ECHINOZOANS

By J. Wyatt Durham, K. E. Caster, Harriet Exline, H. B. Fell, A. G. Fischer, D. L. Frizzell, R. V. Kesling, P. M. Kier, R. V. Melville, R. C. Moore, D. L. Pawson, Gerhard Regnéll, Georges Ubaghs, and Carol D. Wagner

CONTENTS

Subphylum ECHINOZOA Haeckel in Zittel, 1895

[Diagnosis prepared by H. B. Fell]

Fundamentally globoid, including secondarily discoid and cylindroid echinoderm forms that entirely lack arms, brachioles, or outspread rays such as characterize most crinozoans and asterozoans. Earliest members with mouth and anus at opposite ends of body but these are secondarily displaced in many later forms. Meridional water vessels traversing body wall in direction of anus, such vessels originally lying on surface of theca but in later Paleozoic and all post-Paleozoic groups sinking into its substance. Skeleton, nervous system, reproductive organs, and muscular system tending to be differentiated into meridional systems, although underlying bilateral symmetry is discernible generally and in course of evolution may become expressed strongly. *L.Cam.(Olenellus Zone)-Rec.*

GENERAL FEATURES AND RELATIONSHIPS OF ECHINOZOANS

By H. Barraclough Fell and Raymond C. Moore

[Harvard University; University of Kansas]

INTRODUCTION

Echinozoans are fundamentally globoid, cylindroid, or discoid echinoderms which entirely lack outspread rays, such as characterize asterozoans, and arms or brachioles,[1] such as occur in most crinozoans.

Earliest echinozoan classes have the mouth and anus at opposite extremities of the body, thus defining an anteroposterior axis, but in some later classes these orifices of the alimentary tract are found to be secondarily displaced. Meridionally disposed water vessels traverse the body wall in the direction of the anus, such vessels originally lying on the surface of the theca (as interpreted by Fell, strongly doubted by Dur-

---

[1] The calcareous scale-covered podia of ophiocistioids cannot be compared closely with the arms of crinoids, supported by an internal skeleton of solid ossicles, or with similar structures of other crinozoans.

HAM) but in later Paleozoic and all post-Paleozoic groups sinking into its substance. Skeletal elements, reproductive organs, and the muscular and nervous systems tend to be differentiated in meridional patterns, although an underlying bilateral symmetry almost invariably is evident.

The echinozoans are defined as a subphylum and included classes are designated Helicoplacoidea (L.Cam.), Edrioasteroidea (L.Cam.-L.Carb.), Ophiocistioidea (L.Ord.-U.Ord.), Cyclocystoidea (M.Ord.-L.Sil.), Holothuroidea (?M.Ord., Dev.-Rec.), and Echinoidea (M.Ord.-Rec.).

BACKGROUND

Until recently, zoologists customarily have divided the phylum Echinodermata into two contrasted subphyla, respectively named Pelmatozoa and Eleutherozoa. The Pelmatozoa, predominantly represented by fossil forms, have been construed to include groups that throughout all or at least part of their postlarval life are attached in fixed manner to the substrate and that carry the oral and anal openings of the spirally twisted gut on the upwardly directed surface of the body or the anus may be located laterally on the theca (this side being defined as posterior). Crinoids, cystoids, blastoids, and the much less common fossil groups known as eocrinoids, paracrinoids, and edrioblastoids are typical pelmatozoans. The Eleutherozoa comprise almost exclusively free-living echinoderms in which the mouth is directed downward or anteriorly and the anus (if present) is usually placed on the upper surface or posteriorly at end of the body opposite the mouth. Best-known eleutherozoans are the sea urchins (echinoids), sea cucumbers (holothurians), starfishes (asteroids), and brittle stars (ophiuroids).

The various pelmatozoan and eleutherozoan groups differ from one another so widely that the task of elucidating their interrelationships and defining the nature of their presumed common ancestry has been extremely difficult. Recent morphological and paleontological studies by FELL (4-6) have led to definite conclusion that the star-shaped members of the so-called eleutherozoans are so interrelated as to comprise a single grouping classifiable as a subphylum, and for it the name Asterozoa is available. Similarly, other evidence implies that the globoid, cylindroid, and discoid so-called eleutherozoans are probably interrelated also, and these may be associated in another subphylum named Echinozoa. Consequently, the too-inclusive "Eleutherozoa" are an outmoded polyphyletic assemblage and the name should be abandoned for taxonomic purposes. On the other hand, if confined to characterization of life habit only, the descriptive noun and adjective "eleutherozoan" are conceded to have usefulness.

The discovery of a class of echinoderms named Helicoplacoidea by DURHAM & CASTER (3), found in oldest known (*Olenellus* Zone) fossil-bearing rocks of California, has shown that primitive, free-living members of the Echinodermata already had become differentiated in earliest Cambrian time. The morphological characters of the Helicoplacoidea partly resemble those of Echinoidea, Holothuroidea, and Edrioasteroidea, suggesting a relationship of all four classes to a common ancestral stock. This stock, then, is inferred to be the source of eleutherozoan helicoplacoids, holothurians, and echinoids on one hand and to prevailingly pelmatozoan edrioasteroids on the other. On the basis of common features of body form, however, especially absence of ray-like and armlike extensions from it, all are assignable to the subphylum Echinozoa.

The Echinozoa represent an ancient stock, modern representatives of which are the Holothuroidea and Echinoidea, whereas the Asterozoa are of later origin, interpreted by FELL (6) to have been derived from pinnulate pelmatozoans belonging or allied to the Crinoidea. Recent studies of dendrochirote holothurians (PAWSON & FELL, 12), partly discussed in the later section of this volume devoted to Holothuroidea (p. *U*641), indicate the essentially archaic nature of this group and point to possibly significant relationships with the Cambrian helicoplacoids. Also, some observed parallelism of the psolid dendrochirotes and edrioasteroids serves to reinforce judgment that the Edrioasteroidea belong with echinozoan echinoderms, rather than the subphylum Pelmatozoa, where previously they have been placed (4, 7).

Relationships of the early Paleozoic Homalozoa examined critically by UBAGHS

(13) are doubtful. These are asymmetrical echinoderms which in specialized forms show a tendency toward bilateral symmetry, though none fully attain it. They were evidently free-living (eleutherozoan) in habit (Fig. 90,*1*), for none fixed permanently to the substrate are known. Classification as homalozoans is not based on life habit of the animals.

In summation, Fell (7) has pointed out that four contrasted structural patterns are clearly discernible in echinoderms as follows (see also chapter by Ubaghs on "General Characters of Echinodermata," *Treatise,* Part S).

(1) A **homalozoan pattern,** represented by early Paleozoic forms with skeletal parts arranged asymmetrically or displaying some degree of bilateral symmetry, is seen in classes named Homostelea (Fig. 90,*1*), Stylophora, and Homoiostelea, formerly grouped together as "Carpoidea." They are assigned to the subphylum named Homalozoa Whitehouse, 1941. Other classes named Cyamoidea, Cycloidea, and Machaeridia, have very doubtful status.

(2) A **crinozoan pattern** comprises prevailingly globoid forms with partial radiate meridional symmetry from which ambulacral feeding appendages (arms,

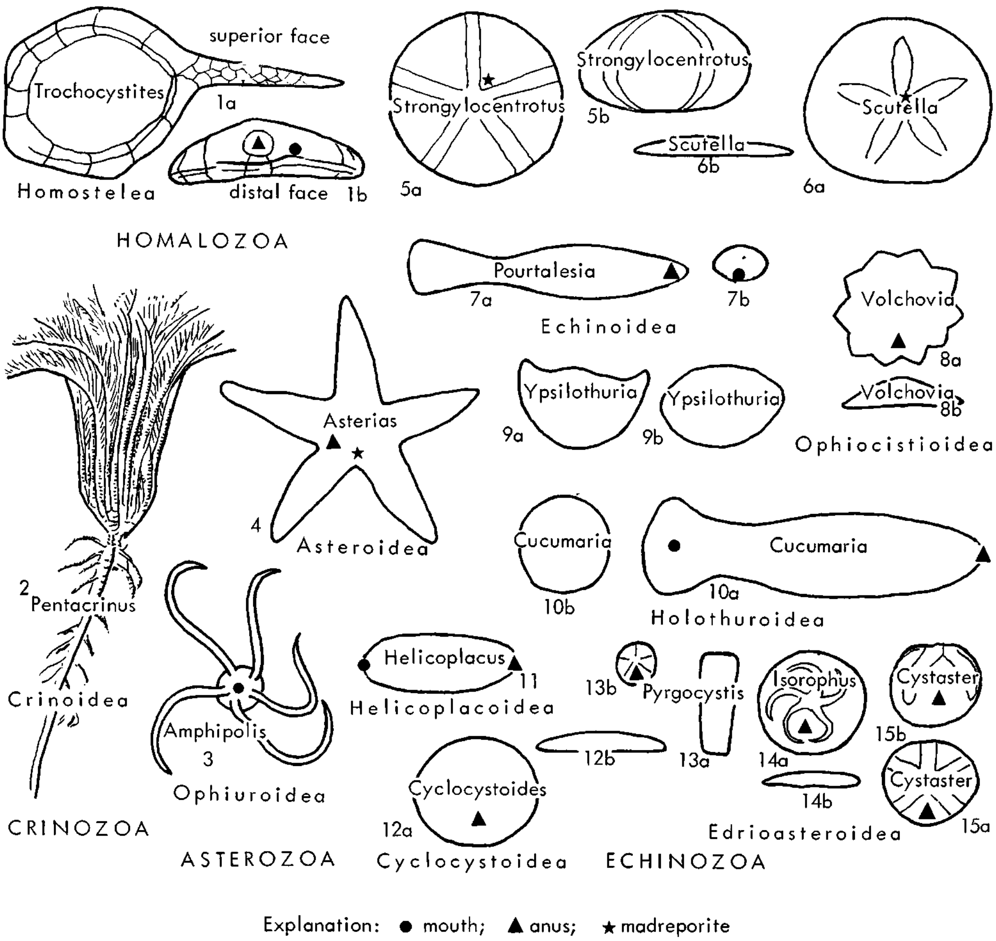


Fig. 90. Types of thecae representative of echinoderm subphyla (diagrammatic, not to scale).——*1.* Homalozoa (carpoid).——*2.* Crinozoa (crinoid).——*3,4.* Asterozoa (ophiuroid, asteroid).——*5-15.* Echinozoa (*5-7,* echinoids; *8,* ophiocistioid; *9,10,* holothurians; *11,* helicoplacoid; *12,* cyclocystoid; *13-15,* edrioasteroids).

brachioles) extend upward or outward. Most of them are attached to the substrate in fixed location throughout postlarval life, but some are free-moving (eleutherozoan) as adults. They include classes named Eocrinoidea, Paracrinoidea, Cystoidea, Crinoidea (Fig. 90,*2*), Edrioblastoidea, and Blastoidea. These are grouped in the subphylum Crinozoa MATSUMOTO, 1929 (=Pelmatozoa LEUCKART, 1848, *partim*).

(3) An **asterozoan pattern** is characterized by radially divergent axes of symmetry expressed by relatively broad to elongate narrow extensions of the body spread laterally outward. Commonly the central body surrounded by its rays has a star-shaped outline. Three subclasses named Somasteroidea, Asteroidea (Fig. 90,*4*), and Ophiuroidea (Fig. 90,*3*) are recognized, grouped together in the class Stelleroidea and the subphylum Asterozoa HAECKEL in ZITTEL, 1895.

(4) An **echinozoan pattern** consists of globoid, cylindroid, and discoid forms with well-marked radial meridional symmetry which entirely lack outspread extensions comparable to the arms or brachioles of crinozoans or the rays of asterozoans. The classes Helicoplacoidea (Fig. 90,*11*), Holothuroidea (Fig. 90,*9,10*), Ophiocistioidea (Fig. 90,*8*), Cyclocystoidea (Fig. 90, *12*), Edrioasteroidea (Fig. 90,*13-15*), and Echinoidea (Fig. 90,*5-7*) are divisions of the subphylum Echinozoa HAECKEL in ZITTEL, 1895. Most echinozoans are free-moving throughout life, but some edrioasteroids and dendrochirote holothurians are recognized as sessile animals.

In agreement with FELL (7), it seems evident that the mode of life adopted by various echinoderm assemblages is not acceptable as the governing criterion for classification of them in first-rank divisions (subphyla), even though this may affect morphological features importantly. Eleutherozoan tendencies exclusively characterize Homalozoa, Asterozoa, and nearly all Echinozoa, whereas they are confined to a minority of Crinozoa (comatulid and various other crinoids, possibly a few blastoids and cystoids). Clearly, the four patterns of symmetry which have been described briefly are entirely unrelated to these tendencies. Free-living echinoderms acquire locomotor mechanisms that facilitate quest for food by browsing on algae, by preying on other animals, and by swallowing large quantities of mud in order to extract its small organic content. This is accompanied generally by the development of jaws or special oral appendages suited to gross (macrophagous) feeding. The anus, if present, tends to be placed remote from the mouth, commonly on the opposite side of the body. Among sessile echinoderms locomotor organs are partly or entirely lost, forcing the animals to depend on such planktonic food sources as sea currents may provide. Feeding is of microphagous type, food particles being carried by some ciliary or comparable mechanism with aid of the tube feet along food grooves of appendages and the upper body surface to the mouth. The alimentary canal has a more or less contorted U-shape, with mouth and anus directed upward in locations not far apart. These features characterize most Crinozoa, in contrast to the Asterozoa and Echinozoa.

EVOLUTION OF ECHINOZOA

The oldest known organism classed as an echinozoan is *Helicoplacus* (L.Cam., *Olenellus* Zone, Calif.-Nev.), although a locally associated fossil (edrioasteroid, *?Stromatocystites*) is also classed as an echinozoan (2, p. 52). Eocrinoids are other echinoderms found in this ancient fauna.

The mouth of *Helicoplacus* is located at the broadly rounded end of its fusiform body (therefore interpreted by DURHAM & CASTER, 1963, as anterior) and the anus probably occurs at the tapered opposite extremity (Fig. 91,*1*). The very numerous small plates of the theca are disposed in closely adjoined spiral rows twisted counterclockwise. A single narrow band of minute platelets (bifurcated in some individuals) which winds around the body is interpreted by FELL (7) to denote an external water vessel, although observations by DURHAM (personal communication) indicate a possibility that this water vessel may have been internal. The narrow band of platelets, identified as an ambulacrum, divides the thecal surface into halves that define a sort of bilateral symmetry greatly affected by torsion. It is combined wtih an apparent radial symmetry defined by arrangement of the thecal plates. FELL (7) has noted that simi-

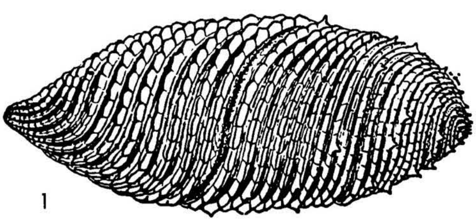


FIG. 91. *Helicoplacus,* L. Cam., USA (Calif.); lat. view of theca (reconstr.), ×0.33 (3).

lar torsion is observed in earliest echinoids (e.g., *Eothuria*) of Ordovician age, although in them the symmetry is overtly radial (more correctly meridional) as defined by the five twisted ambulacral meridians, regularly spaced at intervals of 72 degrees. Analogous torsion also is seen in the Edrioasteroidea, persisting to their extinction in the Lower Carboniferous, but it has not been reported in the Holothuroidea and Ophiocistioidea. The torsion soon was lost in the echinoid line. The oldest known edrioasteroid (*Stromatocystites,* L.Cam., Czech., ?Calif.; M.Cam., France, Sweden) had straight ambulacra, rather than curved ones. Also, the echinoid *Aulechinus,* a contemporary of *Eothuria,* and the somewhat older *Bothriocidaris* exhibit no signs of torsion.

Helicoplacus may have been an eleutherozoan bottom-feeding echinoderm rather similar to a plated dendrochirote holothurian. Its thecal plates formed a complete, robust, flexible test. The varying degrees of expansion and contraction observed in the fossils (3) imply existence of musculature capable of altering thecal shape in a manner comparable to operation of a concertina. Perhaps *Helicoplacus* crept over the sea floor like an annelid. The occurrence of the fossils in a very fine clastic matrix denotes a mud-bottom habitat and suggests that this echinoderm may have been a mud-swallower, like many nondendrochirote holothurians. The small size of the mouth has led DURHAM (personal communication) to guess, rather, that these echinoderms depended for food on small organic particles gathered from surrounding water by a mucus-secreting or ciliary mechanism, such food particles being then passed along the ambulacrum to the mouth. *Helicoplacus* may thus have lived much of the time in an upright position as a somewhat sedentary inhabitant of the muddy sea bottom, only occasionally assuming a horizontal attitude.

In the view of FELL (7), the primitive state of the lone ambulacrum of *Helicoplacus* implies that this structure carried rudimentary tube feet which may have been respiratory organs or possibly only sensory tentacles, like the dorsal tube feet of many holothurians. The completeness of thecal plating and probable rudimentary nature of the tube feet are evidence that no effective respiratory mechanism existed on the body surface. If this is correct, FELL has judged it reasonable to infer that rectal respiration was required, either of the pulsatory crinoid type or by means of respiratory trees, as in holothurians. The distribution of respiratory trees in various orders of holothurians suggests that these structures are related directly to habits of the animals and implies that the earliest holothuroids already had developed such trees. It seems likely, then, that rudimentary respiratory trees were present in the Helicoplacoidea, although the divergent speculations on the significance of nearly all observed morphological features leave much doubt.

The earliest Echinoidea, represented by such forms as *Eothuria,* resemble the helicoplacoids not only in torsion of the body wall, as previously noted, but in the flexible nature of the multiplated theca. Possibly these features indicate derivation of the echinoid line from helicoplacoids. The early Paleozoic echinoids possessed five well-developed ambulacra, on which (as interpreted by FELL) the meridional water vessels lay as external structures (though with internal ampullae for the tube feet). This is doubted by DURHAM and UBAGHS (personal communication) who note that in *Bothriocidaris, Ectinechinus* and *Eothuria* the radial water vessels clearly were internal; in *Aulechinus* they are susceptible of either interpretation.

Structural details of the ambulacral pores of early echinoids show that the tube feet were large and probably suctorial; certainly they were extensile and muscular. Thus they could serve the double function of locomotor and respiratory organs, as in modern echinoids. The fossils exhibit a moderately well-developed jaw mechanism, which shows that the early echinoids were capable of feeding in the manner of their extant endocyclic descendants, biting and grinding organisms in the substrate and chewing algae. Such features demonstrate an eleutherozoan habit and deny pelmatozoan tendencies, for echinoderms provided with feeding mechanisms of this sort rapidly would starve if they adopted a sessile existence.

The Ophiocistioidea developed a rigid skeleton by solid union of adjacent thecal plates in a manner comparable to that seen in modern echinoids. Locomotion was effected by use of the grossly enlarged and plated tube feet of the oral surface. These tube feet, which specially distinguish the class, doubtless also served the function of nutrition by sweeping up detrital material and cramming it into the downwardly directed mouth. The anus, as in endocyclic echinoids, was located on the upper surface next to the margin or midway between it and the apical pole. Habits of the ophiocistioids surely were eleutherozoan, as indicated by their morphology and by lack of any known sessile forms.

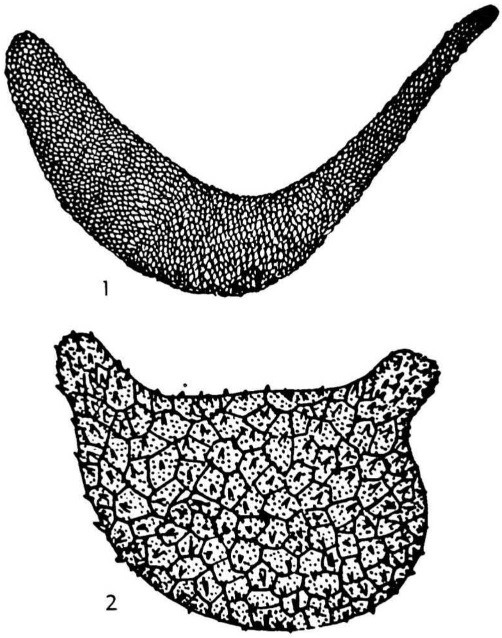


FIG. 92. Holothurians.——*1. Placothuria,* Rec.; lateral view of fine-plated theca, ×3 (Pawson).——*2. Ypsilothuria,* Rec.; lat. view showing large spine-bearing plates of theca, ×3 (Ludwig).

Oldest known fossil remains of Holothuroidea consist of isolated diminutive skeletal plates. However, recent studies (12; see also p. *U*646) indicate strong probability that the Ordovician and later Paleozoic holothurians closely resembled some modern members of the Dendrochirotida (e.g., *Placothuria*; Fig. 92,*1*) and of a new order named Dactylochirotida (12), the latter exemplified by *Ypsilothuria* (Fig. 92,*2*). These holothurians cited for comparison are all heavily plated forms with a complete test made up of large plates which commonly are provided with rigid spinous processes. The early holothurians are judged to be similar also to *Helicoplacus* and to the Ordovician echinoids with flexible theca (e.g., *Eothuria,* originally considered to be a holothurian). Suctorial tube feet probably were lacking in earliest holothurians, judging from their rudimentary state in extant plated genera, but this is uncertain. If such tube feet had not yet been developed, locomotory movement of the animals must have been effected by contraction and expansion of the body wall and its flexible test (7). When they were provided with suctorial tube feet, movement on the echinoid plan would have been possible. Morphological evidence indicates that some kind of jaw apparatus comparable to the echinoid lantern was developed early in evolution of the holothurians, but with development of the dendrochirote type of tentacles, apparently the apparatus was abandoned and its elements served the new purpose of providing attachments for the radial and retractor muscles. In this fashion the organ persisted in later holothurians as the calcareous ring surrounding the pharynx.

Probably the many-branched dendrochirote type of tentacle was evolved from initially simple tube feet of finger-like form in the oral region (12). Repeated dichotomy could lead to the very complex dendritic tentacles of the Dendrochirotida, which are efficient for collecting planktonic food and conveying it to the mouth by ciliary action accompanied by contractions of the tentacles and spooning movements of the two ventral tentacles. The dendrochirotids, whether motile or not, are able to trap sufficient nourishment by filtering of sea water, provided that currents replace the

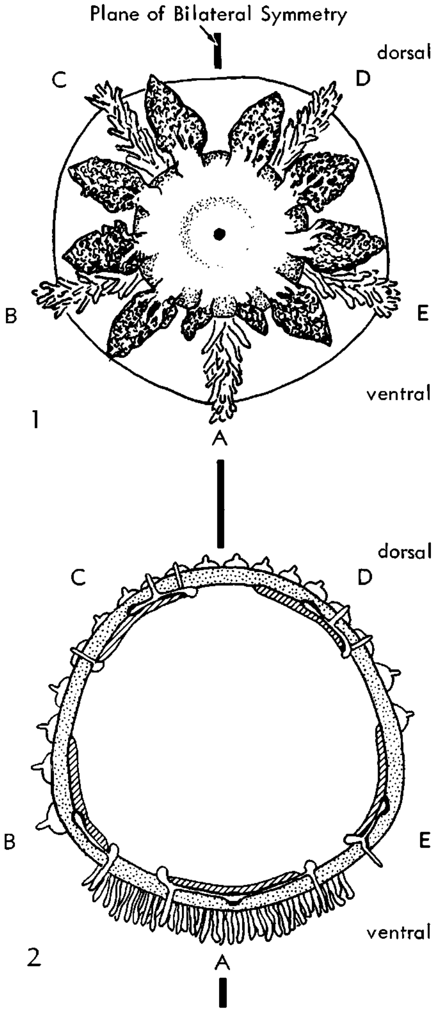


FIG. 93. Anterior and cross section views of holothurians showing differentiation of ventral and dorsal sides and vertical plane of bilateral symmetry. ——*1. Cucumaria,* Recent dendrochirotidan from front, showing pair of reduced ventral tentacles and crowded tube feet of five rays (*A-E,* designations of rays, Carpenter system) (diagram.).——*2.* Cross section (diagram.) of body of *Holothuria,* Rec. aspidochirotidan, showing ventral locomotory tube feet and paxillate tube feet of dorsal and lateral surfaces (*A-E,* Carpenter designations of rays).

surrounding water so as to bring fresh supplies of food particles. From the dendrochirotids more than one line of evolution is possible, for they have the means of adopting either eleutherozoan or pelmatozoan habits. If a locomotor system is retained, the oral tentacles can be adapted to serve for collection of food, operating in various ways. In the Cucumariidae, for example, the body may be held erect, attached only by the posterior tube feet, with tentacles around the upraised mouth spread outward in the manner of a sea anemone (Fig. 93,*1*). In holothurians that adopt a

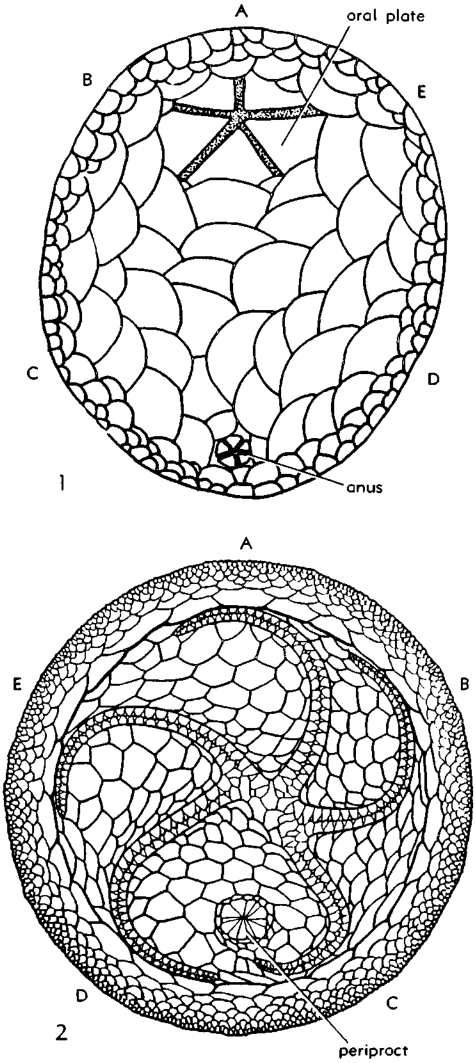


FIG. 94. Comparison of psolid holothurian with edrioasteroid (diagram.). ——*1.* Dorsal view of *Psolus,* a dendrochirotidan, showing oral and anal plates near opposite extremities and imbricated nature of other thecal plates (*A-E,* Carpenter designations of rays).——*2. Isorophus,* upper (oral) surface of typical edrioasteroid showing prominent curved ambulacra and periproct in posterior *(CD)* interray (10).

