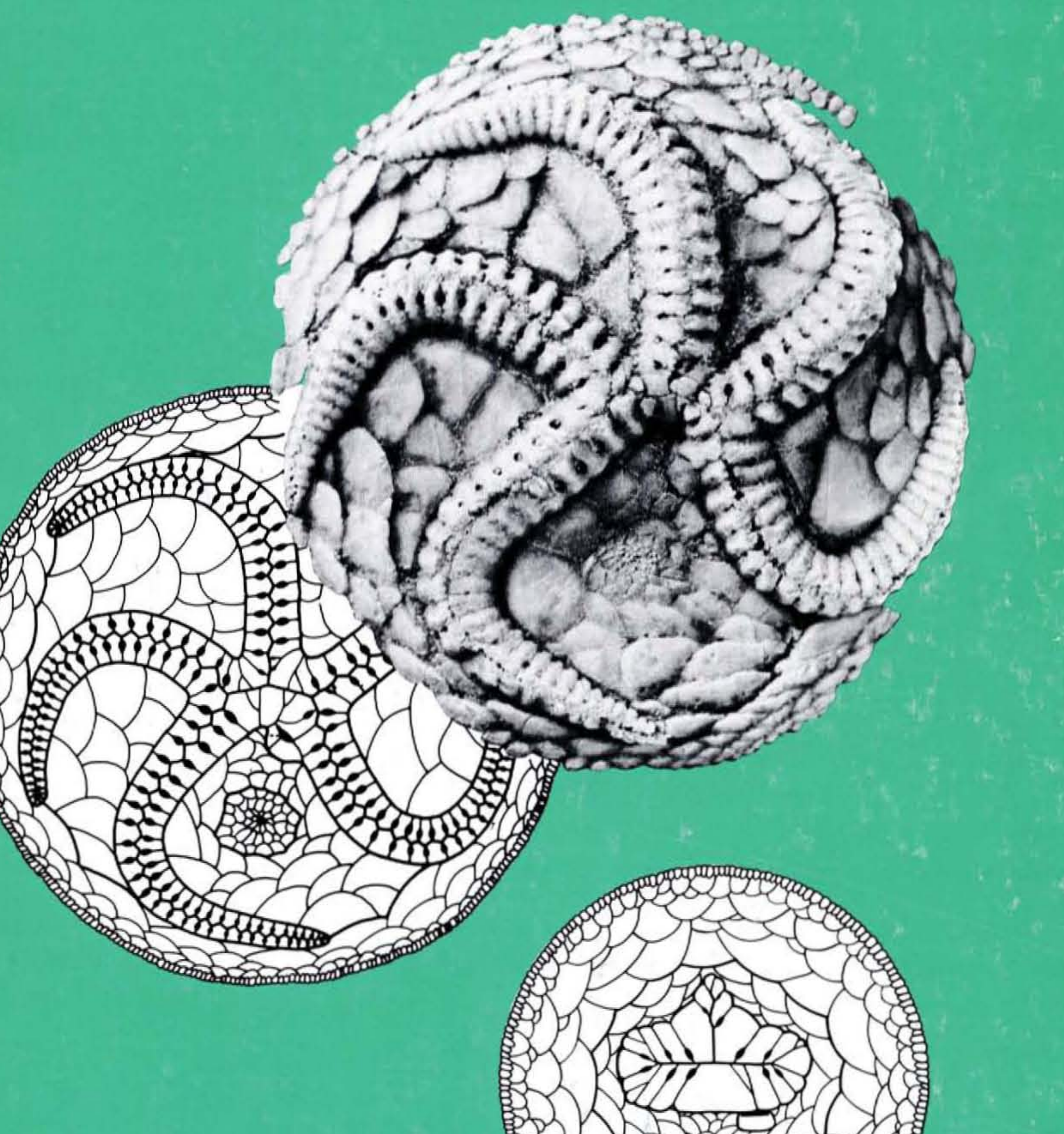
A Study of North American Edrioasteroidea

Bruce M. Bell, Senior Scientist



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ABSTRACT

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 (13 only with reservations), whereas the remaining 25 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 46 edrioasteroid species here described are grouped into the following nine subdivisions of the class. (I) Order Edrioasterida Bell, *ord. nov.*, with a subgloboid theca; oral frame formed by 10 compound plates; hydropore penetrates two posterior plates of the oral area 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 intrathecal 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 intrathecal extensions; hydropore structure in or near the posterior oral area, opening between plates along sutures; ambulacra formed by uniserial floorplates without passageways, and by biserial or multiple series of coverplates with intrathecal 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 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 coverplates form cyclic sets of two to seven plates.

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ABBREVIATIONS

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

AMNH	American Museum of Natural History, New York, New York
CFM	Field Museum of Natural History, Chicago, Illinois
CFMP CFMPE	Field Museum Paleontology Collection
CFMUC	University of Chicago Walker Museum deposited at the Field Museum
GSC	Geological Survey of Canada, Ottawa, Ontario
IUPC	Indiana University, Department of Geology, Paleontology Collection, Bloomington, Indiana
ISGS	Illinois State Geological Survey, Urbana, Illinois
ISM	Illinois State Museum, Springfield, Illinois
MCZ	Museum of Comparative Zoology, at Harvard College, Cambridge, Massachusetts
NYSM	New York State Museum, Albany, New York
ROM	Royal Ontario Museum, Toronto, Ontario
SUIC	University of Iowa, Department of Geology, Paleontology Collection, Iowa City, Iowa
UCMP	Museum of Paleontology, Department of Geology, University of Cincinnati, Cincinnati, Ohio
UCLAPC	University of California, Los Angeles, Department of Geology, Paleontology Collection, Los Angeles, California
UIPC	University of Illinois, Department of Geology, Paleontology Collection, Urbana, Illinois
UMMP	University of Michigan, Museum of Paleontology, Ann Arbor, Michigan
USNM	United States National Museum, Washington, D.C.
USNMS	United States National Museum, Springer Collection
YPM	Peabody Museum of Natural History, Yale University, New Haven, Connecticut

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 65 of the approximately 115 described edrioasteroid species, supplemented by numerous additional undescribed specimens.

Of the 65 described species that were examined, only 40 are recognized here, and 13 of these only with reservations. The remaining 25 species are here placed in synonymy. Six new species are described.

The original 65 species included types for 18 of the approximately 29 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 22 genera and 46 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 groupings, 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 12 others, described primarily on the arrangement of pedunculate 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 Stromatocystitidae suggests that they probably represent a new order. The Pyrgocystidae and Lispidecodidae have unusual thecal shapes, but both belong to the Isorophida, and probably to 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, because of the scarcity of specimens in most collections, new descriptions have usually included little comparative data and those are 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 Radiaria," 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" owing to "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*, meaning "a herd of crinoids" (New Latin from Greek *agelê* herd, *krinon* lily).

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 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. 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 separation 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 19th 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 "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 aperture 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 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 19th century. Most treated the edrioasteroids quite summarily, often using their own terms for the group. Among these were 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 with Edrioasteroidea in 1903. [Regnéll (1966) reports that 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) gallicized 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 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: "Cystoids 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 semispheroidal, and tapered underneath into a short stem, . . . [central] pentagonal mouth, . . . [ambulacra with] pinnules." Haeckel (1896b, p. 110-111) divided the Agelacystida into two subfamilies. (1) 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).*" (2) 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 (tenax), Asterocystis (tuberculata), Asteroblastus (stellatus), Edriocystis (bigsbyi), Mesites (pusireffskyi).*" Haeckel's summation of the morphology of the Agelacystida is confusing owing to the inclusion of four true cystoids along with the edrioasteroids, hence the description of pinnules, 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 " -cystis " 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 (translated from German).

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 absent 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, 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 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) and *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)] 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.
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 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. Owing to 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 contribution 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), who presented a major summary of morphology, discussed evolutionary development, and gave comparative descriptions of many species; Raymond (1915, 1921), who contributed several new Middle Ordovician species; Williams (1918), who reviewed *Agelacrinites*, including an ontogenetic series for one species; and, finally, Bassler (1935, 1936), who published two papers which 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 were 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.

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 24 genera and 92 species. Seven of these genera and 30 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.

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 floorplates 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 onto aboral surface; floorplates arranged in two series, one on each side of the ray, and alternating along the median line. [Bassler notes that the only actually diagnostic feature of the family is the presence of the biseries of floorplates.]

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

Family CYATHOCYSTIDAE Bather (1899)

Edrioasteroidea in which the aboral portion consists of a 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), in which they compiled the stratigraphic occurrence of the group and a bibliographic index of genera and species (in which they recognized 23 genera and 92 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 *Lepidodiscus 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 20 species of edrioasteroids, and most recently (1967) he described two new families; Lispidecodidae for the new

Lispidecodus 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 20 species demonstrates the taxonomic significance of the structure. Moreover, his splendid reconstructions of 13 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 of the Edrioasteroidea. This work is largely a literature compilation, owing 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 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 27 described genera.

Morphology

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.

adradial — direction toward the adradial suture.

adradial suture — zone of contact between the oral-ambulacral series plates and interambulacral plates; 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; separates the lower from the upper side of theca; commonly the greatest horizontal circumference of the theca.

ambulacral bifurcation plates — see bifurcation plates.

ambulacral coverplates — plates which cover the ambulacral groove and roof the ambulacral tunnel; may be a single or multiple biseries, or a cyclic series of plates.

ambulacral floorplates — plates which underlie the ambulacral groove and floor the ambulacral tunnel; may be a uniseries or a 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 the theca.

