and laterally. Adjacent floorplates are in contact around the central lumen. Intra-thecal extensions from the overlying oral plates may also participate in frame formation, but these have not been observed in the specimens which expose the frame structure.

The hydropore structure is a large, transversely elongate elevation which rises from the posterior edge of the central oral rise (pl. 49, fig. 6). In large adults it extends distally from the axial midline of the theca along the right posterior half of the oral area and the proximal posterior side of ambulacrum V. The posterior side of the mound is formed by three to six large plates, either modified interambulacrals incorporated into the oral area, or, multiple hydropore oral plates. The anterior side of the hydropore structure is formed by the elevated, adradial ends of six or seven plates of the oral-ambulacral series. Perradially these plates form the posterior side of the right half of the transverse oral midline and the proximal

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part of the perradial line of ambulacrum V. The central parts of these plates are depressed and form a deep trough which separates the oral-ambulacral rise from the hydropore protuberance. One or two anterior plates which form the left end of the hydropore prominence may not reach the transverse oral midline because smaller, medial orals apparently lie proximal to these plates. The anterior edges of these smaller, central orals form the center of the posterior side of the transverse oral midline.

In younger adults (text fig. 52A, pl. 50, fig. 1-2), the hydropore structure is formed by only three large posterior plates and four anterior ones. Apparently the additional plates in the anterior part of the hydropore structure seen in larger adults are the expanded adradial ends of small medial orals of the smaller specimens. These plates appear to increase rapidly in size during ontogeny, and extend adradially into the hydropore structure. Additional proximal posterior coverplates of ambulacrum V may also be incorporated into the adult structure. In some larger adults, the posterior side of the structure continues to be formed by only three large plates. In others, additional plates are added. These are probably new plates inserted into the structure between existing ones. Elevation of the hydropore protuberance may be less pronounced in smaller individuals.

Poorly preserved stone-canal passageways have been observed in two specimens (pl. 50, fig. 10-12, pl. 51, fig. 3-4). Apparently expanding rapidly in diameter inwardly, the inner end of the funnel-shaped passageway is a large, ovate opening. The structure appears to

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Text Figure 52 Lepidodiscus laudoni (Bassler), 1936.

S.U.I.C. 12545.

A. Oral area and adjacent structures, (X20), pl. 50, fig. 2.

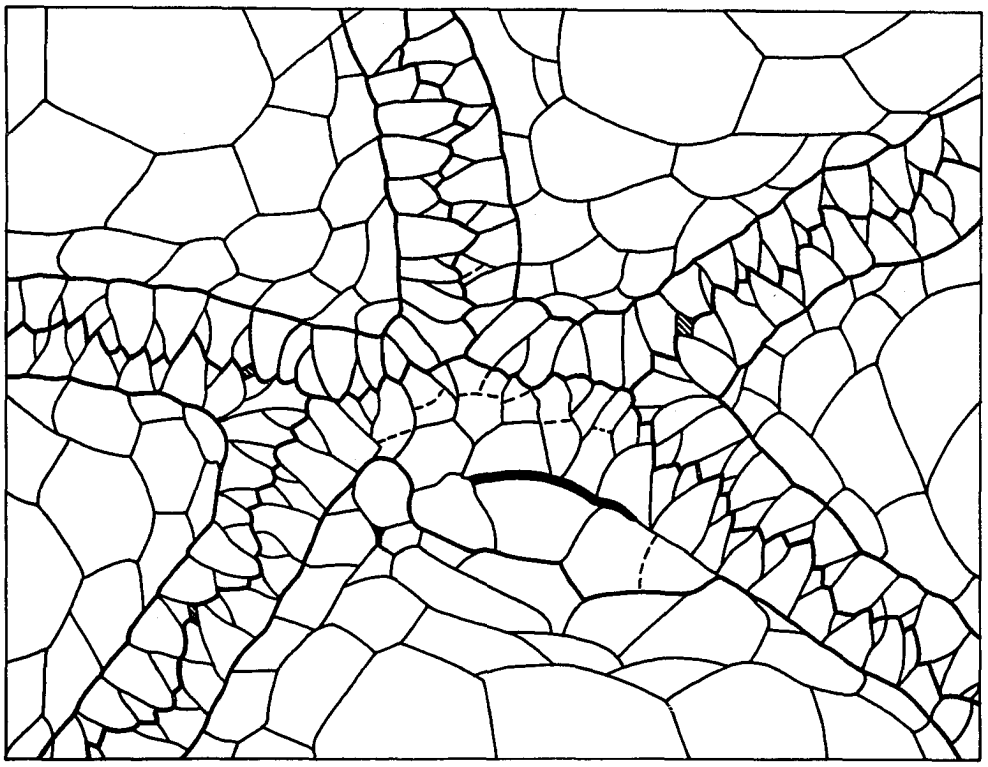
B. Segment of ambulacrum V, (X25), pl. 50, fig. 4. Proximal end is to the left. 1 through 6 are the first through the sixth sets of ambulacral coverplates, respectively.

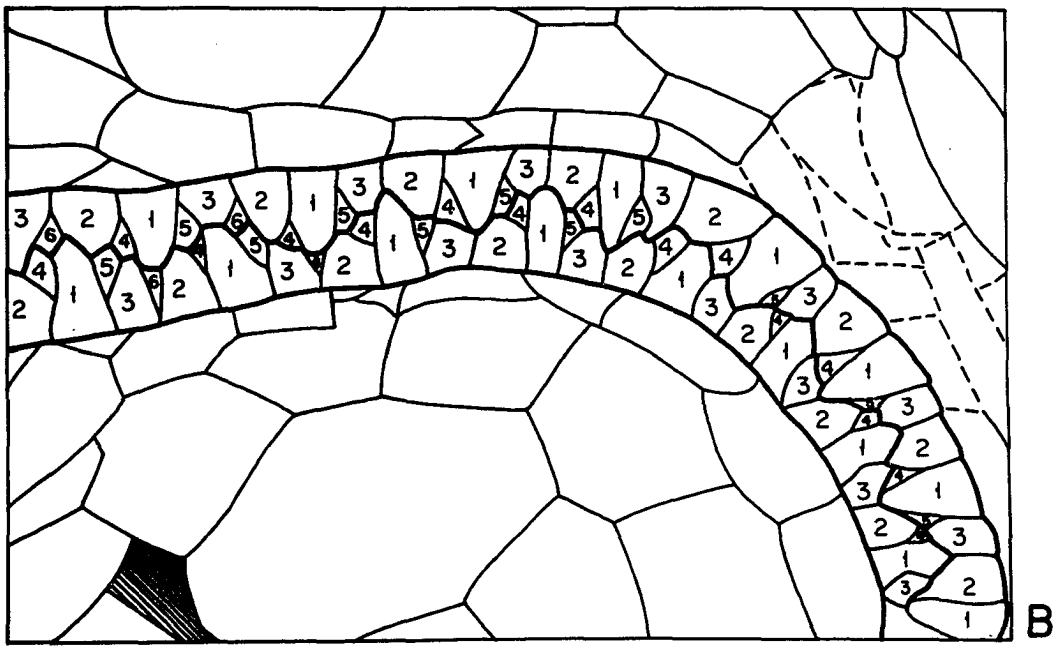
Text Figure 53 Lepidodiscus laudoni (Bassler), 1936.

A. Distal segment of ambulacrum I, S.U.I.C. 12546, (X25), pl. 50, fig. 9. The distal end is to the right.

B. Central segment of ambulacrum IV, S.U.I.C. 12545, (X25), pl. 50, fig. 3. The proximal end is to left. 1 through 6 are the first through the sixth sets of ambulacral coverplates, respectively.

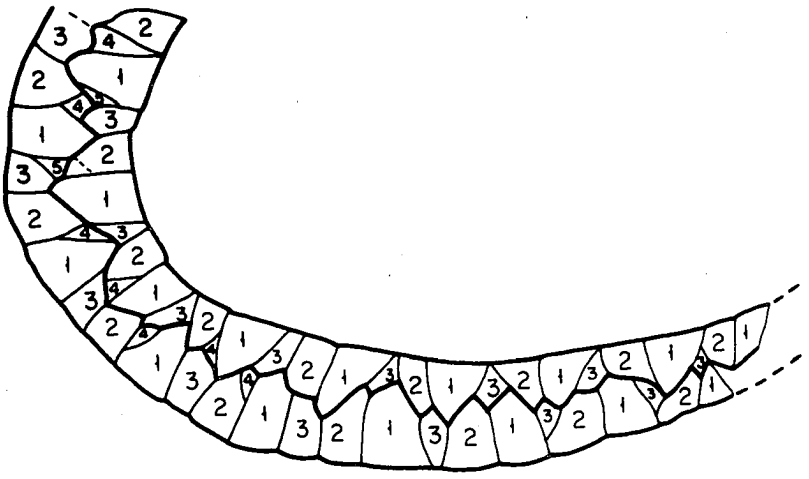
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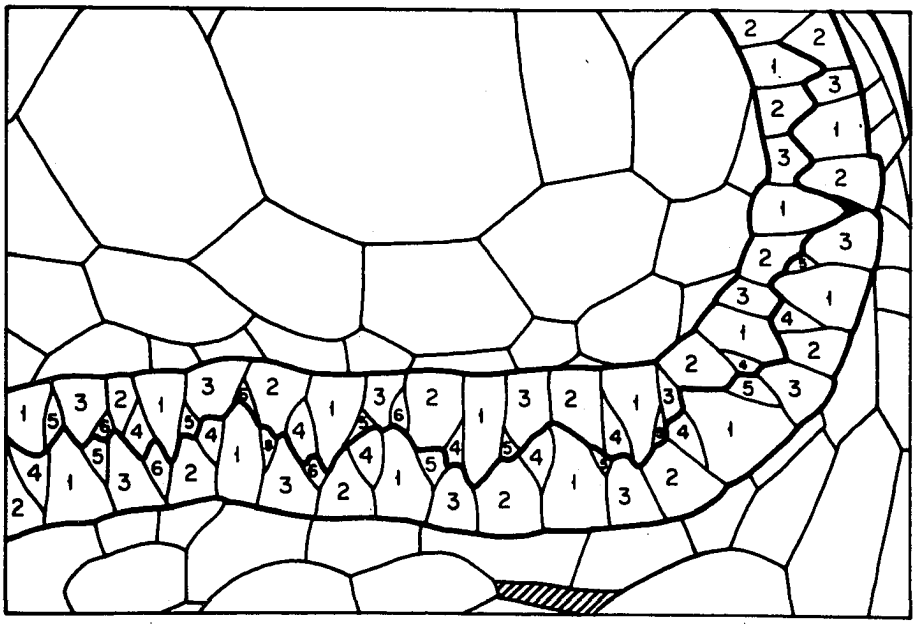


Text Figure 52

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A



B

Text Figure 53

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be formed by the proximal two floorplates of ambulacrum V and the intra-thecal parts of several other elements, probably hydropore structure plates.

Curvature of the long moderately narrow ambulacra is commonly uneven. A proximal straight sector is followed by pronounced curvature as the ambulacra become concentric with the ambitus of the upper oral surface.

The ambulacral coverplates form six-plate cycles; those on opposite sides of the perradial line alternate, offset by half the length of a cycle. The broadly undulating zigzag perradial line is accentuated by the upturned perradial ends of the coverplates which form a small, sharply defined perradial ridge which extends the length of the ambulacra. The perradial edges of the individual plates of the cycle commonly align evenly and form the single, wide, smooth, perradial undulation for each cycle. However, any of the six plates of the cycle may form a discrete perradial point, and thereby superimpose small serrations on the broader undulations.

Coverplate shapes, sizes and relative positions are similar to those of L. squamosus (text fig. 52B, 53A-B, pl. 49, fig. 3-4, pl. 50, fig. 3-4). Ehlers and Kesling (1958, p. 267) described these plates in detail, numbering them sequentially, proximal to distal.

> "The first plate is small and short. It is located where the zigzag central line is near the edge of the ambulacrum. This plate is rectangular, . . . trapezoidal or pentagonal, . . . [or] deeply indented to fit around the apex of the central line. The second plate is typically subpentagonal . . . The

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> third plate is small. It fits between the proximal parts of the second and fourth plate and borders on the central line. In most cycles it is triangular, . . . [or] subrhombic. The fourth plate is the longest and largest . . . The sides are parallel and more or less perpendicular to the edge of the ambulacrum, its proximal end . . . may be straight, bluntly tapering, sharply acuminate or, in rare cases, indented. The fifth plate is almost a mirror image of the third and is situated between the fourth and sixth plates; the sixth plate is a mirror image of the second."

The ambulacral coverplates of small adult specimens of L. laudoni more closely resemble the description for the coverplates given for L. squamosus than that presented above for L. laudoni (text fig. 52B, 53A-B). Notably, most plates form small but discrete perradial points which alter plate outlines to shapes more common in L. squamosus. Moreover, in small L. laudoni, plate shapes are more constant from cycle to cycle and the perradial elevation of the coverplates is less pronounced.

The mode of coverplate insertion and the sequential identity of the coverplate sets is preserved in the distal sectors of the ambulacra of two small adult L. laudoni (text fig. 53A). Coverplate sets are described below in order of insertion; parenthetic numbers refer to Ehlers' and Kesling's proximal to distal, sequential numbering, cited above.

The first formed or primary coverplates (fourth) are developed

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singly at the distal tip of each ambulacrum and move alternately left and right. Secondary coverplates (second) are inserted along the proximal margins of the alternating primaries. Their zone of insertion lies one or more primary plates from the distal tip of the ambulacrum. Next, tertiary set elements (sixth) are inserted along the distal margins of the alternate primaries. Their insertion zone lies two or three "two-plate cycles" proximal to the insertion zone of the secondaries. Coverplates of the quaternary set (third) are inserted between the perradial tips of primaries and secondaries, the insertion zone being four cycles proximal to that of the tertiaries. In contrast with the first three sets of plates, the tertiaries are confined to the perradial part of the ambulacrum and rarely enlarge sufficiently to reach the adradial suture line. Quintary, or fifth set, coverplates (fifth) follow, inserted between the perradial tips of plates of the primary and tertiary sets. Occasionally these plates are inserted in the same cycle as the quaternaries. Commonly their insertion zone lies one to three cycles proximal to the quaternary insertion zone. Like the quaternaries, plates of the quintary set are limited to the perradial part of the ambulacrum. The sixth, and final, set of coverplates (first) are inserted along the proximal side of the secondary set plates; the proximal margin of the sixth set plates is in contact with the distal edge of the tertiary plate of the adjacent, next proximal cycle. These final elements are inserted three to six cycles proximal to the zone of insertion of the quintary set plates.

In larger adult specimens, the successive insertion zones tend to

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be separated by the minimum numbers of cycles cited above, whereas in younger specimens the maximum numbers are more common. Apparently in very large adults distal additions of primary coverplates nearly cease, and the following zones thus migrate distally until complete six-plate cycles are very near the distal tip of the ambulacrum.

Proximally, the cyclic coverplate pattern is less apparent, with many of the smaller cycle plates enlarged to nearly equal the size of the primary plates. Occasional cycle irregularities occur throughout the length of the ambulacrum. These are usually due to the insertion of an extra coverplate and a corresponding modification of adjacent plate shapes. Occasional omissions of cycle plates are also encountered.

Blade-like intra-ambulacral extensions are produced inward from the ambulacral tunnel faces of the coverplates. The configuration of the inner parts of these extensions are unknown. The adradial ends of the larger coverplates which externally reach the adradial suture line appear to be shaped similar to those of L. squamosus (text fig. 49C).

Small, thin, elongate interambulacrals laterally overlap the depressed, upper adradial margins of the ambulacral coverplates. Irregular in the smaller adult specimens, these small interambulacrals are regularly spaced in the larger adults and extend furthest perradially over the central plates of each cycle. Thus, the adradial suture lines of the ambulacra are sinuous in large adults. Commonly, adjacent large thick interambulacrals extend under the thin adradial interambulacrals and abut the lateral edges of the ambulacral floorplates.

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The thick, uniserial floorplates are sub-rectangular in plan view, and are axially elongate. Contiguous plates abut along vertical sutures. The upper surface of each floorplate is centrally concave downward, U-shaped in cross-section, with steep lateral sides and a nearly horizontal central floor. Wide, upper lateral margins which form the articulation zones, flank the central trough and slope slightly toward the trough. A small ridge appears to extend along each flat upper margin, parallel to the axis of the ambulacrum. Apparently it aids in the articulation of the floorplates with the bases of the overlying coverplates and may fit into a shallow groove on the bases of the overlying coverplates. The convex inward lower surfaces of the floorplates bear large lateral nodes. These project laterally outward and downward into the thecal cavity under the adjacent interambulacral plates. Two lateral nodes are developed on each floorplate, one on each side.

Adjacent interambulacral plates laterally abut the uppermost lateral margins of the lower surfaces of the floorplates. The zone of contact between these two sets of plates may be irregularly sinuous with small nodes and depressions on the floorplate edges which fit into complementary grooves and ridges along the abutted margins of the interambulacrals (pl. 51, fig. 5-8). The small thin interambulacrals which laterally overlap the adradial ends of the coverplates hide this floorplate-interambulacral plate junction in nondisrupted specimens.

The interambulacral plates are large, polygonal and tessellate in the central sectors of the interambulacra. Marginally, they are

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more squamose and may imbricate slightly, particularly along the adradial suture line boundaries. Distally, the interambulacrals extend past the ambitus of the upper oral surface onto the lower side of the upper gibbous part of the theca. Immediately below the ambitus the interambulacrals become thinner, more elongate, and slightly imbricate. These plates of the transition zone form two or three irregular circlets. Distal to these, numerous, very thin, sub-rectangular plates, which are highly imbricate, are arranged in vertical columns that form the elongate peduncular zone. The transition from polygonal, tessellate to elongate-imbricate takes place through three or four "circlets" of transition zone plates. This contrasts with the more gradual transition zone found in the clavate Discocystis kaskaskiensis in which seven or eight "circlets" of transition are required.

The valvular anal structure of L. laudoni comprises an inner and outer circlet of regularly alternating, triangular plates. Outer plates widely overlap inner ones along tightly fitting oblique sutures and expose only a thin central strip of the inner plates. In large adults the bases of the outer plates are commonly in contact externally, the overlapped inner plates being exposed only in the more central sector of the structure. Thus, externally, the inner anals commonly appear lanceolate. The external shape of the inner plates varies within the structure due to the variable degree of overlap by the outer plates. Large adults average ten plates in each circlet.

A peripheral rim is formed at the base of the peduncular zone. The large plates of the proximal circlet and the smaller plates of the

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following one or two circlets are elongate, concentric with the thecal margin. The small plates of the distal three or four circlets are radially elongate. Large vertical ridges are found on the bases of at least the large, geniculate plates of the proximal circlet of the rim.

External plate surfaces are smooth.

Specimens:

U.S.N.M. S-3886 (A-B). Type series of Lepidodiscus laudoni (Bassler) (1936, p. 21, pl. 3, fig. 7-8, as Discocystis laudoni). Gilmore City Formation, Kinderhookian Series, Mississippian. Gilmore City, Iowa.

U.S.N.M. S-3886-B. Lectotype of L. laudoni (Bassler). 29.4 mm axial by 30.1 mm transverse diameter.

Pl. 49, fig. 1-4.

The lectotype is incomplete, but preserves: the oral-hydropore region; the proximal parts of all the ambulacra, I and V complete; interambulacra 4 and 5; and, the anal structure. These structures include most of the taxonomically important features, and thus, the loss of the distal parts of ambulacra II-IV and interambulacra 1-3 do not hinder interpretation. The lower part of the theca is completely hidden. Thecal collapse has accentuated the height of the oral-ambulacral structures and partially has disrupted the interambulacrals. However, the oral-ambulacral plating has been little disrupted with the exception of minor plate shifting in the central posterior part of the oral region. Plates immediately posterior to the center of the oral region appear to form an elevated connection between the hydropore

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protuberance and the central oral rise. This feature has not been found in most other specimens, and is apparently preservational.

U.S.N.M. S-3886-A. Lectoparatype of L. laudoni. 29.5 mm axial by 28.4 mm transverse diameter.

Pl. 49, fig. 5-6.

This specimen is more complete than the lectotype, missing only the distal part of ambulacrum III and many of the peduncular zone and peripheral rim plates. However, the oral, hydropore, and oral frame structures, and the proximal parts of all five ambulacra are completely disrupted. The completely collapsed specimen is nearly free of matrix and exposes both the upper oral surface and parts of the peduncular zone plates on the lower side of the specimen. Where lower surface plates are missing, the inner side of the upper oral surface is exposed, including: the floorplates of ambulacra I-II; interambulacrals in 1, and parts of 2 and 5; part of the anal structure; and, the disrupted oral frame area. This individual complements the lectotype and preserves the distal curvature of ambulacra II-IV, the ambulacral floorplates, and some of the lower surface peduncular zone plates. Ambulacral coverplates are mostly well-preserved in the central and distal parts. Interambulacrals are little disrupted in 1 and 5. Preservationally formed striations are common on the smaller, nearly vertical, collapsed interambulacrals which flank the adradial sutures of the ambulacra. Ambulacrum II bifurcates as it approaches the ambitus and forms two equal distal branches. This is the only specimen

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of L. laudoni in which an extra or anomalous ambulacrum has been observed.

U.S.N.M. S-3884. L. laudoni illustrated by Bassler (1936, pl. 3, fig. 6) as Discocystis kaskaskiensis. "Chester Group", Chesterian Series, Mississippian. Grayson County, Kentucky. 33.8 mm axial by 27.2 mm transverse diameter.

Pl. 49, fig. 7-12.

The specimen is preserved with the upper oral surface imbedded in matrix and exposes the lower side of the theca. As viewed from the lower side, the right half of the specimen preserves the exterior of the peduncular zone plates, although the basal rim is missing. These peduncular zone elements have been lost from the left side, which exposes the inner sides of the upper oral surface plates, including the floorplates of ambulacra IV and V, and interambulacral plates of 4, and parts of 3 and 5. The central oral frame region is unfortunately obscured by tenacious matrix.

A small distal segment of ambulacrum IV, separated from the remainder of the theca by several missing plates, exposes the ambulacral coverplate pattern when viewed obliquely.

Bassler (1936) illustrated this individual as a Discocystis kaskaskiensis. However, the ambulacral coverplate pattern seen in the distal fragment of ambulacrum IV (pl. 49, fig. 9-10) is that of L. laudoni. A five-plate cycle is preserved, comparable to the part of the ambulacrum seen in text fig. 53B, distal to the insertion zone of the final set of cycle plates. Moreover, the thin, imbricating

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plates of the peduncular zone appear to be separated from the ambitus by only a few interambulacrals pertaining to the transition zone as is the case in other L. laudoni.

S.U.I.C. 12545, 12546. L. laudoni. The type specimens of Discocystis priesti Strimple (1967). Pella beds, (St. Louis or Ste. Genevieve Limestone), Meramecian Series, Mississippian. Abandoned County quarry, N.W. $\frac{1}{4}$, N.W. $\frac{1}{4}$, sec. 9, T.25N., R.18W., Marian County, west of Harvey, Iowa.

S.U.I.C. 12545. Holotype of Discocystis priesti Strimple. 15.5 mm axial by 15 mm transverse diameter.

Text fig. 52A-B, 53B, 54B, pl. 50, fig. 1-7.

The specimen is a small adult Lepidodiscus laudoni. The clavate theca has collapsed and the upper oral surface is depressed against the lower, collapsed peduncular part of the theca. Plate disruption is most pronounced in the medial parts of ambulacra I and II, and the adjacent interambulacra . However, the oral-hydropore area, and many of the ambulacral coverplates are little disrupted and preserve the distribution patterns of the plates. Abrasion of the oral region has leveled off the upper ends of the plates. Text fig. 52A-B, 53B outline the plating of the oral-hydropore area and the ambulacral coverplate sequence. The complete six-plate cycles of coverplates are developed proximally.

This edrioasteroid has been separated from the brachiopod upon which it rested in life, and exposes the lower oral surface plates,

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below the ambitus. The interambulacrals of the sub-ambital transition zone form the outer or proximal part of the lower surface and are in two or three irregular "circlets". The transition plates are succeeded by the thin, sub-rectangular, imbricate plates of the peduncular zone. Only the upper or proximal parts of the columns of plates of the peduncular zone are visible when the specimen is whitened (pl. 50, fig. 5), because the center of the lower surface is covered with secondary calcite. This externally preserves the impression of the brachiopod shell on which the specimen rested. However, when the specimen is under xylene (pl. 50, fig. 6), the secondary calcite becomes transparent and exposes the more distal or lower parts of the theca (text fig. 54B). Under the secondary calcite, the plates of the peripheral rim are preserved in life orientation, their basal surfaces directed downward against the resting site (i.e., the basal surface is exposed when viewed from the lower side of the specimen). During collapse the outer or external sides of the plates of the lower peduncular zone were depressed against the outer surface of the peripheral rim plates. These lower peduncular zone plates are thus hidden from view in the collapsed specimen and now lie directly above the peripheral rim plates (i.e., under them when viewed from the lower surface of the specimen). As seen from the lower side of the specimen, the large plates of the proximal rim circlet are nearest the center of the specimen, surrounded by the more distal circlets of plates. The rim includes six or seven circlets, the plates decreasing in size outward, i.e., distally. The large geniculate plates of the proximal circlet, located

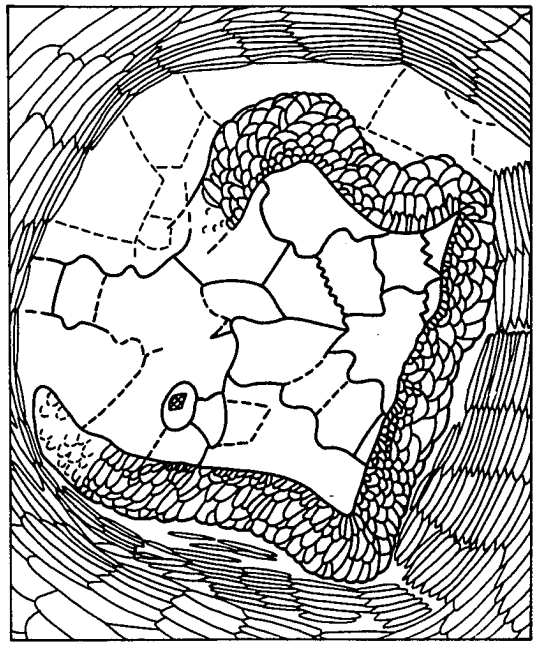
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Text Figure 54 Lepidodiscus laudoni (Bassler), 1936

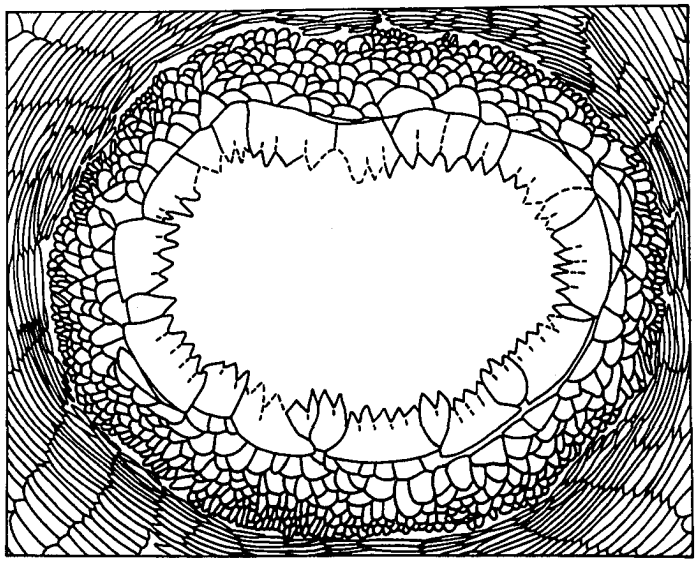
A. Central part of lower surface of S.U.I.C. 12546, (X10), pl. 50, fig. 11.

B. Central part of lower surface of S.U.I.C. 12545, (X10), pl. 50, fig. 7.

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A



B

Text Figure 54

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nearest the center of the lower side, bear large vertical ridges on their basal surfaces. These plates are tilted outward slightly and thus the proximal ends of the ridges appear to extend toward the center of the specimen as acuminate projections. The plates of the surrounding, more distal, rim circlets are also geniculate, but basal ridges were not observed. The smallest rim plates form the outermost or distal circlet of rim plates which lie furthest from the center of the lower surface. Surrounding these plates, the external sides of the central peduncular zone plates are exposed.

The proximal circlet of rim plates surrounds a non-plated, central, oral area, filled with secondary calcite. This zone is the center of the aboral surface and was probably covered by a soft membrane, in contact with the adjacent brachiopod surface. The inner sides of a few of the plates of the upper oral surface can be seen through the secondary calcite which fills the collapsed thecal cavity.

S.U.I.C. 12546. Paratype of Discocystis priesti Strimple. 11.6 mm axial by 10.7 mm transverse diameter.

Text fig. 53A, 54A, pl. 50, fig. 8-12.

This specimen is another small adult L. laudoni. The clavate theca has collapsed, depressing the upper oral surface against the collapsed lower peduncular zone. Freed from its resting site, the specimen exposes both the upper and lower parts of the theca. The oral and hydropore plates, interambulacrum 3 elements, and, some of the peduncular zone plates are disrupted.

The upper oral surface structures are comparable to those found

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in specimen S.U.I.C. 12545. Text fig. 53A shows the mode of cyclic coverplate insertion in the distal part of ambulacrum I. During collapse, the upper oral surface was depressed, but it maintained some of its original upward convexity. The peduncular zone and peripheral rim plates have been pressed against the inner surface of the convex upward upper oral surface; their external surfaces thereby are convex upward inside the upper surface plates (text fig. 54A). The distal peduncular zone and adjacent rim plates now lie within the thecal cavity area, surrounding the oral frame. However, in contrast with the above specimen, the peripheral rim has not maintained its life orientation. Rather, the proximal rim circlets remain in life orientation, but the distal circlets of smaller plates have curled down and under the proximal rim plates. Thus, when viewed from the lower side of the specimen, the external surfaces of the distal rim plates are exposed. The larger plates of the proximal circlet are almost entirely hidden beneath the outer circlet plates. The basal surfaces of two large proximal rim plates, along with their large, vertical ridges, are seen projecting inward from the rim, adjacent to ambulacrum IV. Distorted during preservation, the rim follows an irregular course of nearly straight segments joined by abrupt angles. Moreover, a small section of the rim appears to be missing in the area of ambulacra I and II. Thus the segment of the rim lying on the inner surface of interambulacrum I appears to end, as does the segment lying adjacent to the proximal part of ambulacrum III. Many of the plates of the distal peduncular zone are missing or hidden, thereby separating the rim from the peduncular

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ular zone. Along the anterior margin of the rim, the inner sides of the upper oral surface plates are exposed between the rim and the peduncular plates. The peculiar preservation of the rim in this specimen led Strimple (1968, p. 262) to describe it as a "long slender tube . . . presumed to be the stone canal."

In the center of the specimen's lower surface the oral frame and central lumen are exposed (text fig. 54A, pl. 50, fig. 12). Abrasion and etching have obscured some plate boundaries, particularly in the area of ambulacra IV and V. The frame appears to include only the enlarged proximal ambulacral floorplates. The inner end of the stone-canal passageway is exposed along the posterior margin of ambulacrum V, but plate boundaries are not distinct in this area.

The suture line between the proximal and second floorplates of ambulacrum II appears to be crenulate. This suggests a syzygial suture, locking the plates together. Similar suture development has not been observed in any other edrioasteroid specimen, and is only questionably preserved here.

U.I.P.C. Z6-B. Lepidodiscus laudoni. Gilmore City Limestone, Kinderhookian Series, Mississippian. University of Illinois locality Z6, one mile northwest of Gilmore City, Iowa. J. L. Carter, collector (1967). 30 mm axial by 22 mm transverse diameter.

Pl. 51, fig. 1-4.

The theca of this specimen has collapsed; the upper oral surface is nearly flat. The theca is slightly compressed and transversely shortened. The right side is disrupted and partially missing. Plating

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of the oral-hydropore area, ambulacra I-III, V, interambulacra 1, 2 and 5, and the anal structure is well-preserved. The lower side of the specimen preserves the proximal plates of the peduncular zone, pressed against the inner side of the plates of the upper oral surface. The remainder of the peduncular zone and the basal peripheral rim are missing which exposes the inner side of the upper oral surface plates. Proximal floorplates are seen in ambulacra I-II. The oral frame is exposed, but only the left side (right when viewed from the lower side of the specimen) is well-preserved. The tessellate plates of interambulacra 1, 2 and 5 are also exposed. The inner side of the anal structure is largely covered with recalcitrant matrix, but the triangular shape of the plates comprising the inner circlet can be seen.

N.Y.S.M. 12778. L. laudoni. Glen Dean Limestone, Hamburg Group, Chesterian Series, Mississippian. Morrow County, Kentucky. W. H. White, Jr., collector (1968). 24 mm long by 13.2 mm wide.

Pl. 51, fig. 5-8.

This specimen is a fragment of a large adult which exposes the upper, ambulacral tunnel, surfaces of ambulacral floorplates where the coverplates have been eroded away. The deep central trough and sloping lateral articulation zones are exposed. The lateral edges of the inner or lower surfaces of the floorplates appear to abut adjacent interambulacrals along irregular sutures, because complementary ridges and grooves are developed along the zone of contact. Coverplates are preserved proximal to the zone of exposed floorplates and form the typical six-plate cyclic sequence. The distal part of another

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ambulacrum is also preserved. Apparently located distal to the insertion zones of several of the coverplate sets, the cycles in this distal ambulacral segment include two plates distally, three plates in the more proximal part of the segment.

A large suite of L. laudoni specimens from the Monteagle Formation, Ste. Genevieve, Mississippian, of Madison County, Alabama, has also been examined during this study. The specimens range in size from 10 to 40 mm in upper oral surface diameter. Thecal collapse is commonly vertical, depressing the specimens into nearly flat disks. However, some of the specimens apparently toppled sideways, and although laterally compressed, they preserve distended peduncular zones and allow interpretation of thecal height. Specimens approximately 35 mm in upper oral surface diameter average 50 mm in height (see I.U.P.G. 10837-19, pl. 51, fig. 9-10).

Discussion:

Bassler (1936, p. 21) suggested Discocystis laudoni is "distinguished by its narrow, well developed long ambulacra curving decidedly throughout their length", and thereby contrasted with other species of Discocystis in which the "ambulacra are comparatively straight for the first third of their length and curve rather abruptly."

Ehlers and Kesling redescribed Discocystis laudoni (1958) and, like Bassler, they used only the two type specimens. Although primarily interested in the pattern of cyclic ambulacral coverplates overlooked by Bassler, their extensive description of the species included

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most taxonomically important thecal structures. The above redescription of the species follows Ehlers and Kesling in most aspects, although additional specimens have allowed more complete analysis in some areas. Ehlers and Kesling reported the possible occurrence of a genital pore in specimen U.S.N.M. S-3886-B. "The posterior interambulacrum has a polygonal depressed area [to the right of the anal structure], apparently where one or more large interambulacral plates are missing from the specimen, which contains an elongate, narrow opening bordered by plates . . . much smaller than those in the adjacent area" (Ehlers and Kesling, 1958, p. 270). In other examples of L. laudoni this area is covered by large interambulacrals and those specimens which expose the inner side of this area do not have small inner plates below the large outer interambulacrals. Therefore, it appears that the "smaller" interambulacrals and supposed elongate opening in the lectotype results from breakage and depression of larger interambulacrals during preservation. They are not part of a genital pore structure as suggested by Ehlers and Kesling.

The holotype and one paratype of Strimple's Discocystis priesti (1968) are reillustrated here as small adult specimens of Lepidodiscus laudoni (text fig. 52A-B, 53A-B, 54A-B, pl. 50, fig. 1-12). Contrary to Strimple's interpretation, the ambulacral coverplates form six-plate cycles. This and other thecal features of these two specimens agree with those found in the type specimens of L. laudoni. Moreover, Strimple described the occurrence of a long, polyplated stone-canal in S.U.I.C. 12546. As seen in text fig. 54A, pl. 50, fig. 10-12, the

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supposed stone-canal is the outer circlets of peripheral rim plates, curled under the larger, proximal rim plates. Thecal collapse has left the rim pressed against the inner side of the upper oral surface, distorting and breaking the rim. The position, curling, and irregular broken path of the rim apparently misled Strimple as to the true identity of these plates.

Most clavate edrioasteroids are depressed during thecal collapse associated with preservation. The plates of the peduncular zone are usually telescoped together and pressed against the inner side of the upper oral surface. Fortunately, some specimens of Lepidodiscus laudoni from Alabama apparently toppled over sideways when buried. Although laterally compressed, these specimens preserve the original lateral outline of the inflated theca (pl. 51, fig. 9-10). As suspected from depressed specimens, the ambulacra are limited to the convex upward, upper oral surface. Below the ambitus of the upper gibbous part of the théca the transition zone interambulacrals and the following thin, sub-rectangular, imbricate peduncular zone plates form a downwardly tapering cone. Even in compressed specimens the numerous peduncular zone plates are highly imbricated. The basal peripheral rim flares outward against the substrate, but the total diameter of the rim is only one-fourth or less the diameter of the upper gibbous part of the theca. Thus, it must have been firmly attached to the substrate to prevent lateral toppling of the individual during life.

The large number of the thin plates of the peduncular zone, their high degree of imbrication, and the common, depressed preservational

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state, suggest that the theca was capable of great vertical extension and retraction. Specimens preserved in their extended state are often one and one-half times as high as the diameter of the upper gibbous head. The imbrication of the peduncular plates suggests that the theca could easily have been further extended, perhaps reaching heights two or two and a half times the "head" diameter. Depressed specimens preserve the thin imbricating peduncular plates telescoped together, with the upper plates slipped inside the lower ones. The lower plates overlap the contiguous higher elements, so that complete collapse of the peduncular zone requires lateral separation of adjacent lower plates due to the greater diameters of the upper circlets. Partially contracted specimens are also preserved; in these the total thecal height is only half the diameter of the upper gibbous area. These show no evidence of peduncular zone disruption, and thus, at least this degree of contraction was possible in life.

Vertical extension of the theca would raise the food gathering ambulacra above the sea-floor, a condition found desirable in other sedentary suspension feeding echinoderms. Retraction would lower the gibbous "head" and produce greater stability both by reducing the total area exposed to currents and also by lowering the center of gravity. If the peduncular zone were almost completely telescoped together, the ambitus of the upper convex oral surface would be pressed against the substrate. The theca would thereby assume a domal external shape and offer little resistance to turbulent waters and prevent lateral toppling of the theca.

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Support for this proposed contractibility is found in the mode of thecal preservation. Most specimens are depressed. Only a few have toppled sideways and were laterally compressed. Yet, a highly extended rigid clavate theca with a small basal attachment disk would most likely topple sideways during burial, precise vertical depression being quite unlikely. Thus, most specimens apparently contracted prior to burial, probably in response to the turbulent waters carrying the influx of sediment that buried them. Only a few were caught in the extended state and pushed over sideways.

Range and occurrence: Mississippian, of Iowa, Kentucky and Alabama.

Lepidodiscus sampsoni (Miller), 1891

Text fig. 55; plate 51, fig. 11-13, plate 52.

1891 Echinodiscus sampsoni Miller, S. A., Geol. Surv. Indiana, 17th Ann. Rept. (adv. pub.): 76, pl. 12, fig. 16.

1892a Echinodiscus sampsoni Miller, S. A., First Appendix to North American Geology and Palaeontology, Cincinnati: 678, fig. 1225.

1892b Echinodiscus sampsoni Miller, S. A., Geol. Surv. Indiana, 17th Ann. Rept.: 686, pl. 12, fig. 16.

1894 Echinodiscus sampsoni Miller, Keyes, C. R., Missouri Geol. Surv. 4 (1): 133.

1901 Discocystis sampsoni (Miller), Clarke, J. M., New York St. Mus., Bull. 49 (2): 182-198.

1904 Echinodiscus sampsoni Miller, Klem, M. J., St. Louis Acad. Sci., Trans. 14: 73-74.

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1943 Discocystis sampsoni (Miller), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 201.

Diagnosis:

A Lepidodiscus with: clavate or subclavate theca, plates distal to ambulacra squamose, imbricate; cyclic ambulacral coverplates perradially raised, forming small, distinct, perradial ridge; ambulacral floorplates abutting, each with four or more lateral projections on lower side; interambulacrals large, polygonal, tessellate.

Description:

Lepidodiscus sampsoni (Miller) is represented by the incomplete holotype and eight fragmentary or partially disrupted topotypes. The theca appears to have been clavate, with the ambulacra extending down to the ambitus of the convex upward oral surface. Below the ambitus a zone of squamose, imbricate plates apparently forms a short peduncular zone, thought to constrict slightly in diameter downward. A basal peripheral rim flares outward and forms a wide zone of contact with the substrate.

Plate boundaries in the oral region are obscure in available specimens. Text fig. 55B tentatively identifies some oral plate boundaries in the oral and hydropore areas of the holotype. The oral plates are variable in shape and size and apparently imperfectly mimic the ambulacral coverplate pattern. Orals thus appear to grade into the coverplate sequence without apparent break. Around thirty lateral, but only six or seven anterior, orals are included in the region and

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Text Figure 55 Lepidodiscus sampsoni (Miller), 1891

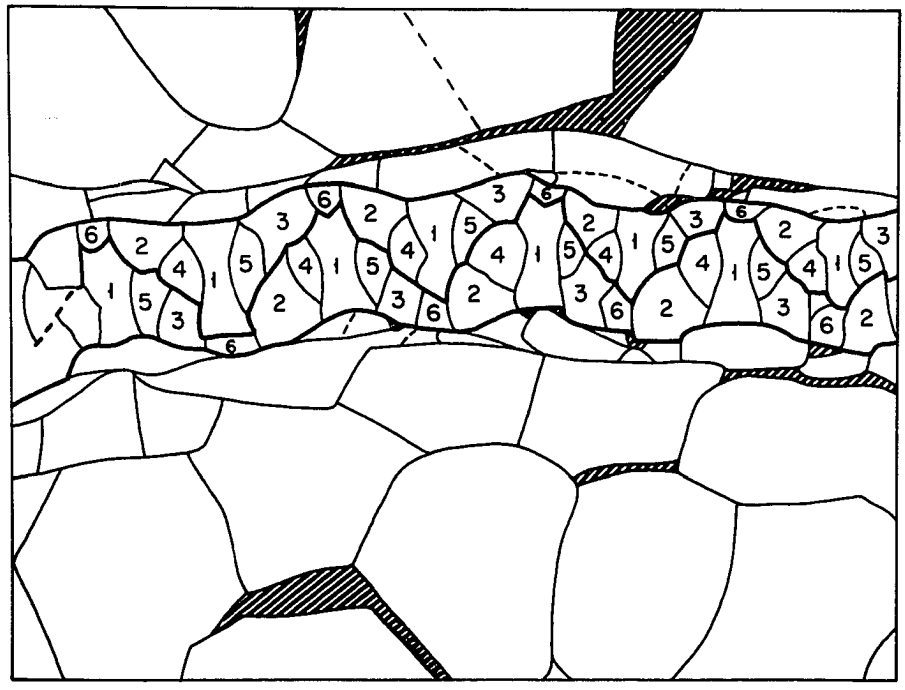
Holotype, C.F.M.-U.C. 7000.

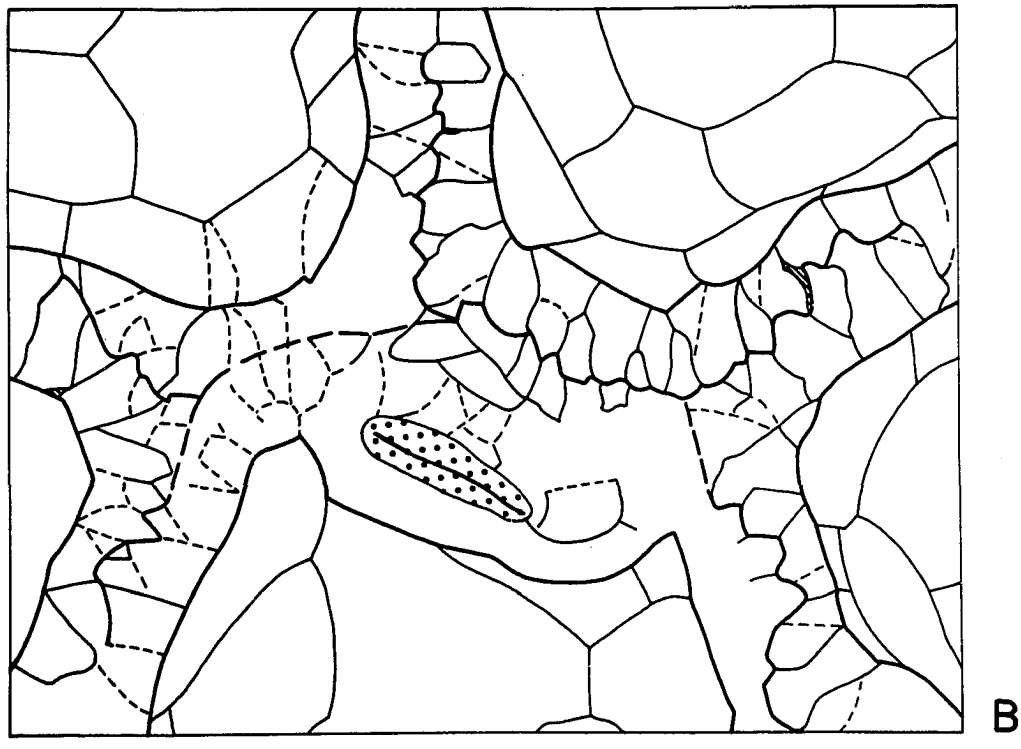
A. Proximal segment of ambulacrum V, (X15), pl. 52, fig. 4.

1. through 6. are the first through the sixth sets of ambulacral coverplates, respectively.

B. Oral area and adjacent structures, (X15), pl. 52, fig. 2. Broken upper ends of the hydropore structure plates are marked by a dotted pattern.

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Text Figure 55

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thereby form a transverse elongation in the oral area outline. Primary orals are not externally differentiated from other orals.

The hydropore structure is a large, elongate mound which arises from the posterior margin of the central oral rise (text fig. 55B, pl. 52, fig. 1-2). It extends in an oblique lateral direction from the right part of the left half of the posterior oral region toward the proximal posterior edge of ambulacrum V. The plates included in the structure are upturned and form the steep, nearly vertical sides of the protuberance. The elongate, slit-like hydropore extends along the summit of the prominence. Plate boundaries are obscure in the holotype, the only specimen which preserves the structure in non-disrupted state. Even in this specimen the summit has been leveled by abrasion which has removed the upper ends of the plates.

Ambulacral curvature is commonly uneven, the straight proximal segments being followed by pronounced curvature near the ambitus of the upper oral surface. Distal to the zone of pronounced curvature, the ambulacra extend concentric with the upper oral surface margin. Distally, ambulacrum V may curve back toward the oral area into inter-ambulacrum 5. Ambulacrum I and perhaps others may also exhibit distal curving back toward the oral region.

The ambulacral coverplates form six-plate cycles (text fig. 55A, pl. 52, fig. 3-4). Those on opposite sides of the perradial line alternate, offset by half the length of a cycle. The alternating cycles form a broadly undulating, zigzag, perradial line. Individual cycle plates occasionally form discrete perradial points which randomly

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superimpose small serrations onto the broader undulations. Plate sizes and shapes are similar to those found in other Lepidodiscus species. Thus, the plate sets described below are considered homologous to those of L. laudoni, although the order of insertion has not been completely verified in specimens of L. sampsoni.

Primary set plates are largest and longest and form the center of each complete six-plate cycle. The adradial bases of the primary plates are broad. The lateral margins converge slowly from the adradial suture line, but near their perradial end, they diverge for a short distance and form an expanded or swollen perradial end. The variable perradial margin may be pointed, nearly straight, or occasionally indented. This plate is opposed by the sixth set plate of the alternate cycle, which has a complementary perradial shape, i.e., sloping, straight, or pointed, respectively.

The moderately large plates of the secondary set lie proximal to the primaries. Their left lateral edges abut the adradial part of the lateral edge of the adjacent primary. These secondaries are sub-triangular to sub-rectangular with: wide adradial bases; nearly parallel, short, lateral margins which are approximately normal to the adradial suture line; and, a broad perradial point. However, commonly only the right side of the angular perradial end extends along the perradial line; the left side is in contact with the adjacent fourth series plate. Occasionally the right side of the pointed perradial end does extend outward perradially and thus the secondary forms a small, discrete, perradial line angulation. The third or tertiary set plates are mirror

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images of the secondaries, but lie distal to each primary cycle plate.

The quaternary set plates, smaller than plates of the first three sets, are sub-triangular to rhomboidal. Commonly limited to the axial part of the ambulacrum, they lie between the perradial ends of the primary and secondary set plates. Perradially, the margin of the quaternaries may be straight and form the sloping central part of the cycle undulation. In others it is angular and forms a small serration along the perradial line. The quintary or fifth set coverplates are mirror images of the quaternaries, lying between the perradial ends of the primary and tertiary plates of each cycle.

The sixth and final element is the smallest plate in the cycle. It lies proximal to the secondary plate along the adradial suture line. It may be rectangular, or pentagonal and perradially pointed, or occasionally sub-triangular. The proximal margin of this plate abuts the distal margin of the tertiary plate of the adjacent, proximal cycle.

The margins of the coverplates which flank the perradial line are upturned and form a small, distinct, perradial ridge along the undulating perradial line. Axially elongate interambulacrals overlap the adradial ends of the coverplates. The interambulacrals regularly extend further out over the central cycle plates and form a concave adradial suture line with the coverplates. The adradial suture lines are thus sinuous and each ambulacrum appears to have an undulating course.

The externally hidden adradial and ambulacral tunnel surfaces of

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the coverplates have not been observed in L. sampsoni.

Ambulacral floorplates are rectangular in plan view and elongate axially (pl. 52, fig. 9-11). Contiguous plates meet along vertical sutures. The inner or lower surface of each floorplate bears four large nodes which arise from the lateral parts of the convex inward lower surfaces. Two nodes are formed on each lateral margin, one directly above the other. The upper node appears to extend out under the adjacent interambulacrals, the upper side of the node in contact with the inner surface of these interambulacrals. The lower rounded node projects laterally and obliquely downward into the thecal cavity. On each plate the two lateral sets of nodes may lie directly across from one another or may be offset with either set proximal to the other. Occasionally additional pairs of nodes may be formed on a floorplate. Although suggested by only two fragmentary specimens, every second suture between the uniserial floorplates appears to be more firmly united, perhaps even fused (pl. 52, fig. 9-11).

The central parts of the interambulacra are formed by large, thick, polygonal, tessellate plates. Along the adradial suture lines, the interambulacrals are smaller, more elongate, and may imbricate slightly toward the adradial line. Distal to the ambulacra, apparently below the ambitus, the plates continuous with the interambulacral series are squamose and imbricate and form a slightly downward constricting, short, peduncular zone.

The valvular anal structure is located near the center of interambulacrum 5. It includes perhaps twelve or more large, triangular

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plates, apparently alternating as inner and outer circlets. Outer circlet plates overlap the inner ones along a narrow zone of overlap which externally exposes most of the upper surfaces of the inner plates.

The basal peripheral rim is formed by six or seven circlets. The structure is poorly preserved in available specimens.

The external surface of the thecal plates is minutely pustulate, reflecting the microstructure of the plates.

Specimens:

C.F.M.-U.C. 7000. Holotype of Lepidodiscus sampsoni (Miller), (1891, p. 76, pl. 12, fig. 16, as Echinodiscus sampsoni). Warsaw Formation, Keokuk Group, Osagean Series, Mississippian, Boonville, Cooper County, Missouri. 38.5 mm axial by 41 mm transverse diameter. Text fig. 55A-B, pl. 52, fig. 1-6.

The holotype is incomplete and preserves only the center of the upper oral surface. Most of the distal parts of the ambulacra, which curve concentrically with the margin of the upper oral surface, are missing, along with the distal interambulacrals and the posterior half of the anal structure. If any of the squamose, imbricate, peduncular zone plates or peripheral rim plates are preserved, they are hidden beneath the upper oral surface plates and matrix.

The upper oral surface of the specimen has collapsed against the substrate. The oral-ambulacral series, which is supported by the frame and ambulacral floorplates, remains elevated as prominent ridges above the collapsed interambulacrals. Oral-ambulacral series plates are little disrupted, but suture lines commonly have been obscured. The

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hydropore protuberance also appears to be intact, but plate boundaries are not discernible, and abrasion has leveled the summit of the structure. Interambulacrals are partially disrupted, especially along the ambulacral margins and the distal parts of the specimen. The ambulacral coverplate pattern is most clearly preserved in the remaining distal segments of ambulacra IV and V. The distal tip of ambulacrum V may be preserved to the left of the anal structure.

U.S.N.M. S-3888 (A-H). Nine specimens, seven of which appear to be fragments or partially disrupted topotypes of L. sampsoni. Warsaw Formation, Keokuk Group, Osagean Series, Mississippian. Booneville, Cooper County, Missouri.

U.S.N.M. S-3888-A. 37.3 mm axial by 36 mm transverse diameter.

Pl. 51, fig. 11.

This specimen has collapsed obliquely; the anterior part of the upper oral surface has been folded under the remainder of the theca. Many of the thecal plates are disrupted but outlines of the major structures are clear. The ambulacra curve, I-IV contrasolar, V solar. The distal tips of ambulacra I and V curve back proximally and extend into interambulacrum 5. The coverplate pattern appears to be like that of the holotype, but is mostly obscured.

U.S.N.M. S-3888-B. 26.4 mm greatest length.

Pl. 51, fig. 13.

This specimen is obliquely compressed. Ambulacra I, II, III, and interambulacra 1 and 2 are exposed on the "upper" side of the specimen.

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The other half of the upper oral surface is folded under the upper side and is completely jumbled. Ambulacral curvature, coverplate pattern, and the large polygonal, tessellate interambulacrals appear to be like those of other specimens of L. sampsoni.

U.S.N.M. S-3888-C. 22.7 mm axial by 22.1 mm transverse diameter.

Pl. 52, fig. 7.

This specimen is partially collapsed. Only the upper oral surface is well-preserved; it retains some of its original convexity. Although most plates appear to be little disrupted, surficial etching has obscured most plate boundaries. The right side of the oral area and the hydropore structure appear to be little disturbed. The ambulacra rise above the interambulacral areas as low rounded ridges. Curvature agrees with the other specimens of this species. Distally, ambulacra I and V curve back proximally into interambulacrum 5. Other ambulacra may be similarly curved distally. The ambulacral coverplate pattern is obscure in all of the ambulacra. The anal structure is elevated into a low, sub-conical mound near the center of interambulacrum 5.

U.S.N.M. S-3888-D. 18.3 mm axial by 20.4 mm transverse diameter.

Pl. 51, fig. 12.

This specimen has collapsed and most plates are disrupted. Depression was oblique, folding the posterior part of the upper oral surface onto the lower side of the specimen. The five curved ambulacra are recognizable, but are disrupted. All of the interambulacrals are jumbled. The specimen does preserve one section of plates of the

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squamose, imbricate peduncular zone, distal to ambulacra III and IV. A small, anterior segment of the peripheral rim lies adjacent to these peduncular zone plates.

U.S.N.M. S-3888-F. 21 mm axial by 10.5 mm transverse diameter.

Pl. 52, fig. 8.

This specimen has collapsed and is laterally compressed. Plates are mostly jumbled. However, several of the large proximal rim plates are seen along the posterior margin of the theca. Small adjacent plates, now disrupted, probably represent the more distal plates of the rim.

U.S.N.M. S-3888-G. 17.5 mm long by 10.9 mm wide.

Pl. 52, fig. 9-10.

This specimen is a fragment of a large adult and exposes seven ambulacral floorplates and adjacent interambulacrals. The specimen suggests every second floorplate suture is more tightly joined, perhaps even fused. The large lateral knob-like nodes are found on the floorplates, four per plate.

U.S.N.M. S-3888-H. 12.5 mm long.

Pl. 52, fig. 11.

Another fragment of an ambulacrum, this specimen also exposes the ambulacral floorplates. Each appears to bear six or eight inner surface lateral nodes rather than four, as seen in the above specimen. Every second floorplate suture again appears to be more tightly joined.

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Discussion:

S. A. Miller (1891, p. 76) briefly described Echinodiscus sampsoni as: "circular", interambulacra flat, depressed; ambulacra higher than wide; interambulacrals large, tessellate; "orals" [anals] partially preserved, located over one-half inch from the central pole; ambulacra long, proximally straight, curved distally; ambulacral coverplates numerous, small, "thrown into a waving line on top". The accompanying illustration depicts the broken outline of the theca, the tessellate, polygonal interambulacrals, and, the adradially undulating course of the ambulacra. Ambulacral plating is not shown.

The incomplete nature of the holotype, combined with the superficial original description, relegated Lepidodiscus sampsoni (Miller) to obscurity, for most subsequent authors have ignored it. Thought to be similar to Discocystis kaskaskiensis, most authors listed L. sampsoni under the genus Discocystis (the name substituted for the preoccupied Echinodiscus) without redefinition of the thecal features.

Lepidodiscus sampsoni (Miller) remains inadequately known. However, location of several topotypes in the United States National Museum has allowed confirmation of the ambulacral curvature direction. Moreover, these topotypes preserve the squamose, imbricating plates of the short peduncular zone, and parts of the basal peripheral rim. Two fragmentary specimens expose the only view of the ambulacral floorplates. Unfortunately, the topotypes are either poorly preserved or fragmentary, and do not preserve many thecal details that are also obscure on the fragmentary holotype.

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L. sampsoni is differentiated from other clavate Lepidodiscus species by its peduncular zone which is short, only slightly constricted, and composed of moderately thick, squamose, imbricate plates. Moreover, individual plate shapes in the six-plate cycles of ambulacral coverplates are distinctive. Most apparent is the unique shape of the elongate plates of the primary set which perradially expand in width.

The hydropore protuberance may also be unique for apparently it extends far into the left half of the posterior oral region. In most other species of Lepidodiscus, this structure ends at or near the axial midline. Unfortunately, the details of the hydropore plating are unknown. Oral and anal area plating are also inadequately represented in the available specimens.

Range and occurrence: Osagean Series, Mississippian of Boonville, Missouri.

Ulrichidiscus Bassler, 1935

1935 Ulrichidiscus Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 8, pl. 1, fig. 7.

1936 Ulrichidiscus Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 22.

1938 Ulrichidiscus Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 190.

1943 Ulrichidiscus Bassler, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 209.

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1966 Ulrichidiscus Bassler, Regnéll, G., in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U171, text fig. 128-5.

Type species: Agelacrinus pulaskiensis Miller and Gurley, 1894.

Diagnosis:

Agelacrinitidae with: high domal or sub-clavate theca; numerous oral plates, primary orals undifferentiated; large hydropore structure separated from central oral rise; ambulacra curved, I-V contrasolarly, coverplates form seven-plate cyclic sequence; interambulacrals polygonal or squamose, tessellate or slightly imbricate; valvular anal structure with two circlets of plates.

Description:

Ulrichidiscus is monotypic. Therefore, separation of generic and specific taxobases is uncertain. Features outlined in the above diagnosis are inferred to be of generic rank from extablished taxobases of related Agelacrinitidae genera.

Discussion:

Diagnostic features of Ulrichidiscus noted by Bassler (1935, p. 8) were: "Body semiglobose with the oral side occupied by five narrow but well-defined, very long ambulacra all strongly curving to the left, with a well-defined anal pyramid of many long triangular plates in one circlet, and interambulacral areas composed of polygonal but slightly imbricating plates". Regnéll (1966) repeated Bassler's definition,

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adding thecal size of the type species and noting the large size of the interambulacrals.

In addition to the characters noted by Bassler, the cyclic ambulacral coverplates in a seven-plate series separates Ulrichidiscus from other genera of Agelacrinitidae.

Range and occurrence: Glen Dean Limestone, Hamburg Group, Chesterian Series, Mississippian of Kentucky.

Ulrichidiscus pulaskiensis (Miller and Gurley), 1894

Text fig. 56-58; plate 53, plate 54, fig. 1-7.

1894 Agelacrinus pulaskiensis Miller, S. A. and Gurley, F. E., Illinois St. Mus. Bull. 5: 16, pl. 3, fig. 18.

1897 Agelacrinus pulaskiensis Miller and Gurley, Miller, S. A., Second Appendix to North American Geology and Palaeontology, Cincinnati: 733.

1935 Ulrichidiscus pulaskiensis (Miller and Gurley), Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 8, pl. 1, fig. 7.

1936 Ulrichidiscus pulaskiensis (Miller and Gurley), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 22.

1938 Ulrichidiscus pulaskiensis (Miller and Gurley), Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 190.

1943 Ulrichidiscus pulaskiensis (Miller and Gurley), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 209.

1966 Ulrichidiscus pulaskiensis (Miller and Gurley), Regnéll, G., in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U171, text fig. 128-5.

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Diagnosis:

An Ulrichidiscus with: large, high domal, or subclavate theca; distal oral plates reflect ambulacral coverplate pattern and appear to grade into proximal ambulacrals; large separate hydropore structure protuberance formed by many plates, anterior hydropore plates do not reach transverse oral midline perradially; ambulacra long, moderately narrow; valvular anal structure large, formed by alternate inner and outer circlet plates.

Description:

Ulrichidiscus pulaskiensis is represented by only four specimens, the moderately well-preserved holotype, and three presumed topotypes. The theca appears to have been either a highly convex dome, or subclavate. The ambulacra curve distally concentric with the margin of the convex upper oral surface. Distal to the ambulacra, numerous irregular circlets of squamose imbricate plates form an elongate zone which was either nearly vertical or perhaps slightly constricting downward, thereby forming a sub-clavate theca. Distal to this zone, the peripheral rim flares outward in contact with the substrate. The diameter of the upper oral surface reached thirty millimeters. The diameter of the basal peripheral rim probably equalled or exceeded that of the upper oral surface.

The transversely elongate oral area includes numerous plates (text fig. 56A, 57, pl. 53, fig. 5, 12). Primary orals are not differentiated externally. Most orals are smaller than or equal in size to the proximal ambulacral coverplates. Those which form the anterior

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Text Figure 56 Ulrichidiscus pulaskiensis (Miller and Gurley), 1894
Holotype, C.F.M.-U.C. 6419.

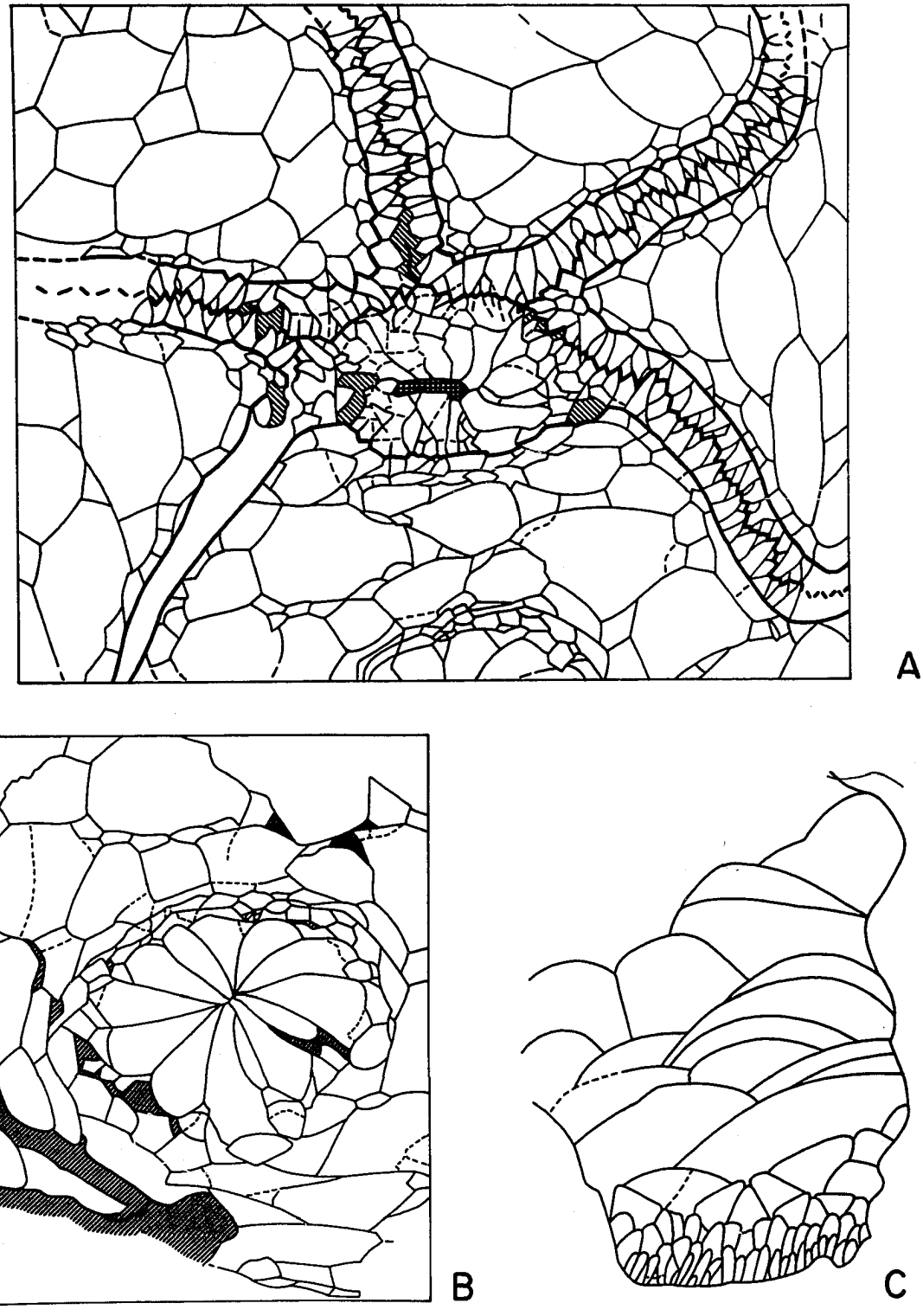
A. Oral area and adjacent structures, (X10), pl. 53, fig. 5.