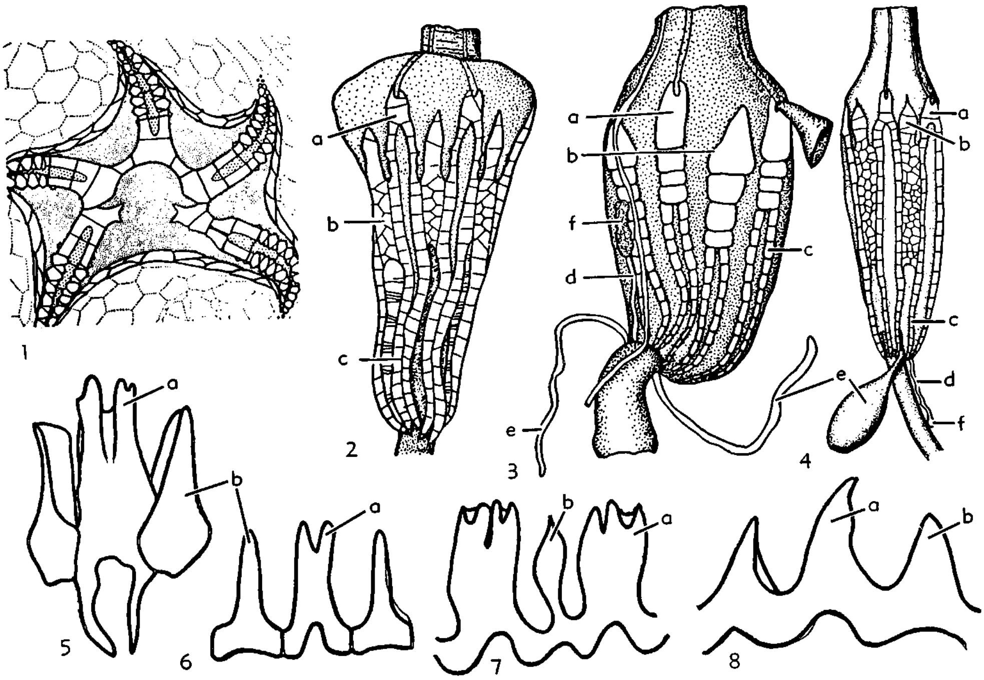


FIG. 95. Calcareous rings of edrioasteroid and holothurians.——*1.* Oral side of *Isorphus,* U.Ord. edrioasteroid, showing calcareous ring and associated ambulacral plates (10).——*2-4.* Side views of pharyngeal region of dendrochirotidan holothurians *Pentadactyla, Placothuria,* and *Neothyonidium,* showing calcareous rings and associated structures, all Rec. (Pawson).——*5-8.* Diagrammatic outlines of part of calcareous rings of *Euthyonidiella, Psolus, Thyonidium,* and *Mitsukuriella,* from side (all Rec. dendrochirotidan holothurians) (*5,7,8,* from Heding & Panning, 1954; *6,* Pawson). [Explanation: *a,* radial piece of calcareous ring; *b,* interradial piece; *c,* posterior process of radial; *d,* madreporic duct (or stone canal); *e,* Polian vesicle; *f,* madreporite.]

horizontal attitude the lower and upper sides are not determined at random or changed from time to time. The lower (ventral) side bears abundant locomotory tube feet, whereas the upper (dorsal) and lateral surfaces have much less numerous (paxillate) tube feet associated with low pimple-like elevations (Fig. 93,*2*). Aspidochirote forms can readily evolve from dendrochirotids, thus permitting gross mud-swallowing and a markedly eleutherozoan habit (7).

Another possibility is for the locomotory system to be converted to a purely adhesive role, thus leading to a sessile (pelmatozoan) habit, though no known holothurian fully attained this. It is illustrated by the psolid dendrochirotes, some genera of which exhibit a flattened limpet-like body which adheres by its broad ventral surface to a firm substrate (Fig. 94,*1*). They may be classed as statozoans (temporarily fixed), rather than true pelmatozoans (permanently fixed). The exposed dorsal and lateral surfaces are covered by a test composed of robust imbricated plates. The mouth and anus are placed on the upper surface and commonly protected by valvate plates similar to those of edrioasteroids and various cystoids.

The whole body, in fact, is somewhat comparable to that of an edrioasteroid, except for its lack of external ambulacral plates (Fig. 94,*2*). Morphological features of the psolids are closer to those of the Edrioasteroidea than to characters of many Holothuroidea and Echinoidea. They chiefly differ from edrioasteroids in the same way that distinguishes them from echinoids, namely, in the internal placement of their water vessels, as a result of which the psolid test lacks ambulacral plates. The

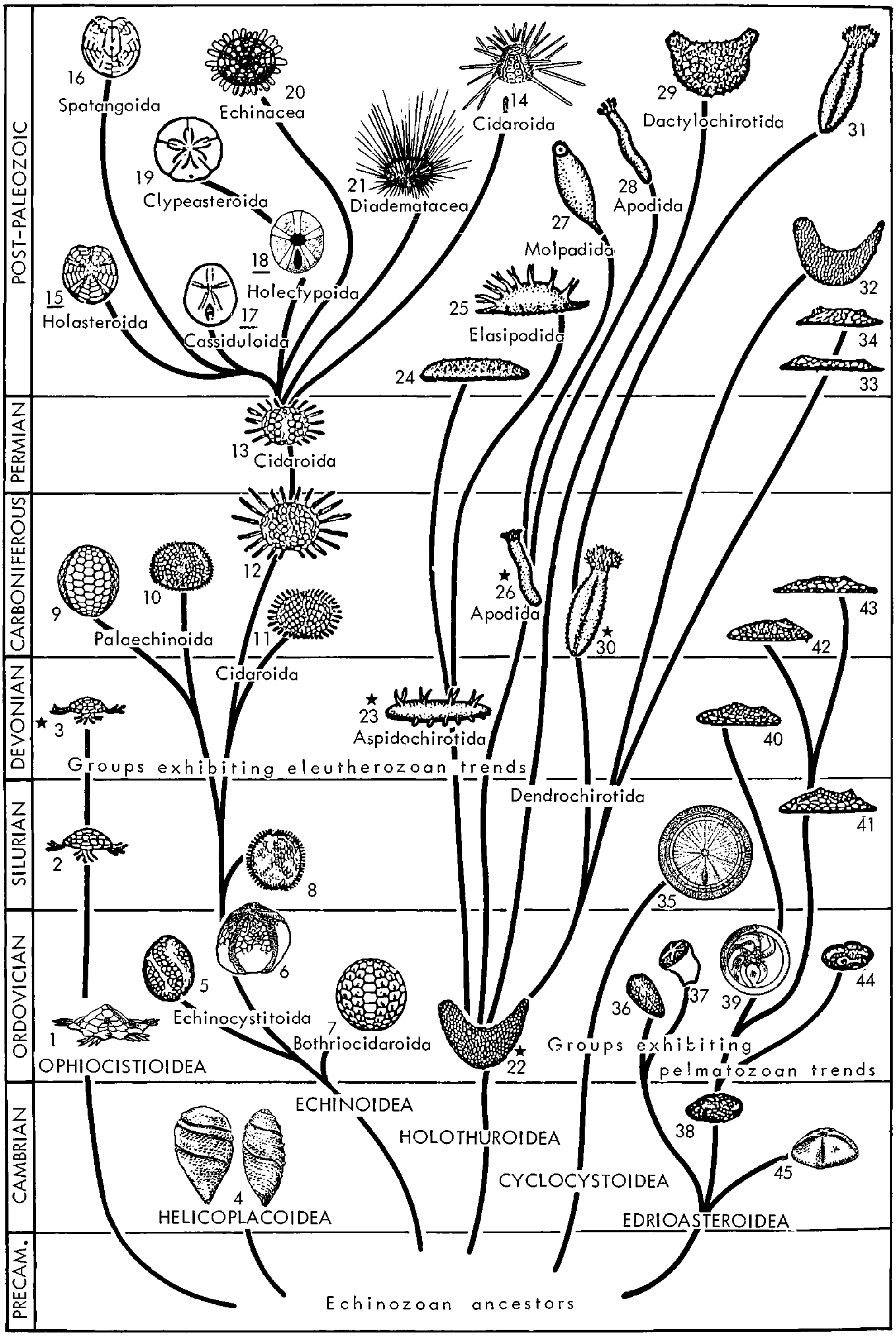


FIG. 96. Diagram representing postulated phylogenetic relationships of echinozoan classes and orders (modi-

(Continued on facing page.)

edrioasteroids and psolids are similar derivatives from an early echinozoan stock and both developed pelmatozoan characters in response to adopting a sessile mode of life (7). However, we must not overlook the fact that latest known edrioasteroids are some 300 million years older than earliest recorded psolids. This is a great hiatus in the fossil record.

Comparative studies of pharyngeal skeletal elements found in the dendrochirote holothuroids suggest that original representatives of the class must have possessed external ambulacra formed by modified thecal plates similar to those of edrioasteroids illustrated by KESLING & MINTZ (10) (Fig. 95,*1*). Seemingly, the evolution of large dendrochirote tentacles required the existence of a protective mechanism suited to allow withdrawal of them into the body. This was achieved by the introvert, which comprises a telescoping of the anterior part of the body with retraction induced by muscles derived from the radial muscle group. Evolution of the introvert implies a conversion of the original external ambulacral areas of the test into internal structures surrounding the pharynx and these structures serve for insertion of the retractor muscles. In primitive dendrochirotes the pharyngeal skeleton is still recognizable (in the opinion of PAWSON and FELL) as equivalent to the ambulacral plates of an edrioasteroid, but in most surviving holothurians the mechanism is very much reduced or vestigial (Fig. 95,*2-8*).

Although the edrioasteroids (Fig. 94,*2*; 95,*1*) adopted a habit similar to that of psolid holothurians (Fig. 92), as previously noted, their ambulacral tracts remained external, instead of sinking inward, and this permitted an alternative method of feeding suited to the pelmatozoan way of life. The feeding mechanism was provided by the whole complex of tube feet distributed along the five ambulacra which extended outward from the mouth as meridians on globoid forms (see Fig. 102,*2a,b*) but confined to the upper (oral) surface generally, as on discoid forms (Fig. 94,*2*). Each ambulacrum carried a median groove that was bordered on either side by tube feet which must have functioned in manner similar to those of crinoids, waving about in the water so as to entrap small organic particles on their mucous surface, sweeping this food inward to the mouth along food grooves of the ambulacra. FELL (7) has stressed that no introvert structure evolved in edrioasteroid stocks, and consequently tentacles of dendrochirote type doubtless never developed.

In the holothurian line, radial water vessels early became concentrated into internal canals and this occurred also in postechinocystitoid echinoids. Hence, among forms that adopted pelmatozoan habits a preexisting dendrochirote nutritive mechanism inevitably was demanded, and in holothurians external ambulacra never were involved. The fact pointed out by BASSLER (1) that a fully plated ventral sole is retained by Cambrian edrioasteroids may be taken as evidence of an originally spherical form of the test, and the ambulacra of these early members of the class were more simple than in later forms. The development of such pelmatozoan features as cover plates along the ambulacra indicates specialization analogous to that seen in somasteroids and crinoids (7).

A comparison of dissections of psolids with edrioasteroids suggests some reasonable inferences concerning the internal anatomy of the latter. Lacking evidence to the contrary, FELL (7) assumed that edrioasteroids had a gonad placed in the posterior *(CD)* interray. In psolids the gonopore lies

---

(Fig. 96. *Continued from facing page.)*

fied from Fell). [Explanation: Highly conjectural reconstructions of some genera indicated by star. Numbers are for identification of genera selected to illustrate class and order groups, forms known only as fossils in post-Paleozoic part of chart marked by underlined numbers. 1, *Volchovia;* 2, *Sollasina;* 3, *Rhenosquama;* 4, *Helicoplacus;* 5, *Eothuria;* 6, *Aulechinus;* 7, *Bothriocidaris;* 8, *Echinocystites;* 9, *Palaechinus;* 10, *Pholidocidaris;* 11, *Lepidocidaris;* 12, *Archaeocidaris;* 13, *Miocidaris;* 14, *Cidaris;* 15, *Holaster;* 16, *Echinocardium;* 17, *Nucleolites;* 18, *Holectypus;* 19, *Arachnoides;* 20, *Colobocentrotus;* 21, *Diadema;* 22, *Thuroholia;* 23, *Protocaudina;* 24, *Stichopus;* 25, *Deima;* 26, *Thallatocanthus;* 27, *Molpadia;* 28, *Chiridota;* 29, *Ypsilothuria;* 30, *Calclamna;* 31, *Cucumaria;* 32, *Placothuria;* 33, *Lepidopsolus;* 34, *Psolus;* 35, *Cyclocystoides;* 36, *Cystaster;* 37, *Cyathocystis;* 38, *Walcottidiscus;* 39, *Isorophus;* 40, *Agelacrinites;* 41, *Hemicystites;* 42, *Lepidodiscus;* 43, *Hemicystites;* 44, *Edrioaster;* 45, *Stromatocystites.*]

on the introvert, just behind the mouth. The corresponding position in edrioasteroids is that in which a pore is known to occur, although hitherto this pore has been supposed to be a hydropore. Since psolids respire (at least in part) by means of respiratory trees, it seems likely that similar trees occurred in edrioasteroids, and it is probable that the hydropore was internal, as in dendrochirote holothurians. Irrespective of these inferences, in FELL's opinion the Edrioasteroidea should be recognized as bona fide members of the subphylum Echinozoa, exhibiting various pelmatozoan features no more fundamental than the same features in psolid holothurians, where undoubtedly they constitute purely secondary responses to demands of a sessile habit.

Inferred relationships of the echinozoan classes are illustrated approximately and very diagrammatically in Figure 96. The reconstructions of forms most highly subject to conjecture are prominently marked by asterisks.

Subsequent chapters in this volume of the *Treatise* contain discussions of varying length which express the views of their authors on distinctive features of the several classes of Echinozoa, with appropriate morphological comparisons within and between the classes. Also, more detailed consideration of evolution and phylogeny is presented. Important literature is cited in a composite list of references for Echinoidea and in separate lists for other classes.

REFERENCES

Bassler, R. S.

(1) 1935, *The classification of the Edrioasteroidea:* Smithsonian Misc. Coll., v. 93, no. 8, p. 1-11, pl. 1.

Durham, J. W.

(2) 1964, *Occurrence of the Helicoplacoid*[*e*]*a (Echinodermata):* Geol. Soc. America, Spec. Paper 76, p. 52.

———, & Caster, K. E.

(3) 1963, *Helicoplacoidea: a new class of echinoderms:* Science, v. 140, p. 820-822, text-fig. 1.

Fell, H. B.

(4) 1962, *A classification of echinoderms:* Tuatara, v. 10, p. 138-140.

(5) 1963, *The phylogeny of sea-stars:* Royal Soc. London, Philos. Trans., ser. B, v. 246, p. 381-435, pl. 50-51, text-fig. 1-16.

(6) 1963, *The evolution of the echinoderms:* Smithsonian Inst., Ann. Rept. 1962, p. 457-490, pl. 1-3.

(7) 1965, *Early evolution of the Echinozoa:* Harvard Univ., Museum Comp. Zoology, Breviora, v. 219, p. 1-17, text-fig. 1-13.

(8) 1965, *The Echinodermata:* in PARKER & HASWELL, Textbook of Zoology, 7th ed. (in press), Macmillan (London, New York).

Jaekel, Otto

(9) 1918, *Phylogenie und System der Pelmatozoen:* Paläont. Zeitschr., v. 3, no. 1, p. 1-128, text-fig. 1-114.

Kesling, R. V., & Mintz, L. W.

(10) 1960, *Internal structures in two edrioasteroid species, Isorophus cincinnatiensis (Roemer) and Carneyella pilea* [*pileus*] *(Hall):* Michigan Univ., Museum Paleontology, Contrib., v. 15, no. 14, p. 315-348, pl. 1-9, text-fig. 1-4.

Matsumoto, Hikoshichirô

(11) 1929, *Outline of the classification of the Echinodermata:* Tohoku Imper. Univ., Sci. Repts., ser. 2 (Geology), v. 13, no. 2, p. 27-33.

Pawson, D. L., & Fell, H. B.

(12) 1965, *A revised classification of the dendrochirote holothurians:* Harvard Univ., Museum Comp. Zoology, Breviora, v. 214, p. 1-7.

Ubaghs, Georges

(13) 1961, *Sur la nature de l'organe appeletige ou pedoncle chez les Carpoides Cornuta et Mitrata:* Acad. Sci. Paris, Comptes Rendus, v. 253, p. 2738-2740, text-fig. 1-5.

Whitehouse, F. W.

(14) 1941, *The Cambrian faunas of northeastern Australia; Part 4, Early Cambrian echinoderms similar to the larval stages of Recent forms:* Queensland Museum, Mem., v. 12, pt. 1, p. 1-28, pl. 1-4, text-fig. 1-9.

Zittel, K. A. von

(15) 1900 [1896-1900], *Text-book of palaeontology* (transl. and ed. C. R. Eastman), v. 1, ed. 1, 706 p., 1476 text-fig. (Echinodermata, p. 122-250, text-fig. 217-402, publ. 1896), Macmillan & Co., Ltd. (London, New York).

HOMOLOGY OF ECHINOZOAN RAYS

By Raymond C. Moore and H. Barraclough Fell

[University of Kansas; Harvard University]

INTRODUCTION

An important subject in the study of Echinozoa relates to the homology of their five ambulacral rays as seen both in different classes of the subphylum and in representatives of other echinoderm subphyla. If corresponding parts of the theca in various groups can be distinguished reliably, morphological comparisons are facilitated and advances may be made in solving questions of phylogeny and evolution. Are uniform means of designating homologous skeletal parts possible, and if so, to what extent is it desirable to adopt them?

As a first step, consideration must be given to orientation. The oral face of most echinozoans is directed downward, as in the myriad kinds of echinoids and the small group of ophiocistioids. In others, such as the edrioasteroids and cyclocystoids, it is pointed upward, and in the holothurians it is directed sideward. The mode of life of helicoplacoids may have resembled that of holothurians, moving about with the long axis of the body parallel to the substrate, or alternatively the long axis of the body may have been subvertical most of the time. An anterior extremity is definable in the holothurians, irregular echinoids, and seemingly in the helicoplacoids, whereas anterior and posterior directions are ill-defined or determined somewhat arbitrarily by conventions in the regular echinoids, edrioasteroids, ophiocistioids, and cyclocystoids. Nevertheless, a plane of bilateral symmetry can be recognized in all, and its orientation is identifiable as normal to the substrate. The part of the plane that coincides with one of the ambulacral rays or that approximately marks its median position is considered anterior and the part that bisects an interray is classed as posterior, because in many, if not most, forms this interray contains the anus. Right and left sides then can be differentiated but with opposite signification in forms having the oral face upward as compared with those in which it is downward. Partly for this reason, right and left as directional terms are not favored, even though formerly much used for crinoids and other Crinozoa and though judged by Fischer (1952) to be a preferred method in referring to parts of echinoids.

The Lovén system of marking the rays and interrays of echinoids, explained and illustrated in the subsequent chapter on echinoid morphology (p. *U*220), has been employed very widely by specialists and in our opinion wisely has been adopted in the *Treatise* for descriptions and figures of members of the Echinoidea. This is because its application to both regular and irregular echinoids is trustworthy and unambiguous (Fig. 97). In this system the plane of bilateral symmetry passes through the anterior ray (designated III) and posterior interray (designated 5), which in irregular echinoids contains the anus. In clockwise order on the oral surface interrays (Arabic numbers) and rays (Roman numbers) are 5 (posterior), I, 1, II, 2, III (anterior), 3, IV, 4, and V. The arrangement of rays in many irregular echinoids shows a well-defined grouping of the three anterior rays, forming a so-called trivium, and the two posterior rays, making an opposed bivium (Fig. 97,*D,E*). Between rays of the bivium is interamb 5 containing the anus. The plane of bilateral symmetry, which coincides with the Lovén plane, is emphasized, whereas this is much less readily discerned in the regular echinoids, among which it is positively determinable by the symmetrical pattern of large and small plates of rays at the peristomial margin and by location of the madreporite in interamb 2.

A trivium and bivium are defined by junction of the oral plates of many crinoids (e.g., *Haplocrinites*, Fig. 98,*1*) and by the pattern of ambulacral grooves or plate rows on the tegmen of numerous crinoids (e.g., *Cyathocrinites,* Fig. 98,2; modern *Antedon,* and others). In our view it is highly significant that the grouping of pelmatozoan rays in threesome and twosome is not by any means at random, for as in irregular echinoids the median ray of the trivium invariably coincides with the anterior part of the plane of bilateral symmetry and likewise the interray enclosed by the bivium

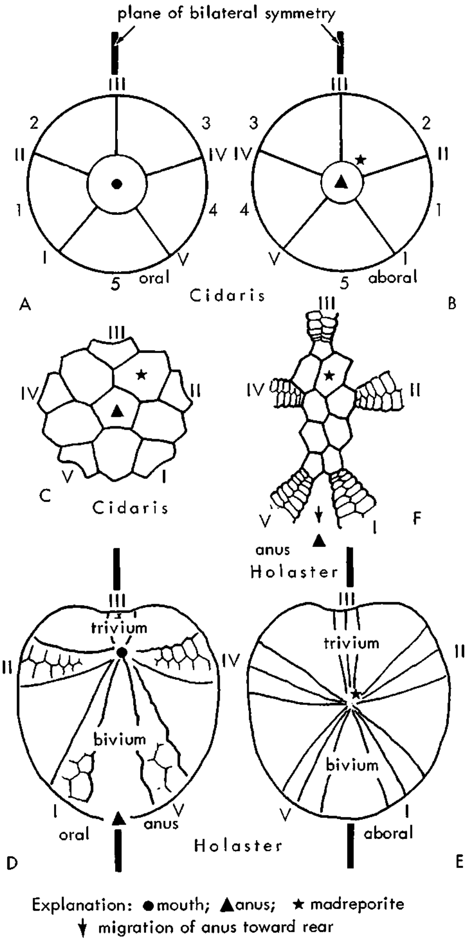


Fig. 97. Lovénian numerical notations for rays and interrays of regular echinoid *(Cidaris, A-C)* and irregular echinoid *(Holaster, D-F)*, latter showing trivium and bivium; enlargements of apical systems shown in *C* and *F*.

contains the anus. It may also contain other small openings identified as hydropore, gonopore, or hydrogonopore. If the Echinozoa, as well as Asterozoa, have been derived from ancestral echinoderms that gave rise also to the Crinozoa, it is not surprising to find in the different subphyla common features of bilateral symmetry, and this should aid in reaching trustworthy conclusions concerning homologies. Reasonable proof of the descent of members belonging to one subphylum from stocks classified in another is not demanded, for the purpose here is simply to find common denominators. The anteroposterior plane of bilateral symmetry is thought to be paramount among these.