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

ambulacrum — morphologically and functionally unified group of structures which form each of the endothecal subvective 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; extends anteriorly from the oral pole.

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.

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 outward flaring peripheral rim; the nonplated aboral surface is restricted to the area underlying (distal to) the peripheral rim, and 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 the 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 the 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 the 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 the 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; 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 the upper side of the theca; the distal edge of the oral surface forms the thecal ambitus. The nonplated aboral surface forms the entire lower side of the theca. Lateral view: concave-convex or planoconvex; 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 the ambitus onto the 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 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 the lower side of the 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 subcircular.

endothecal — ambulacra between thecal plates, in contact with both the interior and the exterior of the 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 an unusually large theca and perhaps by modification of some thecal structures.

hydropore — external opening through the theca which links the hydrovascular 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 forms the posterior edge of the hydropore.

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

inner side of oral surface — 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.

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

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

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

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

peristome — thecal elements surrounding mouth.

perradial — direction toward the perradial line.

perradial line — 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 of ambulacra, I-II and IV-V; the anterior radius continues as ambulacrum III.

primary orals — large oral plates with intrathecal extensions which participate in the formation of the underlying oral frame and have a fixed position in the theca relative to ambulacral 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 the term is applied; opposite of distal.

right lateral primary ambulacral radius — primary ambulacral radius which extends from the oral pole out to the right ambulacral bifurcation plate along the 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 intrathecal extensions, commonly with a fixed position relative to the 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 ambulacral curvature.

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

stone canal passageway — opening through which the stone canal extended; leads from the hydropore to the interior of the theca; formed by the inner parts of the hydropore structure plates in combination with additional elements, commonly the adjacent ambulacral floorplates.

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

submarginal ambulacral suture — zone of contact between the ambulacral coverplates and floorplates in the Edrioasterida.

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

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

suture — plane formed by the junction of connected plates.

suture line — surficial line on the 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, as tiles in a floor.

test — sum of all the mesodermal skeletal plates.

theca — enclosing body surface structures consisting of the body wall with mesodermal skeleton of discrete plates, and the nonplated 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 plane perpendicular to the oral-aboral axis and through the ambitus.

transition plate — see peripheral rim transition plates.

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 the oral region between opposing anterior and posterior orals perpendicular to the anterior primary ambulacral radius; extends from the proximal tip of one lateral ambulacral bifurcation plate to the other.

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

valvular anal structure — anal structure commonly formed by an inner and an outer circlet of large, subtriangular plates; outer circlet elements alternate with and overlap the plates of the inner circlet along beveled, tightly 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.

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 nonplated 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 nonplated aboral surface. However, in clavate or "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 nonplated 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 relation 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. S347) in the "Treatise on Invertebrate Paleontology," are the 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 indicates 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.

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 most distal 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 nonplated 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, with 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 semiflexible 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 "nondomal" Isorophida are clavate, with a gibbous upper area, a downwardly constricting pedunculate zone below the ambitus, 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 nonplated 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). Postmortem 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 (text fig. 1A, D, F, G, H). The oral area is elevated above the interambulacra with the highest part of this central oral rise at the oral pole.

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 (text fig. 1D, F). 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 vs. 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 (text fig. 1A, D). 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 primary orals plus a large, right posterior hydropore oral (text fig. 1A). 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 (text fig. 1D). Additional secondary oral plates may also be present along both oral area midlines. Hydropore orals are absent in this family. The

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Text figure 1. ISOROPHIDA

A. *Carneyella pilea* (Hall), 1866, UCMP 40465, (x 5), pl. 17, fig. 7.*

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

B. Reconstruction of a segment of an ambulacrum of *Carneyella pilea* (Hall), oblique view with proximal coverplates removed to expose the floorplates and the ambulacral trough (approximately x 20).

C. *Lebetodiscus dicksoni* (Billings), 1857, GSC 437, (x 3), pl. 1, fig. 10.

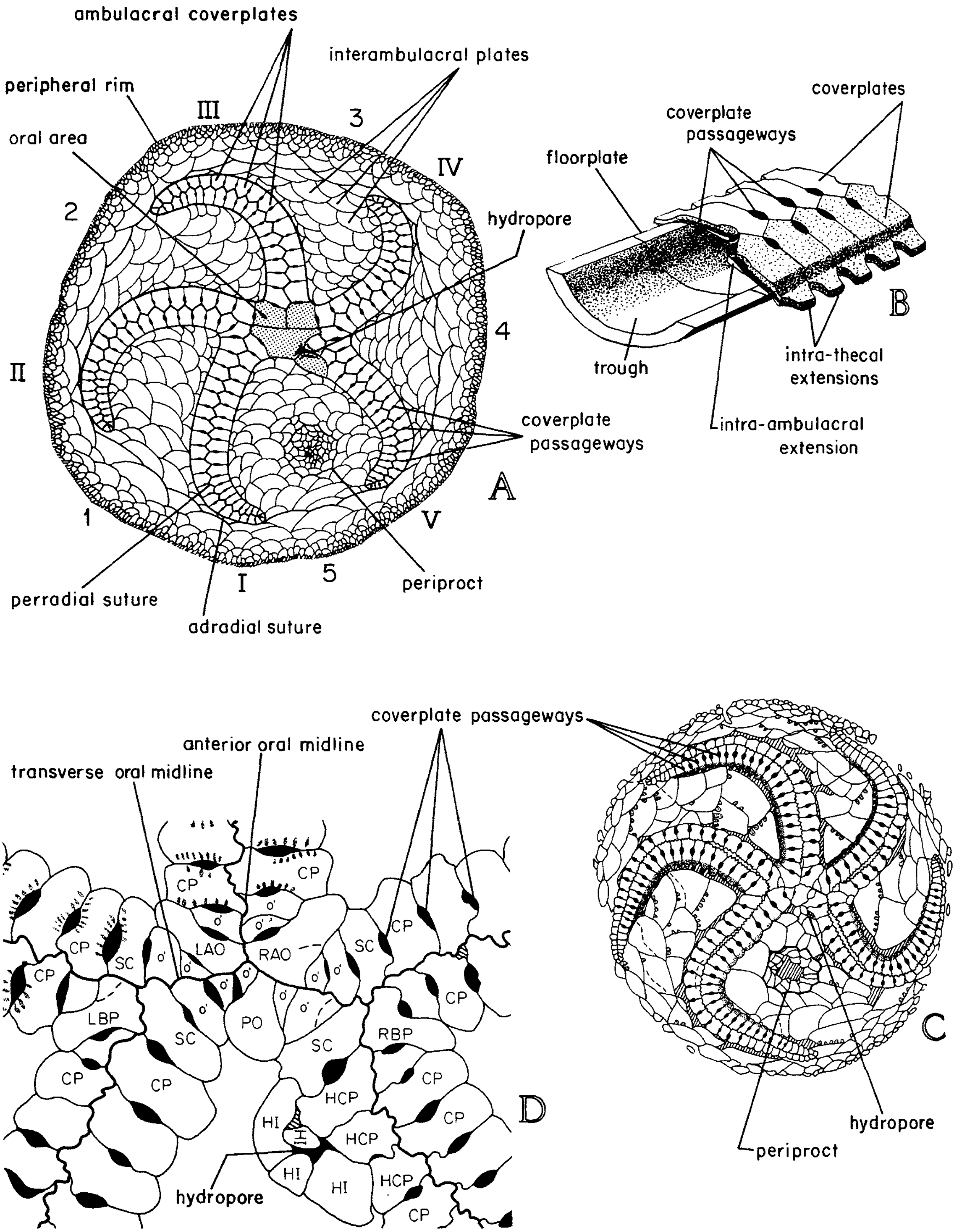
D. *Foerstediscus splendens* Bassler, 1936, USNM 4079, oral area, (x 10), pl. 5, fig. 4. CP, ambulacral coverplate; HCP, hydropore ambulacral coverplate; HI, hydropore interambulacral plate; LAO, left anterior primary oral plate; LBP, left lateral bifurcation plate; o′, secondary oral plate; PO, posterior primary oral plate; RAO, right anterior primary oral plate; RBP, right lateral bifurcation plate; SC, lateral shared coverplate.