B. Anal area and adjacent interambulacral plates, (X10), pl. 53, fig. 7.

C. Segment of the basal peripheral rim and adjacent pedunculate zone plates, (X10), pl. 53, fig. 3.

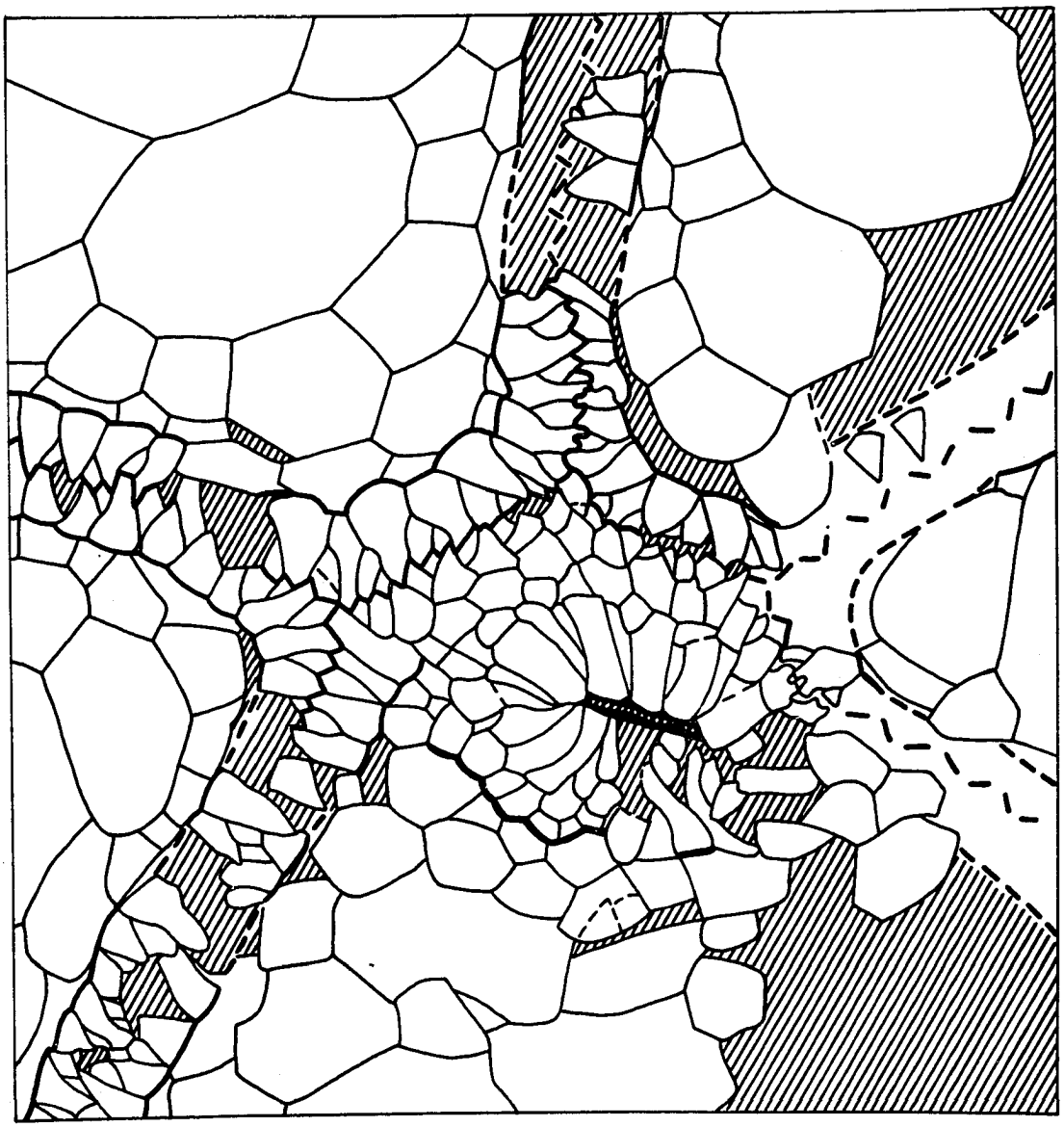
Text Figure 57 Ulrichidiscus pulaskiensis (Miller and Gurley), 1894
Oral area and adjacent structures, U.S.N.M. S-3193-A, (X14), pl. 53, fig. 12.

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Text Figure 56

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Text Figure 57

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oral midline and the anterior side of the transverse oral midline partially mimic the cyclic ambulacral coverplate pattern. Thus, distally, they appear to grade into the ambulacrals without apparent separation between the two series. The posterior side of the area, posterior to the transverse oral midline, includes many more plates than the anterior side. A zone of small orals, one to two plates wide, flank the adradial ends of those orals which perradially form the posterior margin of the transverse oral midline. The hydropore structure plates lie posterior to these elements, further widening the posterior side of the oral area. In contrast, only a single series of plates form the anterior side of the transverse oral midline.

The anterior oral midline extends directly outward along the axial midline of the theca. In contrast, the transverse oral midline is V-shaped with the anteriorly directed central point meeting the anterior oral midline. The perradial tips of those oral plates which flank the oral midlines are flexed upward and form a small, distinct central ridge.

The large, transversely elongate, hydropore protuberance arises from the posterior margin of the central oral rise (text fig. 56A, 57, pl. 53, fig. 5, 12). It extends along two-thirds of the posterior side of the oral area, from the proximal posterior edge of ambulacrum V over to the left half of the oral region. The structure is formed by many, elongate plates, including approximately twelve wide and twenty narrow ones, all sloping upward to form the steep sides of the prominence. The wide plates reach the summit of the elevation where

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they are laterally in contact. One or two narrow plates are wedged between the basal ends of each two contiguous large plates and appear to end externally just below the summit of the structure. The large outer plates may overlap the more narrow ones. The hydropore opens along the summit of the transversely elongate protuberance.

The large, moderately narrow, ambulacra curve contrasolarly. Commonly, curvature is gradual and is initiated near the oral region. The distal parts gradually become concentric with the margin of the upper oral surface. Occasionally, curvature is more abrupt with a straight proximal zone followed by a pronounced curved area as the ambulacrum approaches the upper oral surface margin. The distal part of each long ambulacrum is concentric with the margin of the adjacent ambulacrum, but they remain separated by several interambulacrals.

The ambulacral coverplates form seven-plate cyclic sets. Cycles on opposite sides of the perradial line alternate, offset by half the length of a cycle, and form a broadly undulating, zigzag, perradial line. Individual plates of the cycles are perradially pointed, superimposing small serrations along the large undulations. Homologous plates in adjacent cycles vary somewhat in shape but maintain a constant relationship to the other plates of the cycle.

Actual plate shapes are shown in text fig. 56A and 56B. These are somewhat regularized in text fig. 58A, which tentatively identifies the plates by their order of insertion. Plates of set one, two and three are generally sub-triangular with broad adradial bases and pointed perradial ends. Plates of set one are the largest and longest,

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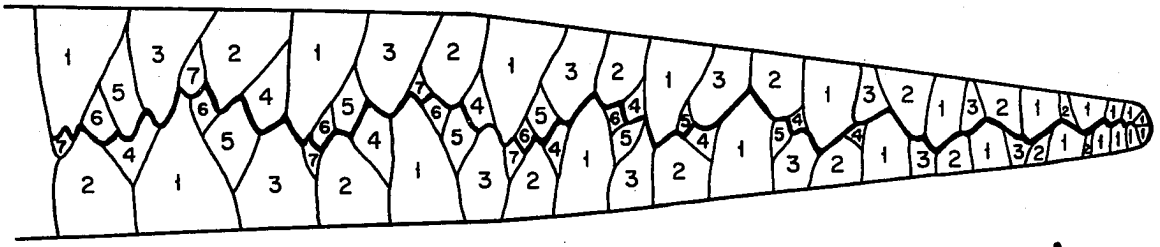
Text Figure 58 Ulrichidiscus pulaskiensis (Miller and Gurley), 1894

A. Model of ambulacral coverplate development showing the mode of formation of the seven-plate cycles.

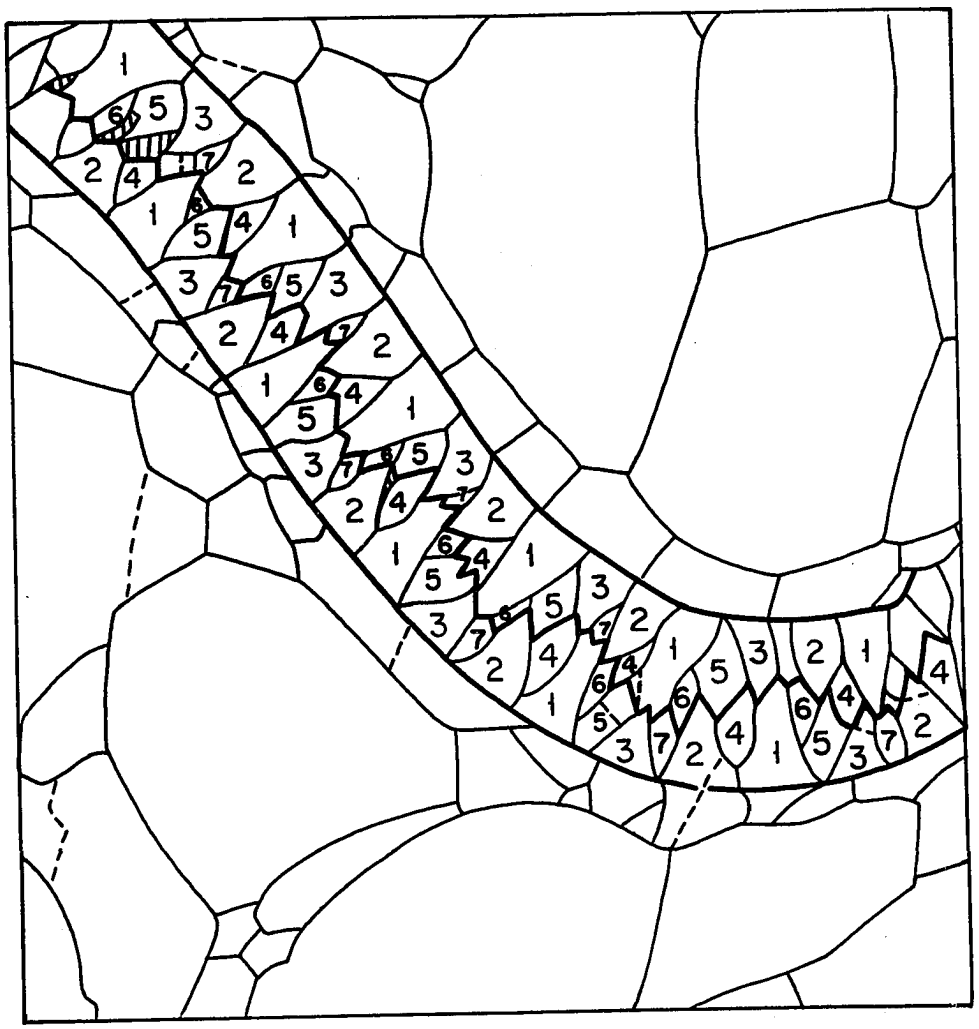
B. Proximal segment of ambulacrum V and adjacent interambulacrals, holotype, C.F.M.-U.C. 6419, (X25), pl. 53, fig. 6.

1. through 7. are the first through seventh sets of ambulacral coverplates, respectively.

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A



B

Text Figure 58

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plates of set two and three are nearly equal in shape and are intermediate in size. Plates of set four and five are often similar in size, both smaller than the plates of sets two and three. Plates of set six and seven are commonly very small. Modifications of those plate shapes shown in the text figures occur when a single plate forms two perradial points and the angular perradial tip of an opposing cycle plate fits between the double points.

The order and position of insertion of the coverplate sets is tentatively reconstructed in text fig. 58A, a schematic regularization of the distal part of an ambulacrum. In the drawing, one new set is included in each successive cycle, except for the distal most plates. Specimens suggest the plates of the first set (primary) are added singly at the distal tip and move alternately left and right. Plates of the second set (secondaries) are added about three primary plates from the ambulacrum tip. They are inserted along the proximal sides of the primaries. Third set plates (tertiaries) are added three or four two-plate cycles proximal to the insertion zone of the secondary set, and are inserted along the distal sides of the primaries. After four to seven three-plate cycles, the plates of the fourth (quaternary) and fifth (quintary) sets are added in adjacent cycles, four inserted between the perradial tips of primary and secondary plates, five between the perradial tips of primary and tertiary set plates. In a few instances, the elements identified as plates of the fifth set appear to be added before those of the fourth set. Plates of the sixth set are inserted one or two five-plate cycles proximal to the zone of

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insertion of the plates of the fifth set. These sixth set plates are formed between the perradial tips of the primaries and the quintaries. The seventh and final set of plates is inserted two six-plate cycles proximal to the insertion zone of the sixth set. These plates of the seventh set are added proximal to the tip of the secondaries and thus, distal to the tips of the plates of the third set of the adjacent, proximal cycle.

The interpretation of the coverplate insertion zones is based on isolated segments of ambulacra in three specimens. It thus remains tentative, particularly for the fourth and fifth sets, and perhaps also for the sixth and seventh sets. Fracturing of larger plates may be responsible for some of the apparent irregularity in the insertion sequence. In the proximal part of the ambulacra, anomalous plates occasionally appear to be present. These may also be due to fractures rather than to sutures.

Sutures between contiguous plates of the cycles appear to be vertical, without suggestion of lateral overlap. Thus, smaller coverplates are apparently limited to the axial part of the ambulacra both externally and internally. Inner surfaces of the coverplates have not been observed.

Isolated ambulacral floorplates are exposed on the jumbled lower surface of one specimen (pl. 53, fig. 10). Apparently the floorplates are extremely thick. The upper surface is centrally concave downward and forms a deep central trough which is flanked by narrow, upper lateral margins that slope slightly toward the trough. The lower or

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inner surfaces of the floorplates expand laterally and have a broad base. Below the laterally expanded zone, the inner surface may be evenly convex inward. Sutures between contiguous floorplates are vertical.

The interambulacral plates are large and polygonal in the central parts of the interambulacra, and smaller and more squamose where they flank the adradial sutures. Interambulacrals abut one another, or are slightly imbricate. Distal to the ambulacra, the plates of the marginal or peduncular zone are large, thick, squamose and imbricate.

The valvular anal structure is unusually large, and fills the entire central part of interambulacrum 5. Well-preserved only in the holotype (text fig. 56B), it includes approximately fourteen large, triangular plates which alternate as inner and overlapping outer circlet members. Some of the inner ones may have been hidden during preservation.

The peripheral rim forms the base of the theca; it includes five or six circlets. The very large plates of the proximal circlet are surrounded by small, externally triangular plates; the apices of adjacent ones are directed alternately proximal and distal. The outer three or four circlets include small plates, either radially elongate (text fig. 56C, pl. 53, fig. 3), or similar to the second circlet plates, externally triangular with adjacent plates pointing alternately proximal and distal (pl. 54, fig. 1). A few isolated large plates, exposed on the jumbled lower side of specimen U.S.N.M. S-3193-A, are tentatively identified as proximal rim plates. They are geniculate and

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appear to bear small vertical, basal ridges, perhaps five per plate.

Thecal plate exteriors are smooth, except for minute pustulation which reflects the microstructure of the plates.

Specimens:

C.F.M.-U.C. 6419. Holotype of Ulrichidiscus pulaskiensis (Miller and Gurley) (1894, p. 16, pl. 3, fig. 18, as Agelacrinus pulaskiensis), "Kaskaskia Group", Chesterian Series, Mississippian. Pulaski County, Kentucky. 23.8 mm axial by 24.3 mm transverse diameter.

Text fig. 56A-C, 58B, pl. 53, fig. 1-7.

The holotype is moderately well-preserved. The upper oral surface retains much of its original convexity. However, plates distal to the ambulacra have been folded under and pressed against the inner sides of the upper plates. Many of these lower plates are missing. The oral region and entire lower side of the specimen was covered with resistant matrix prior to this study.

Fracturing of the oral and some hydropore structure plates obscures the relationship of some of the plates in this area (text fig. 56A). The outline of all five ambulacra is distinct, but coverplates are well-preserved only in the proximal parts of ambulacra III-V. Interambulacral and anal plates are little disrupted (text fig. 56B). One complete section of the plates distal to the ambulacra, including the basal peripheral rim, is preserved on the lower side of the specimen (pl. 53, fig. 2-3). The total length of this series is approximately 15 mm. Added to the convex upper oral surface height, approximately 13 mm, the total non-collapsed thecal height appears to have been at

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least 25-30 mm.

U.S.N.M. S-3193 (A-C). Three specimens of U. pulaskiensis, believed to be topotypes. Chesterian Series, Mississippian. Pulaski County, Kentucky.

U.S.N.M. S-3193-A. 30.6 mm axial by 22.5 mm transverse diameter.

Text fig. 57, pl. 53, fig. 8-13.

This specimen is separated from its resting site. The left two-thirds of the upper oral surface is well-preserved, but most of the right third is disrupted and in part folded under the remainder of the specimen. The lower surface of the specimen is a mass of jumbled thecal plates which expose several isolated ambulacral floorplates and some of the geniculate rim plates. On the upper surface, most of the oral area and hydropore structure plates are in place. The ambulacral coverplate sequence is preserved in parts of ambulacra I-IV. Interambulacra 1 and 2 are also well-preserved. The anal structure is completely disrupted.

U.S.N.M. S-3193-B. 28.6 mm long by 16.8 mm wide.

Pl. 54, fig. 1-6.

The specimen is a fragment of a large individual, resting on a small rugose coral. It includes parts of three ambulacra, adjacent interambulacrals, the squamose, imbricate marginal plates, and an adjacent section of the peripheral rim. Distal sectors of the ambulacra preserve the insertion zones of several ambulacral coverplate sets. The marginal zone of squamose imbricate plates, proximal to the

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peripheral rim, appears to be much shorter in this specimen than in the holotype, and suggests the theca may have been domal.

U.S.N.M. S-3193-C. Upper oral surface: 27.4 mm greatest diameter by 22.5 mm. Peripheral rim: 24.9 mm greatest diameter by 18.3 mm.

Pl. 54, fig. 7.

This individual, also resting on a rugose coral, is poorly preserved. The upper oral surface is almost totally disrupted. Partially disrupted distal sections of two ambulacra are retained. Below the ambitus of the upper oral surface, the squamose, imbricate marginal plates and the basal peripheral rim plates are preserved in part. This individual also appears to have been less highly elevated than the holotype, but the marginal zone does constrict downward to form a short pedunculate zone.

Discussion:

The original description of Agelacrinus pulaskiensis Miller and Gurley (1894, p. 16) was very generalized; they recorded: the high convexity of the theca; the peduncular or marginal zone plates squamose and imbricate (thought by them to be the peripheral rim plates); interambulacrals large, imbricate; five long, narrow ambulacra, "four sinistral and one dextral", with a single biseries of coverplates; numerous small orals; twelve anal plates; and, plate surfaces "finely granular". In contrast with the written description, an accompanying line drawing of the holotype shows ambulacrum V curving contrasolarly, as is the case.

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Bassler (1935) noted the contrasolar curvature of all five ambulacra in this species. For this reason he designated a new genus Ulrichidiscus, for the species.

The expanded description of U. pulaskiensis presented here is based on restudy of the holotype, after removal of matrix which had obscured the oral area and entire lower surface of the specimen. Three new specimens, believed to be topotypes, are also included. Thecal shape is still uncertain for the specimens suggest either a highly convex upward domal form or a sub-clavate theca with a short, slightly constricting peduncular zone. Taxonomically distinctive features include the shape of the transverse oral midline, the large number of posterior oral plates, the plating of the hydropore structure, the ambulacral coverplate sequence and the large size of the anal structure. Internal thecal features are mostly unknown.

Range and occurrence: Chesterian Series, Mississippian of Pulaski County, Kentucky.

Cooperidiscus Bassler, 1935

1935 Cooperidiscus Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 8, pl. 1, fig. 9.

1936 Cooperidiscus Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 22.

1938 Cooperidiscus Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 72.

1943 Cooperidiscus Bassler, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 199.

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1944 Cooperidiscus Bassler, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, pl. 49, fig. 16.

1966 Cooperidiscus Bassler, Regnéll, G., in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U169, text fig. 128-2.

Type species: Lepidodiscus alleganius Clarke, 1901.

Diagnosis:

Agelacrinitidae with: transversely elongate oral area, probably formed by numerous, small plates; large hydropore protuberance posterior to central oral rise; five long, extremely narrow ambulacra, curved, I-V solar; two or more sets of ambulacral coverplates; interambulacrals numerous, squamose, imbricate; valvular anal structure with two circlets of plates.

Description:

Cooperidiscus Bassler (1935) is monotypic. Therefore, separation of generic and specific taxobases is uncertain. Features cited in the above diagnosis are in part inferred to be of generic rank from established generic taxobases for related genera of Agelacrinitidae. Cooperidiscus is the only Agelacrinitidae in which all of the ambulacra curve solarly.

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Cooperidiscus alleganius (Clarke), 1901

Text fig. 59; plate 54, fig. 8-11, plate 55, fig. 1-6.

1901 Lepidodiscus alleganius Clarke, J. M., New York St. Mus., Bull. 49 (2): 194-195, pl. 10, fig. 1-5.

1910 Agelacrinus (Lepidodiscus) alleganius Clarke, Grabau, A. W. and Shimer, H. W., North American Index Fossils, Invertebrates, New York, 2: 472.

1914 Lepidodiscus alleganius Clarke, Foerste, A. F., Denison Univ., Sci. Lab. Bull. 17 (art. 14): 399-456, pl. 6, fig. 2a-b.

1935 Cooperidiscus alleganius (Clarke), Bassler, R. S., Smithsonian Misc. Coll. 93 (8): 8, pl. 1, fig. 9.

1936 Cooperidiscus alleganius (Clarke), Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 22.

1938 Cooperidiscus alleganius (Clarke), Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 72.

1943 Cooperidiscus alleganius (Clarke), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 199.

1944 Cooperidiscus alleganius (Clarke), Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, pl. 49, fig. 16.

1966 Cooperidiscus alleganius (Clarke), Regnéll, G., in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U169, text fig. 128-2.

Diagnosis:

A Cooperidiscus with: convex upward upper oral surface; large

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hydropore structure arising from the posterior margin of the central oral rise, apparently formed by numerous plates; ambulacra distally become concentric with margin of upper oral surface but remain widely separated from each other; interambulacra wide.

Description:

Cooperidiscus alleganius (Clarke) is known only from external molds preserved in coarse sandstone. The critical plates of the oral-ambulacral series are poorly preserved in all known specimens.

The upper oral surface of the theca is convex upward. It includes the oral-ambulacral structures, hydropore, anal area, and interambulacral plates. The lower part of the theca, below the ambitus, was described by Clarke (1901) as being concave upward, entirely covered by squamose, imbricate plates which overlap proximally. Greatest observed upper surface diameter is 44.5 mm.

The transversely elongate oral region forms the central oral rise. It apparently comprises numerous, small plates, but none of the specimens preserves the details. The faint impressions of finely serrate oral midlines are seen on two specimens (pl. 55, fig. 4, 6). The course of the transverse oral midline, beginning at the lateral bifurcation plates, appears to be angled anteriorly (almost V-shape); the central point intersects the proximal end of the short, straight anterior oral midline.

The large, transversely elongate, hydropore structure arises from the posterior margin of the central oral rise. It appears to extend from the proximal posterior margin of ambulacrum V across most

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of the posterior side of the oral region. The structure probably includes many plates, oriented oblique to the thecal surface, that form the steep sides of the protuberance. The hydropore opening may be an elongate, anteriorly arched, arcuate slit which extends along the summit of the protuberance.

The ambulacra are long and extremely narrow. In proportion to thecal diameter, they appear to be less than half as wide as the ambulacra of any other known edrioasteroid. All five ambulacra curve solarly. Proximal parts are nearly straight, followed by a rapidly curving zone. Distally they become concentric with the margin of the upper oral surface, but each ambulacrum remains widely separated from adjacent ambulacra by a wide zone of interambulacrals. Irregular minor sinuations are not uncommon along the course of the ambulacra in some specimens, particularly in the distal parts.

The ambulacral coverplate sequence appears to include at least two sets of plates which perhaps form either an alternating double biseries, or more likely a two-plate cyclic series. Text fig. 59A attempts to outline the coverplate sutures in the medial part of ambulacrum IV of the holotype. The drawing is regarded as highly tentative due to the poor preservation, although this is the best preserved material available. The coverplates are preserved steeply inclined to the thecal surface and form sharply defined, narrow ridges. This orientation further obscures the plate pattern. The coverplate series may be much more complex than suggested in text fig. 59A.

The wide interambulacra are covered with numerous, squamose,

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Text Figure 59 Cooperidiscus alleganius (Clarke), 1901

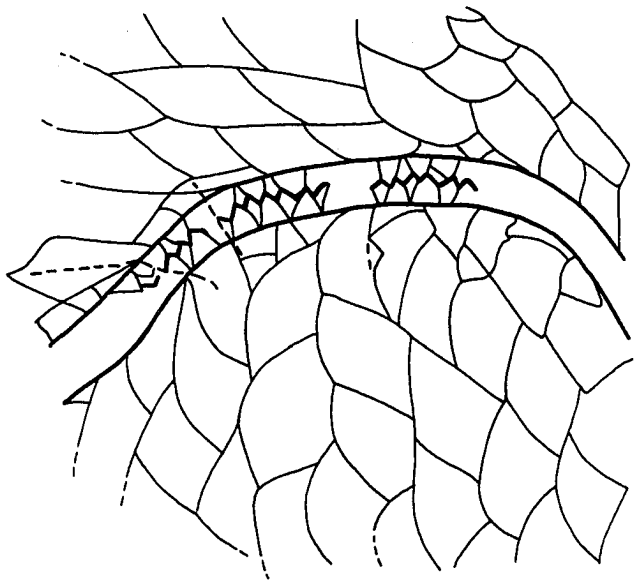
A.-B. Lectotype, N.Y.S.M. 4962.

A. Central segment of ambulacrum IV and adjacent interambulacrals, (X7), pl. 54, fig. 11.

B. Anal structure and adjacent plates, (X7), pl. 54, fig. 10.

C. Lectoparatype, N.Y.S.M. 4959, anal area and adjacent parts of interambulacrum 5 and ambulacra I and V, (X5), pl. 55, fig. 2.

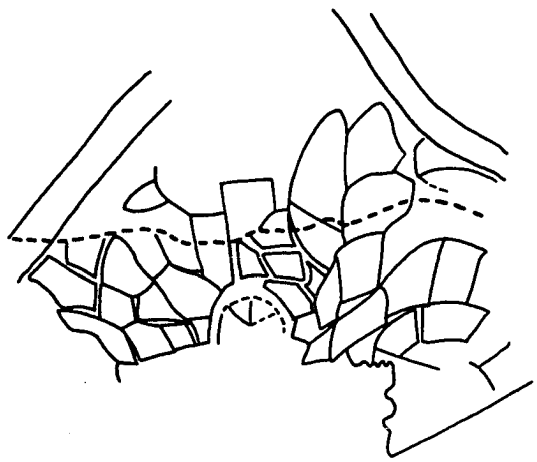
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A



B



C

Text Figure 59

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imbricate plates. These extend between the distal parts of the ambulacra, and apparently continue onto the lower side of the theca.

The valvular anal structure includes ten, large, triangular plates in the lectotype (text fig. 59B, pl. 54, fig. 10). There are suggestions of alternate, overlapping outer and overlapped inner circlets.

Plate surfaces appear to have been smooth.

Specimens:

N.Y.S.M. 4962. Lectotype of Cooperidiscus alleganius (Clarke) (1901, pl. 10, fig. 4, as Lepidodiscus alleganius). "Chemung SS", probably Canadaway or Conneaut Group, Chautauguan Series, Upper Devonian. Loose at Alfred, New York. 33.6 mm axial by 38.5 mm transverse diameter.

Text fig. 59A-B, pl. 54, fig. 8-11.'

This specimen, one of five in Clarke's type series, is here designated the lectotype. It and all following specimens are external molds, preserved in coarse sandstone. The lectotype preserves the upper oral surface. Ambulacra I and II are poorly preserved, as is the oral area and the proximal part of the other three ambulacra. The coverplate pattern has been tentatively interpreted from the curved, medial part of ambulacrum IV. The serrate perradial line is also seen in the distal part of ambulacrum V, but individual coverplate boundaries are not clear. The anal structure is preserved in the posterior interambulacrum. The squamose, imbricate interambulacrals distally appear to extend past the ambitus, onto the lower surface of the specimen.

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N.Y.S.M. 4959. Lectoparatype of C. alleganius (Clarke) (1901, pl. 10, fig. 1). "Chemung SS", probably Canadaway or Conneaut Group, Chatauquan Series, Upper Devonian. Loose at Alfred, New York. 27.4 mm axial by 25.3 mm transverse diameter.

Text fig. 59C, pl. 55, fig. 1-2.

This specimen was described by Clarke (1901) as a juvenile with straight ambulacra that extend to the margin of the upper oral surface. The specimen appears to be only the central sector of the upper oral surface of a large adult, the distal curved parts of the ambulacra and the adjacent interambulacrals being missing. The specimen preserves the shape of the oral-hydropore region and the proximal parts of the ambulacra, but all plate boundaries within these areas are obscure. Only the proximal interambulacral plates are distinct. The anterior half of the anal structure is preserved along the posterior margin of the preserved portion of interambulacrum 5.

U.S.N.M. 34131 (A-B). "Upper Chemung SS", probably Chatauquan Series, Upper Devonian. West Beech Woods Creek, 1½ miles south of Sabinsville, Clymer Township, Tioga County, Pennsylvania.

U.S.N.M. 34131-A. Lectoparatype of C. alleganius (Clarke) (1901, pl. 10, fig. 3). 33.6 mm axial by 40.7 mm transverse diameter.

Pl. 55, fig. 3-4.

This large adult preserves only the collapsed, axially compressed, upper oral surface. The outline and elevated form of the oral area and hydropore structure are preserved, but plate boundaries are indistinct.

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The oral midlines and the hydropore opening are preserved as faint impressions. The ambulacra show minor sinuations along their course, particularly distally. The anal structure is elevated into a small, conical mound. Suggestions of inner circlet plates are exposed.

U.S.N.M. 34131-B. Specimen of C. alleganius on slab adjacent to U.S.N.M. 34131-A. 44.5 mm axial by 41 mm transverse diameter.

Pl. 55, fig. 5-6.

This large individual also preserves only the collapsed and laterally compressed upper oral surface. The oral areas and hydropore structures are distinct, but suture lines are obscure. The anterior and transverse oral midlines, and the hydropore opening are preserved as faint impressions. The ambulacral coverplate pattern is not recognizable. The anal area and some adjacent interambulacrals are missing.

Discussion:

Clarke's (1901) original description of Lepidodiscus alleganius reported: the transversely elongate oral area; the long, narrow, solarly curved ambulacra with sinuous perradial lines; squamose, imbricate interambulacrals; and ten, triangular anal plates. Moreover, he included two specimens, now missing, purported to be molds of the lower side of the theca. Clarke suggested that the lower surface was slightly concave upward, and entirely covered with squamose, proximally imbricate plates.

Re-investigation of the available type specimens and latex pulls

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of these has added little to Clarke's description, except for the identification of the hydropore protuberance. Plating of the oral area, hydropore structure, and ambulacra is poorly preserved in all of the specimens.

Clarke's statement that in two specimens, now missing, a plated aboral thecal surface was seen is enigmatic. If correct, this is the only species of Agelacrinitidae, indeed, the only Isorophida, in which the aboral surface has been shown to be fully plated. Clarke's drawings of these specimens suggest that the center of the lower side was poorly preserved in both. Thus, it seems likely that the theca was clavate, and a small, basal peripheral rim was overlooked.

Range and occurrence: Upper Devonian of northwestern Pennsylvania and southwest New York.

Genus and Species Indeterminate

Plate 56.

Two fragments of an extraordinarily large edrioasteroid species were collected by N. Gary Lane from the Madera Formation, Magdalena Group, Upper Pennsylvanian of New Mexico. Although probably a new species, the specimens are considered too incomplete to designate a new taxon. They are described here because only one other Pennsylvanian edrioasteroid species has been reported, Agelacrinites hybolopus Fraunfelter and Utgaard (1970), from the Conant Limestone member of the Jamestown Cyclothem, Carbondale Formation, Middle Pennsylvanian of southern Illinois.

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Specimens:

U.C.L.A.P.C. 48166, 48167. Two fragmentary specimens. Road cut on east side of dirt lumber truck road in Guadalupe Canyon, 9.5 miles north of junction of Guadalupe Canyon Road with New Mexico Rt. 4, Guadalupe Canyon, New Mexico. Madera Formation, upper part, Magdalena Group, Virgilian Series, Pennsylvanian.

U.C.L.A.P.C. 48166. 39.3 mm long by 22.8 mm wide.

Pl. 56, fig. 1-8.

The upper surface of the specimen includes segments of three ambulacra and the adjacent large, polygonal interambulacrals. These interambulacrals continue around the marginal ambitus of the theca onto the lower surface. Distal to the large polygonal lower interambulacrals, a few thin, elongate, imbricate, peduncular zone plates are preserved. The inner sides of the upper and lower surface plates have been pressed together during thecal collapse.

U.C.L.A.P.C. 48167. 17.1 mm long by 14 mm wide.

Pl. 56, fig. 9-11.

This fragment preserves two ambulacral segments, and adjacent interambulacrals. The lower surface of the fragment includes only the large polygonal plates adjacent to the ambital region. The upper and lower surface plates have been pressed together during collapse.

The two fragments, probably from different individuals, demonstrate that the theca was clavate. The upper oral surface included the oral-ambulacral structures, large, thick, polygonal, tessellate

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interambulacrals, and presumably the anal structure. Similar interambulacrals form the ambitus and the proximal part of the lower surface. Distal to these elements, elongate, thin, rectangular, imbricate plates apparently formed a peduncular zone, probably similar to that of Discocystis kaskaskiensis. If the arc formed by the ambitus of the larger specimen is used to define the circumference of the complete theca, the diameter obtained is over 70 mm, one of the largest for any edrioasteroid.

The ambulacral coverplates are disrupted in all but two small parts of one ambulacrum in the larger specimen. These two areas demonstrate that the coverplates are cyclic, there being three or four plates per cycle in this part of the ambulacrum. However, the variability in shape, size and arrangement seen in the two small segments suggests preservational distortion of the coverplate series. Therefore, confident description of the cyclic elements is impossible.

The ambulacral floorplates are uniserial, axially elongate, and unusually thick. A deep, steep-sided trough is incised into the upper surface of each floorplate. The uppermost lateral margins which flank the trough are somewhat less steeply inclined and thereby form a very narrow zone of articulation with the bases of the overlying coverplates. The lateral sides of the floorplates abut the thick interambulacrals. These adradial sutures are oblique planes, slanting downward and away from the ambulacral axis, the floorplates widening downward. The lower, basal surfaces of the floorplates appear to be nearly flat, parallel with the inner flat surfaces of adjacent interambulacrals.

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This Pennsylvanian form shows similarity to the Mississippian Discocystis kaskaskiensis. Both have clavate thecae, thin, elongate, imbricate plates of the peduncular zone, and perhaps also a three- or four-plate cyclic series of ambulacral coverplates. However, only the distal ambulacral coverplates are preserved in the Pennsylvanian species, and thus, the cycles may be incomplete. The shape of the ambulacral floorplates appears to be unique in the Pennsylvanian species.

Family Uncertain

Hadrochthus Bell, gen. nov.

Diagnosis:

Isorophina with: highly domal theca; oral area formed by few plates, primary orals differentiated externally; small hydropore structure semi-integrated with central oral rise; broad ambulacra straight, coverplates large, forming a single alternating biseries; interambulacrals large, thick, polygonal, tessellate; valvular anal structure formed by one circlet of plates.

Description:

Hadrochthus is monotypic. Therefore, separation of generic and specific taxobases is uncertain. Features outlined in the above diagnosis are in part inferred to be of generic rank from established taxobases for other Isorophina genera.

Etymology: Hadrochthus is compounded from the Greek hadros, meaning stout or thick, referring to the large size and great thickness of the thecal plates, and ochthos, meaning mound, referring to the domal theca.

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Range and occurrence: Mason City Member, Shell Rock Formation, Upper Devonian of Iowa.

Hadrochthus commensalus Bell, sp. nov.

Text fig. 60; plate 57.

Diagnosis:

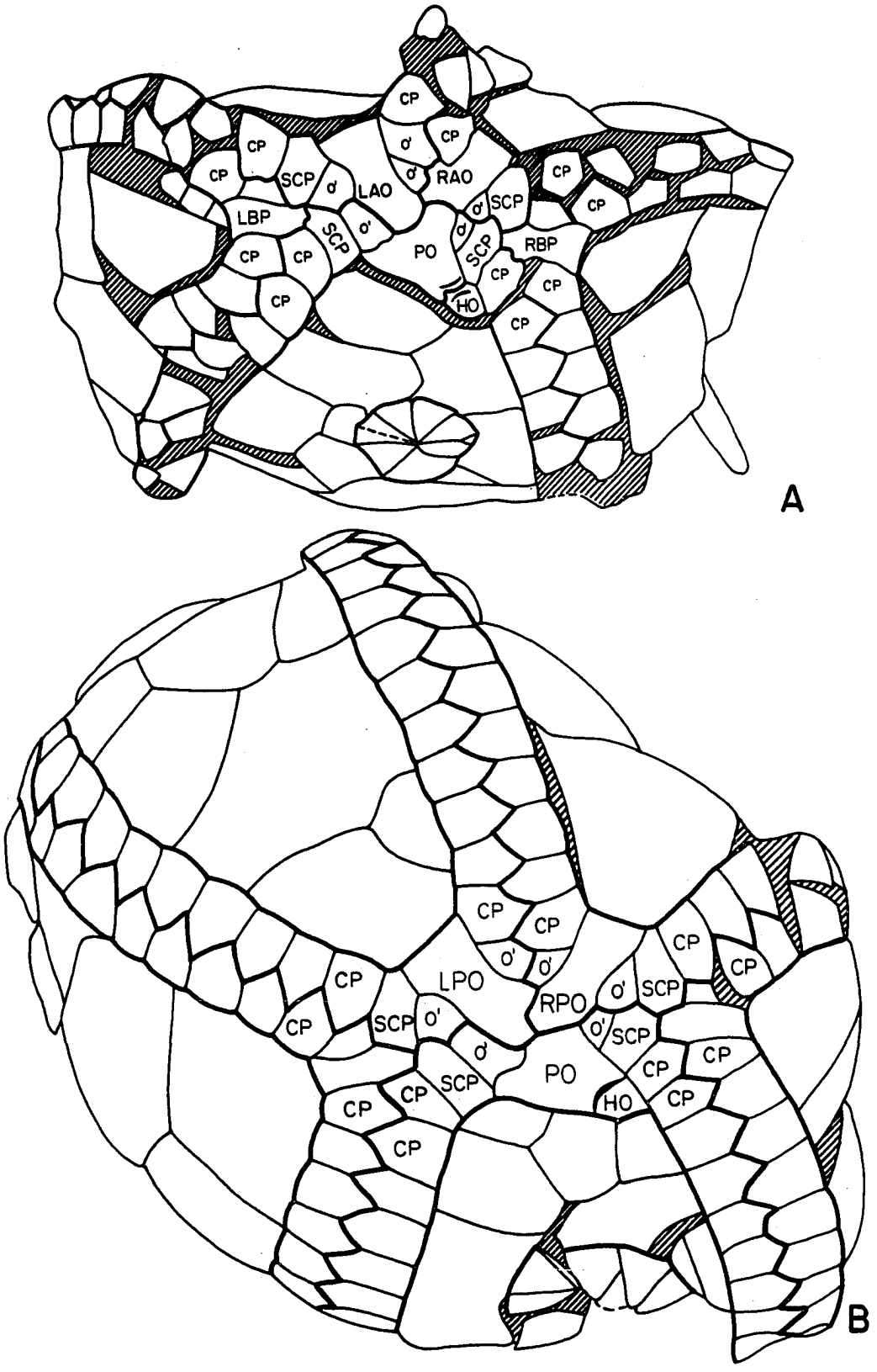
A Hadrochthus with: moderate sized, highly convex, domal theca; oral area formed by three large primary orals, two pairs of lateral shared coverplates, four secondary orals, and one small hydropore oral; small hydropore protuberance in right posterior oral region, semi-integrated with the central oral rise, formed by two plates; anal plates large and triangular.

Description:

The moderate sized, highly convex, domal theca of H. commensalus reaches 15 mm in diameter.

The oral area includes fourteen plates (text fig. 60A-B). Three large primary orals form the center, all adradially in contact with the adjacent interambulacra. Two are anterior primaries which meet each other laterally along the proximal end of the anterior oral midline. A single very large, posterior primary oral meets both anterior primaries along the center of the transverse oral midline. However, it may be offset to the right and abut a larger part of the right than the left anterior oral. A small plate lies adjacent to the proximal part of the left side of the large posterior primary oral. Perradially, this plate abuts a large sector of the proximal end of the left anterior

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Text Figure 60

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Text Figure 60 Hadrochthus commensalus Bell, sp. nov.

A. Paratype (1), S.U.I.C. 80003, (X8), pl. 57, fig. 4.

B. Holotype, S.U.I.C. 80002, (X10), pl. 57, fig. 1.

CP. ambulacral coverplate; HO. hydropore oral plate; LAO. left anterior primary oral plate; LBP. left lateral bifurcation plate; o'. secondary oral plate; PO. posterior primary oral plate; RAO. right anterior primary oral plate; RBP. right lateral bifurcation plate; SCP. lateral shared coverplate.

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primary oral. This small element, tentatively identified here as a secondary oral, might represent a fourth primary oral, homologous to the left posterior primary oral found in Isorophidae.

Two pairs of lateral shared coverplates flank the central primaries along the transverse oral midline, one pair on each side. These shared coverplates reach the adradial suture line where they are laterally in contact with the adjacent, primary orals. One pair of secondary orals, one plate anterior and one posterior to the transverse midline, perradially separate each of the two pairs of shared coverplates from the central primaries. Two small anterior secondary orals lie along the anterior oral midline between the anterior orals and the proximal coverplates of ambulacrum III. The two anterior secondaries may lie on the left side of the midline, or they may be opposed, one on each side. A small, right posterior hydropore oral completes the oral sequence. Proximally it abuts the right distal margin of the large posterior primary oral. Laterally it abuts the adradial end of the second, and sometimes also part of the first proximal, posterior coverplate of ambulacrum V.

The small hydropore structure lies in the right posterior corner of the oral area, adjacent to the proximal posterior margin of ambulacrum V (text fig. 60A-B). Involving only two plates, it is a small, semi-integrated elevation, arising from the posterior slope of the oral rise. The anterior side is formed by the right posterior end of the large posterior primary oral. The adjacent left anterior margin of the small hydropore oral forms the posterior side of the structure. The

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contiguous edges of these two plates are thickened and form a small, elongate elevation. The hydropore opening lies along the summit of the protuberance at the junction of the two plates. Commonly, the opening is arcuate, convex proximally (text fig. 60B). In one specimen it appears to be sinuous (text fig. 60A).

The wide ambulacra are straight and drape down the highly convex upper oral surface to the proximal margin of the peripheral rim. The ambulacral coverplates form a single alternating biseries. Each coverplate is large, sub-pentagonal, with a pointed perradial end. Adjacent coverplates laterally abut along vertical sutures.

The inner sides of the coverplates are inadequately known, observed only in partially disrupted specimens. Apparently, large blade-like intra-ambulacral extensions are produced into the large ambulacral tunnel from the perradial ends of the coverplates. The length and shape of the inner parts of these extensions are unknown. The adradial ends of the coverplates abut the adjacent thick interambulacrals along nearly vertical adradial sutures. These adradial faces may be modified by a groove incised into the edge of the coverplates which extends the length of the adradial face of each coverplate. A corresponding rounded ridge may be present on the opposing edge of each interambulacral. The inner, adradial ends of the coverplates rest on the upper lateral margins of the ambulacral floorplates. The coverplates apparently end adjacent to the edges of the floorplates and thus are not produced inward as intra-thecal extensions.

A single isolated ambulacral floorplate is preserved on the

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disrupted lower side of the holotype (pl. 57, fig. 2). It suggests the uniserial floorplates are trough-shaped. The upper side is convex downward, with narrow, lateral margins which slope inward less steeply than the sides of the deep, central trough. These lateral margins apparently abut the inner, adradial ends of the overlying coverplates. The inner sides of the floorplates appear to be evenly convex inward, without lateral nodes.

The interambulacrals are large, unusually thick, polygonal plates which abut along vertical sutures.

The valvular anal structure lies near the center of interambulacrum 5. It is formed by seven or eight large, thick, triangular plates which apparently form a single circlet.

The peripheral rim includes five circlets of plates. The very large plates of the proximal circlet, and the much smaller ones of the second, are externally elongate concentric with the thecal margin. Plates of the following three circlets progressively diminish in size outward and are elongate radially.

Most thecal plates appear to be smooth externally. However, two disrupted interambulacrals, preserved on the lower side of the holotype, have been shoved into the thecal cavity and thus protected from abrasion. These bear large rounded tubercles. Although the outer ends of the tubercles are large, they are attached to the plates by short, narrow, constricted "necks". All of the specimens of this species are much abraded. Thus, it is not impossible that large tubercles may have been present on many of the plates, but have been lost.

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Specimens: S.U.I.C. 80002, 80003, 32293, 32299. Middle of the Mason City member, Shell Rock Formation, Senecan Series, Upper Devonian. Thomas William Quarry, N.W. $\frac{1}{4}$, sec. 28, T. 96N., R. 18W., Floyd County, three miles southwest of Norra Springs, Iowa.

S.U.I.C. 80002. Holotype of Hadrochthus commensalus Bell. 14.7 mm axial by 13.8 mm transverse diameter.

Text fig. 60B, pl. 57, fig. 1-3.

The holotype preserves the central part of the upper oral surface with little plate disruption. However, the distal parts of the oral surface, including most of the right anterior third of the theca, have been folded under the upper side. The peripheral rim is missing. The oral and hydropore areas are well-preserved, along with most of ambulacra I, II, III and V. Only the proximal end of IV is not disrupted. Interambulacra 1 and 2 are well-preserved also. The anal structure is disrupted, some of the posterior plates missing. The upper surface of the specimen has been severely abraded.

The lower side of the specimen preserves several disrupted plates which have been pushed into the thecal cavity; these include one ambulacral floorplate and two interambulacrals which bear large external nodes. The specimen is believed to have rested on the theca of a cystoid, Adocetocystis williamsi.

S.U.I.C. 80003. Paratype (1) of H. commensalus. 15.1 mm axial by 15 mm transverse diameter.

Text fig. 60A, pl. 57, fig. 4-7.

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The specimen has been laterally compressed. One surface, referred to here as upper, preserves the oral area, ambulacra I, II, IV and V, interambulacra 1, 4 and 5, and the anal structure. The reverse or lower side preserves the proximal parts of ambulacrum III and interambulacra 2 and 3. The remainder of the theca, including the peripheral rim, is missing.

The oral area, hydropore structure, anal structure, and proximal parts of ambulacra I and V, are well-preserved, their plates nearly in place. Other thecal elements are disrupted to varying degrees, although most of the plates of interambulacrum 5 are nearly in place. The specimen has been extensively abraded. Although now free, it is believed to have been attached to the theca of a cystoid, Adocetocystis williamsi.

S.U.I.C. 32293. Paratype (2) of H. commensalus. 11.7 mm axial by 11 mm transverse diameter.

Pl. 57, fig. 8-10.

This specimen has collapsed; the oral surface is depressed and has been pushed anteriorly. The distal parts of ambulacra II, III and IV and interambulacra 2 and 3 have overridden the anterior section of the peripheral rim. Although many of the plates are disrupted, the oral area and parts of the ambulacra preserve the plate relationships. The posterior half of the peripheral rim is well-preserved. Ambulacrum III, which arches out over the anterior edge of the theca, has been separated from adjacent interambulacrals, and exposes the grooved, adradial ends of the coverplates along the left side of the ambulacrum. The specimen is resting on a paratype (S.U.I.C. 32293) of the cystoid

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Adocetocystis williamsi.

S.U.I.C. 32299. Paratype (3) of H. commensalus. 7.1 mm axial by 6.5 mm transverse diameter.

Pl. 57, fig. 11-12.

This specimen is partially collapsed and irregularly compressed. It retains some of the original convexity of the oral surface, but the distal parts of the ambulacra and interambulacra have been crushed inward along the proximal margin of the peripheral rim. Many plates are disrupted, but the proximal parts of ambulacra I, III, IV and the center of V preserve the coverplate relationships. The two anterior primary orals and some of the anal area plates are identifiable. The specimen is resting on a paratype (S.U.I.C. 32299) of the cystoid Adocetocystis williamsi.

Discussion:

Thecal plating in Hadrochthus commensalus Bell is simple. Like specimens in the Lebetodiscina, the ambulacral coverplates form a single alternating biseries. Moreover, the oral area includes relatively few plates with primary orals differentiated, and the hydropore structure is formed by only two plates. However, H. commensalus lacks ambulacral coverplate passageways, and the anal structure is valvular. Thus, it is included here within the suborder Isorophina, but does not appear to belong to either of the two families recognized in this study. With only a single species exhibiting these features, it seems unwise to propose a new family. Thus, H. commensalus is not assigned to a

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family here.

As the only species of Isorophina known to have a single alternating biseries of coverplates (in the adult stage), H. commensalus may be either primitive, or highly specialized. In view of the unusual thickness of the thecal plates and the apparently commensal relationship with the cystoid Adocetocystis williamsi, H. commensalus is thought to be a highly specialized form.

Evidence for the suggested commensal relationship between H. commensalus and the cystoid Adocetocystis williamsi is circumstantial. All specimens of H. commensalus appear to have been attached to the theca of one of these cystoids. All of the specimens are from a single locality. Koch and Strimple (1968) have presented a detailed reconstruction of this site, apparently an intertidal or perhaps very shallow sub-tidal area. The substrate is an eroded limestone surface, with large, rounded knobs of limestone separated and undercut by deep, interconnected solution channels. The cystoids attached to the undersides of the knobs. Apparently they were able to extend out and upward above the knobs for feeding. Thousands of specimens of another edrioasteroid species (Agelacrinites hanoveri Thomas, 1924) are found resting on the upper surfaces of the limestone knobs. Thus, favorable substrate conditions existed for edrioasteroid growth within the area, but H. commensalus occurs only on cystoid thecae. Therefore, it seems that some type of commensal relationship existed between H. commensalus and the cystoid, without which the edrioasteroid was not able to survive.

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Range and occurrence: Shell Rock Formation, Senecan Series, Upper Devonian of north central Iowa.

Order Isorophida Bell

Suborder and Family Uncertain:

(?) Hemicystites carbonarius Bassler, 1936

Text fig. 61A; plate 55, fig. 7-10.

1936 Hemicystites (?) carbonarius Bassler, R. S., Smithsonian Misc. Coll. 95 (6): 15, pl. 4, fig. 10-11.

1943 Hemicystites (?) carbonarius Bassler, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 203.

1944 Hemicystites (?) carbonarius Bassler, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131, pl. 49, fig. 14.

Description:

Hemicystites carbonarius is known from eight specimens, seven of which preserve only the peripheral rim and a completely disrupted central thecal area. The single individual with partially preserved oral surface features is a juvenile (text fig. 61A). The theca is domal, the largest specimen 10.5 mm in diameter. The oral region appears to include four or five large plates in the juvenile. An asymmetrical right posterior bulge in the oral area outline suggests the presence of a hydropore structure. The five ambulacra appear to be straight. Ambulacral coverplates may form a double biseries. Interambulacrals are squamose and imbricate plates. The anal structure lies

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Text Figure 61

A. Hemicystites carbonarius Bassler, 1936, type series specimen, U.S.N.M. 91837-b-6, (X15), pl. 55, fig. 10.

B.-E. Agelacrinites hanoveri Thomas, 1924.

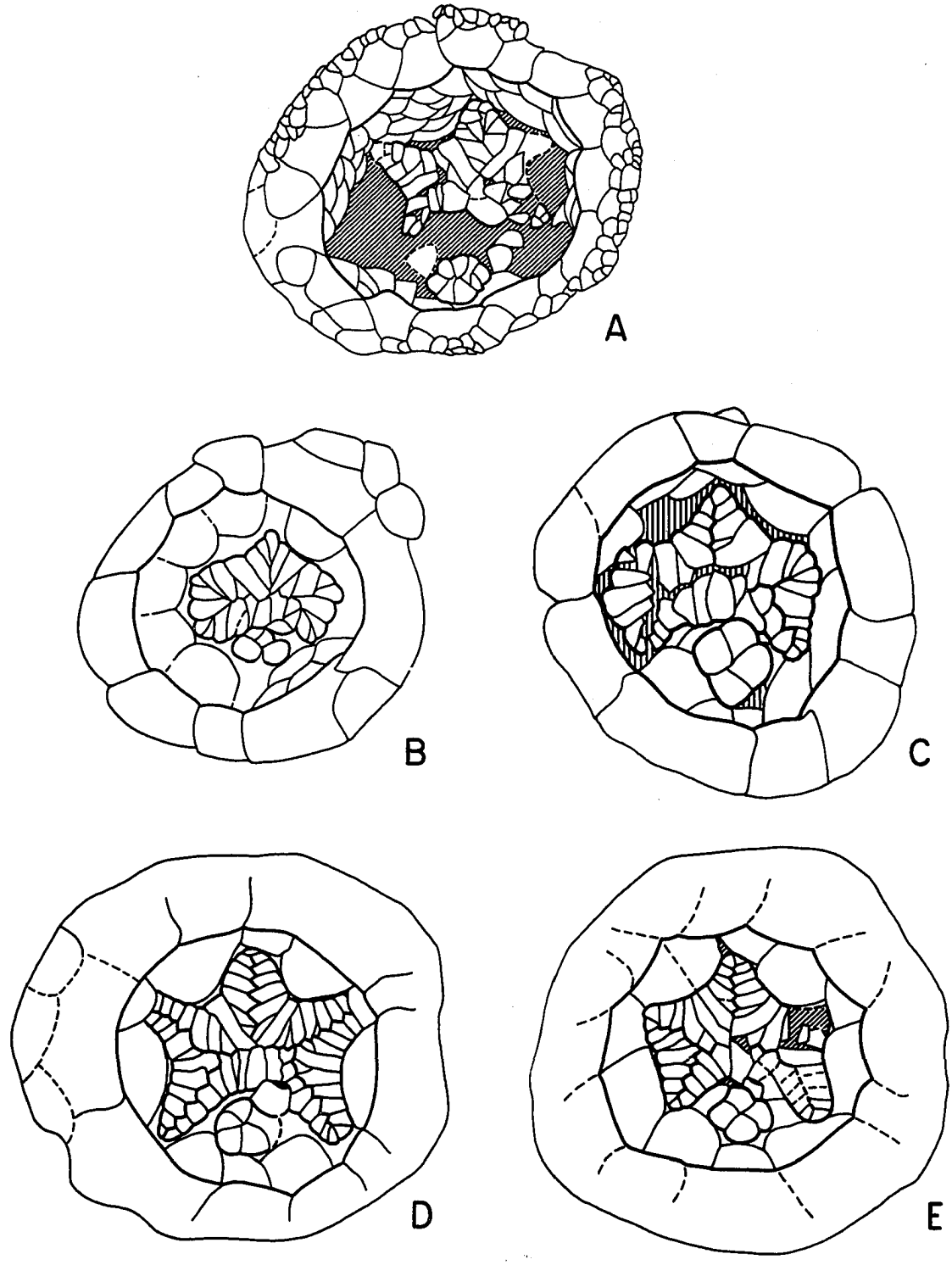
B. Juvenile, S.U.I.C. 35162, (X20), pl. 55, fig. 11.

C. Juvenile, S.U.I.C. 1906, (X15), pl. 55, fig. 13.

D. Juvenile, S.U.I.C. 35163, (X15), pl. 55, fig. 14.

E. Juvenile, S.U.I.C. 35164, (X15), pl. 55, fig. 12.

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Text Figure 61

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in the posterior part of interambulacrum 5 and is formed by at least six sub-triangular plates.

The peripheral rim includes approximately five circlets. Plates of proximal circlet are very large and alternate as proximal and distal subcirclet members. These and the smaller plates of the following two circlets are externally elongate concentric with the thecal margin. The tiny plates of the distal two circlets are radially elongate.

Specimens:

U.S.N.M. 91837. Type series of Hemicystites carbonarius Bassler (1936, p. 15, pl. 4, fig. 10-11). Bluefield shale, Bluefield Group, Chester Series, Mississippian [not Pennsylvanian as listed by Bassler, 1936, and authors]. 4/5 mile east of Adds Valley, West Virginia. Two fragments that were originally one slab.

Fragment A. Two specimens. (Pl. 55, fig. 7)

A-1. 10.5 mm greatest diameter by a perpendicular of 10.5 mm (Pl. 55, fig. 8.)

A-2. 6.6 mm greatest diameter.

Fragment B. Six specimens. (Pl. 55, fig. 9.)

B-1. 9.4 mm greatest diameter by a perpendicular of 7.3 mm.

B-2. 7.0 mm greatest diameter.

B-3. 8.2 mm greatest diameter.

B-4. 4.8 mm greatest diameter

B-5. 4.2 mm greatest diameter.

B-6. 3.5 mm axial by 4.2 mm transverse diameter. (Pl. 55, fig. 10.)

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Text fig. 61A, pl. 55, fig. 7-10.

All eight specimens of H. carbonarius are resting upon a fragment of a large "cephalopod shell" (Bassler, 1936, p. 15) that originally was one larger fragment, but is now broken into two pieces. All specimens have collapsed. Seven of the eight are poorly preserved, the peripheral rim the only interpretable feature in any of these. The eighth specimen is only partially disrupted, but it is a juvenile.

Discussion:

Hemicystites carbonarius Bassler (1936) is here restricted to the type specimens which are too poorly preserved to define the species characters or even to allow recognition of generic or familial relationships. Bassler's generic assignment of Hemicystites carbonarius seems unlikely in view of the great difference in age of his Mississippian specimens and the Middle Silurian Hemicystites parasiticus Hall.

Order Edrioasterida Bell, ord. nov.

Diagnosis:

Edrioasteroidea with: "echinoidal" shaped theca, ambulacra extend past ambitus into subambital zone; oral frame formed by large, compound plates, 5 radial, 5 interradial; hydropore structure located along right posterior margin of oral area, opening sutural but elongate perpendicular to suture line so as to penetrate adjacent plates; ambulacra include alternating biseries of coverplates without intra-thecal or intra-ambulacral extensions; and, biserial floorplates with sutural

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passageways which connect ambulacral tunnel with thecal cavity.

Description:

The Edrioasterida have a semi-globoid, "echinoidal" theca that can be divided into five areas: the upper oral surface which ends at the ambitus; the sub-ambital zone; the resting zone; the incurved zone; and, the distal membrane. The center of the upper oral surface is nearly horizontal; the distal parts gradually increase in inclination down to vertical plates at the ambitus. The sub-ambital zone gradually constricts in diameter, downward. It forms approximately one-third of the total thecal height. In the sub-ambital zone, the sides of theca curve inward toward the center of the lower side. The resting zone lies distal to the sub-ambital zone. Only one or two plates wide, this area is parallel to the horizontal, central upper oral surface, and the exterior side of the plates of the resting zone are parallel to, and apparently rest on, the underlying substrate. Distal to the resting zone the thecal surface curves upward, away from the substrate, and inward toward the center of the theca for a short distance. A thick membrane, imbedded with numerous minute platelets is attached to the distal edges of the innermost plates of the incurved zone. This plated membrane apparently extended downward toward, and probably attached to, the substrate. It is not continuous across the lower surface, and a large circular central gap is surrounded by the attaching, distal edge of the plated membrane.

The oral area, hydropore structure, proximal parts of the ambulacra, and the anal structure are on the upper oral surface. Distally,

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the ambulacra extend past the ambitus into the sub-ambital zone, but either terminate or curve laterally before they reach the resting zone.

The oral area includes external covering orals continuous with the ambulacral coverplate series and externally exposed parts of the oral frame. The covering orals form the center of the area and are similar to the ambulacral coverplates in size and shape. They apparently vary in number. Perradially, the orals form the transverse and anterior oral midlines. Adradially they meet the externally exposed parts of the oral frame and form a sub-marginal suture line on the thecal surface; distally, this suture line is continuous with that between the adradial ends of the ambulacral coverplates and exposed parts of the ambulacral floorplates.

The large central oral frame is formed by ten compound plates, each formed by the fusion of numerous plates; a minimum of 55 fused elements comprises the frame of Edrioaster bigsbyi. The proximal margin of the frame is pentagonal to ovoid, transversely elongate, and surrounds the pentagonal to oval central lumen. The lumen extends downward from the proximal ends of the ambulacral tunnels to open into the underlying thecal cavity. The distal margin of the frame is subpentagonal in outline and is continuous with the five radiating ambulacra.

Five frame plates are radial and lie at the proximal ends of the ambulacra, and five are interradial. Each radial plate is formed by the fusion of several proximal pairs of the biserial, ambulacral floorplates of the adjacent ambulacrum. They expand proximally, both inward

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and laterally. Adjacent radials may be in contact around the innermost proximal part of the frame rim, under the interradial elements. These radials also extend distally out under the proximal, unfused ambulacral floorplates.

The interradial frame plates lie between the radials. These elements are formed by the fusion of ambulacral floorplates and the proximal interambulacral plate of each interambulacrum. Each interradial includes floorplates from both adjacent ambulacra. Apparently, opposing members of the most proximal pairs of biserial floorplates of each ambulacrum separate along the perradial suture line. Opposing pair plates migrate laterally away from each other and become incorporated into different interradial frame plates. Thus each interradial includes floorplates from one side of the biseries of both adjacent ambulacra. These floorplates are fused to each other and form the proximal ends of the interradials. The adradial ends of these fused "half pairs" of floorplates are also fused to the adjacent proximal plate of each interambulacrum to form a single large frame interradial.

Viewed externally, when oral coverplates are in place, only the interradial plates of the frame are exposed. Of these, only the external surface of the fused interambulacral and the adradial ends of the "half pairs" of proximal floorplates are exposed. The proximal pairs of non-fused floorplates in each ambulacrum abut the distal-lateral margin of the interradial frame plate. Thus, the radial frame plates are entirely hidden beneath the proximal ambulacral and oral coverplates.