A system for designating the rays and interrays of echinozoans, similar to that devised by Lovén in being somewhat arbitrarily defined, uses capital letters instead of numerals. This was introduced by P. H. Carpenter (1884) for identifying main divisions of the thecal skeleton of crinoids and the procedure has been found equally well suited to other pelmatozoans. Various authors have extended the Carpenter system to echinozoans and even to asterozoans (e.g., Cuénot, 1948; Hyman, 1955; Ailsa Clark, 1963), but in a manner decidedly open to question. As applied to crinoids (Fig. 98), the Carpenter letters are very simple, unambiguous, and convenient. The ray coinciding with the anterior part of the plane of bilateral symmetry (opposite to the interray containing the anus) is marked by *A*, and then on the oral surface other rays are designated in clockwise succession by *B*, *C*, *D*, and *E*. Interrays can be indicated in terms of their bordering rays, as *AB*, *BC*, etc. To echinoderm workers this is elementary; they do not need to be reminded that in aboral views of crinoids the sequence of Carpenter letters runs counterclockwise.

CARPENTER LETTERS APPLIED TO ECHINOIDS

As previously stated, the Lovén system of ray and interray designation has been adopted as "official" in the *Treatise* for application to the Echinoidea. Even so, correlation of the Lovén numerals with Carpenter letters needs to be considered in order to indicate homologies between members of this class and representatives of the Crinozoa, as well as other echinozoan classes and possibly the Asterozoa. Crinoids, blastoids, edrioasteroids, echinoids, holothurians, ophiocistioids, asteroids, and ophiuroids have been depicted with parts marked by letters of the Carpenter system, and whereever this is done erroneously by presumed authorities, they and others are led to false conclusions concerning homologies.

What guides are available for determining homologous parts of echinoderm tests? Among forms that display entirely perfect pentameral symmetry of the skeleton—fos-

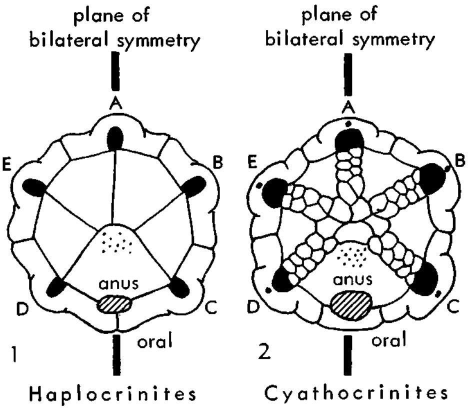


FIG. 98. Oral views of crinoids showing bilateral symmetry and designation of rays by letters of the Carpenter system.

sils rarely if ever provide evidence of soft parts—no clues are provided for distinguishing one ray or interray as different from others. The *A* ray cannot be discriminated and accordingly others are unidentifiable. Such perfect symmetry is found in some crinozoans that in them it is possible only to determine oral (ventral) and aboral (dorsal) sides of the test. The vast majority of echinoderms exhibit one or more asymmetrical features, which in turn may lead to recognition of bilateral symmetry superposed on the basic pentameral symmetry of the phylum. Here we may employ as guides for recognizing significant departures from perfect pentameral symmetry any single excentrically located structure (e.g., mouth, anus, hydropore, gonopore, madreporite, etc.), any distinctive skeletal element (e.g., posterior oral plate differing in shape and size from other orals), and any groups of such features (e.g, insert oculars on one side of periproct of echinoid, exsert oculars on other sides). Greatest in value is modification of thecal outline and the pattern of rays and interrays (e.g., trivium, bivium) in some manner that clearly defines overriding bilateral symmetry with respect to the anteroposterior plane perpendicular to the oral and aboral surfaces of the theca. This may be accompanied and accentuated by such surface features as fascioles, grouped areas of specialized spines, and tracts of particular kinds of pedicellariae. In varying degree this pattern is clearly evident in all of the subphyla, possibly excepting the Homalozoa, and it is discernible in nearly all echinoderm classes. Reliable recognition of ray homologies depends on correct correlation of the available guides.

In order to determine the correct application of Carpenter letters to echinozoans, attention may be directed first to regular echinoids and later extended to the irregular forms, inasmuch as all kinds of irregular echinoids indubitably constitute modifications derived from primordial regular ancestors, chiefly represented by the Paleozoic Cidaroida. Then, we will turn to the classes Edrioasteroidea, Cyclocystoidea, Ophiocistioidea, and Holothurioidea. The spirally twisted theca of the Helicoplacoidea lacks evidence of differentiated rays and therefore is not considered here.

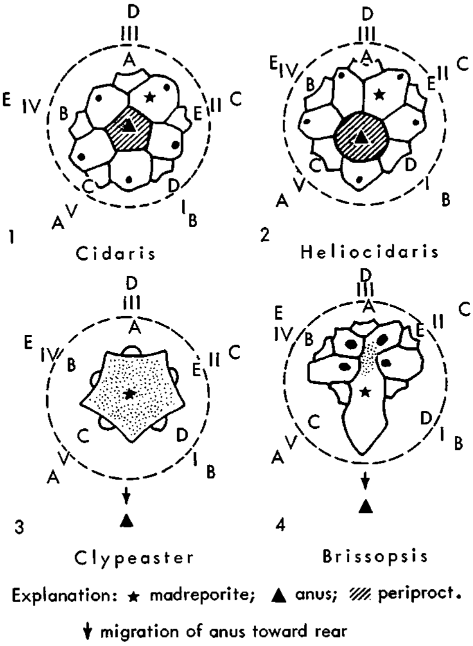


FIG. 99. Apical systems of regular echinoids (*Cidaris, Heliocidaris, 1,2*) and irregular echinoids (*Clypeaster, Brissopsis, 3,4*) showing Lovénian numerals for designation of rays accompanied on inner side by Carpenter letters recognized by *Treatise* and on outer side different placement of these letters according to common usage of authors. The diagrams show (in *1*) nearly perfect radial symmetry, (in *2*) incipient bilateral symmetry marked by exsert oculars II, III, IV and insert oculars I and V, (in *3*) central "monobasal" madreporite, and (in *4*) rearward migration of madreporite.

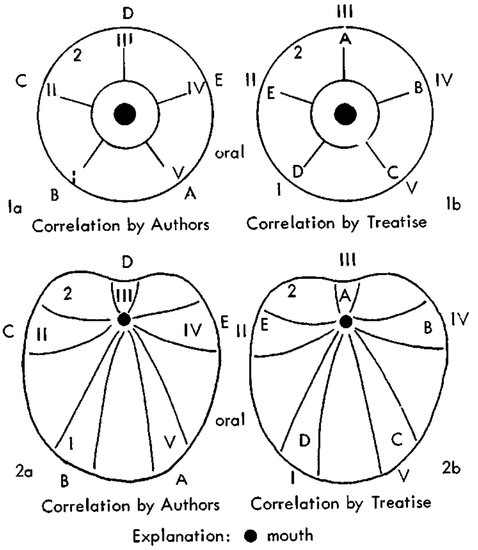


Fig. 100. Oral views of regular and irregular echinoids showing divergent correlation of Carpenter letters with Lovénian numerals by authors and by *Treatise*.

Regular echinoids have been regarded universally as a group that differs markedly from nearly all irregular echinoids. Their nearly perfect pentaradiate symmetry is disturbed only by differentiation of one of the genitals in the ocular ring as a madreporite. It lies next to the periproct in the Lovén interamb 2 (Fig. 97,*C*; 99,*A*). Regular urchins creep over the substrate with any ray forward and they can reverse the direction of their movement without turning around (Hyman, 1955, p. 550), although some have a very slight preference for locomotion with the III ray in front. Application of the Lovén numerals to the rays and interrays of the regular echinoids has been accepted by all on the basis of the single clue furnished by position of the madreporite, for if this element of the theca prevailingly (not quite universally) occurs in interamb 2 of irregular echinoid tests, it is entirely reasonable to infer the same location for it in the tests of regular echinoids. Then, other Lovén numerals for the rays and interrays can be assigned with measurable confidence (Fig. 97,*A-C*). This is not the last word with respect to the regular echinoids, however, for in many of them signs of incipient bilateral symmetry corresponding to that marked by the anterolateral axis of irregular echinoids (ray III, interray 5) can be recognized, though it has been overlooked as a significant feature by specialists (Fig. 97,*D-F*; 99,*2*).

Granting that application of the Lovén numerical designations of rays and interrays in irregular and regular echinoids is the same, as agreed by all authors who have employed this system, substitution of Carpenter letters for the numerals is unacceptable—certainly so if the letters are placed in the manner adopted by such authors as Cuénot (1948), Hyman (1955), and Ailsa Clark (1963). The disposition of letters for rays shown in Figure 100,*1a,2a* is based on the assumption that interamb 2 (Lovén), which typically contains the madreporite, corresponds to interray *CD* (Carpenter), which typically contains the excentric anus and may also have a hydropore, gonopore, or hydrogonopore. No account is taken of pervasive bilateral symmetry defined by the anteroposterior axial plane, expressed not only by the location of various excentric structures but commonly by characters of the whole skeleton. In our view correct placement of Carpenter letters, identical in crinozoans and echinozoans, is unequivocally indicated by relationships to the fundamental anteroposterior bilateral symmetry. Thus *A* (Carpenter) corresponds to III (Lovén), rather than to V, and the posterior interray *CD* (Carpenter) is equivalent to interamb 5 (Lovén), and not to interamb 2 (Fig. 100,*1b,2b*). The importance of these conclusions with respect to ray homologies is obvious, especially in connection with studies of echinoderm evolution and phylogeny.

With an initially skeptical approach, one of us (Fell, who is author of the *Treatise* chapters on cidaroids and other echinoid groups) undertook a special study of the regular echinoids aimed at finding out whether this group furnishes independent evidence that the axis passing through amb III and interamb 5 corresponds to the anteroposterior axis defined by ray *A* and interray *CD* of the Carpenter system. Some of the results were communicated to Moore in a letter (7 January 1963), excerpts from which follow.

"Propositions that seem pertinent initial statements are the following. (1) Lovénian symmetry is a universal characteristic of echinoids, with only very minor exceptions. (2) *Bothriocidaris,* if not an echinoid in strictest sense, is so close to one that all writers who have referred to it in the past decade are unanimous in regarding it as best classified among echinoids and at least susceptible to analysis as an echinoid. [Evidence published by MYANNIL (1962) indicates beyond doubt that *Bothriocidaris* is an echinoid.] (3) *Bothriocidaris* exhibits full Lovénian symmetry. (4) Cidaroids, as the only known group of Paleozoic echinoids to cross into the Mesozoic, must be the ancestors of all post-Paleozoic echinoids. (5) The plane of bilateral symmetry of all post-cidaroid echinoids passes through amb III and interamb 5 (Lovénian notation). It is required to ascertain whether the post-cidaroid plane of symmetry presents a stable relationship to other structures in all known echinoids including Paleozoic forms in which the Lovénian plane has proved recognizable, and whether the madreporite (or hydropore) presents a similar stable relationship.

"My approach to this problem is outlined in succeeding paragraphs. (1) It is self-evident that if any morphological proof of the fundamental character of the plane of bilateral symmetry in post-cidaroid echinoids exists, such proof can only be sought in the apical system of regular echinoids, for it is in this region that the first observable signs of movement of the anus into an interambulacrum are found, and it is such movement that enables us to recognize the anteroposterior axis. (2) LOVÉN established his law on the basis of the plate arrangement of the ambulacra at the peristome in spatangoids, among which bilateral symmetry is conspicuous. He extrapolated backward on the basis of the position of the madreporite in spatangoids, showing that if a regular echinoid is oriented with the madreporite in the same relative position, then the only possible plane of symmetry yielding the Lovénian sequence is that passing through the apex, amb III, and interamb 5, which defines the anteroposterior axis and plane in spatangoids and also exists in regular echinoids. By extending his inquiry to the apical region, LOVÉN was able to show that a bilateral symmetry generally exists in adapical, as well as adoral, parts of the test, and that it corresponds to the plane derived by him from adoral plate arrangement. (3) Cidaroids generally have been regarded as exhibiting aborally an almost perfect radial symmetry, not susceptible to Lovénian analysis. Therefore, it has been inferred that the anteroposterior axis and plane is a feature evolved in post-cidaroid groups. Since the madreporite is necessarily to be regarded as a pre-cidaroid structure, its significance as a morphological "marker" has been given much importance, and as others are lacking, it has been used as the main reference point in attempting to correlate echinoid orientation with that used in other groups.

"I have investigated the symmetry of the apical system of regular echinoids as part of my *Treatise* assignment, paying special attention to signs of incipient bilateral symmetry. I have reached the judgment that the common method of describing the apical system of any regular echinoid by statements such as 'oculars I and V insert' actually puts the cart before the horse. As pointed out by MORTENSEN in the first volume of his monograph on Echinoidea, the embryonic cidaroid apical system is monocyclic, with all oculars inserted between genitals (one comprising the madreporite) so as to form a single ring. With increasing growth the genitals overtake the oculars, intruding upon the periproct so as to exclude the oculars effectively from this region, thus converting the apical system into a dicyclic type. The dicyclic type clearly is secondary to the monocyclic.

Post-cidaroid echinoids generally inherit a dicyclic type of apex as their juvenile pattern, but commonly they tend to depart from it (as a tertiary modification) by developing one or more insert oculars in adults. Why is this so? The answer, in my opinion, is found by referring to such groups as the pygasteroids, nucleolitids, and others in which the first signs of migration of the anus out of the apex can be observed. The postembryonic development of the surviving nucleolitid *Apatopygus* shows in the life history of the animal how the anus leaves the apex, beginning to descend interamb 5, with new plates introduced between the periproct and apical system. No one can doubt that this is an example of recapitulation and that it was the way in which the so-called irregular echinoids arose, with conspicuous bilateral symmetry coming to involve the whole test. I interpret the 'insert oculars I and V' to mean, not that these oculars moved back inward so as to adjoin the periproct, but that in virtually all regular echinoids a constant tendency exists for the periproct to *move out* toward oculars I and V. Resorption of the neighboring genitals occurs and the emargination of their adapical edges is the real reason why oculars I and V come into contact with the periproct. Hence, it is easy to understand why irregular echinoids arose from more than one stock of regular echinoids, as stressed by DURHAM & MELVILLE (1957); it was because the periproct for some reason tends constantly to move toward oculars I and V, which is rearward in spatangoids and all other irregular echinoids. Accordingly, any tendency in a regular echinoid for oculars I and V to become insert must be treated as prima-facie evidence of an anteroposterior axis.

"With these considerations in mind, I have re-examined the apical systems of all cidaroids available to me, studying also the photographic plates in MORTENSEN's monograph and plates in my own earlier papers. Soon, most decisive witness to the existence of an anteroposterior axis in the cidaroids became evident, despite my earlier belief that this

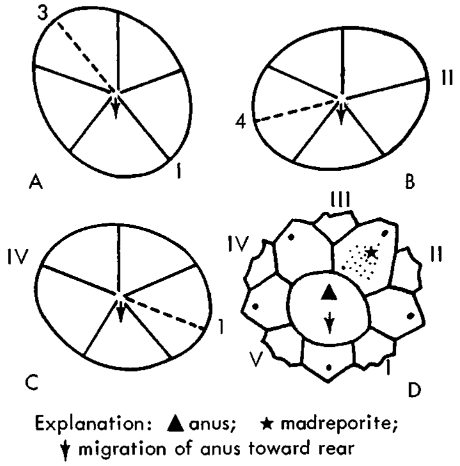


Fig. 101. "Misshapen" regular echinoids of the Echinometridae indicated by outlines of thecae in aboral views showing elongation in three different directions *(A-C)* and enlarged apical system belonging to these with exsert and insert oculars which denote bilateral symmetry with respect to the anteroposterior plane.

was not so. A recurrent tendency of oculars I and V toward *failure to become exsert* during growth constitutes evidence that this axis is present in many genera of such diverse subfamilies of the Cidaridae as the Histocidarinae (most primitive surviving group), Goniocidarinae, Stereocidarinae, Rhabdocidarinae, and Ctenocidarinae, as well as other families. Therefore, I do not doubt that it is a universal features of the cidaroids, even though expressed sporadically, some adults showing insert oculars I and V, others with all oculars exsert but I and V nearest to the periproct, and still others with evenly disposed insert or exsert oculars.

"If differences among the oculars are due to purely chance variations during growth, all oculars should be affected equally, but this is not the case. An unmistakable bias—almost an exclusive one—caused only oculars I and V to become insert, or rather, to fail in being exsert. Unavoidably, therefore, I must conclude that an anteroposterior axis of symmetry already exists in the cidaroids. It is defined by the recurrent tendency of oculars I and V to remain next to the periproct, or expressed otherwise, by the recurrent tendency of the cidaroid periproct to move rearward in the direction of interamb 5. That this anteroposterior axis of the cidaroids exactly matches the Lovénian axis on the oral surface cannot be emphasized too strongly, for it means that we are dealing here with a true plane of symmetry identical with the one found in all post-cidaroid echinoids [Fig. 99].

"A test now can be applied to the reasoning which has been outlined. Certain regular echinoids (e.g., Parasaleniidae, Echinometridae) are 'misshapen' in exhibiting a bilateral symmetry of the whole test expressed by markedly oval outlines in many species when viewed from the oral or aboral sides. In the Echinometridae (Mortensen, v. 3, pt. 3, p. 278, fig. 130) the axis of elongation plainly differs from that of spatangoids and other irregular echinoids, for in different forms it is observed to coincide with amb I and interamb 3, or with amb II and interamb 4, or with amb IV and interamb 1 [Fig. 101]. Now if the bilateral symmetry associated with elongation of the test in any of these directions is as fundamental as that postulated for symmetry with respect to the amb III and interamb 5 axis, the insert oculars ought then to be located in the appropriate ambulacra—not in I and V. *But this is not so* [Fig. 101,*D*]. Instead, the echinometrids are entirely characterized by insertion of oculars I and V, just as in other cidaroid groups. Hence, the slightly displaced periproct completely ignores the new symmetry along axes other than that marked by amb III and interamb 5, remaining faithful to this latter. Thus, I conclude that the amb III-interamb 5 plane of symmetry is a fundamental feature of all orders of echinoids from the Cidaroida onward. It was already present in at least one of the Paleozoic orders, for we know that cidaroids as defined in the strictest sense range back into the Permian (Miocidaridae), and the Archaeocidaridae, which generally are classed as cidaroids, extend back to the Lower Carboniferous and possibly to the Silurian.

"Including the Bothriocidaroida, three orders of Paleozoic echinoids in addition to the Cidaroida are discriminated. The Lovénian law seems to be observed exactly in *Bothriocidaris,* as stressed by Jackson, Hawkins, Mortensen, and Durham & Melville. Fossils now available to show characters of the Paleozoic orders Echinocystitoida and Palaechinoida are too fragmentary to allow determination of the presence in them of Lovénian symmetry. The archaic *Bothriocidaris* (Ord.) at least already exhibited the same anteroposterior plane of symmetry that is manifested in the Cidaroida and in post-cidaroid groups, as indicated by the potential, incipient, or consummated migration of the anus into interamb 5.

"What about the madreporite, to which so far relatively little notice has been given? In *Bothriocidaris,* which we might reasonably expect to show such a structure in interamb 5, it is located rather in one of the ambulacra, not even in interamb 2, as customarily in echinoids. By definition, a posterior direction is indicated by the location of the anus, and observation of other echinoderms indicates that the hydropore tends to move into the interambulacrum containing the anus. The hydropore itself thus may be regarded as a marker of posterior direction, though of secondary value. When we trace the post-Paleozoic history of the echinoid hydropore (madreporite), we find that it fulfills expectations, albeit belatedly and in a most uncertain, devious manner, experimenting, so to speak, with various locations but ultimately yielding to interamb 5 after crossing the middle of the apical disc. It set out from genital 2 (seemingly reached as a post-bothriocidaroid translocation), toyed briefly with genital 4 (with pores developed on both genitals 2 and 4, as seen in juvenile *Apatopygus*, MORTENSEN, Vid. Medd. 73, p. 187, fig. 20), or invaded all of the genital plates, producing pores in each of them simultaneously (e.g., *Discoidea*, MORTENSEN, monograph) and even converted all of them into a single compound 'monobasal' plate at the apex [Fig. 99,*3*], or it sailed across the apex into interamb 5 with a long trailing lobe joined to its old host (genital 2) [Fig. 99,*4*]. The last-mentioned arrangement represents the so-called ethmolytic condition of spatangoids. Finally, the madreporite may swallow up all of the residual genitals, pushing a long process into the posterior interambulacrum (e.g., *Palaeopneustes, Heterobrissus*, and other spatangoids of more specialized nature).

"This brief sketch shows that the history of the hydropore (madreporite) in echinoids is one of continuing migration, with interamb 2 its longest occupied home and interamb 5 its ultimate destination. As a trigonometric landmark, the madreporite is hopeless. As an indicator of posterior direction and position, the anus is far superior in guidance to correct orientation, for its morphologic relationships are entirely consistent. By its influence on the behavior of oculars I and V, the anus very early indicated the tendency to migrate into interamb 5, enabling us to recognize the anteroposterior axis and plane of bilateral symmetry in many of the oldest regular echinoids. The great adventure in evolution of the echinoid anus was its slide from dead-center location on the aboral surface to a place on the underside of the test within sight of the mouth, where finally it halted futile pursuit of the mouth, which was seeking to escape forward.

"In summation, it seems to me that inescapably we must recognize the anteroposterior plane passing through amb III and interamb 5 of Lovénian notation as the fundamental plane of symmetry in all echinoids. Therefore, corresponding notations of the Carpenter system equate amb *A* with amb III, interamb *AB* with interamb 3, amb *B* with amb IV, and so on. Interamb *CD* is not the equivalent of interamb 2, as commonly supposed by authors, but corresponds to interamb 5."

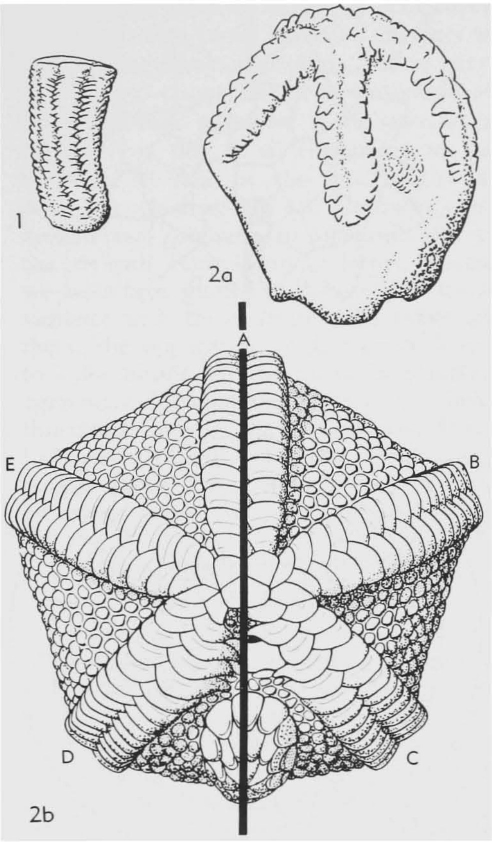


FIG. 102. Edrioasteroids, showing side view of cylindroid form *(1)* and *D*-ray side view and oral view *(2a,b)* of globose form, anteroposterior plane of bilateral symmetry strongly defined in all, not to scale (*1*, from Aurivillius; *2a*, from Jaekel; *2b*, from Kesling).