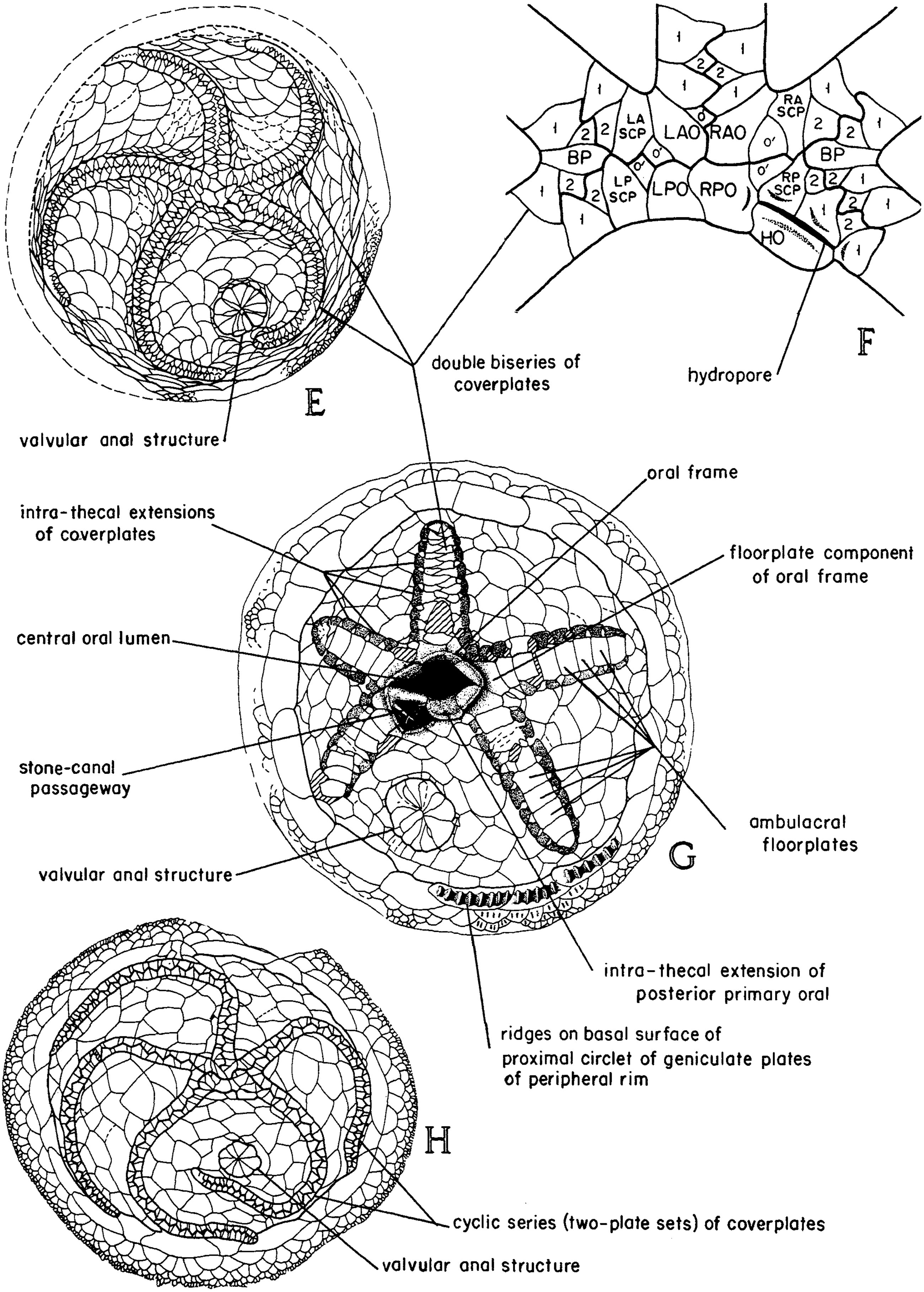
E. *Isorophus cincinnatiensis* (Roemer), 1851, UCMP 40470, (x 3), pl. 28, fig. 8.

F. Reconstruction of the oral area of *Isorophus cincinnatiensis* (Roemer) (approximately x 10). 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.

G. *Isorophusella pleiadae* (Sinclair and Bolton), 1965, GSC 14680-1, (x 12), pl. 36, fig. 1. Inner side of the oral surface.

H. *Agelacrinites hamiltonensis* Vanuxem, 1842, NYSM 362-A, (x 2.5), pl. 40, fig. 1.


ambulacral coverplates
interambulacral plates
peripheral rim
oral area
III
3
IV
2
hydropore
4
II
coverplate passageways
A
1
V
I
5
periproct
perradial suture
adradial suture
coverplates
coverplate passageways
floorplate
B
trough
intra-thecal extensions
intra-ambulacral extension
coverplate passageways
anterior oral midline
transverse oral midline
CP
o'
LAO
RAO
SC
PO
LBP
RBP
HCP
HI
hydropore
D
C
hydropore
periproct


E
F
G
H
LA SCP
LAO
RAO
RA SCP
BP
LP SCP
LPO
RPO
RP SCP
HO
double biseries of coverplates
hydropore
valvular anal structure
oral frame
intra-thecal extensions of coverplates
floorplate component of oral frame
central oral lumen
stone-canal passageway
ambulacral floorplates
valvular anal structure
intra-thecal extension of posterior primary oral
ridges on basal surface of proximal circlet of geniculate plates of peripheral rim
cyclic series (two-plate sets) of coverplates
valvular anal structure

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 (text fig. 1F, H). 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 (text fig. 1F). 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 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 asymmetrical 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 a 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 (text fig. 1G). 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 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 bladelike extensions that divide it into right and left halves, or into a small subchamber between the central lumen and the posterior part of the thecal cavity.

The transversely elongate oral frame is subovate 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 semicircular 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 intrathecal extensions from the primary oral plates. The anterior half of the frame is formed by the proximal floorplates of ambulacra II, III, IV, and the intrathecal 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 intrathecal 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, ending 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 intrathecal 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 inward and laterally. Their anterior edges flare outward laterally and form the wide contact zone with 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 intrathecal extensions of the posterior primary oral (or orals), and occasionally also by hydropore plates. These intrathecal extensions end far above the innermost edges of adjacent floorplates and thereby leave a large posterior interradial gap. The disposition of the intrathecal 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 part of the thecal cavity. Additional bladelike extensions from the coverplates extending down into the center of the posterior gap have been observed in some forms and these subdivide the gap into right and left halves. The intrathecal 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 intrathecal 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 (text fig. 1A, C, D, F, H). It lies near the proximal posterior edge of ambulacrum V. It is a slitlike opening along the contact zone 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 subtypes. 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 (text fig. 1A, F, H). The other type lies distal to the oral area, along the posterior side of ambulacrum V, and is formed by ambulacral and interambulacral plates (text fig. 1C, D). The first of these is more common. 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, in which 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.

In the Carneyellidae the posterior edge of the opening is bounded by the anterior edge of the hydropore oral (text fig. 1A). 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 (text fig. 1F). 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 slitlike 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 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), owing 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 (text fig. 1H). 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 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, the anterior ends of which 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 (text fig. 1C, D). 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 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 slitlike opening in this type of hydropore structure is variable and ranges from nearly parallel to the midline of ambulacrum V to parallel to the transverse axis of the theca.

" Peripheral " hydropore structure plates in the Lebetodiscidae may be ambulacral coverplates which are shortened to accommodate the intrusion of hydropore interambulacrals into the edge of the ambulacrum, or occasionally they may be 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 slitlike hydropore into the thecal cavity (text fig. 1G). 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 subcircular to subtriangular 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, with the hydropore distal to the center of the large inner opening of the passageway.

The stone canal passageway is formed by the intrathecal parts of the plates of the hydropore structure, one or two underlying ambulacral floorplates, and occasionally, additional elements. The upper 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 intrathecal extensions from one or more posterior hydropore structure plates.

The structure of the stone canal passageway is adequately known in only a few species, because of 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 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 sideshoot 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 appears to be of taxonomic importance. They would seem to be ontogenetic "accidents." The 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 belongs to the Isorophida, it is unique.

The ambulacra of the Isorophida are formed by a uniseries of floorplates overlain by sets of coverplates (text fig. 1B). The ambulacral tunnel is enclosed between these two sets of plates.

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 (text fig. 1A, B, C, D). 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 (text fig. 1E, F, G). The Agelacrinitidae coverplate sequence is commonly cyclic, with two to seven serially repeated sets of plates forming the cycles (text fig. 1H). 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.

Bladelike intra-ambulacral extensions commonly extend from the inner, ambulacral tunnel surfaces of the coverplates (text fig. 1B, G). 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 adjacent 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 required sequential (or peristaltic) operation of the coverplates, the individual plates being 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 as 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 Agelacrinitidae. However, these may not interlock adjacent or opposing elements. This being so, the coverplate movement in agelacrinitids may have differed from that in 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, intrathecal extensions of the coverplates commonly pass between the lateral edges of the floorplates and adjacent interambulacrals into the thecal cavity (text fig. 1B, G). In the Lebetodiscina, those extensions form the inner ends of the coverplate passageways. The intrathecal extensions interlock the coverplates into the theca and may be an important part of the articulating apparatus for movement of the coverplates. In the Isorophidae, only coverplates of the primary set appear to develop large intrathecal extensions which interlock the coverplates into the theca, and probably also participate in the articulatory apparatus (text fig. 1G). Most, and perhaps all Agelacrinitidae lack intrathecal 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 intrathecal 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 (Agelacrinitidae, some Isorophidae) 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 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 constitute 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 (text fig. 1A-D). 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 the 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*).

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 is 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, bladelike, 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 slitlike (*e.g.*, *Cryptogoleus*).

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

At least two genera, *Lebetodiscus* and *Foerstediscus*, have accessory structures, called "lateral depression series," associated with the external foramina of the passageways (text fig. 1D). These are rows of external basinlike 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.

FLOORPLATES

The ambulacral floorplates of all Isorophida are a tightly sutured uniseries which forms a solid ambulacral floor, without passageways into the thecal cavity (text fig. 1B, G). 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 interambulacrals 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 only slightly, 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, with 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 clavate species.

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 (text fig. 1A, C). 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 subconical mound. The periproct was merely a flexible zone around the anus.