The hydropore structure lies along the right posterior margin of

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the oral area, near the proximal, posterior side of ambulacrum V. The opening is a small elliptical slit which extends across the suture between two plates, elongate normal to the suture line. The anterior or proximal hydropore plate is the interambulacral part of the posterior interradial plate of the oral frame. The posterior hydropore plate abuts the right posterior margin of the frame plate and also the proximal floorplates of ambulacrum V. This posterior plate is a modified proximal interambulacral and may be fused to the adradial end of one or more proximal posterior floorplates of ambulacrum V. The two hydropore plates are thickened around the opening and form a raised rim.

The ambulacra are broad and long, and extend past the ambitus into the sub-ambital zone. They are curved in all known species. The coverplates commonly form a single alternating biseries which meet along a zigzag or sinuous perradial line. The adradial ends of the coverplates meet the exposed parts of the floorplates along sub-marginal suture lines. The beveled lower side of the adradial ends of the coverplates rest on articulation zones formed by the upper sides of the floorplates. Except for these thin, beveled zones, the coverplates are uniform in thickness and lack both intra-thecal and intra-ambulacral extensions.

The single, alternating biseries of ambulacral floorplates are covered perradially by the coverplates, but their adradial ends are externally exposed. The perradial ends of opposing floorplates slope steeply inward to form a deep central ambulacral trough which is

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roofed by the coverplates. The pointed perradial ends of the alternate floorplates form a zigzag perradial suture line along the floor of the trough.

Adradially, the thick floorplates abut adjacent interambulacrals along vertical or slightly oblique sutures to form the adradial suture of the ambulacrum. The exposed upper surface of the floorplates slopes upward to the sub-marginal suture line. Perradial to the sub-marginal suture line, the upper surfaces of the floorplates form the articulation zone on which the coverplates rest. These flank each side of the ambulacral trough, and slope slightly inward toward the ambulacral midline.

Sutural passageways connect the ambulacral tunnel with the thecal cavity. One passageway extends inward along each lateral suture between adjacent floorplates. Thus, two rows of passageways penetrate each ambulacrum, one along each margin of the ambulacral trough.

The upper ends of the floorplate passageways open into small, subcircular pits which are centered over the lateral sutures. These pits lie along the upper margin of the trough, at the inner edge of the floorplate articulation zones. The inner ends of the passageways open into depressions, elongated normal to the ambulacral axis, which lie along the inner (thecal cavity side) suture lines between the floorplates.

In some species the upper pits of the passageways open into deep sutural grooves which extend down the sides of the ambulacral trough along the lateral sutures between adjacent floorplates. The grooves

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open into small lower pits which form a single row flanking each side of the floor of the ambulacral trough. Passageways do not extend inward from these lower pits. Additional grooves may also occur within the ambulacral trough. Commonly a shallow lateral groove flanks each side of each deep sutural groove, separated from it by a small ridge. Moreover, a shallow groove may extend from the perradial sides of the lower pits along the perradial ends of the lateral suture lines between floorplates. This groove intersects the perradial floorplate suture. This central suture line may also be slightly depressed to form a shallow zigzag perradial groove.

Interambulacral plates are large, thick, polygonal and tessellate.

The anal structure is a periproct in interambulacrum 5. It is formed by several irregular circlets of plates.

Small polygonal plates, continuous proximally with the large interambulacrals, form the resting zone and the proximal part of the incurved zone of the theca. Plates in the distal circlet of the incurved zone are commonly larger than the more proximal ones, and form an irregular distal circlet. The distal margin of these plates tapers to a thin edge which points toward the center of the lower surface of the theca. The thick basal membrane, imbedded with numerous minute platelets, is attached to the distal edge of the distal plates of the incurved zone.

Discussion:

Species embraced in the Order Edrioasterida were first separated from other edrioasteroids into the Family Edrioasteridae by Bather

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(1898). He cited as the important differentia: (1) the absence of a definite border of plates which define the margin of the upper oral surface, i.e., peripheral rim, and (2) the extension of the ambulacra below the ambitus onto the lower side of the theca. In Bather's 1900 summary of the Class Edrioasteroidea, he also mentioned the small size of the attachment area.

Jaekel (1899) recognized only two families of edrioasteroids, the Thecoidea and Agelacrinitidae. Edrioasterida species were placed in the first, along with stromatocystids, cyathocystids, and Cystaster.

In 1914 Bather published a more complete description of his Family Edrioasteridae which summarized his extensive investigation of Edrioaster, Dinocystis, and Lebetodiscus. Family features mentioned include: the relatively thin thecal plates; the lack of permanent attachment of the theca; ambulacra which extend onto lower surface of theca and are formed by movable coverplates and biserial floorplates with sutural pores; interambulacrals continuous with plates on the lower side of the theca; a central lower surface covered by a flexible integument with minute plates; and, a hydropore piercing the proximal interambulacral plate of interambulacrum 5.

Subsequent works have recognized Bather's Edrioasteridae, although Lebetodiscus, which was included originally, has been placed in various other families by most. Jaekel (1918) recognized the Edrioasterida as defined by Bather, but excluded Lebetodiscus. Bassler (1935) in agreement with Spencer (1904), cited the biserial ambulacral floorplates as one of the most important diagnostic features. Regnéll (1966)

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emended Bather's description only by adding: a description of the thecal shape ("tam-o-shanter" with centrally excavate aboral surface); that the interambulacrals are polygonal and tessellate; and that the coverplates correspond in position with the floorplates. Kesling (1967) accepted thecal shape, lack of a peripheral rim, and the biserial floorplates as the important taxobases.

In the Edrioasteridae of Bather, as recognized here, several features found throughout are judged to be ordinal taxobases. Hence the Order Edrioasterida is proposed. Four primary features differentiate the Edrioasterida from the Isorophida.

First, the oral frame of the Edrioasterida is formed by 10 compound plates that include numerous fused proximal ambulacral floorplates (50 to 60 in Edrioaster bigsbyi) and five proximal interambulacrals. Oral covering plates do not participate in frame formation. The Isorophida oral frame is formed by only five major elements: a single, enlarged proximal floorplate of each ambulacrum. Commonly, it also includes intra-thecal extensions from the overlying oral covering plate.

Second, the edrioasterid hydropore is a sutural slit, elongated normal to the suture between the two hydropore plates, and it penetrates these plates. The isorophid hydropore opens along the junction between two or more plates, the opening being formed by the edges of the plates. Thus, it does not penetrate the plate structure.

Third, the ambulacral coverplates of the Edrioasterida rest on the upper sides of floorplates and do not extend out to the adradial

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suture. Thus, the upper faces of the adradial ends of the floorplates are exposed externally. Moreover, the coverplates are more or less uniform in thickness except where the beveled adradial ends meet the underlying floorplates. The isorophid coverplates rest on the upper lateral margins of the floorplates, and commonly extend past them into the theca as intra-thecal extensions. The coverplates thus form the external part of the adradial suture and thereby entirely cover the floorplates which can be seen only from the inner side of the theca. Commonly the ambulacral tunnel surfaces of the coverplates are thickened to form complex intra-ambulacral extensions.

Fourth, the ambulacral floorplates of the Edrioasterida are biserial. Sutural passageways extend between the floorplates from the ambulacral tunnels into the thecal cavity. The isorophid floorplates are uniserial and lack passageways of any sort.

Other edrioasterid thecal features, including thecal shapes, oral plate patterns, ambulacral coverplate patterns, interambulacral plate characteristics, anal structure features, and hydropore structure features, may eventually prove to be familial taxobases. However, all genera and species included here are now judged to belong to one family.

The Edrioasterida hydropore opening is described here as lying in the right posterior part of the oral area. In contrast, former descriptions (Bather, 1914, Kesling, 1960) place this structure in the proximal part of interambulacrum 5. This change reflects only a modification of terminology. The anterior of the two hydropore plates

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is fused to floorplates to form the posterior interradial oral frame plate. This is considered to be incorporated into the posterior oral area. The more posterior, right hydropore plate appears to be fused to the posterior proximal floorplates of ambulacrum V in some species; in others it is free but intrudes into the edge of the ambulacrum and the adjacent floorplates are adradially shortened where they abut this plate. So modified, this posterior plate is also considered to be an oral area element. As noted by Kesling (1960, p. 148), "If they [the two hydropore plates of Edriophus levis (Bather)] are regarded as part of the ambulacral and peristomial region, then the hydropore is located within a posterior expansion of the peristomial region."

Two European species, Edrioaster buchianus (Forbes) and Dinocystis barroisi Bather, appear to belong to the Family Edrioasteridae, but were not restudied during this investigation. Published descriptions suggest that Edrioaster buchianus belongs to the genus Edriophus. Unfortunately, the coverplates are not preserved in the known specimens, which are only molds of the upper oral surface. It may well be that these specimens are conspecific with Edriophus levis.

Dinocystis barroisi is separated generically from other Edrioasterida by the contrasolar curvature of all five ambulacra. Moreover, the resting and incurved zones of the theca appear to be formed by squamose, imbricate plates. This species is also represented only by molds, with the ambulacral and oral covering plates not preserved.

Range and occurrence: Middle Ordovician of eastern North America and Europe.

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Family Edrioasteridae Bather, 1898

Type genus: Edrioaster Billings, 1858.

Characters of the Order.

Edrioaster Billings, 1858

1842 [non] Agelacrinites Vanuxem, L., Nat. Hist. of New York, pt. IV, Geology 3: 158, fig. 80.

1854 Agelacrinites Vanuxem, Billings, E. K. [partim], Canadian Jour. Industry, Sci. and Art: 271-273 [non text fig. 10-12].

1857 Cyclaster Billings, E. K. [partim], Geol. Surv. Canada, Rept. Progress 1853-1856: 292-294.

1858a Edrioaster Billings, E. K. [partim], Geol. Surv. Canada, Fig. and Descriptions of Canadian Organic Remains, dec. 3: 82-83, 85, pl. 8, fig. 1, 1a, 2, 2a.

1860 Agelacrinites Vanuxem, Chapman, E. J. [partim], Canadian Jour. Industry, Sci. and Art (n.s.), 5: 361-365.

1889 Edrioaster Billings, Miller, S. A., North American Geology and Palaeontology, Cincinnati: 242.

1894 Aesiocystites Miller, S. A. and Gurley, F. E., Illinois St. Mus. Bull. 5: 13-15, pl. 2, fig. 10-12.

1896b Edriocystis Haeckel, E. [partim], Die Amphorideen und Cystoideen, Leipzig, 1: 117-118, pl. 3, fig. 35-36.

1899 Edrioaster Billings, Jaekel, O. [partim], Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 44-46, pl. 2, fig. 4, 4a.

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1900a Edrioaster Billings, Bather, F. A. [partim], in A Treatise on Zoology, E. R. Lankester (ed.), London, pt. III, Echinoderma: 209, text fig. 6-1, -2, -3; Aesiocystis Miller and Gurley, idem, ibid.: 208-209.

1903 Edrioaster Billings, Delage, Y. and Herouard, E., Traité de Zoologie Concréte, T. 3, Echinodermes, Paris: 414-415, text fig. 548-550.

1903 Edrioaster Billings, Steinmann, G., Einführung in die Paläontologie, Leipzig: 192-193, text fig. 264D-E.

1907 Edrioaster Billings, Steinmann, G., Einführung in die Paläontologie, 2nd edition, Leipzig: 213-214, text fig. 299d-e.

1908 Edrioaster Billings, Bather, F. A. [partim], Geol. Mag. (n.s.), dec. 5, 5: 543-550.

1914 Edrioaster Billings, Bather, F. A. [partim], Geol. Mag. (n.s.), dec. 6, 1: 115-125, 162-171, text fig. 1, 3-4, pl. 10, fig. 1-11, pl. 11, fig. 1-2, pl. 13, pl. 14, fig. 1-3.

1915a Edrioaster Billings, Bather, F. A. [partim], Geol. Mag. (n.s.), dec. 6, 2: 211-215, 259-266, text fig. 1a.

1915b Edrioaster Billings, Bather, F. A. [partim], Geol. Mag. (n.s.), dec. 6, 2: 316-322.

1915c Edrioaster Billings, Bather, F. A. [partim], Geol. Mag. (n.s.), dec. 6, 2: 393-403, text fig. 3.

1915 Edrioaster Billings, Bassler, R. S. [partim], United States Nat. Mus. Bull. 92, 1: 473-474; Aesiocystites Miller and Gurley, idem, ibid.: 19.

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1935 Edrioaster Billings, Bassler, R. S. [partim], Smithsonian Misc. Coll. 93 (8): 9.

1938 Edrioaster Billings, Bassler, R. S., Fossilium Catalogus I: Animalia, pars 83, Gravenhage, Holland: 92.

1943 Edrioaster Billings, Bassler, R. S. and Moodey, M. W. [partim], Geol. Soc. America, Spec. Pap. 45: 201-202.

1944 Edrioaster Billings, Shimer, H. W. and Shrock, R. R., Index Fossils of North America, New York: 131-133, pl. 49, fig. 24.

1946 Edrioaster Billings, Wilson, A. E., Geol. Surv. Canada Bull. 4:22.

1953 Edrioaster Billings, Piveteau, J., Traité de Paléontologie, Paris, 3: 654-655, text fig. 7-8.

1960 Edrioaster Billings, Kesling, R. V. [partim], Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 145-146, text fig. 1, 14a [non pl. 1, fig. 1-2].

1963 Edrioaster Billings, Müller, A. H., Lehrbuch der Paläozoologie, Bd. 2, Invertebraten, Teil 3, Jena, East Germany: 280, text fig. 386.

1966 Edrioaster Billings, Regnéll, G. [partim], in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: U171, text fig. 111, 116-1, 118-1, 119-1, 3, 120-1, 131-1a, b.

Type species: Cyclaster bigsbyi Billings, 1857.

Diagnosis:

Edrioasteridae with: "echinoidal" theca, oral plates similar to ambulacral coverplates in size and shape; right posterior hydropore

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structure plate intrudes into proximal posterior edge of ambulacrum V, abutting, but free from floorplates; ambulacra curved, I - IV contrasolar, V solar, elevated above interambulacra with adradial edges steep, ambulacral coverplates in single, alternating biseries; plates of distal circlet of incurved zone large.

Description:

Only the type species, Edrioaster bigsbyi, is placed in the genus without question. Thus, for diagnostic purposes, the genus is essentially monotypic, and has the characters of the type species. Separation of generic and specific traits is uncertain. The features cited in the above diagnosis are in part inferred to be of generic rank from taxobases established for other edrioasteroid genera.

Discussion:

Billings (1854) reviewed published descriptions of "Trenton limestone" edrioasteroids, and described additional, new specimens which he had examined. Included was a reconstruction (1854, fig. 10) based on several specimens, labeled Agelacrinites from the Trenton Limestone, Bytown. His specimens apparently represent two species, Edrioaster bigsbyi (Billings) and Edriophus levis (Bather). The reconstruction is dominated by features of the latter, the ambulacra all curved solarly, and the thecal plates are smooth. Billings concluded that large, "globoid" Trenton species apparently belonged to a new genus which fit published descriptions of neither Agelacrinites Vanuxem (1842) nor Hemicystites Hall (1852).

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Billings later proposed (1857) the genus Cyclaster (type species C. bigsbyi Billings). The following year he substituted the name Edrioaster for the preoccupied Cyclaster. Billings' generic description (1857, p. 292) was brief: "body sessile, circular, discoid, covered with numerous irregularly polygonal plates; mouth large, subpentagonal [oral frame]; five ambulacral areas, each composed of two series of oblong plates [floorplates] and having two rows of large pores which penetrate to the interior."

Billings apparently included in his new genus specimens recognized here as representing 4 species of 3 genera. In the generic discussion he refers to Sowerby's 1825 illustration of a then unnamed specimen of Lebetodiscus dicksoni and to the type specimen of Edriophus buchianus (Forbes) (1848). In addition, Billings' description of the type species, Cyclaster bigsbyi, includes specimens representing not only Edrioaster bigsbyi (Billings), but also specimens of Edriophus levis (Bather), i.e., specimens with some ambulacra curved contrasolarly (I-IV) and with tuberculate plates as in Edrioaster bigsbyi, and others with all ambulacra curved solarly and the thecal plates smooth as in Edriophus levis.

Billings (1858) not only introduced the name Edrioaster, but also "corrected" parts of his 1857 description. He here reports four rows of ambulacral "pores" rather than two. The original two rows identified by Billings as pores lie along the sutures between floorplates at the perradial edge of the zone of articulation with the overlying coverplates. Sutural passageways do extend into the thecal

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cavity along these zones, each originating at the base of a small pit centered over the floorplate sutures. Two lower rows of small pits, perradial to these upper pits, are found near the perradial floorplate suture line, one along each side of the floor of the ambulacral trough. The lower pits are also centered over the lateral sutures between the floorplate and are connected to the upper pits by a deep groove which extends along the floorplate lateral sutures. However, in contrast to Billings' description, these end blindly. Thus, only one set of passageways is developed on each side of each ambulacrum.

Billings (1858) also mentioned that in 1857 he had misinterpreted Forbes' description of Agelacrinus buchianus and thus erroneously referred a specimen of Agelacrinites dicksoni to the genus Edrioaster. It is ironical that this specimen, collected by Bigsby, had inspired the trivial name bigsbyi, but fortunately it had not been designated type of the new species.

Edrioaster Billings was a commonly accepted genus during the last half of the Nineteenth Century. However, Chapman (1860) referred E. bigsbyi to Agelacrinites, and Haeckel (1896) arbitrarily changed the spelling of the generic name to Edriocystis.

Miller and Gurley (1894) proposed the genus Aesiocystites for a new species A. priscus. The few available specimens of this species are poorly preserved, but appear to conform to the generic traits of Edrioaster.

Bather published a series of papers (1898-1915) describing in great detail several edrioasteroid species, including Edrioaster

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bigsbyi (Billings), Edriophus buchianus (Forbes) and Edriophus levis (Bather). Bather included all three species, plus Edriophus saratogensis (Ruedemann) in the genus Edrioaster. His emended generic diagnosis (1914, p. 170) recorded: "An Edrioasteroid with pores of subvective groove within the tract protected by coverplates; with interradials all tessellate and separated from the central apical region by a frame of stouter plates; on the apical face the peripheral plates are variable in size but not minute, the central plates are minute and tend to imbricate." Ambulacral curvature, coverplate shapes, thecal size and prosopon were relegated to trivial taxobases.

Bassler (1935) emended the diagnosis of Edrioaster and restricted the genus to species with ambulacra curved I-IV contrasolar, V solar. However, in spite of his definition, he listed Agelacrinites buchianus, Edrioaster levis, and Edrioaster saratogensis as species belonging to Edrioaster, although all three have ambulacra I-IV curved solarly.

Recent references to Edrioaster have been based on Bather's description without restudy of specimens. Most comprehensive is Regnéll's (1966, p. U171) diagnosis which recognizes variable ambulacral curvature but suggests species with solar curvature "possibly should be separated generically".

Edrioaster is here restricted to species with ambulacra curved I-IV contrasolar, V solar. Only the type, E. bigsbyi, is included with certainty. Aesiocystites priscus is included with question due to the poor preservation of all available specimens which has obscured the details of most plate boundaries in the critical oral-ambulacral

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series.

Range and occurrence: Trenton Group, Middle Ordovician, of eastern North America.

Edrioaster bigsbyi (Billings), 1857

Text fig. 62-63; plate 58-59.

1854 Agelacrinites sp. Billings, E. K. [partim], Canadian Jour. Industry, Sci. and Art: 271-273 [non text fig. 10-12].

1857 Cyclaster bigsbyi Billings, E. K. [partim], Geol. Surv. Canada, Rept. Progress 1853-1856: 293-294.

1858a Edrioaster bigsbyi (Billings), E. K. [partim], Geol. Surv. Canada, Fig. and Descriptions of Canadian Organic Remains, dec. 3: 82-83, 85, pl. 8, fig. 1, 1a, 2, 2a.

1860 Agelacrinites bigsbyi (Billings), Chapman, E. J., Canadian Jour. Industry, Sci. and Art (n.s.) 5: 361-365.

1896b Edriocystis bigsbyi (Billings), Haeckel, E., Die Amphorideen und Cystoideen, Leipzig, 1: 117-118, pl. 3, fig. 35-36.

1899 Edrioaster bigsbyi (Billings), Jaekel, O., Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 44-46, pl. 2, fig. 4, 4a.

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Diagnosis:

An Edrioaster with: large, "echinoidal" theca; 9 or more oral plates; ambulacral coverplates sub-pentagonal, perradial ends pointed; interambulacrals large, polygonal, tessellate, periproct formed by several irregular circlets; thecal plates with large, rounded, external nodes.

Description:

The large echinoidal theca of Edrioaster bigsbyi (Billings) reaches diameters of over 45 mm (reconstruction, text fig. 2).

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The oral plates which cover the central oral area are missing or disrupted in available specimens. However, Bather (1914) illustrated a now missing individual which preserves seven oral plates. Obviously missing at least two or more additional orals, his specimen suggests nine or more orals form the central oral area. The orals are similar in shape and size to the proximal ambulacral coverplates. Four or five central orals may be somewhat larger than the others. Distally the oral plates appear to grade into the proximal ambulacral coverplate series without apparent division between the two sets of plates.

The oral frame of E. bigsbyi is poorly exposed in available specimens (pl. 58, fig. 1-5, pl. 59, fig. 5). Distally the frame is pentagonal in outline, confluent with the ambulacral structures. The proximal rim of the frame appears to be sub-pentagonal with five large rounded lobes surrounding the central lumen. However, only the outline of the inner side of the frame has been seen as an impression through the distal membrane of the lower side of the theca (pl. 59, fig. 2, 8, 10).

The frame comprises ten compound plates, five radials and five interradials. Each of the five radials is formed by the fusion of three or four pairs of proximal floorplates from the adjacent ambulacrum (text fig. 62A-B, pl. 58, fig. 2-5). These pairs of floorplates are fused to one another both laterally and perradially, obliterating the sutures. However, four to six passageways penetrate each compound radial. These passageways are believed to be homologous to the floorplate passageways of the ambulacral floorplates, and thus mark the

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Text Figure 62 Edrioaster bigsbyi (Billings), 1857

A. Lectotype, G.S.C. 1407, (X5), pl. 58, fig. 4. Axial cross-section view.

B. Lectotype, G.S.C. 1407-a, (X5), pl. 58, fig. 5.

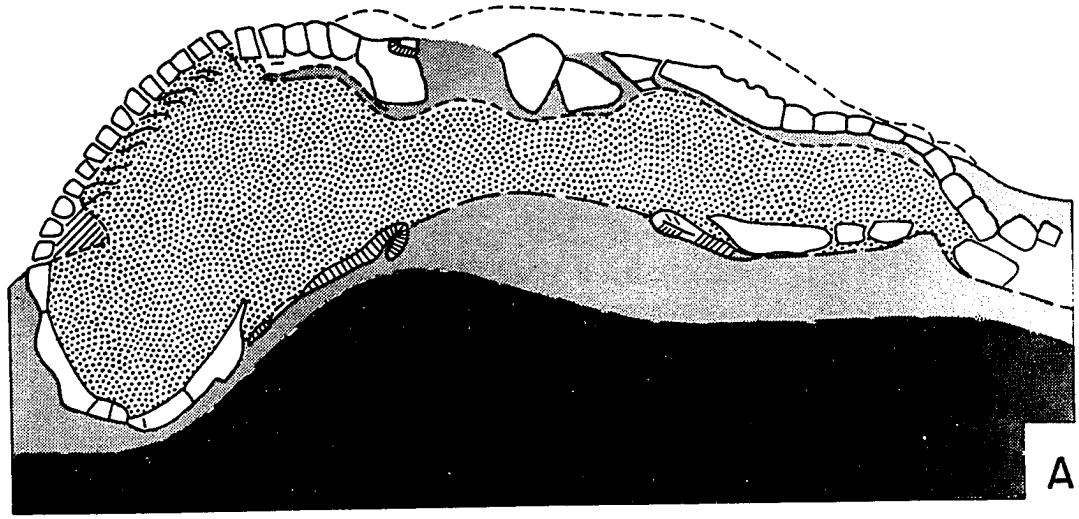
Dark shading marks firm carbonate substrate; light shading marks softer, dark shale which buried the specimen; dotted pattern marks fine-grained, light-colored, carbonate filling of thecal cavity.

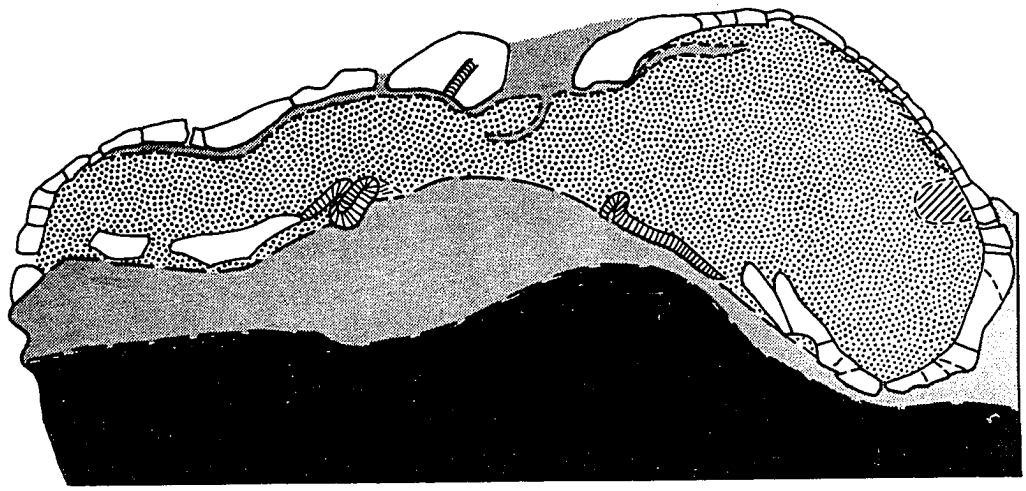
Text Figure 63 Edrioaster bigsbyi (Billings), 1857

A. Lectotype, G.S.C. 1407-a, (X4), pl. 58, fig. 6. Lateral cross-section view cutting ambulacrum II and adjacent structures. Dark shading marks firm carbonate substrate; light shading marks softer, dark shale which buried the specimen; dotted pattern marks fine-grained, light colored, carbonate filling of thecal cavity.

B. Lectoparatype, G.S.C. 1407-e, (X10), pl. 58, fig. 12. Segment of one ambulacrum exposing the upper surface of the floorplates. A cross-section of the ambulacrum is shown at the left end of the specimen. The shaded upper floorplate exposes the proximal sutural face of the plate, with the sutural passageway, groove and pits. The striped, lower floorplate face is a section through the center of the alternate, opposing floorplate.

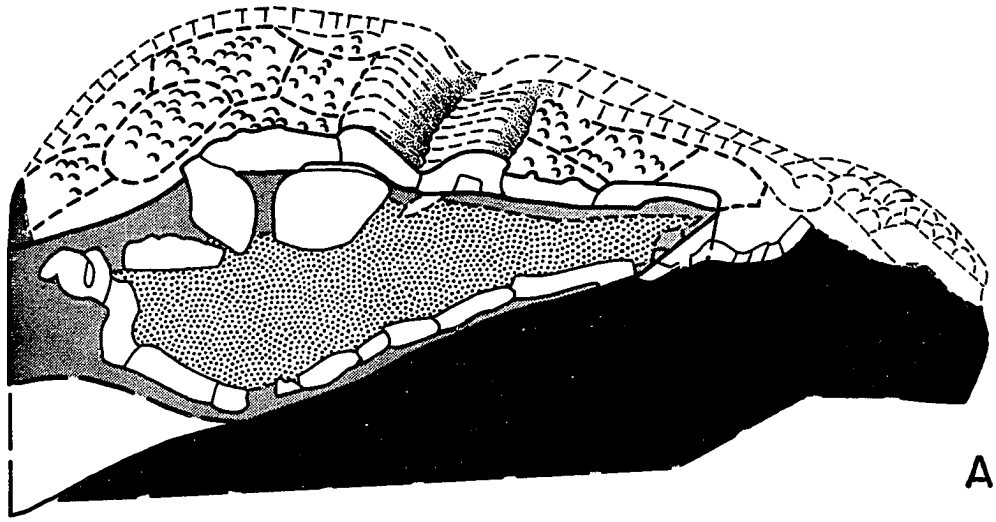
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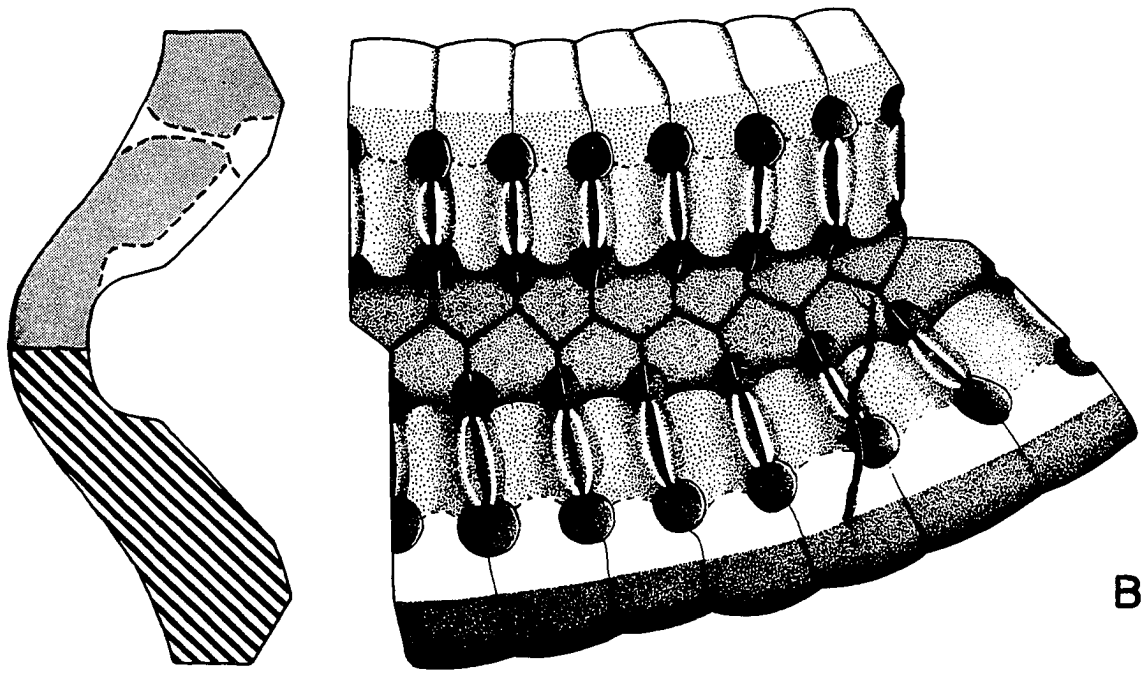




Text Figure 62

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Text Figure 63

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position of the now fused lateral sutures between the floorplate components of the radial plates of the frame.

The compound radial plates extend inward proximally to form the radial sectors of the thick proximal wall of the rim of the frame. The innermost edge of each radial extends into the thecal cavity over twice as far as the adjacent (non-fused) proximal floorplates of the ambulacra. Distally each radial becomes thinner and narrower, and this tapered part extends out under the proximal three or four pairs of floorplates of the adjacent ambulacrum. The center of the upper surface of this tapered, distal sector of each radial is exposed axially where the proximal two or three pairs of non-fused floorplates of the adjacent ambulacrum are perradially separated, with the opposing members of each pair pulled away from one another along the perradial suture.

The five interradial frame plates alternate with the radials. Each compound interradial is formed by the fusion of four proximal floorplates and a large proximal interambulacral plate. The floorplates form the proximal sector of the compound interradial and the interambulacral plate forms the distal part. The floorplates that are incorporated into the interradial plates represent "half-pairs", i.e., the opposing pair members of two pairs of proximal floorplates of each ambulacrum have been separated perradially and those on one side of the perradial line have been incorporated into the interradial plate which flanks one side of the ambulacrum, whereas the opposing members of the pairs of floorplates have been incorporated into the interrad-

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ial which flanks the other side of that ambulacrum. Three passageways penetrate the proximal end of each interradial and demonstrate that four floorplates have been fused together laterally, two from each adjacent ambulacrum. These fused floorplates are proximally enlarged and extend inward over twice as far as the adjacent proximal non-fused floorplates of the ambulacra. The interradial sectors of the inner rim of the frame are formed by the proximal inner ends of the fused floorplates of each interradial plate. The inner edge of the rim of the frame is thus formed by alternating radials and interradials. The upper parts of the fused floorplates of the interradials abut the proximal, lateral edges of the proximal non-fused floorplates of each adjacent ambulacrum. Adradially the fused floorplates of the proximal part of the compound interradial are fused to the proximal plate of the adjacent interambulacrum. This interambulacral forms the largest part of the compound interradial plate and extends distally much further than the adjacent compound radial plates of the frame.

The compound frame plates thus represent numerous fused elements. The five radials each have six to eight fused floorplates and the five interradials each represent four fused floorplates and one interambulacral. Thus fifty to sixty individual floorplates and five interambulacral plates are included in the structure.

When proximal ambulacral coverplates and the oral covering plates are in place, the upper, adradial ends of the fused floorplate sectors of each interradial plate of the frame remain exposed externally. Like the adradial portions of the adjacent ambulacral floorplates, these are

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abruptly elevated above the level of the interambulacrals and form a small ridge continuous with the ambulacral ridges. The distal margin of this ridge marks the line of fusion of the floorplates with the proximal interambulacral plate of each interambulacrum, although all traces of the original suture have been obliterated.

The hydropore is a small elliptical opening along the right posterior margin of the oral area, shared by two plates (pl. 59, fig. 5). It is elongate normal to the suture between two plates: the interambulacral part of the posterior interradial plate of the oral frame, and an adjacent, posterior, polygonal plate. The left anterior margin of this posterior plate abuts the right posterior margin of the posterior interradial frame plate. Its right edge intrudes into the adradial edge of the proximal posterior side of ambulacrum V where it abuts one or two proximal floorplates which are thus shorter than adjacent floorplates. Distally this posterior plate abuts interambulacrals. This posterior hydropore plate is constant in position from one specimen to another and is considered to be part of the oral series, as are the modified interambulacral plates incorporated into the compound interradial frame plates. The edges of the two hydropore structure plates are thickened around the opening and form a small raised rim.

The stone-canal passageway leads inward from the hydropore and penetrates both plates of the hydropore structure. It appears to extend obliquely inward in a proximal direction; it is thus housed primarily by the posterior interradial frame plate. The inner edge of this posterior interradial is enlarged and apparently modifies the

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inner end of the passageway, but this area is inadequately exposed in available specimens.

The five, long, broad ambulacra extend from the oral region, past the ambitus, into the sub-ambital thecal zone. All are curved, I-IV contrasolarly, V solarly. Curvature is uneven; the proximal upper surface parts are commonly straight or nearly so, followed by pronounced curvature immediately distal to the ambitus. The distal parts of the ambulacra extend along the sub-ambital zone concentric with the ambitus. Ambulacrum V commonly curves back onto the upper oral surface and ends near the left posterior edge of the anal area. The proximal, upper oral surface parts of the ambulacra may be gently curved, often in the opposite direction to that of the major distal direction of curvature. Bather (1914, p. 122) presented detailed descriptions of these minor proximal undulations in several specimens. His data show the proximal flexures of each ambulacrum to vary in degree and even direction from one specimen to another, and thereby to have no taxonomic importance. Moreover, in partially inflated specimens, such as the lectotype, these proximal parts are nearly straight, suggesting that much of the apparent minor curvature is preservational, produced during thecal depression.

The ambulacra form low rounded ridges on the thecal surface. Their adradial edges are steeply inclined and rise abruptly from the adjacent interambulacra.

The ambulacral coverplates form a single alternating biseries. Each plate is sub-pentagonal; the perradial end is pointed and inter-

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digitates with the opposing alternate coverplates to form a prominent zigzag perradial line (pl. 59, fig. 15-16). Lateral sides are straight and parallel, and they extend normal to the ambulacral axis. The slightly convex adradial ends of the coverplates meet the exposed adradial ends of the ambulacral floorplates and form subtlely scalloped sub-marginal suture lines with the exposed parts of the floorplates. The lower edge of the adradial ends of the coverplates are beveled to fit tightly against the slightly inwardly sloping upper lateral surface of the floorplates, along the articulation zone. Otherwise the coverplates appear to be of uniform thickness, without intra-ambulacral extensions. Commonly the coverplates are either lost or collapsed into the ambulacral groove during preservation.

Bather (1914, p. 162) described an additional set of coverplates termed "accessory coverplates". He described them as small plates wedged between the adradial ends of the coverplates and floorplates, and supposedly lying adjacent to the lateral adradial edges of the coverplates. These elements occur only sporadically along the ambulacra, supposedly often hidden from view. Topotype G.S.C. 1407-d has these elements in the proximal part of ambulacra I and II. The coverplates are slightly disrupted and overlap one another laterally. Where ever one of these small plates occur, the adradial corner of the adjacent coverplate is unusually rounded. It now appears that these supposed plates are merely fragments broken from the coverplates during preservation.

The biserial ambulacral floorplates are elongate and sub-rectang-

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ular in plan view (text fig. 63B). Their perradial ends are pointed and form a central, zigzag, floorplate perradial suture. The long, straight, lateral edges of each floorplate are nearly parallel to one another and extend normal to the ambulacral axis. The adradial ends are irregularly convex outward and abut adjacent interambulacrals. Each floorplate lies directly under a corresponding coverplate. Thus, lateral sutures of the plates and the zigzag perradial lines of both series are aligned, one above the other. The adradial ends of the longer floorplates extend past the ends of the coverplates, and are thereby exposed externally between the adradial and sub-marginal ambulacral suture lines.

The floorplates form a broad central ambulacral trough. Opposing alternate floorplates slope downward from the zone of articulation with the coverplates to the center of the ambulacral trough. The rate of slope is gradual along the upper sides of the trough. However, a short, steeply inclined zone flanks the nearly horizontal perradial area and thus a narrow U-shape trough is incised into the center of the broad ambulacral trough.

The sectors of the floorplates which form the upper lateral margins of the deep ambulacral trough are nearly horizontal and slope only slightly perradially. This is the articulation zone on which the bases of overlying coverplates rest. The zone lies in part along and in part adradial to the upper ends of the floorplate passageways. Adradial to the coverplate articulation zone, the floorplates slope away from the ambulacral trough and form the externally exposed

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adradial zone of the floorplates. The pronounced adradial slope of this area forms the abrupt sides of the externally elevated ambulacra which rise above the adjacent interambulacra.

The floorplates are thickest under the articulation zone, thinning conspicuously toward their perradial ends (text fig. 63A-B). Thus, the inside inward convexity of the ambulacra is less pronounced than the external corresponding concavity of the ambulacral trough. Perradially, opposing alternate floorplates abut along vertical sutures. Adradially, they abut adjacent interambulacrals along vertical or perhaps oblique sutures which may slope toward the ambulacral axis.

The floorplate passageways begin in small, sub-circular, steep-walled pits which are centered over the lateral sutures between adjacent floorplates. These pits lie along the perradial edge of the coverplate articulation zone. Their adradial ends are partly roofed by the bases of the overlying coverplates whereas the perradial sides of the pits are open into the upper lateral margin of the ambulacral tunnel. The passageways extend inward from the floor of these pits along the floorplate sutures. Their inner ends expand and open into the thecal cavity as sutural depressions elongate normal to the ambulacral axis. Bather (1914, p. 124) reported these inner surface depressions are larger than the upper pits.

The small pits which mark the upper ends of the floorplate passageways form two rows along each ambulacrum, one flanking each edge of the ambulacral tunnel. Two additional rows of pits, perradial to the passageway pits also occur (text fig. 63A-B). One row of these

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lower depressions lies along each steep wall of the central U-shaped axial depression in the center of the broad ambulacral trough. These sub-central pits are less clearly defined than the passageway pits and their perradial edges open toward the central axial trough.

The upper and lower rows of pits on each side of the ambulacrum are connected by deep grooves which extend along the lateral sutures of the floorplates. Moreover, a shallower groove flanks each side of each sutural groove. The three grooves extend toward the center of the ambulacral trough parallel to one another, normal to the ambulacral axis. A small ridge separates each shallow lateral groove from the adjacent deep sutural groove.

The lower series of less well-defined pits end blindly, but apparently misled earlier workers to suggest that four rather than only two rows of passageways penetrate each ambulacrum. The floorplate grooves, which extend along the walls of the ambulacral trough between the upper and lower lateral pits, were first described by Bather (1914, p. 123). In contrast with the above description, he reported that the shallower grooves which flank each sutural groove diverge as they extend downward toward the center of the ambulacral trough.

The perradial edges of the floorplates are slightly depressed and form a subtle groove along the zigzag perradial suture line. The lateral edges of the floorplates, perradial to the lower pits, are also slightly depressed and thus form very subtle grooves which extend from the lower pits along the lateral sutures to intersect the perradial suture line grooves at each zig and zag point.

Interambulacral plates are large, polygonal and tessellate.

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Smaller polygonal plates, continuous with the interambulacrals, form the resting and proximal part of the incurved thecal zones.

The resting zone is two or three plates wide. Distal to these, three or four irregular circlets form the incurved zone of the theca which is flexed upward above the substrate and extends inward toward the center of the theca. The last (distal) circlet includes approximately twelve large plates which form a well-ordered circlet. The distal margins of these plates taper to a thin edge. The proximal edge of the lower-surface membrane is attached to the distal tapered edge of these large plates. This membrane is imbedded with numerous minute plates, slightly elongate concentric with the thecal margin. The membrane apparently flexed downward and attached to the substrate. The membrane is not in evidence across the center of the lower surface, and a small central zone surrounded by the distal margin of the plated membrane thus represents the aboral surface of the theca. The five-part lobation of the basal membrane described by Bather (1914) is merely the impression of the inner edge of the oral frame seen through the membrane which is pressed against that structure during thecal collapse.

The periproct lies in the posterior part of the upper oral surface part of interambulacrum 5. It includes a large number of plates which are smaller than the surrounding interambulacrals. These form three or four irregular circlets. The central plates are elongate and sub-triangular and may be more regular.

External thecal plate surfaces are covered by rounded nodes which occur irregularly on the plates. This pustular prosopon appears to be

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limited to upper oral surface and sub-ambital thecal zones; the plates of the resting and incurved zones are apparently smooth externally.

Specimens:

G.S.C. 1407, 1407a, 1407c-h. Eight pieces representing six specimens. "Cobourg beds, Trenton Limestone", Trenton Group, Mohawkian Series, Middle Ordovician. Ottawa, Ontario.

The collection of the Geological Survey of Canada now includes six specimens of Edrioaster bigsbyi (G.S.C. 1407). Two of these are from Billings' (1858) original type series and were illustrated in his publication. Bather (1914) designated specimens G.S.C. 1407-1407a, which are two pieces of one individual, the "holotype", i.e., lectotype. The other specimen, illustrated by Billings (G.S.C. 1407e-1407f, two fragments of one specimen) is thus a lectoparatype. The other four specimens are topotypes, and may have been in Billings' original type series; they were not illustrated by him.

When Bather restudied Edrioaster bigsbyi he indicated that the collection of the Geological Survey of Canada included ten specimens. Bather's description was based on three of these ten, referred to as "A", "B" and "C". These three individuals, plus a fourth, are now missing. However, Bather's "B" and "C" closely resemble specimens G.S.C. 1407-d and G.S.C. 1407-c, respectively. Most of Bather's work was based on specimen "A"; his drawing of this specimen (see text fig. 2) suggests it is better preserved than any of the remaining individuals.

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G.S.C. 1407-1407a. Lectotype of E. bigsbyi (Billings) (1857, p. 293-294, 1858, pl. 8, fig. 1, 1a).

1407. 39.3 mm "axial" (along cut surface) by 20.5 mm "transverse" diameter (normal to cut section, from oral area out to edge of theca).

Text fig. 62A, pl. 58, fig. 1, 3-4.

1407a. 37.2 mm "axial" (along axial line cut section) by 11.5 mm normal to axial cut, out to second lateral cut.

Text fig. 62B, 63A, pl. 58, fig. 1-2, 5-6.

The lectotype exposes the upper oral surface of the theca. It has been cut into three sections, one now missing. One cut nearly follows the axial midline of the theca, slicing the proximal part of ambulacrum III, the oral area, interambulacrum 5, and part of the anal structure. The right half of the theca is labeled G.S.C. 1407 (pl. 58, fig. 1). The left side of the theca was cut a second time along its left edge. The cut extends through the distal parts of interambulacra 1 and 2 and the distal upper oral surface sector of ambulacrum II. The small left edge fragment of the specimen is missing. The large fragment which preserves most of the left half of the theca is labeled G.S.C. 1407-a (pl. 58, fig. 1). The cut surfaces of this specimen expose sectional views of both upper oral surface plates and also the thecal zones below the ambitus.

The specimen is only partially collapsed and retains most of the original thecal shape. All oral and ambulacral coverplates are missing which exposes the ambulacral tunnel surface of the floorplates and the upper parts of the oral frame plates. The ambulacral and interambulac-

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ral plates are nearly in life position. Resistant matrix obscures part of the specimen. Abrasion has modified the floorplate pits and grooves, and has also broken the upper edges of some elements, particularly the posterior floorplates of ambulacrum V. The left posterior edge of the theca is missing, including the ambital part of ambulacrum I and adjacent interambulacral. The anal structure is disrupted. The prominent nodose prosopon is preserved on the interambulacrals.

The axial section of G.S.C. 1407 (text fig. 62A, pl. 58, fig. 4) shows: (1) the sutural passageways which extend between the floorplates of the right side of ambulacrum III, (2) a section view of the anterior radial oral frame plate, with an oblique view of the upper end of one passageway which extends down the sloping proximal side of the plate; this groove is open to the central lumen along its upper side but the oblique view makes it appear to be a small tube in part roofed by the plate; (3) sectional views of the posterior interradial frame plate and the proximal tips of two other frame elements; (4) sectional views of the posterior interambulacral plates and a few of the anals; (5) sectional views of the plates which form the resting and incurved zone of the theca with the posterior plates partially disrupted; (6) sectional views of the partially disrupted lower surface, plated integument which extends toward the center of the lower surface and then curves downward toward the substrate.

The opposing side of the axial cut, seen on specimen G.S.C. 1407a, exposes a slightly different view, separated from the first by the width of cutting instrument. It exposes (text fig. 62B, pl. 58, fig. 5):

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(1) a more central view of ambulacrum III floorplates, proximal to the passageways; (2) sectional view of the anterior radial oral frame plate; (3) section view of the posterior interradial oral frame plate which exposes one of the passageways that penetrate this compound plate; (4) sectional views of posterior interambulacrals, resting zone, and incurved zone plates; and (5) sectional view of the basal flexible membrane which has curled back on itself distally, but proximally is still attached to the thin distal edge of the distal circlet of plates of the incurved zone. Both axial section views of the lectotype preserve a series of thin curved slivers of calcite immediately beneath the floorplates of ambulacrum III. Most are convex toward the oral area, but some recurve and are S-shaped in section view. Apparently one calcite sliver is present for each ambulacral floorplate. If they are not preservational in origin, the relationship of these slivers to other thecal structures is unknown.

The lateral section view of the G.S.C. 1407-a (text fig. 63A, pl. 58, fig. 6) exposes a cross-section view of ambulacrum II and adjacent interambulacral plates. Interambulacrals adjacent to the anterior side of the ambulacrum are disrupted and the resultant oblique section view gives the deceptive appearance of large thick plates adjacent to and under the ambulacral plates. The lower part of the section exposes plates of the sub-ambital zone.

G.S.C. 1407 e-f. Lectoparatype of E. bigsbyi (Billings) (1857, p. 293-294, 1858, pl. 8, fig. 2, 2a).

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1407-e. 17.7 mm along cut by 20.9 mm normal to cut.

Text fig. 63B, pl. 58, fig. 7, 11-13.

1407-f. 18.2 mm along cut by 5.8 mm normal to cut.

Pl. 58, fig. 7-10.

The lectoparatype is a small fragment of a large specimen which preserves the sub-ambital sectors of two ambulacra and a few adjacent interambulacrals. Only ambulacral floorplates are preserved. The fragment was cut in two so as to separate the two ambulacral segments. The upper edge of the ambulacrum on specimen G.S.C. 1407-f has been ground obliquely and then polished to expose sectional views of the adradial parts of the floorplates. Grinding was deep enough along the left proximal four floorplates to expose the floorplate passageways which extend from the ambulacral tunnel into the thecal cavity.

The upper sides of the ambulacral floorplates are well-preserved in both ambulacra and expose the upper and lower rows of pits as well as the grooves and ridges connecting these pits. The subtle central perradial line groove is also preserved and is connected to the lower pits by the shallow lateral sutural grooves between adjacent floorplates. This specimen clearly demonstrates that the two shallow lateral grooves flanking the deep sutural groove which connects the upper and lower pits, are parallel and do not diverge downward as described by Bather.

G.S.C. 1407-c. Topotype of E. bigsbyi. 36 mm axial by 35 mm transverse diameter.

Pl. 59, fig. 1-5.

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This specimen exposes both the upper and lower sides of the theca, but it is depressed and the inner surfaces of upper and lower side are pressed together. The upper side preserves most of the upper oral surface except for the distal part of the right anterior margin of the theca. Most oral and ambulacral coverplates are missing except for the proximal coverplates of ambulacrum V. However, these are partially disrupted, collapsed down into the ambulacral trough. Many ambulacral floorplates are well-preserved and completely free of matrix in ambulacrum II. Some of the ambulacrals are displaced, apparently disrupted during thecal collapse. Interradial plates of the oral frame are partially exposed and reveal the upper ends of the passageways and associated grooves which mark the line of fusion between the floorplates which form these compound elements. The hydropore is apparently enlarged by abrasion and only remnants of the small rim are preserved. The right posterior hydropore plate is clearly not fused to the proximal ambulacrals, but does intrude into the edge of the ambulacrum. Interambulacrals are little disrupted. The anal structure plates are partially jumbled but apparently formed three or four irregular circlets. The distal tip of ambulacrum V curves back onto the upper surface and ends near the anal structure in interambulacrum 5.

The lower surface of the specimen preserves the collapsed sub-ambital, resting, and incurved thecal zones. The distal parts of ambulacra I-IV and adjacent interambulacra of the sub-ambital zone are partially disrupted. The resting and incurved zones appear to total only three irregular circlets of plates. The distal circlet of the

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incurved zone is formed by eleven large plates. The basal flexible membrane is poorly preserved.

G.S.C. 1407-d. Topotype of E. bigsbyi. 43 mm axial by 41.8 mm transverse diameter.

Pl. 59, fig. 15-17.

This specimen is buried in matrix and only part of the depressed upper oral surface of the theca is exposed. Ambulacra I, II, III and V are seen along with interambulacral plates of 1, 2 and 3. A small segment of ambulacrum IV curves back up onto the upper oral surface in interambulacrum 3. The oral region is disrupted, along with the proximal plates of ambulacrum V. This individual preserves the ambulacral coverplates, but they have been twisted laterally during preservation and are now imbricated with adjacent coverplates. The nodose prosopon is preserved on the interambulacrals, ambulacral coverplates and the few oral coverplates. Small elements described by Bather as "accessory coverplates" lie between the adradial ends of the coverplates and underlying floorplates. These appear to be the broken adradial corners of the coverplates and thus not discrete plates.

G.S.C. 1407-g. Topotype of E. bigsbyi. 38.4 mm axial by 29.1 mm transverse diameter.

Pl. 59, fig. 7-12.

This specimen exposes both the upper and lower sides of the completely collapsed theca. Parts of the ambital area are missing, including the right posterior third of the theca and a small segment of

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the left anterior zone. The ambulacral coverplates are missing, thereby exposing the floorplates and oral frame elements. These are not well-preserved, but show partially eroded pit rows and grooves. Interambulacrals preserve the nodose prosopon. The lower surface of this specimen exposes the collapsed resting and incurved zone plates. Moreover, parts of the basal flexible membrane are preserved. The minute, elongate platelets imbedded in this membrane are well-preserved. They are elongate concentric with the thecal margin and proximally imbricate. The integument is "lobate", reflecting the large oral frame plates which are pressed against the inner side of the membrane. The distal edge of the membrane is not well-preserved in this specimen, but apparently attached to substrate. It thus surrounded a small central, open, basal zone, the aboral surface of the theca.

G.S.C. 1407-h. Topotype of E. bigsbyi. 32.4 mm long by 23 mm wide. Pl. 59, fig. 13-14.

This specimen has been laterally compressed, hiding the lower surface of the theca between the two halves of the upper oral surface. Compression followed a line through interambulacrum 4, the oral area and ambulacrum II. One side of the specimen exposes interambulacra 2, 3, and part of 4, ambulacra III and parts of II and IV. The opposing surface exposes interambulacra 5 and 1, and parts of ambulacra I, II, IV and V.

Many of the thecal plates have been partly dissolved which exposes impressions of the inner surfaces of these plates preserved in the matrix which fills the thecal cavity. Some of the ambulacral coverplates

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are preserved in segments of the ambulacra, but all are collapsed down into the ambulacral trough. The anal structure is disrupted. The nodose prosopon is well-preserved on both interambulacrals and ambulacral coverplates.

U.M.M.P. 10347. Illustrated Specimen of E. bigsbyi by Hussey (1928, p. 78, pl. I, fig. 4). Trenton Group, Mohawkian Series, Middle Ordovician. Escanaba River, 3 miles north of Escanaba, Michigan, Locality 8, zone 2, 1927 expedition of Museum of Paleontology, University of Michigan. 33.5 mm axial by 25.6 mm transverse diameter.

Pl. 59, fig. 6.

This specimen preserves only the left half of the upper oral surface of the theca. Some ambulacral coverplates are preserved, others are missing and expose the upper, ambulacral-tunnel sides of the floorplates. Thecal prosopon is well-preserved. This specimen extends the range of species into Michigan.

Discussion:

Billings' (1854) description of an Agelacrinites outlined the major features of what was to become Edrioaster bigsbyi. An accompanying illustration reconstructs the dominant structures of what is now Edriophus levis (Bather). In 1857, Billings described Cyclaster bigsbyi. Included in this definition are: thecal shape, ambulacral floorplate and coverplate structure, floorplate passageway structures, interambulacral and anal area plating. However, Billings described ambulacral curvature as variable, contrasolar in some, but all solar in others,

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and thecal plates either smooth or pustulose. This analysis incorporated traits of both Edrioaster bigsbyi and Edriophus levis. Billings (1857) referred to several specimens but did not illustrate any of them.

In 1858 Billings revised his original description and replaced the preoccupied Cyclaster with Edrioaster. In this paper he suggested that each ambulacrum had four rows of floorplate passageways. He (1857) had already established the presence of sutural passageways leading inward from the upper rows of floorplate pits. Apparently this led him to suppose that similar passageways led from the two lower rows of pits which he observed in better preserved specimens. This latter assumption was shown to be erroneous by Bather (1914); passageways led inward only from the upper pits.

Billings' 1858 paper included the first illustrations of the type specimens of Edrioaster bigsbyi. Of the two illustrated, that on pl. 3, fig. 1, 1a, was designated the lectotype by Bather (1914, p. 116), the other, plate 3, fig. 2, 2a, a lectoparatype. (The lectotype had been cut into three pieces when Billings' illustration was prepared, for fig. 1a is an axial section view of specimen G.S.C. 1407). The small fragment of the left side was apparently missing then also.

Bather's (1914) reinterpretation of Edrioaster bigsbyi was very complete. This came after he had described the related species Edrioaster levis and Dinocystis barroisi and redescribed Edrioaster buchianus (Forbes). Bather's extensive description of Edrioaster bigsbyi was based primarily on three specimens from the Geological Survey of Canada

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which are now missing, supplemented by three British Museum specimens. It covered most important thecal features. Among the few significant differences between Bather's and the present redescription of Edrioaster bigsbyi are the following seven items. (1) The ambulacra extend into the sub-ambital zone, but this area was still elevated above the sea-bottom; only the resting zone was in contact with the substrate. Thus, the ambulacra did not come into contact with the sea-floor as Bather suggested. (2) The basal membrane was flexible and distally attached to the underlying substrate. There is no evidence that it extended entirely across the lower side of the theca as Bather suggested. (3) The interradial plates of the oral frame include not only fused floorplates, as noted by Bather, but also the fused proximal plate of each interambulacrum. (4) The hydropore penetrates the interambulacral part of the posterior interradial plate of the oral frame and a second, modified, right proximal "interambulacral," or hydropore plate, which intrudes into the proximal posterior edge of ambulacrum V. Thus, the two plates of the hydropore structure are modified interambulacrals that belong to the oral-ambulacral series; Bather described both hydropore plates as interambulacrals. (5) Bather's "accessory coverplates", small triangular elements supposedly lying between the adradial ends of the coverplates and underlying floorplates, are interpreted here as fragments of the adradial corners of the biserial ambulacral coverplates, in spite of Bather's rejection of this interpretation. (6) Bather described the upper and lower rows of ambulacral floorplate pits and the deep sutural groove connecting them. However,

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he described the two shallow grooves which flank each deep sutural groove as diverging downward. The lectoparatypes clearly show all three grooves are parallel and extend normal to the ambulacral axis. Bather also described the passageways as mere "pin-pricks", although the narrowest diameter seen in exposed sectional views averages .22 mm. (7) The nodose prosopon described by Bather on the external surfaces of the interambulacrals also covers the orals and the ambulacral cover-plates.

Bather described all of the specimens he studied in great detail; he gave extensive analyses of size ranges of individual structural elements and of the minor proximal undulations of the ambulacra. Bather's statistics suggest such features vary intra-specifically.

Later works have relied upon Bather's descriptions and illustrations of Edrioaster bigsbyi as definitive for the species. Moreover, many texts and summary works have used Bather's description as diagnostic of the characters of all edrioasteroids. Bather's reconstruction of E. bigsbyi has been refigured many times in these summary works as typifying the Class.

Discussion:

Edrioaster bigsbyi (Billings) is not a common or "typical" edrioasteroid, in spite of the impression that frequent citation has created. The related species, Edriophus levis (Bather) is not uncommon and has often been misidentified as Edrioaster bigsbyi.

Four fundamental thecal features are not well-exposed in the few available specimens of Edrioaster bigsbyi. First, the perradial ends

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of the ambulacral coverplates are crushed in all specimens; the supposedly simple, angular perradial ends are perhaps more complex. Second, the oral coverplates are missing or disrupted in all known specimens. Third, the plates of the oral frame may not be fully revealed in the partially covered and sectional views seen in the specimens illustrated here. Fourth, the inner elliptical ends of the floorplate passageways are known only in Bather's (1914) illustrations, not on the specimens now available.

The complex series of ambulacral floorplate pits and grooves suggest several possible alternative functions. The seemingly most plausible interpretation suggests a dual function. Extensions from the central radial canals, which extend under the ambulacral floorplates, passed upward through the sutural passageways into the upper series of pits. Bulbous, distendable vesicles would have been housed in these upper pits. Their expansion would have exerted pressure against the lower surfaces of the overlying coverplates and thus opened these plates to expose the food groove for feeding. Lateral tubules apparently extended from these upper vesicles downward along the deep sutural grooves, ending in extensible podia housed in the lower pits. These probably were extended upward during feeding, used as food gathering devices. The thin-walled podia no doubt also functioned as respiratory structures, with gases and perhaps fluids exchanged with the sea water through their thin walls.

Bather's interpretation of the floorplate structures contrasts with the above. He thought the radial water canals extended along the

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floor of the ambulacral tunnels, on the upper surfaces of the floorplates. Lateral branches supposedly extended along the lateral sutural grooves up to the upper pits. Here, each branch connected to a podial structure with a tubule extending into the theca via the sutural passageways. This ended in an internal ampulla. Large extensible podia arose from the upper pits. These supposedly pushed open the coverplates and then functioned as food gathering and respiratory structures. Bather's interpretation suggests no function for the lower pits. Moreover, the hydropore opens through the stone-canal into the thecal cavity and no evidence has been found to suggest that radial canals passed up through the central lumen to reach the proximal ends of the ambulacral tunnels. Thus, the radial canals are here assumed to lie under the ambulacral floorplates, in the thecal cavity. This corresponds to their position in the Lebetodiscina. Bather's suggestion that large extensible podia were housed in the upper pits is functionally problematic. The coverplates articulate with the floorplates along the zone housing the pits and almost completely roof them over, even when open, and thus they leave little room for the upward extension of podia. Neither of the above two interpretations explains the two shallower grooves which flank each deep sutural groove that extends between the upper and lower rows of floorplate pits.

The coverplates of Edrioaster bigsbyi rest upon the floorplates and appear to lack intra-thecal and intra-ambulacral extensions. Thus, it is conceivable that they could be moved individually, in sequence, randomly, or they may have moved as a unit, all opening and closing

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at once. Thus, unlike the Isorophida, their structure did not limit movement to a fixed pattern.

Range and occurrence: Trenton Group, Middle Ordovician, of Ontario and Michigan.

Edrioaster priscus (Miller and Gurley), 1894

Plate 60, fig. 1-6.

1894 Aesiocystites priscus Miller, S. A. and Gurley, F. E., Illinois St. Mus. Bull. 5: 13-15, pl. 2, fig. 10-12.

1915 Aesiocystites priscus Miller and Gurley, Bassler, R. S., United States Nat. Mus. Bull. 92, 1: 19.

1943 Edrioaster priscus (Miller and Gurley), Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 202.

Diagnosis (tentative):

An Edrioasteridae with: small "echinoidal" theca; ambulacra curve I-IV contrasolar, V solar, curvature uneven, long proximal parts straight, distal parts curve abruptly, distal tips directed back toward oral area; thecal plates smooth.

Description:

All specimens known of Edrioaster priscus (Miller and Gurley) are replaced by beekite which has destroyed most plate sutures. Only major structural units of the theca are recognizable. The whereabouts of the four specimens of the type series is unknown. Three specimens from

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the same area as the types are illustrated here.

The theca is relatively small; diameters range from 15 to 19 mm. The upper oral surface of the "echinoidal" theca is highly convex. The sub-ambital zone appears to be very narrow, and the ambulacra appear to extend beyond it onto the resting zone. This appearance may be due to preservational compression of the lower thecal zones. The incurved zone is also narrow, and leaves a relatively large non-plated central area on the lower surface. A membrane similar to that of Edrioaster bigsbyi may have been attached to the distal plates of the incurved zone and presumably extended downward and attached to the substrate.

The oral region includes oral covering plates which are continuous with the ambulacral coverplate series and oral frame plates. The oral frame is transversely elongate and surrounds an ovoid central lumen which leads from the proximal ends of the ambulacral tunnels down into the thecal cavity. Presumably it is formed by ten compound plates, five radial and five interradial.

The hydropore structure is probably similar to that of Edrioaster bigsbyi, but cannot be confidently identified on the available specimens.

The five ambulacra rise abruptly above the adjacent interambulacra and form prominent ridges on the thecal surface. The ambulacra curve, I-IV contrasolarly, V solarly, but curvature is limited to the distal quarter of each ambulacrum. The proximal parts are straight and are draped down over the convex upper oral surface. They extend into the sub-ambital and perhaps also the resting zone. The distal

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segments curve abruptly, the distal tip of each directed back toward the oral region. However, all appear to end in the sub-ambital zone and none recrosses the ambitus onto the upper oral surface.

Remnants of the contact faces between ambulacral plates suggest the biserial coverplates and floorplates are similar to those found in Edrioaster bigsbyi.

The interambulacral plates appear to be large, polygonal and tessellate. These plates are continuous with the apparently polygonal tessellate plates of the resting and incurved thecal zones.

The anal structure, apparently a periproct, is located near the distal edge of the center of the upper oral surface part of interambulacrum 5. It may be slightly elevated and form a low rounded mound.

Thecal plate surfaces appear to have been smooth.

Specimens:

Y.P.M. 28455-28456 (old 2361). Two of seven specimens from one locality. "Lower Trenton", Trenton Group, Mohawkian Series, Middle Ordovician. Curd's farm, Mercer County, Kentucky. Fischer Collection, O. C. Marsh Donor.

Y.P.M. 28455. 16.3 mm axial by 17.1 mm transverse diameter by 10.7 mm high.

Pl. 60, fig. 6.

The type locality is listed by Miller and Gurley only as Mercer County. Therefore, this and the following specimen may be topotypes.

This individual appears to be little, if at all, depressed, and

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thus preserves the original thecal shape. Oral and ambulacral coverplates are preserved along most of the length of the ambulacra. Only the outline of the oral area, ambulacra and anal structures are distinct for nearly all plate sutures have been destroyed.