CARPENTER LETTERS APPLIED TO EDRIOASTEROIDS

The ambulacral rays of some edrioasteroids, for example as seen on the globose test of *Cystaster* (Fig. 102,*2*). are straight and they diverge radially in nearly perfect pentamerous manner. Actually, the interray containing the prominent anal pyramid of *Cystaster* is wider than others. Bilateral symmetry with respect to the vertical plane that bisects this interamb and that coincides with the opposite ambulacrum is clearly evident. The oral surface is directed upward, and Carpenter letters are applicable without any question, beginning with *A* for the ray in the plane of anteroposterior bilateral symmetry and proceeding clockwise for designation of others in alphabetical sequence. An aperture next to peristomial plates at summit of the test is located in interray *CD*, like the anus. It has been distinguished as a hydropore by KESLING (1960) but designated noncommittally as "third aperture" by REGNÉLL (p. *U*150). If the supposition

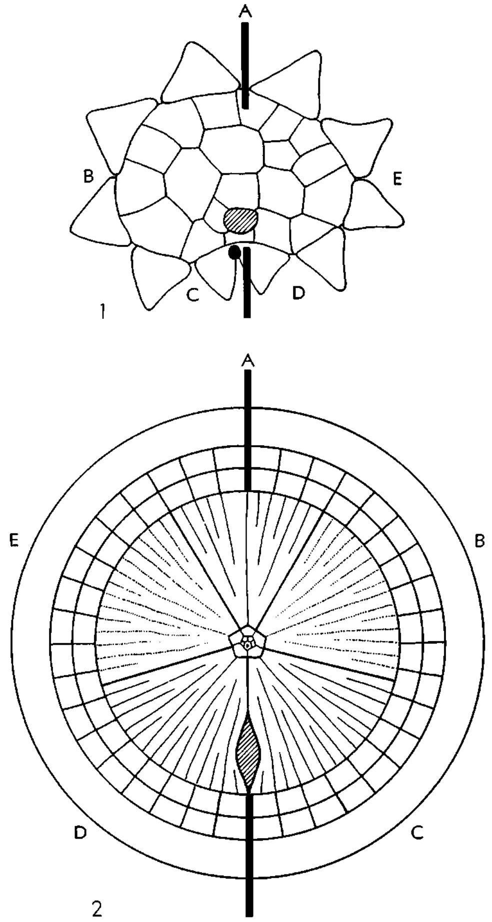


Fig. 103. Ophiocistioidea and Cyclocystoidea showing anterodorsal plane of bilateral symmetry.——*1*. *Volchovia* (ophiocistioid), aboral view showing application of Carpenter letters to rays, reconstr., ×0.5 (from Gekker).——*2*. *Cyclocystoides*, oral surface, reconstr., showing Carpenter letters, ×2.25 (from Kesling).

expressed by Fell & Moore (p. *U*117) is correct, that respiration of the edrioasteroids probably resembled that of holothuroids, utilizing internal respiratory trees not preservable in fossils, this opening may very well be a gonopore. Whatever its physiological function may have been, this structure fits in with the *A-CD* plane of symmetry.

The same symmetry is definable on the oral surface of cylindroid edrioasteroids (e.g., *Pyrgocystis,* Fig. 102,*1*) and discoid forms, which include a majority of genera belonging to the class. The latter are characterized by more or less strongly curved ambulacra, as well known. Bilateral symmetry defined by the anteroposterior plane is less evident, but nonetheless uniformly marked by location of the anus in interray *CD*.

CARPENTER LETTERS APPLIED TO OPHIOCISTIOIDS

Ubaghs (p. *U*176) has reported that notation of rays and interrays of the ophiocistioids presents no difficulty or ambiguity. In *Volchovia* (Fig. 103,*1*), for example, the anteroposterior plane of bilateral symmetry is defined by the arrangement of plates on the aboral surface and position of the anus, supplemented by presence in the same interray of a small aperture doubtfully identified as a hydropore, gonopore, or hydrogonopore. Carpenter letters have been employed by Ubaghs, therefore, in describing fossils of this class.

CARPENTER LETTERS APPLIED TO CYCLOCYSTOIDS

Although most specimens of cyclocystoids are not very well preserved, enough is known concerning structure of their tests to establish definitely nearly perfect pentameral symmetry of the many-branched rays (Fig. 103,*2*). No system of notation for the rays has been adopted by authors, however, even though a vertical plane of bilateral symmetry transecting the nearly flat discoid test is recognized. This coincides with the mid-line of one of the rays and an opening in the opposite interray that must be the anus. Accordingly, the ray just mentioned is here defined by the letter *A* of the Carpenter system and other rays can then be distinguished in customary manner. Three cyclocystoid genera have been described, but in the view of Kesling (p. *U*188) they are synonymous and in the *Treatise* all are included in *Cyclocystoides.*

CARPENTER LETTERS APPLIED TO HOLOTHURIANS

The holothurians prevailingly comprise cylindroid echinozoans, as indicated by their common name sea cucumbers; some are decidedly wormlike in form and others thick discoid to globoid. They differ in mode of life from echinoids and eleutherozoan

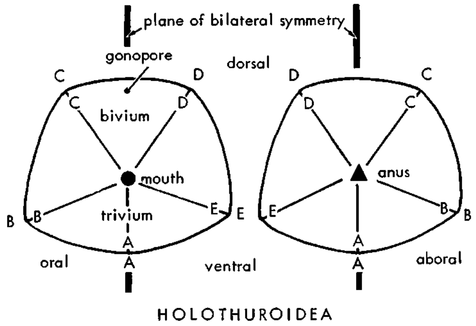


FIG. 104. Diagrammatic oral and aboral views of holothurian showing plane of bilateral symmetry and Carpenter letters for designation of rays belonging to trivium and bivium.

echinoderms generally in displaying a strongly marked fore and aft orientation, with the mouth at one extremity and the anus at or near the other. The animals crawl or burrow with one of their sides lowermost and the opposite side directed upward. Accordingly, the lower side is designated as ventral and the other as dorsal. Three rays on the lower side are differentiated as a trivium and the opposite two comprise a bivium, and between rays of the bivium a gonopore commonly is recognized near the anterior end of the body.

Authors who have employed Carpenter letters for the different rays of holothurians agree in adopting *A* for the median ventral ray, others then being identified in clockwise sequence around the mouth. This results in application of *C* and *D* to rays of the bivium (Fig. 104). The tenuous basis for this agreed application of Carpenter letters seems to be the premise that the gonopore corresponds to the genital plate of the echinoid apical disc which prevailingly (but not exclusively) includes the madreporite, and on the additional premise that the interray containing the echinoid madreporite corresponds to the Carpenter *CD* interray. The first-mentioned premise may be correct, whereas the second is judged by us to be incorrect. The truly significant, and therefore basic, consideration is that the obvious vertical plane of bilateral symmetry in the holothurian body which coincides with the median ventral ray (middle one of the trivium) and which bisects the bivium is identical in its relationships to the vertical anteroposterior plane of symmetry recognized in all echinoids (now including regulars as well as irregulars), in crinoids, and in nearly all other crinozoans. The placement of the holothurian gonopore is the same as in crinoids but not at all equivalent to the common location of the madreporite in echinoids which would call for finding the holothurian gonopore in interamb *AB* of the trivium. Fortuitously, it seems, because we have been guided by criteria entirely at variance with those accepted by other authors, the application of Carpenter letters to holothurians happens to be in complete agreement. Designation of the rays of holothurians adopted in the *Treatise* is as shown in Figure 104, and this is identical to designation given by CUÉNOT, HYMAN, and others.

CARPENTER LETTERS APPLIED TO ASTEROZOANS

So uncertain and insecure is identification of individual rays and interrays of somasteroids, asteroids, and ophiuroids that authors generally have declined to use any system of notations for them. In many of these echinoderms radial symmetry appears to be perfect, with no clue whatever for the adoption of orientation other than oral and aboral. Asteroids commonly possess an easily distinguished madreporite in one of the interrays on the aboral side of the body, and in addition, some show the presence of an anus, also located on the aboral surface in the interray at left (in aboral view) of the one containing the madreporite. Some asteroids (e.g., *Acanthaster*) carry several madreporites scattered about on the aboral side. Ophiuroids commonly appear to be perfectly symmetrical radially, but the presence of a madreporite in one of the interrays next to the mouth can be determined. Several genera of the suborder Euryalina (order Phrynophiurida), however, have five madreporites, one in each interray, or similarly disposed hydropores not associated with any skeletal element may be found (e.g., *Trichaster*) (HYMAN, 1955, p. 613).

In asteroids and ophiuroids having a single madreporite, authors (e.g., CUÉNOT, 1948; HYMAN, 1955; AILSA CLARK, 1963) have accepted this as basis for defining the interray containing it as *CD* (Fig. 105).

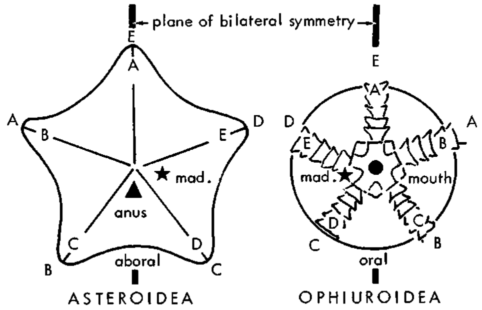


Fig. 105. Diagrammatic aboral view of asteroid and oral view of ophiuroid showing doubtfully identified plane of bilateral symmetry and application of Carpenter letters to rays, inner letters as here identified and outer letters according to authors.

Guidance for conclusions on homology is the same as accepted by these and other authors—firmly fixed location of the madreporite in all echinoderm groups—even though this has been shown by us to be untrustworthy, commonly serving to mislead rather than to point out homologous skeletal parts correctly. Since the rays of no asterozoans are grouped in trivia and bivia, and since a vertical plane of bilateral symmetry defined by such arrangement is unavailable to help us, only guesswork concerning orientation remains for use. When account is taken of earliest known asterozoans, which in all classes exhibit structural affinities with pinnulate crinoids (Fell, 1963) and which indicate interrelationships pointing to a common ancestry, judgment is reached that location of the anus outweighs that of the madreporite as marker for orientation. Thus we are led to apply Carpenter notations of rays as shown in Figure 105,*1* (letters distributed outside of the outline) for asteroids, and on assumption that the interray bearing a madreporite in ophiuroids corresponds to the madreporite-bearing interray in asteroids, Carpenter letters may be applied to ophiuroids as shown in Figure 105,*2*. Whereas great confidence can be expressed as to the correctness of ray and interray homologies for echinozoans as here presented, surely this cannot be extended to include the asterozoans, at least on the basis of present knowledge.

SUMMARY

A vertical plane of bilateral symmetry which is clearly defined in the Crinoidea and various other classes of the Crinozoa provides the basis for applying in uniform manner letter symbols introduced by Carpenter for the different rays and interrays. The system is especially suited for description and illustration of echinoderms belonging to this subphylum, many of which display arrangement of the rays in a well-marked trivium and bivium. The anus is invariably located in the *CD* interray, defined as posterior, and commonly a hydropore or gonopore or both occur in the same interray (Fig. 98; 106,*1*).

An identical plane of bilateral symmetry is demonstrated to exist in echinoids, incipiently expressed in the regular echinoids (Fig. 97,*B,C*; 99,*1,2*; 101; 106,*2,3*) but strongly marked in the irregular echinoids (Fig. 97,*D-F*; 99,*4*; 106,*6,7*), most of which display grouping of the anterior three rays in a trivium and the posterior two rays in a bivium, the latter enclosing the anus. The Lovén system of notation, using Roman numerals for rays and Arabic numerals for interrays, is adopted in the *Treatise* (Fig. 97; 100; 106,*2,6*), but correlation of it with the Carpenter system is indicated (Fig. 100, *1b,2b*; 106,*2,6*). In addition, authors' application of Carpenter letters to echinoids in manner judged to be entirely erroneous is discussed and illustrated (Fig. 99; 100; 106,*3,7*). Reasons are presented for relegating the madreporite to a very subordinate status as a structure to be considered in studies of homology, and accordingly conclusions mainly or entirely based on this are rejected.

The application of Carpenter letters to edrioasteroids (Fig. 102), ophiocistioids (Fig. 103,*1*), and cyclocystoids (Fig. 103,*2*) offers no problems and is straightforward.

For the holothurians (Fig. 104; 106,*4*) recognition of far-reaching homologies and use of Carpenter ray notations to express them are curious in that identical conclusions have been reached in different ways, one being quite faulty and the other strongly supported by trustworthy evidence. The faulty approach is that generally accepted by authors, based on trust in the significance of gonopore placement, in our opinion erroneously correlated with the madreporite-bearing genital 2 element of the echinoid apical disc. The differentiation of holothurian rays into a ventrally oriented trivium and dorsal bivium defines a fundamental vertical plane of bilateral symmetry equivalent to that in echinoids, crinoids, and most other echinoderm classes. The presence of a gonopore in the *CD* interray corresponds to the gonopore in crinoids, for example, and not to genital 2 of echinoids.

Asterozoans are doubtfully oriented in terms of Carpenter ray notations, but phylo-

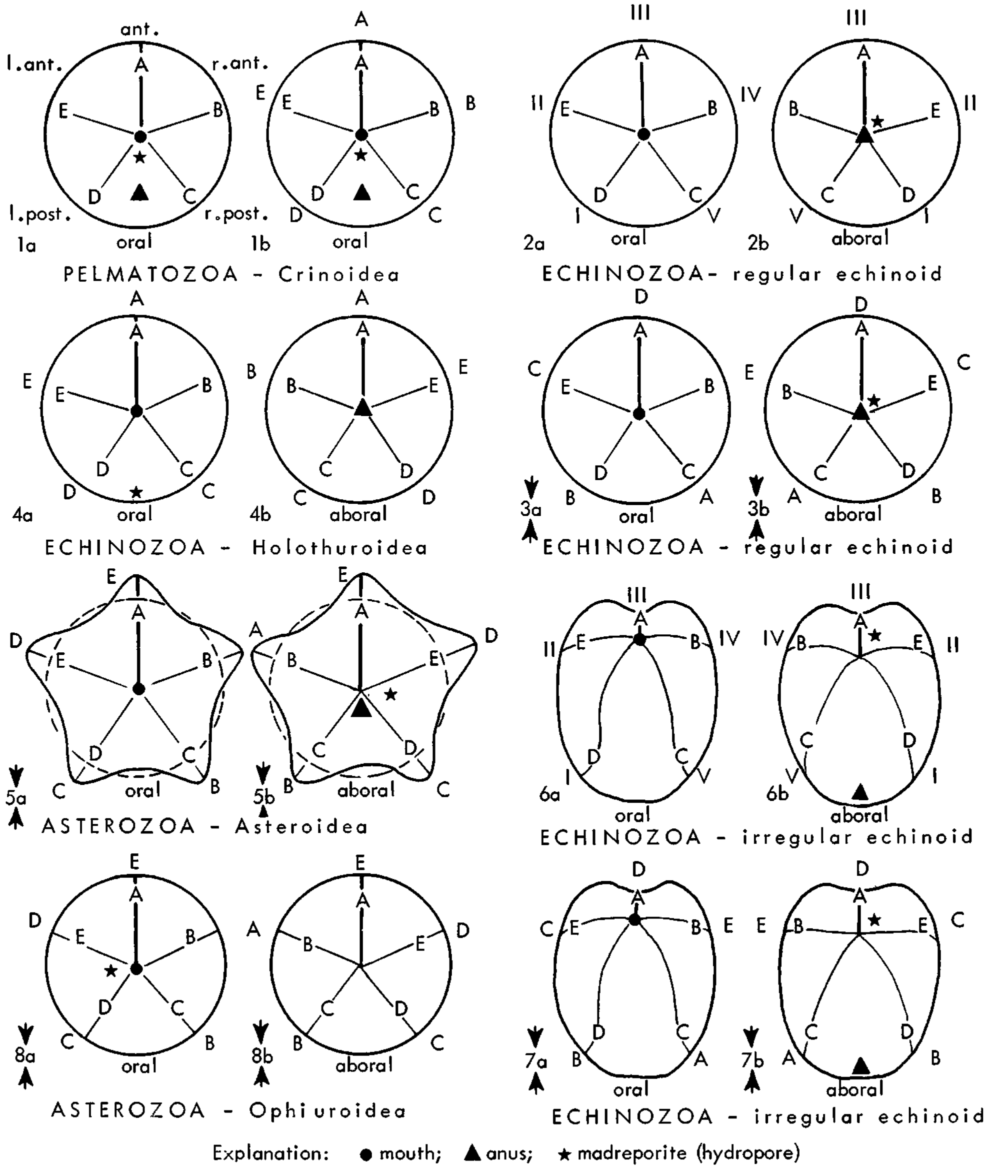


FIG. 106. Summary of ray designations applied to echinozoans and other echinoderms brought together for comparison. [Ray designations outside of test outlines indicate usage of authors; those inside of these outlines show designations adopted in the *Treatise,* except that for echinoids Carpenter letters merely indicate correlation with *Treatise*-adopted Lovénian numerals. Arrows pointing to some figures call attention to ray designations which are judged to be erroneous.]

genetic considerations support tentative identification of the anus-bearing interray of asteroids with the *CD* interray of crinozoans and interamb 5 of echinoids (Fig. 105,*1*; 106,*5*). Correlation of madreporite placement in ophiuroids with that observed in asteroids indicates that the interray bearing this structure is *DE* (not *CD*), granting the orientation of asteroids just stated.

REFERENCES

Agassiz, Alexander

(1) 1872-74, *Revision of the Echini:* Harvard Univ., Museum Comp. Zoology, Mem., v. 3, p. 1-762, pl. 1-38.

Bather, F. A.

(1a) 1900, *The Echinoderma:* in E. R. Lankester, ed., A Treatise on Zoology, pt. 3, 344 p., 309 text-fig., A. & C. Black (London).

Carpenter, P. H.

(2) 1884, *Report upon the Crinoidea collected during the voyage of H.M.S. Challenger during the years 1873-1876:* Rept. Scientific Results Explor. Voyage H.M.S. Challenger, Zoology, v. 11, xii+442 p., 62 pl., 21 text-fig.

Clark, Ailsa M.

(3) 1962, *Starfishes and their relations:* British Museum (Nat. History), 119 p., 16 pl., 30 text-fig. (London).

Clark, H. L.

(4) 1925, *A catalog of the Recent sea-urchins in the British Museum:* British Museum (Nat. History), 278 p., 12 pl. (London).

Cuénot, Lucien

(5) 1948, *Anatomie, éthologie, et systématique des échinodermes:* in Traité de zoologie, P.-P. Grassé (ed.), v. 11, p. 1-275, text-fig. 1-312, Masson (Paris).

Durham, J. W.

(6) 1955, *Classification of clypeasteroid echinoids:* California Univ., Publ. Geol. Sci., v. 31, p. 73-198, pl. 3-4, 38 text-fig.

———, & Melville, R. V.

(7) 1957, *A classification of echinoids:* Jour. Paleontology, v. 31, p. 242-272, text-fig. 1-9.

Fell, H. B.

(8) 1963, *The phylogeny of sea-stars:* Royal Soc. London, Philos. Trans., ser. B, v. 246, p. 381-435, pl. 50-51, text-fig. 1-16.

Gregory, J. W.

(9) 1900, *Echinoidea,* in E. R. Lankester, A. Treatise on Zoology, Part III, the Echinoderma: p. 282-332, text-fig. 1-47, A. & C. Black (London).

Hawkins, H. L.

(10) 1931, *The first echinoid:* Biol. Reviews, v. 6, p. 443-458.

Hyman, L. H.

(11) 1955, *The invertebrates: Echinodermata:* vii & 763 p., 280 text-fig., McGraw-Hill (New York).

Jackson, R. T.

(12) 1896, *Studies of Palaeechinoida:* Geol. Soc. America, Bull., v. 7, p. 171-254, pl. 2-9, 5 text-fig.

(13) 1912, *Phylogeny of the Echini, with a revision of Paleozoic species:* Boston Soc. Nat. History, Mem., v. 7, p. 1-490, pl. 1-76, 256 text-fig.

(14) 1929, *The status of Bothriocidaris:* Harvard Univ., Mus. Comp. Zoology, Bull, v. 69, p. 481-512.

Jaekel, Otto

(15) 1918, *Phylogenie und System der Pelmatozoen:* Paläont. Zeitschr., v. 3, no. 1, p. 1-128, text-fig. 1-114.

Kesling, R. V.

(16) 1960, *Hydropores in edrioasteroids:* Michigan Univ., Museum Paleontology, Contrib., v. 15, no. 8, p. 139-192, pl. 1-13, text-fig. 1-14.

Kier, P. M.

(17) 1962, *Revision of the cassiduloid echinoids:* Smithsonian Misc. Coll., v. 144, no. 3, 262 p., 44 pl., 184 text-fig.

Lovén, Sven

(18) 1874, *Etudes sur les Echinoidées:* K. Svenska Vetenskapsakad. Handl., v. 11, no. 7, p. 1-91, pl. 1-53.

Mortensen, Theodor

(19) 1928, *Bothriocidaris and the origin of echinoids:* Vidensk. Medd. Dansk Naturh. Foren., v. 86, p. 93-124.

(20) 1928-51, *A monograph of the Echinoidea:* v. 1, Cidaroidea, 551 p., 173 text-fig., atlas 24 pl. (1928); v. 2, Bothriocidaroida, Melonechinoida, Lepidocentroida, and Stirodonta, 647 p., 377 text-fig., atlas 89 pl. (1935); v. 3, no. 1, Aulodonta, 370 p., 197 text-fig., atlas 77 pl. (1940); v. 3, no. 2, Camarodonta, 533 p., 321 text-fig., atlas 56 pl. (1943); v. 3, no. 3, Camarodonta, 446 p., 215 text-fig., atlas 66 pl. (1943); v. 4, no. 1, Holectypoida, Cassiduloida, 363 p., 14 pl., 326 text-fig. (1948); v. 4, no. 2, Clypeasteroida, 471 p., 258 text-fig., atlas 72 pl. (1948); v. 5, no. 1, Spatangoida, 432 p., 25 pl., 315 text-fig. (1950); v. 5, no. 2, Spatangoida, 593 p., 286 text-fig., atlas 64 pl. (1951); index to v. 1-5, 63 p. (1951),

C. A. Reitzel (Copenhagen); Milford, Oxford Univ. Press (London).

(21) 1931. *Bothriocidaris and the ancestry of echinoids, a reply:* Vidensk. Medd. Dansk Naturh. Foren, v. 90, p. 313-352.

Nichols, David

(22) 1959, *Changes in the Chalk heart-urchin Micraster interpreted in relation to living forms:* Royal Soc. London, Philos. Trans., ser. B, v. 242, p. 347-437, 1 pl., 46 text-fig.

(23) 1962, *Echinoderms:* 200 p., 26 text-fig., Hutchinson (London).

Regnéll, Gerhard

(24) 1945, *Non-crinoid Pelmatozoa from the Paleozoic of Sweden:* Lunds Geol.-Mineral. Inst., Medd., v. 108, viii+255 p., 15 pl., 30 text-fig. (Lund).

Zittel, K. A. von

(25) 1900 [1896-1900], *Text-book of palaeontology* (transl. and ed. C. R. Eastman), v. 1, ed. 1, 706 p., 1476 text-fig. (Echinodermata, p. 122-250, text-fig. 217-402, publ. 1896), Macmillan & Co., Ltd. (London, New York).

HELICOPLACOIDS

By J. Wyatt Durham and Kenneth E. Caster

[University of California (Berkeley); University of Cincinnati]

Class HELICOPLACOIDEA Durham & Caster, 1963

[Helicoplacoidea Durham & Caster, 1963, p. 820]

Free-living, fusiform to pyriform placoid echinoderms with spirally pleated, expansible and flexible test; apical and oral poles at opposite extremities; columns of plates disposed spirally; ambulacra and "interambulacra" present, new "interambulacral" plates originating at apical pole and becoming more oral in position as subsequent plates are added, origin of ambulacral plates obscure, but possibly similar. *L.Cam.(Olenellus Zone).*

In the retracted state the known species of this specialized extinct group are pyriform, but when expanded they become fusiform. The plates are not firmly sutured to one another as in the echinoids and many pelmatozoans, and in the expanded state (Fig. 107) the body was flexible, much as in the holothurians. Because the plates were not sutured to one another the test usually became disassociated upon death. In consequence, the small isolated plates are much more abundant in the fossil record than partial or entire tests.

The "interambulacral" areas are composed of three columns of plates extending from the oral to the apical pole. In the retracted state (Fig. 108,*A*) the central column is external and the two lateral columns folded internally; in order to expand, the lateral column folded outward laterally and formed the floors of troughs adjacent to the ridgelike medial column (Fig. 108,*B*). The three columns of an area originate from a single center in the apical area. The minute plates when first recognizable appear in a multiserial (?triserial) column. As the apical pole becomes more distant and the plates grow larger, the single column differentiates into three columns, with the medial plates forming the central column. In each of the two described species there are 10 "interambulacral" areas.

The principal ambulacrum makes at least two full spiral turns, starting at the mouth, but does not reach to the apical pole. The secondary ambulacrum first appears about 180 degrees along the spiral from the mouth and then continues for approximately another 180 degrees, being separated from the first by two "interambulacral" areas throughout most of its length. In one specimen (Fig. 109,*B*) the two ambulacra clearly join, apparently adapically (although theoretical objections can be made to this interpretation), and the principal ambulacrum continues. In the retracted state the medial "interambulacral" columns imbricate adapically posterior to the branching of the ambulacrum, and slightly adorally anterior to this point. The ambulacra are composed

FIG. 107. *Helicoplacus gilberti* DURHAM & CASTER, L.Cam. (*Olenellus* Zone), USA (Calif.); well-preserved adoral portion of theca showing clockwise spiral torsion of plate rows interpreted as "interambulacral" and small part of ambulacrum, oral pole upper right at center of spiral, ×6.6 (2).

of four or more rows of small plates. As yet no podial pores have been recognized certainly, although possible grooves for tube feet seem to be present on adjacent ambulacral plates on one poorly preserved specimen.