In the Isorophina there is a radial, valvular anal structure (text fig. 1E, G, H). Commonly it is formed by two imbricating circlets of triangular or subtriangular 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 and out, thereby opening the central anus. The large, lateral overlap of adjacent anals would permit the structure to open widely without these anals losing contact with each other.

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 (text fig. 1A, C, E, G, H). 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 subcirclets. The lateral edges of plates in the distal subcirclet overlap the lateral edges of the two adjacent proximal subcirclet members. Thus although plates of both subcirclets are subequal in size, the externally exposed part of the distal ones is much larger than that of adjacent, proximal subcirclet plates. Commonly the distal subcirclet elements are externally squamose, the proximal plates subtrapezoidal.

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. 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 subcirclets, five to seven second circlet plates overlap each distal plate, whereas only three or four overlap the externally narrower plates of the proximal subcirclet. Thus the scallops of the line adjacent to distal subcirclet plates are much wider than, and alternate with, those adjacent to proximal subcirclet 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 because of 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, semicircular " 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 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 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 led 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 (text fig. 1G). The ridges are elongate normal to the thecal margin and commonly are sharp crests which are in contact with the underlying substrate. Seven to 10 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 collapse 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 semigloboid 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 subambital 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 nonplated aboral surface of the Isorophida. The Edrioasterida are 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 subambital 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 surface. "Echinoidal" thecae appear to have been only slightly, 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 (text fig. 2A). 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 (text fig. 2A). 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 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 submarginal suture line which is continuous with the adjacent proximal ends of the ambulacral submarginal suture lines.

Oral frame and central lumen

A massive oral frame, surrounding a central lumen, forms the inner part of the oral region (pl. 61, fig. 2, 5, 7–9). 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 subovate and transversely elongate. It extends down into the thecal cavity further than any other structure. The distal margin of the frame is subpentagonal, 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 subpentagonal 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 fused sutures and allow

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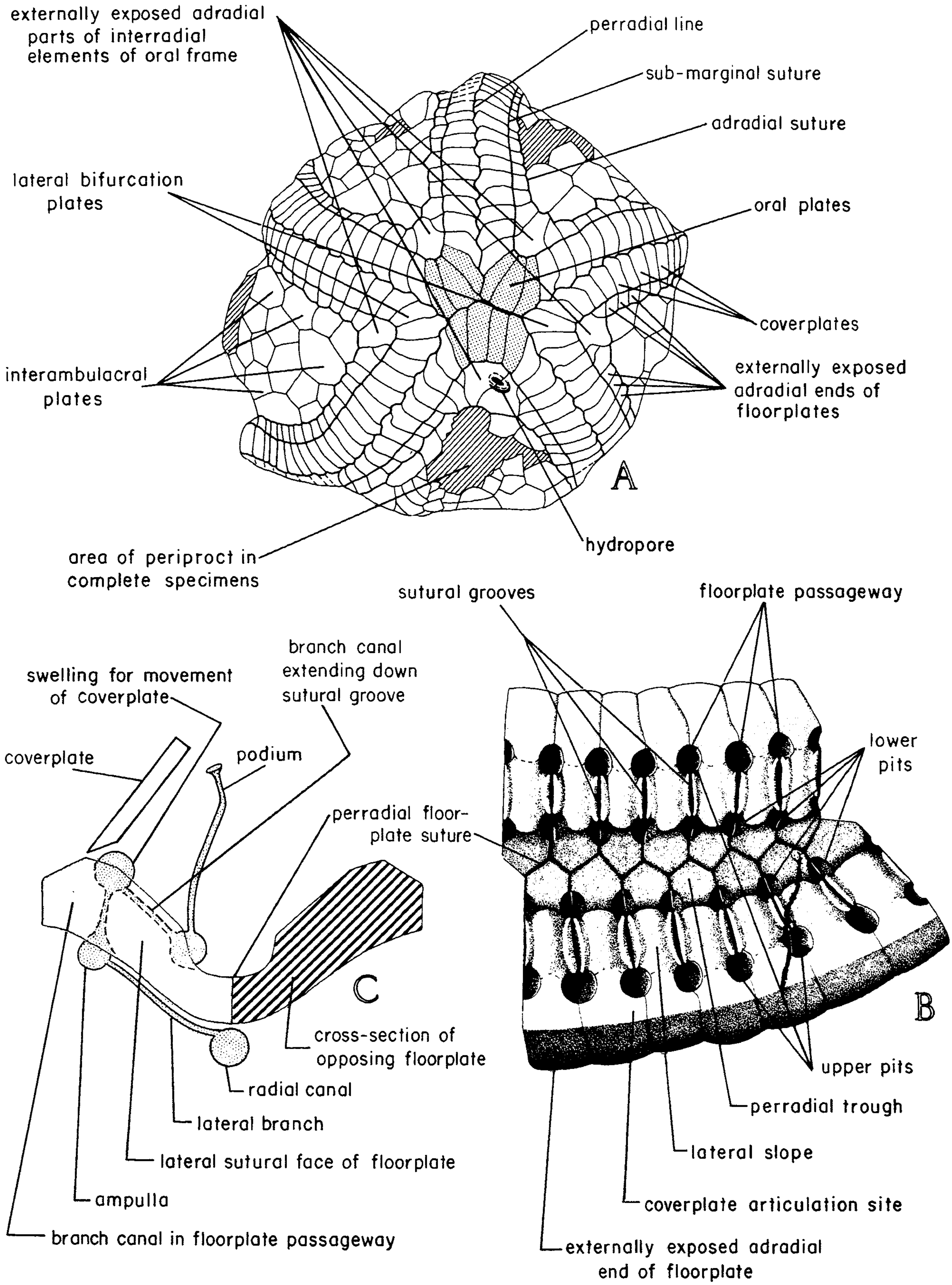
Text figure 2. EDRIOASTERIDA

A. *Edriophus levis* (Bather), 1914. UCMP 40479; (x 3), pl. 62, fig. 1.

B. *Edrioaster bigsbyi* (Billings), 1857. GSC 1407-E. (x 8), segment of one ambulacrum which exposes the upper surface of the floorplates.

C. *Edrioaster bigsbyi* (Billings), 1857. GSC 1407-E. (x 8), cross section of the ambulacrum seen in fig. B. The left floorplate shows its proximal sutural face with the coverplate passageway, sutural groove, and pits. The right floorplate (diagonally lined) is a section through the center of the alternate opposing floorplate. Parts of the hydrovascular system presumed present in life and one open coverplate have been reconstructed.


externally exposed adradial parts of interradial elements of oral frame
perradial line
sub-marginal suture
adradial suture
lateral bifurcation plates
oral plates
coverplates
interambulacral plates
externally exposed adradial ends of floorplates
A
area of periproct in complete specimens
hydropore
sutural grooves
floorplate passageway
branch canal extending down sutural groove
swelling for movement of coverplate
coverplate
podium
perradial floor-plate suture
lower pits
C
cross-section of opposing floorplate
radial canal
lateral branch
lateral sutural face of floorplate
ampulla
branch canal in floorplate passageway
B
upper pits
perradial trough
lateral slope
coverplate articulation site
externally exposed adradial end of floorplate

determination of the number of floorplate pairs included in each compound plate. The proximal edge 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 are 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 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 margins 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 the 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 (text fig. 2A). 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 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 (pl. 61, fig. 5). It penetrates both plates which bound the hydropore. Apparently the passageway is oval in cross section and expands in diameter inward. The inner end of the passageway appears to be 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 subambital 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 their 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 (text fig. 2B, C). 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.

Coverplates

The ambulacral coverplates form a single alternating biseries of plates which meet perradially along a zigzag or sinuous line (text fig. 2A, C). 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 submarginal 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 intrathecal 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, with 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.

Floorplates

The ambulacral floorplates are an alternating biseries (text fig. 2B). 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 zigzags.

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 submarginal 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 (text fig. 2B, C). 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, subcircular 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 (text fig. 2B, C). 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 subcircular 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 (text fig. 2C). 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 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, with smaller ones lying along the ambulacral sutures. The tessellation of the interambulacral areas suggests relative rigidity. Distally the interambulacra extend into the subambital 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 seem 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 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 elongate concentric with the thecal margin. The membrane apparently extended downward and distally attached to the underlying substrate. It surrounds a small, nonplated 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.

Preservation

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 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 the 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 circlets. 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 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, with the subambital, 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, with 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 is most often 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 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 plates are most severely etched. The results can be quite misleading if not properly appreciated.

Etched specimens expose subsurficial 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 on the taxonomically important coverplates. The external surfaces are removed, exposing 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.

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 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, pl. 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 nonskid 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 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 that 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 theca (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 the central basal zone seems to have been 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 have one or more ambulacra curved in a direction opposite to the others, which destroys the spiral aspect. The ontogeny of species with curved ambulacra suggests curvature in 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 Cuénot (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 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. This 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, and two lateral primary 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 lateral 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) 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 extant 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 " postmetamorphic 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 proved, 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 a great extent that extant larvae are of no help in interpreting phylogenies within the phylum beyond establishment of the " dipleurula "-like, bilateral ancestor. Fell convincingly supports his conclusion by contrasting phylogenetic inferences from the extant larval types with the contradictory phylogenies suggested by the morphology of postlarval 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 postlarval 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 confined 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 phylum. 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 work. 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 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 postmetamorphic 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 such as pentaradial, etc., which he would probably term "pentameridional" 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 dominated by the second type. Thus the growth gradients of larvae which yield the symmetry of the adult members of these three subphyla, support 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 vs. 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 plane of bilateral symmetry of postlarval 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, partly 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 incorrectly placed.