Y.P.M. 28456. 19.1 mm axial by 17.8 mm transverse diameter, 11.3 mm high.

Pl. 60, fig. 1-3.

The specimen apparently preserves the original inflated shape of the theca. Oral and most ambulacral coverplates are missing, exposing the central oral lumen, the upper side of the oral frame, and the ambulacral grooves. Remnants of the ambulacral coverplates suggest an alternating biseries, similar to that of Edrioaster bigsbyi. A few sutures between the apparently alternating, biserial floorplates have been identified, and suggestions of the upper ends of floorplate passageways are present. Interambulacral plate suture lines are preserved in some areas, and the slightly disrupted anal structure is preserved in interambulacrum 5.

The lower side of the specimen preserves the distal parts of ambulacra I, III, IV, V, which show the pronounced distal curvature. The incurved thecal zone is partially visible. Matrix obscures the center of the lower side.

C.F.M.-U.C. 33380. "Curdsville, Trenton Limestone", Trenton Group, Mohawkian Series, Middle Ordovician. 1.5 miles south of High Bridge, Mercer County, Kentucky. 15.2 mm axial by 13.6 mm transverse diameter

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by 10 mm high.

Pl. 60, fig. 4-5.

This is an incomplete specimen; the left third of the theca is missing. Ambulacra III, IV and V and part of I are preserved with the coverplates in place. All sutures have been destroyed. The lower side of the specimen may preserve part of an attachment membrane which extends from the incurved zone down toward the substrate.

Discussion:

Miller and Gurley (1894) based the species Aesiocystites priscus on four specimens, illustrating two of these. Both the generic and specific descriptions were brief and generalized. Features included were: thecal shape, oral area and ambulacral disposition, and anal structure location. They also described: alternating biserial ambulacral coverplates; orals similar to ambulacral coverplates; ambulacral grooves beneath coverplates deep; and, interambulacrals polygonal and abutting. The new genus Aesiocystites was contrasted with Hemicystites.

Subsequent to Bather's (1914) description of Edrioaster bigsbyi, most authors have considered Aesiocystites to be a junior synonym of Edrioaster (i.e., Bassler, 1935; Bassler and Moodey, 1943; Regnéll, 1966). The thecal shape, course of the ambulacra, and suggested structure of the ambulacral plates support this conclusion. Unfortunately, until specimens that preserve the plates are located, this interpretation remains questionable.

It is not impossible that specimens identified as Edrioaster

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priscus are young adults of Edrioaster bigsbyi. The only observable thecal features separating the two species are thecal size, details of the thecal shape, and the nature of the ambulacral curvature. All of these could be explained as ontogenetic.

Range and occurrence: Trenton Group, Mohawkian Series, Middle Ordovician, of Mercer County, Kentucky.

Edriophus Bell, gen. nov.

1842 [non] Agelacrinites Vanuxem, L., Nat. Hist. of New York, pt. IV, Geology 3: 158, fig. 80.

1854 Agelacrinites Vanuxem, Billings, E. K. [partim], Canadian Jour. Industry, Sci. and Art: 271-273, text fig. 10-12.

1857 Cyclaster Billings, E. K. [partim], Geol. Surv. Canada, Rept. Progress 1853-1856: 292-294.

1858a Edrioaster Billings, E. K. [partim], Geol. Surv. Canada, Fig. and Descriptions of Canadian Organic Remains, dec. 3: 82-83, 85.

1899 Edrioaster Billings, Jaekel, O. [partim], Stammesgeschichte der Pelmatozoen, Bd. 1, Thecoidea und Cystoidea, Berlin: 44-46, text fig. 9.

1914 Edrioaster Billings, Bather, F. A. [partim], Geol. Mag. (n.s.) dec. 6, 1: 115-125, 162-171, text fig. 2, pl. 12, fig. 1-2.

1915a Edrioaster Billings, Bather, F. A. [partim], Geol. Mag. (n.s.) dec. 6, 2: 211-215, 259-266.

1915b Edrioaster Billings, Bather, F. A. [partim], Geol. Mag. (n.s.) dec. 6, 2: 316-322.

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1915c Edrioaster Billings, Bather, F. A. [partim], Geol. Mag. (n.s.) dec. 6, 2: 393-403.

1943 Edrioaster Billings, Bassler, R. S. and Moodey, M. W. [partim], Geol. Soc. America, Spec. Pap. 45: 201-202.

1960 Edrioaster Billings, Kesling, R. V. [partim], Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 147-148, pl. 1, fig. 1-4.

Type species: Edrioaster levis Bather, 1914.

Diagnosis:

An Edrioasteridae with: "echinoidal" theca; oral plates similar to and continuous with ambulacral coverplates; right posterior plate of hydropore structure apparently fused to proximal posterior floorplates of ambulacrum V; ambulacra curved, I-V solar; ambulacral coverplates form a single alternating biseries, each perradially elevated.

Description:

Only the type species, Edriophus levis (Bather) is placed in the genus without question. Thus, for diagnostic purposes the genus is essentially monotypic and has the characters of the type species; separation of generic and specific traits is uncertain. The features cited in the above diagnosis are in part inferred to be of generic rank from taxobases established for other edrioasteroid genera.

Discussion:

The genus Edrioaster Billings originally included species with ambulacra curved I-IV contrasolar, V solar, as well as those with I-V

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solar. The latter type includes three species: Edrioaster levis Bather, Edrioaster saratogensis Ruedemann and Agelacrinites buchianus Forbes. Only the first is represented by well-preserved specimens, and is here selected as the type species of the new genus Edriophus.

The direction of ambulacral curvature is the most apparent difference between Edriophus and Edrioaster. Other generic differences probably include the structure of the oral frame, structure of the hydropore plates, the shape of the ambulacral coverplates, the ambulacral groove structures formed by the floorplates and perhaps the features of the oral plates.

Unfortunately, with only one well-known species, the amount of variability in supposedly generic features is uncertain. Edriophus saratogensis is represented by only a few fragmentary specimens, all preserved as molds, and is of no help in establishing generic features. Edriophus buchianus is known from two incomplete specimens which were not available during this study. Bather's detailed description of that species establishes the ambulacral curvature as like that of Edriophus levis. Other thecal features mentioned by Bather are quite similar to those seen in Edriophus levis and thus, it is not impossible that the two are conspecific. Unfortunately the ambulacral coverplates of Edriophus buchianus are unknown. Therefore, even restudy of the type specimens is not likely to resolve this problem.

Etymology: Edriophus is compounded from the Greek Edrio, seat, and ophis, serpent, referring to the sinuous perradial ridge formed by the tips of the ambulacral coverplates of this "seat-star".

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Range and occurrence: Trenton Group, Mohawkian Series, Middle Ordovician of New York and Ontario.

Edriophus levis (Bather), 1914

Text fig. 64; plate 61-63.

1854 Agelacrinites sp. Billings, E. K. [partim], Canadian Jour. Industry, Sci. and Art: 271-273, text fig. 10-12.

1857 Cyclaster bigsbyi Billings, E. K. [partim], Geol. Surv. Canada, Rept. Progress 1853-1856: 293-294.

1858a Edrioaster bigsbyi (Billings), E. K. [partim], Geol. Surv. Canada, Fig. and Descriptions of Canadian Organic Remains, dec. 3: 82-83, 85.

1914 Edrioaster levis Bather, F. A., Geol. Mag. (n.s.), dec. 6, 1: 115-125, 162-171, text fig. 2, pl. 12, fig. 1-2.

1915a Edrioaster levis Bather, F. A., Geol. Mag. (n.s.), dec. 6, 2: 259-266.

1943 Edrioaster levis Bather, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 202.

1960 Edrioaster levis Bather, Kesling, R. V., Univ. Michigan, Contrib. Mus. Paleont. 15 (8): 147-148, pl. 1, fig. 1-4.

1966 Edrioaster levis Bather, Regnéll, G., in Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, 1: text fig. 115-2.

Diagnosis:

An Edriophus with: large "echinoidal" theca; approximately ten

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orals, with four central orals apparently larger than other orals; orals raised perradially to form a small ridge along oral midlines; oral frame formed by five compound interradial oral frame plates, partly exposed externally, and five compound radial frame plates which lie in part below the interradials; radials in contact around inner edge of frame rim; ambulacral coverplates are perradially elevated to form a distinct perradial ridge; proximal side of perradial end of each coverplate produced proximally as small lobe; interambulacrals large, polygonal, tessellate; periproct formed by several irregular circlets of plates, central elements larger, elongate; thecal plates smooth.

Description:

The "echinoidal" theca of Edriophus levis (Bather) is large, averaging 40 mm in diameter, with larger individuals over 55 mm (text fig. 64).

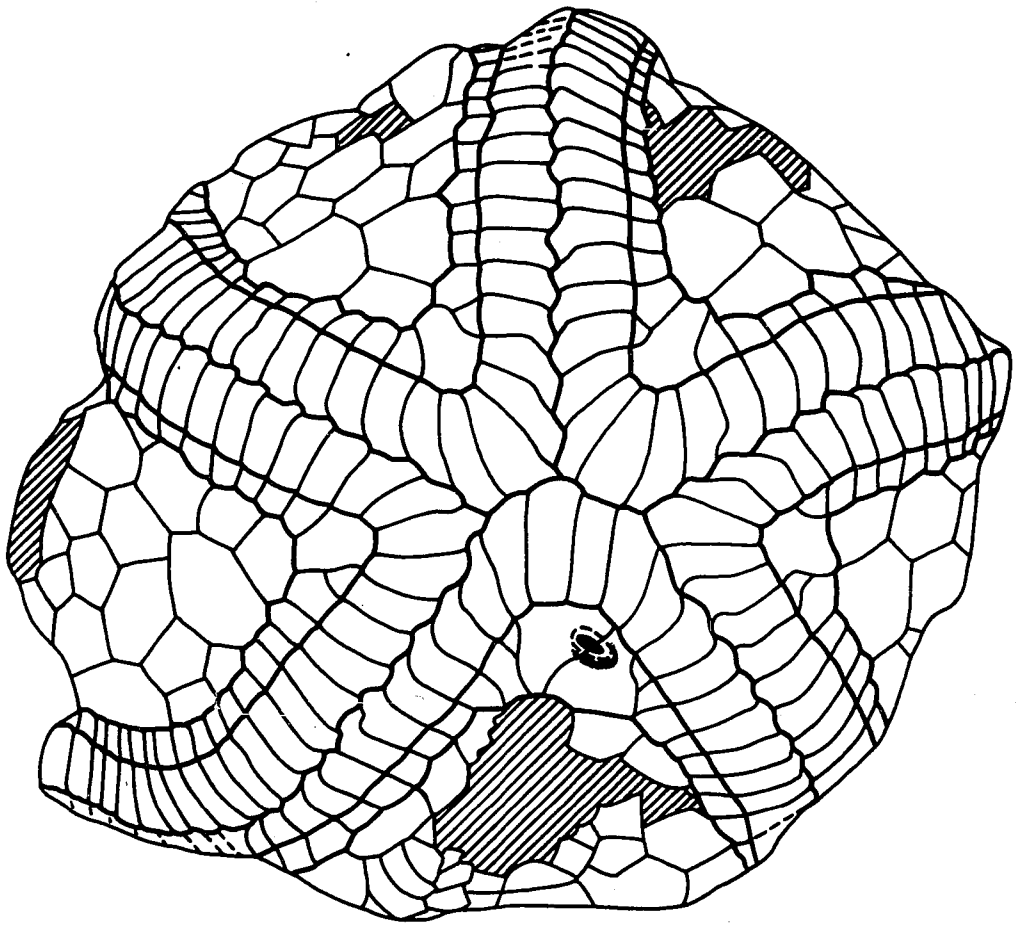
The oral area includes approximately ten covering orals which are continuous with the ambulacral coverplate series (pl. 61, fig. 4, pl. 62, fig. 3, 5, 9-10). Three or four central orals are somewhat larger than the others. Two are anterior, one on either side of the anterior oral midline. These centrally abut one or two large posterior plates along the center of the transverse oral midline. The central orals are flanked by smaller plates, about equal in size to the proximal ambulacral coverplates. Commonly one pair of the smaller orals lies adjacent to each side of centrals along the transverse oral midline, proximal to the point of bifurcation of the two lateral pairs of

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Text Figure 64 Edriophus levis (Bather), 1914

U.C.M.P. 40479, (X5), pl. 62, fig. 1.

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Text Figure 64

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ambulacra. A third pair lies along the anterior midline and separates the central orals from the adjacent proximal coverplates of ambulacrum III. Occasionally one of these smaller anterior orals may reach the transverse oral midline, and thus it separates the two larger anterior central orals. The orals are perradially raised, and form a small, distinct ridge along each of the oral midlines.

The large transversely elongate oral frame of Edriophus levis is sub-pentagonal in outline, being distally continuous with the ambulacra (pl. 61, fig. 2, 5, 7-9). The proximal margin is ovoid and surrounds the large central lumen which extends down from the proximal ends of the ambulacral tunnels and opens into the thecal cavity. The five compound radial plates are formed by the fusion of three or more pairs of proximal ambulacral floorplates. Four passageways penetrate each radial plate and mark the fused lateral sutures between the floorplate components of these compound plates. The radials are enlarged proximally and extend both downward into the thecal cavity and also laterally; the inner proximal edges of adjacent radial elements are in contact around the innermost, proximal edge of the frame rim. Only the two posterior radials are not in contact; the lower edge of the posterior interradial forms this part of the frame rim. Distally the radials extend out under the proximal three or four pairs of ambulacral floorplates of the contiguous ambulacra. The radials taper gradually and each has a blunt termination. Small triangular sectors of the upper sides of the distal parts of the radials, pointed distally, are exposed when the oral frame is viewed from above with the oral and proximal

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ambulacral coverplates removed. These wedges are seen between the perradially separated, opposing members of the proximal two or three pairs of ambulacral floorplates.

The five compound interradial frame plates alternate with the radials. Each is formed by the fusion of approximately six floorplates and the proximal plate of each interambulacrum. As in Edrioaster bigsbyi, the floorplates incorporated into each interradial plate are "half-pairs". The originally opposed members of the proximal three pairs of floorplates in each ambulacrum were separated perradially. Opposing members were thus incorporated into different interradials, with pair members of the right side fused into the adjacent interradial to the right, and the left pair ones into the adjacent interradial on the left. Commonly five passageways penetrate each interradial plate, marking the fused sutures between the six floorplates. The fused floorplates are also fused adradially to the proximal plate of each interambulacrum.

The interradial frame plates lie adjacent to the upper part of the alternate radials and also extend above the radials so that the adradial ends of the floorplate sectors and all of the interambulacral plate sectors of each interradial are exposed externally, distal to the ends of the oral coverplates. Except in the posterior interradius, the inner proximal ends of the interradials are wedged between the adjacent radials. They end before reaching the inner edge of the frame rim which is formed by the laterally expanded radial plates. In the posterior interradius, the interradial plate does reach the inner frame edge

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and separates the inner ends of the two adjacent posterior radials.

The oral frame of Edriophus levis is thus formed by sixty or more fused floorplates and five fused interambulacrals. It differs from the frame of Edrioaster bigsbyi not only by the addition of at least two extra floorplates in each interradial, but also by the greater proximal expansion of the radials, which are laterally in contact under the interradials (except posteriorly) around the inner edge of the frame rim. Moreover, the externally exposed adradial ends of the frame plates slope gradually down to the interambulacra, and thus do not form a steeply sloping, abrupt border as in Edrioaster bigsbyi.

The hydropore is a small elliptical opening along the right posterior margin of the oral area and is shared by two plates (text fig. 64, pl. 61, fig. 4, pl. 62, fig. 1-3, 9-10, pl. 63, fig. 7-8, 11, 13). It is elongate normal to the suture between the interambulacral part of the posterior interradial of the frame and an adjacent right posterior hydropore plate. The left margin of this posterior plate is fused to one or more (? three) floorplates of the proximal posterior side of ambulacrum V. Distally this plate abuts interambulacrals.

The hydropore may be shared equally by the two plates, or it may extend further into either plate. The rounded anterior end of the elongate opening is wider than the posterior end, which occasionally is pointed. The margins of both plates of the hydropore structure are thickened around the opening and form a small, distinct, raised rim.

The hydropore opens down into the stone-canal passageway. This

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is apparently formed by the two plates of the hydropore structure. The passageway expands rapidly inward and opens into the thecal cavity by way of a large elliptical to circular exit which lies adjacent to the distal edge of the right posterior margin of the oral frame.

The five long, broad ambulacra curve solarly. They extend outward from the oral area past the ambitus into the sub-ambital thecal zone. Curvature is uneven; the proximal part of each is straight, but curvature is initiated gradually before the ambitus is reached. Distally, they extend along the sub-ambital zone concentric with the thecal margin. Occasionally the distal end of an ambulacrum may appear to curve back onto the upper oral surface, but this feature is found only in extremely depressed specimens, suggesting that it may be preservational.

The ambulacra are slightly elevated above adjacent interambulacra, but their adradial margins slope downward gradually and merge with the interambulacral areas.

The single alternating biseries of ambulacral coverplates roofs the ambulacral tunnel (text fig. 64, pl. 61, fig. 1, pl. 62, fig. 1-5, 7-10, pl. 63, fig. 1-13). The coverplates are more or less sub-rectangular. The adradial ends are straight or slightly convex outward. The straight, parallel sides extend normal to the ambulacral axis. The perradial ends of the coverplates are sinuous, each plate being centrally or distally concave, with the proximal part produced toward the oral area along the perradial line as a rounded to proximally angular-lobe. The proximal perradial lobe of an opposing, alternate

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coverplate fits into the distal or central concavity of the coverplate. Moreover, the perradial ends of the coverplates are abruptly upturned and form a pronounced, narrow median ridge which extends along the sinuous perradial line.

The elevation of the perradial ends of the coverplates, and their sinuous shape, each with a proximal lobe, apparently strengthens the coverplates when the ambulacra are closed. This is suggested by the common preservation of the ambulacral coverplates in place in this species, whereas in Edrioaster bigsbyi these plates are commonly lost or disrupted.

The adradial ends of the coverplates rest on the upper surface of the floorplates and form a nearly straight sub-marginal ambulacral suture line. The larger floorplates extend past the adradial ends of the coverplates and are exposed externally between the sub-marginal and adradial sutures. The lower edge of the adradial ends of the coverplates are beveled and fit tightly against the slightly inwardly sloping upper lateral margin of the floorplates, along the articulation zone. Coverplates appear to be uniform in thickness and lack both intra-thecal and intra-ambulacral extensions.

Bather (1914) described an additional series of small median ambulacral coverplates. These are not plates, but fragments of the upturned perradial ends of the coverplates.

The ambulacral floorplates form an alternating biseries (pl. 63, fig. 1-2, 5-6). Each plate is elongate and sub-rectangular in plan view. The pointed perradial ends of the alternating floorplates form

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a central zigzag perradial suture. The long, straight, lateral edges of each floorplate are parallel to one another and extend normal to the ambulacral axis. The adradial ends abut adjacent interambulacrals along straight or slightly convex sutures. Adjacent floorplates may vary in length, and thus form an irregular adradial suture line. This variability in length appears to be more common along the proximal parts of the ambulacra. Floorplates and coverplates correspond exactly, each floorplate lying directly under a corresponding coverplate. Bather (1914) suggested that the coverplates were proximally offset from the floorplates, with each lying on parts of two floorplates and extending over the lateral suture between the two floorplates. This interpretation was apparently based upon specimens in which the coverplates were partially disrupted and crushed down into the ambulacral tunnel. Well-preserved specimens which have not been crushed preserve the coverplates over the floorplates, the contact surfaces between coverplates being directly above the lateral sutures between the floorplates.

The floorplates are similar in shape to those of Edrioaster bigsbyi (text fig. 63B). Opposing plates slope downward centrally and form a broad ambulacral trough. The slope is gradual along the upper sides of the trough. However, a short, steeply inclined zone flanks the nearly horizontal perradial area and thus forms a relatively narrow U-shaped groove incised into the center of the broad trough.

The upper lateral margins of the floorplates are nearly horizontal and slope only slightly perradially. This is the articulation zone

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on which the beveled bases of the overlying coverplates rest. It lies in part over and in part distal to the upper ends of the floorplate passageways. The adradial end of the zone is marked by the line of contact with the adradial ends of the coverplates, and forms the submarginal ambulacral suture line.

Adradial to the articulation zone, the externally exposed parts of the floorplates slope gradually downward toward the interambulacra. The floorplates abut adjacent interambulacrals along vertical sutures, and form the adradial suture line along the thecal surface.

The floorplates are thickest under the articulation zone and thin conspicuously toward their perradial ends. Thus, the inwardly directed convexity of the inner side of the floorplates is less pronounced than the central concavity of the upper surface. The perradial contact of the alternate floorplates is by vertical sutures.

The floorplate passageways originate in small, rounded or elliptical pits centered over the lateral sutures between adjacent floorplates. These pits lie along the perradial edge of the articulation zone. Their adradial ends are partly roofed by the bases of the overlying coverplates, and their perradial sides open into the upper lateral edge of the ambulacral tunnel. The passageways extend inward from the floor of the pits along the sutures. Their inner ends expand rapidly and open into the theca as large elliptical depressions along the sutures between adjacent floorplates; they commonly exceed half the length of the floorplates.

The small upper pits of the passageways form two rows along each

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ambulacrum, one along each upper lateral edge of the ambulacral tunnel. As in Edrioaster bigsbyi, there are two additional rows of small depressions along each ambulacrum, perradial to the passageway pits. They lie along the steep walls of the U-shaped axial depression and are less well-defined than the upper pits. Their perradial side is open to the central trough. These depressions end blindly. They are not connected with passageways.

The upper and lower rows of pits are connected by deep grooves which extend along the lateral suture lines of the floorplates. Due to partial erosion of all available specimens, additional details of the floorplate pits and connecting grooves are not known. The presence of lateral grooves flanking each sutural groove, like those found in Edrioaster bigsbyi, has not been established.

The perradial edges of the floorplates may be slightly depressed to form a subtle groove along the zigzag perradial line of the floorplates. However, this groove is even less apparent than in Edrioaster bigsbyi.

Interambulacral plates are large, polygonal and meet along vertical sutures. Smaller polygonal plates continuous with the interambulacrals form the resting and proximal part of the incurved thecal zones. These distal zones have been observed only in collapsed specimens. Apparently their combined width is small and involves only two or three irregular circlets of plates. The distal circlet may be formed by somewhat larger plates than the adjacent one. As in Edrioaster bigsbyi, a flexible membrane is attached to the distal edge of the

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last circlet and likewise is imbedded with numerous minute, squamose plates which are slightly elongate concentric with the thecal margin. The membrane extends downward, and its distal edge apparently attached to the substrate. It thus surrounds a small, sub-circular, central non-plated area.

The periproct is located near the center of the upper oral surface part of interambulacrum 5 (pl. 61, fig. 1, pl. 62, fig. 6). It includes three irregular circlets. The outer two are formed by small, irregularly polygonal plates which distally abut large interambulacrals. The central circlet appears to be formed by elongate, sub-lanceolate plates which are acuminate centrally.

External thecal plate surfaces appear to be smooth.

Specimens:

U.C.M.P. 40477-40480. Hull Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Quarry 3 miles north of Kirkfield, Ontario. (Specimens from near the floor of the quarry.) Kopf Collection.

U.C.M.P. 40477. 41.8 mm axial by 42.2 mm transverse diameter.

Pl. 61, fig. 1-6.

The specimen has collapsed; the upper and lower surface plates are pressed together. The upper oral surface is well-preserved, although a few plates on the left side are missing. The hydropore structure is partly disrupted. The lower surface of the specimen is partly covered with matrix. The inner surface of the oral frame is exposed centrally. The inner sides of the proximal floorplates of ambu-

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lacrum V are exposed where the marginal plates are missing. The oral frame is partially disrupted; the inner lateral ends of adjacent radials are no longer in contact. The inner side of several posterior plates of the oral cover are exposed through the central lumen. One segment of the distal plated membrane is preserved adjacent to the oral frame under interambulacrum 3.

U.C.M.P. 40478. 39 mm axial by 39 mm transverse.

Pl. 61, fig. 7-9.

This specimen is also collapsed, the upper and lower surface plates being pressed together. The lower surface preserves the distal parts of the ambulacra; most of the coverplates are missing and hence the ambulacral groove parts of the floorplates are seen. The inner sides of the adjacent sub-ambital interambulacrals are also preserved intact. Centrally, the oral frame and proximal ambulacral floorplates are exposed. The oral frame is well-preserved, and both the radial and parts of the interradial plates can be seen. The inner surfaces of two posterior oral covering plates are seen through the transversely elongate central lumen. The ambulacral floorplates show the large, elongate inner openings of the floorplate passageways.

U.C.M.P. 40479. 27.5 mm axial by 27 mm transverse diameter.

Text fig. 64, pl. 62, fig. 1-3.

This specimen is smaller than most other representatives of the species. It exposes only the upper side of the theca, but it is only partially collapsed and preserves most of the original convexity of

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the upper oral surface. The central plates of the upper oral surface are well-preserved except for interambulacrum 5 and the anal structure; the orals and ambulacral coverplates are slightly pulled apart perradially but ambulacral and oral midline ridges are preserved. The hydropore is surrounded by a raised rim. The anterior end of the opening is large and rounded, the posterior end acuminate. It is sub-equally shared by the two hydropore plates. Plate surfaces are minutely pustulose.

U.C.M.P. 40480. 55.3 mm axial by 51 mm transverse diameter.

Pl. 62, fig. 7-10.

This large individual exposes only the upper oral side of the collapsed theca. A large crack separates the disrupted anterior part of the theca from the posterior part. The oral region and proximal parts of the ambulacra and interambulacra are well-preserved. Orals and ambulacral coverplates are in place. The perradial and oral midline ridges are well-preserved. The hydropore structure is partly eroded. The opening is shared equally by the two plates, but the anterior part is much wider than the acuminate posterior end.

G.S.C. 18659. Illustrated Specimen of Edriophus levis by Sinclair (1964, A.A.P.G. Guidebook, pl. 3, fig. 21). Hull Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Quarry 3 miles north of Kirkfield, Ontario. 40 mm axial by 45 mm transverse diameter.

Pl. 63, fig. 1-6.

This specimen exposes the collapsed and partially disrupted upper oral surface. Ambulacral coverplates are missing along parts of

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ambulacra II, III and IV, which exposes the ambulacral groove surfaces of the floorplates. Although partially eroded, these preserve the upper and lower rows of pits and the connecting sutural grooves. When the specimen is under xylene, the recrystalized proximal coverplates of ambulacrum IV become transparent and reveal the upper lateral parts of the underlying floorplates. This view demonstrates that the adradial ends of the coverplates are located just adradial to the upper row of floorplate pits.

U.S.N.M. S-3197 (A-B). Hull Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Quarry 3 miles north of Kirkfield, Ontario.

U.S.N.M. S-3197-A. 55.7 mm axial by 55.4 mm transverse diameter.

Pl. 63, fig. 7-8.

This specimen exposes the collapsed upper oral surface. Coverplates are preserved, but in part have caved into the ambulacral tunnel. Distal parts of the ambulacra and interambulacra are disrupted. The oral plates are well-preserved, only slightly depressed, and the hydropore structure, with raised rim, is well-preserved. It is subequally shared by both plates, although the anterior end is somewhat larger.

U.S.N.M. S-3197-B. 52 mm axial by 53.5 mm transverse diameter.

Pl. 62, fig. 4-5.

A second large specimen preserved in a manner similar to that of A. The oral plates are well-preserved.

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U.S.N.M. Acc. no. 212887. Hull Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Quarry 3 miles north of Kirkfield, Ontario. 43.7 mm axial by 49.6 mm transverse diameter.

Pl. 62, fig. 6.

This individual has collapsed but is moderately well-preserved and exposes the upper oral surface plates. The anal structure shows the two irregular outer circlets of smaller polygonal plates and the larger, elongate anals of the central circlet. A few plates are missing from the left posterior sector of the structure.

U.M.M.P. 5731. Edriophus levis illustrated by Kesling (1960, pl. 1, fig. 1-2 as Edrioaster bigsbyi). Hull Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Quarry 3 miles north of Kirkfield, Ontario. 30.5 mm axial by 32.8 mm transverse diameter.

Pl. 63, fig. 9-10.

This specimen was illustrated by Kesling (1960) as an Edrioaster bigsbyi to demonstrate the location and structure of the hydropore. This and other misidentifications have led to the erroneous conclusion that specimens of Edrioaster bigsbyi are common. The theca is only partially collapsed; the upper oral surface retains its original convexity. The anterior third of the specimen is missing and the oral and proximal anterior thecal plates are crushed. The illustration shows the specimen under xylene, which reveals the upper parts of three of the interradial oral frame plates.

U.M.M.P. 26428. Illustrated Specimen of Edriophus levis by Kesling

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(1960, pl. 1, fig. 3-4). Hull Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Quarry 3 miles north of Kirkfield, Ontario. 38.8 mm axial by 47.6 mm transverse diameter.

Pl. 63, fig. 11-13.

The specimen exposes only the collapsed, upper oral surface. Most of interambulacrals are disrupted or missing. Kesling illustrated an oral surface view (pl. 1, fig. 3, specimen whitened) and a close-up of the oral area and partially disrupted hydropore structure. An oral surface view of the specimen under xylene is presented here for comparison with Kesling's plate. The proximal part of ambulacrum I is well-preserved (pl. 63, fig. 12). The coverplates are in place and their sinuous perradial ends are elevated and form the perradial ridge. The externally exposed adradial ends of the floorplates flank the adradial ends of the coverplate. The surfaces of the thecal plates appear to be minutely pustulose.

Over 50 other specimens of Edriophus levis were examined during this investigation. One (R.O.M. 18854) is from the "Trenton Limestone" at Hull, Quebec. The others are all from the quarry three miles north of Kirkfield, Ontario, Kopf Collection, University of Cincinnati, Museum of Paleontology. The holotype of Edriophus levis designated by Bather (British Museum no. E. 15900) is listed as Trenton Limestone, Kirkfield, Ontario. It is probably from the quarry three miles north of town, and thus the other Kirkfield quarry specimens are probably topotypes.

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Discussion:

Specimens of Edriophus levis were first included in Edrioaster bigsbyi Billings. Billings' (1854) description of Agelacrinites sp. includes characters of both species. An accompanying "reconstruction" (1854, text fig. 10) depicts the upper oral surface of Edriophus levis which lacks ambulacral coverplates. Billings' 1857 and 1858 descriptions of Edrioaster bigsbyi also include characters of both Edriophus levis and Edrioaster bigsbyi; i.e., ambulacra all solar, or I-IV contrasolar, V solar, and thecal plates smooth or with large nodes.

Bather (1914) restricted Edrioaster bigsbyi to specimens with ambulacra curved I-IV contrasolar, V solar, and thecal plates with large nodes. He proposed the name Edrioaster levis for the others with ambulacra I-V solar and thecal plates smooth. Bather's detailed description of the new species and extensive comparison of it with Edrioaster bigsbyi includes most thecal features. The present redescription of Edriophus levis differs in only six features. (1) The hydropore opens down into the thecal cavity through the stone-canal which penetrates both plates of the hydropore structure, not merely the anterior one as suggested by Bather. Moreover, both hydropore plates are modified interambulacrals that have been incorporated into the oral-ambulacral series. The anterior plate is the interambulacral part of the posterior interradial of the oral frame. The posterior plate is fused to the proximal posterior floorplate of ambulacrum V. Thus, the hydropore location is described as in the right posterior extension of the oral area, not in the proximal part of interambulacrum 5. (2) The compound

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interradial plates of the oral frame include not only fused floorplates, as Bather suggested, but also the proximal plate of each interambulacrum which is fused to the adradial ends of the floorplates. (3) The ambulacral coverplates form a single alternating biseries. The irregular "median coverplates" described by Bather are perradial fragments of the large coverplates and not discrete plates. (4). The coverplates and floorplates correspond one-to-one, each coverplate being centered over a floorplate. Bather's conclusion that the coverplates are proximally offset from the floorplates, with each coverplate over parts of two floorplates, apparently was based on partially disrupted specimens in which the coverplates had been shifted laterally and partly collapsed downward into the ambulacral tunnel. (5) The anal structure includes three irregular circlets of plates. Plates of the outer two are irregularly polygonal, but in contrast with Bather's description, the plates of the central circlet are elongate. (6) Bather described the thecal plates as scrobiculate. Most specimens appear to have smooth plate surfaces. A few individuals do have minutely pustulose surfaces, but this appears to be due to differential weathering which reveals the microstructure of the plates; the stroma canals are now filled with more resistant secondary calcite, hence stand in relief after etching.

Kesling (1960) described the hydropore opening, and suggested it was essentially similar to that of Edrioaster bigsbyi. The hydropore plates "are closely associated with the peristomial region . . . If they are regarded as part of the ambulacra and peristomial region, then the hydropore is located with a posterior expansion of the peristomial

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region." (Kesling, 1960, p. 147-148). This is in agreement with the present interpretation. It should be noted, however, that Kesling's comparison of the hydropore structure of Edrioaster bigsbyi with that of Edriophus levis was based on two specimens, both examples of Edriophus levis.

Edriophus levis Bather is closely related to Edrioaster bigsbyi. Differences include ambulacral disposition, the make-up of the oral frame and the hydropore structure, the shape of the ambulacral coverplates, the details of the floorplate features, and prosopon. The coverplate shape would appear to denote significant functional difference, for the proximal extensions and pronounced elevation of the perradial ends of the coverplates apparently increased the strength of the coverplate series. Thus, most specimens of Edriophus levis preserve the coverplates, whereas these elements are commonly missing from specimens of Edrioaster bigsbyi. This probably signifies weaker coverplate articulation in the latter and probably correlates with different modes of operation.

Range and occurrence: Trenton Group, Middle Ordovician of Ontario.

(?) Edriophus saratogensis (Ruedemann), 1912

Text fig. 65; plate 60, fig. 7-14.

1912 Edrioaster saratogensis Ruedemann, R., New York St. Mus., Bull. 162: 86-88, pl. 3, fig. 2-4.

1914 Edrioaster saratogensis Ruedemann, Bather, F. A., Geol. Mag. (n.s.) dec. 6, 1: 162-171.

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1915 Edrioaster saratogensis Ruedemann, Bassler, R. S., United States Nat. Mus. Bull. 92, 1: 474.

1943 Edrioaster saratogensis Ruedemann, Bassler, R. S. and Moodey, M. W., Geol. Soc. America, Spec. Pap. 45: 202.

Diagnosis (tentative):

An Edrioasteridae with: small "echincidal" theca; seven or more oral plates similar to and continuous with proximal ambulacral coverplates; hydropore elongate, penetrating two plates in right posterior oral area; ambulacra curved, I and probably II-V solar, coverplates form a single alternating biseries; interambulacrals polygonal, tessellate; plates externally finely pustulose.

Description:

Edriophus saratogensis (Ruedemann) is represented by four semicomplete and three fragmentary specimens, all preserved as molds (text fig. 65A-D). Except for one small segment of the inner surface of the lower side, only the upper oral surface features are preserved.

The "echinoidal" theca is small, diameters ranging from 10 to 17 mm. The upper oral surface is convex upward. Apparently a downward constricting sub-ambital zone, which includes the distal ends of the ambulacra, was present below the ambitus. The resting and incurved zones, if both are developed, have not been observed.

The oral area is formed by the oral covering plates and externally exposed parts of oral frame plates (text fig. 65A-C, pl. 60, fig. 7-12). Seven or more central oral covering plates roof the central

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Text Figure 65 (?) Edriophus saratogensis (Ruedemann), 1912

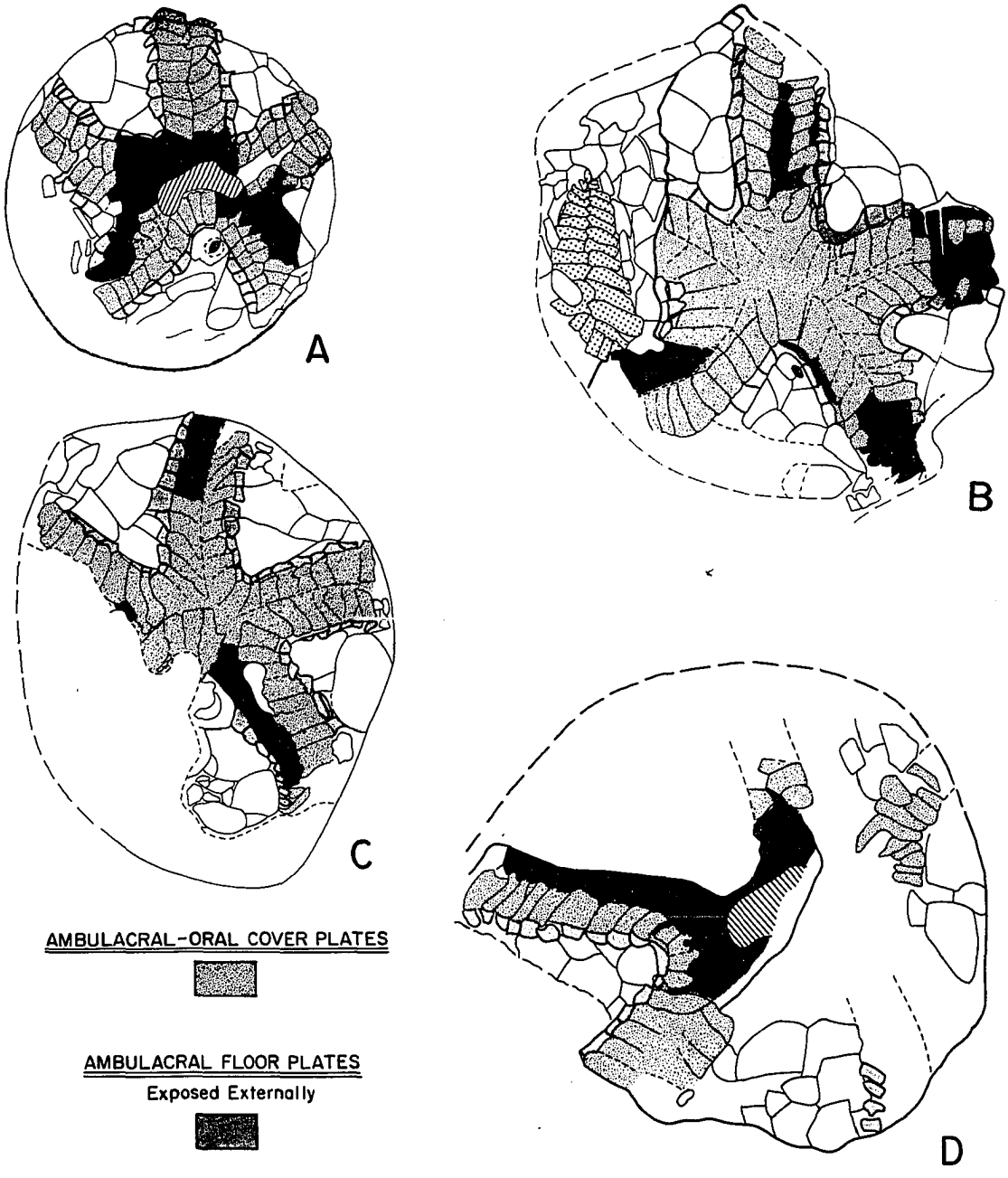
A. Holotype, N.Y.S.M. 7385, (X5), pl. 60, fig. 7.

B. Paratype (2), N.Y.S.M. 7387, (X5), pl. 60, fig. 11.

C. Paratype (1), N.Y.S.M. 7386, (X5), pl. 60, fig. 9.

D. N.Y.S.M. 12779, (X5), pl. 60, fig. 13.

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Text Figure 65

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oral lumen. These plates apparently are similar in size and shape to the proximal ambulacral coverplates. The orals are distally continuous with the ambulacrals. The three or four orals which lie in the center of the area and abut perradially, may be somewhat larger than the others.

The transversely elongate oral frame surrounds the oval central lumen. This extends downward from the proximal ends of the ambulacral tunnels and opens into the thecal cavity below (text fig. 65A, D, pl. 60, fig. 7-8, 13-14). The frame appears to be similar to that of Edriophus levis, formed by five compound interradial plates and presumably five compound radials, although the latter have not been seen. The interradials appear to be formed by the fusion of four floorplates and the proximal plate of the adjacent interambulacrum. The upper ends of the passageways which mark fused sutures are exposed in four interradials of specimen N.Y.S.M. 7385. Apparently three passageways penetrate each plate which suggests four floorplates are fused together in each. Adradially these plates are fused to the proximal interambulacral plate. When the oral coverplates are in place, only the adradial edges of the floorplates and the adjacent fused interambulacral part of the interradial plates are exposed externally. These adradial ends of the fused floorplates rise steeply above the interambulacrals and form an abrupt margin to the central oral rise. This abrupt margin is continuous with the steep adradial margins of the ambulacra.

The hydropore structure lies in the right posterior part of the oral region and is formed by two plates (text fig. 65A, pl. 60, fig. 7-8). The left anterior one is the interambulacral part of the posterior

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interradial plate of the oral frame. The right posterior element is a polygonal to sub-triangular plate, apparently fused to the adradial ends of the proximal posterior floorplates of ambulacrum V.

The hydropore is a small elliptical opening which extends across and normal to the suture between the two plates of the hydropore structure. The opening is shared equally by both. A small raised rim may have surrounded the opening.

The five wide ambulacra are elevated above the interambulacra; their adradial margins are steeply inclined to the adjacent interambulacral plates (pl. 60, fig. 7-14). Proximally the ambulacra are straight. They extend past the ambitus onto the lower side of the theca. All appear to be curved. Ambulacrum I is known to be solar, II-V believed also to be solar, although the distal parts of these have not been clearly observed.

The coverplates form a single alternating biseries. The plates are believed to be sub-rectangular. Their adradial ends are straight and meet the externally exposed parts of the floorplate along the sub-marginal suture. The straight lateral margins of the coverplates are parallel and extend perradially normal to the sub-marginal suture line. The perradial ends of the coverplates are believed to be pointed, and interdigitate with the alternate coverplates to form a zigzag perradial line. However, the coverplates have been crushed downward into the ambulacral tunnels in all known specimens, making observation difficult.

The biserial, alternating floorplates are sub-rectangular in outline (pl. 60, fig. 9-12). Their adradial ends are straight and parallel to the ambulacral axis. The straight lateral sides are

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parallel and extend normal to the adradial suture. Perradially, these plates are bluntly pointed and form a median zigzag perradial floorplate suture line. The externally exposed adradial ends of the floorplates, adradial to the sub-marginal suture, slope steeply upward from the adjacent interambulacrals and form the abrupt adradial margins of the ambulacra. Perradially, the floorplates slope downward from the sub-marginal suture and form a deep central ambulacral trough. Large elongate depressions are formed along the sutures between adjacent floorplates. One row of depressions lies along the upper edge of each side of the ambulacral trough. Sutural passageways are believed to extend into the thecal cavity from the floor of each lateral depression. The inner sides of the floorplates appear to have sloped downward into the thecal cavity and the inner sides of the ambulacra are thus convex inward. Elongate depressions are also formed on the lower, thecal cavity, sides of the floorplate along the sutures between the adjacent floorplates. These are believed to be the inner ends of the sutural passageways.

The interambulacrals are irregular polygonal plates and are relatively few in number. The central interambulacrals are large, whereas those flanking the ambulacra are much smaller.

A small part of the right side of the anal structure appears to be preserved in specimen N.Y.S.M. 7386, near the center of interambulacrum 5. It includes several small, irregularly polygonal plates.

The external surfaces of the interambulacrals appear to have been covered with small pustules. The ambulacral coverplates may also have

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been pustulose.

Specimens:

N.Y.S.M. 7385, 7386, 7387, 12779. "Snake Hill shale and sandstone", Trenton Group, Mohawkian Series, Middle Ordovician. Loose slabs collected under the cliff on the shore of Lake Saratoga, Snake Hill, Saratoga County, New York.

All specimens are preserved as molds in a fine to medium "graywacke" sandstone. N.Y.S.M. 7385 and 7386 are on one slab; N.Y.S.M. 7387, 12779 and 3 other fragmentary specimens are preserved on a second.

N.Y.S.M. 7385. Holotype of Edriophus saratogensis (Ruedemann) (1912, pl. 3, fig. 2, as Edrioaster saratogensis). 10.2 mm axial by 9.2 mm transverse diameter.

Text fig. 65A, pl. 60, fig. 7-8.

The holotype preserves the upper oral surface of a small individual. It apparently retains most of the original convexity of the upper side of the theca. The ambulacra extend straight out from the oral region. Distally a slight solar curvature appears to be initiated as they disappear from sight. The left posterior edge of the specimen is disrupted, including ambulacrum I and the adjacent interambulacrals. Some of the oral and most of the ambulacral plates are preserved, but they have perradially collapsed downward into the ambulacral groove. Parts of the proximal margins of all but the posterior interradial plates of the frame are exposed where oral covering plates are missing.

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These show the upper ends of the passageways, three per interradial. A few proximal floorplates of ambulacrum II and V are exposed. The hydropore structure has been partially disrupted, which gives the appearance that the opening is elongate parallel to the suture between the two plates of the hydropore structure. The plates of interambulacrum 2 are less disrupted than the others.

N.Y.S.M. 7386. Paratype (1) of Edriophus saratogensis (Ruedemann) (1912, pl. 3, fig. 3, as Edrioaster saratogensis). 14 mm axial by 11.2 mm transverse diameter.

Text fig. 65C, pl. 60, fig. 9-10.

This specimen preserves the upper oral surface of a partially collapsed and laterally compressed individual. The left posterior third of the theca is missing, including interambulacrum 1 and half of 5, ambulacrum I and half of II, and the hydropore structure. Most of the oral covering plates are present. The preserved segments of the ambulacra include coverplates, but these have been perradially collapsed into the ambulacral tunnel. The floorplates of the proximal posterior part of ambulacrum V are exposed and reveal the upper elongate sutural depressions which mark the upper ends of the sutural passageways. The plates of interambulacrum 2 are less disrupted than the others. Part of the right side of the anal structure appears to be preserved near the center of interambulacrum 5.

N.Y.S.M. 7387. Paratype (2) of Edriophus saratogensis (Ruedemann) (1912, pl. 3, fig. 4, as Edrioaster saratogensis). 15 mm axial by 14 mm

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transverse diameter.

Text fig. 65B, pl. 60, fig. 11-12.

This specimen has collapsed and is somewhat laterally compressed. It exposes the upper oral surface of the theca except for the left margin where the plates of the upper oral surface are hidden beneath the thecal cavity filling which preserves the impression of the inner sides of a small section of the lower side of the specimen. This area includes the distal, solarly curved part of ambulacrum I. The upper oral surface preserves the proximal parts of all but ambulacrum II. Orals and ambulacral coverplates are preserved, but have perradially collapsed down into the ambulacral grooves. The median perradial ends of the coverplates of ambulacrum III are missing, exposing the perradial ends of the underlying floorplates. Floorplates are also exposed in the distal ends of the proximal sectors of ambulacra IV and V. The hydropore structure is present, although the two participating plates are slightly pulled apart. The inner surface of the distal floorplates of ambulacrum I show the elongate inner opening of the sutural passageways.

N.Y.S.M. 12779. Specimen on slab with paratype (2). 13.7 mm axial by 14.6 mm transverse diameter.

Text fig. 65D, pl. 60, fig. 13-14.

This individual is very fragmentary and preserves only part of the collapsed upper oral surface. It includes most of the proximal part of ambulacrum II and small parts of the other four. It also exposes the proximal margin of the left anterior side of the oral frame

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and a few of the plates of interambulacrum 5. The collapsed ambulacral coverplates are preserved on the posterior side of ambulacrum II, whereas the anterior side exposes the partially eroded floorplates.

Three other fragments of edrioasteroids are preserved on the same slab as N.Y.S.M. 7387 and 12779. These fragments preserve bits of the original calcite plates.

Discussion:

Ruedemann's (1912) original description of this species outlined the major thecal structures. In contrast with the above description, he reported: ambulacra "four solar and one contrasolar". The direction of curvature has been established only for ambulacrum I, solar, but the slight curvature of the ambital and the distal, upper oral surface parts of the other four ambulacra suggest all are solarly curved. Ruedemann also described the "sub-ambulacral plates" [? floorplates] as polygonal or hexagonal, similar to the interambulacrals. The floorplates, where exposed, appear to be elongate, sub-rectangular and perradially pointed. Describing the anal structure, Ruedemann (1912, p. 87) reported it as "small, consisting of four triangular plates". The anal structure is seen only in specimen N.Y.S.M. 7386. It appears that only a few plates of the right edge of the structure are preserved. Ruedemann apparently assumed these represented the complete structure.

Unfortunately the few known specimens of this species are too incomplete and too poorly preserved to allow a definitive description of the species. If the ambulacra are all curved solarly, as the specimens suggest, it probably belongs to the genus Edriophus. If the

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specimens are full-sized adults, the species is readily distinguished from Edriophus levis by its small size. Difference in the structural details of the oral frame, ambulacral floorplates and ambulacral coverplates would also be expected.

Range and occurrence: Trenton Group, Middle Ordovician of Saratoga County, New York.

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PLATES

Photographs have bot been retouched. Where necessary, line drawings locate sutures. These are included as text figures and are identified in the plate legend. Each drawing was prepared by tracing an enlargement of the photograph seen in the corresponding plate figure. Photographs described as whitened show the specimen coated with a thin sublimate of ammonium chloride; those denoted as in xylene show the specimen submerged in xylene. Views labeled oral surface are of the exterior of the upper side of that surface unless otherwise identified. Specimens are thought to be adults unless otherwise noted.

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PLATE 1

Lebetodiscus dicksoni (Billings), 1857

1-2. G.S.C. 1407-b, holotype.

1. Oral surface, X6, whitened.

2. Oral surface, X6, in xylene (text fig. 3b).

3-5. R.O.M. 18855-b.

3. Oral surface, X2, whitened.

4. Disrupted ambulacral coverplates that expose their ambulacral tunnel faces; each has three perradial ridges; the isolated interambulacral plate, right center, has two rows of sub-marginal, distal depressions, X4, whitened.

5. Lateral view of isolated ambulacral coverplate, X15, whitened.

6. R.O.M. 18855-a, oral surface, X3, whitened.

7-8. Y.P.M. 28451.

7. Ambulacrum II with small posterior branch, X5, whitened.

8. Oral surface, X3, whitened.

9-11. G.S.C. 437.

9. Oral surface, X3, whitened.

10. Oral surface, X3, in xylene (text fig. 1A, 3A).

11. Oral region, X5, in xylene.

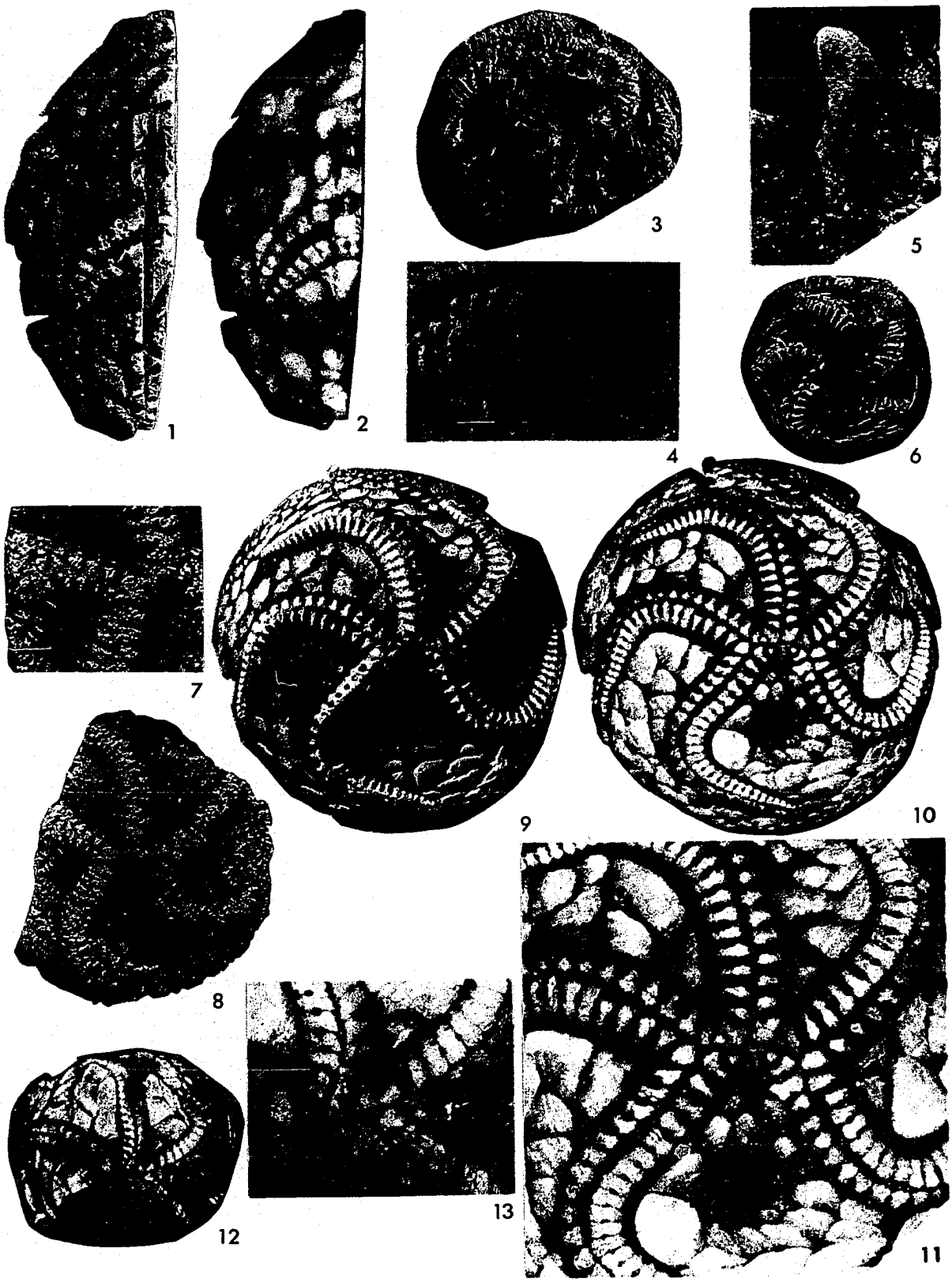
12-13. R.O.M. 18848-a.

12. Oral surface, X2, in xylene.

13. Oral area, X5, in xylene.

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PLATE 1



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PLATE 2

Lebetodiscus dicksoni (Billings), 1857

1-6. G.S.C. 1414 [holotype of Lepidoconia loriformis (Raymond), 1915].

1. Oral surface, X2, whitened.
2. Oral surface, X2, in xylene (text fig. 4B).
3. Oral region, X5, in xylene.
4. Oblique view of ambulacrum II, X8, whitened (text fig. 4D).
5. Oblique view of the proximal coverplates of ambulacrum I which have well-preserved lateral depression series, X8, whitened.
6. Oblique view of right anterior segment of peripheral rim, X6, whitened (text fig. 4C).

7-9. R.O.M. 161t-a-1 (= G.S.C. 1415).

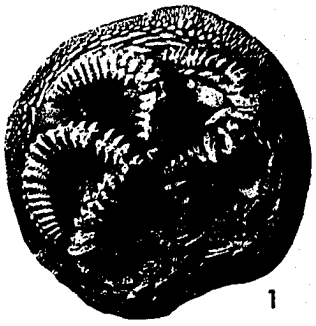
7. Oral surface, X2, whitened.
8. Oral surface, X2, in xylene (text fig. 4A).
9. Oral region, X6, in xylene.

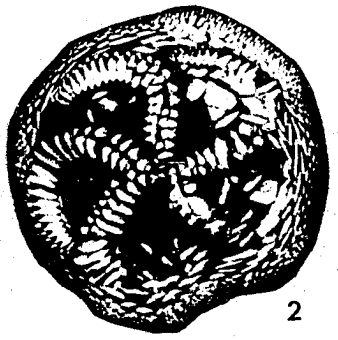
10-13. G.S.C. 1412.

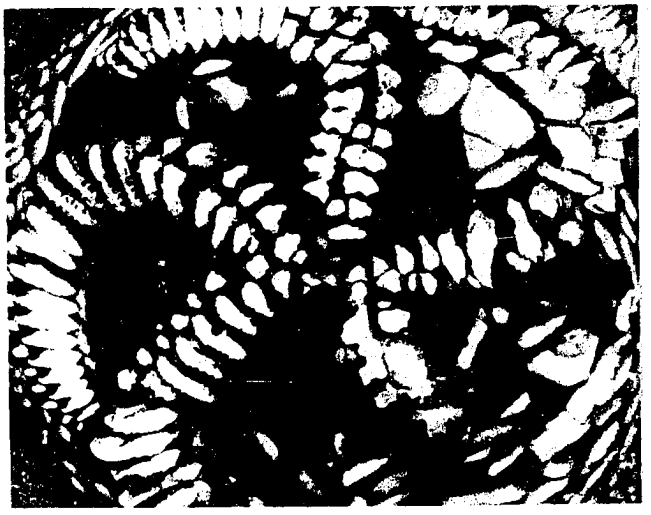
10. Oral surface, X2, whitened.
11. Oral surface, X2, in xylene.
12. Proximal segment of ambulacrum IV, inner or thecal cavity side, proximal end up, X15, in xylene (text fig. 4E).
13. Proximal segment of ambulacrum IV, exterior side, proximal end up, X15, in xylene (text fig. 4F).

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PLATE 2

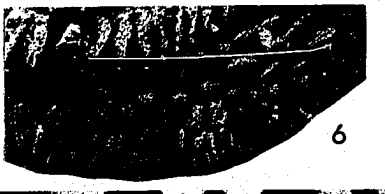

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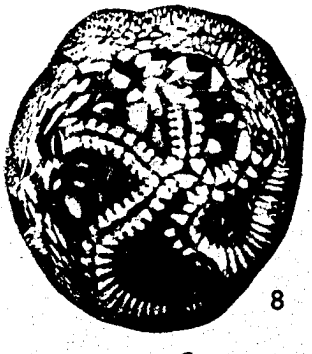

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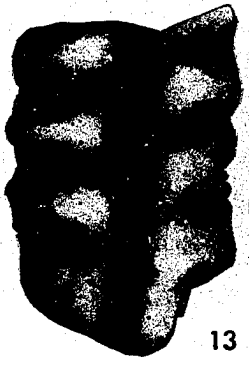

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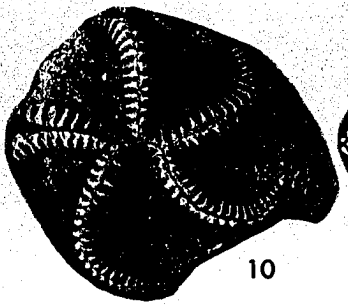

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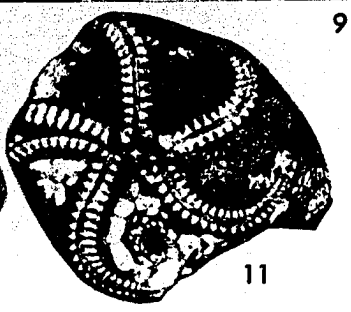

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PLATE 3

Foerstediscus grandis Bassler, 1935

1-2. U.S.N.M. S-3191, holotype.

1. Oral surface, X3, whitened.

2. Oral surface, X3, in xylene (text fig. 5C).

3-5. R.O.M. 543t-a.

3. Oral surface, X4, whitened.

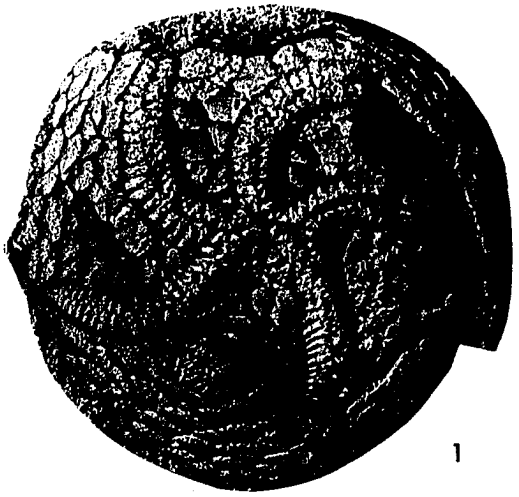
4. Oral surface, X4, in xylene (text fig. 5B).

5. Oral region, X9, in xylene (text fig. 5A).

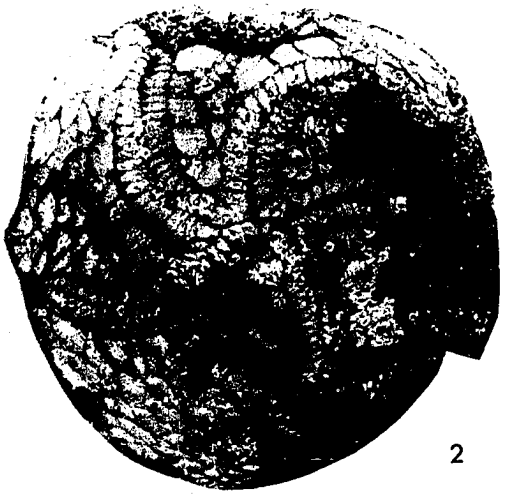
6. Y.P.M. 28452, oral surface, X3, whitened.

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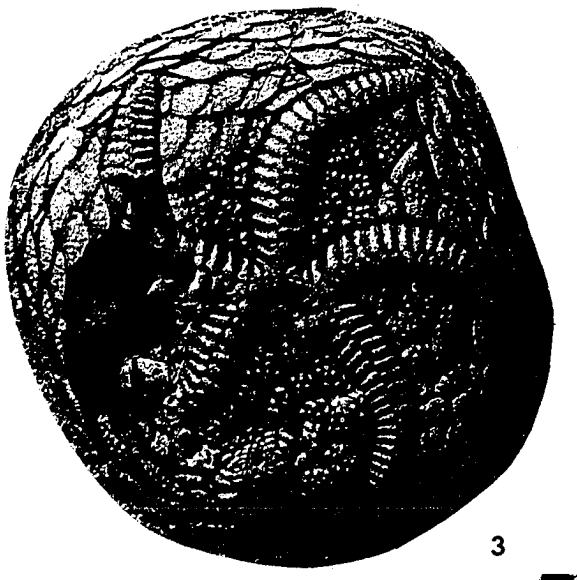
PLATE 3



1



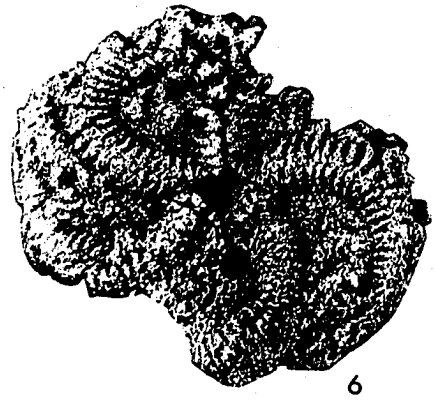
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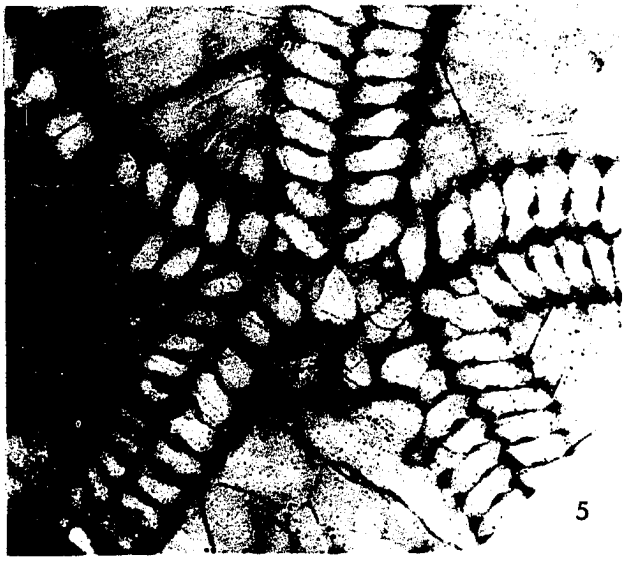
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6



5

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PLATE 4

Foerstediscus grandis Bassler, 1935

1-2. U.S.N.M. S-3889-A ("cotype" of Foerstediscus parvus Bassler, 1936).