Anal and genital orifices have not been recognized. The structure of the peristome is uncertain, but the mouth apparently was not more than 1 mm. in diameter. No supportive or masticatory structures have been recognized in the oral area. Likewise no tentacular or brachial appendages have been found, and no evidence of any attachment area for such structures has been discovered.

The symmetry of the test, at least as far as the "interambulacra" are concerned, is radial, modified by torsion to a spiral form. However, the single primary ambulacrum imposes a distinct bilaterality upon the

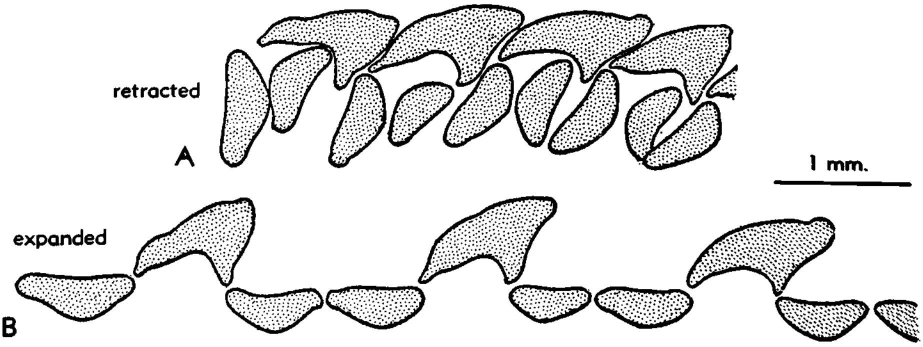


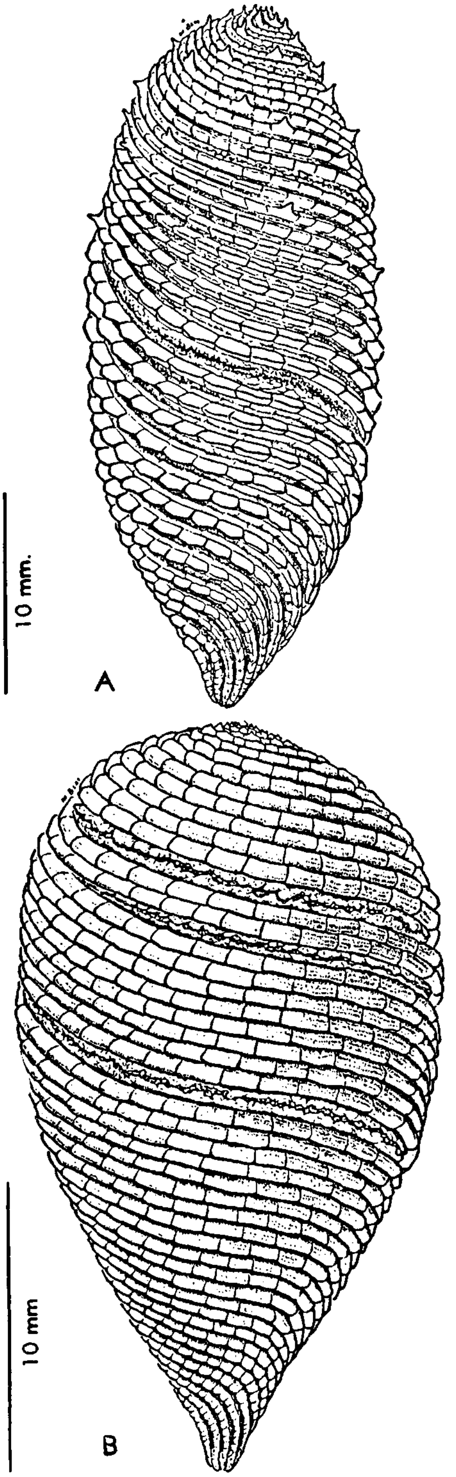
FIG. 108. Diagrammatic sections of thecal plates of *Helicoplacus gilberti* parallel to oral-aboral axis, showing *(A)* infolded "interambulacral" columns in retracted state of theca, and *(B)* spread-out lateral "interambulacral" columns in expanded state of theca, ×18 (1).

original radial pattern of the "interambulacra." Nevertheless, it should be noted that the two "interambulacral" areas separating the branch for most of its length from the primary ambulacrum are strongly suggestive of possible subsequent development of a pentameral pattern. If a similar branching were repeated three additional times, and if the appearance of branching were accelerated in ontogeny, the result would be the usual pentameral echinoderm pattern.

The small area of the ambulacra in comparison with the total bulk of the animal suggests that the ambulacra were primarily respiratory structures. Inasmuch as most living echinoderms have a ciliated epidermis, it seems probable that the integument was likewise ciliated in this group. The small mouth indicates that *Helicoplacus,* the type and presently only known genus of the class, was a small-particle-feeder. This seems likely in view of the lack of indication of other food-gathering organs, and it may be inferred that *Helicoplacus* was usually in the expanded state, with organic particles gathered by its cilia being passed along the spiral "interambulacral" grooves towards the mouth. Presumably, only in times of danger from predators or in encountering an unfavorable environment or in periods of inactivity would the retracted state be assumed.

The small size of the apical pole, the fact that it is the point of origination for new plates, the lack of any specialized structure for adhesion, and the small-particle size of the enclosing sediments indicate that the known helicoplacoids were free-living. Their mode of life is unknown. They may have been stationary, with the apical pole buried in the soft substrate upon which they lived, or they may have lain on the sea floor, crawling about like many holothurians. Another possibility is that they rested passively on the sea floor when in the retracted state but when expanded slowly pulsed through the water by rhythmic contractions of the accordion-like test. With respect to the last-suggested hypothesis it may be noted that in the completely expanded state the volume of the body was probably more than twice that of the retracted state and the specific gravity of individuals then may not have been much above that of sea water.

In California *Helicoplacus* occurs in the same beds as the eocrinoid *Eocystites,* as well as various trilobites, a few archaeocyathids, and inarticulate brachiopods. Stratigraphically, the shales in which it occurs are intercalated in a thick sequence of archaeocyathid-bearing beds, and the known occurrences are located at levels about one-third of the thickness of the sequence above the base of the olenellid-trilobite-bearing beds. In nearby western Nevada, a *Stromatocystites*-like edrioasteroid occurs in association with numerous disarticulated plates of *Helicoplacus.* Seemingly, these occurrences of Edrioasteroidea, Eocrinoidea, and Helicoplacoidea represent the oldest known records of the Echinodermata. The presence of these dissimilar echinoderm types close to the beginning of the good fossil record



indicates that differentiation within the phylum must have been initiated before the beginning of the Cambrian. The free-living character of *Helicoplacus* suggests that, contrary to usual concepts, ancestral echinoderms may have been free-living. Whatever their character, the common ancestor must have had the potential to give rise to such divergent types as *Helicoplacus, Eocystites,* and the edrioasteroids.

Because of the highly specialized nature of the expansion-contraction mechanism which is judged to distinguish the Helicoplacoidea, this group probably represents a branch of the echinoderm stock that left no descendants. The imbrication of the test in the retracted state, however, is strongly reminiscent of such edrioasteroids as *Lepidodiscus* and *Agelacrinus,* suggesting that the Edrioasteroidea may be related to the Helicoplacoidea. Also, it seems possible that the holothurians might have been derived from the immediate, pretorsion ancestor of the helicoplacoids. The test of the adherent but flexible holothurian *Psolus,* with its heavy imbricating plates, is suggestive of the retracted test of *Helicoplacus.* The origination of new plates from the apical pole, the lack of circumoral appendages, and the probable body shape of the pretorsion ancestor also suggest such early echinoids as *Aulechinus* and the equivocal echinoid-holothurian *Eothuria.* If these similarities are significant, they suggest that the Edrioasteroidea, as well as the Helicoplacoidea, belong in the subphylum Echinozoa and that this group probably was derived from the immediate pretorsion ancestor of the Helicoplacoidea.

Family HELICOPLACIDAE
Durham & Caster, n. fam.

Characters of the class. *L.Cam. (Olenellus Zone).*

Helicoplacus Durham & Caster, 1963, p. 82c [**H. gilberti*; OD]. Test of 10 "interambulacra" and single ambulacrum with short branch; peristome

Fig. 109. Side views (reconstr.) of species of *Helicoplacus,* both L.Cam. (*Olenellus* Zone), USA (Calif.), showing strong torsion of theca, oral extremity at top, pointed aboral end directed downward.——*A. H. curtisi* Durham & Caster, partially expanded, a spinose species (1).——*B.* **H. gilberti* Durham & Caster, individual in retracted state (1).

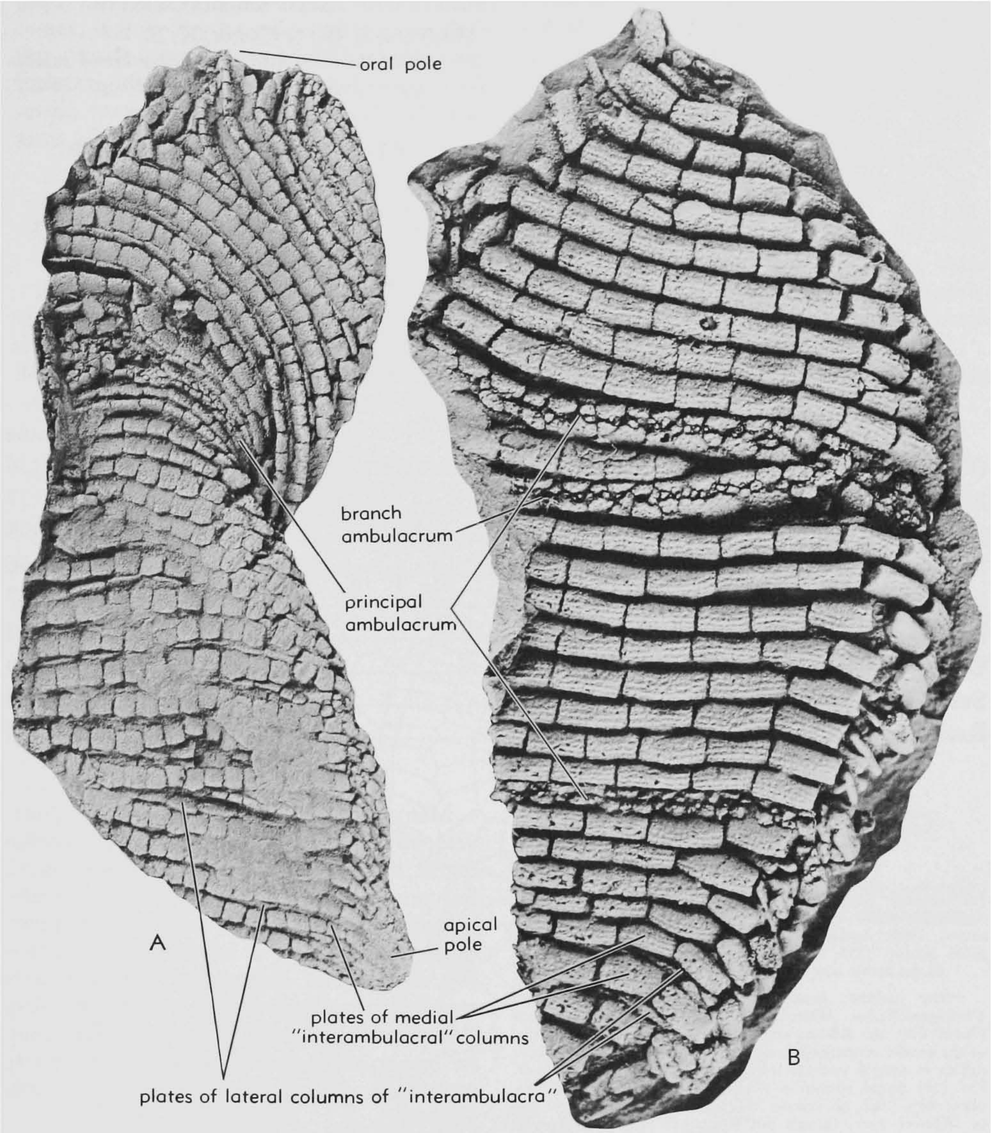


FIG. 110. Specimens of *Helicoplacus,* L.Cam. (*Olenellus* Zone), USA (Calif.).——*A*. Flattened, nearly complete specimen, *H.* sp., showing pointed apical pole and partly dissociated upper part of test with oral pole, ×4 (2).——*B.* **H. gilberti* DURHAM & CASTER, incomplete flattened specimen with branching ambulacrum, lowermost ambulacrum being continuation of this, ×7 (2).

small; type-species with longitudinal ribs on plates of medial "interambulacral" column; random nonarticulating spines on plates of medial interambulacral column, especially near peristome. *L. Cam. (Olenellus Zone),* USA (Calif.-W. Nev.).——FIG. 107; 108, 109, 110,A. **H. gilberti*; 107, flattened and expanded oral pole of incomplete specimen, oral area at center of spiral, showing a few plates of incomplete ambulacrum in lower right, and spines on random plates of medial interambulacral column, ×6.6 (2); 108,*A*,*B*, sections of test parallel to oral-aboral axis, in retracted state *(A)* showing infolded "interambulacral" columns, and in expanded state *(B)* showing lateral "interambulacral" columns in expanded position, both ×18 (1); 109,*B*, restoration, retracted state ×3.75 (1); 110,*B*, incomplete, flattened specimen showing branching of ambulacrum, lowermost ambulacrum same as uppermost but on next volution, ×7 (2).——Fig. 109,*A*. *H. curtisi*; restoration of spinose species partially expanded, ×2.5 (1).——Fig. 110,*A*. *H.* sp., flattened, nearly complete specimen, showing apical pole and partially dissociated oral pole, ×4 (2).

REFERENCE

Durham, J. W., & Caster, K. E.

(1) 1963, *Helicoplacoidea, a new class of echinoderms:* Science, v. 140, no. 3568, p. 820-822, text-fig. 1, photo on cover.

ADDITIONAL SOURCE OF ILLUSTRATIONS

(2) **Kier, P. M.**, n.

EDRIOASTEROIDS

By Gerhard Regnéll

[Lunds Universitet, Lund, Sweden]

CONTENTS

Class EDRIOASTEROIDEA Billings, 1858

[as suborder Edrioasteridae] [=Thyroidea Chapman, 1860; Agelacrinoidea S. A. Miller, 1877; Cystasteroidea Steinmann, 1890; Agelacystida Haeckel, 1895 *(partim)*; Thecoidea Jaekel, 1895; Cystostelleroidea Steinmann, 1903] [excludes forms now referred to class Edrioblastoidea[1]]

Many-plated echinoderms with well-developed (normally) quinqueradiate endothecal ambulacral system; no thecal pores, but pores may be present between ambulacral elements (thus not piercing substance of plates); no arms or brachioles; anal opening in posterior interradius, generally covered by valvular pyramid; a third aperture, interpreted generally as a hydropore, may be recognizable between mouth and anus; unstalked (Fig. 111,*1*). *L.Cam.-L.Carb. (Miss.).*

INTRODUCTION

The pelmatozoan nature of the Edrioasteroidea, although some of them show eleutherozoic tendencies in mode of life, is clearly demonstrated by the following observations. Even so, the class here is included in the dominantly eleutherozoan subphylum Echinozoa.

(1) The adoral surface, with mouth, anus, and a third opening, was directed upward. In some genera the theca was modified so as more or less to simulate a stem.

(2) The Edrioasteroidea fed as whirlers, according to Remane (Spencer, 38), that is, food was brought to the mouth by a subvective system of ciliated grooves protected by cover plates.

(3) Evidence is found in some genera

---

[1] The stalked genus *Astrocystites* Whiteaves, 1897 (=*Steganoblastus* Whiteaves, 1897) has formerly been placed with the Edrioasteroidea as the single representative of the family Astrocystitidae Bassler, 1935. Since *Astrocystites* differs in several respects from typical Edrioasteroidea R. O. Fay (14) found reason to institute a new class, Edrioblastoidea Fay, 1962, to reecive the genus. This procedure will be followed here, though not without a certain reluctance.

(e.g., *Edrioaster*) of an aboral motor nerve center, but it may be assumed *a priori* that this system is strongly reduced because it has little or no importance in sessile or almost sessile forms wanting a stem and movable arms (7, pt. 7).

The most significant features of the Edrioasteroidea, by which they differ from all other pelmatozoans, are the nature of ambulacral structures and absence of all exothecal appendages.

MORPHOLOGY

GENERAL FEATURES OF THECA AND AMBULACRA

As in other noncrinoid pelmatozoans, the viscera are enclosed in a capsule, termed **theca.** However, unlike the theca of the Rhombifera, this is not closed, for the ambulacra are lodged between the thecal skeletal elements and do not rest upon them (Fig. 111,*2*). It may be that, morphogenetically, the ambulacral skeleton is not different from the other thecal plates.

As mentioned already, the **adoral surface**

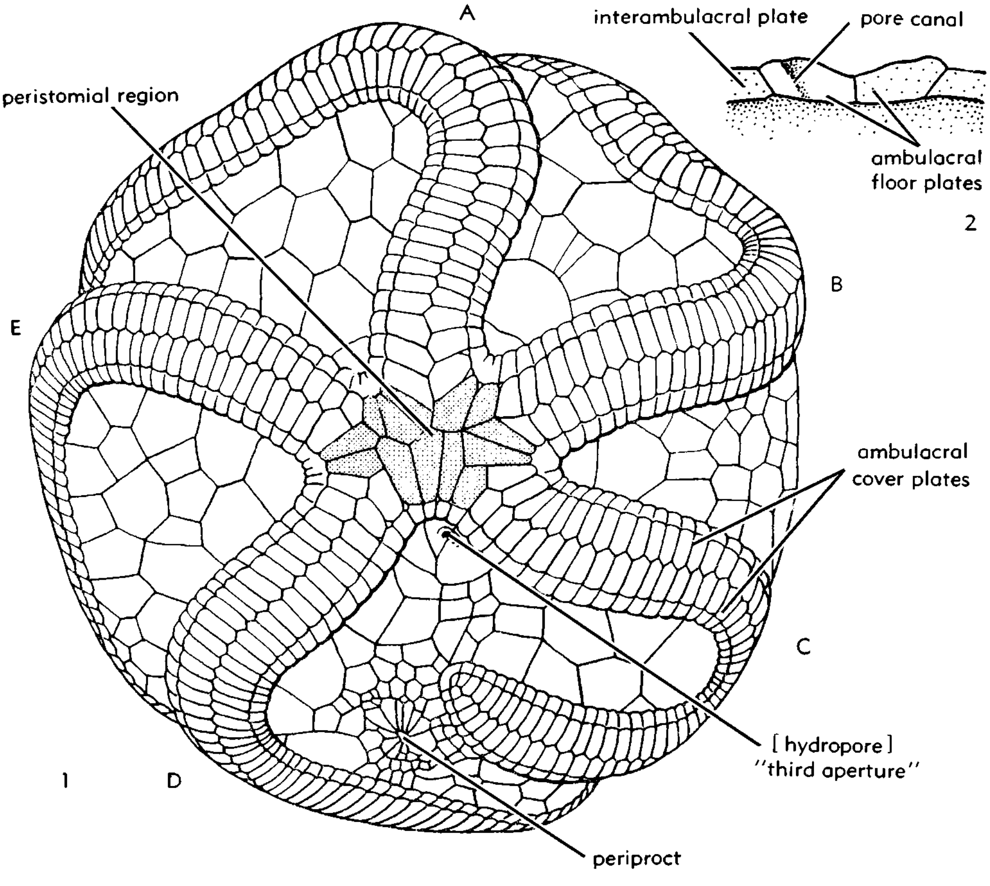


FIG. 111. Typical edrioasteroid, *Edrioaster bigsbyi* (BILLINGS), M.Ord., Ontario, illustrating some morphological features.——*1*. Adoral surface showing ambulacra with biserially arranged cover plates adjoined on each side by row of adambulacral plates, interambulacral areas distinguished by relatively large irregularly arranged plates; ambulacra marked by letters of Carpenter system; ill-differentiated plates of peristomial region unshaded; posterior interambulacrum with low anal pyramid (periproct) and near peristome with "third aperture" interpreted as hydropore; ×2.5 (after 24, modified from 7, pt. 4).——*2*. Transverse section of ambulacral floor plates showing their relation to adjoining interambulacrals; floor plate at left viewed on its sutural surface, showing pore canal, floor plate at right viewed on cut surface; ×5 (7, pt. 4).

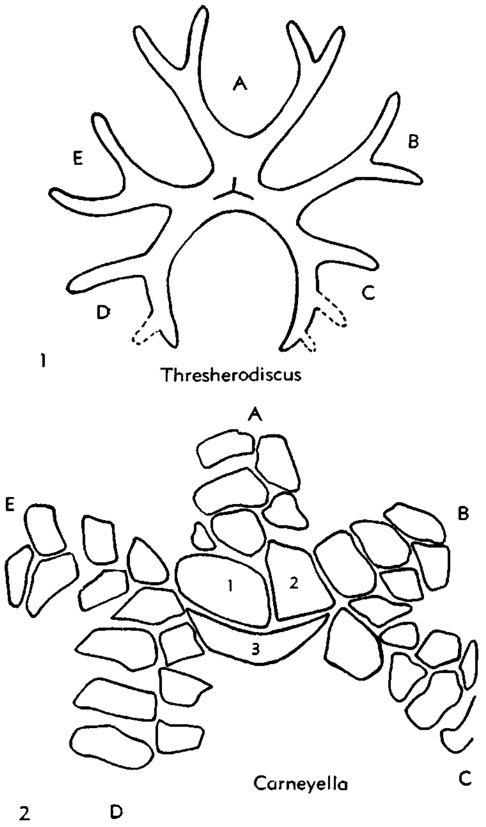


FIG. 112. Trimerous arrangement of ambulacra rarely exhibited by edrioasteroids.——*1.* Pattern of rays shown in diagram of adoral surface of *Thresherodiscus ramosus* FOERSTE (M.Ord., Ontario), ×4 (16).——*2.* Adoral part of theca of *Carneyella pileus* (HALL) (U.Ord., Ohio), with somewhat disguised trimerous disposition of rays owing to separation by large orotegminal plates (left and right anterior, *1,2;* posterior, *3*), ×8 (40).

(known also as oral, ventral, or actinal surface—"adoral" should be preferred to "oral" because the latter term refers primarily to the area occupied by the mouth and its skeleton, the peristome) contains the apertures of the thecal wall and was directed upward (hence sometimes referred to as "upper surface"), whereas the **aboral surface** (known also as apical, adapical, dorsal, or abactinal surface) was directed downward ("lower surface"). In most genera, the ambulacral grooves are restricted to the adoral surface and do not reach the aboral surface except in the family Edrioasteridae.

In the oldest known edrioasteroid, *Stromatocystites* (L.Cam.-M.Cam.), and in many later genera, the theca is depressed semiglobular, having the shape of a slightly convex disc. The theca developed variously, however, being either very thin and almost flat in some forms (e.g., *Agelacrinites*), or saclike in others (e.g., *Cystaster*). The tendency to elevate the adoral surface over the sea bottom has found its extreme expression in *Pyrgocystis.* In this genus the theca is transformed into a high turret, the height of which is many times the diameter of the adoral surface.

Pentamerous symmetry in these forms is demonstrated mainly in the disposition of the ambulacral grooves, which differentiate the theca into 5 ambulacral (radial) and 5 interambulacral (interradial) fields, called **ambulacra** and **interambulacra,** respectively. One or more extra rays may occur in several genera. The ambulacra will be referred to by the letters *A-E* in agreement with the system introduced by P. H. CARPENTER (1884). The ambulacrum opposite to the posterior interradius *(CD)* is designated by *A*; ambulacra *B-E* follow in clockwise direction when the oral surface is directed upward. The interambulacra have the symbols *AB, BC,* etc. (Fig. 111,*1*).