Moore and Fell (1966) reevaluated the methods of ambulacral identification in the Crinozoa, Asterozoa, and Echinozoa to allow the consistent and accurate identification of the antero-posterior plane. Their reevaluation 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 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 ambulacral 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 owing to their lack of an apparent five-part form, which thereby deletes 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 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; rather it is found in the D-E interradius of the Asterozoa and the 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, namely 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 (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 as 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-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 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 exothecal ambulacral appendages, (2) forms with " radial " (directed outward) extensions of the body, 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, as the members apparently lack any consistent pattern of symmetry. Within this framework the edrioasteroids, without 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, are 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 " is still uncertain. Moreover, 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 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 centrally. 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 that 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), in which 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 inasmuch as many other echinoderms show such a condition.

HYDROVASCULAR SYSTEM

The hydrovascular system in edrioasteroids is presumed to have included a hydropore, a stone canal, a 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 leaving a trace in the skeleton.

An opening into 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 in 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. 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, 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 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 bigsby*, 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 basinlike 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 extending 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 basinlike depressions which flank the floor of the ambulacral 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 accommodated 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 basinlike 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.

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, the outer circlet plates alternating and overlapping inner plates along tightly fitting, beveled edges. Because of this 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 reflects 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 developed some sort of anal respiratory tree 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. U118) 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, and reports, " the rectum projects as the tubular papilla and the rectal tube is in the living animal seen to undergo 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 0.5 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 trilobed 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. In Lebetodiscina one, and in Isorophidae two, posterior primary orals form the straight posterior side of the area 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 does 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.

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 0.5 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 of coverplates 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 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 number of coverplates per ambulacrum being quite variable.

The ambulacra continue to lengthen as floorplates and coverplates are added at their distal tips, and through 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 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 oral surface area, in contrast with the youngest known juveniles, in which 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 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 of 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.

Diagnostic Summary of Edrioasteroid Taxa Included

CLASS EDRIOASTEROIDEA BILLINGS, 1858

Polyplated, thecate, sedentary Echinodermata with:

— anal structure in posterior interambulacrum (5)
— triradiate or (? secondary) pentaradial symmetry
— endothecal ambulacral-oral system composed of two distinct sets of thecal elements:
  a) coverplates
  b) floorplates
  forming five (±) ambulacra and a central oral structure
— hydropore structure located in or near right posterior side of oral area
— accessory hydrovascular sutural passageway systems commonly present
— interambulacral areas polyplated, without regular order
— anal structure in posterior interambulacrum (5)

A. Order ISOROPHIDA Bell, *ord. nov.*
Edrioasteroidea with:

1) theca domal, discoidal, or clavate; aboral surface nonplated
2) oral frame formed by five proximal, ambulacral floorplates, (±) intrathecal 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 elements; hydropore opening along junctions between edges of plates and elongate parallel to plate margins
4) ambulacra composed of:
  a) uniserial floorplates without sutural passageways
  b) biserial or multiple series of coverplates with intrathecal and/or intra-ambulacral extensions 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

A-I. Suborder LEBETODISCINA Bell, *subord. nov.*
Isorophida with:

1) three central primary oral plates
2) ambulacral coverplates forming single, alternating biseries; with intra-ambulacral and intrathecal extensions
3) sutural passageways developed between coverplates, extending directly from thecal cavity to exterior of theca
4) ambulacral floorplates imbricate, each floorplate proximally overlapping distal end of adjacent floorplate
5) anal structure a periproct

A-I-a. Family LEBETODISCIDAE Bell, *fam. nov.*
Lebetodiscina with:

1) theca domal, discoidal, or clavate
2) oral area including two pairs of lateral shared coverplates; secondary orals commonly present
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 forming 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

A-I-a(1) 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, a few distal to ambulacra
8) thecal plates smooth

(1.1) *L. dicksoni* (Billings), 1857
Type species
Character of genus

A-I-a(2) Genus *Foerstediscus* Bassler, 1935

1) theca domal, oral surface highly convex
2) oral area commonly includes two sizes of secondary oral plates
3) hydropore structure as in *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

(2.1) *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 interambulacrum (5)
4) prosopon of prominent nodes covers interambulacral and marginal plates

(2.2) *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

(2.3) *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

A-I-a(3) 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 peripheral rim

(3.1) *B. orthokolus* Bell, *sp. nov.*
Type species
Characters of genus

A-I-a(4) 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 — 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 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

(4.1) *S. vorticellatus* (Hall), 1866
Type species
Characters of genus

A-I-a(5) Genus *Cystaster* Hall, 1871

1) theca discoidal to clavate
2) secondary oral plates absent
3) hydropore structure formed by four plates — two proximal coverplates of posterior side of ambulacrum V, and two large interambulacrals

4) ambulacra straight; draped down thecal surface in clavate forms

5) coverplate passageways' external foramina very elongate

6) lateral depression series absent

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

(5.1) *C. granulatus* Hall, 1871

Type species

1) theca clavate

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

(5.2) *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

A-l-b. Family CARNEYELLIDAE Bell, *fam. nov.*

Lebetodiscina with:

1) thecal domal

2) oral area including 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 forming low, rounded ridges

5) ambulacral coverplates of moderate thickness

6) ambulacral tunnel low and wide

7) coverplate passageways oblique

8) peripheral rim plates geniculate

A-I-b(1) Genus *Carneyella* Foerste, 1917

1) ambulacra curved, I-IV contrasolar, V solar

2) ambulacral terminations confined to interambulacral areas

3) coverplate passageways' external foramina elliptical to slitlike

4) anal structure a periproct

(1.1) *C. pilea* (Hall), 1866

Type species

1) prosopon of small, irregular tubercles and small, perradial coverplate ridges

(1.2) *C. faberi* (Miller), 1894

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

(1.3) *C. ulrichi* Bassler and Shideler, 1936

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

(1.4) (?) *C. valcourensis* Clark, 1920

Characters obscure

A-I-b(2) Genus *Cryptogoleus* Bell, *gen. nov.*

1) ambulacra straight

2) ambulacral terminations commonly penetrate proximal circlet of peripheral rim

3) coverplate passageways' external foramina slitlike, difficult to detect

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

(2.1) *C. chapmani* (Raymond), 1915

Type species

1) theca large

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

(2.2) *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

(2.3) *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, appear bulbous or knobby
- *5*) thecal plates smooth or with subdued pitting, occasional large nodes present

(2.4) *C. youngi* (Raymond), 1915
Characters uncertain

(2.5) *C. platys* (Raymond), 1915
Characters uncertain

(2.6) *C. billingsi* (Chapman), 1860
Characters uncertain

A-II. Suborder ISOROPHINA Bell, *subord. nov.*

Isorophida with:
- *1*) four large, central primary orals, or numerous small, undifferentiated central orals
- *2*) ambulacral coverplates forming multiple, alternating biseries or cyclic series of two to seven sets of plates; coverplates with intra-ambulacral and/or intrathecal extensions
- *3*) coverplate passageways absent
- *4*) ambulacral floorplates commonly abutting along vertical sutures, rarely imbricate
- *5*) anal structure valvular

A-II-a. Family ISOROPHIDAE Bell, *fam. nov.*

Isorophina with:
- *1*) thecal 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 forming simple alternating, multiple biseries of two or three sets of plates
- *5*) interambulacrals commonly squamose and imbricate

A-II-a(1) 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, with gradual distal taper
- *4*) interambulacrals of moderate size; squamose and imbricate

(1.1) *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 reach adradial suture line externally
- *4*) interambulacrals moderate in size

(1.2) *I. austini* (Foerste), 1914
- *1*) theca small
- *2*) five or more secondary orals
- *3*) proximal secondary ambulacral coverplates nearly as large externally as primaries, reach adradial suture line externally
- *4*) interambulacrals moderate in size

(1.3) *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

A-II-a(2) Genus *Isorophusella* Bassler, 1935
- *1*) ambulacra straight or slightly curved
- *2*) ambulacral coverplates form a regular, alternating, double biseries
- *3*) ambulacra of moderate to broad width, with gradual distal taper
- *4*) interambulacrals squamose, imbricate

(2.1) *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

(2.2) *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

(2.3) *I. pleiadae* (Sinclair and Bolton), 1965
1) theca small
2) external oral surface not observed

A-II-a(3) Genus *Hemicystites* Hall, 1852
1) ambulacra straight
2) ambulacral coverplates form double alternating biseries
3) ambulacra wide
4) interambulacrals squamose, imbricate

(3.1) *H. parasiticus* Hall, 1852
Type species
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, form perradial ridge
6) interambulacrals of moderate size
7) valvular anal structure large

A-II-a(4) Genus *Rectitriordo* Bell, *gen. nov.*
1) ambulacra straight
2) ambulacral coverplates form regular triple biseries
3) ambulacra of moderate width
4) interambulacrals squamose, imbricate

(4.1) *R. kirkfieldensis* Bell, *sp. nov.*
Type species
1) oral surface highly convex
2) oral area includes approximately 13 secondary orals
3) interambulacrals relatively large
4) distal rim plates subtriangular in external outline