1. Oral surface, X7, whitened.

2. Oral surface, X7, in xylene (text fig. 5D).

3. U.S.N.M. S-3889-B ("cotype" of Foerstediscus parvus Bassler, 1936), oral surface, X7, whitened.

4-5. U.S.N.M. S-3889-C (type series specimen of Foerstediscus parvus Bassler, 1936).

4. Oral surface, X7, whitened.

5. Oral surface, X7, in xylene.

6-7. U.S.N.M. S-3889-D (type series specimen of Foerstediscus parvus Bassler, 1936).

6. Oral surface, X7, whitened.

7. Oral surface, X7, in xylene.

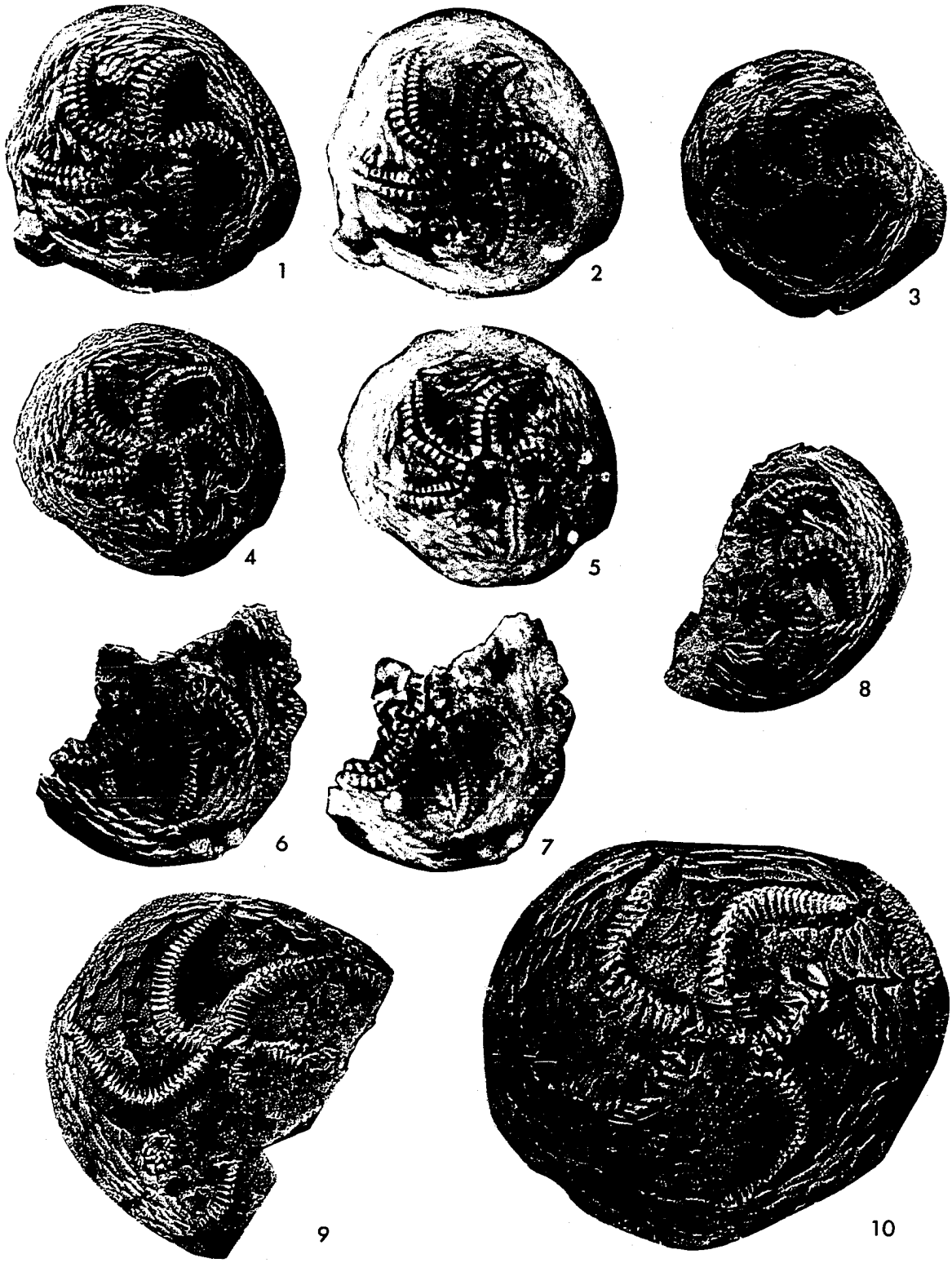
8. U.S.N.M. S-3889-E (type series specimen of Foerstediscus parvus Bassler, 1936), oral surface, X6, whitened.

9. U.C.M.P. 40433, oral surface, X2, whitened.

10. U.C.M.P. 40434, oral surface, X3, whitened.

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PLATE 4



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PLATE 5

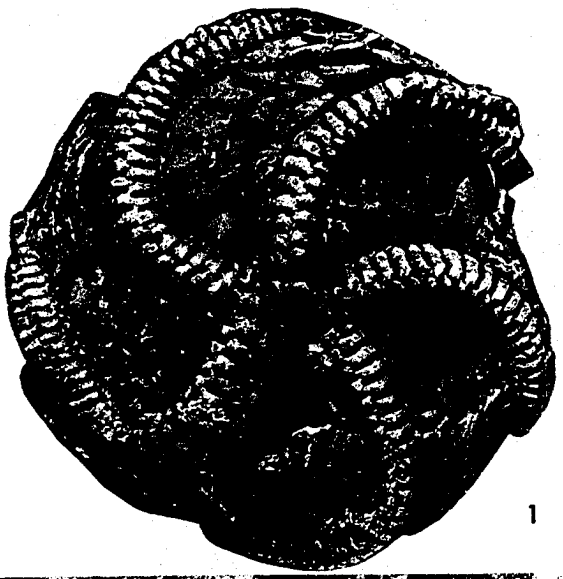
Foerstediscus splendens Bassler, 1936

1-6. U.S.N.M. S-4047, holotype.

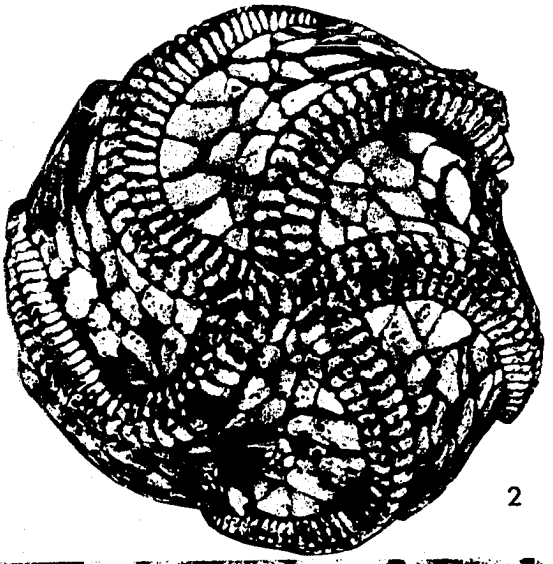
1. Oral surface, X3, whitened.
2. Oral surface, X3, in xylene (text fig. 6B).
3. Oral region, X9, whitened.
4. Oral region, X9, in xylene (text fig. 6A).
5. Segment of the peripheral rim adjacent to the tip of ambulacrum I, X8, whitened.
6. Coverplate passageways and remnants of lateral depression series in the proximal parts of ambulacra III and IV, X8, whitened.

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PLATE 5



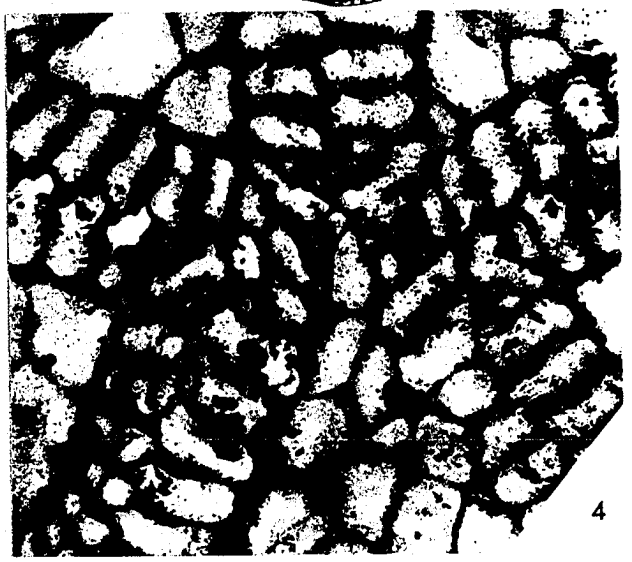
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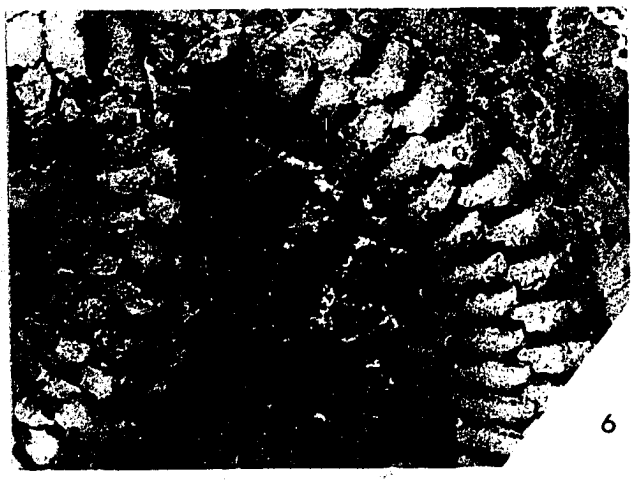
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PLATE 6

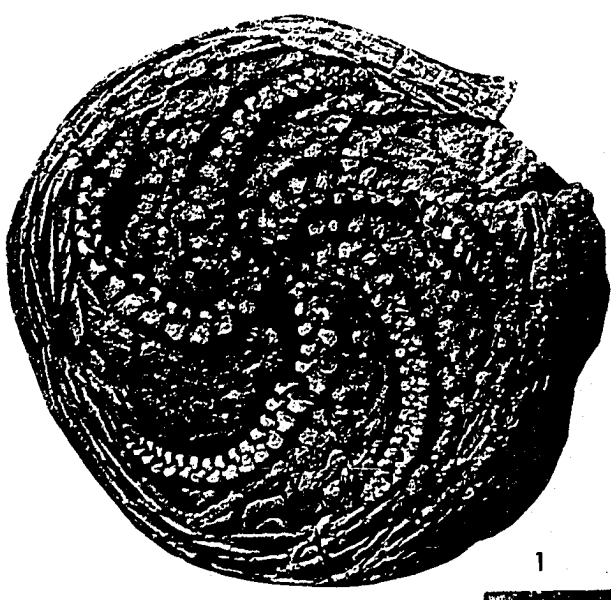
Foerstediscus solitarius Bell, sp. nov.

1-5. U.S.N.M. 140853, holotype.

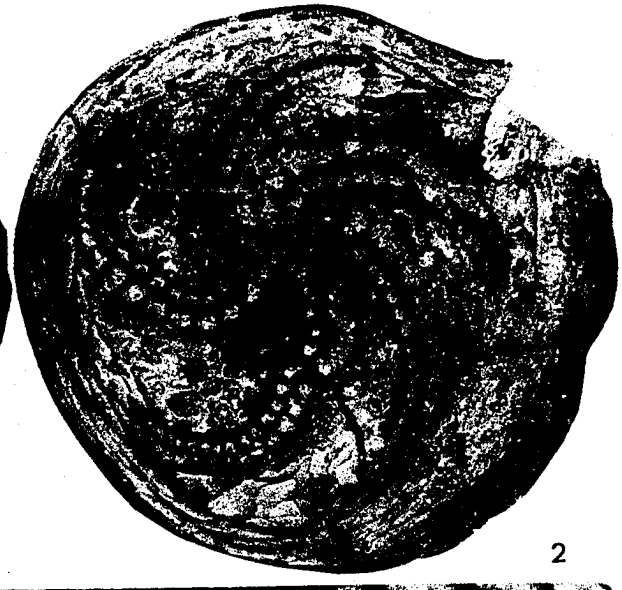
1. Oral surface, X8, whitened (text fig. 7A).
2. Oral surface, X8, in xylene.
3. Segment of peripheral rim distal to the tip of ambulacrum III, X20, whitened.
4. Oral region, X15, in xylene (text fig. 7B).
5. Oral region, X15, whitened.

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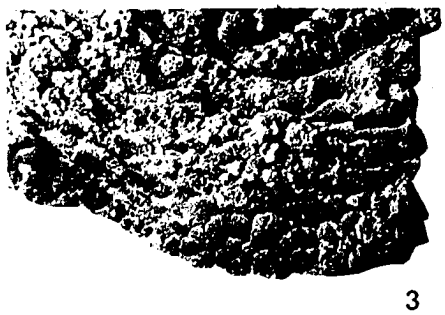
PLATE 6



1



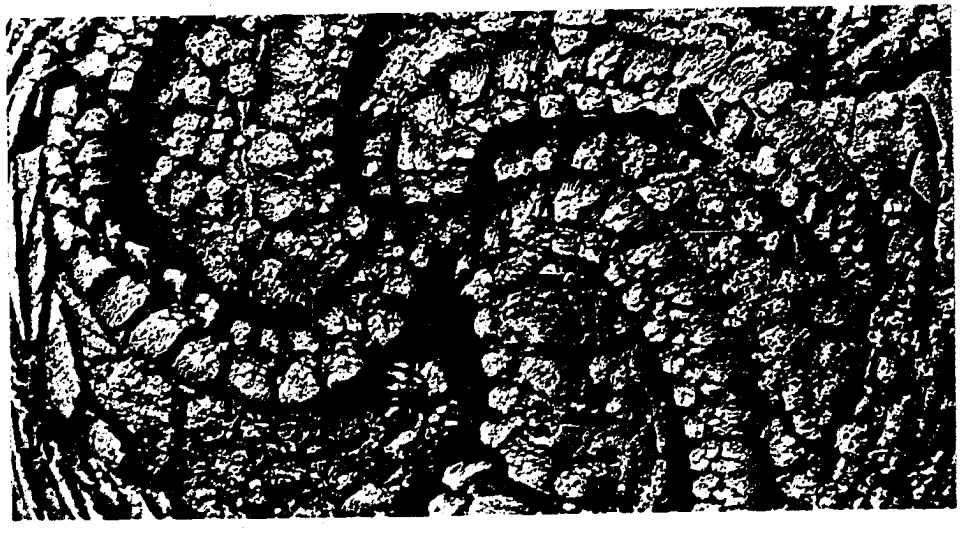
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4



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PLATE 7

Belochthus orthokolus Bell, *gen. et sp. nov.*

1-3. R.O.M. 18874, holotype.

1. Oral surface, X6, whitened.

2. Oral surface, X6, in xylene (text fig. 8E).

3. Oral region and ambulacrum IV, X15, in xylene.

4-5. R.O.M. 28179, paratype (1).

4. Oral surface, X7, whitened.

5. Oral surface, X7, in xylene.

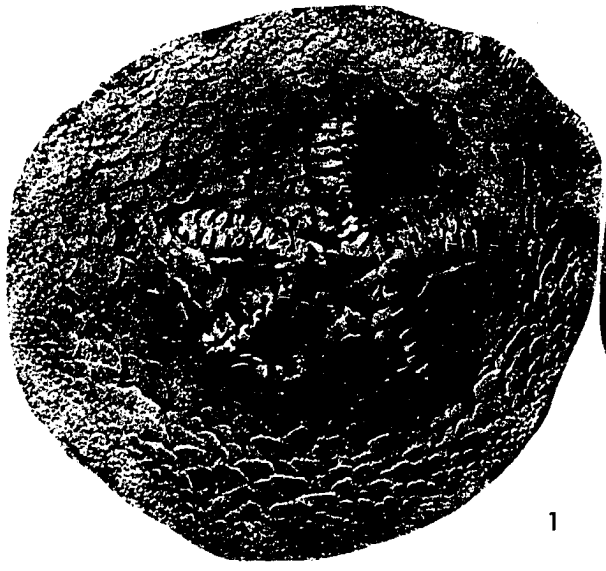
6-7. U.S.N.M. S-3894-c, paratype (3).

6. Oral surface, X9, whitened.

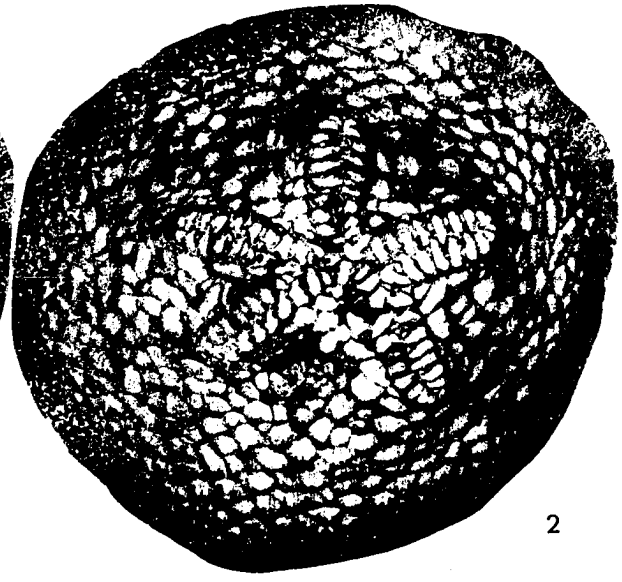
7. Oral surface, X9, in xylene.

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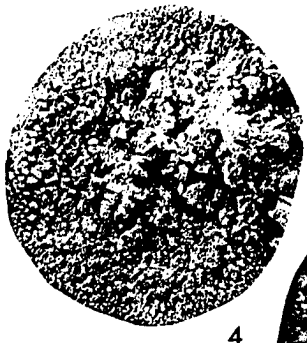
PLATE 7



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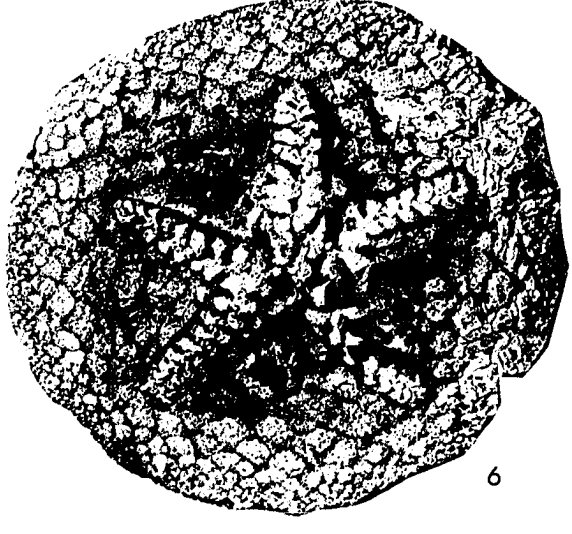
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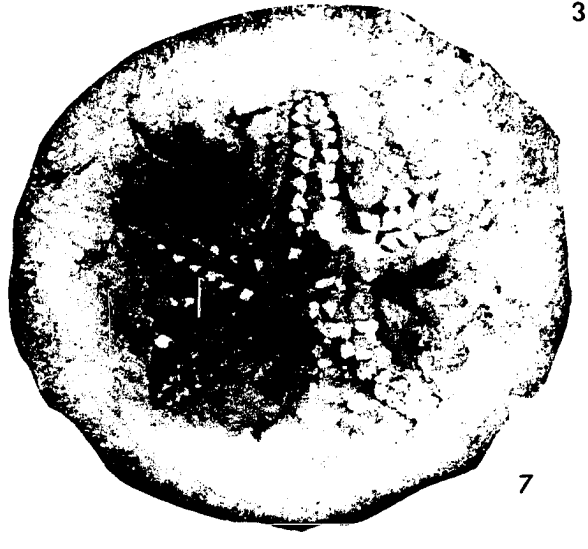
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PLATE 8

Belochthus orthokolus Bell, *gen. et sp. nov.*

1. N.Y.S.M. 12774, juvenile, oral surface, X25, whitened (text fig. 8A).

2-3. R.O.M. 160t-c-2, juvenile.

2. Oral surface, X46, whitened.

3. Oral surface, X46, in xylene (text fig. 8B).

4-5. R.O.M. 160t-c-1, juvenile.

4. Oral surface, X24, whitened.

5. Oral surface, X24, in xylene (text fig. 8C).

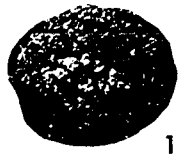
6-7. N.Y.S.M. 12773, young adult.

6. Oral surface, X14, in xylene (text fig. 8D).

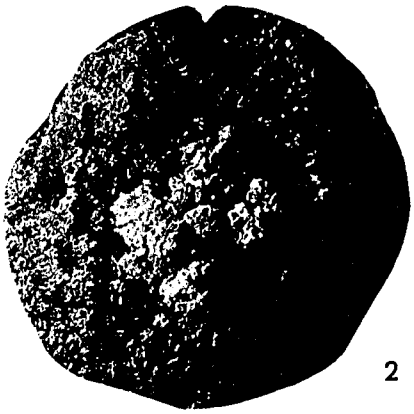
7. Oral surface, X14, whitened.

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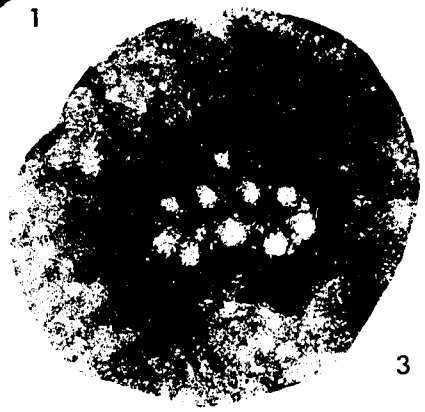
PLATE 8



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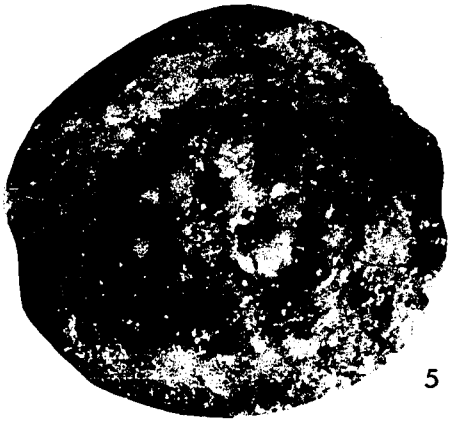
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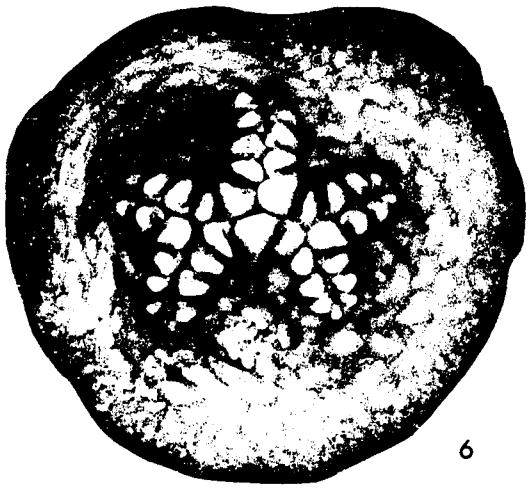
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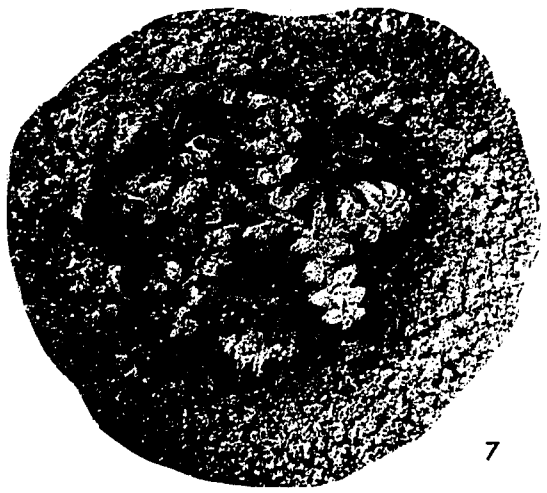
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PLATE 9

Streptaster vorticellatus Hall, 1866

1-2. A.M.N.H. 1192, holotype.

1. Oral surface, X5, whitened.

2. Oral surface, X5, in xylene.

3. M.C.Z. 520, oral surface, X4, whitened (text fig. 9A).

4-6. U.S.N.M. 87164 (holotype of *Streptaster reversata* Foerste, 1914).

4. Oral surface, X3, whitened.

5. Oral surface, X3, in xylene.

6. Hydropore interambulacral plate with grooves on the face which abuts the ambulacral coverplate components of the hydropore structure, X10, whitened.

7-9. M.C.Z. 514 [holotype of *Streptaster septembrachiatus* (Miller and Dyer), 1878].

7. Oral surface, X3, whitened (text fig. 9B).

8. Oblique view of the oral surface, X2, whitened.

9. Oblique view of the oral surface, opposite side from fig. 8, X2, whitened.

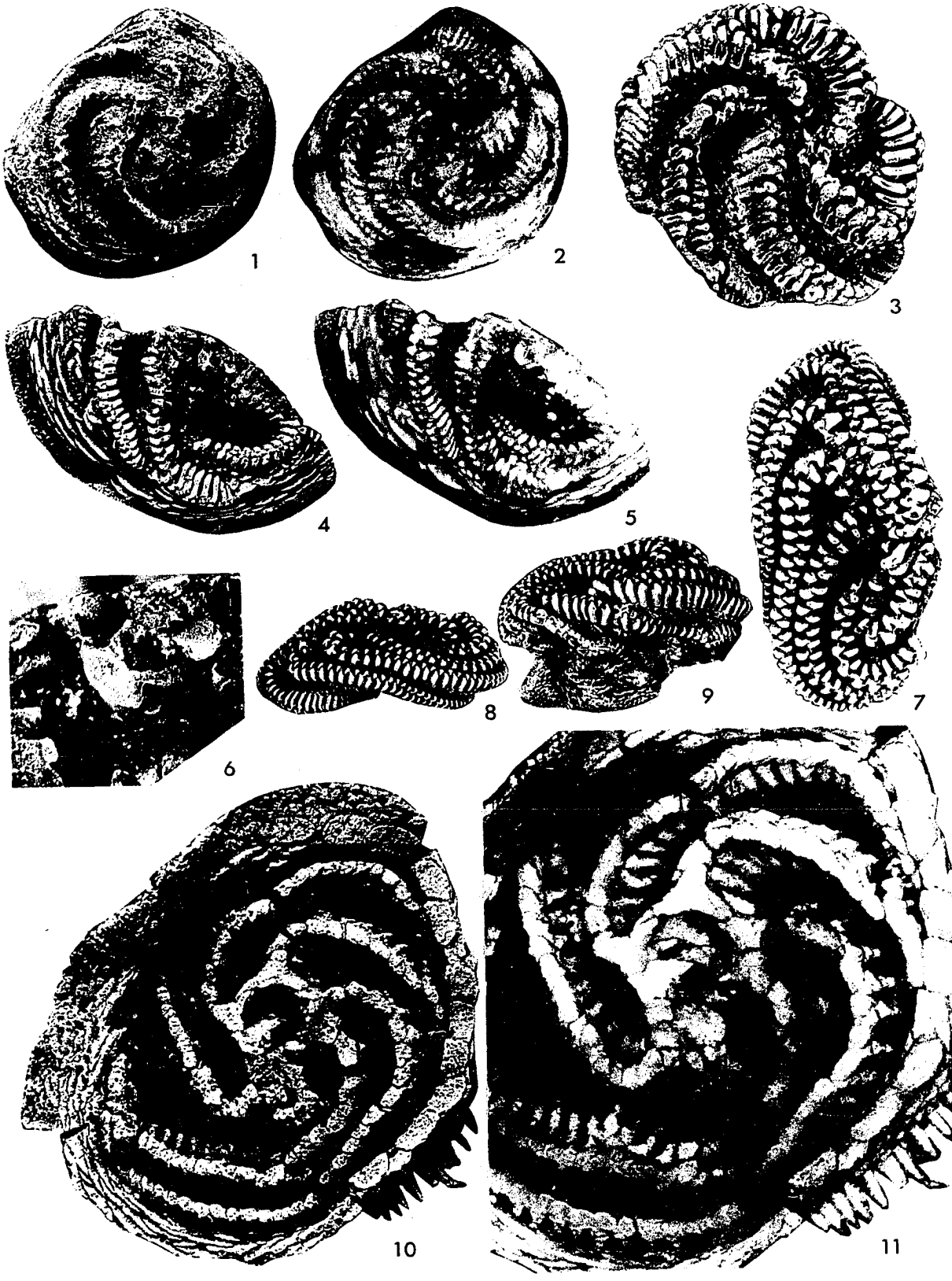
10-11. U.S.N.M. 87165.

10. Inner side of oral surface, X4, whitened. Coverplate spines project laterally from the upper side of the oral surface along the lower right edge of the specimen.

11. Inner side of oral surface, X6, in xylene.

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PLATE 9



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PLATE 10

Streptaster vorticellatus Hall, 1866

1-5. A.M.N.H. 13267/1-c.

1. Oral surface, X3, whitened.
2. Inner side of oral surface; coverplates protrude from the exterior side of the oral surface beyond the margin of the peripheral rim, X3, whitened.
3. Oral region, X7, whitened. Note small spines and spine basins on the summits of the coverplates.
4. Distal tip of ambulacrum II and adjacent segment of ambulacrum I, X10, in xylene. Note coverplate passageways and last formed pair of small distal coverplates.
5. Lateral view of a distal segment of ambulacrum I with adjacent interambulacral and rim plates missing; the tall coverplates are resting on the lateral edges of the upper sides of the imbricate floorplates, proximal end to left, X10, in xylene.

6-7. A.M.N.H. 13267/1-e.

6. Oral surface, X6, whitened. Note large, erect spines on many ambulacral coverplates.
7. Segment of ambulacrum I with several large spines on coverplates, proximal end to right, X15, whitened.

8-9. I.U.P.C. 10493.

8. Oral surface, X5, whitened.
9. Oral region, X10, whitened. The interambulacral plate of the hydropore structure is rotated so as to reveal the

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Plate 10 (cont.)

grooved face which fits against the coverplate components of the structure.

10. U.C.M.P. 36532, young adult, oral surface, X7, in xylene.

11. U.C.M.P. 40437, oral surface with large spines preserved on many of the coverplates, X7, whitened.

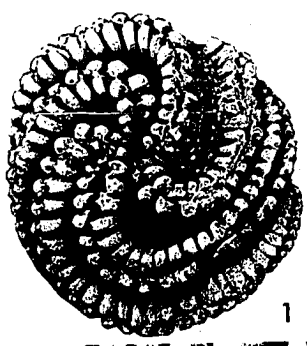
12. U.C.M.P. 40438, oral surface, X4, whitened. Note the proportionately small coverplate spines and deep coverplate basins.

13. C.F.M.-U.C. 54065, oral surface, X4, whitened.

14. U.C.M.P. 24700, oral surface, X3, whitened. Specimen resting on a fragment of a bryozoan.

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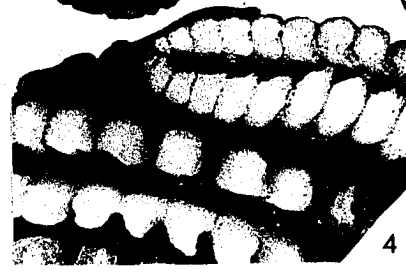
PLATE 10


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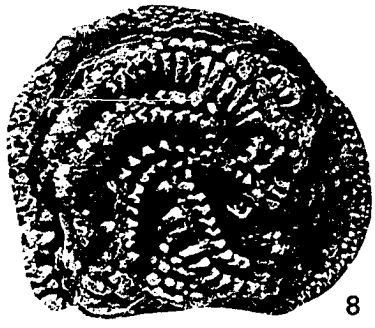

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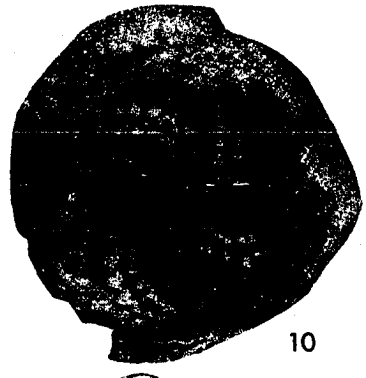

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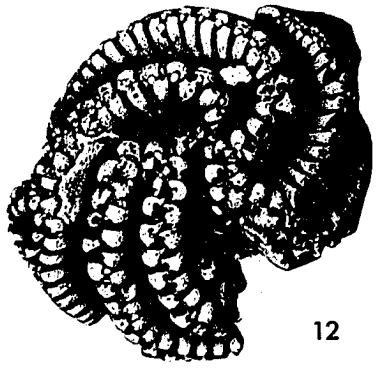

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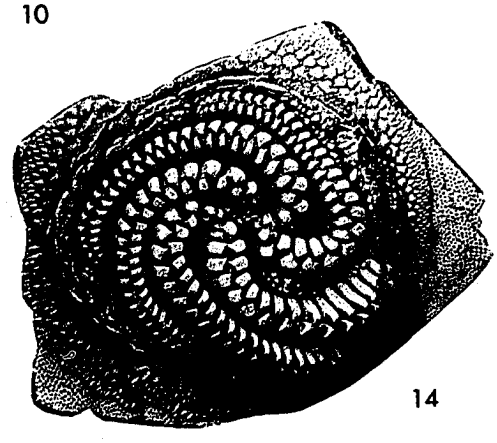

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PLATE 11

Cystaster granulatus Hall, 1871

1-3. M.C.Z. 521-C, lectotype.

1. Lateral view with ambulacrum II toward viewer, X4, whitened.

2. Lateral view with ambulacrum IV toward viewer, X4, whitened.

3. Lateral view with anus toward viewer, X4, whitened.

4-5. M.C.Z. 521-B, lectoparatype.

4. Oral surface, X4, whitened.

5. Oral surface, X5, in xylene.

6-8. M.C.Z. 521-A, lectoparatype.

6. Lateral view with ambulacrum V toward viewer, X4, whitened.

7. Oral surface, X6, whitened.

8. Oblique view, ambulacrum V toward viewer, X6, in xylene.

9. U.S.N.M. 87628-A (holotype of Cincinnatidiscus turgida Bassler, 1936), oral surface, X5, whitened.

10. U.S.N.M. 87628-B, peripheral rim and the few remaining oral surface plates, X3, whitened.

11. U.S.N.M. 42138 (holotype of Cystaster ulrichi Bassler, 1936), oral surface, X8, whitened (text fig. 10A).

12-13. M.C.Z. 515, lectoparatype.

12. Oral surface, X4, whitened.

13. Oral surface, X4, in xylene.

14-15. U.C.M.P. 40440-a.

14. Oral surface, X5, whitened.

15. Oral surface, X5, in xylene.

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Plate 11 (cont.)

16-17. U.C.M.P. 40448.

16. Oral surface, X5, whitened.

17. Lateral view with ambulacrum IV toward viewer, X6, whitened.

18-19. U.C.M.P. 40442.

18. Oral surface, X5, whitened.

19. Lower side of specimen which includes the exterior of the pedunculate zone, inner side of the peripheral rim and a small central sector of the inner side of the upper oral surface, X5, in xylene.

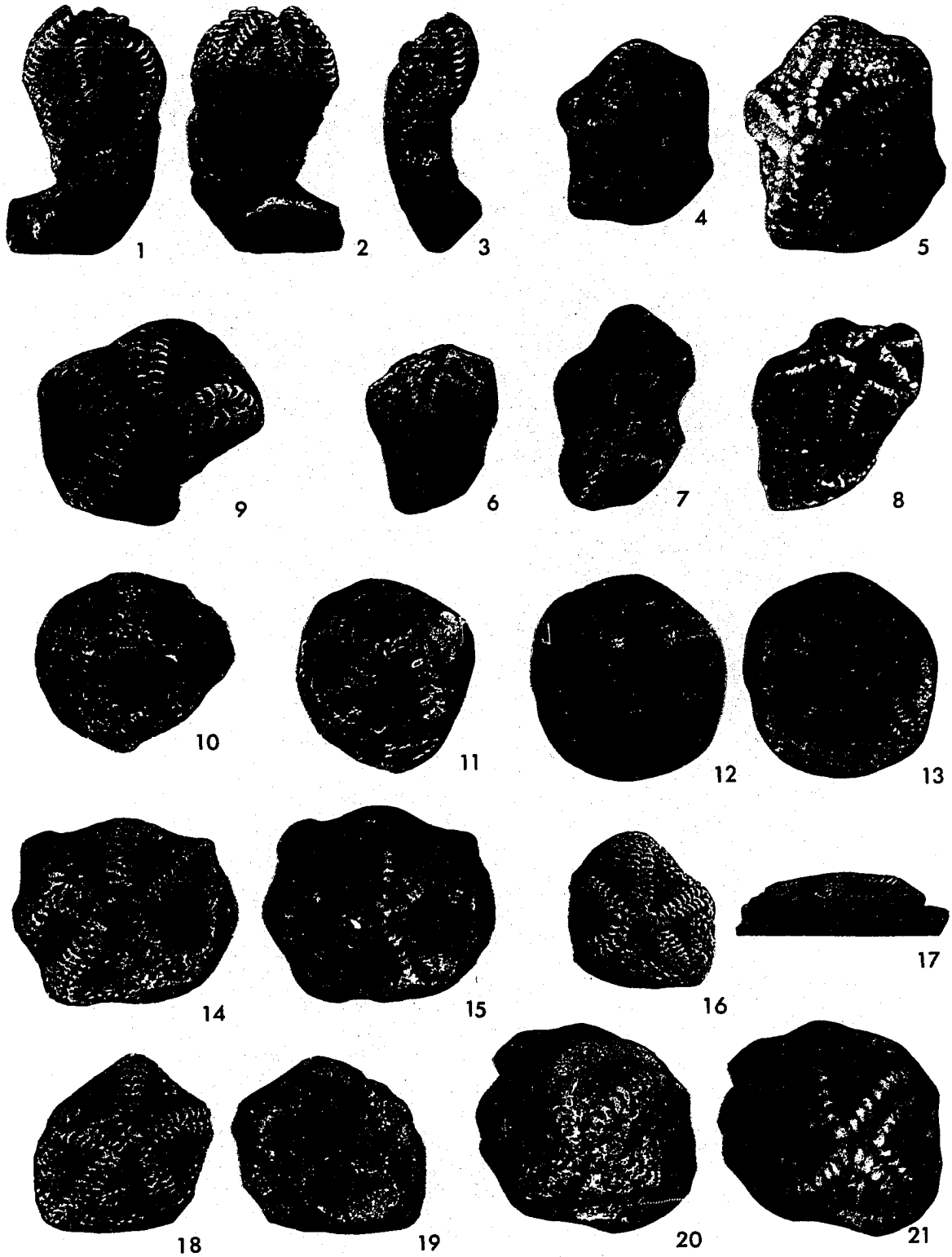
20-21. U.C.M.P. 40439.

20. Oral surface, X7, whitened.

21. Oral surface, X7, in xylene.

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PLATE II



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PLATE 12

Cystaster granulatus Hall, 1871 Fig. 1-10.

1. U.C.M.P. 40447, oral surface, X4, whitened.

2. U.C.M.P. 40441, oral surface, X8, whitened.

3-4. U.C.M.P. 40443.

3. Oral surface, X5, whitened (text fig. 10B).

4. Oral surface, X5, in xylene.

5. U.C.M.P. 40446, oral surface, X4, whitened.

6. U.C.M.P. 40444, oral surface, X6, whitened.

7. U.C.M.P. 40445, oral surface, X4, whitened.

8. A.M.N.H. 13263/1-g, oblique view with interambulacrum II toward viewer, X5, whitened.

9. U.C.M.P. 40450, oral region, X8, whitened.

10. U.C.M.P. 40449 (a-c), oblique view, X2, whitened.

a. = lower left specimen, b. = lower right one, c. = top center one.

Cystaster stellatus (Hall), 1866 Fig. 11-22.

11-12. M.C.Z. 523, holotype.

11. Oral surface, X3, whitened.

12. Oral surface, X3, in xylene (text fig. 11B).

13. A.M.N.H. 1191-A, lectoparatype, oral surface, X7, whitened.

14. A.M.N.H. 1191-B, oral surface, X12, whitened.

15. U.S.N.M. 34413-A (holotype of Cincinnatidiscus edenensis Bassler, 1936), oral surface, X4, whitened.

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Plate 12 (cont.)

16. U.S.N.M. 34413-B (paratype of Cincinnatidiscus edenensis Bassler, 1936), oral surface, X4, whitened.

17-18. U.S.N.M. 87163-A [cotype of Cincinnatidiscus carnensis (Foerste), 1914].

17. Oral surface, X5, whitened.

18. Oral surface, X5, in xylene.

19-20. U.S.N.M. 87163-B [cotype of Cincinnatidiscus carnensis (Foerste), 1914].

19. Oral surface, X5, whitened.

20. Oral surface, X5, in xylene.

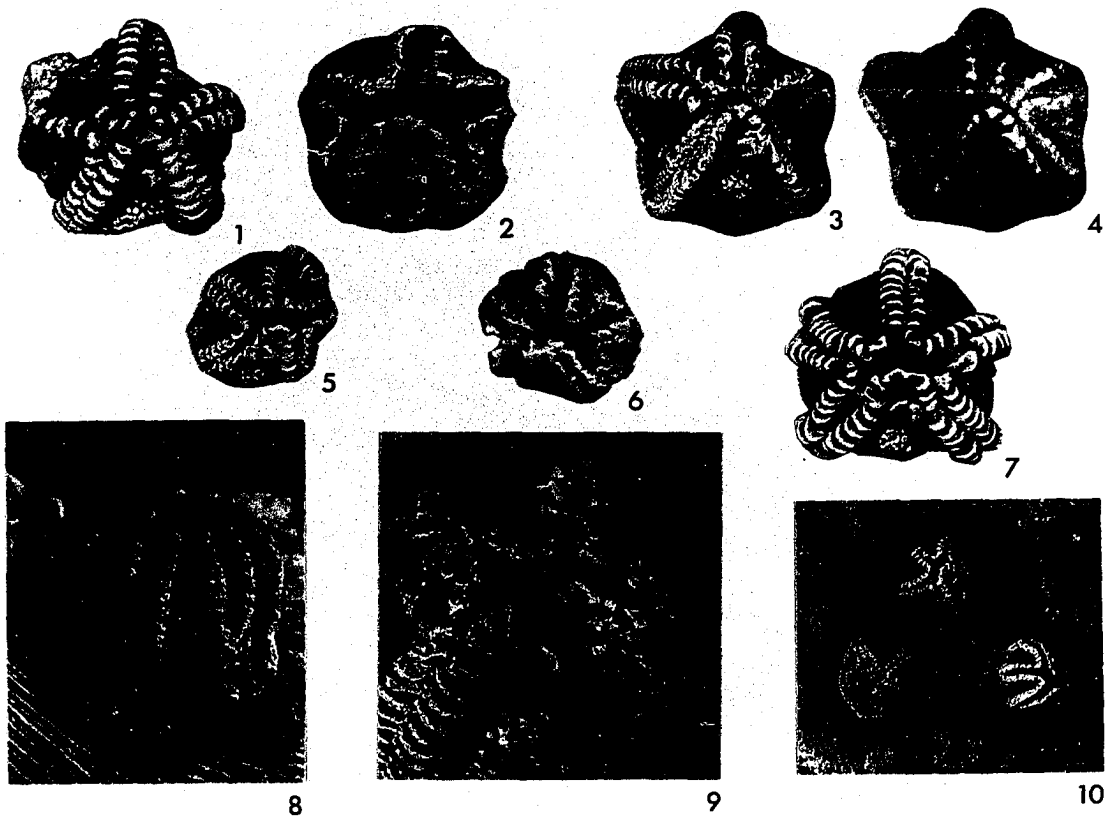
21-22. Y.P.M. 28453.

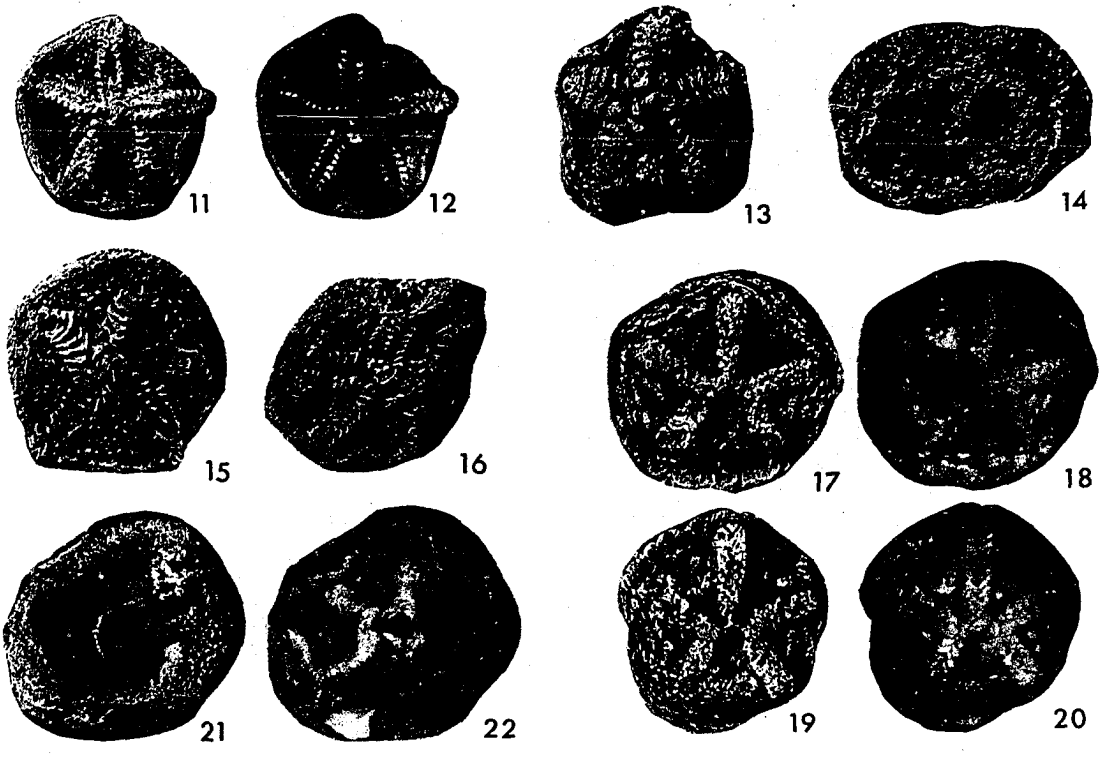
21. Inner side of the oral surface, X4, whitened (text fig. 11C).

22. Inner side of the oral surface, X4, in xylene.

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PLATE 12





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PLATE 13

Cystaster stellatus (Hall), 1866

1-2. U.C.M.P. 40451-A.

1. Central and posterior part of the oral surface, with spines preserved on the summits of the coverplates of ambulacra I-III, X9, whitened.

2. Oral surface, X5, whitened.

3. U.C.M.P. 40451-B, oral surface with spines preserved on the summits of the distal coverplates of ambulacrum V, X5, whitened.

4-5. U.C.M.P. 40462, oral surface with the exterior of the plates of the oral-ambulacral series removed by grinding to expose a subsurficial, sectional view.

4. Oral surface, X5, in xylene. Note the coverplate passageways.

5. Enlargement of ambulacra I-III, X10, in xylene.

6. U.C.M.P. 40459, oral surface with the exterior of the plates of the oral-ambulacral series removed by grinding to expose a subsurficial, sectional view, X5, in xylene (text fig. 11A). Note the coverplate passageways, stone-canal passageway and central oral lumen.

7. U.C.M.P. 40481, oral surface, X4, whitened.

8. U.C.M.P. 40482, oral surface, X4, whitened.

9-10. U.C.M.P. 40452.

9. Oral surface, X4, whitened.

10. Oral surface, X4, in xylene (text fig. 12C).

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Plate 13 (cont.)

11. U.C.M.P. 40453, oral surface, X4, in xylene.

12-13. U.S.N.M. Acc. no. 258129-A.

12. Oral surface, X5, whitened.

13. Oral surface, X5, in xylene (text fig. 12A).

14-15. U.C.M.P. 40454.

14. Oral surface, X6, whitened.

15. Oral surface, X8, in xylene.

16. U.S.N.M. Acc. no. 258129-B, oral surface, X6, in xylene (text fig. 12B).

17-18. U.C.M.P. 40455.

17. Oral surface, X4, whitened.

18. Oral surface, X4, in xylene.

19. U.C.M.P. 40457, oral surface, X6, in xylene.

20-21. U.C.M.P. 40456.

20. Oral surface, X5, whitened.

21. Oral surface, X5, in xylene.

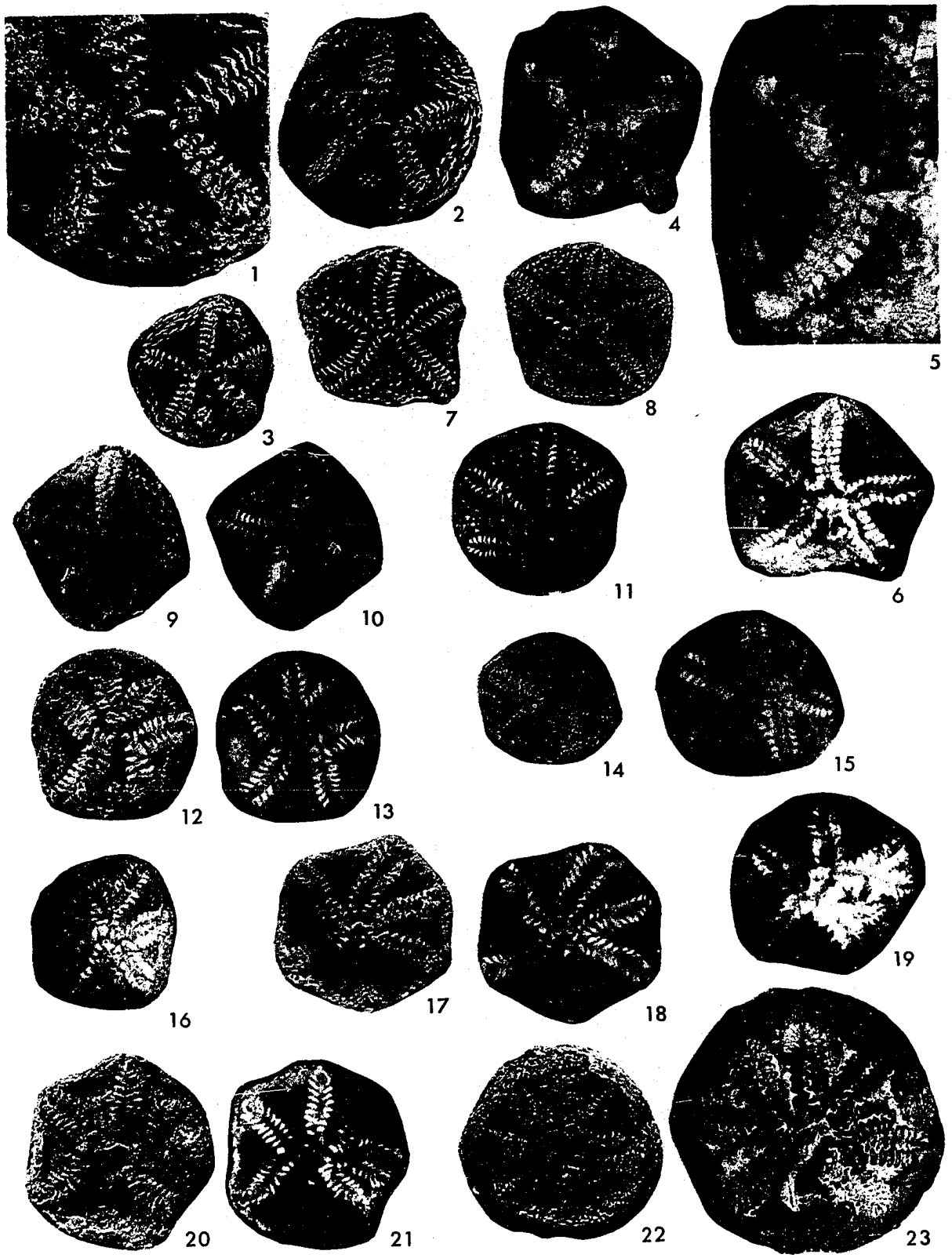
22-23. U.C.M.P. 40458.

22. Oral surface, X6, whitened.

23. Oral surface, X8, in xylene (text fig. 12D).

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PLATE 13



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PLATE 14

Carneyella pilea (Hall), 1866

1-2. M.C.Z. 516-a, lectotype.

1. Oral surface, X3, whitened.

2. Oral surface, X3, in xylene (text fig. 13B).

3-5. A.M.N.H. 1193-A, lectoparatype.

3. Oral surface, viewed normal to the axis of compression, X2, whitened.

4. Upper side of specimen, including ambulacra I and V, interambulacrum 5 with the anus and the posterior half of the oral area, X2, whitened.

5. Interambulacrum 2 with nodes preserved on one plate, X5, whitened.

6-7. M.C.Z. 518-a, (?) lectoparatype.

6. Oral surface, X3, whitened.

7. Inner side of oral surface, X3, whitened.

8-9. U.S.N.M. 40743-C.

8. Oral surface, X5, whitened (text fig. 13D).

9. Ambulacrum IV with medial bifurcation, X10, whitened.

10-12. U.S.N.M. 40743-a (holotype of Carneyella cincinnatiensis Bassler, 1935).

10. Oral surface, X4, whitened.

11. Oral region, X7, whitened. Note surficial pitting of the plates of the oral-ambulacral series.

12. Interambulacral and rim plates with nodose prosopon, X10, whitened.

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Plate 14 (cont.)

13. U.S.N.M. 40743-b, oral surface with nodes preserved sporadically on interambulacral and rim plates, X3, whitened.

14. U.S.N.M. 40743-d, oral surface, X3, whitened.

15. N.Y.S.M. 10683 (holotype of Bassleridiscus mohawkensis Fisher, 1952), oral surface, X3, whitened.

16. U.S.N.M. 42105, juvenile (holotype of Hemicystites curtus Bassler, 1936), oral surface, X10, whitened (text fig. 14C).

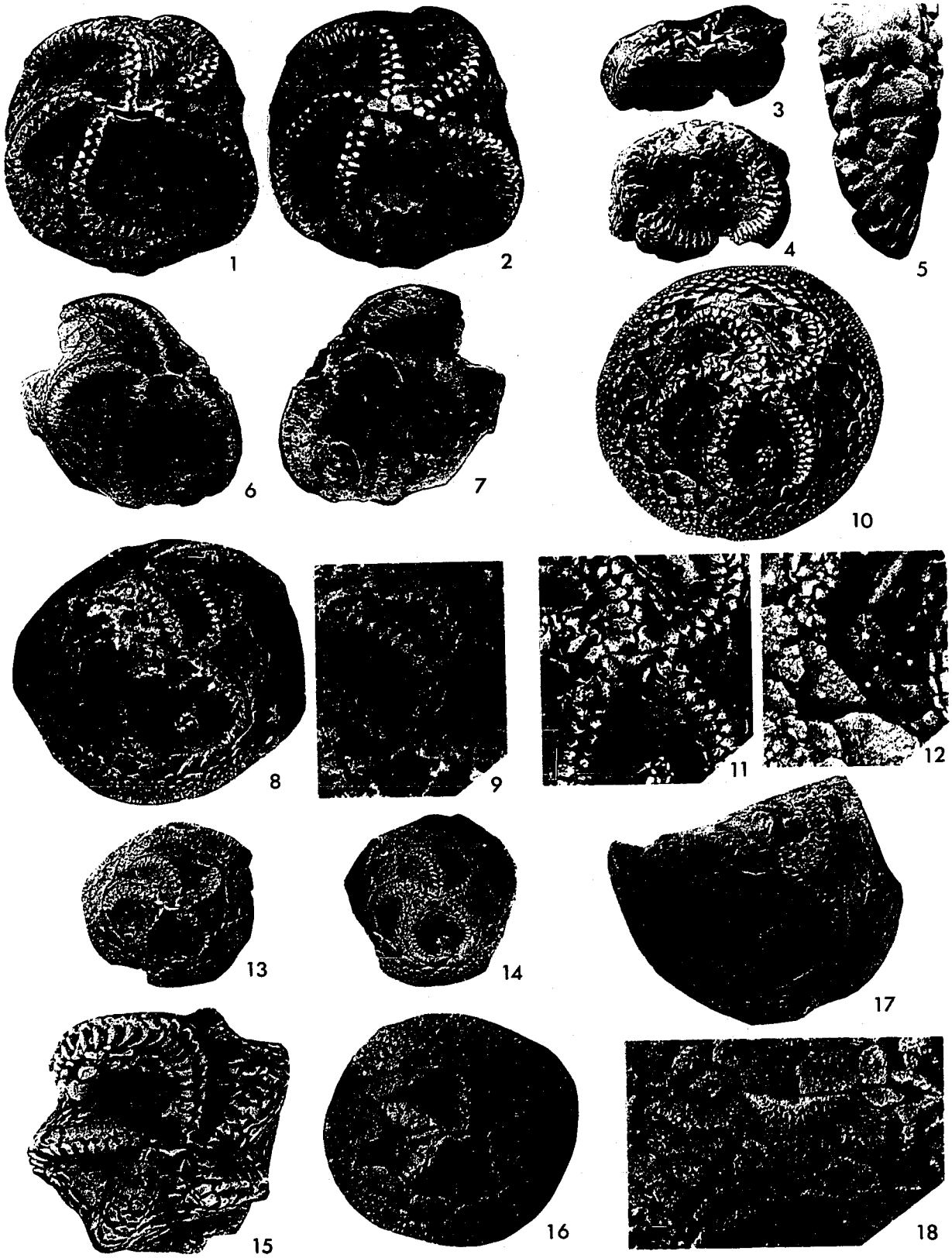
17-18. U.S.N.M. S-3876 (holotype of Carneyella nicklesi Bassler, 1936).

17. Oral surface, X3, whitened.

18. Oral region with surficial pitting well-preserved on the posterior primary oral, X10, whitened.

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PLATE 14



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PLATE 15

Carneyella pilea (Hall), 1866

1-2. U.S.N.M. 42111-A, juvenile or young adult ("cotype" of Hemicystites richmondensis Bassler, 1936).

1. Oral surface, X5, whitened.

2. Oral surface, X5, in xylene (text fig. 14D).

3. U.S.N.M. 42111-B, young adult ("cotype" of Hemicystites richmondensis Bassler, 1936), oral surface, X5, whitened.

4. U.S.N.M. 40742-B, juvenile ("cotype" of Hemicystites richmondensis Bassler, 1936), oral surface, X5, whitened.

5. U.S.N.M. 40742-A-1, juvenile ("cotype" of Hemicystites richmondensis Bassler, 1936), oral surface, X8, whitened.

6. U.S.N.M. 40742-A-2, juvenile ("cotype" of Hemicystites richmondensis Bassler, 1936), oral surface, X8, whitened (text fig. 14A).

7. U.S.N.M. 68333, juvenile ("cotype" of Hemicystites richmondensis Bassler, 1936), oral surface, X8, whitened.

8. U.S.N.M. S-3960 (paratype of Isorophus germanus Bassler, 1936), oral surface, X3, in xylene.

9-10. U.S.N.M. S-3959 (holotype of Isorophus germanus Bassler, 1936).

9. Oral surface, X3, whitened.

10. Oral surface, X3, in xylene (text fig. 14E).

11-13. U.S.N.M. 170362.

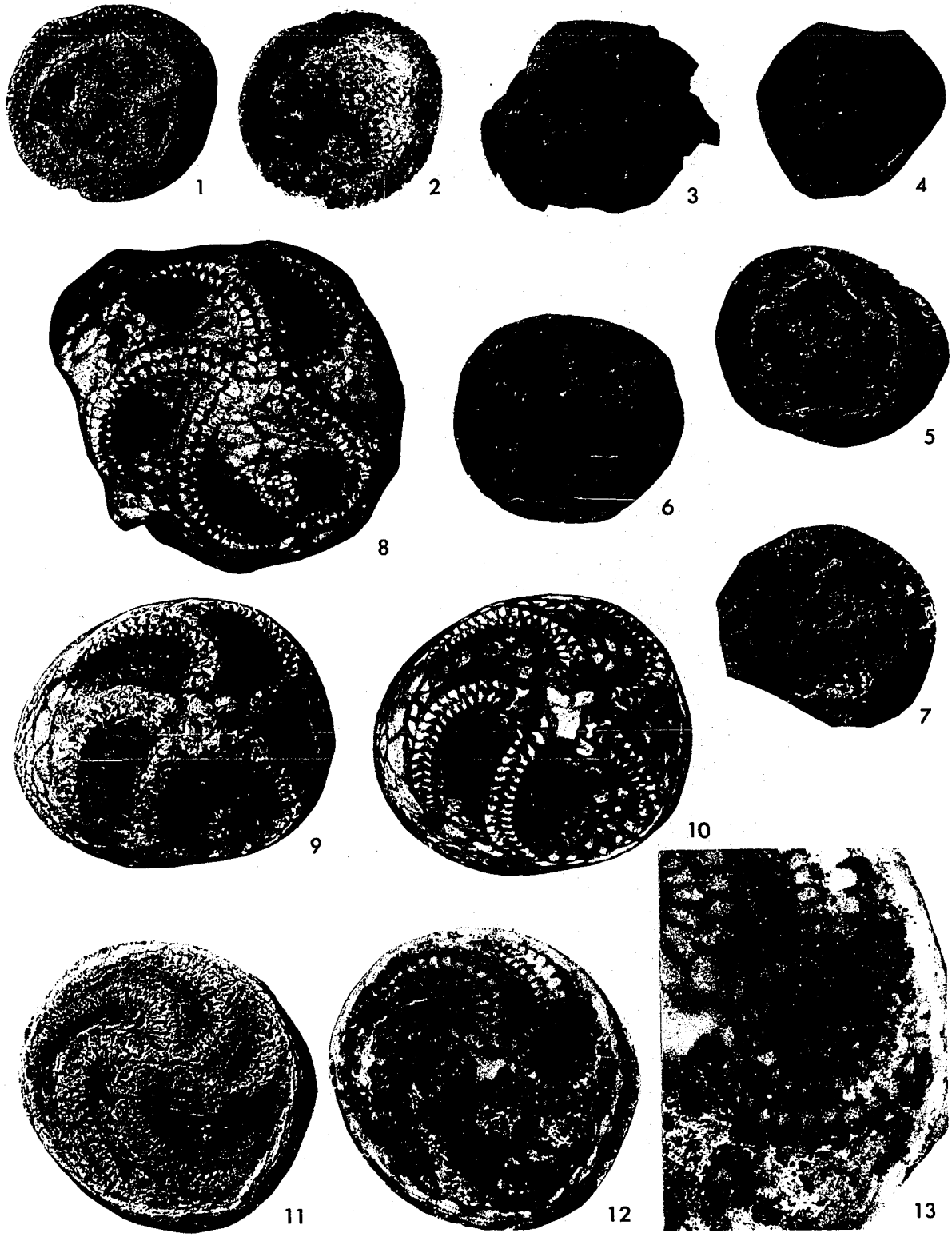
11. Oral surface, X5, whitened.

12. Oral surface, X5, in xylene (text fig. 13E).

13. Ambulacrum V and adjacent areas, X10, in xylene.

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PLATE 15



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PLATE 16

Carneyella pilea (Hall), 1866

1-4. C.F.M.-U.C. 8825.

1. Central part of the inner side of the oral surface, X8, whitened.
2. Central part of the inner side of the oral surface, X8, in xylene.
3. Inner side of the oral surface, X4, whitened.
4. Inner side of ambulacrum V with the floorplates missing, X10, whitened (text fig. 14B).

5-6. C.F.M.-U.C. 8886, small segment of one ambulacrum and a few adjacent interambulacral plates.

5. Coverplates of the oral surface, proximal end of segment on right, X5, whitened.
6. Imbricate floorplates of the inner side of the oral surface, proximal end of segment on left, X5, whitened.

7. U.C.M.P. 34535, oral surface, X3, whitened.

8-10. U.C.M.P. 34537.

8. Oblique view of the proximal part of ambulacrum I and the oral area, showing prosopon, X6, whitened.
9. Oblique view of the oral area, ambulacrum III toward the viewer, showing prosopon on the plates of the oral-ambulacral series, X6, whitened.
10. Oral surface, X3, whitened.