Pentamerism is not reflected generally by the arrangement of thecal plates. A trimerous disposition of the radial extensions, with one anterior ray and two forking lateral ones, is apparent in *Thresherodiscus* (M. Ord.) (Fig. 112,*1*) and it can be distinguished in *Carneyella* (M.Ord.-U.Ord.) (Fig. 112,*2*) *Dinocystis* (U.Dev.), and *Lepidodiscus squamosus* (Miss.). This has been interpreted by BATHER and others as an archaic pattern, but that view is not in accord with recent opinion which regards trimerism in echinoderms as a secondary feature. [*Tribrachidium* GLAESSNER, 1959, from the Precambrian of S. Australia, which is characterized by perfect threefold symmetry, has a superficial resemblance to disc-shaped edrioasteroids. However, there is no ground for assuming that *Tribrachidium* developed into some primitive echinoderm. Rather was it an aberrant coelenterate (cf. this *Treatise,* p. *W*228)].

All Edrioasteroidea are small or moderate in size. The thecal diameter of adult specimens varies generally between 5 and 60 mm.; in *Pyrgocystis* it may be less than 5 mm.; the largest of the two known specimens of *Timeischytes* is 4.5 mm.

THECAL SKELETON

As a rule, the interambulacral (interradial) sections are broad as compared with the ambulacral (radial) ones. Their structure therefore largely controls constitution of the theca. Where the ambulacra are exceptionally broad, as in *Hemicystites,* the interambulacra are narrow, in consequence. Very commonly, the posterior *(CD)* interambulacrum differs in shape from the others.

GENERAL CHARACTER

The plates of the interambulacra are called **interambulacrals** (interambulacralia, interradials, interradialia). They may be scalelike and more or less imbricating, which provides the theca with a certain degree of flexibility. In the oldest known family (Stromatocystitidae), flexibility is achieved by other means; as by weak calcification of the skeleton or by presence of stroma strands between the polygonal nonimbricate plates, which thereby admitted some mobility. Attachments of the stroma strands are marked generally by two or three diplopore-like depressions that extend across the sutures of adjoining plates. Because of the superficial resemblance of these structures to diplopores, *Stromatocystites* has been supposed to indicate relationship between edrioasteroids and diploporite Hydrophoridea. This interpretation is quite implausible in view of the fact that true diplopores only exceptionally cross sutures between thecal plates (e.g., *Glyptosphaerites*). It is not more convincing to compare the dumbbell-shaped depressions on edrioasteroid suture faces with the pore canals of the Rhombifera (as suggested by Cuénot, 10).

A weakly calcified theca, with minute plates, is also present in the saclike *Cystaster.*

It is noteworthy that flexibility of the theca among discoidal and hemispherical forms surely is not correlated with their temporary fixation. Otherwise, one might suppose that the purpose of flexibility was to allow the theca to act as a sucking disc, as indeed it may have been in *Stromatocystites.*

The turret-shaped *Pyrgocystis* cannot have been able to relinquish its attachment at an adult stage. In spite of this, its theca is formed by imbricating plates, which are not markedly different from those of the interradial areas of the adoral surface. The skeletal elements in this genus show a tendency, although not absolute, to develop phylogenetically toward greater plasticity without loss of firmness. This is effected by modification of the inosculating plates of early species into obliquely disposed plates arranged in distinct columns separated by grooves and in late forms by dense crowding of small plates without overlapping. Development of this sort seems to have occurred independently in Lower Ordovician and Silurian stocks of *Pyrgocystis.* The improved flexibility of the theca thus acquired may have served for adjustment of the theca to the substratum and for directing the oral region toward food-bearing water currents. It may be that flexibility of the theca had some importance also for the mechanism regulating the opening and closing of the ambulacral grooves.

In forms where the interambulacrals comprise a mosaic of polygonal plates, the theca generally is characterized by greater rigidity. In the Cyathocystidae, the lateral plates are fused into a solid saclike mass cemented to the substratum so as to form, with plates of the adoral surface, an extremely firm theca. The stalked *Astrocystites* has a very rigid theca composed of relatively few plates, which are extraordinarily large and thick as compared with the plates of all Edrioasteroidea (*Astrocystites* now assigned to Edrioblastoidea).

INTERAMBULACRALS

The interambulacrals are either polygonal plates arranged in a mosaic, or scalelike imbricating ossicles. Some genera, however, have interambulacrals intermediate between these types, with polygonal, slightly imbricate plates (e.g., *Walcottidiscus, Ulrichidiscus*). Species with mosaic plates and species with imbricate plates may belong to one and the same genus (e.g., *Lebetodiscus, Isorophus, Agelacrinites*).

In most genera, the interambulacrals are tolerably uniform, but in some they are clearly differentiated in size and shape. The interambulacral plates of *Hemicystites* and *Anglidiscus* have a tendency to become larger in a centrifugal direction, whereas in *Lebetodiscus* and *Thresherodiscus* the largest plates are found near to the center; in *Agelacrinites* they vary strongly in shape.

Minute plates bordering on the valvular plates of the periproct are found in several genera (e.g., *Anglidiscus, Isorophusella*). Not seldom (e.g., *Edrioaster*) an agglomeration of numerous small irregular plates on the right side of the anus marks the position of an expanded rectum.

Further, one or more rows of small adradial plates may line the ambulacra (e.g., *Anglidiscus, Isorophus, Lepidodiscus, Stromatocystites*).

A definite arrangement of the interradial plates is usually not recognizable. A noteworthy exception is found among members of the Cyathocystidae and *Timeischytes* among the Hemicystitidae. *Cyathotheca* and *Cyathocystis* have only one large, triangular plate in each interambulacrum. Whether these have developed from a number of ordinary interambulacrals fused into larger solid plates or are primary structures is not obvious from the fossil material, in which not the slightest indication of sutures can be traced. Yet it is easy to realize that an amalgamation of mosaic interambulacrals (as in *Stromatocystites*) would produce plates like those present in the Cyathocystidae, just as has been suggested to explain the sides of saclike thecae by fusion of lateral plates corresponding to those in *Cystaster*. This seems reasonable. Although corresponding morphologically and functionally to the orals of certain crinoids, the interambulacrals of the Cyathocystidae are not necessarily homologous with orals. *Cyathocystis* also possesses an inner circle of five interradially disposed plates which cover the oral field. These probably do not belong to the interambulacral series, however, for they seem to have originated by coalescence of the most proximal ambulacral cover plates of each two adjoining rays, like the oral cover plates of other Edrioasteroidea.

Timeischytes is remarkable in that all interambulacra save the posterior one are each covered by a single large sublunate or sublinguiform plate. In interambulacrum *CD* five differently shaped interambulacrals are disposed around the anal pyramid.

In forms with imbricating plates, the overlap is invariably in a proximal direction, and greater toward the periphery. A diagonal arrangement of the interambulacrals may be discerned in some species.

Advocating the view that the Edrioasteroidea were derived from some cystoidean ancestor, Foerste (16) observed that imbrication of thecal plates can hardly be considered a primitive feature, because the plates of cystoids have polygonal outlines and are arranged in a mosaic. He suggested that the change was due to "assuming of the sessile habit, together with the enormous shortening of the theca in a vertical direction. This caused the distal edge of one plate to collapse within the proximal edge of the adjoining plate." Without entering now on a discussion of the supposed phylogeny of the Edrioasteroidea, it should be pointed out, in objection to this theory, that an extraordinarily strong imbrication of the thecal plates is found in *Pyrgocystis,* in which the vertical axis of the theca is extremely long.

PERIPHERAL RING

Plates of the adoral surface (excluding those of the ambulacra) commonly are differentiated into interambulacrals proper and distal plates forming a peripheral ring. This is true of most discoidal to hemispherical forms. Naturally, a peripheral ring is lacking among the edrioasteroids in which the ambulacra pass on to the aboral surface.

Generally, plates of the peripheral ring decrease in size in a centrifugal direction. It is a common feature that those nearest to the central part of the adoral surface are even bigger than the interambulacrals and are extended tangentially, especially in *Agelacrinites* and *Timeischytes.* Plates of the border nearest to the periphery are minute.

The outer portion of the peripheral ring undoubtedly was mobile and thus capable of adjusting to the surface of the substratum. The larger plates forming an inner band of the peripheral ring in many Edrioasteroidea had much greater rigidity; they were rather firmly locked horizontally but capable of some vertical extension.

Most plates of the peripheral ring bear one or more processes on their aboral surface. These processes may have served for attachment of muscles of the muscular wall in which the plates were imbedded.

The peripheral ring of *Cyathocystis* is formed by a single row of subquadrate marginals. In *Cyathotheca* it is wanting entirely.

Not seldom the peripheral ring is raised over the central portion of the theca. This is a post-mortem feature due to sinking in of the central body after decay of the animal.

ABORAL SIDE

Among edrioasteroids which lack a definite peripheral ring, the aboral side of the theca is made up of plates more or less continuous with and similar to the interambulacrals.

In *Stromatocystites* the aboral center is occupied by a fairly distinct dorsocentral (not necessarily homologous with the dorsocentral of other echinoderms) surrounded by large polygonal plates; toward the periphery the plates decrease somewhat in size and tend to be more rounded.

The aboral surface of *Cooperidiscus* is bordered by a projecting periphery of more prominent plates. The surface enclosed in this ring is covered with squamose plates, the imbrication of which is centrifugal and thus continuous in direction with the imbrication of the oral face. This suggests that *Cooperidiscus* developed from some more or less globular body covered by plates overlapping in a direction from the base toward the oral pole.

The Edrioasteridae are characterized by differentiation of the aboral surface into three regions: a central area covered with more flexible integument, bearing smaller-than-average plates; a circular frame of relatively stout plates (corresponding to the peripheral ring?); and a peripheral area of plates serially homologous with the interambulacrals of the oral face but a little smaller than the majority of these (Fig. 113,*1*).

In *Pyrgocystis (Pyrgocystis)* the basalmost plates are closely amalgamated so as to form a sort of ferrule (Fig. 113,*2*), while in *P. (Rhenopyrgus)* numerous minute plates are scattered in a coriaceous skin forming a saccate base.

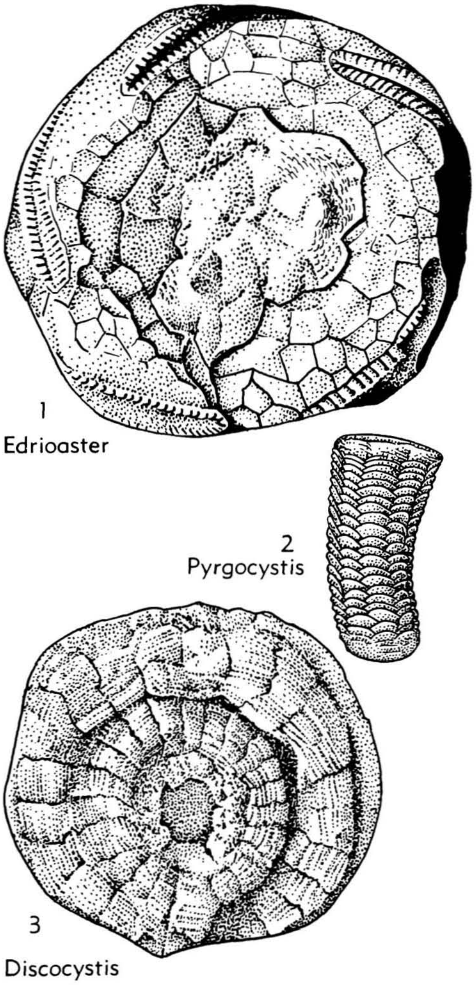


FIG. 113. Aboral surface of edrioasteroids.——*1*. *Edrioaster buchianus* FORBES, M.Ord., Wales, anal interradius at left, ×1.6 (7, pt. 2).——*2*. *Pyrgocystis (Pyrgocystis) sulcata* (AURIVILLIUS), U.Sil. (Wenlock.), Sweden (Gotl.), from side, showing smoothly rounded aboral extremity below, ×3 (2).——*3*. *Discocystis kaskaskiensis* (HALL), U.Miss. (Chester.), USA (Ala.), ×2 (4).

Little information is available about the structure of the aboral side of most other Edrioasteroidea. Conditions similar to those in the Edrioasteridae have been traced in *Lebetodiscus* (7). The lower side of *Discocystis kaskaskiensis* is remarkable in having been described originally as an echinoid, *"Echinodiscus optatus"* WORTHEN & MILLER, 1883. It is composed of many rows of fused imbricating plates (interambulacrals

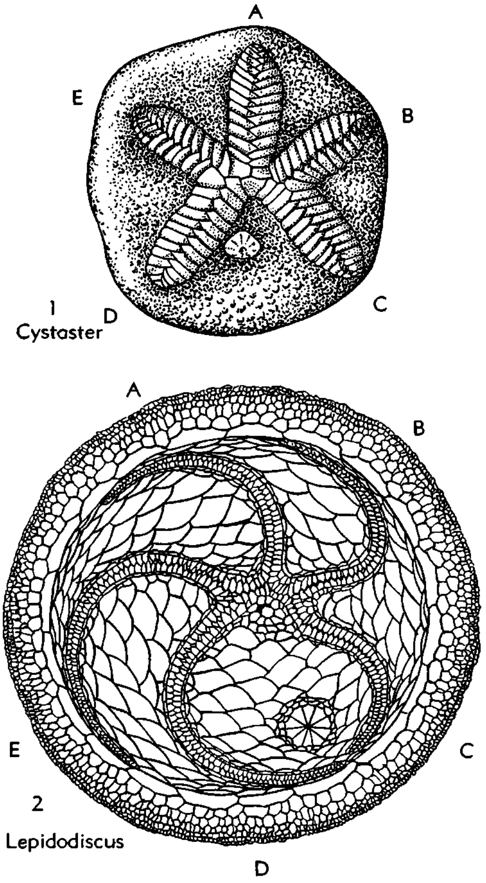


Fig. 114. Edrioasteroids with straight and curved ambulacra.——*1. Cystaster granulatus* Hall, U. Ord., USA (Ohio), a simple type characterized by relatively wide, short, and straight rays, ×4.5 (20).——*2. Lepidodiscus ephraemovianus* (Bogolubov), U.Dev. (Famenn.), USSR, showing contrasolar curvature of long, narrow ambulacra in all rays except *C*, which is solar, ×2.8 (18).

of the adoral surface mosaic) and a central area of attachment (Fig. 113,*3*).

In species attached by the entire aboral surface to some foreign object, the lower surface is, of course, not accessible for investigation in complete specimens. Foerste (16) has reported several specimens of *Carneyella cincinnatiensis* in which a few plates of the adoral surface of the theca were missing. On etching away the clay inside the theca, he found no trace of aboral plates, even though the finest details in sculpture of the shell of *Rafinesquina* supporting the theca were preserved. From this Foerste concluded that "it may be assumed that in those forms which assumed the sessile habit, the original plates of the aboral surface became obsolete, a fleshy surface, unprotected beneath, being much better adapted for attachment to an underlying surface."

AMBULACRA

GENERAL CHARACTER

It has been pointed out above that the thecal skeleton is not completely continuous but is interruped by the skeletal elements of the **ambulacra** enclosing the ambulacral groove (subvective groove, food groove). The ambulacral structures are intercalated between (not extended over) the interradial plates. It is likely, however, that from the outset the floor plates formed part of the thecal wall, having acquired later the appearance of a separate system. According to this view, the grooves were originally epithecal, very much as in the Diploporita.

The primitive condition of the ambulacra, as displayed by *Stromatocystites* and by immature stages of several species assigned to other genera, is characterized by a straight course. Straight ambulacra are further found in the Cyathocystidae, some Hemicystitidae (e.g., *Pyrgocystis, Cystaster, Cincinnatidiscus, Hemicystites,* and *Timeischytes*) (Fig. 114,*1*). In *Isorophus* the ambulacra may be almost straight; in *Thresherodiscus* they are straight and repeatedly branch dichotomously, which is quite unique among the Edrioasteroidea.

In all other genera, the ambulacra are more or less curved. The curve may be **contrasolar** (counter-clockwise, to the left) or **solar** (clockwise, to the right). All rays may curve in the same direction, or they may behave differently in this respect (Fig. 114,*2*). All ambulacra curving in a contrasolar direction are found in *Lebetodiscus, Lepidoconia, Streptaster, Ulrichidiscus,* and *Dinocystis.* There is evidence that contrasolar curvature is a primitive feature among species with curved rays, for in many forms (if not all) in which ambulacrum *B* has a solar curve, its proximal part has a distinct tendency to be directed contrasolarly.

Solar curvature of the rays is characteristic of *Foerstediscus, Cooperidiscus,* and certain species of *Edrioaster* (Fig. 115).

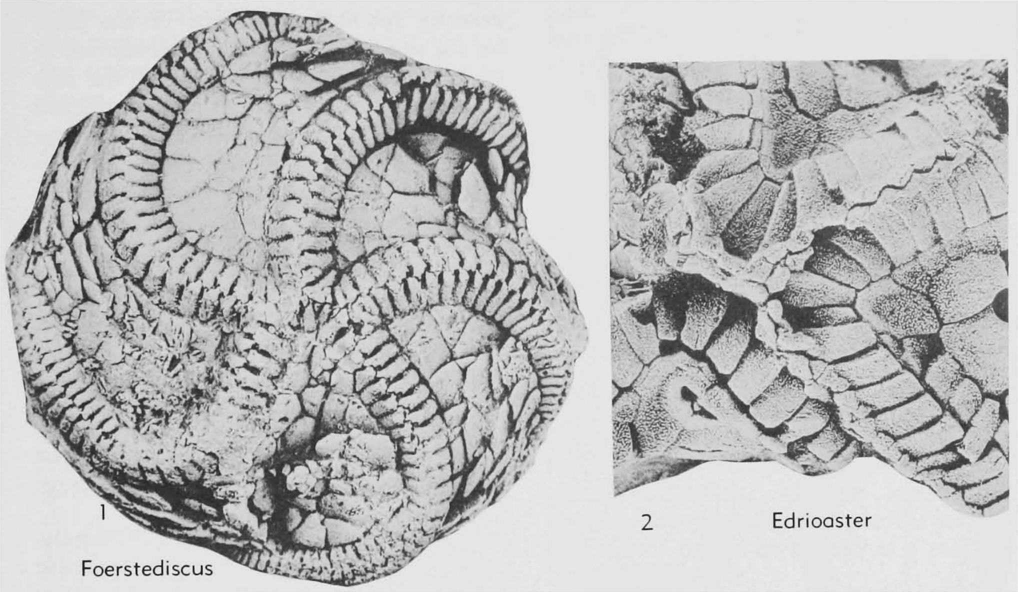


FIG. 115. Adoral views of Middle Ordovician edrioasteroids.——*1. Foerstediscus splendens* BASSLER, showing all ambulacra curved in solar (clockwise) direction, ×2.7 (24).——*2. Edrioaster levis* (BATHER), showing at upper right cover plates of ambulacrum *B* and at lower right those of ambulacrum *C;* relatively large "third aperture" near peristome in posterior interambulacrum at lower left, ×3.3 (24).

Where the rays curve in different directions, the most common case is that the rays *A, B, D,* and *E* are contrasolar and *C* solar (e.g., *Walcottidiscus, Bassleridiscus, Carneyella, Anglidiscus, Isorophus, Lepidodiscus, Discocystis, Edrioaster bigsbyi*). Two rays *(B, C)* that curve in a solar direction and others in a contrasolar direction occur in *Isorophusella* and *Agelacrinites* (and, maybe, *Xenocystites*).

Provided that ambulacra *C* and *D* curve in opposite directions and are long enough to approach each other, their tips are seen to meet approximately on the same level (e.g., *Carneyella* and some *Lepidodiscus*). The distal portion of ambulacrum *C* runs proximally to the distal part of ambulacrum *D* (thus nearest to the periproct) in *Anglidiscus, Discocystis, Edrioaster* and some *Lepidodiscus*. This is also true of some species of *Isorophus* and *Agelacrinites,* whereas in other members of these genera the distal part of ambulacrum *C* passes on the distal side of ambulacrum *D*. There may be a certain variation in this respect.

The diagnostic significance of mode of curvature of the ambulacra has been called in question, most recently by SINCLAIR (36). It is evident that direction of curvature is not constant in all species; nevertheless it seems legitimate to maintain that disposition of the ambulacra follows a pattern characteristic of each genus and species, although curvature is subject to a certain variation in the same way as number of ambulacra, for example.

The solar coiling of ambulacrum *C* has been postulated to originate from a differential pull of gravity on different rays of the growing animal in position attached to the sloping valve of a brachiopod with interradius *BC* assumed to be directed upward and with the anus at right of the mouth. Apart from theoretical considerations, such a position is indicated by the fact that the theca rather commonly exhibits a sag toward the left side.

By slight turning of the theca so that ambulacrum *B* became directed more to the right, this ray as well came under the pull of gravity of that side and acquired a solar curve, too. Once acquired, the mode of curving of the ambulacra might have remained unchanged, on principle, in later generations in the state fixed in ancestral forms and thus unaffected by the more or less at random position of the theca. The deeper explanation of the varying (but apparently specific) orientation of the theca on the sloping surface of the substratum as probably controlling the bend of the rays is not obvious, nor is it easy to comprehend the origin of solar or contrasolar curvature affecting all rays of a theca (7).

The ambulacra are grooves underlain by floor plates, and both walled in and roofed over by cover plates which could open or close at will.

AMBULACRAL FLOOR PLATES

The plates forming the ambulacral grooves are known as **floor plates** (ambulacrals, ambulacralia *auctorum*, adambulacrals, adambulacralia *auctorum*—terms that should be avoided because of their inconsistent usage—subambulacral plates).

In the primitive condition (e.g., *Stromatocystites*), these are arranged in a double series (two rows) of alternating plates meeting in a perradial (mid-radial) line. Biserial floor plates are further met within the Edrioasteridae and, doubtfully, in the Cyathocystidae. The perradial suture is more or less zigzag. In the Edrioasteridae a lateral pore occurs between successive floor plates on each side, thus not piercing the plates but situated in the tangential suture between them (Fig. 116,*1*). The Stromatocystitidae are probably devoid of such pores, whereas the Cyathocystidae are not known in this respect.

The Hemicystitidae and Agelacrinitidae, on the other hand, are characterized by a single row of concave floor plates (Fig. 116,*2*) which may partly have become fused but still separated at intervals. An apparent exception to the rule that no pores are present between the uniserial floor plates is offered by *Anglidiscus*, according to a statement by Anderson (1) (Fig. 116,*3*). Bather (7) pointed out that the floor plates of *Lebetodiscus* were disposed in a double series of alternating plates with intervening

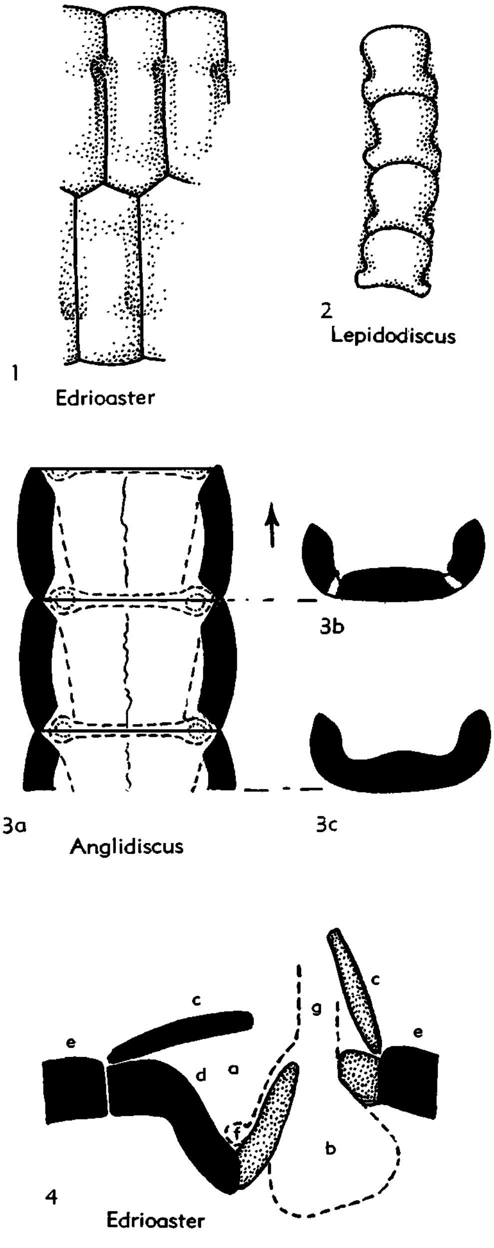


Fig. 116. Ambulacral floor plates of edrioasteroids.——*1. Edrioaster bigsbyi* (Billings), M.Ord., Ontario; upper (adoral) surface of floor plates showing grooves that lead from pore depressions to perradial canal, ×10 (7, pt. 4).——*2. Lepidodiscus beecheri* (Clarke), Miss., USA (Pa.); lower (aboral) side of floor plates, ×6 (9).——*3. Anglidiscus fistulosus* (Anderson), L.Carb., Eng., diagrams of floor plates, arrow pointing toward mouth, ×30 (1); *3a,* plan of mature floor plates from center of ambulacrum; *3b,c,* transverse sections of floor plate at suture and through center.——*4. Edrioaster* sp., diagrammatic transverse section across ambulacrum showing relations of cover plates, floor plates and inferred water vessel (ampulla) with its connection to tube foot through pore (natural suture surfaces stippled, cut surfaces solid black, supposed soft parts indicated by broken line) [*a,* ambulacral groove; *b,* ampulla; *c,* cover plate; *d,* floor plate; *e,* interambulacral plate; *f,* perradial water vessel; *g,* tube foot] (7, pt. 2).

pores. As first observed by Raymond (28), this proposal is due to misinterpretation of the ambulacral skeletal structure in this instance.