A-II-a(5) Genus *Curvitriordo* Bell, *gen. nov.*
1) ambulacra curved, I-IV contrasolar, V solar
2) ambulacral coverplates form triple biseries
3) ambulacra of moderate width
4) interambulacrals squamose, imbricate

(5.1) *C. kentuckyensis* (Bassler), 1936
Type species
1) Triple biseries of ambulacral coverplates formed by regularly alternating pairs of three sets of plates; opposing pair members in contact perradially

(5.2) *C. shideleri* (Bassler), 1936
1) Triple biseries of ambulacral coverplates formed by alternating pairs of three sets of plates; opposing pair members of primary and secondary sets separated perradially by pairs of tertiary coverplates

A-II-b. Family Agelacrinitidae Chapman, 1860
Isorophina with:
1) theca domal or clavate
2) oral plates either numerous with 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 forming complex multiple biseries or cyclic sets
5) interambulacrals squamose-imbricate or polygonal-tessellate

A-II-b(1) Genus *Agelacrinites* Vanuxem, 1842
1) theca domal
2) fifteen or more oral plates which include two or more apparently 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, subpolygonal, slightly imbricate
7) valvular anal structure with two circlets of alternating plates

(1.1) *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 form regular to irregular two-plate cycles
5) interambulacrals large
6) thecal plates with prominent to subdued ridge and node prosopon

A-II-b(2) Genus *Krama* Bell, *gen. nov.*

1) theca domal
2) sixteen or more oral plates which include four large primary orals, one hydropore oral, and lateral secondary orals which resemble ambulacral coverplate sequence
3) hydropore structure semi-integrated
4) ambulacra curved, I-III contrasolar, IV-V solar; of moderate width
5) ambulacral coverplate sequence a mixture of cyclic sets and biserial pairs
6) interambulacrals squamose, imbricate
7) valvular anal structure formed by two circlets of alternating plates

(2.1) *K. devonicum* (Bassler), 1936

Type species

1) theca of moderate size
2) hydropore structure formed by three or more plates
3) ambulacral coverplate series which includes three-plate cycles and one late-developing fourth set added as biserial pairs
4) interambulacrals relatively large
5) anal plates centrally elevated to form small central protuberance

A-II-b(3) 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 form two- or three-plate irregular cycles, coverplates steeply inclined
6) interambulacrals squamose, imbricate
7) valvular anal structure formed by three circlets which form highly elevated cone

(3.1) *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, which include two posterior elements

(3.2) *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, which include one large posterior element

(3.3) (?) *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

(3.4) (?) *P. alpenensis* (Bassler), 1936

Characters unknown

A-II-b(4) Genus *Discocystis* Gregory, 1897

1) theca clavate
2) numerous small orals, primaries undifferentiated
3) large hydropore protuberance separate from oral rise
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

(4.1) *D. kaskaskiensis* (Hall), 1858

Type species

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

A-II-b(5) Genus *Lepidodiscus* Meek and Worthen, 1868

1) theca highly convex, domal, or clavate
2) numerous small orals, primaries undifferentiated
3) large, elongate hydropore structure separate 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

(5.1) *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

(5.2) *L. laudoni* (Bassler), 1936
1) theca large, clavate; pedunculate zone plates numerous, imbricate, subrectangular, very thin, and in vertical columns
2) ambulacral coverplates perradially raised, form small perradial ridge
3) ambulacral floorplates abutting; each with two lower-surface, lateral protuberances
4) central interambulacrals polygonal, tessellate

(5.3) *L. sampsoni* (Miller), 1891
1) theca clavate or subclavate, pedunculate zone plates squamose, imbricate, without regular order
2) ambulacral coverplates perradially raised, form a perradial ridge
3) ambulacral floorplates abutting; each with four or more inner surface, lateral protuberances
4) interambulacrals large, polygonal, tessellate

A-II-b(6) 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

(6.1) *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

A-II-b(7) 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

(7.1) *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

A-II-b(8) Genus and species indeterminate
Pennsylvanian fragments

A-II-c. Family Uncertain

A-II-c(1) 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 single alternating biseries
6) interambulacrals large, thick, polygonal, tessellate
7) valvular anal structure formed by one circlet

(1.1) *H. commensalus* Bell, *sp. nov.*
1) theca small to moderate in size
2) fourteen oral plates which include 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

A-III. Suborder and Family Uncertain
(?) *Hemicystites carbonarius* Bassler, 1936
1) theca small, domal
2) characters not interpretable

B. Order EDRIOASTERIDA Bell, *ord. nov.*
Edrioasteroidea with:
1) thecal shape "echinoidal," oral surface plates extending below ambitus onto lower side of theca
2) oral frame formed by 10 compound plates which include numerous floorplates and five modified proximal interambulacrals
3) hydropore structure located in posterior part of oral area, formed by two plates; hydropore opening elongate perpendicular to suture line and 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 intrathecal or intra-ambulacral extensions; 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; attached to substrate; peripheral rim not present

B-I-a. Family EDRIOASTERIDAE Bather, 1898
Characters of the order

B-I-a(1) Genus *Edrioaster* Billings, 1858
1) ambulacra curved, I-IV contrasolar, V solar
2) ambulacral coverplates perradially angular, form right-angle, zigzag, perradial lines
3) right posterior hydropore plate abuts adradial ends of proximal posterior floorplates of ambulacrum V

(1.1) *E. bigsbyi* (Billings), 1857
Type species
1) theca large
2) thecal plates with large, rounded nodes
3) ambulacral curvature initiated above ambitus

(1.2) *E. priscus* (Miller and Gurley), 1894
1) theca small
2) thecal plates smooth
3) ambulacral curvature initiated below ambitus

B-I-a(2) Genus *Edriophus* Bell, *gen. nov.*
1) ambulacra curved, I-V solar
2) ambulacral coverplates perradially sinuous and elevated, form sinuous perradial ridge
3) right posterior hydropore plate fused to adradial ends of proximal posterior floorplates of ambulacrum V

(2.1) *E. levis* (Bather), 1914
Type species
1) theca large
2) thecal plates smooth

(2.2) (?) *E. saratogensis* (Ruedemann), 1912
1) theca small
2) thecal plates finely pustulose

Systematic Paleontology

Class EDRIOASTEROIDEA Billings, 1858

Diagnosis

Polyplated, thecate, sedentary Echinodermata with: initially triradiate and subsequently pentaradiate symmetry; five (±) endothecal ambulacra radiating 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; hydropore opening 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, periproctal 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 nonplated central aboral surface, without a stem or stalk.

The ambulacra are formed by outer coverplates and underlying floorplates. Edrioasteroids lack exothecal appendages. The central covering orals are distally continuous with the ambulacral coverplate series. The oral frame is formed by enlarged proximal ambulacral floorplates and commonly, also by intrathecal extensions from the overlying orals. In certain species (Edrioasterida), the oral frame includes 10 large compound plates. Ambulacral coverplate passageways (in Lebetodiscina) or floorplate passageways (in 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 formed by the right posterior plates of the oral area. In certain forms (Lebetodiscidae) it is 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 largest interambulacral plates are in the central and distal parts of each interambulacrum.

Discussion

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 of edrioasteroids including described taxa not covered in this study

Class EDRIOASTEROIDEA Billings, 1858

Lower Cambrian — Pennsylvanian. Australia, Belgium, Canada, Czechoslovakia, England, France, Germany, Scotland, Sweden, United States, U.S.S.R.

Order ISOROPHIDA Bell

Suborder LEBETODISCINA Bell

Family LEBETODISCIDAE Bell

Black River Group, Mohawkian Series, Middle Ordovician — Keyser Group, Cayugan Series, Upper Silurian. Australia, Canada (Ontario), Czechoslovakia, United States (Indiana, Kentucky, Minnesota, Ohio, Pennsylvania).

Family CARNEYELLIDAE Bell

Chazy Group, Mohawkian Series, Middle Ordovician — Richmond Group, Cincinnatian Series, Upper Ordovician. Canada (Ontario), United States (Illinois, Indiana, Kentucky, Minnesota, New York, Ohio, Tennessee).

Suborder ISOROPHINA Bell

Family ISOROPHIDAE Bell

Chazy Group, Mohawkian Series, Middle Ordovician — Clinton Group, Niagaran Series, Middle Silurian. Canada (Ontario, Quebec) ?Czechoslovakia, United States (Indiana, Kentucky, Minnesota, New York, Ohio, Tennessee, Virginia).

Family AGELACRINITIDAE Chapman, 1860

Helderberg Group, Helderbergian Series, Lower Devonian — Magdalena Group, Virgilian Series, Pennsylvanian. Canada (Alberta, Ontario), England, Germany, United States (Alabama, Illinois, Indiana, Iowa, Kentucky, Michigan, New Mexico, New York, Pennsylvania, West Virginia), U.S.S.R.

Order EDRIOASTERIDA Bell

Family EDRIOASTERIDAE Bather

Trenton Group, Mohawkian Series, Middle Ordovician. Canada (Ontario, Quebec), United States (Kentucky, Michigan, Minnesota, New York). (?) " Psammites du Controz," Upper Devonian. Belgium.