11. C.F.M.-P. 6504, young adult, oral surface, X5, whitened (text fig. 13C).

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Plate 16 (cont.)

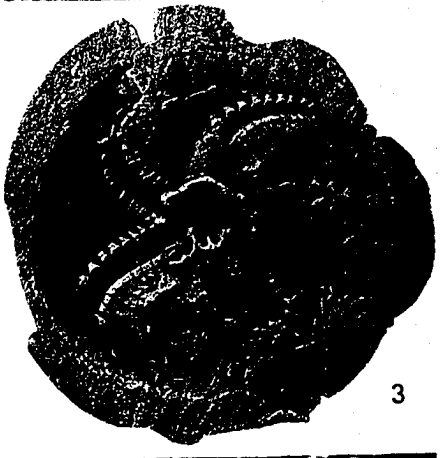
12. C.F.M.-U.C. 54062, oral surface, X4, whitened.

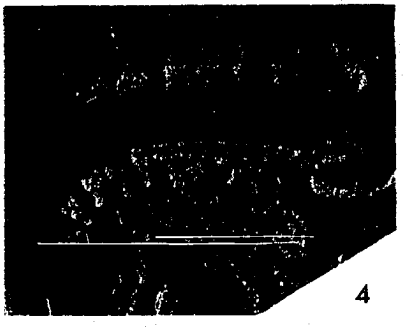
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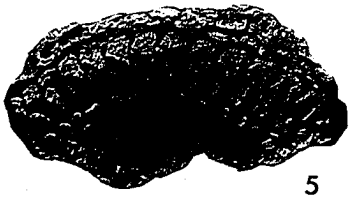
PLATE 16


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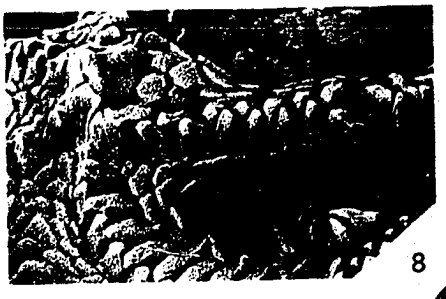

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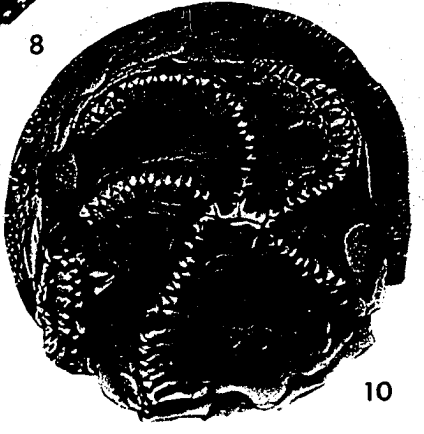

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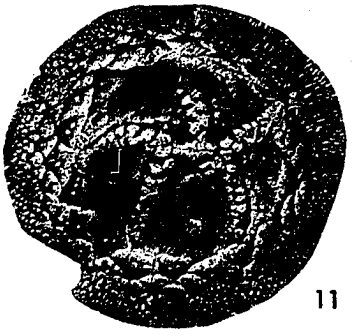

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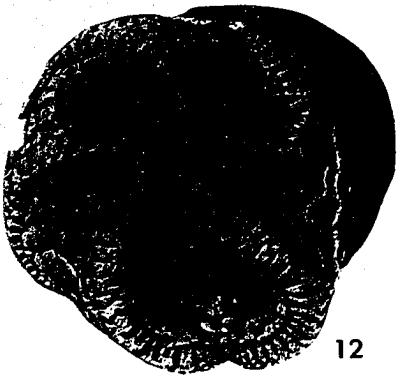

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PLATE 17

Carneyella pilea (Hall), 1866 Fig. 1-9.

1-4. U.C.M.P. 26324, specimen resting on a segment of crinoid stem with the peripheral rim and the distal parts of interambulacra 1-4 and ambulacra II and IV flexed under the upper or oral side of the theca.

1. Oral side of theca, X3, whitened.
2. Oral side of theca, X3, in xylene.
3. Lower side of theca, X3, whitened.
4. Lower side of theca, X3, in xylene.

5. U.C.M.P. 40463, oral surface, X3, in xylene.

6-7. U.C.M.P. 40465.

6. Oral surface, X3, whitened.
7. Oral surface, X3, in xylene (text fig. 1B).

8-9. U.C.M.P. 40464.

8. Oral surface, X2, in xylene (text fig. 13A).
9. Ambulacrum IV with many of the coverplate passageways preserved clearly, X7, in xylene.

Carneyella faberi (Miller), 1894 Fig. 10-13.

10-11. C.F.M.-U.C. 8821, holotype.

10. Oral surface, X3, whitened (text fig. 15B).
11. Anterior part of the oral surface with the nodose prosopon preserved on ambulacral, interambulacral and rim plates, X10, whitened.

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Plate 17 (cont.)

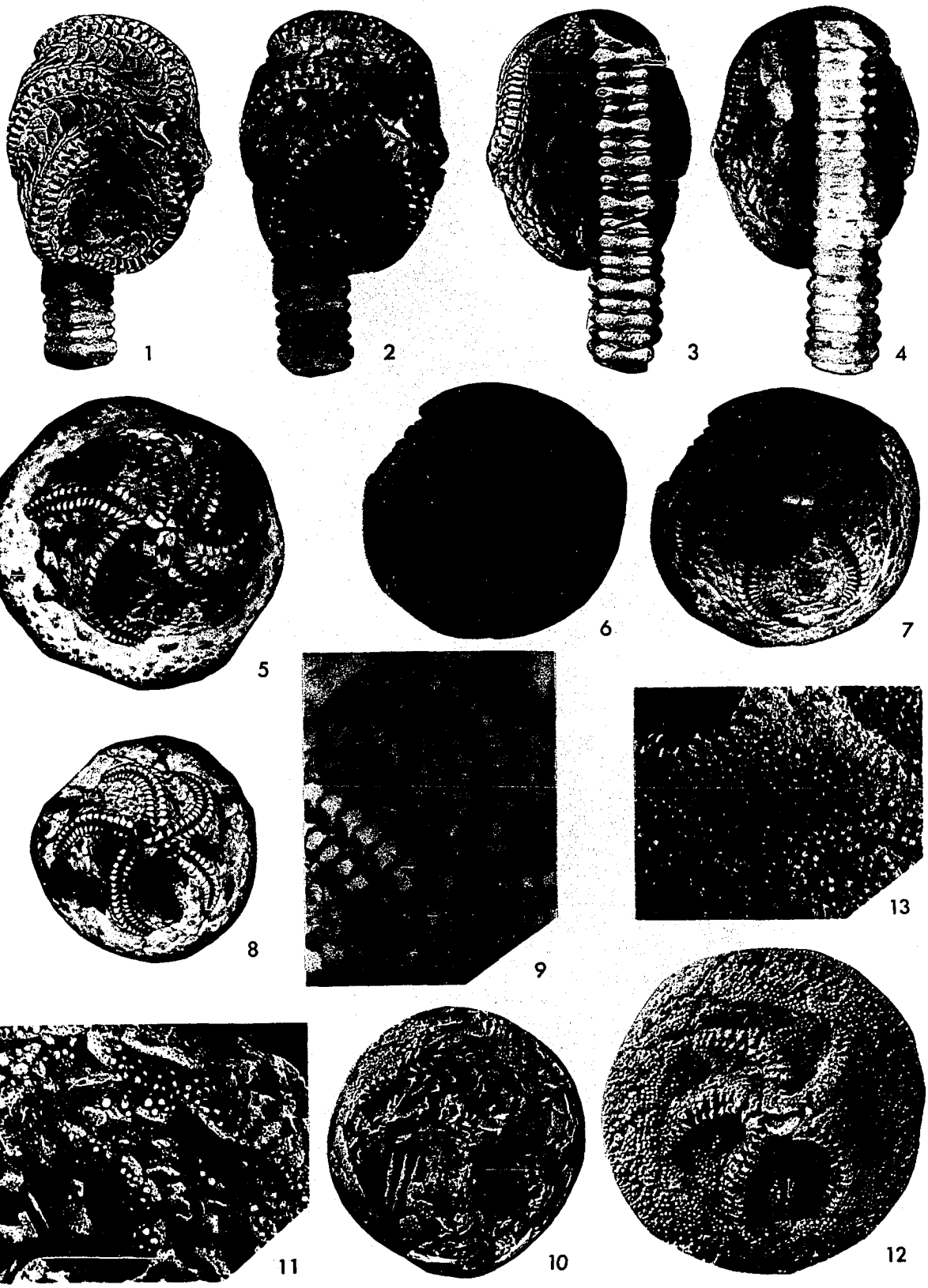
12-13. U.S.N.M. 87162 (holotype of Agelacrinus vetustus Foerste, 1914).

12. Oral surface, X5, whitened.

13. Interambulacrum 4 and adjacent areas with the plates covered by nodose prosopon, X10, whitened.

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PLATE 17



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PLATE 18

Carneyella faberi (Miller) 1894 Fig. 1-5.

1-5. U.S.N.M. S-3965 (holotype of Carneyella foerstei Bassler and Shideler, 1936).

1. Oral surface, X3, whitened.
2. Oral surface, X3, in xylene.
3. Oblique view of ambulacrum I and adjacent structures, X5, whitened.
4. Oblique view of the proximal coverplates of the anterior side of ambulacrum I, X20, whitened.
5. Hydropore region, X10, whitened.

Carneyella ulrichi Bassler and Shideler, 1936 Fig. 6-10.

6-10. U.S.N.M. S-3964, holotype.

6. Oral surface, X4, whitened.
7. Oral surface, X4, in xylene.
8. Oblique view of the proximal coverplates of ambulacrum IV and parts of the oral area and hydropore structure, X10, whitened.
9. Oblique view of the medial coverplates of the anterior side of ambulacrum II, X10, whitened.
10. Oblique view of the proximal plates of the right side of interambulacrum 5, X10, whitened.

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Plate 18 (cont.)

? Carneyella valcourensis Clark, 1920 Fig. 11-12.

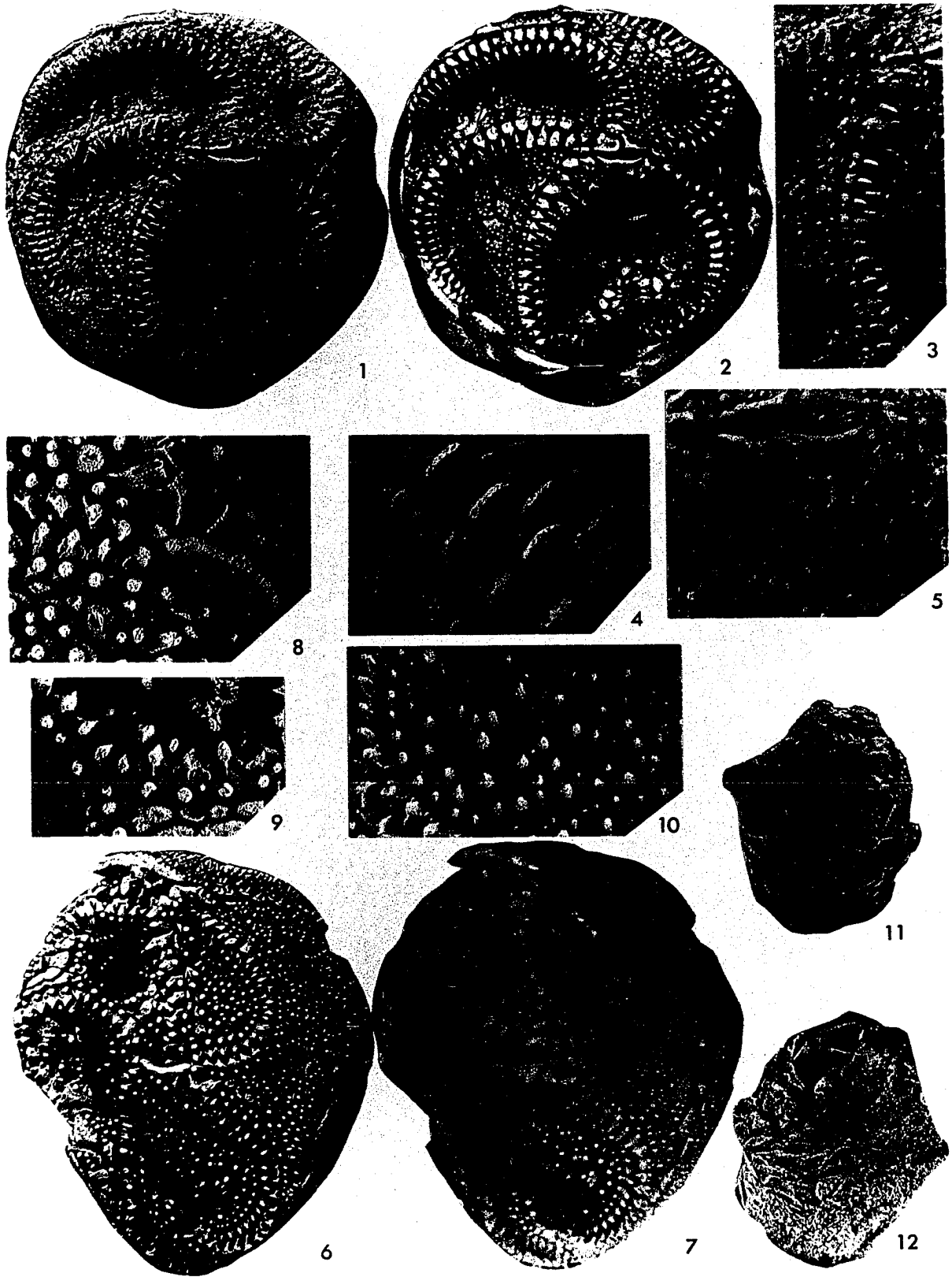
11-12. M.C.Z. 532, holotype.

11. One side of the laterally compressed theca, X4, whitened.

12. Reverse side of the theca, X4, whitened.

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PLATE 18



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PLATE 19

Cryptogoleus chapmani (Raymond), 1915

1-4. G.S.C. 3235-a, holotype.

1. Oral surface, X5, whitened.
2. Oral surface, X5, in xylene (text fig. 17B).
3. Oral region, X10, whitened.
4. Oblique view of the posterior part of the peripheral rim, X10, whitened.

5-6. G.S.C. 3235-b.

5. Oral surface, X3, whitened.
6. Oral surface, X2, in xylene.

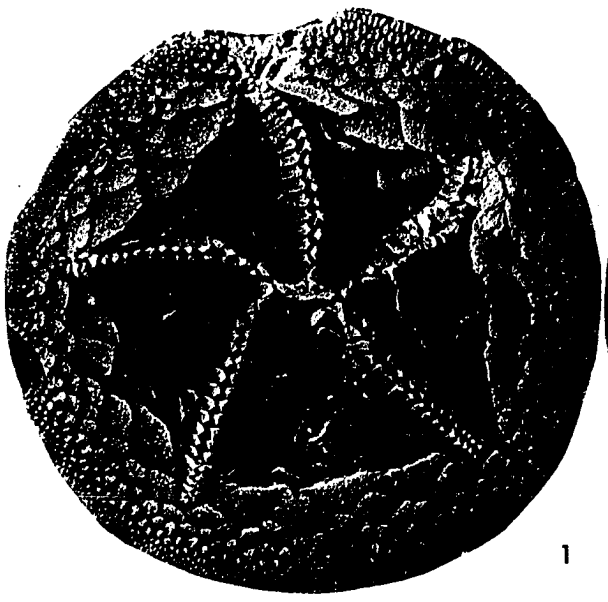
7-8. G.S.C. 1414-b.

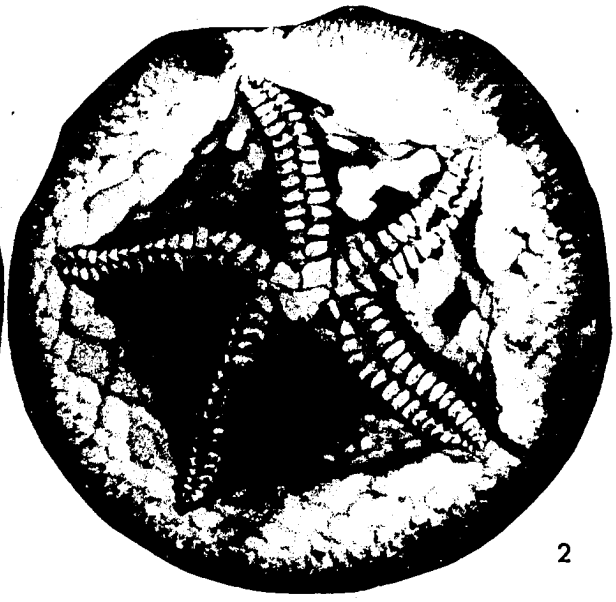
7. Oral surface, X2, whitened.
8. Oral area and ambulacra III-V, X5, in xylene.

9. R.O.M. 28178, small adult, oral surface, X5, whitened.

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PLATE 19


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PLATE 20

Cryptogoleus chapmani (Raymond), 1915

1. G.S.C. 3235-e, f, juveniles, oral surface, X25, whitened; e. on left, anterior edge of theca up (text fig. 18B), f. on right, anterior edge of theca to the left (text fig. 18A).

2-3. R.O.M. 160t-b-F, juvenile.

2. Oral surface, X20, whitened (text fig. 18C).

3. Oral surface, X20, in xylene.

4-5. G.S.C. 3235-C, juvenile.

4. Oral surface, X21, whitened.

5. Oral surface, X21, in xylene (text fig. 18D).

6-9. R.O.M. 28177, small adult.

6. Oral surface, X3.5, in xylene.

7. Oral surface, X3.5, whitened.

8. Ambulacrum III with proximal floorplates exposed where coverplates are missing, X10, in xylene (text fig. 17A).

9. Oblique view of part of peripheral rim distal to interambulacrum 3, X10, whitened.

10-11. U.S.N.M. S-3954 (lectotype of Agelacrinites rectiradiatus Shideler, 1918).

10. Oral surface, X4, whitened (text fig. 18E).

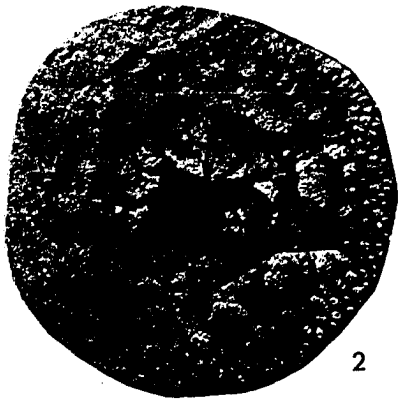
11. Oral region, X5, in xylene.

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PLATE 20



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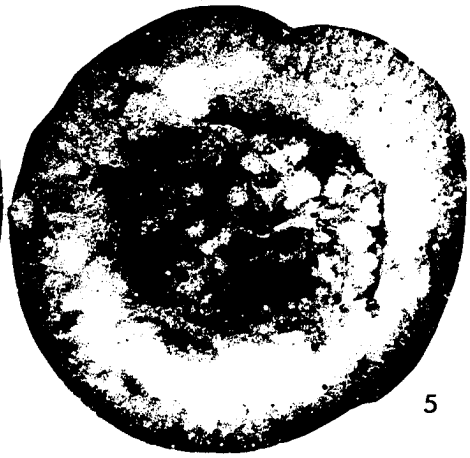
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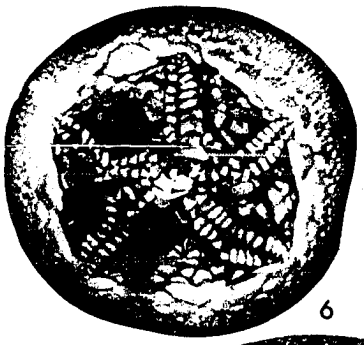
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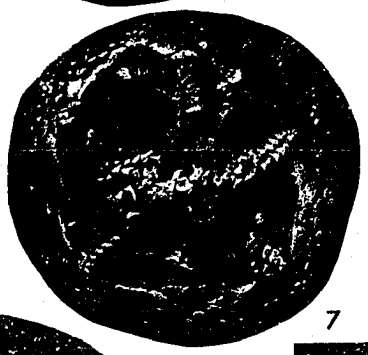
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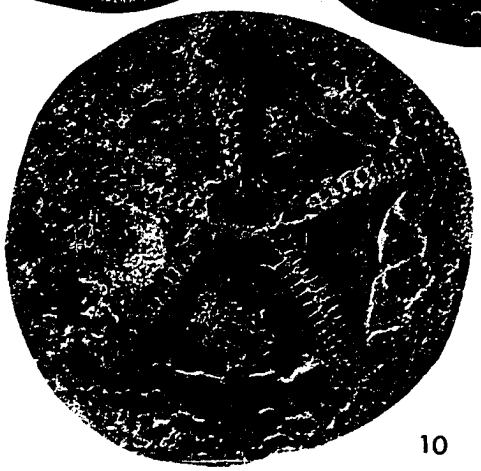
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PLATE 21

Cryptogoleus reticulatus Bell, *sp. nov.*

1-2. R.O.M. 28176, holotype.

1. Oral surface, X7, whitened.

2. Oral surface, X7, in xylene (text fig. 19A).

3-4. G.S.C. 5140, paratype.

3. Oral surface, X7, whitened.

4. Oral surface, X7, in xylene (text fig. 19B).

5. U.C.M.P. 35222-a, oral surface, X5, in xylene.

6-7. U.C.M.P. 35222-d.

6. Oral surface, X10, whitened.

7. Oral surface, X10, in xylene.

8-9. U.C.M.P. 35222-c.

8. Oral surface, X5, whitened.

9. Oral surface, X6, in xylene.

10-11. U.C.M.P. 35222-b.

10. Oral surface, X5, whitened.

11. Oral surface, X5, in xylene.

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PLATE 21



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PLATE 22

Cryptogoleus multibrachiatus (Raymond), 1915

1-3. G.S.C. 7789, holotype.

1. Oral surface, X8, whitened.

2. Oral surface, X8, in xylene (text fig. 20B).

3. Oral-ambulacral region, X12, in xylene.

4-5. U.S.N.M. S-3894-a.

4. Oral surface, X7, whitened.

5. Oral surface, X7, in xylene.

6-7. G.S.C. 7789-a.

6. Oral surface, X5, whitened.

7. Oral surface, X5, in xylene (text fig. 20A).

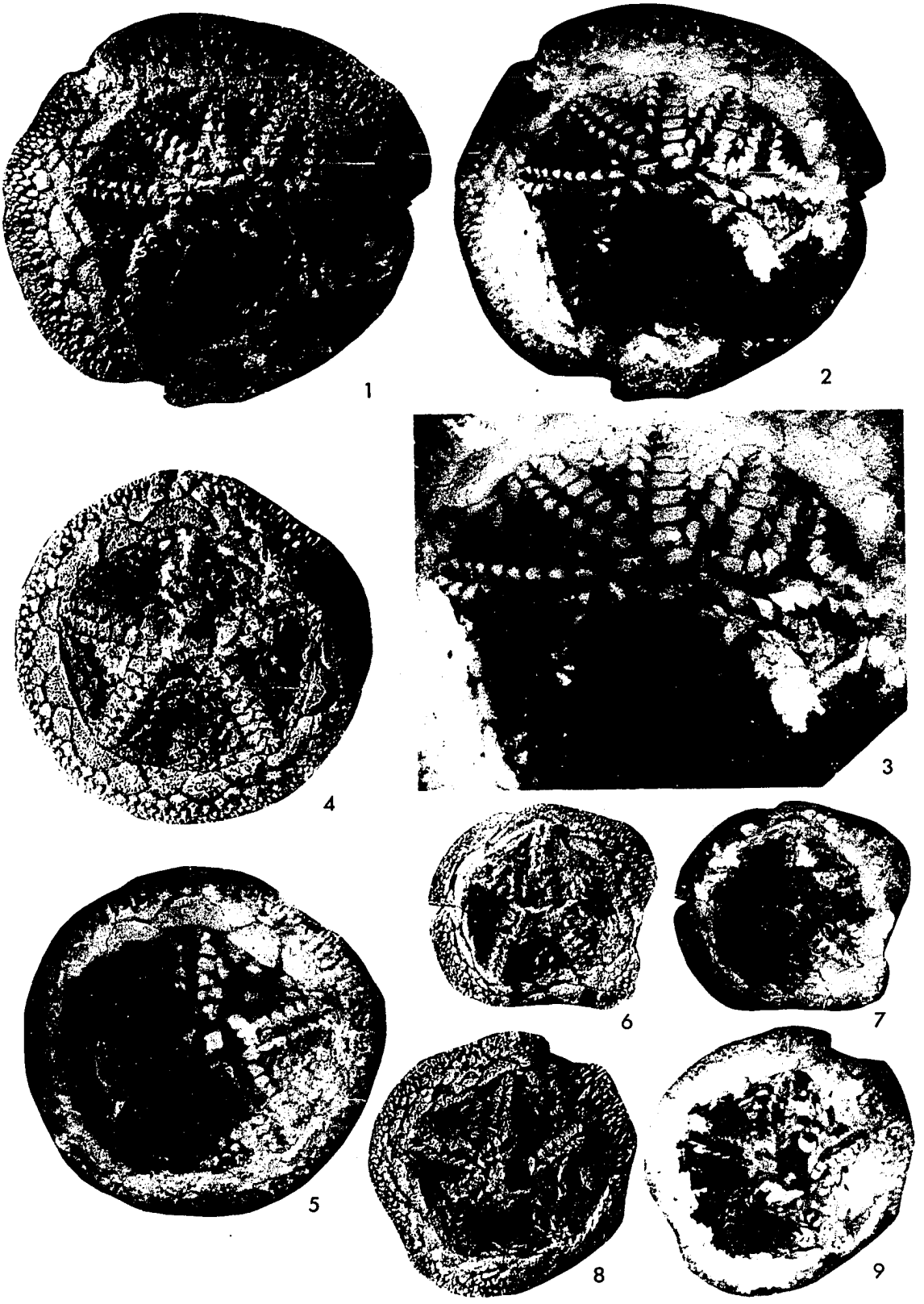
8-9. U.S.N.M. S-3894-b.

8. Oral surface, X5, whitened.

9. Oral surface, X5, in xylene.

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PLATE 22



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PLATE 23

Cryptogoleus youngi (Raymond), 1915 Fig. 1-3.

1-3. G.S.C. 3234, holotype.

1. Oral surface, X5, whitened.
2. Oral surface, X5, in xylene (text fig. 21).
3. Oral region and ambulacrum III, X10, in xylene.

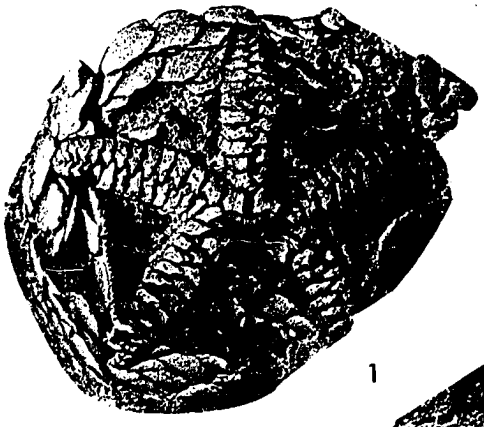
Cryptogoleus platys (Raymond), 1915 Fig. 4-7.

4-7. G.S.C. 7941, holotype.

4. Oral surface, X3, whitened.
5. Oral surface, X3, in xylene.
6. Oral region, X7, in xylene (text fig. 22B).
7. Ambulacrum IV, X7, in xylene (text fig. 22A).

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PLATE 23



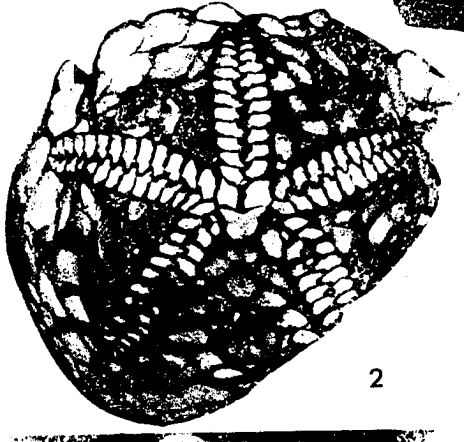
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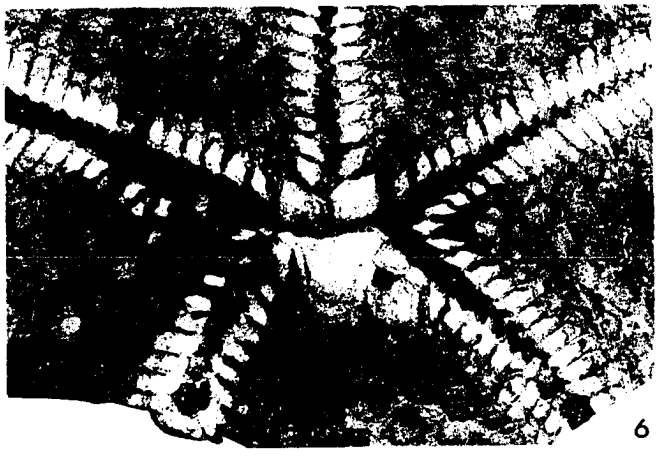
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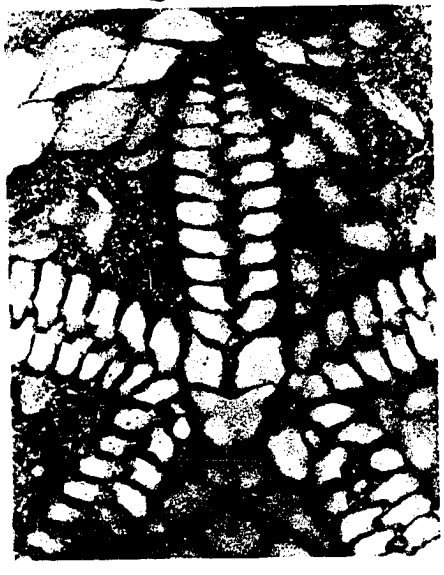
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PLATE 24

Isorophus cincinnatiensis (Roemer), 1851

1. A.M.N.H. 1194, oral surface, X3, whitened.

2-3. U.C.M.P. 34539.

2. Oral surface, X3, whitened.

3. Oral region, X6, whitened.

4-5. M.C.Z. 517.

4. Oral surface, X3, whitened.

5. Anal area, X10, whitened.

6-8. U.C.M.P. 26536.

6. Inner side of the oral surface, X5, whitened.

7. Inner side of the oral surface, X5, in xylene (text fig. 24B).

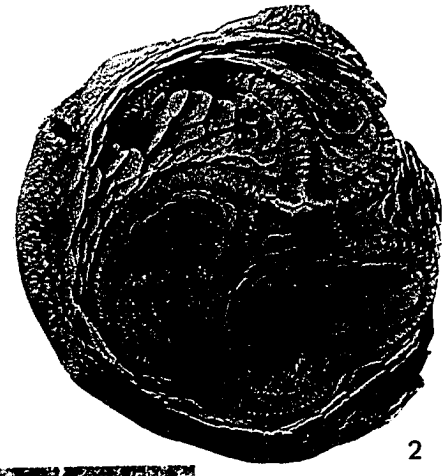
8. Oral frame and adjacent area, X10, whitened.

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PLATE 24



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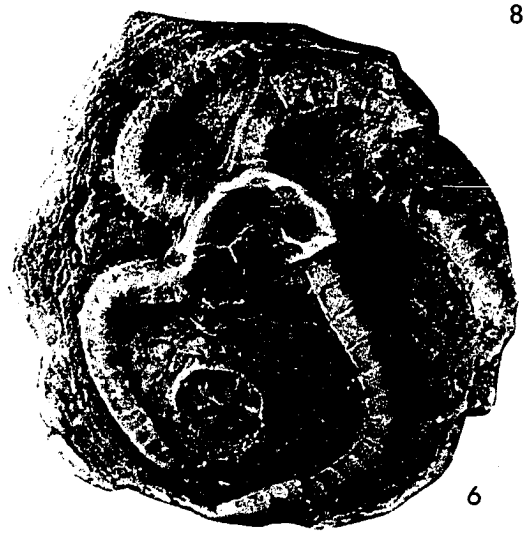
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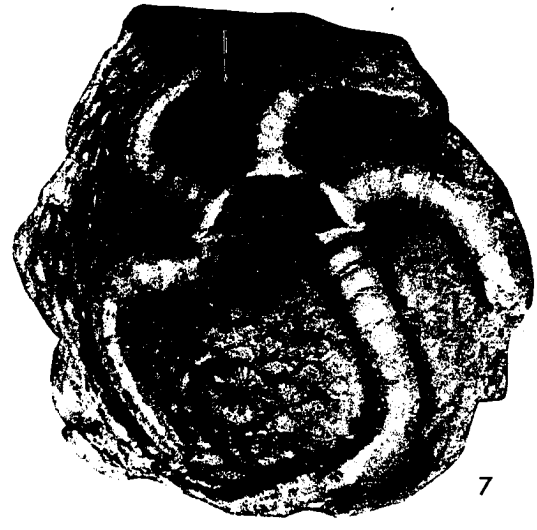
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PLATE 25

Isorophus cincinnatiensis (Roemer), 1851

1-2. A.M.N.H. 13266/1-x.

1. Inner side of the oral surface, X5, whitened.

2. Oral frame and adjacent areas, X10, whitened.

3-4. C.F.M.-U.C. 54068, young adult.

3. Inner side of the oral surface, X8, whitened.

4. Inner side of the oral surface, X8, in xylene (text fig. 24A).

5-6. U.S.N.M. 91838.

5. Inner side of the oral surface, X2, whitened.

6. Anterior section of peripheral rim and adjacent areas with ridges on basal surfaces of rim plates, X4, whitened.

7-8. A.M.N.H. 13266/1-r.

7. Inner side of the oral surface, X2, whitened.

8. Right anterior section of peripheral rim, X10, whitened. The proximal plates of the rim are tilted so that their basal surfaces are nearly vertical and the basal ridges are viewed end-on.

9. U.S.N.M. S-3900, geniculate plates of the peripheral rim which have been tilted backward to expose the inner side of the upper part of the plates; basal surfaces are now vertical and their ridges are viewed end-on, X6, whitened.

10-11. U.S.N.M. 40746-G.

10. Oral surface, X3, whitened.

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Plate 25 (cont.)

11. An ambulacrum with coverplates missing which exposes the secondary filling of the ambulacral tunnel and the upper sides of the lateral margins of the floorplates, X10, whitened.

12-14. U.C.M.P. 40474, segment of one ambulacrum and a few adjacent interambulacral plates.

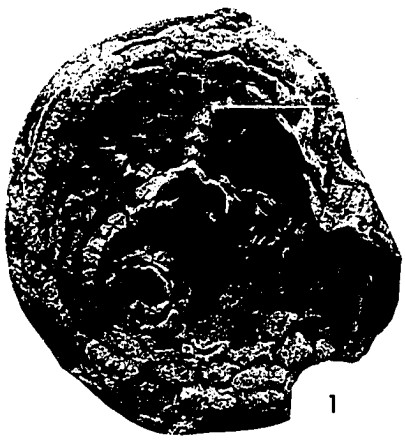
12. Oral surface, proximal end to right, X5, whitened.

13. Inner side of oral surface, proximal end to left, X5, whitened.

14. Oblique view, proximal end to left, X5, in xylene.

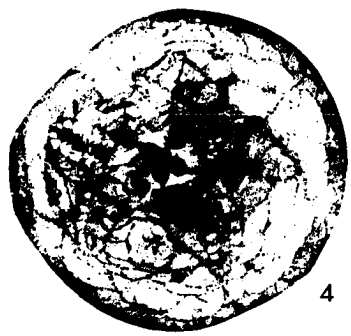
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PLATE 25

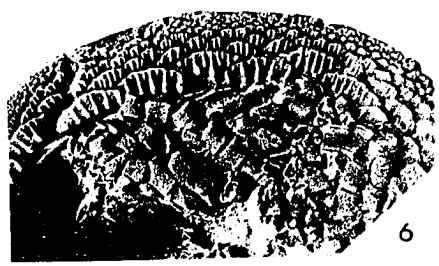

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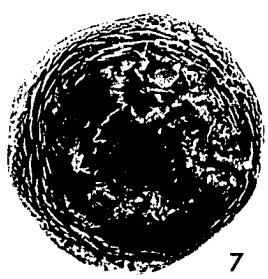

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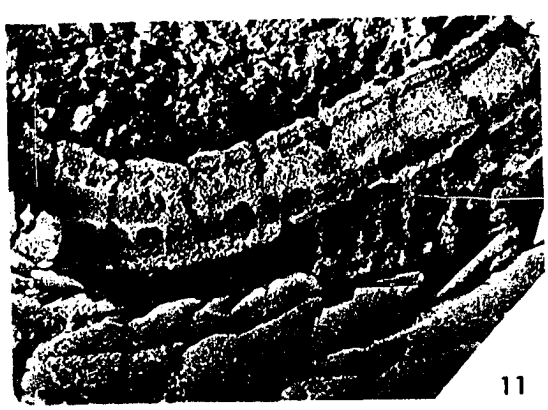

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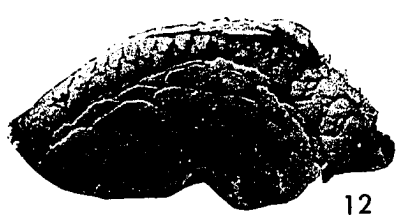

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PLATE 26

Isorophus cincinnatiensis (Roemer), 1851

1-2. U.S.N.M. 91839-B.

1. Oral surface, X5, whitened.

2. Oral surface, X5, in xylene (text fig. 25A).

3-4. U.S.N.M. 91839-A (holotype of Isorophus tennesseensis Bassler, 1936).

3. Oral surface, X5, whitened.

4. Oral surface, X5, in xylene (text fig. 25B).

5-6. U.S.N.M. 40746-H.

5. Inner side of the oral surface, X5, whitened. Floorplates are missing from ambulacrum V.

6. Inner side of anal structure, X10, whitened.

7-8. C.F.M.-U.C. 1004, gerontic adult (may be one of the specimens of the type series of Agelacrinus holbrooki James, 1878).

7. Oral surface, X2, whitened.

8. Ambulacrum I, X6, whitened (text fig. 25D).

9-12. U.S.N.M. 40744, gerontic adult.

9. Oral surface, X2, whitened.

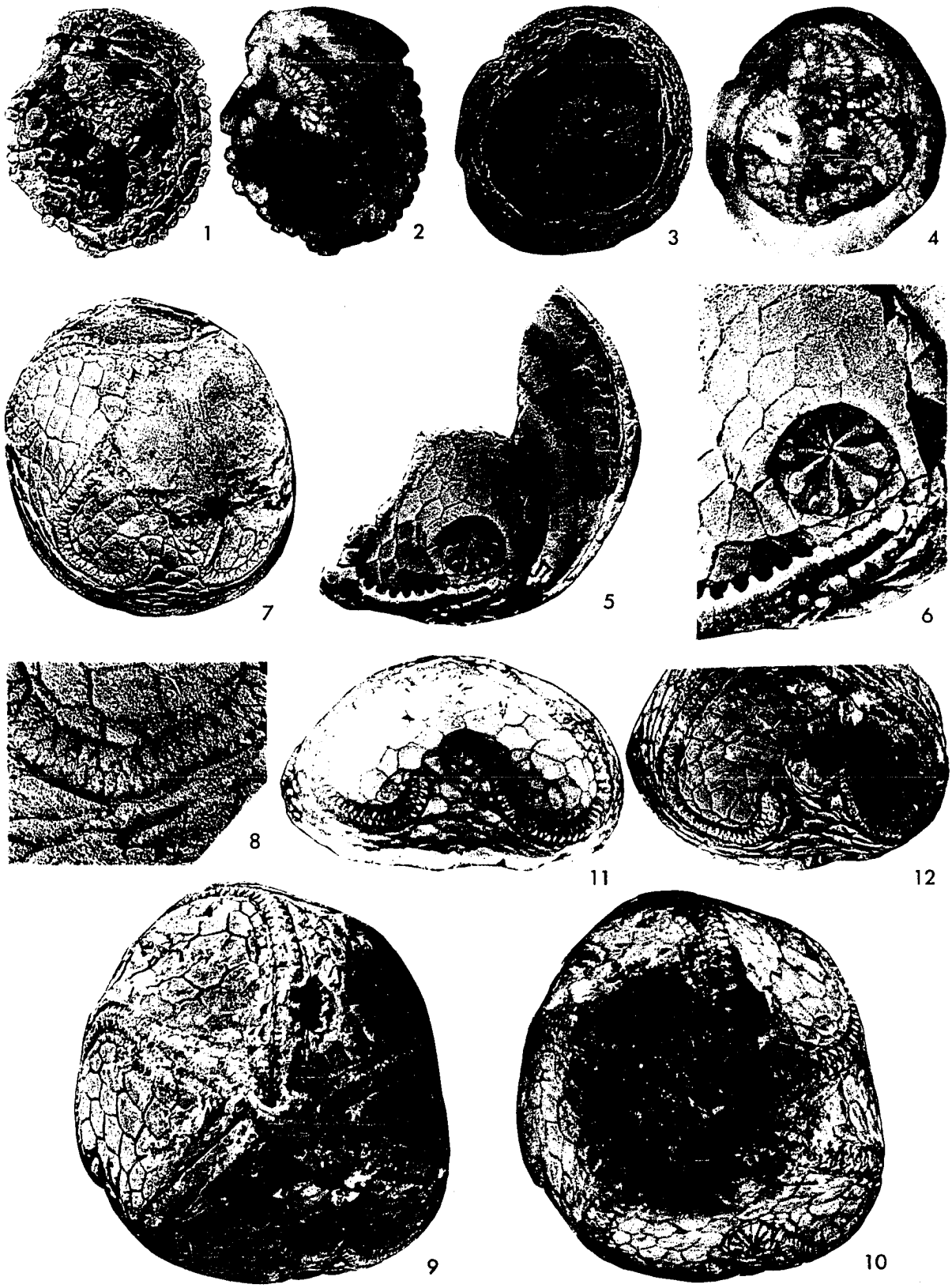
10. Oral surface, X2, in xylene.

11. Lateral view of posterior end of theca, X2, in xylene.

12. Oblique view of posterior third of theca, X2, whitened.

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PLATE 26



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PLATE 27

Isorophus cincinnatiensis (Roemer), 1851

1-3. A.M.N.H. 13269, young adult.

1. Oral surface, X5, whitened.

2. Oral surface, X5, in xylene.

3. Oral region, X10, whitened.

4-5. A.M.N.H. 13268/1-z.

4. Oral surface, X3, whitened.

5. Oral surface, X3, in xylene.

6-7. C.F.M.-PE 16328.

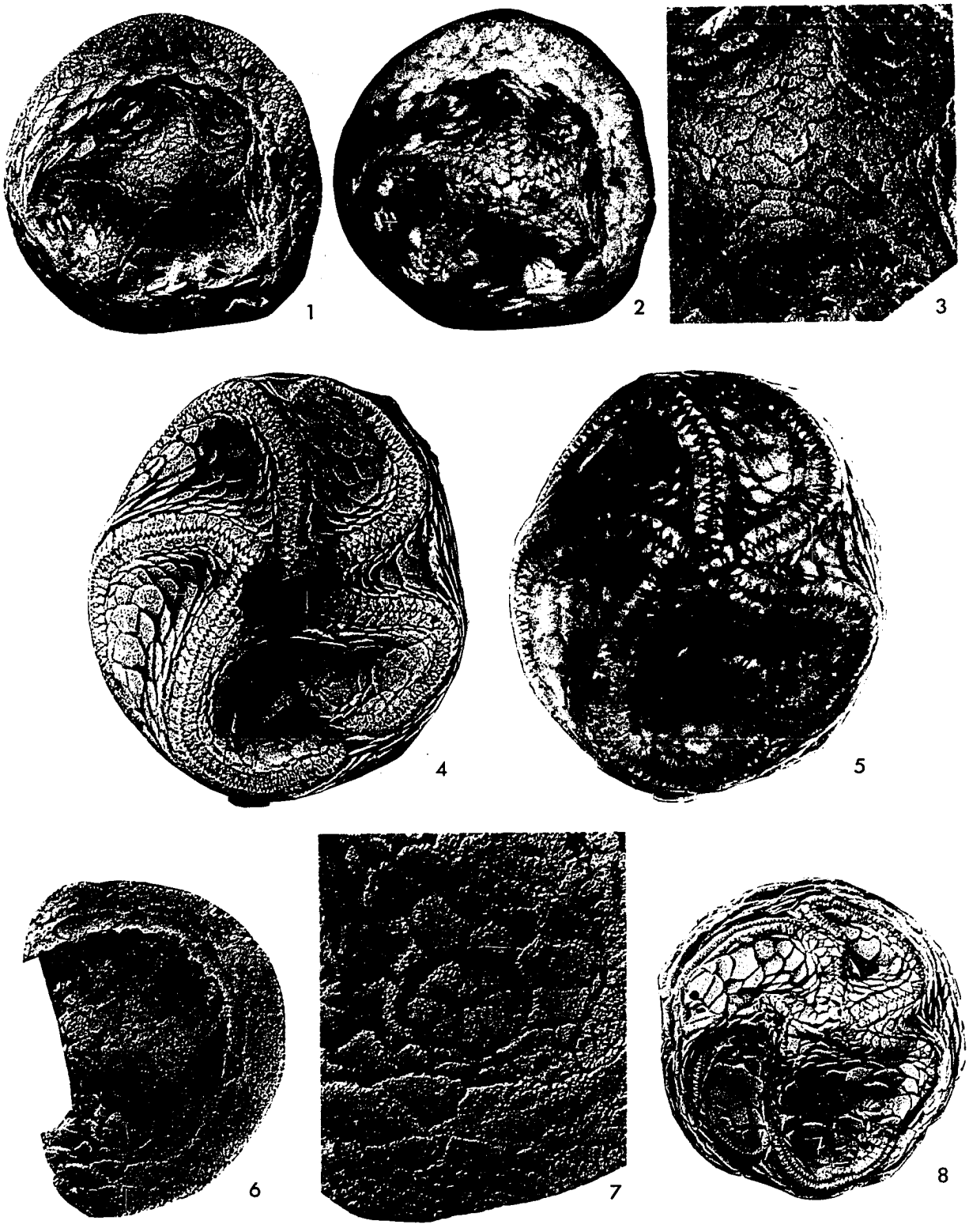
6. Oral surface, X6, whitened.

7. Anal area, X15, whitened.

8. U.C.M.P. 7781, gerontic adult, oral surface, X2, whitened. Cylindrical hole in large, distal plate of interambulacrum 2 appears to be a boring.

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PLATE 27



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PLATE 28

Isorophus cincinnatiensis (Roemer), 1851

1-2. U.C.M.P. 40467.

1. Oral surface, X2, whitened.

2. Oral surface, X2, in xylene.

3-4. U.C.M.P. 40468.

3. Oral surface, X3, whitened.

4. Oral surface, X3, in xylene.

5-6. U.C.M.P. 40469.

5. Oral surface, X3, whitened.

6. Ambulacrum V and adjacent structures, X6, whitened.

7-9. U.C.M.P. 40470.

7. Oral surface, X3, whitened.

8. Oral surface, X3, in xylene (text fig. 1C, 23B).

9. Oral region, X6, in xylene.

10. U.C.M.P. 40473, oral surface, X2, whitened.

11. U.C.M.P. 40472, oral surface with burrow filling in the disrupted right side of theca, X2, whitened.

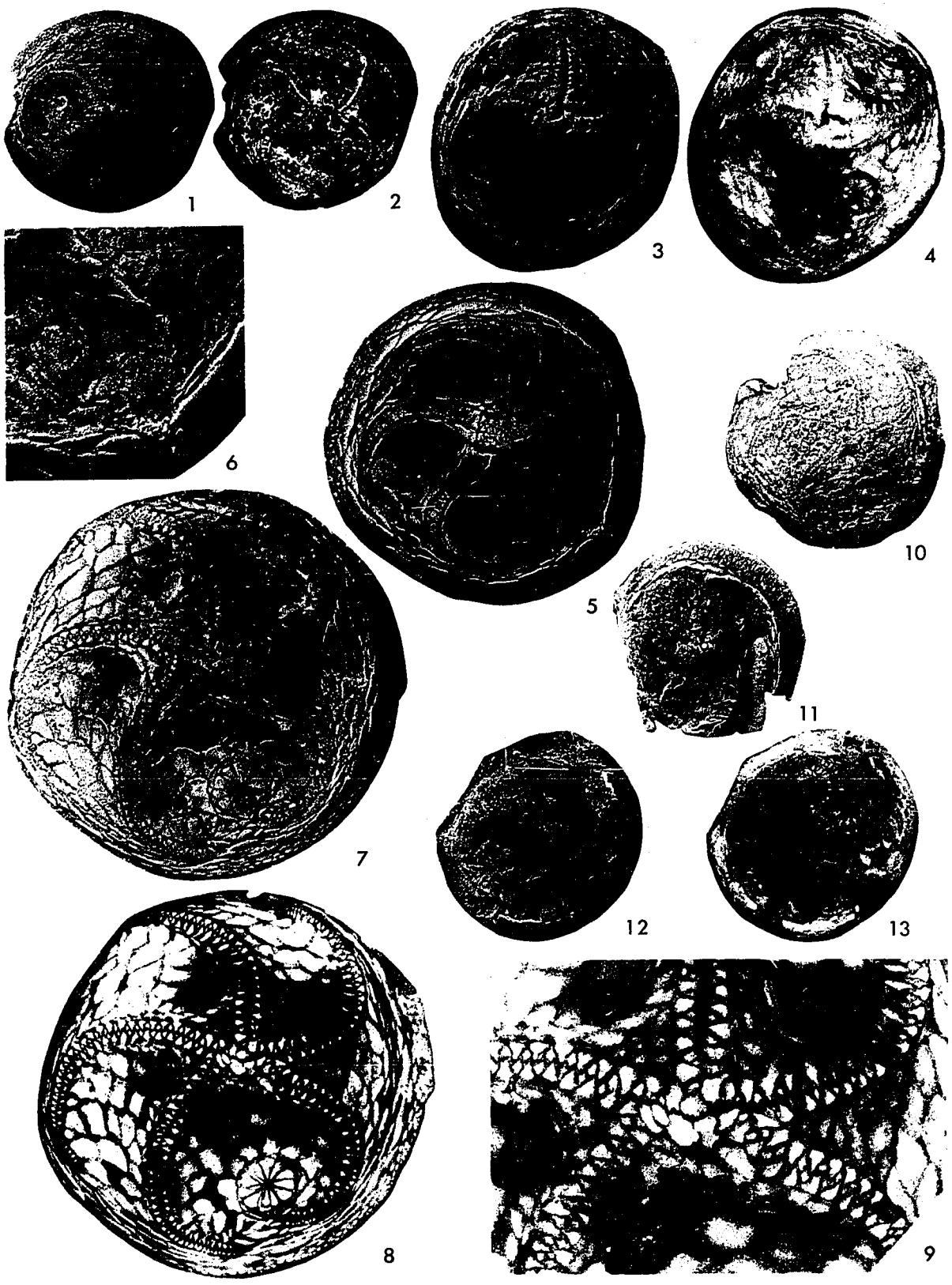
12-13. U.C.M.P. 40471.

12. Oral surface with burrow filling in the disrupted posterior part of theca, X2, whitened.

13. Oral surface with burrow filling in the disrupted posterior part of theca, X2, in xylene.

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PLATE 28



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PLATE 29

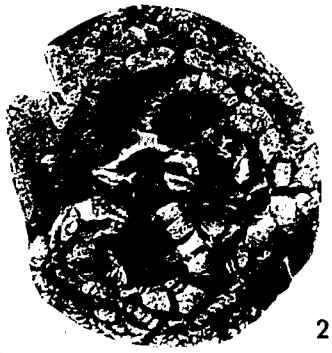
Isorophus austini (Foerste), 1914

1. U.S.N.M. 70162-C-1, lectotype, oral surface, X6, whitened.
2. U.S.N.M. 70162-B, lectoparatype, inner side of the oral surface, X6, whitened.
3. U.S.N.M. 70162-A, lectoparatype, oral surface, X6, whitened.
4-5. U.S.N.M. S-3961.
   4. Inner side of the oral surface, X6, whitened.
   5. Inner side of the oral surface, X6, in xylene.
6-8. U.S.N.M. 70162-D.
   6. Oral surface, X10, whitened.
   7. Oral surface, X10, in xylene (text fig. 26).
   8. Oral-ambulacral region, X15, whitened.
9. U.S.N.M. 70162-C-3, lectoparatype, oral surface, X6, whitened.
10. U.S.N.M. S-3963-B, oral surface, X4, whitened.
11. U.S.N.M. S-3963-C, oral surface, X5, whitened.

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PLATE 29

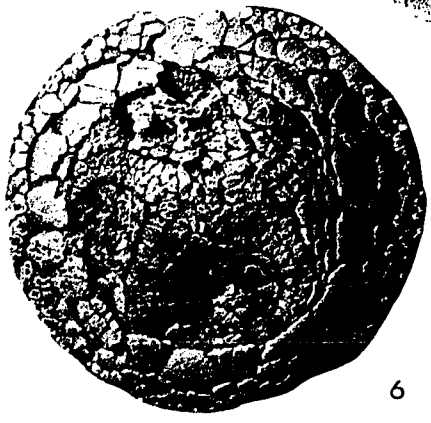

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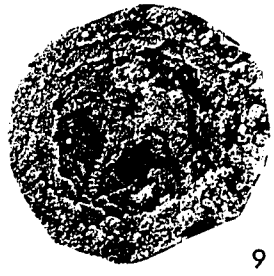

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PLATE 30

Isorophus austini (Foerste), 1914 Fig. 1-2.

1. U.S.N.M. 91841, oral surface, X6, whitened.

2. U.S.N.M. S-3963-A, oral surface, X6, whitened.

Isorophus warrenensis (James), 1883 Fig. 3-9.

3. U.S.N.M. S-3957-A, lectotype, oral surface, X4, whitened.

4-5. U.S.N.M. S-3957-D, lectoparatype.

4. Oral surface, X4, whitened.

5. Oral surface, X4, in xylene (text fig. 27B).

6. U.S.N.M. S-3957-E, lectoparatype, oral surface, X4, whitened (text fig. 27C).

7. U.S.N.M. 70165, oral surface, X3, whitened.

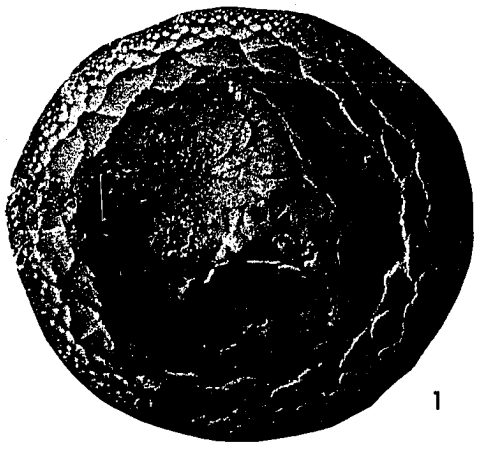
8-9. U.S.N.M. S-3957-C, lectoparatype.

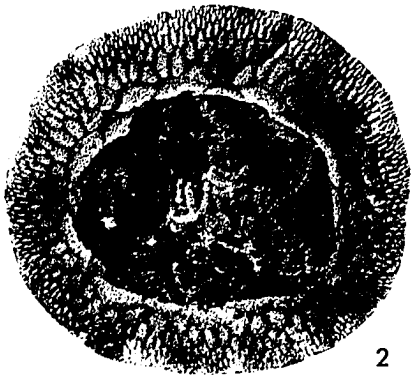
8. Oral surface, X5, whitened (text fig. 27A).

9. Oral-ambulacral region, X10, whitened.

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PLATE 30


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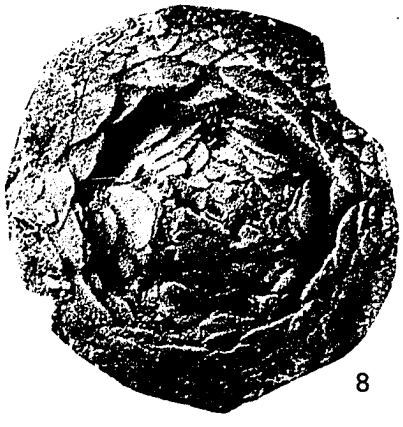

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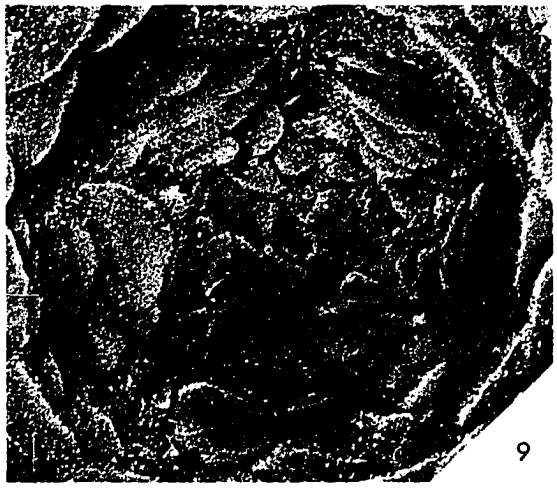

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PLATE 31

Isorophusella incondita (Raymond), 1915

1-3. G.S.C. 1409-A, holotype.

1. Oral surface, X4, whitened.

2. Oral surface, X4, in xylene (text fig. 28B).

3. Oral region, X9, in xylene (text fig. 28A).

4-5. G.S.C. 1409-B, paratype (1).

4. Oral surface, X6, whitened.

5. Oral surface, X6, in xylene.

6-7. G.S.C. 1409-D, paratype (3).

6. Oral surface, X4, whitened.

7. Oral surface, X4, in xylene.

8-10. G.S.C. 1409-C, paratype (2).

8. Oral surface, X6, whitened.

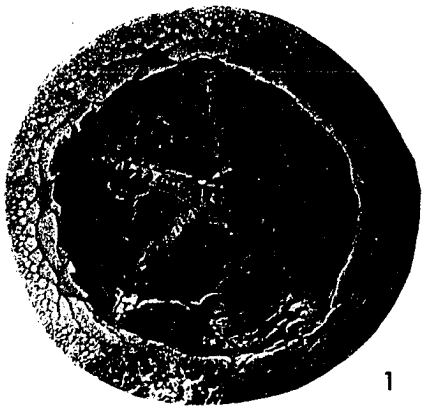
9. Oral surface, X6, in xylene.

10. Oral-ambulacral region, X10, in xylene (text fig. 29A).

11. U.S.N.M. 42114-A-1, advanced juvenile (holotype of Hemicystites paulianus Bassler, 1936), oral surface, X10, whitened (text fig. 29D).

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PLATE 31


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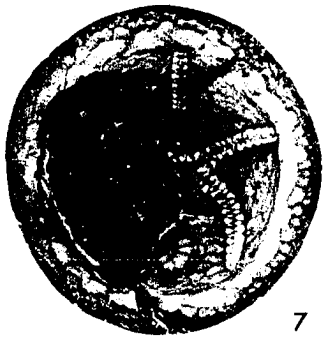

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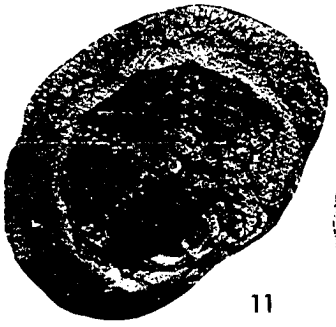

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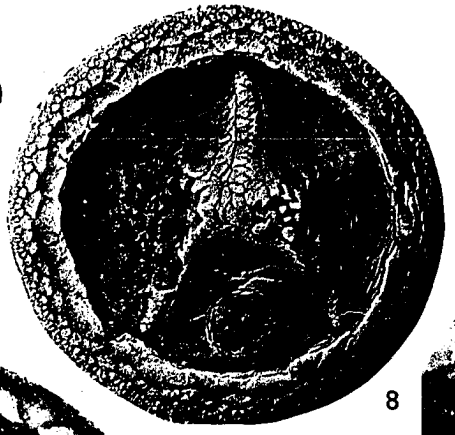

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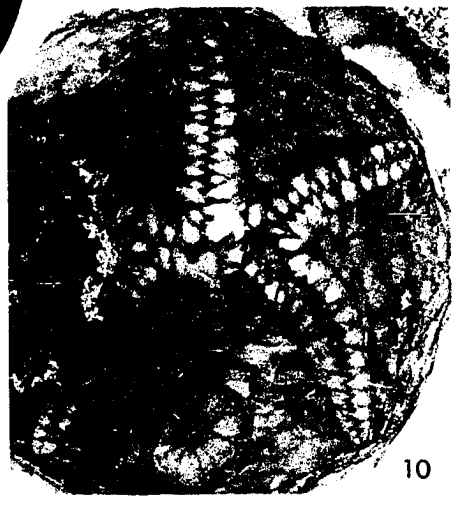

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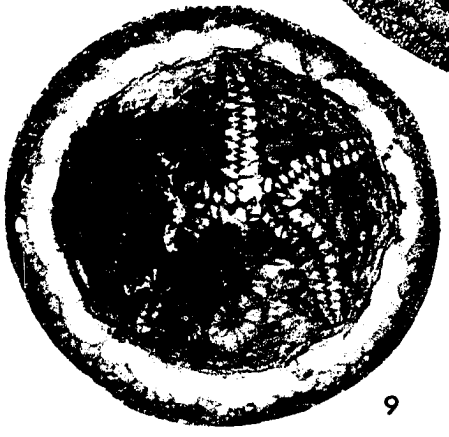

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PLATE 32

Isorophusella incondita (Raymond), 1915

1-3. M.C.Z. 105 (holotype of Carneyella raymondi Clark, 1919).

1. Oral surface, X8, whitened (text fig. 29E).
2. Oral-ambulacral region, X12, whitened.
3. Anterior two-thirds of oral-ambulacral region, X12, in xylene.

4-5. U.C.M.P. 40475.

4. Section view of oral surface exposed by etching, X4, whitened.
5. Section view of oral surface exposed by etching, X4, in xylene (text fig. 29B).

6-7. R.O.M. 160t-h.

6. Oral surface, X4, whitened.
7. Anal structure and adjacent region, X20, whitened.

8-9. R.O.M. 18873-A.

8. Oral surface, X5, whitened.
9. Ambulacrum I with small posterior branch, X12, in xylene (text fig. 29C).

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PLATE 32



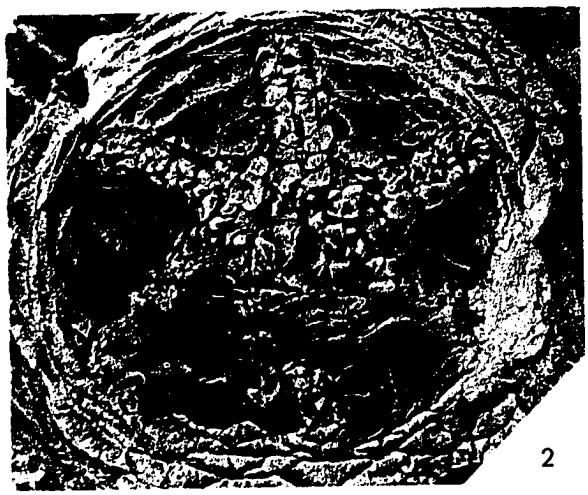
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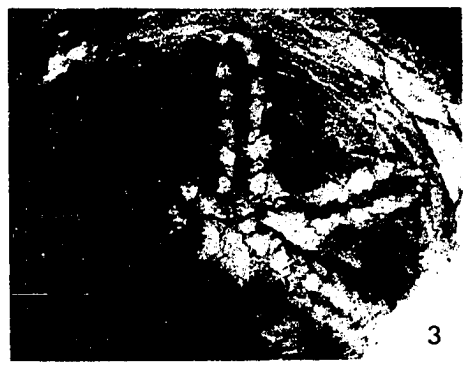
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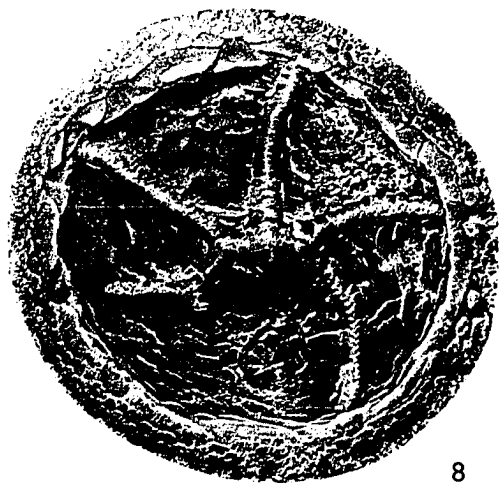
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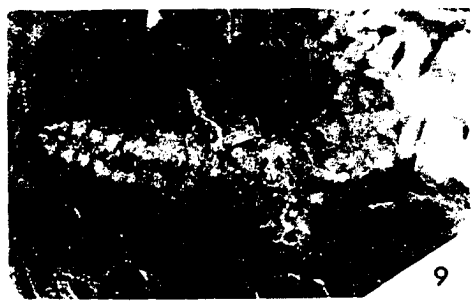
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PLATE 33

Isorophusella incondita (Raymond), 1915

1. R.O.M. 160t-b-E, very young juvenile, oral surface, X40, whitened (text fig. 30A).

2. N.Y.S.M. 12775, very young juvenile, oral surface, X35, whitened (text fig. 30B).

3-4. R.O.M. 160t-c-16, young juvenile.