The floor plates of *Stromatocystites* are fairly polymorphous but invariably more or less elongated in a radial direction, alternating irregularly. These structures are more fully known in the Edrioasteridae, thanks to Bather's thorough investigations. *Edrioaster bigsbyi* may be taken as an example (condensed from Bather). In this species the floor plates are elongate at right angles to the perradius. Their outer margins are convex and their abutting margins straight. The plates rise sharply up from the interradial areas, forming a rounded margin on each side of the groove and then they dip almost straight down to the perradial suture. Proximally, the depression thus formed is more marked, whereas distally it becomes slighter and almost disappears. The suture between two floor plates on the same side of the groove is depressed from a point just within the rounded margin right down to the perradial suture. The depression is deepest at its outer end, where also it is slightly expanded in circular manner to form a pore under lateral margins of the cover plates. The perradial suture also is depressed. At the extreme distal end of a ray, the floor plates diminish considerably in size but continue to alternate and are arranged fanwise. The canals of the lateral pores passing into the thecal cavity run obliquely downward about parallel with the sutures between the floor plates and the adjacent interambulacrals, that is, sloping from the exterior inward toward the perradius. The pores must have been podial pores housing a tube foot connected with a perradial water vessel and an endothecal ampulla (Fig. 116,*4*).

Other members of the Edrioasteridae agree, on principle, with *Edrioaster bigsbyi* with regard to structure of the floor plates, though, of course, minor differences occur.

It is evident that the development of floor plates as described is largely influenced by the presence of a tube-foot ampulla system. Where such a system is absent, as in the Hemicystitidae (*Anglidiscus* apparently making a bewildering exception) and the Agelacrinitidae, the skeletal elements beneath the ambulacral groove are less differentiated. As pointed out above, the floor plates are uniserial in the families just referred to. There is hardly anything to indicate whether the uniseriality arose by a "straightening" of the biserial row or by fusion of a pair of more or less opposed plates of the biserial row.

In some forms the uniserial floor plates exhibit a considerable overlap in a proximal direction as seen from above. Foerste (16), who paid much attention to intimate structure of the Edrioasteroidea, observed that the "proximal overlapping suggests that the floor plates may be modified thecal plates belonging to the upper face of the theca—the food grooves extending over the thecal plates themselves, without intermediate flooring." However that may be, the ambulacral system has to be treated as a morphological unity.

Not uncommonly, the individual floor plates (speaking of the uniserial type only) were formed in fact by fusion of two primitive floor plates, one proximal and another distal. The floor plates are not invariably broad enough to underlie the entire width occupied by the cover plates and thus basal extensions of the cover plates may project beyond their margins (e.g., *Carneyella pileus*). The floor plates are quadrangular or are much wider than long (in distal and proximal regions of the ambulacra). The median portion of their adoral surface is excavated radially. The (ambulacral) groove thus formed may be fairly wide (e.g., *C. cincinnatiensis*) or extremely narrow (e.g., *Streptaster,* in which each whole ambulacrum is very narrow). A much fainter groove has been stated to run, in several species, along the border of the floor plates, on each side of the ambulacral groove. These lateral grooves had some connection with the fulcra of the cover plates, by means of which the latter were opened and closed over the ambulacral furrow.

AMBULACRAL COVER PLATES

Irrespective of the biseriality or uniseriality of the floor plates, the ambulacral **cover plates** (adambulacrals, adambulacralia *auctorum*, —cf. "Ambulacral Floor Plates" above—*Saumplättchen*) are invariably biserial, although this is concealed in some very few special examples. These plates form the walls and roof of the canal made up of the ambulacral skeletal elements.

The cover plates stand on the upper margin or outer extension of the floor plates, which, more or less, form lateral shelves (Fig. 116,*4*). In various genera (e.g., *Edrioaster*), the cover plates have been reported to articulate on a beveled facet just within the edge of the radial groove. Primarily, a single cover plate matches each floor plate among those arranged biserially and a pair of cover plates corresponds to each floor plate among those arranged uniserially. The crowding and doubling of the cover plates seen in many edrioasteroid species is correlated with the aforementioned fusion in a radial direction of uniserial floor plates (40).

In *Anglidiscus* and, less pronounced, in *Lepidodiscus lebouri,* there is an apparent uniseriality of the cover plates in the proximal region of the ambulacrum (Fig. 117,*1*). However, as observed by ANDERSON (1) in *Anglidiscus,* structural details indicate that this is very likely a masked biserial arrangement. This interpretation is corroborated by the fact that, in *Anglidiscus,* a gradual transition is observed in a distal direction into very regular pentagonal plates interlocking along the perradius.

The type of cover plates last mentioned is characteristic of many early Edrioasteroidea, although the cover plates may, of course, vary a good deal in general outline according to width of the ambulacrum, number and length of the floor plates, and

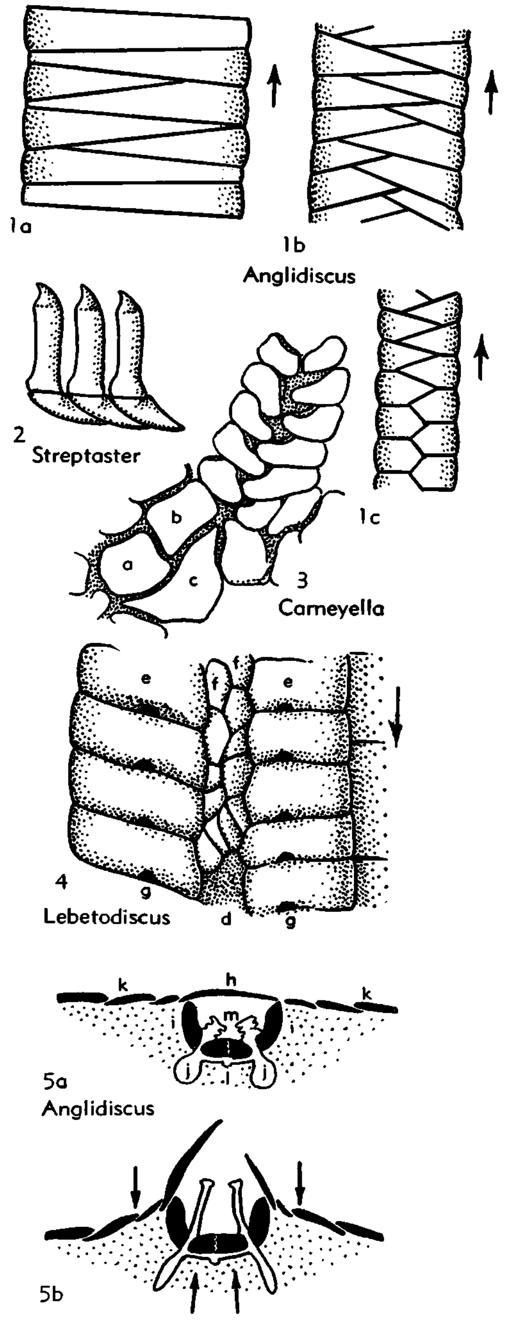


FIG. 117. Form and relationships of edrioasteroid cover plates.——*1. Anglidiscus fistulosus* (ANDERSON), L.Carb., Eng., showing development of cover plates in different parts of single ambulacrum, arrows pointing toward mouth, ×28 (1); *1a-c,* proximal, medial, distal.——*2. Streptaster septembrachiatus* MILLER & DYER, U.Ord., USA (Ohio), 3 vertically disposed palisade-like cover plates borne by ambulacral floor plates, seen from side, enlarged (16).——*3. Carneyella pileus* (HALL), U.Ord., USA (Ohio); peristomial region with orotegminals (*a, b,* left and right ant.; *c,* post.), proximal part of ambulacrum *B* showing boot-shaped lateral cover plates, ×12 (37).——*4. Lebetodiscus dicksoni* (BILLINGS), M.Ord., Ontario, part of ambulacrum, arrow pointing toward mouth (*d,* ambulacral groove; *e,* lateral cover plate; *f,* median cover plate; *g,* pore between lateral cover plates), ×6 (7, pt. 3).——*5. Anglidiscus fistulosus;* hypothetical transverse sections of ambulacral groove and adjacent skeletal elements indicating supposed mechanism of cover-plate movements, enlarged; *5a,* animal deflated, with groove closed; *5b,* animal inflated, with groove open (*h,* ambulacral cover plate; *i,* ambulacral floor plate; *j,* ampulla; *k,* interambulacral plate; *l,* radial canal; *m,* tube foot) (1).

other characters. They are very regular and symmetrical in the Edrioasteridae as well. In *Stromatocystites* they are still little advanced, being minute and less regular.

However, in many species examined in this respect, the cover plates are differentiated further morphologically. They are more or less boot-shaped, with the "sole" of the boot proximal and the "toe" admedian (Fig. 117,*3*). In consequence, they cannot effect closure of the groove as completely as do the symmetrical cover plates of the Edrioasteridae, Cyathocystidae (e.g., *Cyathocystis*), and others. But this drawback is counteracted in many instances by the presence of additional cover plates along the median line (first and foremost in *Lebetodiscus, Carneyella,* and *Thresherodiscus,* further in *Isorophus, Isorophusella,* and *Edrioaster*) The ordinary cover plates have been interpreted by Foerste (16) to be distinguished as "lateral cover plates," in opposition to "median" or "intercalated cover plates" (Fig. 117,*4*). Those last mentioned are smaller, and only their triangular tips may be seen intercalated between the tips of the lateral cover plates, interlocking along the perradius. Some evidence indicates that the additional cover plates abutted against the floor plates by means of facets. However, a perfect closing mechanism could also be achieved in forms provided with both medial and lateral projections of the lateral cover plates proper, as described by Sinclair (36) in a new species of *Foerstediscus.* The medial projections interlock in a closely fitting perradial zigzag suture.

Streptaster is affected by a conspicuous elongation of its cover plates so as to cause a palisade-like effect, especially along the concave curvature of the distal parts of the rays, when observed in lateral view (Fig. 117,*2*). A similar tendency is obvious in *Bassleridiscus.*

In *Timeischytes* only four or five cover plates occur on each side of the perradial line.

The movements of the cover plates may have been brought about by the action of muscles. Small processes interpreted as points of muscular attachment have been recognized at the lateral end of the lower side of the cover plates in several species (36, 40). It has also been suggested, however, that the movements were less due to muscular activity of the cover plates than to contraction and relaxation of the thecal skeleton as a whole in forms with overlapping interambulacrals. The lateral edges of the cover plates appear to have been overlain, in some forms, by inner edges of the adradial interambulacrals. Inflation of the test would result in "pressure on the outer edge of the covering plates, causing them to rotate about the upper edge of the flooring plates, so that their inner ends become elevated and the ambulacral groove uncovered" (1) (Fig. 117,*5*). Whether the specifically developed cover plates in the distal part of the ambulacra in *Anglidiscus,* stretching over the entire width of the ambulacrum, were actually affected by the movement mechanism may be questioned.

Pores between the ambulacral cover plates appear in some few genera (e.g., *Lebetodiscus, Lepidoconia*). In *Lebetodiscus,* a single large pore occurs in the suture between each pair of lateral cover plates (Fig. 117,*4*), whereas in *Lepidoconia* there are 5 pores. In so far as can be ascertained, these are opposite on either side of each plate, but those of adjacent plates are alternate (41).

As opposed to the pores connected with the floor plates, those of the cover plates cannot possibly have been openings for tube feet, for obvious reasons. They may have played a role for circulation of water carrying food particles to the subvective groove. The most probable explanation may be that they were outlets for excessive water rather than intakes for water. But why the genera mentioned, and only those, were provided with such pores remains obscure.

PERISTOME

From a strictly morphological point of view, plates constituting the peristome should not be separated from the ambulacral and, in part, interambulacral skeleton. Yet it is convenient to deal separately with elements integrated in the peristomial (and substomial) structures. These have been described and discussed fully by Bather (7), following whom very little information has been added until 1960, when a study by Kesling & Mintz (26) was published.

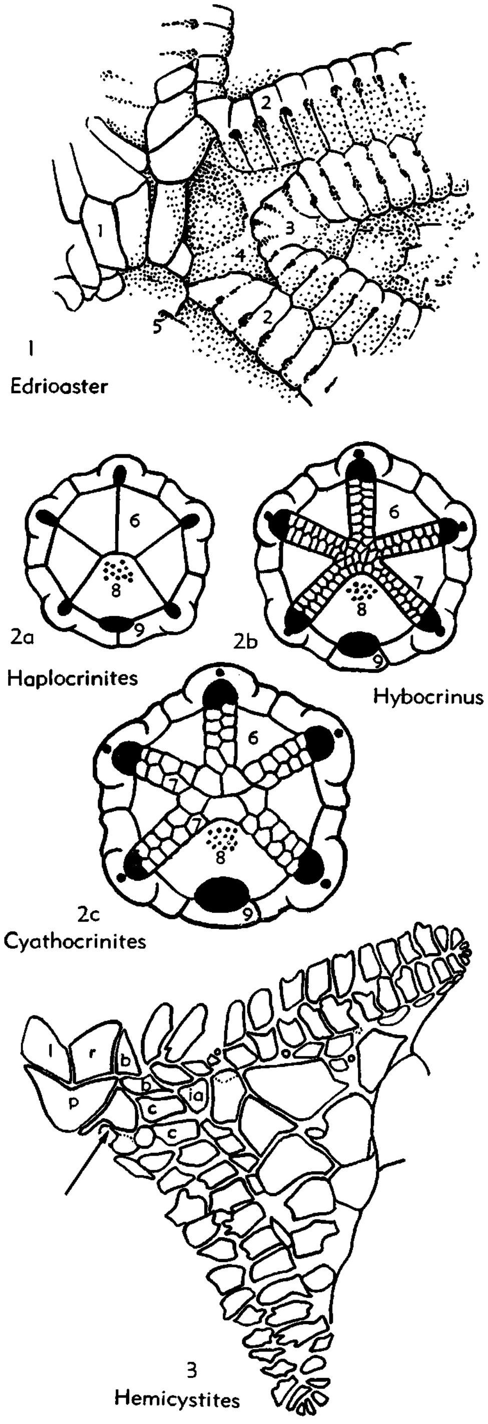


FIG. 118. Morphological features of peristomial region, viewed from above (adorally).——*1. Edrioaster bigsbyi* (BILLINGS), with proximal parts of *B* and *C* ambulacra at right (*1,* ambulacral cover plate; *2,* ambulacral floor plate; *3,* interradial peristomial element; *4,* radial peristomial element; *5,* "third aperture"), ×4 (7, pt. 4).——*2.* Stages in evolution of crinoid tegmen for comparison (diagrammatic); *2a, Haplocrinites; 2b, Hybocrinus; 2c, Cyathocrinites* (*6,* deltoid or oral plate; *7,* ambulacral cover plate; *8,* madreporite, *9,* periproct) (6).——*3. Hemicystites rectiradiatus* (SHIDELER), part of adoral surface, arrow indicating probable location of "third aperture" (inferred hydropore) (*l,p,r,* left, posterior, and right orotegminals); (*b,c,* ambulacral cover plates of *B* and *C* ambulacra, respectively; *i,a,* interambulacrals), ×9 (40).

The peristome is more or less similarly developed in all genera examined. The internal peristomial skeleton consists of a firm subcircular or subpentagonal mouth frame ("substomial chamber"), through which the gullet receiving the ambulacral grooves passed into the stomach. This was evidently attached to the inner adcentral border of the mouth frame. This frame is made up of five perradial plates, triangular as viewed from above (after removal of the plates covering the mouth) (Fig. 118,*1*), and five interradial plates, seen only in aboral aspect. Morphogenetically, all plates mentioned, apart from the elements in interradius *CD,* are undoubtedly fused portions of floor plates. In the interradius *CD* (posterior) the frame is integrated by part of the large interradial plate that is pierced by the canal interpreted generally as a hydropore canal (stone canal), and, contingently, by further peristomial interradial plates.

Also the peristomial cover plates forming a tegmen were derived mainly from the primitive ambulacral elements, namely cover plates which were modified along somewhat different lines in various groups of Edrioasteroidea.

BATHER (6, p. 100) has outlined three stages in the evolution of the tegmen in Crinoidea (Fig. 118,*2*): (1) tegmen composed of five large plates (deltoids or orals) covering the ambulacra and mouth (e.g., *Haplocrinites*); (2) deltoids as in the preceding but the ambulacra with alternating cover plates and the mouth covered by an indefinite number of modified ambulacral cover plates (e.g., *Hybocrinus*); (3) as in the preceding but with plates covering the mouth enlarged and reduced in number, usually five (e.g., *Cyathocrinites*).

A certain parallelism may be pointed out between development of the orotegminal plates in the Crinoidea and Edrioasteroidea, although the phylogenetic significance of this is not very evident in the latter. In the Stromatocystitidae the peristomial cover does not agree with the primitive type just indicated but consists of four large plates and an indefinite number of smaller ones. Whether the large plates held a definite position cannot be made out on the evidence available.

However, the first stage recognized by BATHER is apparent in *Cyathotheca.* The second stage is represented by the Agelacrinitidae, Edrioasteridae, and, perhaps, by the Stromatocystitidae. The third stage is found first and foremost in *Cyathocystis,* but also the Hemicystitidae can properly be included. Both in *Cyathocrinites* and in the Hemicystitidae the mouth slit opens transversely with respect to the sagittal plane (Fig. 118,*3*). The posterior orotegminal, located in interradius *CD,* is the largest one, its adcentral margin forming more or less a straight line transversely to the sagittal plane. In *Cyathocystis* five orotegminals are seen, as in *Cyathocrinites,* but in the Hemicystitidae the number is reduced to three, according to interpretation by BASSLER and others. The anterolateral orotegminals, which are thus smaller in size than the posterior one, were probably derived morphogenetically from ambulacral coverplate elements belonging to the ambulacra *E, A,* and *B.* They border on each other by a straight suture in the perradius of the anterior ambulacrum *(A).*

KESLING & EHLERS (25) and EHLERS & KESLING (13) have the opinion that, in *Carneyella pileus,* one additional plate, namely that designated by FOERSTE (16) as plate "X" and representing according to him one of the interambulacral plates in the posterior interambulacrum, is probably part of the peristomial region. This would be true also of *Hemicystites* and related genera. A still greater number of peristomial cover plates are present in *Timeischytes,* including two large, elongate, subpentagonal ones in the anterior part of the peristome and six diversiform plates in the posterior part of the peristome. However, these orotegminals are arranged in a definite pattern unique of its kind. Additional investigation is required before it can be stated that all genera included in the Hemicystitidae are characterized by having more than three plates covering the peristome.

PERIPROCT

In disc-shaped edrioasteroids the periproct is invariably located on the same surface as the peristome. Also in the saclike Cyathocystidae it lies on the adoral surface, whereas in *Cystaster* it has a lateral position. It is located in the posterior interambulacrum *(CD).* In many genera (the bulk of these belonging to the Hemicystitidae, apart from *Cystaster* and *Anglidiscus* and further in *Ulrichidiscus, Discocystis, Isorophusella, Agelacrinites, Dinocystis,* and others) it lies fairly central in this interambulacrum, whereas in others (e.g., *Stromatocystites, Lepidodiscus, Cooperidiscus, Edrioaster,* and others) it is more or less close to the posterior margin of the interambulacrum. In *Timeischytes* the pyramid is in contact with the peristomial region and occupies a good deal of the posterior interambulacrum. *Cyathotheca* differs from all other known Edrioasteroidea in that the periproct occupies a lunate area of the adoral surface behind the posterior orotegminal. In *Cyathocystis* the anal opening lies on the border of the posterior and adjacent marginals.

Not uncommonly, two sets of periproctal plates can be recognized, namely the circumanal plates proper, which form a more or less pyramidal cover of the anal opening **(anal pyramid),** and the distal periproctal plates surrounding the anal pyramid (e.g., *Lebetodiscus, Anglidiscus, Foerstediscus, Isorophusella,* and others). But in many genera the anal area is occupied entirely by the anal pyramid. On the other hand, no distinct anal pyramid may be present, the anus being covered by a number of irregular plates (e.g., *Edrioaster*) (Fig. 119,*1*). The construction of the anal cover in *Cyathotheca* is unknown, but the anal opening differs from that of all other Edrioasteroidea in being lunate. Otherwise, the periproct—whether consisting of a simple pyramid or of numerous plates—is more or less circular, oval, or polygonal in outline. The shape of the anal pyramid is dependent

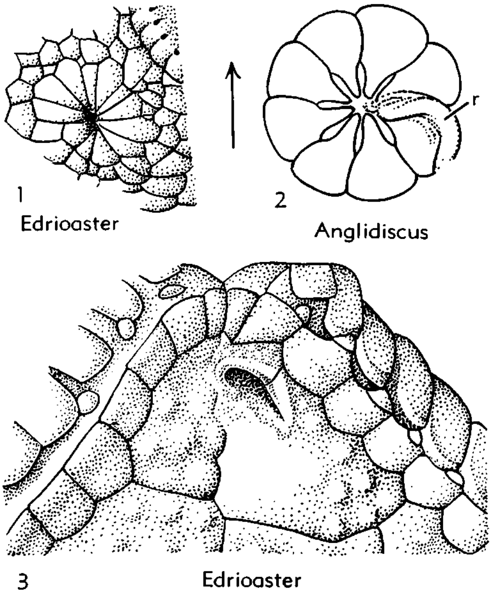


FIG. 119. Features of periproct and "third aperture." ——*1.* Periproct of *Edrioaster bigsbyi* (BILLINGS), M.Ord., Ontario, ×6.5 (7, pt. 4).——*2.* Inner side of anal pyramid of *Anglidiscus fistulosus* (ANDERSON), L.Carb., Eng., showing at right impression (r) which may denote rectum, arrow pointing toward mouth); ×16 (1).——*3.* Part of posterior interambulacrum of *Edrioaster bigsbyi* adjacent to peristome, showing so-called third aperture, ×6 (7, pt. 4).

on the number of plates composing it. Mostly, these are regularly triangular pieces. In *Timeischytes* they are only four in number; in *Cyathocystis* they are five, but other genera have a pyramid made up by 6 to 15 plates. The distal periproctal plates are usually smaller and more irregular in outline than those of the pyramid, and this is true also of plates protecting the vent in genera devoid of a regular anal pyramid.

The structure of the anal pyramid warrants the conclusion that respiration through the anus played at least a certain role in edrioasteroids (Fig. 119,*2*).

THIRD APERTURE

The noncommittal designation "third aperture" (the other two apertures in the thecal wall of the adoral surface being the mouth and anus) has been preferred for the small opening which for a long time has been known to be present in the posterior interambulacrum, behind the mouth, notably in the Edrioasteridae (Fig. 111, 131). It is reasonable to assume that a third aperture was present in many other Edrioasteroidea, although not noticed—possibly obliterated—in the actual fossil material. Lately, KESLING (24) has published a very careful study of a number of edrioasteroids in which he was able to demonstrate the presence, in the right posterior part of the peristomial region or in the nearby part of the posterior interambulacrum, of a structure that he interpreted as a hydropore. Additional comments were presented by KESLING & MINTZ (26). However, in some genera an external pore may have been wanting throughout ontogeny. If so, we have to reckon with a stone-canal opening in the body cavity, perhaps differentiated into a number of weak tubes hanging down from the water ring, as in most holothurians.

The structure of the third aperture was well known only in *Edrioaster* prior to the appearance of KESLING's (24) 1960 paper. BATHER (7, pt. IV) reported the presence of a small, obliquely transverse, slightly curved slit that crossed at right angles the suture between two plates at the adoral end of the interradius *CD* (Fig. 119,*3*). A slight widening and deepening of the aperture in an adoral direction indicates that the canal for which it served as intake (or outlet, according to the function assigned to the pore) passed obliquely through the test from right to left.

To illustrate the nature of the third aperture in different edrioasteroids (Fig. 120) it may be well to quote in full the paragraphs of KESLING (24) in which he summarizes the six basic types of hydropores (the third aperture is referred to throughout as the "hydropore") that his study has led him to recognize.