Others:

Family STROMATOCYSTITIDAE Bassler, 1936

[*Stromatocystites* Pompeckj, 1896; *Walcottidiscus*, Bassler, 1935] Lower Cambrian (" *Olenellus* beds ") — Middle Cambrian. Canada (British Columbia, Newfoundland), Czechoslovakia, France, Germany, Sweden, U.S.S.R.

Family CYATHOCYSTIDAE Bather, 1899

[*Cyathocystis* Schmidt, 1879; *Cyathotheca* Jaekel, 1918] ? Lower Ordovician; Chazy Group, Mohawkian Series, Middle Ordovician. United States (Oklahoma, Tennessee), U.S.S.R. (Estonia). Upper Ordovician or Lower Silurian. Sweden.

Family PYRGOCYSTIDAE Kesling, 1967

[*Pyrgocystis* Bather, 1915]

? Lower Ordovician; Chazy Group, Mohawkian Series, Middle Ordovician — Middle Devonian. Czechoslovakia, England, Germany, Scotland, Sweden (Gotland), United States (Minnesota, New York), U.S.S.R.

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 intrathecal extensions from primary orals; hydropore structure in or posterior to right posterior 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 intrathecal extensions, and uniserial floorplates; ambulacral coverplate passageways present in some; margin of oral surface a peripheral rim.

Description

The 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 is elevated above the interambulacra and forms the central oral rise which is distally continuous with the elevated ambulacral ridges.

The external 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 transversely elongate oral frame underlies the external orals and surrounds a large central lumen. The proximal rim of the frame, which extends down into the thecal cavity, is ovate. Distally the frame is continuous with the floorplate series of each ambulacrum, which imparts a pentagonal outline to the frame.

The hydropore 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 intrathecal 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 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 intrathecal 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 either by 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 an interambulacrum.

The peripheral rim is 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 discussion 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 forming single, alternating biseries, coverplates with both intra-ambulacral and intrathecal extensions; ambulacral coverplate passageways present; ambulacral floorplates imbricate; anal area a periproct.

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 the three large, central primary orals and either a single large hydropore oral or sets of lateral shared coverplates and secondary orals. The oral frame includes both proximal floorplates and intrathecal extensions from at least the primary orals.

The hydropore structure is formed by oral-ambulacral series plates, and in some species 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 intrathecal 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, subcircular openings to elongate slits.

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

Interambulacral plates are squamose and imbricate.

The anal periproct is formed by several irregular 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 (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 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 to 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 that 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 being 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 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 basinlike lateral depressions led 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 in both families of three primary orals, a single biseries of coverplates, the coverplate passageway system, the imbricate floorplates, and a periproctal 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, and 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 forming 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 from 10–20 mm adult diameter. Commonly the oral surface appears to have been nearly hemispherical with the marginal plates almost vertical in many specimens.

The oral area includes 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 comprises the adradial ends of one or two modified ambulacral coverplates and a variable number of interambulacral plates, at least one of which is 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 (text fig. 3). 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 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 pitlike 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, the 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 workers had included all the Isorophida in a single family, the Agelacrinitidae.

Bassler (1936) and subsequent authors included in the Hemicystitidae several other species which are excluded from the Lebetodiscidae. Most of these are included here in the Carneyellidae. 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* is not included in the present 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 possible 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 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.*

In contrasting the differences between the Lebetodiscidae and the Carneyellidae, the 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, thereby forming high ambulacral ridges and a high, narrow ambulacral tunnel and orienting the large coverplate passageways almost normal to the thecal surface; 4) squamose peripheral rim plates. The Carneyellidae are characterized by: 1) oral area with only the three primary orals and one hydropore oral (no shared coverplates or secondary orals); 2) hydropore structure located in the right posterior part of the oral region, formed by ambulacral coverplates and orals (rather than interambulacrals); 3) ambulacral coverplates of moderate thickness, thereby forming low, rounded ambulacral ridges and low, wide ambulacral tunnels, thus making the coverplate passageways nearly parallel to the thecal surface; 4) peripheral rim plates geniculate.

RANGE AND OCCURRENCE: Middle Ordovician through Upper Silurian of eastern North America and Australia.

Genus *Lebetodiscus* Bather, 1908

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

1857 *Agelacrinites* Vanuxem, Billings, E., Geol. Surv. Canada, Rept. Prog. 1853–1856: 294–295.

1858b *Agelacrinites* Vanuxem, Billings, E., Geol. Surv. 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 State 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.

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 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., Geol. Surv. Canada, Rept. Prog. 1853-1856: 294-295.

1858b *Agelacrinites dicksoni* Billings, E., Geol. Surv. 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.

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 State 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., 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 coverplates; hydropore structure formed by second proximal posterior coverplate 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.

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, both of 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 passageways which are along the anterior edges of the two anterior primary orals are open, as in all of the ambulacral coverplate passageways. Conversely, the other four (two flanking the lateral edges of the anterior primaries and the 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 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, GSC 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, slitlike 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 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 in which 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 intrathecal 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, sinuous, perradial line. In external plan view the plates are subrectangular; their perradial ends are bluntly pointed (text fig. 3C-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. 3C-F, H, pl. 1, fig. 5, pl. 2, fig. 4, 5). The exterior arches outward and forms a rounded, submedian 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. 3H). 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 halfway down to the underlying floorplate. The middle ridge is largest, flanked by two smaller ridges which are subequal in size.

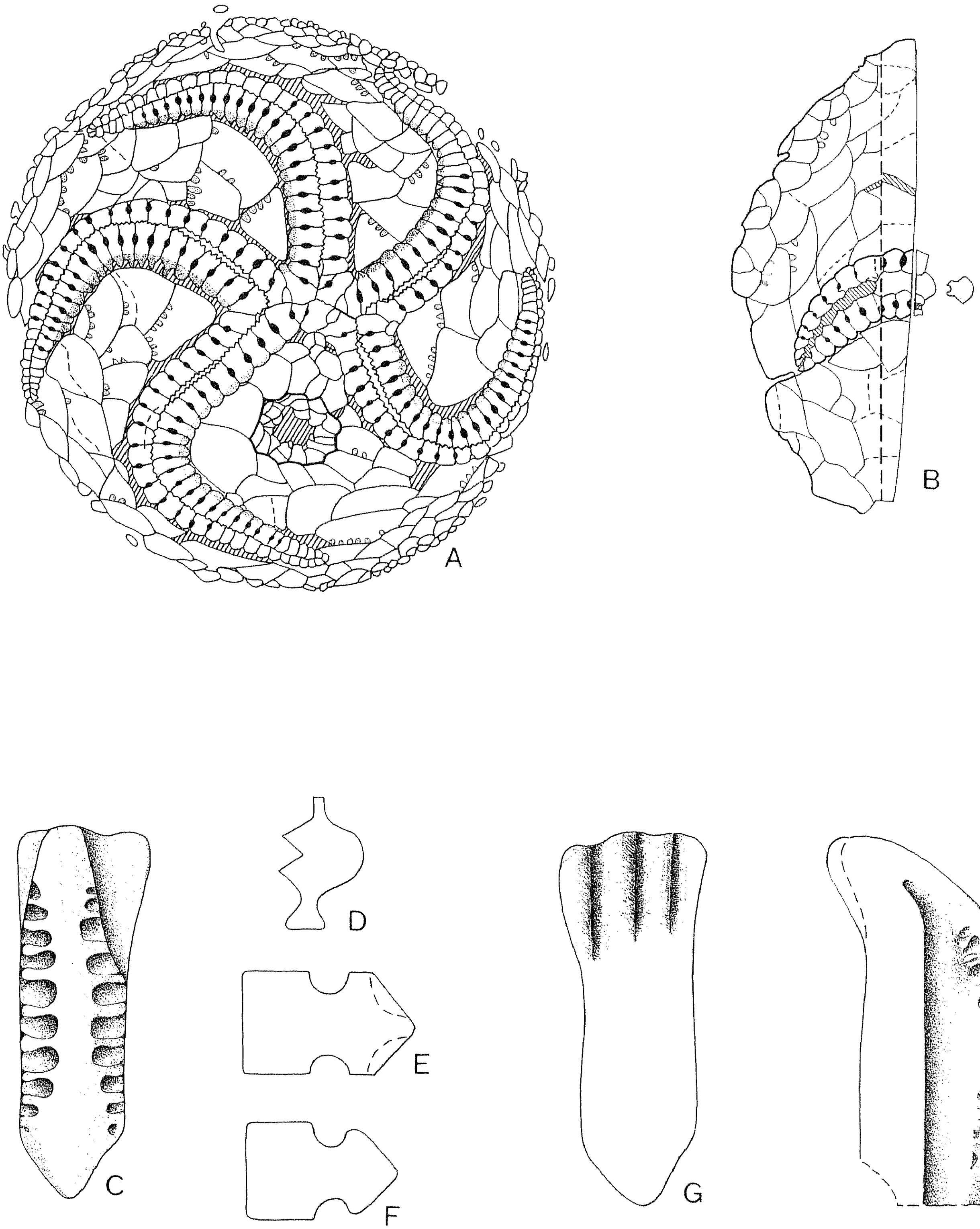
The intra-ambulacral ridges on opposing alternate coverplates interdigitate along the perradial line when the coverplates are closed. The area of interlocking is not great, but the ridges fit tightly together and seal the ambulacrum. In etched specimens the upper ends of these interlocking ridges are exposed and form small serrations along the perradial line.