3. Oral surface, X25, whitened.

4. Oral surface, X25, in xylene (text fig. 30C).

5-6. R.O.M. 160t-c-12, juvenile.

5. Oral surface, X25, whitened.

6. Oral surface, X25, in xylene (text fig. 30D).

7. R.O.M. 160t-c-3, juvenile, oral surface, X20, in xylene (text fig. 30E).

8-9. R.O.M. 160t-c-11, juvenile.

8. Oral surface, X15, whitened.

9. Oral surface, X15, in xylene (text fig. 30F).

10. R.O.M. 160t-b-D, juvenile, oral surface, X15, whitened (text fig. 31A).

11-12. R.O.M. 160-c-4, juvenile.

11. Oral surface, X15, whitened.

12. Oral surface, X15, in xylene (text fig. 31B).

13-14. R.O.M. 160t-c-8, juvenile.

13. Oral surface, X15, whitened.

14. Oral surface, X15, in xylene (text fig. 31C).

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Plate 33 (cont.)

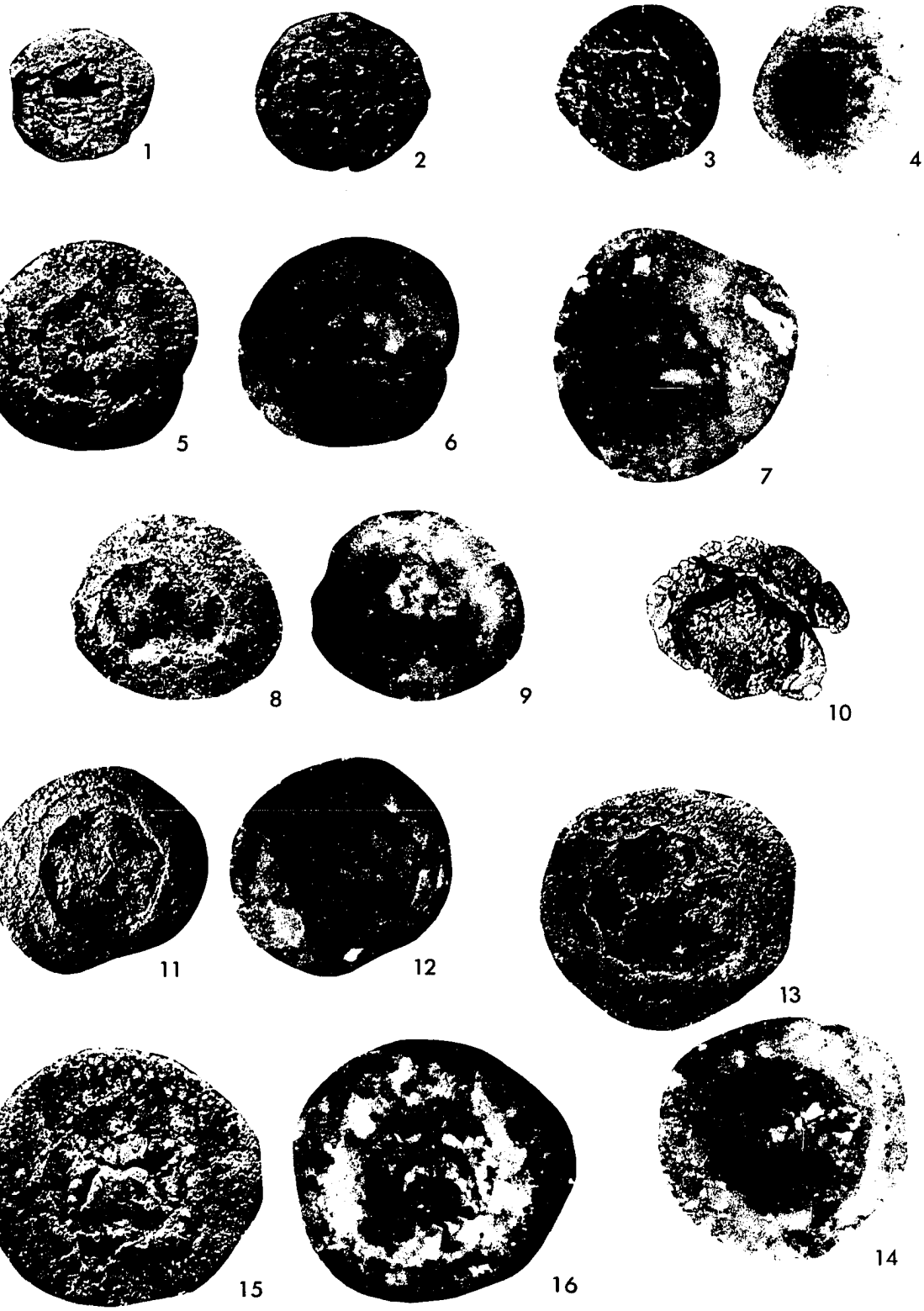
15-16. G.S.C. 3235-D, juvenile.

15. Oral surface, X15, whitened.

16. Oral surface, X15, in xylene (text fig. 31D).

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PLATE 33



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PLATE 34

Isorophusella incondita (Raymond), 1915

1-2. R.O.M. 160t-c-9, juvenile.

1. Oral surface, X15, whitened.

2. Oral surface, X15, in xylene (text fig. 31E).

3-4. R.O.M. 160t-c-15, juvenile.

3. Oral surface, X15, whitened.

4. Oral surface, X15, in xylene (text fig. 31F).

5-6. R.O.M. 160t-c-10, juvenile.

5. Oral surface, X15, whitened.

6. Oral surface, X15, in xylene (text fig. 32A).

7-8. R.O.M. 160t-b-C, advanced juvenile.

7. Oral surface, X15, whitened (text fig. 32B).

8. Oral surface, X15, in xylene.

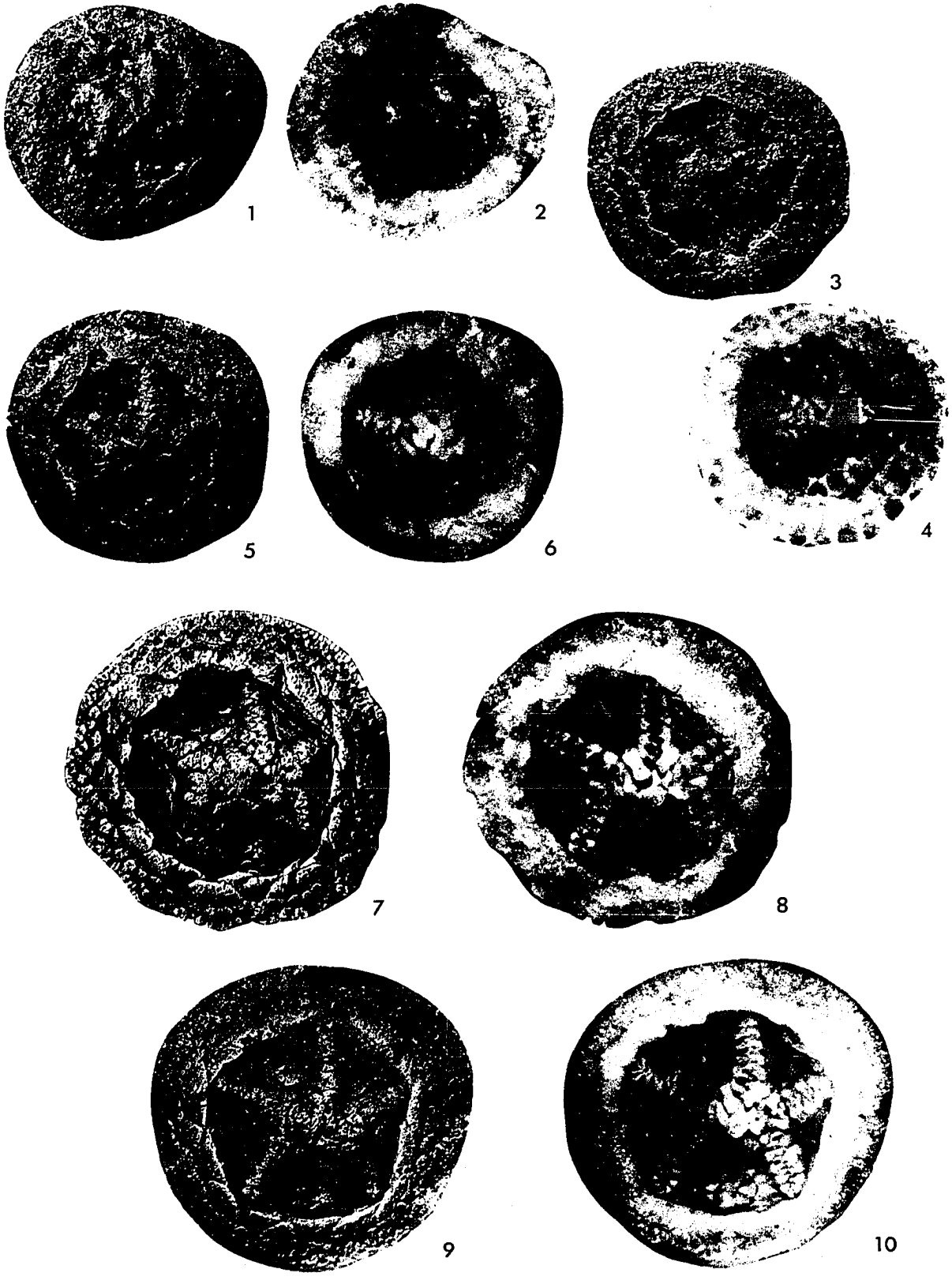
9-10. N.Y.S.M. 12776, advanced juvenile.

9. Oral surface, X11, whitened.

10. Oral surface, X11, in xylene.

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PLATE 34



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PLATE 35

Isorophusella incondita (Raymond), 1915 Fig. 1-4.

1-2. R.O.M. 160t-b-B, young adult.

1. Oral surface, X8, whitened.

2. Oral surface, X8, in xylene.

3-4. R.O.M. 160t-b-A, adult.

3. Oral surface, X10, whitened.

4. Oral-ambulacral region, X15, in xylene.

Isorophusella trentonensis (Bassler), 1936 Fig. 5-6.

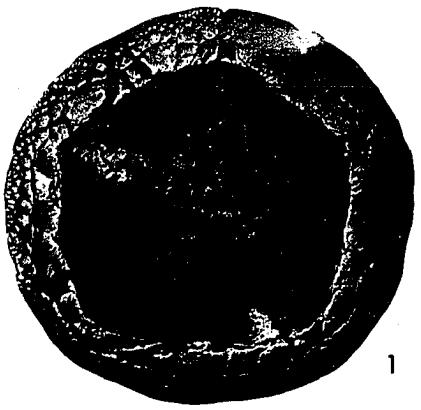
5-6. U.S.N.M. 91843, holotype.

5. Oral surface, X7, whitened.

6. Oral surface, X7, in xylene (text fig. 33).

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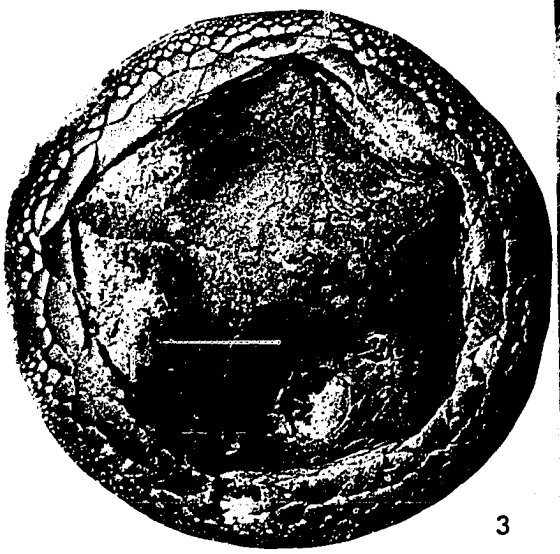
PLATE 35



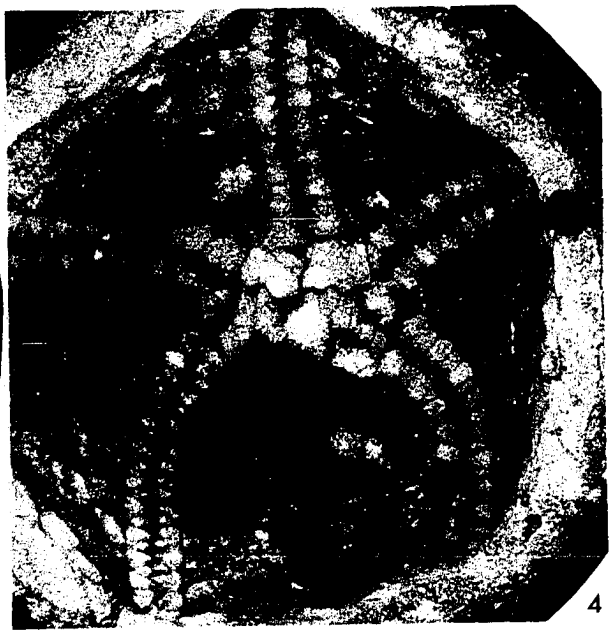
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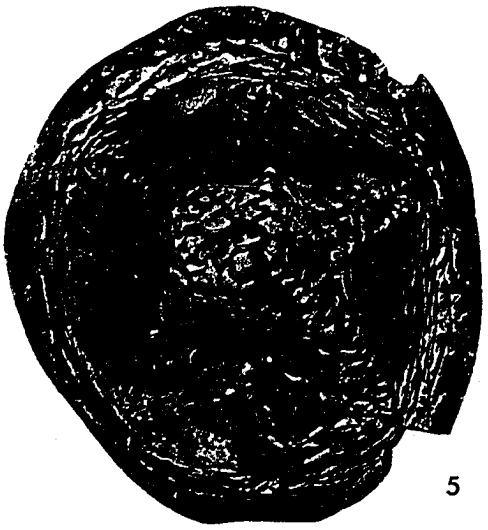
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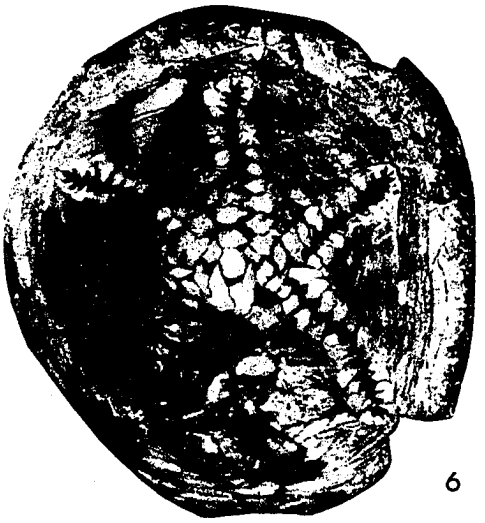
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PLATE 36

Isorophusella pleiadae (Sinclair and Bolton), 1965

1-3. G.S.C. 14680-1, holotype.

1. Inner side of the oral surface, X10, whitened (text fig. 34).

2. Oral frame, ambulacra II-IV and adjacent areas, X15, whitened.

3. Inner side of the oral surface, X9, in xylene.

4. G.S.C. 14680 (1-7) as preserved on the filling of the siphuncular sheath of an endoceroid endocone (cephalopod), X1, whitened.

5. G.S.C. 14680-2, paratype, inner side of the oral surface, X8, whitened.

6. G.S.C. 14680-3, paratype, inner side of the oral surface, X6, whitened.

7. G.S.C. 14680-4, paratype, inner side of the oral surface, X9, whitened.

8. G.S.C. 14680-5, paratype, inner side of the oral surface, X7, whitened.

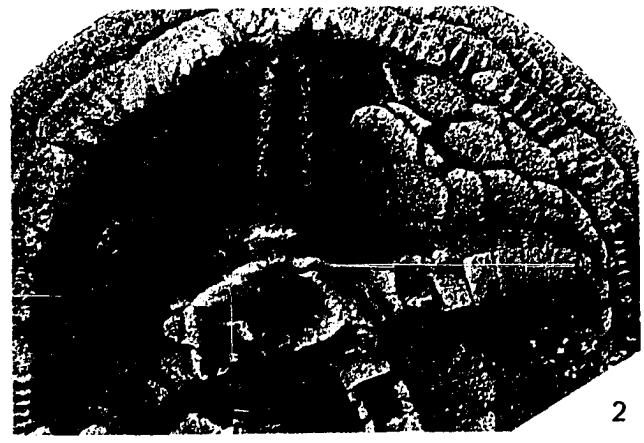
9. G.S.C. 14680-6, paratype, inner side of the oral surface, X8, whitened.

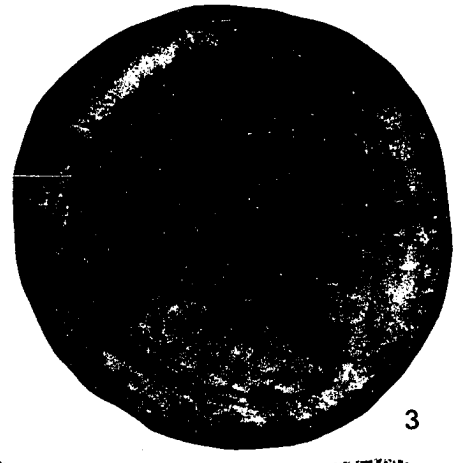
10. G.S.C. 14680-7, paratype, inner side of the oral surface, X8, whitened.

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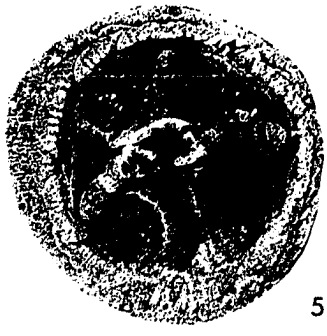
PLATE 36


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PLATE 37

Hemicystites parasiticus Hall, 1852

1. Unretouched copy of Bassler's (1936, pl. 4, fig. 5) photograph of the holotype, oral surface, X6, apparently whitened.
2. U.S.N.M. S-3183-A, oral surface, X7, whitened (text fig. 35B).
3. U.S.N.M. S-3183-B, oral surface, X9, whitened (text fig. 35A).
4. U.S.N.M. S-3183-C, oral surface, X8, whitened.
5. U.S.N.M. S-3183-E, oral surface, X8, whitened.
6. U.S.N.M. S-3183-F, oral surface, X10, whitened.
7. U.S.N.M. S-3183-D-2, inner side of the oral surface, X10, whitened.
8. U.S.N.M. S-3183-D-1, inner side of the oral surface, X6, whitened.
9. U.S.N.M. S-3183-D-3, inner side of the oral surface, X6 whitened.

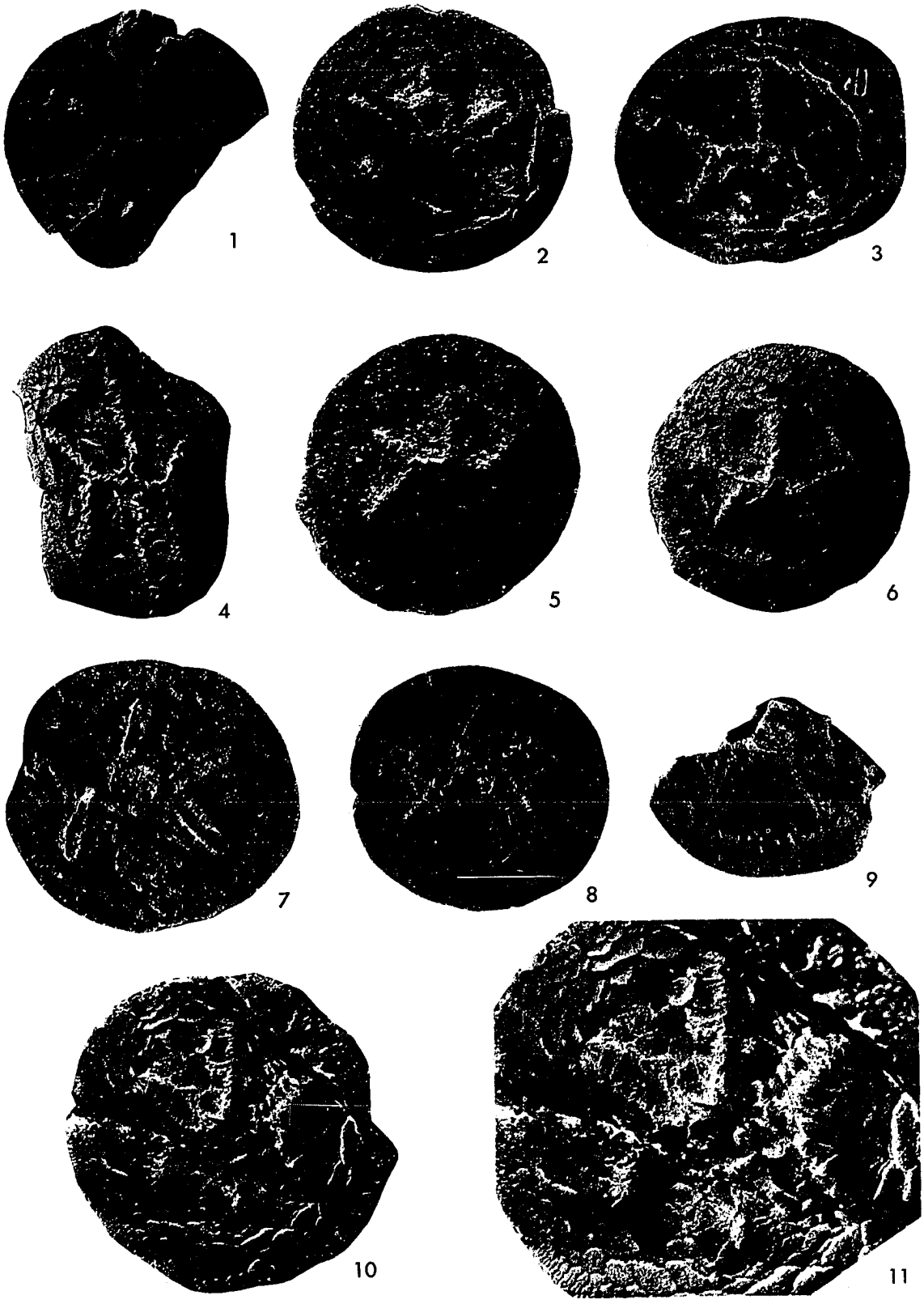
10-11. U.C.M.P. 37217.

10. Oral surface, X8, whitened.

11. Oral-ambulacral region, X12, whitened.

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PLATE 37



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PLATE 38

Rectitriordo kirkfieldensis Bell, *gen. et sp. nov.*

1-6. U.C.M.P. 40476, holotype.

1. Oral surface, X2, whitened.
2. Oral surface, X2, in xylene (text fig. 36A).
3. Oblique view of right anterior section of peripheral rim, X4, whitened (text fig. 37A).
4. Oral region, anterior toward upper right corner of the photograph, X7, in xylene (text fig. 36B).
5. Ambulacrum II and adjacent areas, X8, in xylene.
6. Distal part of ambulacrum IV, X9, in xylene.

7-8. U.S.N.M. S-3894-D, paratype.

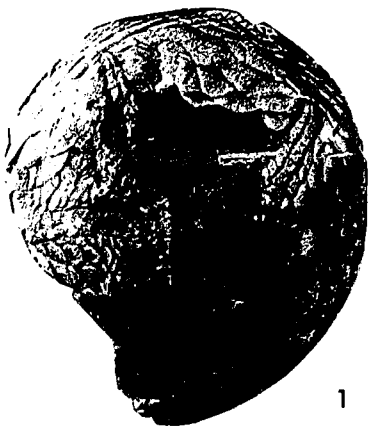
7. Oral surface, X5, whitened.
8. Oral surface, X5, in xylene.

9-10. U.S.N.M. S-3889-G, paratype.

9. Oral surface, X5, whitened.
10. Oral surface, X5, in xylene (text fig. 37B).

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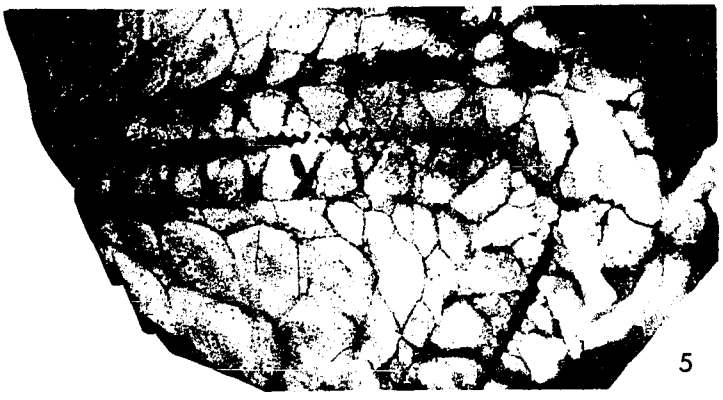
PLATE 38

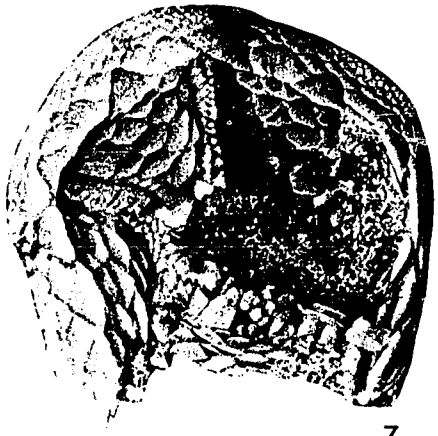

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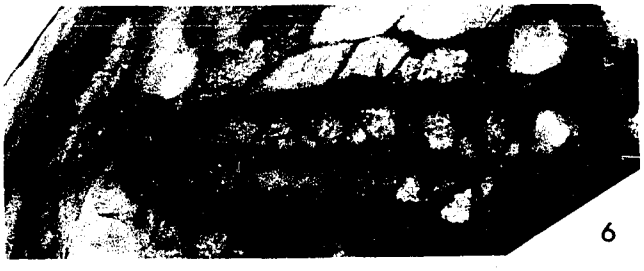

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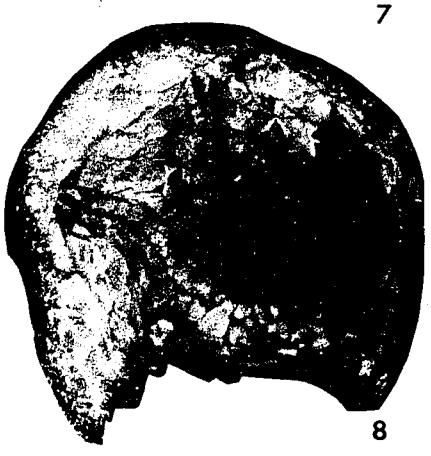

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PLATE 39

Curvitriordo kentuckyensis (Bassler), 1936 Fig. 1-7.

1-5. U.S.N.M. S-3967-A, holotype.

1. Oral surface, X2, whitened.
2. Oral surface, X2, in xylene.
3. Oral region, anterior somewhat left of center of the photograph, X6, in xylene (text fig. 38).
4. Oral region, anterior slightly left of center of the photograph, X6, whitened.
5. Oblique view of the left posterior part of the peripheral rim, X6, whitened.

6-7. U.S.N.M. S-3967-B, paratype.

6. Oral surface, X2, whitened.
7. Oral surface, X2, in xylene.

Curvitriordo shideleri (Bassler), 1936 Fig. 8-9.

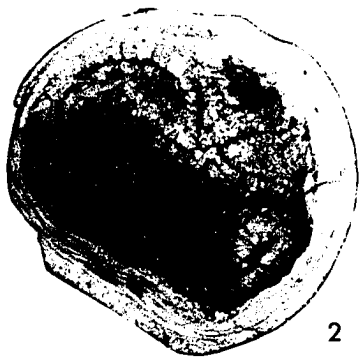
8-9. U.S.N.M. S-3958, holotype.

8. Oral surface, X4, whitened.
9. Oral surface, X5, in xylene (text fig. 39).

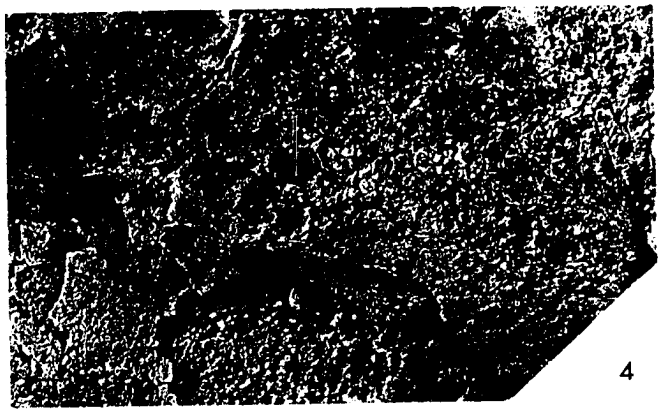
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PLATE 39

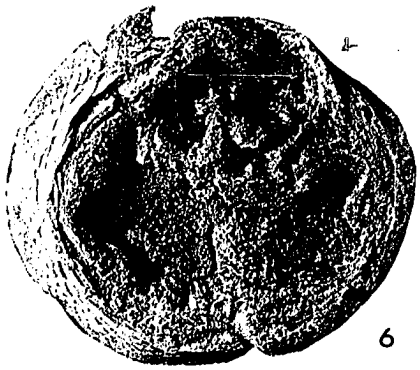

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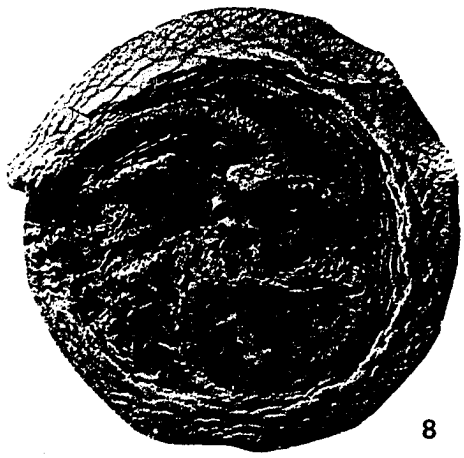

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PLATE 40

Agelacrinites hamiltonensis Vanuxem, 1842

1-2. N.Y.S.M. 362-A, lectotype.

1. Oral surface, X3, whitened latex pull (text fig. 1D, 40A).

2. Oral region, X8, whitened latex pull (text fig. 40B).

3. N.Y.S.M. 362-E, juvenile, lectoparatype (4), oral surface, X5, whitened latex pull (text fig. 41A).

4. N.Y.S.M. 362-D, juvenile, lectoparatype (3), oral surface, X5, whitened latex pull (text fig. 41C).

5. N.Y.S.M. 362-C, lectoparatype (2), oral surface, X4, whitened latex pull (text fig. 41B).

6. N.Y.S.M. 362-B, lectoparatype (1), oral surface, X2, whitened latex pull (text fig. 41E).

7. U.S.N.M. 85190-A, oral surface, X3, whitened latex pull (text fig. 41D).

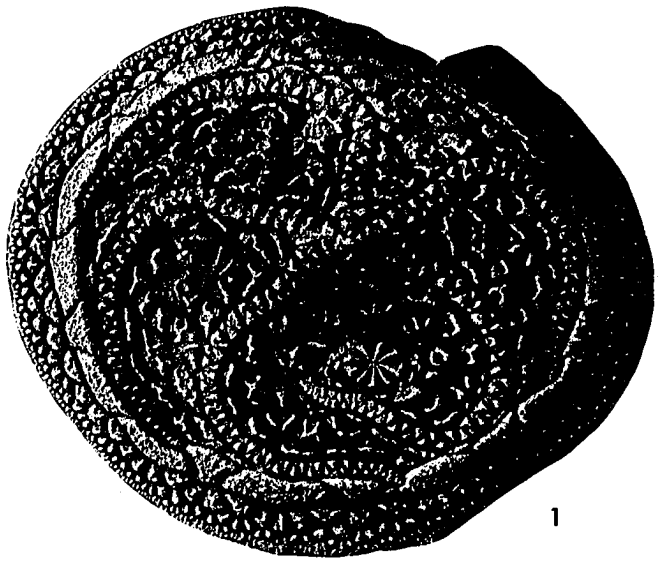
8-9. U.S.N.M. 85190-B, the specimen retains some anterior plates whereas other plates are gone; this gives the viewer a partial composite of both the inner and the exterior side of the oral surface.

8. Composite view of oral surface, X3, whitened latex pull.

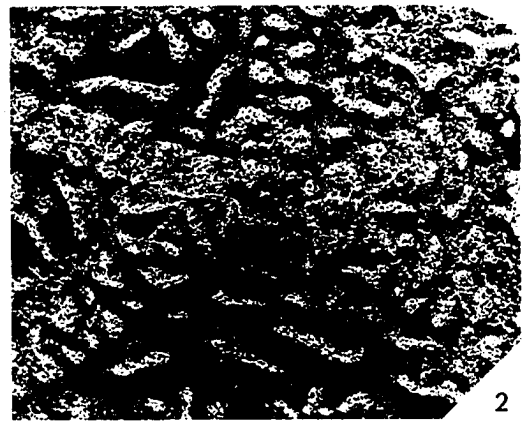
9. Composite view of oral surface, X3, whitened gutta-percha squeeze.

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PLATE 40



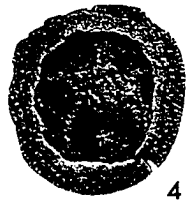
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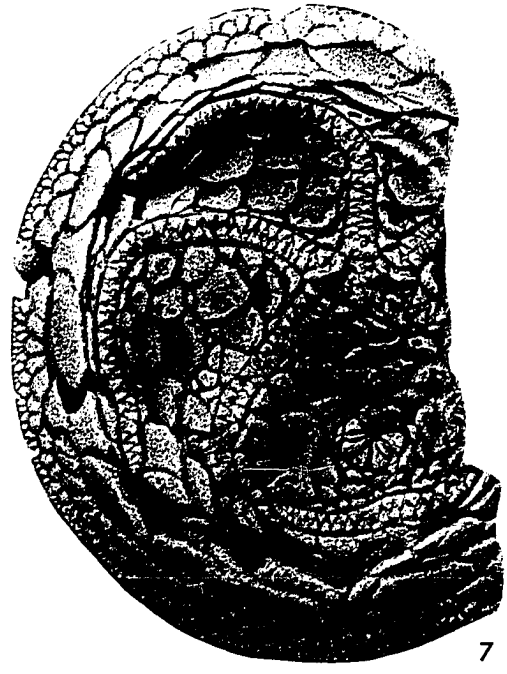
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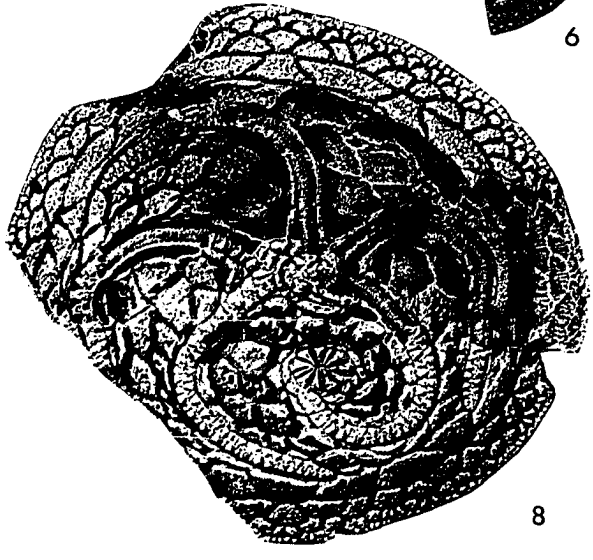
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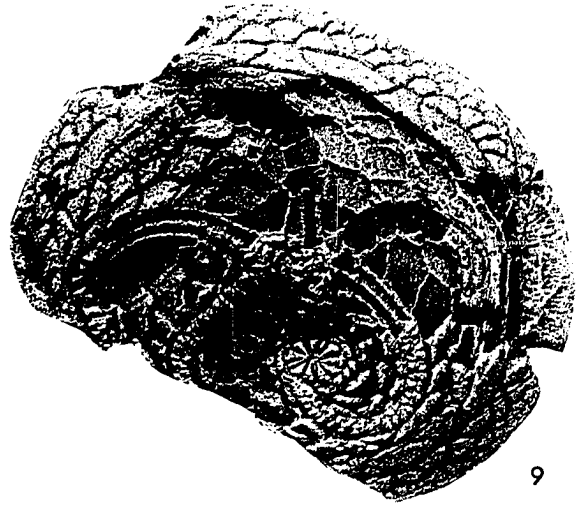
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P L A T E 41

Agelacrinites hamiltonensis Vanuxem, 1842 Fig. 1-5.

1-2. U.S.N.M. 85190-I.

1. Inner side of the oral surface, X4, whitened latex pull.

2. Oral frame and adjacent structures, X10, whitened latex pull.

3-4. U.S.N.M. 85190-G-1.

3. Oral surface, X3, whitened latex pull.

4. Ambulacrum III and adjacent area, X5, whitened latex pull.

5. U.S.N.M. 85190-J, inner side of the oral surface, X3, whitened latex pull.

Krama devonicum (Bassler), 1936 Fig. 6-8.

6. U.M.M.P. 17295, holotype, oral surface, X12, whitened (text fig. 44D).

7-8. U.M.M.P. 35390, juvenile.

7. Oral surface, X20, whitened (text fig. 44A).

8. Oral surface, X20, in xylene.

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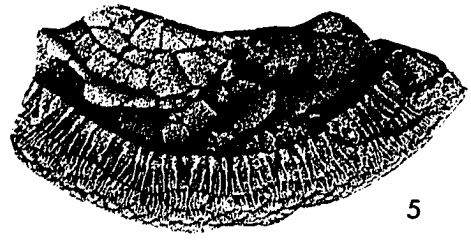
PLATE 41



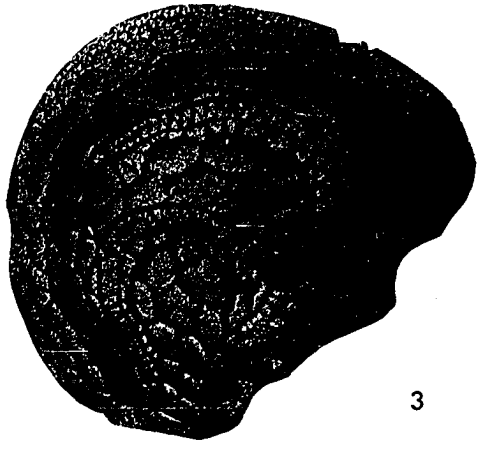
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PLATE 42

Krama devonicum (Bassler), 1936

1-2. U.M.M.P. 21123, juvenile.

1. Oral surface, X10, whitened (text fig. 44B).

2. Oral surface, X10, in xylene.

3. U.S.N.M. 94643, juvenile, oral surface, X10, whitened.

4. U.M.M.P. 57678, young adult, X8, whitened.

5-6. U.C.M.P. 36118, young adult.

5. Oral surface, X10, whitened.

6. Oral surface, X10, in xylene.

7-8. U.M.M.P. 21203.

7. Oral surface, X8, whitened (text fig. 45A).

8. Oral region and ambulacrum III, X16, whitened.

9-11. U.M.M.P. 57679.

9. Oral surface, X7, whitened (text fig. 45B).

10. Oral area, X14, whitened.

11. Oral area, X14, in xylene.

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PLATE 42

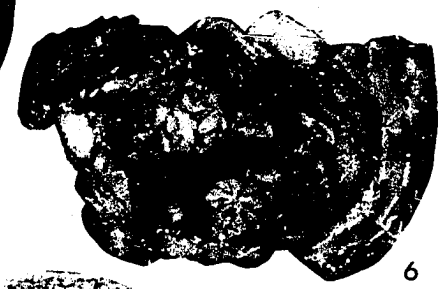

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PLATE 43

Krema devonicum (Bassler), 1936

1-3. U.M.M.P. 4796.

1. Oral surface, X4, whitened (text fig. 45D).
2. Oral surface, X4, in xylene.
3. Ambulacrum V, X12, whitened (text fig. 45C).

4-5. U.M.M.P. 5677-A.

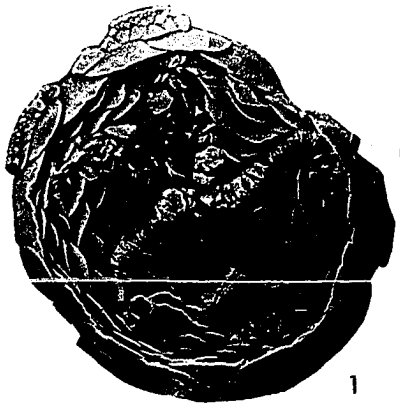
4. Oral surface, X4, whitened.
5. Oral surface, X4, in xylene (text fig. 45E).

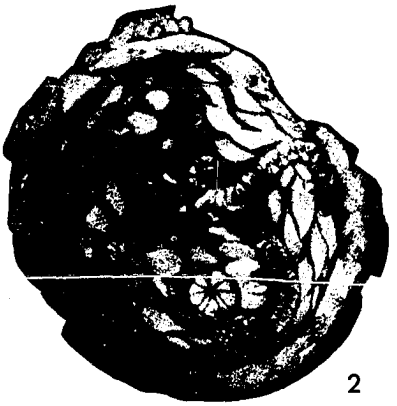
6-11. U.S.N.M. S-3478 (holotype of Agelacrinites southworthi Bassler, 1936).

6. Oral surface, X3, whitened.
7. Oral surface, X3, in xylene.
8. Proximal part of ambulacrum III, X10, whitened.
9. Proximal part of ambulacrum III, X10, in xylene (text fig. 44C).
10. Oral region, X10, whitened.
11. Oral region, X10, in xylene (text fig. 42).

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PLATE 43


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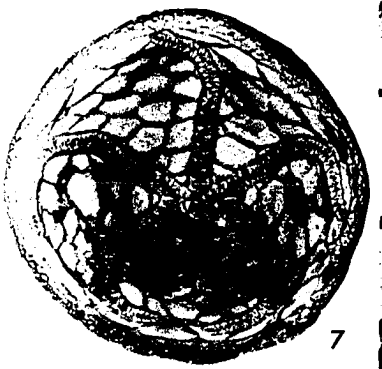

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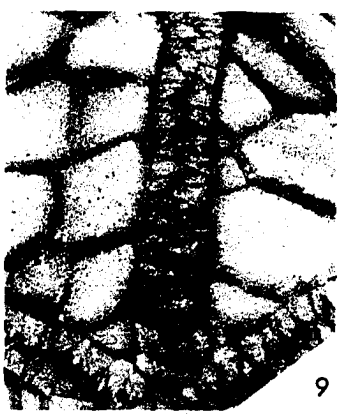

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PLATE 44

Postibulla legrandensis (Miller and Gurley), 1894

1. C.F.M.-U.C. 6495-A, lectotype, oral surface, X6, whitened.
2. C.F.M.-U.C. 6495-B, juvenile, lectoparatype, oral surface, X10, whitened (text fig. 46A).
3. U.S.N.M. S-3881-B-2, oral surface, X10, whitened.
4. U.S.N.M. S-3881-A-2, oral surface, X4, whitened.
5. U.S.N.M. S-3881-E, oral surface with ambulacral coverplates eroded away, X6, whitened.

6-7. U.S.N.M. S-3881-B-1.

   6. Oral surface, X4, whitened.
   7. Oral region, X12, whitened.

8. U.S.N.M. S-3881-C-1, oral surface, X7, whitened.

9-10. G.S.C. 25143.

   9. Oral surface, X10, whitened (text fig. 46B).
   10. Oral region, X20, whitened.

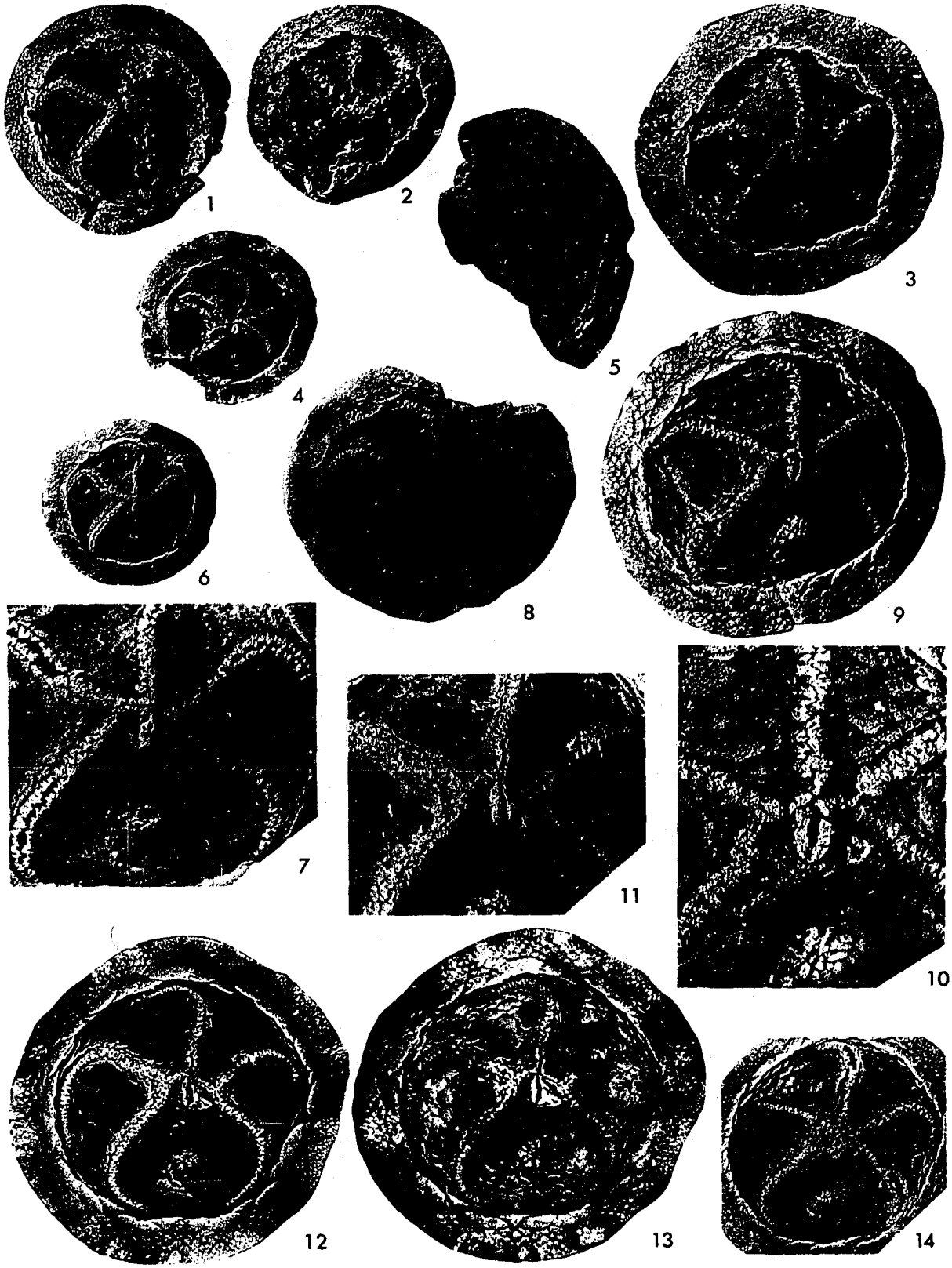
11-13. N.Y.S.M. 12777.

   11. Oral region, X10, whitened.
   12. Oral surface, X6, whitened.
   13. Oral surface, X6, in xylene.

14. U.S.N.M. S-3881-A-1, oral-ambulacral region, X6, whitened.

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PLATE 44



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PLATE 45

Postibulla keslingi Bell, sp. nov. Fig. 1-10.

1-2. U.M.M.P. 35387, holotype.

1. Oral surface, X6, whitened (text fig. 47B).

2. Oral region, X12, whitened.

3-4. U.M.M.P. 35379, young adult, paratype (3).

3. Oral surface, X12, whitened (text fig. 47A).

4. Oral-ambulacral region, X24, whitened.

5-6. U.M.M.P. 35377, paratype (2).

5. Oral surface, X6, whitened.

6. Oral region, X12, whitened.

7-9. U.S.N.M. 111225, paratype (1).

7. Oral surface, X6, whitened (text fig. 47C).

8. Oral surface, X6, in xylene.

9. Oral region, X12, whitened.

10. U.M.M.P. 35389, juvenile, oral surface, X12, whitened.

?Postibulla alpenensis (Bassler), 1936 Fig. 11.

11. U.M.M.P. 17296, holotype, oral surface, X6, whitened.

?Postibulla jasperensis (Harker), 1953 Fig. 12-14.

12-14. G.S.C. 10051, holotype.

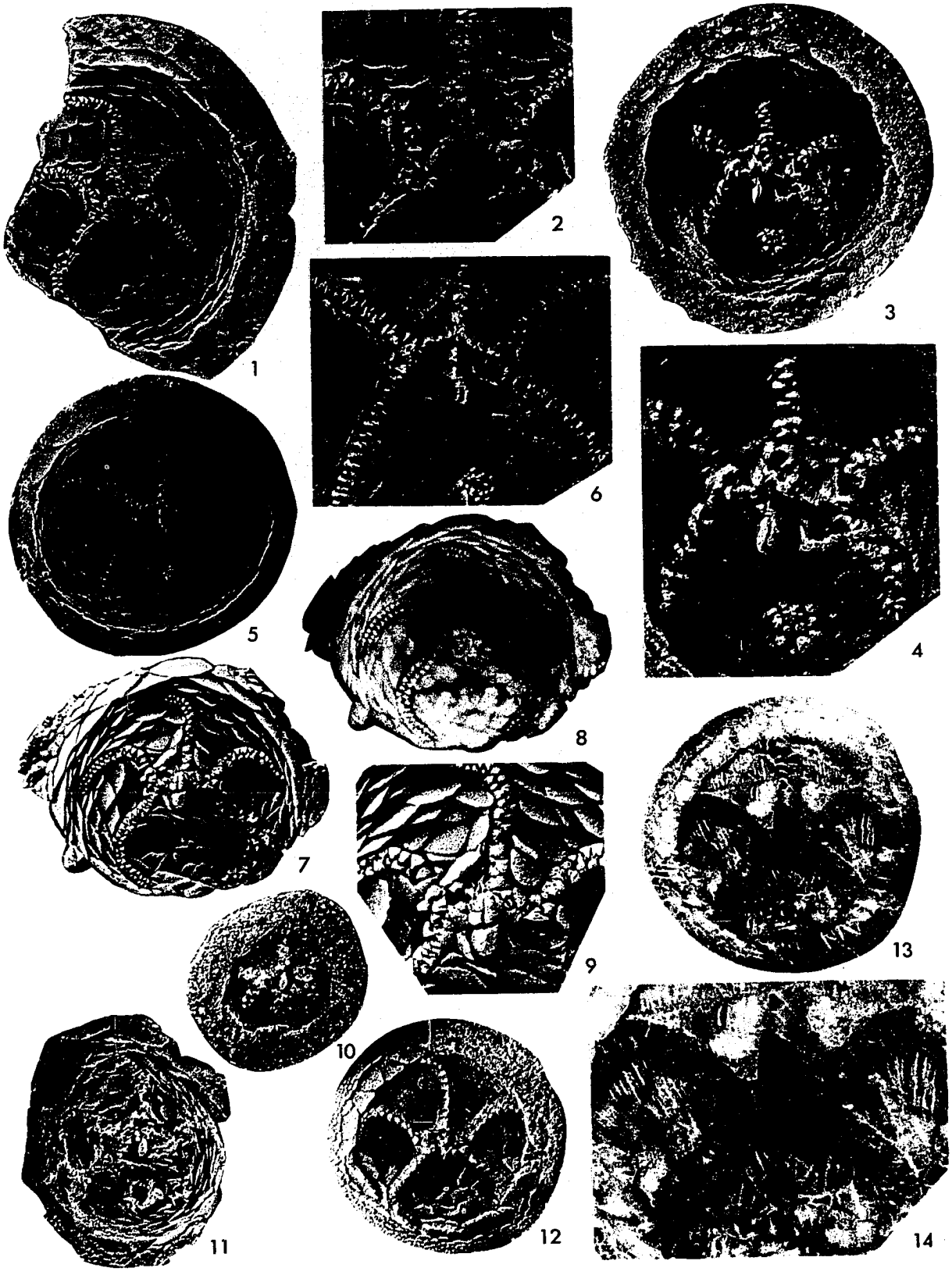
12. Oral surface, X6, whitened.

13. Oral surface, X7, in xylene (text fig. 48).

14. Oral region, X12, in xylene.

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PLATE 45



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PLATE 46

Discocystis kaskaskiensis (Hall), 1858

1-7. I.S.M. 10037, holotype.

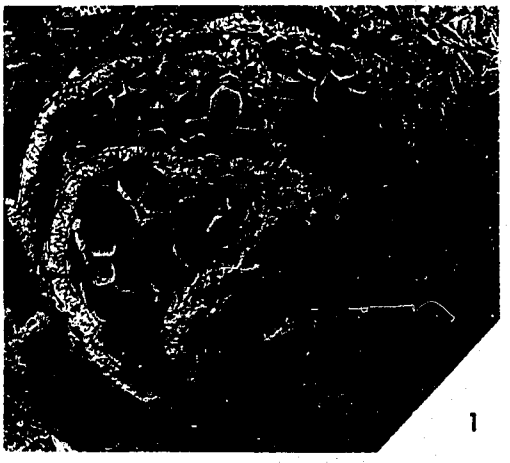
1. Oral surface, X2, whitened.
2. Oral surface, X2, in xylene.
3. Oral region, X8, in xylene (text fig. 49A).
4. Distal segment of ambulacrum III, X10, in xylene (text fig. 50B).
5. Proximal segment of ambulacrum V, X10, whitened.
6. Proximal segment of ambulacrum V, X10, in xylene (text fig. 50C).
7. Anal area, X8, in xylene (text fig. 49B).

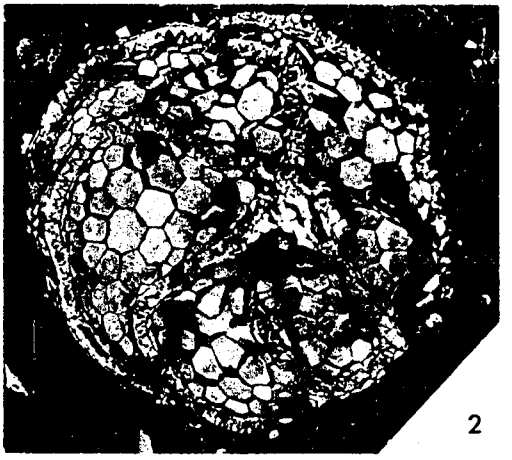
8-9. U.S.N.M. S-3883.

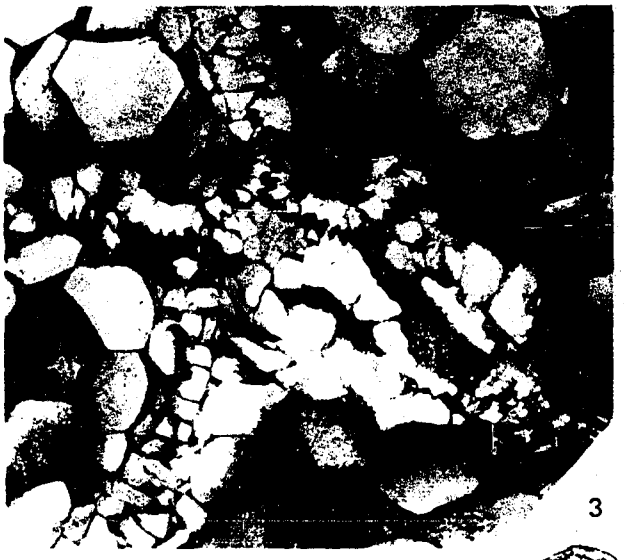
8. Inner side of the oral surface, X2, whitened.
9. Inner side of the oral surface, X2, in xylene.

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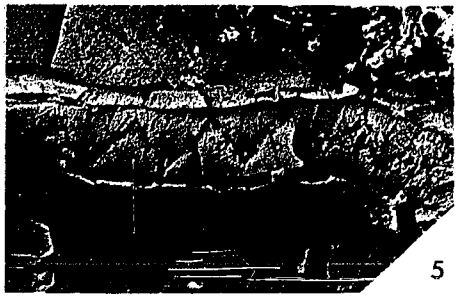
PLATE 46


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PLATE 47

Discocystis kaskaskiensis (Hall), 1868 Fig. 1-8.

1-5. U.S.N.M. S-3885, a fragmentary specimen which exposes the exterior of the upper oral surface of a narrow marginal zone that includes parts of two ambulacra and adjacent interambulacrals, and the inner side of plates of part of the sub-ambital transition zone and pedunculate zone.

1. Entire specimen, X2, whitened.
2. Entire specimen, X2, in xylene.
3. Part of the longer ambulacral segment, X5, in xylene (text fig. 50A). Note the four lateral nodes of the underlying floorplates which are exposed along the upper edge of the left end of the ambulacrum where the interambulacral plates are missing.
4. Left end of the longer ambulacral segment and part of the shorter one with interambulacrals between them, X5, in xylene.
5. Left end of the longer ambulacral segment and adjacent interambulacrals, X7, whitened.

6-8. I.S.G.S. 2478 (holotype of Echinodiscus optatus Worthen and Miller, 1883).

6. Exterior of part of the lower side of the oral surface, X2, whitened.
7. Exterior of part of the lower side of the oral surface, X2, in xylene.

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Plate 47 (cont.)

8. Oblique view of the ambital part of the specimen which includes a short segment of an ambulacrum, X6, in xylene.

Lepidodiscus squamosus Meek and Worthen, 1868 Fig. 9-10.

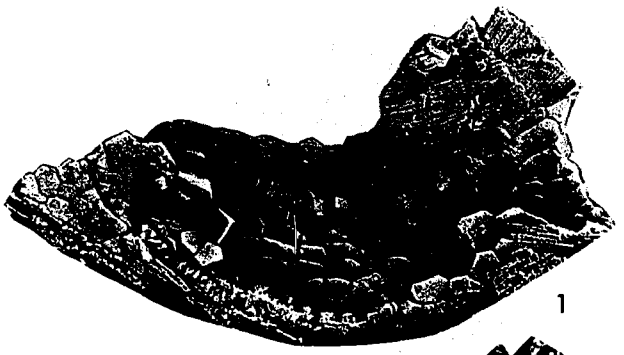
9-10. U.M.M.P. 5420, holotype.

9. Oral surface, X2, whitened.

10. Oral surface, X2, in xylene.

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PLATE 47


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PLATE 48

Lepidodiscus squamosus Meek and Worthen, 1868

1-2. U.M.M.P. 5420, holotype.

1. Oral region, X5, in xylene (text fig. 51B).
2. Medial segment of ambulacrum III, proximal end to left, X10, in xylene.

3-4. Y.P.M. 24804-a (cotype of Agelacrinites beecheri Clarke, 1901).

3. Inner side of the oral surface, X2.5, whitened latex pull.
4. Inner side of the oral surface, X2.5, whitened natural mold.

5-6. Y.P.M. 24804-b (cotype of Agelacrinites beecheri Clarke, 1901).

5. Oral surface, X3, whitened latex pull.
6. Medial part of ambulacrum III, proximal end to left, X10, whitened latex pull (text fig. 51A).

7-11. Y.P.M. 24803-a (cotype of Agelacrinites beecheri Clarke, 1901).

7. Inner side of the oral surface, X2, whitened natural mold.
8. Oblique lateral view of the inner side of the oral surface, ambulacrum IV toward viewer, X2, whitened natural mold.
9. Inner side of the oral surface, X2, whitened latex pull.
10. Inner side of the right anterior part of the peripheral rim and distal part of ambulacrum IV, proximal end to right, X4, whitened latex pull. Note ridges on the basal surfaces of rim plates.
11. Imbricate floorplates with lateral nodes, distal part of ambulacrum V, proximal end to left, X10, whitened latex pull.

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Plate 48 (cont.)

12-13. Y.P.M. 24803-b (cotype of Agelacrinites beecheri Clarke, 1901).

12. Oral surface, X3, whitened latex pull.

13. Distal part of ambulacrum IV, proximal end to left, X10, whitened latex pull.

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PLATE 48

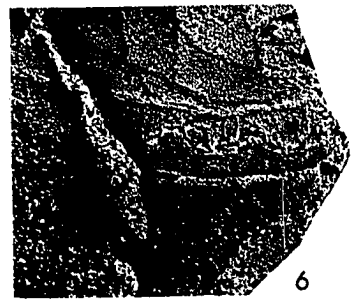

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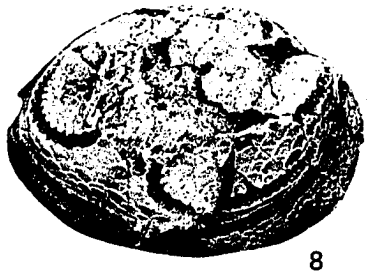

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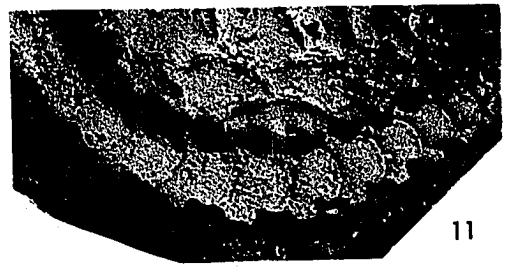

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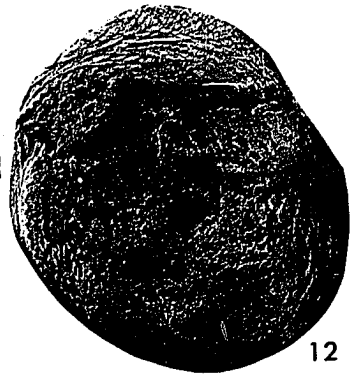

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PLATE 49

Lepidodiscus laudoni (Bassler), 1936

1-4. U.S.N.M. S-3886-B, lectotype.

1. Oral surface, X2, whitened.
2. Inner side of the oral surface, X2, whitened.
3. Exterior of the proximal part of ambulacrum II, proximal end to right, X5, whitened.
4. Exterior of the medial part of ambulacrum I, proximal end to the right, X5, whitened.

5-6. U.S.N.M. S-3886-A, lectoparatype.

5. Oral surface, X2, whitened.
6. Oral region, X7, whitened.

7-12. U.S.N.M. S-3884, a fragmentary specimen giving a composite view, with the left side and central area exposing the inner side of the upper oral surface and the right side showing the exterior side of the plates of the peduncular zone; the small anterior piece which includes a short segment of ambulacrum IV shows the exterior side of the upper oral surface.

7. Entire specimen, X2, whitened.
8. Entire specimen, X2, in xylene.
9. Oblique view of the distal, isolated segment of ambulacrum IV, proximal end to right, X10, whitened.
10. Oblique view of the distal, isolated segment of ambulacrum IV, proximal end to right, X10, in xylene.

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Plate 49 (cont.)

11. Floorplates of the proximal end of ambulacrum V, proximal end to right, X8, whitened.
12. Floorplates of the proximal end of ambulacrum IV, proximal end to right, X6, in xylene.