Text figure 3. *Lebetodiscus dicksoni* (Billings), 1857

A. GSC 437, (x 4), pl. 1, fig. 10. Stippled ends of coverplates are the intrathecal extensions exposed by lateral displacement of adjacent interambulacrals.

B. Holotype, GSC 1407-B, (x 6), 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. 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.


A
B
C
D
E
F
G
H

Large, bladelike intra-ambulacral extensions are produced from the proximal edge of the ambulacral tunnel side of each coverplate (text fig. 3D, 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. Thus these intra-ambulacral extensions are trough-shaped (text fig. 3C, D). The perradial end of each extension is produced 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 halfway 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 when the coverplates were rotated open, with 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 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 intrathecal extensions of the coverplates. These are as thick as the external parts of the coverplates, in contrast with most intrathecal 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 intrathecal 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 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 diminishes 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 sides 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, basinlike 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 subcircular and deeply incised into the external surface of the coverplate. The floor of the basin remains at nearly the same level. Thus owing 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.

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, alternating, or even changing their relative position along the length of a single sutural trough.

Text figure 4. *Lebetodiscus dicksoni* (Billings), 1857

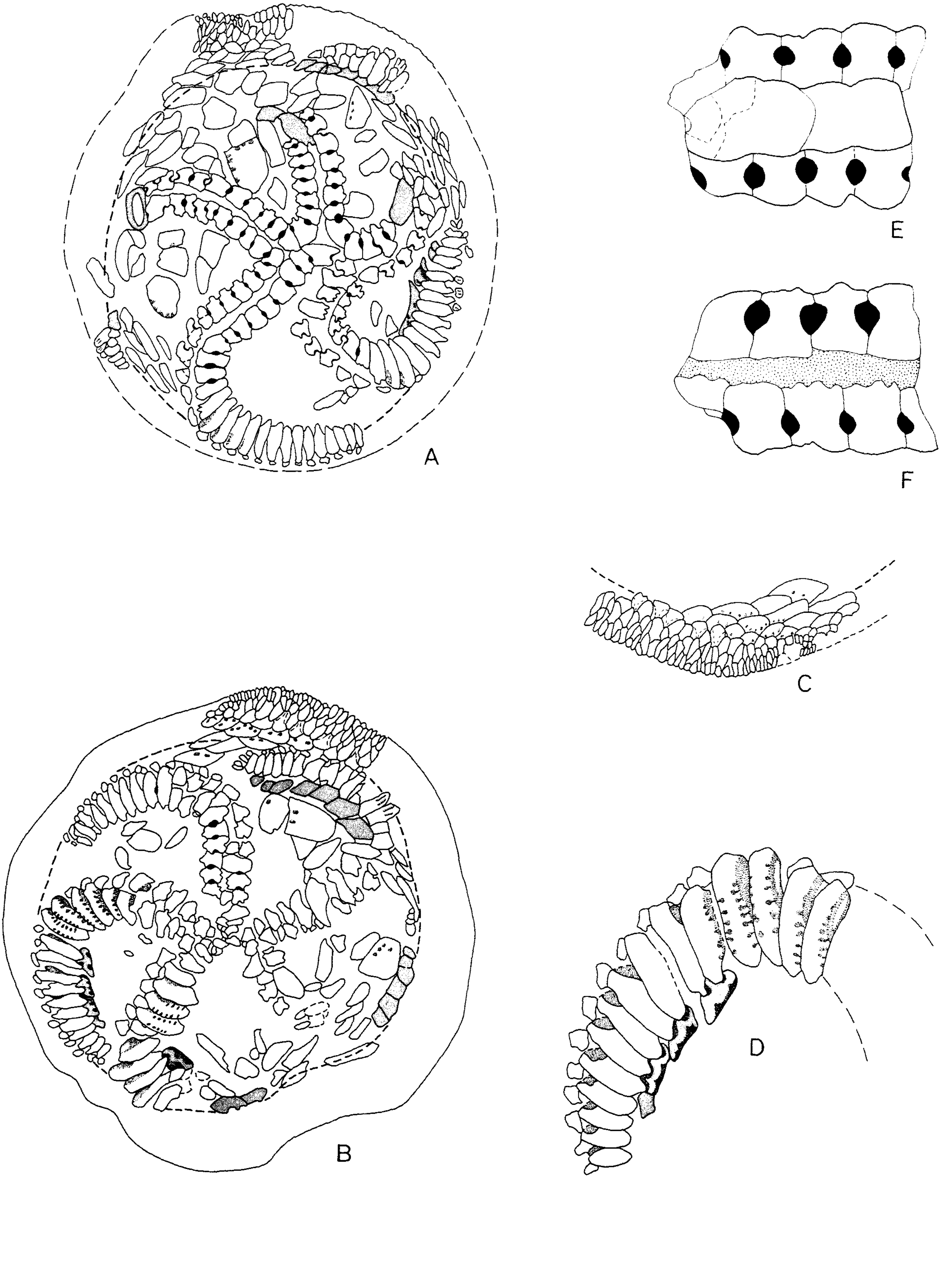
A. ROM 161-t-a (x 4), pl. 2, fig. 8. Ambulacral floorplates are shaded.

B-D. GSC 1414.

- B. Oral surface, (x 4), pl. 2, fig. 2. Ambulacral floorplates are shaded.
- C. Peripheral rim segment, (x 5), pl. 2, fig. 6.
- D. Ambulacrum II, (x 11), pl. 2, fig. 4. Coverplate intra-ambulacral extensions and lateral basins are stippled; floorplates are shaded.

E-F. Segment of ambulacrum IV, GSC 1412, (x 12).

- E. Interior side, pl. 2, fig. 12.
- F. Exterior side, pl. 2, fig. 13. Ambulacral tunnel zone stippled.


A
E
F
C
B
D

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 are 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, subrectangular 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, which flank 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 intrathecal extension of the coverplate.

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 do 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, subpolygonal 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. Usually, they are 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 periproctal 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 they approach it. The structure appears to have been elevated to form a low, conical protuberance.

The peripheral rim comprises seven or eight circlets of squamose 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 next circlet outward 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 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 smooth, except for a fine pitting which reflects the microstructure of the plates where stroma canals intersected the plate surface.

Specimens

GSC 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, together with a bit of the adjacent peripheral rim. The fragment has been sawed from the holotype (some time since the original description) by a vertical cut through the 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 pl. 1, fig. 1, 2 and text fig. 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 it is only a fragment, it is obvious from the structure of the ambulacra that it pertains to *Lebetodiscus dicksoni*. Fortunately, owing to the scarcity of *L. dicksoni*, Raymond (1915, 1921) described in detail the holdings of the Geological Survey of Canada. 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 this fragment with Billings' (1858) original figure of the holotype shows a close similarity between the specimen and the drawing. It should be noted, as Bather

(1908) had previously, that Billings' illustration of the type specimen is much more complete than his written description. Bather evidently saw the type specimen before it was sawed, and indicated 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.

GSC 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.

GSC 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 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 for it the species *L. loriformis* and Wilson (1946) created the genus *Lepidoconia* for Raymond's species.

GSC 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. 10B.

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 was glued back in place. This fragment was removed again and is illustrated here, showing 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 relative to the coverplates than in nonetched specimens. Apparently over half the thickness of the coverplates has been removed.

ROM 161-t-a. A *Lebetodiscus dicksoni* described by Raymond (1915, 1921) and by Wilson (1946) as " GSC 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 to expose a vertical cut through ambulacrum II and an oblique cut through ambulacrum 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 GSC 1415, for the specimen compares well with Raymond's 1915 description, including the ground sections through ambulacra II and III. Wilson (1946) noted that GSC 1415 was missing from the Geological Survey collections and erroneously considered the specimen to be the holotype of the species, which it clearly is not, as noted by Raymond (1915). Dr. Thomas E. Bolton of the Geological Survey of Canada 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).

ROM 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.

ROM 18855 (A-C). Three specimens of *L. dicksoni.* Trenton Limestone, Trenton Group, Mohawkian Series, Middle Ordovician. Hull, Quebec.

ROM 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.

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

YPM 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 that it is 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 is broken. This is the only representative of this species in which an additional ambulacrum is known. The specimen also appears to be 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 Professor 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 described in detail by Bather (1908). It is from the Lower Trenton Group, 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. It is from the Trenton Limestone at Pakenham, Ontario.

Discussion of previous investigations

The designation of the holotype of *Lebetodiscus dicksoni* (Billings), (represented here by specimen GSC 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 Geological Survey of Canada. Billings had only one specimen in his possession, but noted he had seen others. Because 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 collection of the Geological Survey of Canada (the one specifically mentioned in the original description), and a second one, the Bigsby specimen. It is entirely possible that the Bigsby specimen played a part in the original description (*i.e.,* one of his " other specimens " of the species), but this cannot be 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.* GSC 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, ambulacral 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 reillustrated 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 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 probably fragments of plates. This explains why he thought only a few " coverplates " were present in the specimen and that all that could be said about them was that they were tiny and had no regular arrangement. It now appears that Bather's specimen is a typical example of *L. dicksoni.* Unfortunately, it was not available for reexamination 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 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 has misinterpreted the ambulacral coverplates as floorplates, and pointed out that the true floorplates were uniserial, but hidden from view in Bather's specimen. However, Raymond did not deny the existence of the small median plates which Bather reported; 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 redescribing *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 were so long that they nearly touched 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 *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