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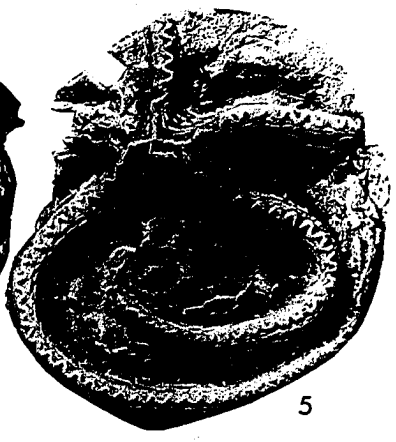
PLATE 49

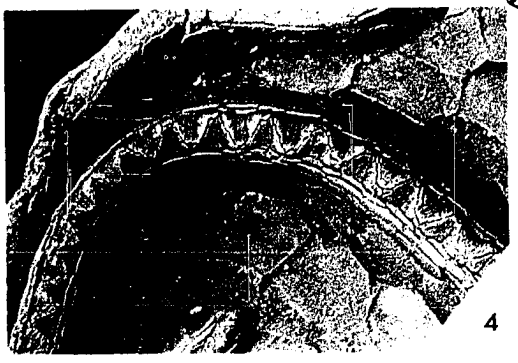

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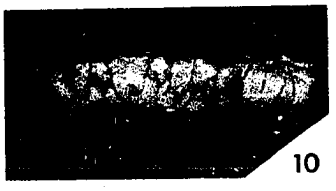

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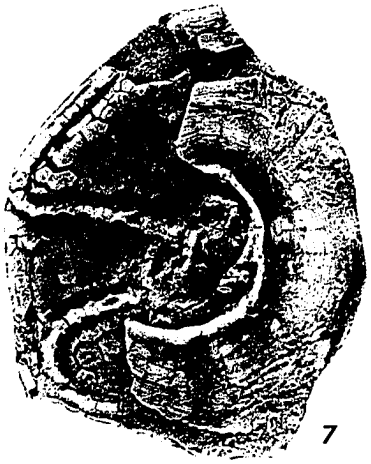

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PLATE 50

Lepidodiscus laudoni (Bassler), 1936

1-7. S.U.I.C. 12545 (holotype of Discocystis priesti Strimple, 1967).

1. Oral surface, X4, whitened.
2. Oral region, X8, whitened (text fig. 52A).
3. Proximal part of ambulacrum IV, proximal end to left, X8, whitened (text fig. 53B).
4. Proximal part of ambulacrum V, proximal end at top, X8, whitened (text fig. 52B).
5. Lower side of the specimen which shows the exterior of the plates of the transition zone, the plates of the proximal part of the peduncular zone and centrally, an impression of the brachiopod on which the specimen rested, X4, whitened.
6. Lower side of the specimen which shows the exterior of the plates of the transition zone, the exterior of the proximal plates of the peduncular zone, the basal surfaces of the plates of the peripheral rim and centrally, the inner side of a few of the plates of the upper oral surface, X4, in xylene.
7. The center of the lower side of the specimen which shows the basal surfaces of the plates of the peripheral rim, including the proximal ends of the basal ridges on the most proximal circlet, surrounded by the exteriors of plates of the peduncular zone; the inner side of a few plates of the upper oral surface are seen in the center, X8, in xylene (text fig. 54B).

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Plate 50 (cont.)

8-12. S.U.I.C. 12546 (paratype of Discocystis priesti Strimple, 1967).

8. Oral surface, X4, whitened.

9. Distal end of ambulacrum I, X8, whitened (text fig. 53A).

10. Lower side of the specimen which shows the exterior side of the plates of the transition zone, parts of the peduncular zone and the peripheral rim; centrally the inner side of the upper oral surface is exposed and includes the central oral frame and some of the ambulacral floorplates and interambulacrals, X4, whitened.

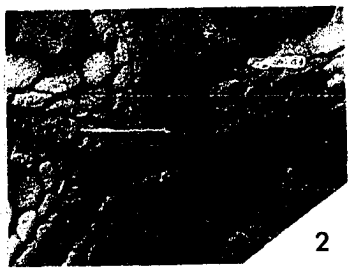
11. Center of the lower side of the specimen, X8, whitened.

12. Center of the lower side of the specimen, X8, in xylene (text fig. 54A).

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PLATE 50

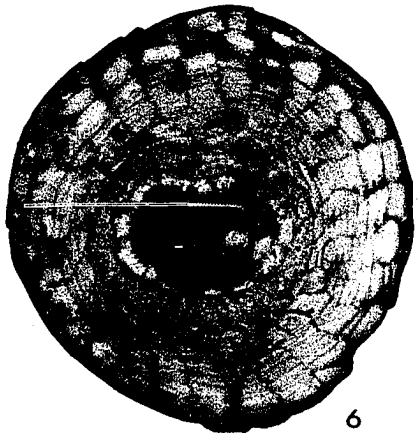

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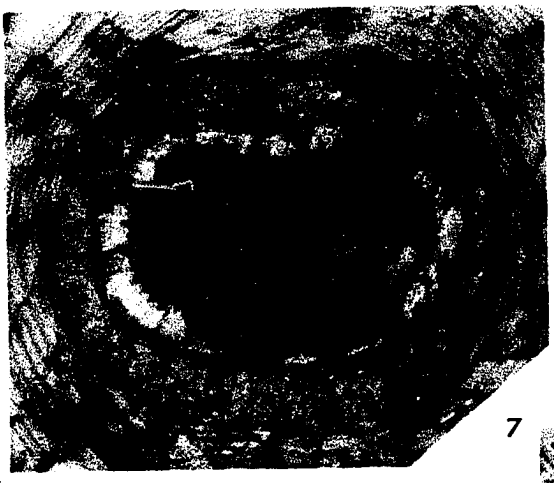

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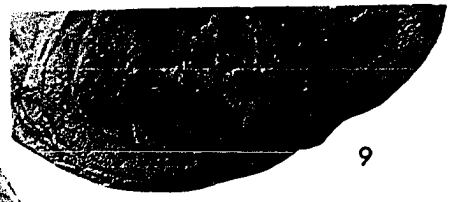

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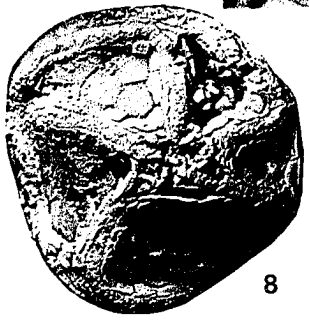

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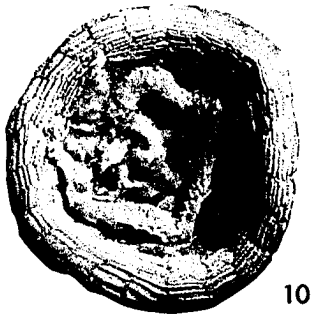

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PLATE 51

Lepidodiscus laudoni (Bassler), 1936 Fig. 1-10.

1-4. U.I.P.C. Z6-B.

1. Oral surface, X2, whitened.
2. Oral region, X6, whitened.
3. Lower side of the specimen; the exterior of the upper part of the peduncular zone surrounds a large central area in which the inner side of the upper oral surface is seen and includes the oral frame, floorplates of the proximal parts of the ambulacra, interambulacrals and the anal structure, X2, whitened.
4. Lower side of the specimen, as viewed in figure 3, X2, in xylene.

5-8. N.Y.S.M. 12778, a fragmentary specimen which includes parts of two ambulacra and adjacent interambulacrals; the coverplates are missing along most of the length of the larger ambulacral segment.

5. Oral surface, X2.5, whitened.
6. Upper sides of the ambulacral floorplates, X5, whitened.
7. Oral surface, X3, in xylene.
8. Upper sides of the ambulacral floorplates, X5, in xylene.

9-10. I.U.P.C. 10837-19.

9. Lateral view of the compressed clavate theca, ambulacrum V toward the viewer, X2, whitened.

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Plate 51 (cont.)

10. Lateral view of the compressed clavate theca, ambulacrum II toward the viewer, X2, in xylene.

Lepidodiscus sampsoni (Miller), 1891 Fig. 11-13.

11. U.S.N.M. S-3888-A, oral surface, X1.5, whitened.

12. U.S.N.M. S-3888-D, oral surface, X2, whitened.

13. U.S.N.M. S-3888-B, "upper" side of the obliquely compressed specimen which shows ambulacra I-III and adjacent areas, X1.5, whitened.

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PLATE 51

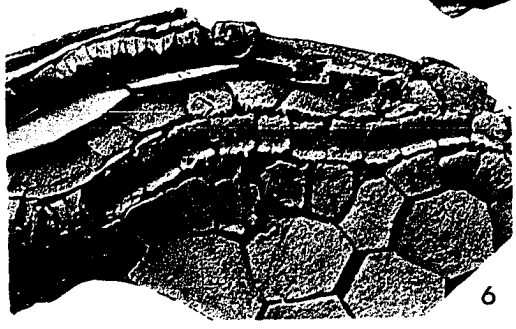

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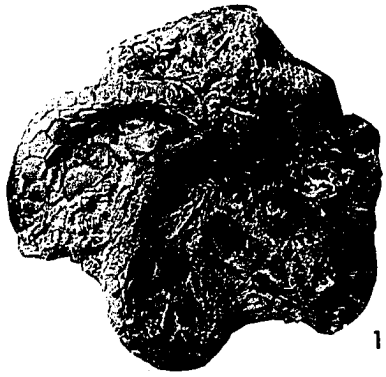

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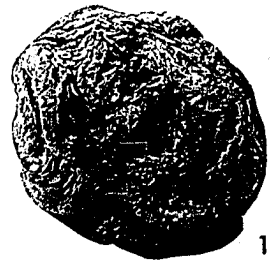

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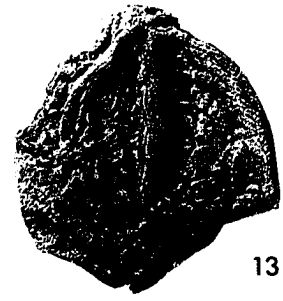

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PLATE 52

Lepidodiscus sampsoni (Miller), 1891

1-6. C.F.M.-U.C. 7000, holotype.

1. Oral surface, X2, whitened.
2. Oral region, X8, whitened, (text fig. 55B).
3. Proximal part of ambulacrum IV, proximal end to left, X8, whitened.
4. Proximal part of ambulacrum V, proximal end to left, X8, whitened (text fig. 55A).
5. Anal area, X8, whitened.
6. Oral surface, X1, in xylene.

7. U.S.N.M. S-3888-C, oral surface, X2.5, whitened.

8. U.S.N.M. S-3888-F, oral surface, X2.5, whitened.

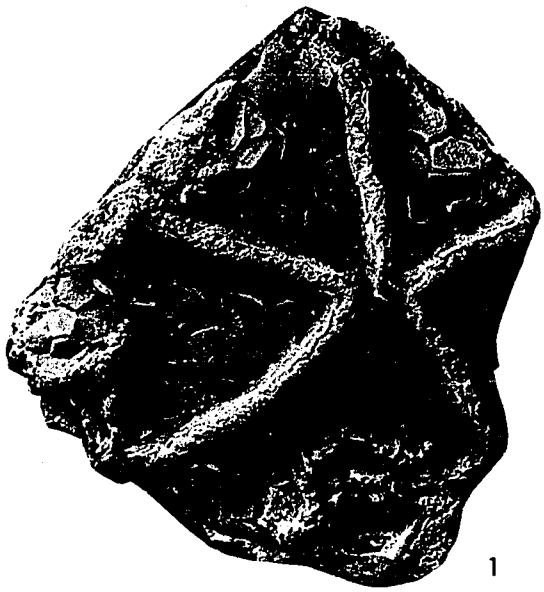
9-10. U.S.N.M. S-3888-G, a section of one ambulacrum and a few adjacent interambulacrals.

9. Inner side of the oral surface which exposes seven floorplates, X4, whitened.
10. Inner side of the oral surface which exposes seven floorplates, X4, in xylene.

11. U.S.N.M. S-3888-H, inner side of the oral surface of a small section of one ambulacrum showing four floorplates, X3, in xylene.

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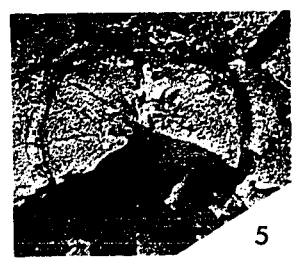
PLATE 52

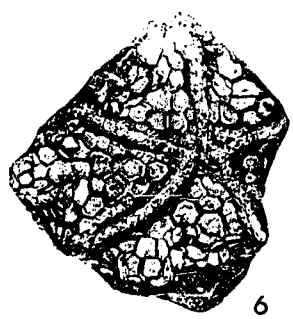

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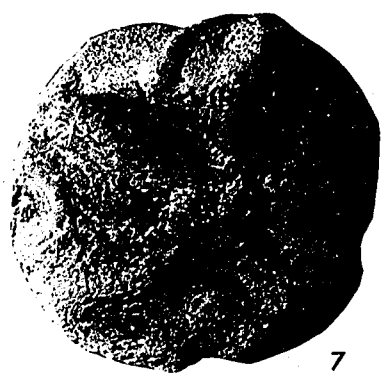

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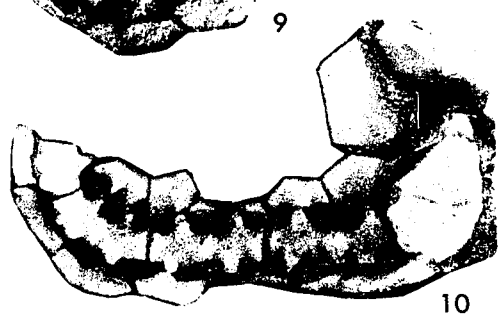

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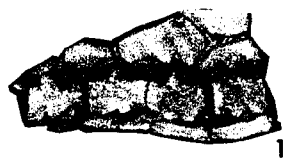

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PLATE 53

Ulrichidiscus pulaskiensis (Miller and Gurley), 1894

1-7. C.F.M.-U.C. 6419, holotype.

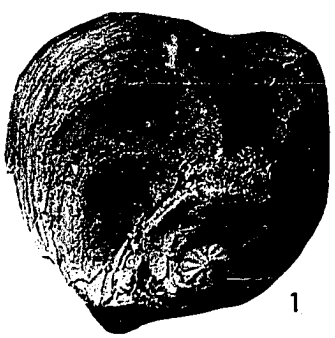
1. Oral surface, X2, whitened.
2. Lower side of the specimen which shows part of the broken peduncular zone and a small section of peripheral rim, X2, whitened.
3. A nearly complete length of the peduncular zone with a segment of the peripheral rim at the base, X4, whitened (text fig. 56C).
4. Oral surface, X3, in xylene.
5. Oral region, X5, in xylene (text fig. 56A).
6. Oblique view of the proximal part of ambulacrum V, proximal end at top, X15, in xylene (text fig. 58B).
7. Anal area, X6, in xylene (text fig. 56B).

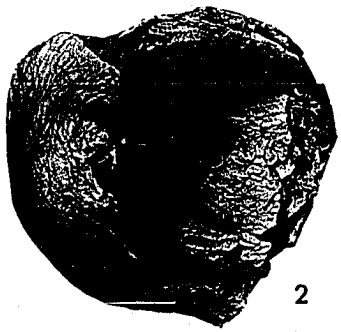
8-13. U.S.N.M. S-3193-A.

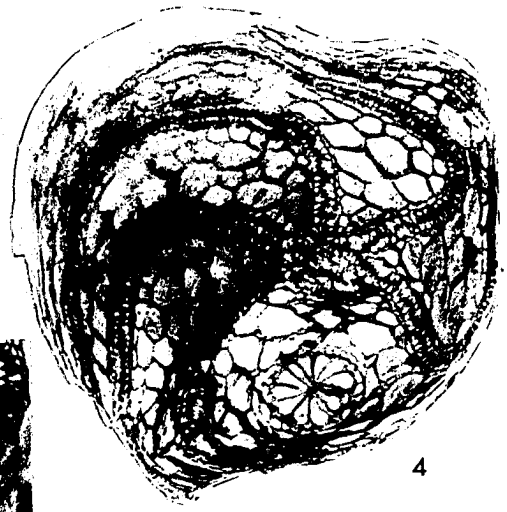
8. Oral surface, X2, whitened.
9. Oral surface, X2, in xylene.
10. Lower side of specimen which preserves disrupted thecal plates, X1.5, whitened.
11. Oral region, X5, whitened.
12. Oral region, X5, in xylene (text fig. 57).
13. Medial section of ambulacrum III, proximal end to right, X10, in xylene.

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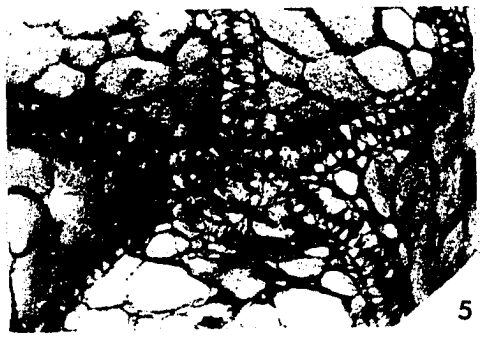
PLATE 53


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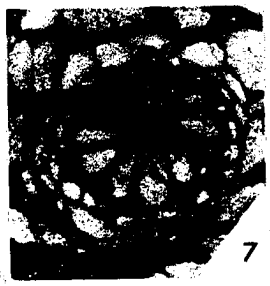

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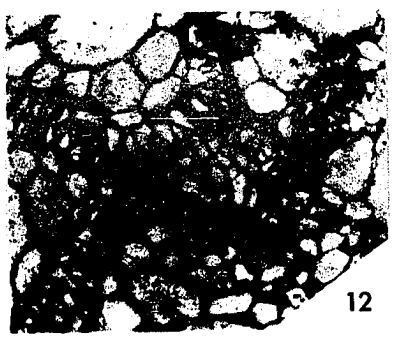

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PLATE 54

Ulrichidiscus pulaskiensis (Miller and Gurley), 1894 Fig. 1-7.

1-6. U.S.N.M. S-3193-B.

1. Oral surface, X2, whitened.
2. Oral surface, X2, in xylene.
3. Distal end of ambulacrum I, X10, in xylene.
4. Proximal segment of ambulacrum I, proximal end to left, X10, whitened.
5. Medial segment of ambulacrum I, proximal end to left, X10, whitened.
6. Distal end of ambulacrum I, X10, whitened.

7. U.S.N.M. S-3193-C, lateral view of the margin of the theca and the upper part of the coral on which the specimen rests, X2, whitened.

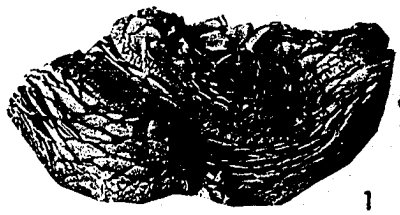
Cooperidiscus alleganius (Clarke), 1901 Fig. 8-11.

8-11. N.Y.S.M. 4962, lectotype.

8. Oral surface, X2, whitened natural mold.
9. Oral surface, X2, whitened latex pull.
10. Anal area, X6, whitened latex pull (text fig. 59B).
11. Medial section of ambulacrum IV, proximal end to left, X6, whitened latex pull (text fig. 59A).

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PLATE 54

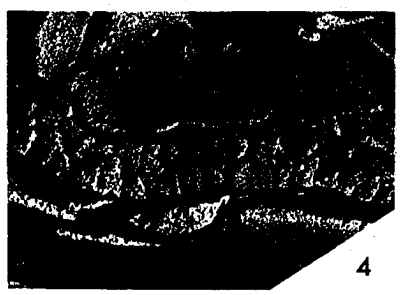

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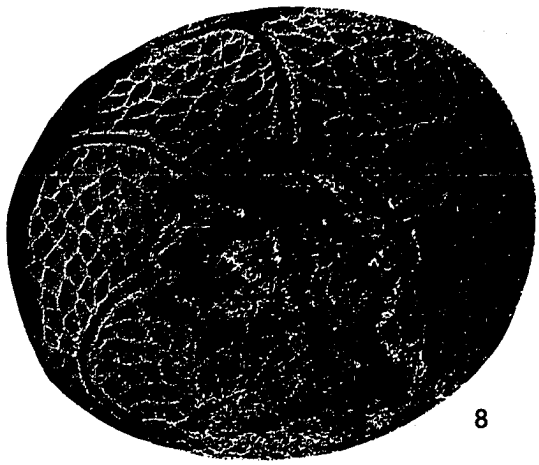

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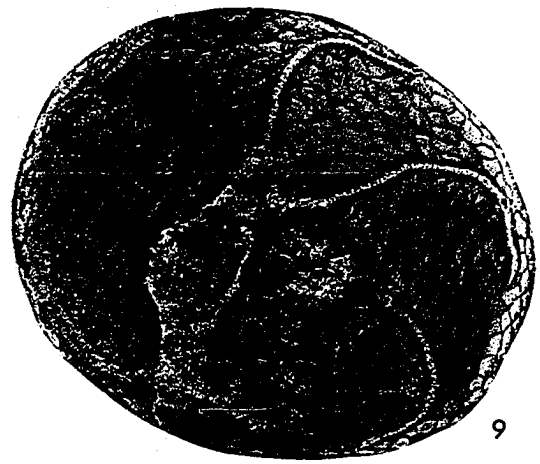

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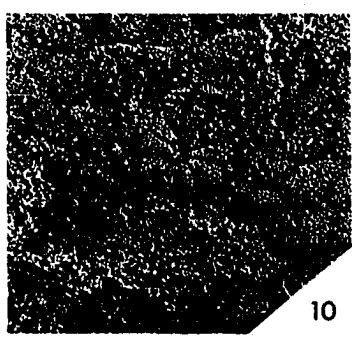

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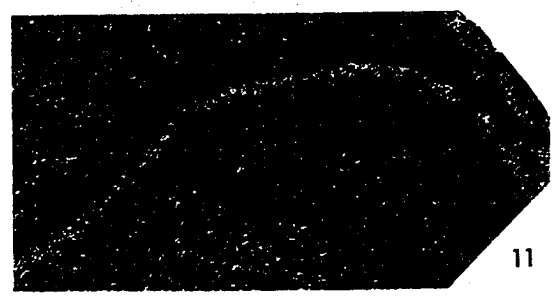

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PLATE 55

Cooperidiscus alleganius (Clarke), 1901 Fig. 1-6.

1-2. N.Y.S.M. 4959, lectoparatype.

1. Oral surface, X2, whitened latex pull.

2. Anal structure and adjacent areas, X3, whitened latex pull (text fig. 59C).

3-4. U.S.N.M. 34131-A, lectoparatype.

3. Oral surface, X1.5, whitened latex pull.

4. Oral region, X3, whitened latex pull.

5-6. U.S.N.M. 34131-B.

5. Oral surface, X1, whitened latex pull.

6. Oral region, X3, whitened latex pull.

Hemicystites carbonarius Bassler, 1936 Fig. 7-10.

7. U.S.N.M. 91837-A, slab with two specimens of the type series, X1, whitened.

8. U.S.N.M. 91837-A-1, syntype, X4, whitened.

9. U.S.N.M. 91837-B, slab with six specimens of the type series, X1, whitened.

10. U.S.N.M. 91837-B-6, juvenile (?), syntype, X10, whitened.

Agelacrinites hanoveri Thomas, 1924 Fig. 11-15.

11. S.U.I.C. 35162, juvenile, X10, whitened (text fig. 61B).

12. S.U.I.C. 35164, juvenile, X10, whitened (text fig. 61E).

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Plate 55 (cont.)

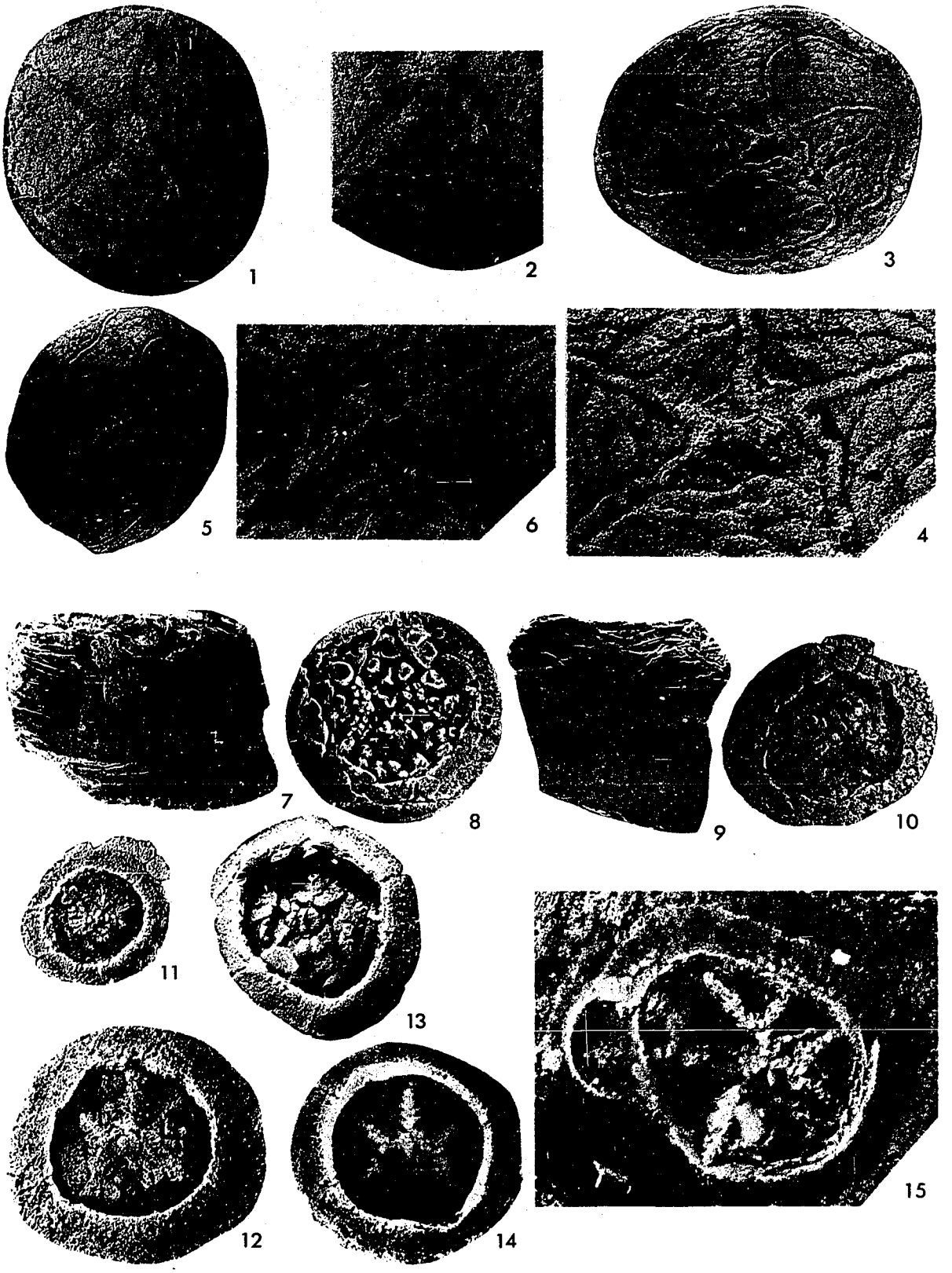
13. S.U.I.C. 1906, juvenile, X10, whitened (text fig. 61C).

14. S.U.I.C. 35163, juvenile, X10, whitened (text fig. 61D).

15. S.U.I.C. 35200, juvenile on left partially overgrown by an advanced juvenile with six ambulacra, X10, whitened.

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PLATE 55



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PLATE 56

Genus and Species Indeterminate.

1-8. U.C.L.A. 48166.

1. Oral surface, X2, whitened.
2. Oral surface, X2, in xylene.
3. Lower side of the specimen which shows plates of the transition zone and a few plates of the peduncular zone that lie along upper edge of specimen, X2, whitened.
4. Coverplates preserved near the left end of the central ambulacral segment, proximal end to left, X10, whitened.
5. Oral surface view of floorplates along the left end of the outer ambulacral segment, proximal end to left, X10, whitened.
6. Oral surface view of floorplates along the left end of the outer ambulacral segment, proximal end to left, X8, in xylene.
7. Oblique view of the proximal end of the outer ambulacral segment which shows a cross-section of a floorplate and the adjacent interambulacrals; transition zone plates have been pressed against the inner sides of the upper oral surface plates, X5, in xylene.
8. Right end of the middle ambulacral segment with a few coverplates on left and the upper sides of the floorplates exposed along the rest of the segment, proximal end to left, X7, whitened.

9-11. U.C.L.A. 48167.

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Plate 56 (cont.)

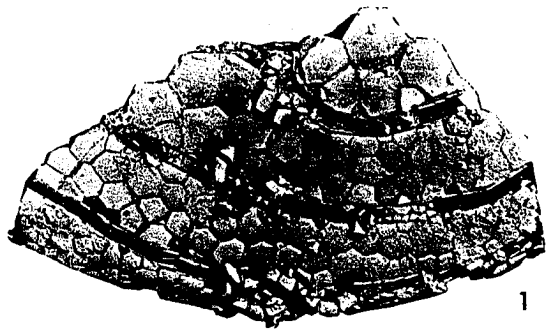
9. Oral surface, X3, whitened.

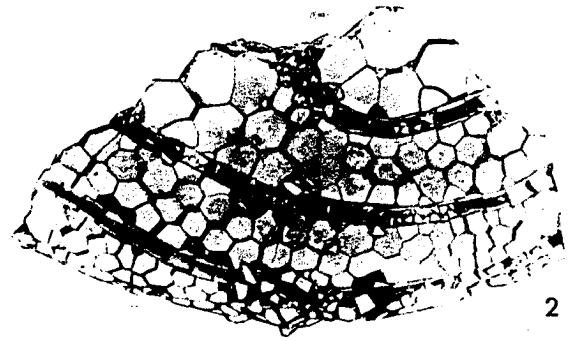
10. Oral surface, X3, in xylene.

11. Lower side of the specimen which preserves some of the plates of the transition zone, X3, whitened.

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PLATE 56


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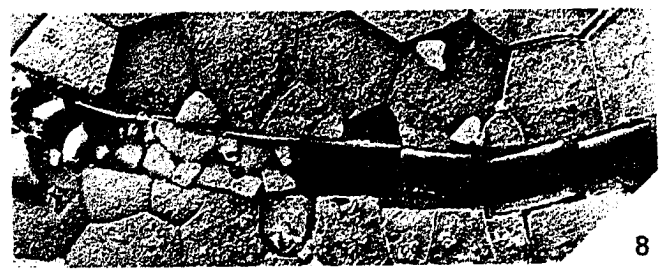

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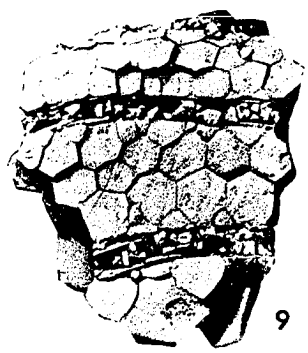

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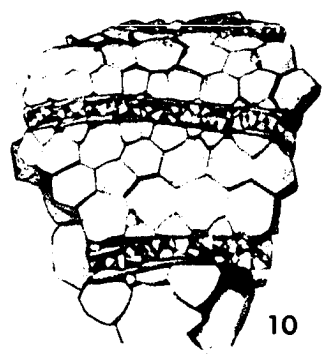

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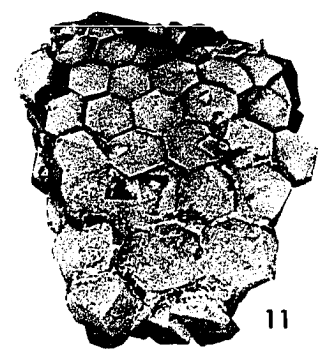

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PLATE 57

Hadrochthus commensalus Bell, gen. et sp. nov.

1-3. S.U.I.C. 80002, holotype.

1. Oral surface, X4, whitened (text fig. 60B).
2. Lower side of specimen with disrupted plates from the upper oral surface; these include interambulacrals with nodes and one floorplate, X4, whitened.
3. Oral region, X8, whitened.

4-7. S.U.I.C. 80003, paratype (1).

4. Oral surface, X4, whitened (text fig. 60A).
5. Oblique view of oral surface with the posterior interambulacrum toward the viewer, X4, whitened.
6. Anal region, X6, in xylene.
7. Oral region, X7, whitened.

8-10. S.U.I.C. 32293, paratype (2).

8. Theca in place on cystoid, X2, whitened.
9. Oral surface, X5, whitened.
10. Lateral view of theca showing the rim on the cystoid, X5, whitened.

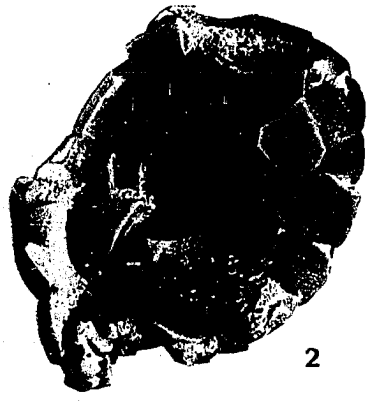
11-12. S.U.I.C. 32299, paratype (3).

11. Theca in place on cystoid, X1, whitened.
12. Oral surface, X8, whitened.

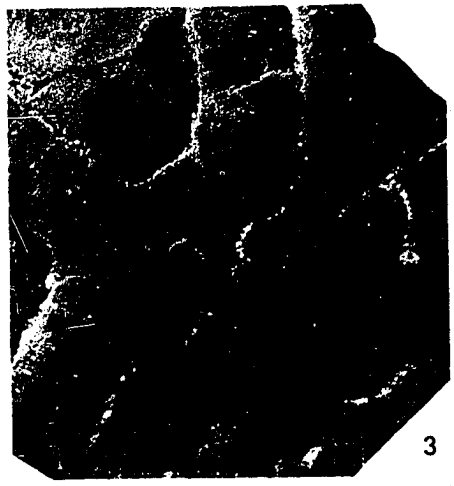
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PLATE 57

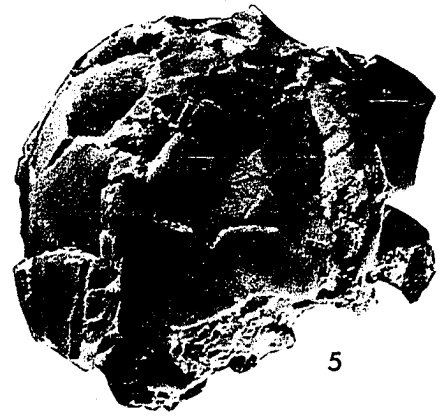

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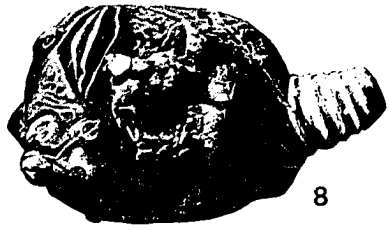

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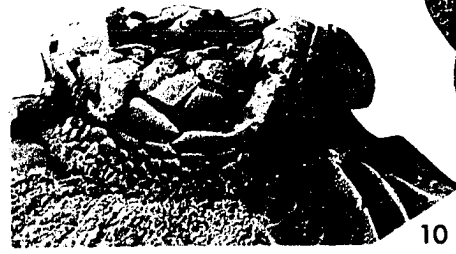

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PLATE 58

Edrioaster bigsbyi (Billings), 1857

1-6. G.S.C. 1407, right half of theca, G.S.C. 1407-a, left half of theca, lectotype, all ambulacral coverplates missing.

1. Oral surface, X1.5, whitened.
2. Oral surface of G.S.C. 1407-a, X2, in xylene.
3. Oral surface of G.S.C. 1407, X2, in xylene.
4. Axial section view of G.S.C. 1407 with ambulacrum III to the left, X2, in xylene (text fig. 62A).
5. Axial section view of G.S.C. 1407-a with ambulacrum III to the right, X2, in xylene (text fig. 62B).
6. Lateral cross-section view of G.S.C. 1407-a with ambulacrum II toward viewer, X2, in xylene (text fig. 63A).

7-13. G.S.C. 1407-e, right half, G.S.C. 1407-f, left half, lectoparatype, ambulacral coverplates missing.

7. Oral surface, X2, whitened.
8. Oblique view of G.S.C. 1407-f which shows the upper side of the floorplates and a polished lateral margin, X3, whitened.
9. Oblique view of G.S.C. 1407-f which shows the upper side of the floorplates and a polished lateral margin, X4, in xylene.
10. View of G.S.C. 1407-f normal to the upper side of the floorplates, X3, in xylene.
11. Upper side of the floorplates of G.S.C. 1407-e, X4, in xylene.

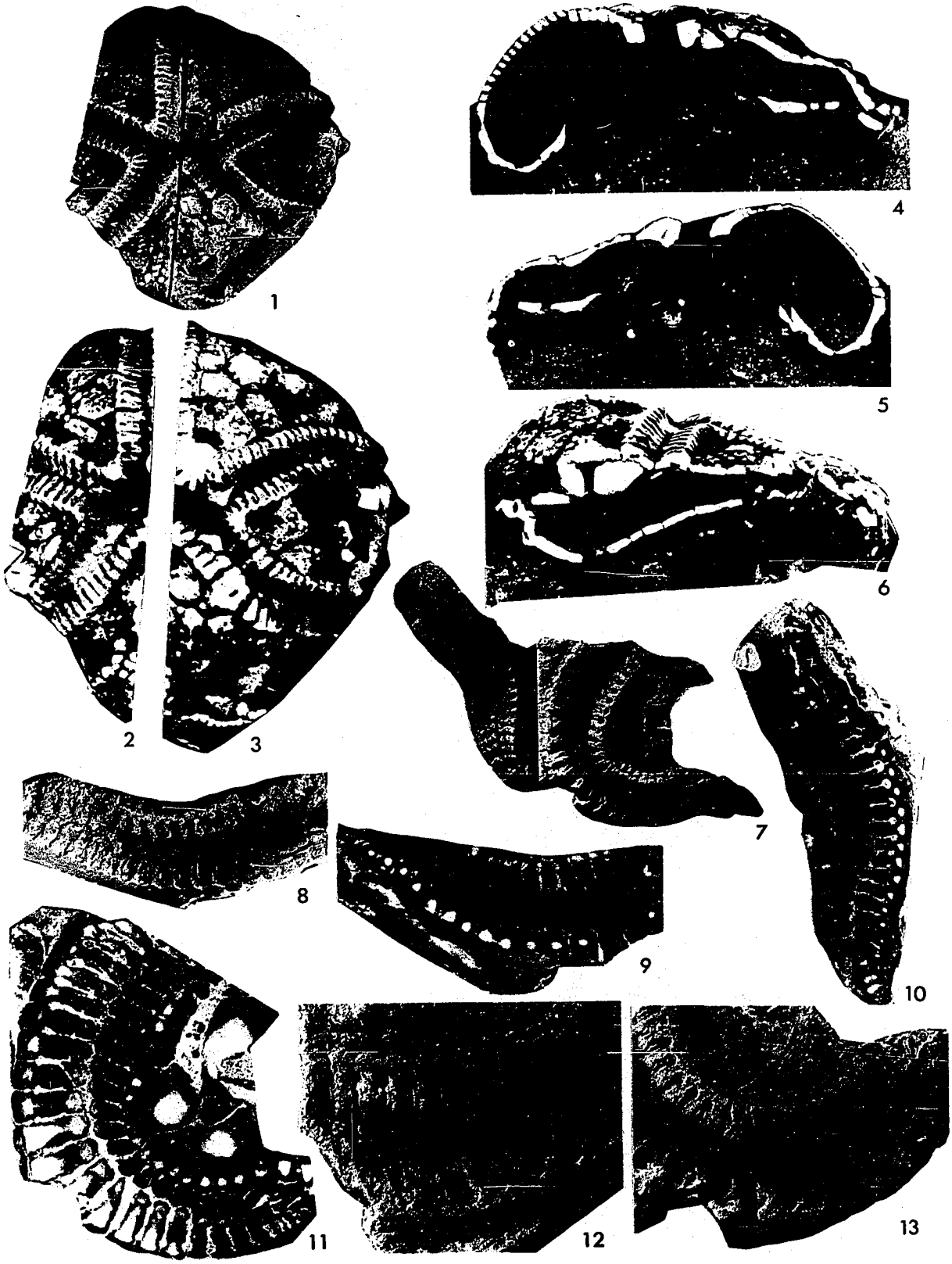
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Plate 58 (cont.)

12. Oblique view of the upper side of the floorplates of the proximal end of G.S.C. 1407-e, X5, whitened (text fig. 63B).
13. Oblique view of the upper side of the floorplates of the distal end of G.S.C. 1407-e, X5, whitened.

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PLATE 58



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PLATE 59

Edrioaster bigsbyi (Billings), 1857

1-5. G.S.C. 1407-c.

1. Oral surface, X1, whitened.
2. Lower side of the oral surface, X1, whitened.
3. Oral surface, X2, in xylene.
4. Lower side of the oral surface, X1.5, in xylene.
5. Oral region, X3, in xylene.

6. U.M.M.P. 10347, oral surface, X1.3, whitened.

7-12. G.S.C. 1407-g.

7. Oral surface, X1, whitened.
8. Lower side of oral surface, X1, whitened.
9. Oral surface, X1.5, in xylene.
10. Lower side of oral surface, X1.5, in xylene.
11. Platelets of a segment of the distal membrane, near the center of the lower side of the specimen, X5, whitened.
12. Platelets of a segment of the distal membrane near the center of the lower side of the specimen, X5, whitened.

13-14. G.S.C. 1407-h, the upper oral surface is compressed laterally.

13. One side of oral surface which includes ambulacra II, III and IV, oral area at bottom center, X1.5, whitened.
14. Opposite side of upper oral surface which includes ambulacra I and V and parts of II and IV, oral area at top center, X1.5, whitened.

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Plate 59 (cont.)

15-17. G.S.C. 1407-d.

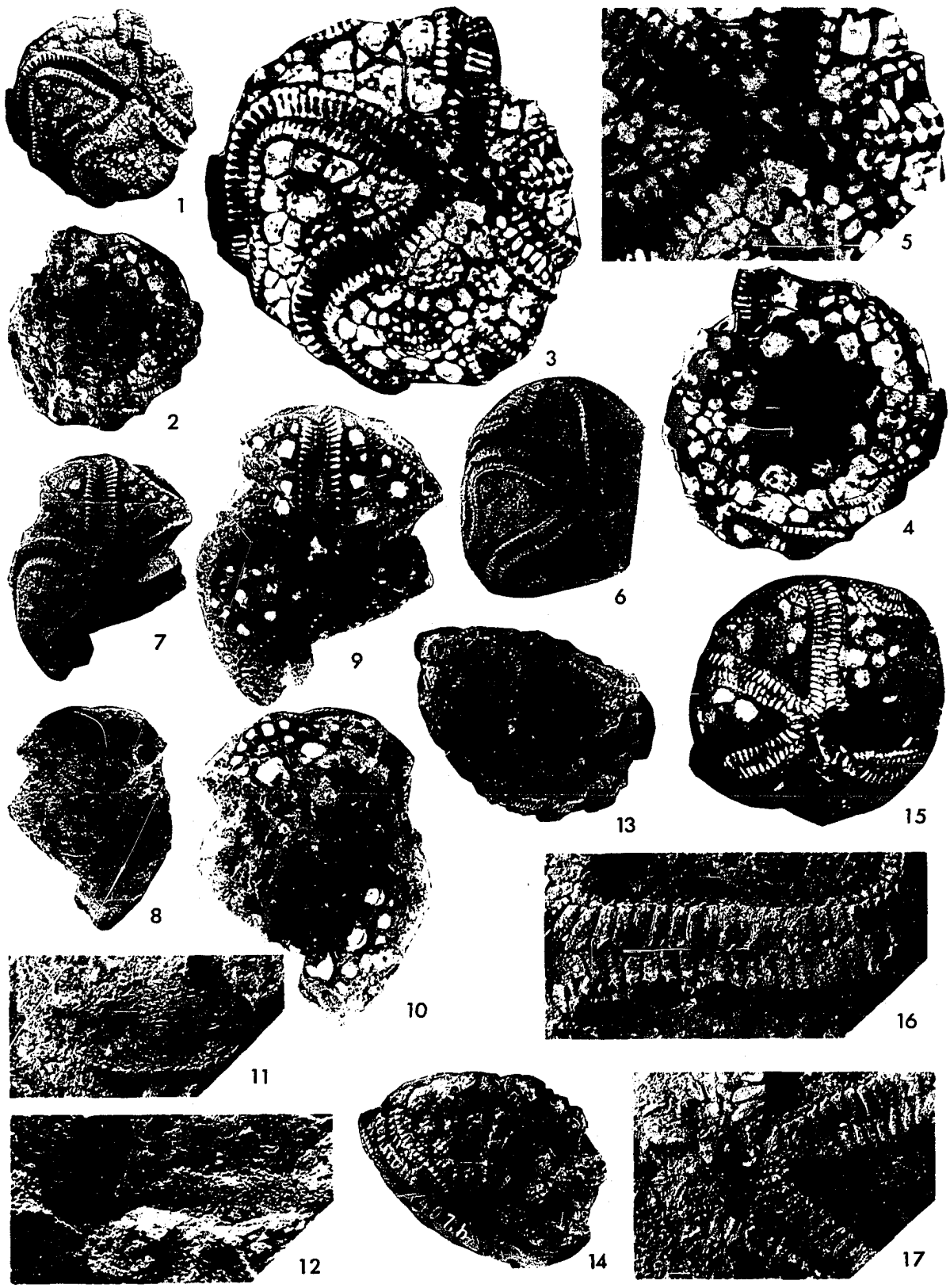
15. Oral surface, X1, in xylene.

16. Ambulacrum III, proximal end to left, X3, whitened.

17. Oral area with oblique lighting to show prosopon, ambulacrum III directed toward the lower right corner, X2, whitened.

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PLATE 59



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PLATE 60

Edrioaster priscus (Miller and Gurley), 1894 Fig. 1-6.

1-3. Y.P.M. 28456.

1. Oral surface, X2, whitened.

2. Lower side of the oral surface, X2, whitened.

3. Ambulacrum III, lit obliquely, distal end to right, X5, whitened.

4-5. C.F.M.-U.C. 33380.

4. Oral surface, X3, whitened.

5. Lower side of oral surface, X3, whitened.

6. Y.P.M. 28455, oral surface, X2, whitened.

Edriophus saratogensis (Ruedemann), 1912 Fig. 7-14.

7-8. N.Y.S.M. 7385, holotype.

7. Oral surface, X4, whitened latex pull (text fig. 65A).

8. Oral surface, X4, whitened natural mold.

9-10. N.Y.S.M. 7386, paratype (1).

9. Oral surface, X3, whitened latex pull (text fig. 65C).

10. Oral surface, X3, whitened natural mold.

11-12. N.Y.S.M. 7387, paratype (2) left margin of theca broken so as to reveal the inner side of the distal part of ambulacrum I which lies below the ambitus.

11. Oral surface, X3, whitened latex pull (text fig. 65B).

12. Oral surface, X3, whitened natural mold.

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Plate 60 (cont.)

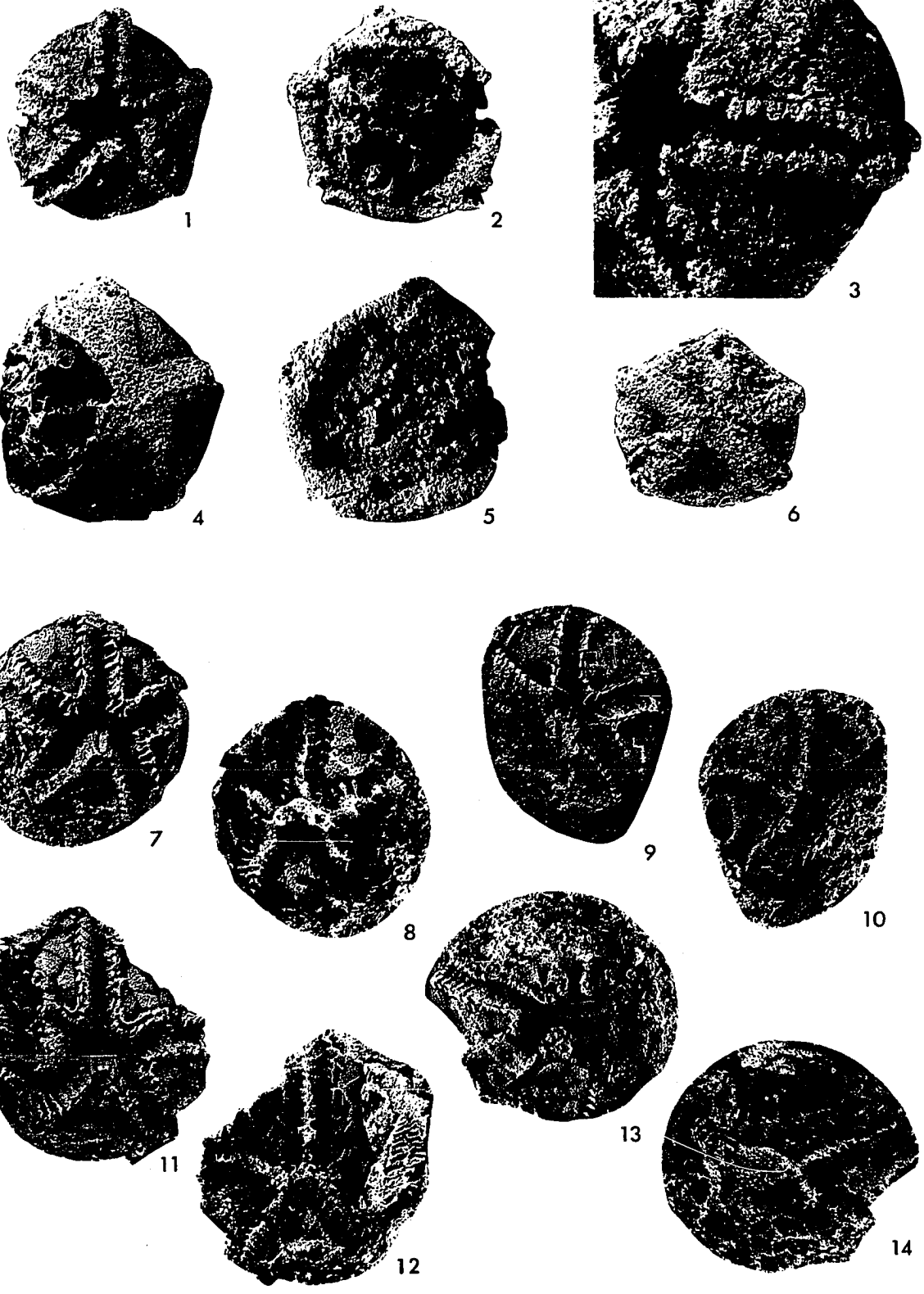
13-14. N.Y.S.M. 12779.

13. Oral surface, X3, whitened latex pull (text fig. 65D).

14. Oral surface, X3, whitened natural mold.

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PLATE 60



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PLATE 61

Edriophus levis (Bather), 1914

1-6. U.C.M.P. 40477.

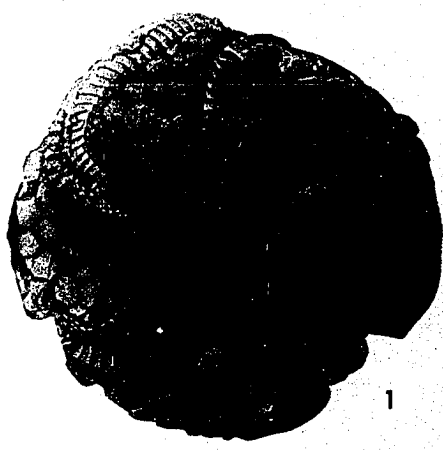
1. Oral surface, X1.5, whitened.
2. Lower side of specimen which exposes part of the lower side of the oral surface and part of the inner side of the upper oral surface; the latter includes the oral frame and the floorplates of ambulacrum V, X1.5, whitened.
3. Platelets of a small segment of the distal membrane preserved on the lower side of the specimen, X3, in xylene.
4. Oral region, X3, in xylene.
5. Oral frame, X2, in xylene.
6. Inner side of the floorplates of ambulacrum V and part of the oral frame, X3, in xylene.

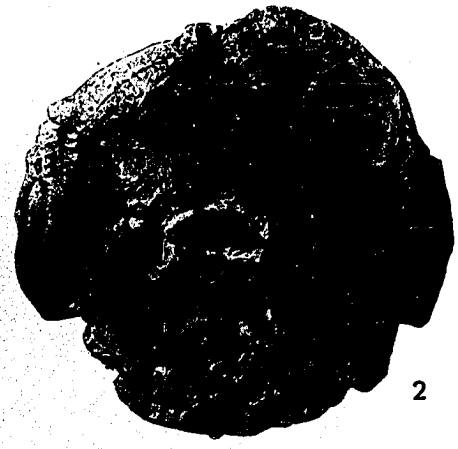
7-9. U.C.M.P. 40478, lower side of the specimen which centrally exposes the inner side of the upper oral surface, this includes the oral frame and proximal parts of the ambulacra; marginally the exterior of plates of the sub-ambital zone are seen and this zone includes the distal parts of the ambulacra.

7. Lower side of the specimen, X1.5, whitened.
8. Lower side of the specimen, X1.5, in xylene.
9. Oral frame, X4, in xylene.

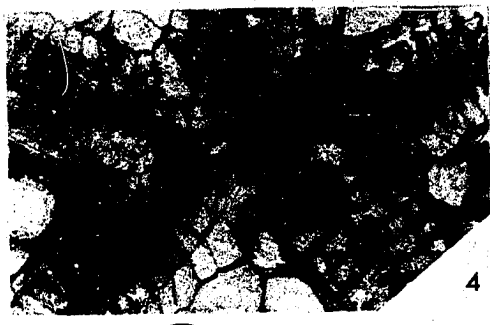
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PLATE 61


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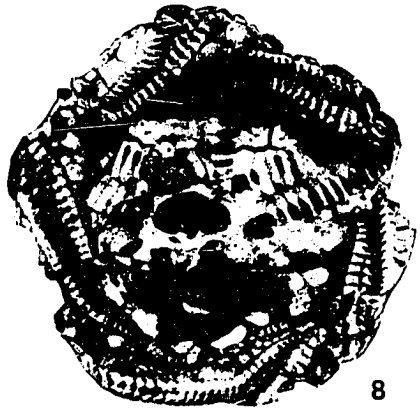

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PLATE 62

Edriophus levis (Bather), 1914

1-3. U.C.M.P. 40479.

1. Oral surface, X2, whitened (text fig. 64).

2. Oral surface, X2, in xylene.

3. Oral region, X3, whitened.

4-5. U.S.N.M. S-3197-B.

4. Oral surface, X1, whitened.

5. Oral region, X2, whitened.

6. U.S.N.M. Acc. no. 212887, anal area, X5, whitened.

7-10. U.C.M.P. 40480.

7. Oral surface, X1, whitened.

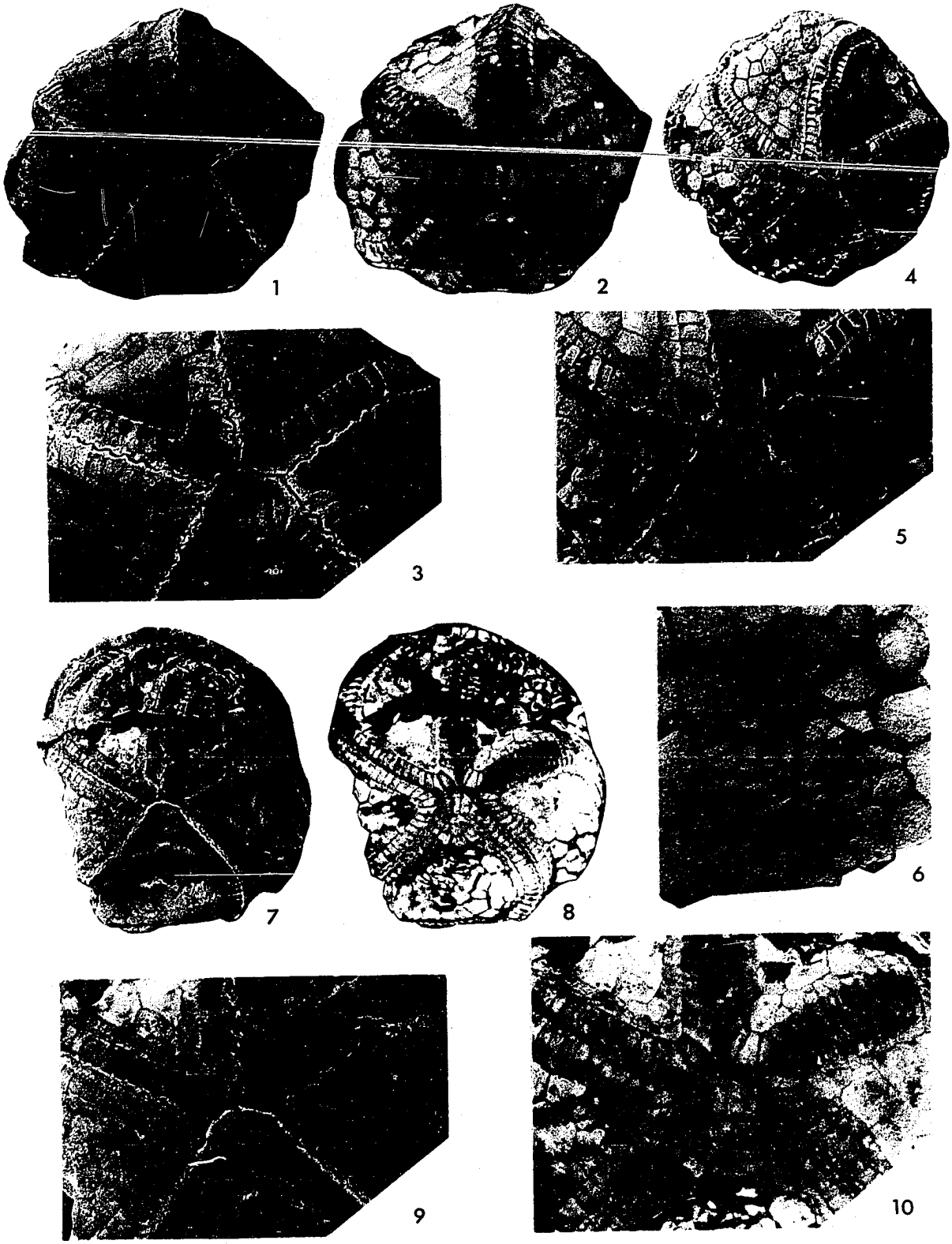
8. Oral surface, X1, in xylene.

9. Oral region, X2, whitened.

10. Oral region, X2, in xylene.

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PLATE 62



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PLATE 63

Edriophus levis (Bather), 1914

1-6. G.S.C. 18659.

1. Oral surface, X1, whitened.
2. Oral surface, X1, in xylene.
3. Medial part of ambulacrum IV, proximal end to left, X4, whitened.
4. Medial part of ambulacrum IV, proximal end to left; the more proximal coverplates are transparent and reveal their alignment with the floorplates, X4, in xylene.
5. Medial part of ambulacrum III, proximal end to left; the upper sides of the floorplates are seen along the right end, X3, whitened.
6. Medial part of ambulacrum II, proximal end at bottom; the upper sides of the floorplates are exposed, X4, in xylene.

7-8. U.S.N.M. S-3197-A.

7. Oral surface, X1, whitened.
8. Oral region, X3, in xylene.

9-10. U.M.M.P. 5731.

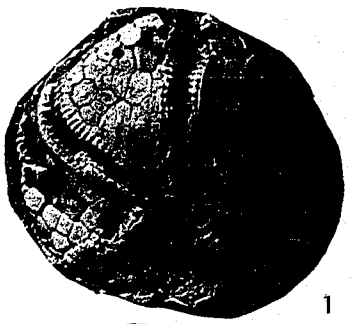
9. Oral surface, X1, whitened.
10. Oral surface, X1.5, in xylene.

11-13. U.M.M.P. 26428.

11. Oral surface, X1.5, in xylene.
12. Proximal part of ambulacrum I, proximal end to left, X4, whitened.
13. Oral region, X4, whitened.

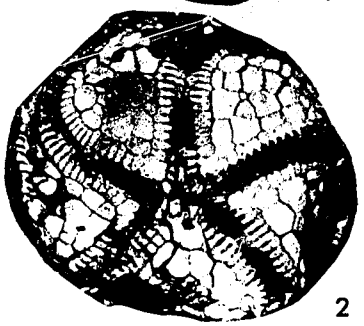
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PLATE 63

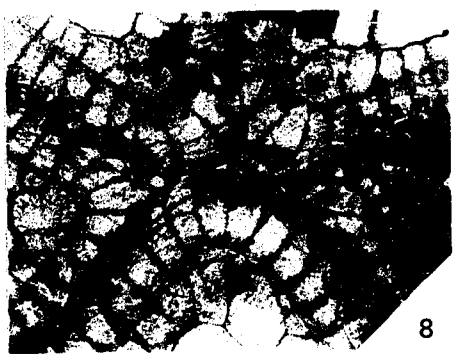

1


3


4

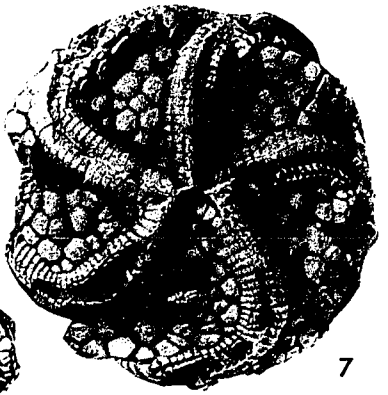

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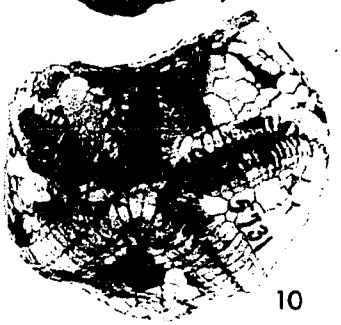

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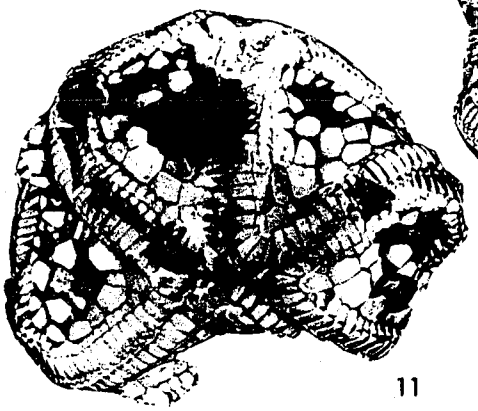

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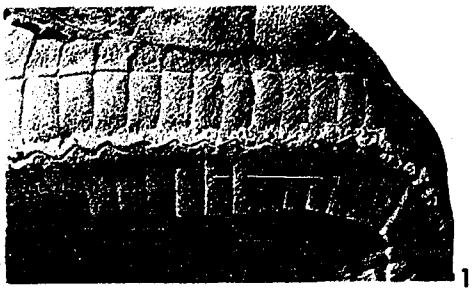

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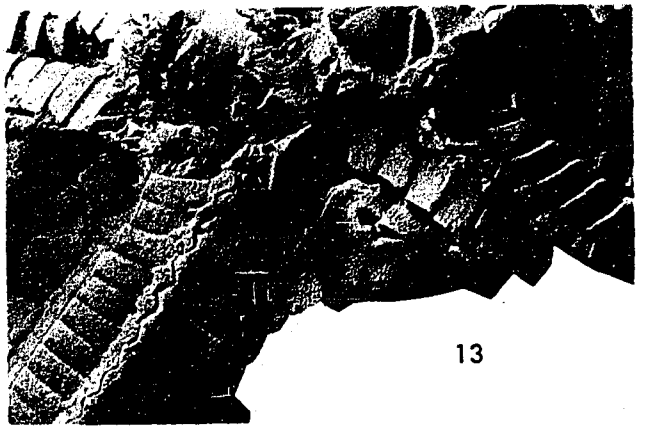

9


7


10


11


12


13

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