> *Type I.*—Hydropore within the posterior interambulacrum, in the right proximal region, consisting of a large permanent opening shared by two plates. *Edrioaster* the only known genus having this type.
>
> *Type II.*—Hydropore within the posterior interambulacrum near ambulacrum V [*i.e.*, ambulacrum *C*], not a large opening. Subtype A, exemplified by *Thresherodiscus*, consists of two large "bordering plates," each semioval, with a long juncture between them. When submersed in xylol, the holotype of *T. ramosus* shows a dark area along the juncture, suggesting that a larger opening underlies the thin margins of these

plates. Subtype B, exemplified by *Foerstediscus splendens,* apparently involves three plates in the posterior interambulacrum around a short slot set perpendicular to the edge of ambulacrum V. The anterior of these plates is fused to another interambulacral plate and, judging from the appearance in xylol, is very thin. The arrangement is such that the larger of the two fused plates may have acted like a hinge.

Type III.—Hydropore a small opening along

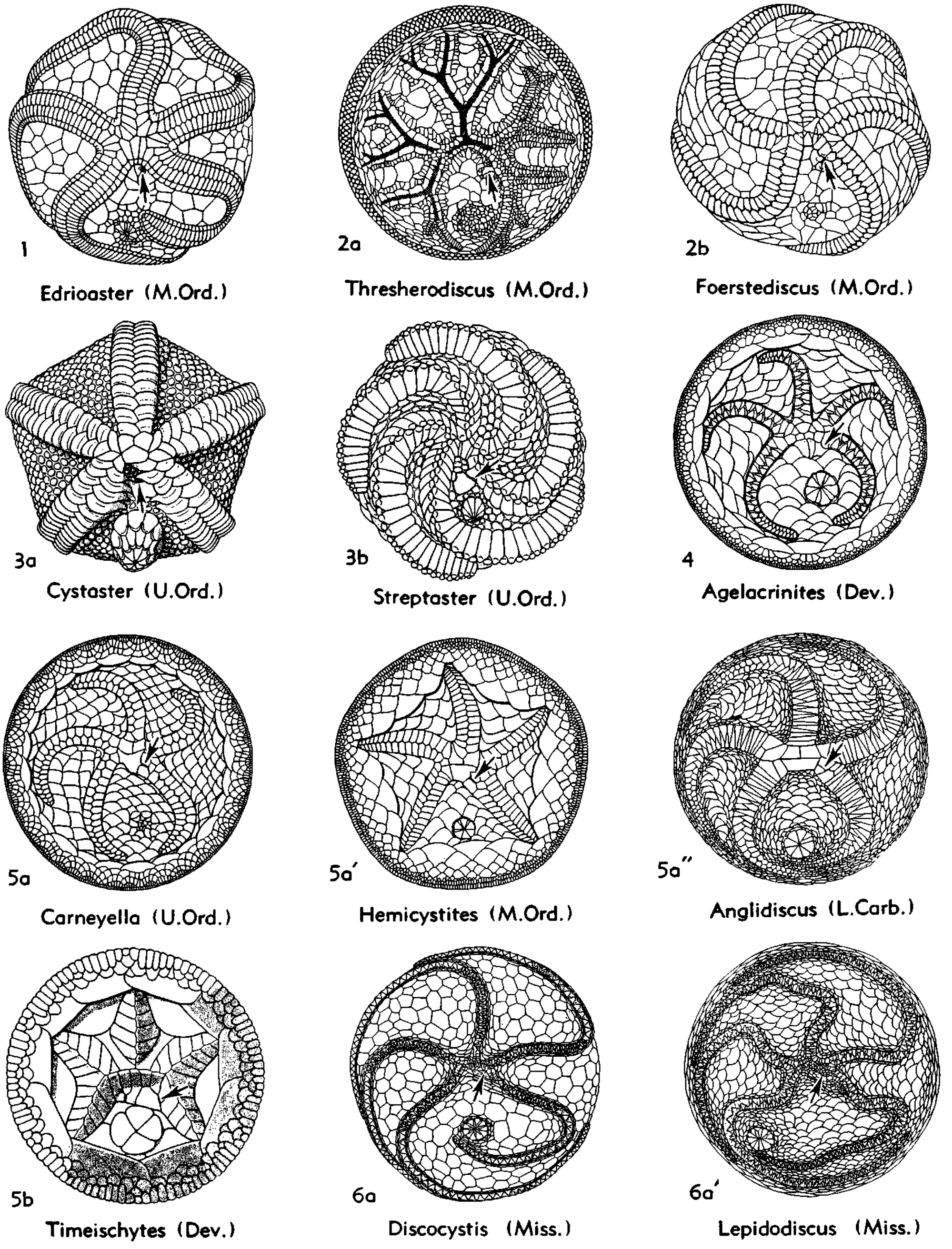


FIG. 120. Types of hydropores distinguished by KESLING, illustrated by restorations: I *(1)*; IIA *(2a)*, IIB *(2b)*; IIIA *(3a)*; IIIB *(3b)*; IV *(4)*; VA *(5a,a′,a″)*, VB *(5b)*; VI *(6a,a′)* (24).

the boundary between the posterior interambulacrum and the edge of ambulacrum V. In subtype A, found in *Cystaster granulatus,* it is bounded posteriorly by a very large interambulacral plate and anteriorly by a long lateral extension of an ambulacral plate. In subtype B, noted in *Streptaster,* the opening is much smaller and extends along the edge of ambulacrum V to the right of an unusually large interambulacral plate.

Type IV.—Hydropore along the juncture between an expanded proximal ambulacral plate and a large plate of the peristomial region. The posterior part of the peristomial region projects into the posterior interambulacrum, but is not distinctly set off from it, and includes two plates with raised edges that form a vaulted structure where they join. Possibly, one of these plates hinged on the other to expose more of the hydropore. *Agelacrinites* is the only genus in which this type occurs.

Type V.—Hydropore along the juncture between a short proximal ambulacral plate and the right posterior plate of the peristomial region. In subtype A, exemplified by *Carneyella pilea, Hemicystites chapmani, Isorophus cincinnatiensis,* and *Anglidiscus fistulosus,* the peristomial plate is aligned with the left series of covering plates of ambulacrum V, so that it appears to be the proximal left plate of the ambulacrum. However, if the plate arrangement is more carefully analyzed, it will be seen that the ambulacrum is sharply indented to accommodate this plate, and the plate must then be regarded as the right posterior extension of the peristomial region. In subtype B, represented by *Timeischytes megapinacotus* and *Hemicystites devonicus,* the right posterior plate is larger and more clearly associated with the peristomial region. Although the proximal plates on the left side of ambulacrum V are shorter than those on the right side of ambulacrum I [*i.e.,* ambulacrum *D*], directly opposite, they do not completely accommodate the anomalous unpaired plate, which does not appear to be a continuation of the ambulacrum.

Type VI.—Hydropore within the right posterior part of the peristomial region. Although this transverse structure is in part bordered by the covering plates of ambulacrum V, it is not closely related to the ambulacrum. *Discocystis laudoni* and *Lepidodiscus squamosus* furnish good examples, and *L. ephraemovianus* also seems to belong to this type (cf. Fig. 120 reproduced from KESLING, 24).

Various alternatives can be suggested in interpreting the nature of the third aperture. Either it was the intake for water feeding the water-vascular system (i.e. a **hydropore**), or it was the outlet for the sexual product (i.e., a **gonopore**). Contingently, it was a common opening for the stone canal and gonoduct (i.e., a **hydrogonopore**).

The hydropore alternative, which is the orthodox and at the same time the prevalent one, includes the possibility that the gametes, if produced in a single gonad, were discharged through the mouth or anus but, if produced in five gonads, through the ambulacral grooves. In this case there was only one stone canal.

The gonopore alternative implies that there was a single gonad, since we would hardly expect a common opening for, say, five gonads. The probable behavior of the stone canal in this case has already been touched upon above. A hydropore piercing the outer wall of the theca may also have been lacking on account of having migrated into the rectum (as probable in the Blastoidea), or into the mouth.

The hydrogonopore alternative, finally, would mean an organization very much the same as in certain cystoids in which the hydrocoelic and genital openings have joined together to form a common aperture lying between the mouth and anal opening, as shown by GISLÉN (19).

It is difficult to decide which alternative should be given preference; in fact, it seems impossible to give a definite answer. In support of interpretation of the third aperture as a hydropore, BATHER (7) pointed out that the presence of this structure correlates with the presence of pores between the ambulacral floor plates, whereas in the Agelacrinitidae the apparent absence of a hydropore is correlated with the absence of pores between the ambulacral floor plates. BATHER's reasoning does not hold good in full any longer because a third aperture is found in several Agelacrinitidae, as demonstrated by KESLING (24). On the other hand, the argument is not decisively weakened by the fact that the Edrioasteroidea very likely had only one gonad (as judged by CUÉNOT, 10, who, also, favors the gonopore hypothesis). Morphologically, the slitlike third aperture in *Edrioaster,* for example, recalls the aperture generally interpreted as a hydropore in the Hydrophoridea, which exhibit two openings between the mouth and anus, that nearest the mouth being considered as the hydropore (cf. GISLÉN, 19).

STEM

A stem of normal pelmatozoan character is not found in any edrioasteroid (*Astrocystites* having been removed to the class Edrioblastoidea). In a few genera, the vertical axis of the theca itself is prolonged very pronouncedly as compared with the disclike theca of most Edrioasteroidea. In the case mentioned, the theca, exclusive of the adoral surface, functionally served as a stem. Such conditions are met within the Cyathocystidae, in which this portion of the theca forms a solid mass, as well as in *Cystaster* and *Pyrgocystis* among the Hemicystitidae. The most extreme manifestation of the tendency toward thecal prolongation shows up in the turret-like form of *Pyrgocystis,* the aboral pole of which is covered with a ferrule-like structure.

ORNAMENT

The ornament of edrioasteroids, if present, commonly is found on all plates of the adoral face but it may be restricted mainly to the interambulacrals and marginals. Spines may have been present in species of various genera. Because of their fragility, however, such structures are not likely to be preserved in the fossil state. As a matter of fact, the only known example of genuine spines is afforded by *Pyrgocystis sardesoni,* in which the ambulacral cover plates were provided with spines articulating on tubercles. Their function as structures protective of the ambulacral groove is not as obvious as in the case of the adambulacral spines in Asteroidea, which have open grooves without cover plates. Spinules seem to have been present on the edges of the turret plates in this and other species of *Pyrgocystis.*

Pustules, produced more or less into papillae or spines, are found in *Carneyella* (especially in *C. vetusta* and *C. ulrichi,* in which the ornament has been interpreted erroneously as a coating of the stromatoporoid *Dermatostroma*) and in *Edrioaster.* Knobs, so small as to be classified as granules, occur on the plate surfaces in *Lepidodiscus.* In *Foerstediscus calderi* all plates are rather coarsely granulose.

Interambulacrals sculptured with heavy ribs, a type of ornament otherwise not typical of the Edrioasteroidea, occur in *Agelacrinites hamiltonensis* and a couple of other species assigned to this genus.

More or less minutely pitted plates are found in *Carneyella* and *Anglidiscus,* and in some species of *Hemicystites* (e.g., *H. paulianus*).

GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO EDRIOASTEROIDEA

[Terms of lesser importance are printed in italics.]

A ray (CARPENTER). Ray (anterior) located opposite interray designated *CD* (posterior) that contains the periproct; corresponds to ray III in system advocated by JAEKEL.

AB interray (CARPENTER). Interray (anterior right) next adjoining *A* ray in clockwise direction when edrioasteroid is viewed from adoral (ventral) side; between *A* and *B* rays; corresponds to interray III-IV in system advocated by JAEKEL.

abactinal. Applied to side of theca or plate opposite actinal (oral) surface of edrioasteroid (syn., aboral, adapical, apical, dorsal).

aboral. Applied to part of theca or plate directed away from mouth, surface of theca opposite that bearing mouth, in edrioasteroids directed downward (syn., abactinal, adapical, apical, dorsal).

actinal. See oral.

adambulacral (adambulacralium, pl. *adambulacralia). See* floor plate.

adapical. See aboral.

admedian. Applied to skeletal element located along median line of ray.

adoral. Applied to surface of theca or plate directed toward mouth.

adradial. Applied to small plates lining ambulacra in some edrioasteroid genera.

ambulacral (ambulacralium, pl., *ambulacralia). See* floor plate.

ambulacral elements. Plates forming ambulacral system.

ambulacral groove. Groove formed by double or single row of floor plates of ambulacra; served to convey food particles to mouth by means of ciliary currents (syn., food groove, subvective groove).

ambulacral system. Organ system peculiar to echinoderms, its main elements being a ring canal encircling the mouth, and 5 radial ambulacral vessels radiating from the ring canal and lodged in the ambulacral grooves.

ambulacrum (pl., **ambulacra**). Any of 5 straight or curved skeletal zones in rays (radii) of theca, enclosing ambulacral groove; adj., ambulacral.

ampulla. Vesicle protruding into perivisceral coelom and associated with a tube foot so that, on contraction of the ampulla, fluid can pass into the tube foot, or, reversely, on contraction of the tube foot, into the ampulla.

anal pyramid. Cover of anal opening composed of several more or less triangular plates forming conical elevation.

apical. See aboral.

arm. Portion of ray extending from theca (not present in Edrioasteroidea).

B ray (Carpenter). Ray (right anterior) next to *A* (anterior) ray in clockwise direction when edrioasteroid is viewed from adoral (ventral) side; corresponds to ray IV in system advocated by Jaekel.

BC interray (Carpenter). Interray (posterior right) next adjoining *B* ray in clockwise direction when edrioasteroid is viewed from adoral (ventral) side; between *B* and *C* rays; corresponds to interray IV-V in system advocated by Jaekel.

brachiole. Biserial, nonpinnulate exothecal appendage springing independently from surface and containing no extension of the body systems; Edrioasteroidea are devoid of brachioles.

C ray (Carpenter). Ray (right posterior) next to *B* ray in clockwise direction when edrioasteroid is viewed from adoral (ventral) side; corresponds to ray V in system advocated by Jaekel.

CD interray (Carpenter). Interray (posterior) next adjoining *C* ray in clockwise direction when edrioasteroid is viewed from oral (ventral) side; between *C* and *D* rays; differs frequently in shape from the other interrays and contains the periproct; corresponds to interray V-I in system advocated by Jaekel.

cover plate. Any of biserially arranged plates forming walls and roof of ambulacral groove (syn., adambulacral, ambulacral, Saumplättchen).

D ray (Carpenter). Ray (left posterior) next to *C* ray in clockwise direction when edrioasteroid is viewed from adoral (ventral) side; corresponds to ray I in system advocated by Jaekel.

DE interray (Carpenter). Interray (posterior left) next adjoining *D* ray in clockwise direction when edrioasteroid is viewed from adoral (ventral) side; between *D* and *E* rays; corresponds to interray I-II in system advocated by Jaekel.

deltoid. *See* oral.

[**diplopore.** Any of double pores piercing thecal plates in Diploporita (Hydrophoridea); absent in Edrioasteroidea but employed for a morphologically remotely similar structure in *Stromatocystites.*]

dorsal. Referring to direction or side away from mouth, in edrioasteroids directed downward. *See* aboral.

dorsocentral. Plate in the aboral center of *Stromatocystites*; not necessarily homologous with dorsocentral of other echinoderms.

E ray (Carpenter). Ray (left anterior) next to *D* ray in clockwise direction when edrioasteroid is viewed from adoral (ventral) side; corresponds to ray II in system advocated by Jaekel.

EA interray (Carpenter). Interray (anterior left) next to *E* ray in clockwise direction when edrioasteroid is viewed from adoral (ventral) side; between *E* and *A* rays; corresponds to interray II-III in system advocated by Jaekel.

eleutherozoic. Applied to free-living echinoderm.

endothecal. Applied to ambulacral plates that pass between thecal plates.

[**epithecal.** Applied to ambulacral plates that *rest on* thecal plates (absent in edrioasteroids).]

[**exothecal.** Applied to structures, like brachioles, not incorporated in theca proper (does not occur in edrioasteroids).]

floor plate. Any of double or single row of plates forming an ambulacral groove (syn., adambulacral, ambulacral, subambulacral).

food groove. *See* ambulacral groove.

gonopore. Simple opening serving as exit from genital system.

hydrogonopore. Supposedly common opening for stone canal and gonoduct.

hydropore. Pore or slit serving as adit to water-vascular system.

interambulacral (*interambulacralium,* pl., *interambulacralia*). Any of thecal plates forming interambulacra (syn., interradial).

interambulacrum (pl., **interambulacra**). Any of 5 interradial sections of theca (syn., interradius, interray); adj., interambulacral.

interradial (interradialium). See interambulacral.

interradius. *See* interambulacrum (syn., interray); adj., interradial.

lateral groove. Faint groove running at each side along border of floor plates in many edrioasteroids; served articulation of cover plates on floor plates.

lateral pore. Any of pores in tangential suture of successive floor plates in Edrioasteridae and some other edrioasteroids; cf. podial pores.

marginal. Any plate in peripheral ring.

oral. Any of 5 interradially disposed plates forming circlet on tegmen surrounding or covering mouth (syn., deltoid); adj., surface of theca bearing mouth, in edrioasteroids directed upward (syn., actinal, adoral, ventral).

orotegminal (orotegminal plate). Any of peristomial cover plates forming tegmen.

pelmatozoan. Applied to echinoderm fixed to substratum, with or without stem.

pentameral. *See* quinqueradiate.

pentamerous. *See* quinqueradiate.

peripheral ring. Peripheral zone formed by distal interambulacral plates in most edrioasteroids.

periproct. Space in *CD* interray in which anal opening is located.

peristome. Space in which mouth opening is located.

perradius. Center line of ambulacrum; adj., perradial.

podial pore. Pore admitting passage of tube foot (podium); lateral pores must have been podial pores.

podium. *See* tube foot.

quinqueradiate. Applied to radial symmetry characterized by 5 rays extending from mouth (syn., pentameral, pentamerous).

radial, radius. Radial plates together with all structures borne thereupon (syn., ray); as adjective, belonging to, or in direction of radius.

ray. *See* radial.

sagittal plane. Plane extending anteroposteriorly and dorsoventrally in mid-line, dividing bilaterally symmetrical animal into two similar halves.

Saumplättchen. See cover plate.

sessile. Of animal fixed to substratum, sedentary.

stone canal. Canal leading from hydropore (madreporite) to ring canal of ambulacral system.

stroma. Endoskeletal mesenchyme.

subambulacral. See floor plate.

substomial chamber. Frame formed by internal peristomial skeleton, through which gullet receiving ambulacral grooves passed into stomach.

subvective groove. See ambulacral groove.

subvective system (Haeckel). Applied to organ system serving transportation of food particles to mouth; from morphological point of view, subvective system cannot be separated from ambulacral system.

suture. Straight line along which adjacent plates meet.

tegmen. Term applied to oral cover of edrioasteroids; strictly roof in crinoid theca.

theca. Capsule of mesodermal skeleton enclosing intestine; in edrioasteroids, the theca is no closed structure, because the skeleton of ambulacra is lodged between the thecal skeletal elements.

thecal plate. Any of numerous plates, mosaic or imbricating, that form theca.

[**thecal pore.** Pore piercing substance of thecal plate (not present in Edrioasteroidea).]

"third aperture." Noncommittal designation for small opening in *CD* interray behind mouth; may represent a hydropore.

trimerous. Applied to radial symmetry characterized by three primary rays extending from mouth, each of two lateral rays giving off two branches.

tube foot. Muscular cylinder protruding through pore between ambulacral floor plates in some Edrioasteroidea; may have served locomotion, and may also have had other function (syn., podium).

valvular. Applied to anal pyramid composed of several more or less triangular plates (valvules).

ventral. *See* oral.

whirler (Remane). Animal feeding by aid of cilia producing an eddy in which particles are eventually caught by other cilia, and, helped by a secretion of mucus, conducted into the place of digestion.

SOFT PARTS

A few points relating to the internal anatomy of the Edrioasteroidea have been touched upon cursorily, mainly in discussing the third aperture. For further information reference may be made to papers by Anderson (1), Foerste (16), Jaekel (22), and Williams (40). Even if we assume that the internal organization was much the same, on principle, in all Edrioasteroidea, it is obvious that the location and extent of several organ systems must have varied considerably in the disc-shaped theca of, say, *Agelacrinites* and the theca of the turret-shaped *Pyrgocystis*.

ONTOGENY

Growth stages have been observed in a number of species, the smallest one measuring no more than 0.7 mm. *(Isorophus austini)* in diameter.

A most prominent feature in the ontogeny of forms with curved ambulacra is that the curvature is acquired gradually, which, in fact, is only what should be expected. Williams (40) studied a series of successively larger (and hence more full-grown) individuals of *Isorophus austini* in abundant specimens, most of which exhibit the aboral side (Fig. 121). In the smallest larva (diam., 1.3 mm.) examined with regard to development of the ambulacral system, only the most proximal floor plate of each ambulacrum was present, encircling the so-called "substomial chamber." During larval development new floor plates are introduced in a distal direction, forming (in this case) a uniserial row. It may be assumed that a pair of ambulacral cover plates was developed simultaneously with addition of a floor plate. On reaching the peripheral limit of the theca, the growing ray, hitherto straight, was turned aside either in a solar or in a contrasolar direction in a way specific of each ambulacrum.

In forms characterized by straight ambulacra, the rays stopped growing at the moment of coming into contact with the peripheral ring or, as in *Stromatocystites,* when the margin of the adoral surface was reached. Contingently, the rays had ceased to extend in a radial direction even before reaching so far.

Williams (40) has noted that differentiation into radial and interradial skeletal elements cannot be recognized in very small specimens. Also, they cannot be oriented properly, because the anal pyramid is not found until in later growth stages.

It should be noted that the proportions between different parts of the theca may shift during development. Thus, in *Isorophus,* the oral area is proportionally broader in immature than in mature forms (4). In larval forms of some species (e.g., *Lepidodiscus buttsi, Agelacrinites hamiltonensis*), the marginal ring is proportionally wider than the central disc of the adoral surface, which is much contracted (9).

The ontogeny of Edrioasteroidea in comparison with other pelmatozoans has been discussed by REGNÉLL (31) elsewhere.

EVOLUTIONARY TRENDS

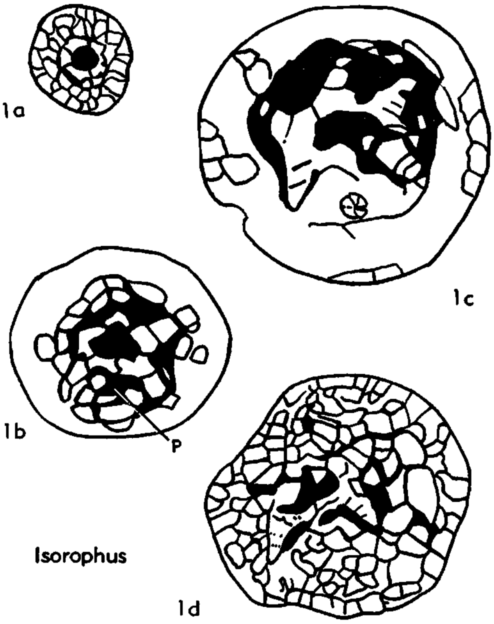


FIG. 121. Successive stages in development of *Isorophus austini* (FOERSTE) shown in aboral views, all ×12 (40).——*1a.* Substomial chamber and peristomial ring of modified floor plates distinct, no other floor plates separable.——*1b.* Stage with additional floor plate in ambulacra *C, D,* and *E,* location of anal pyramid *(p)* indistinct.——*1c.* Stage showing 2 floor plates in each ambulacrum and presence of peristomial ring.——*1d.* Stage with all plates distinguishable, 3 floor plates in ambulacra *C* and *D* but others less complete.

A general trend in respect of thecal construction is not obvious in phylogenetic development of Edrioasteroidea. A tendency towards prolongation of the vertical axis of the theca serves to elevate the adoral surface over the substratum. Contemporaneous with this tendency, however, most evident in *Pyrgocystis* (L.Ord.-L.Dev.), which clearly was a successful edrioasteroid well adapted to environmental requirements, the more or less discoidal type of theca was in existence from the very first appearance of Edrioasteroidea (e.g., *Stromatocystites*) in Early Cambrian time and it persisted throughout most of the Paleozoic (e.g., *Anglidiscus, Lepidodiscus,* U.Miss.). Essentially the same observation applies to hemispherical forms. Thus, once brought into shape, the various modifications of thecal development were remarkably persistent.

Nor is any positively discernible trend distinguished within each of the thecal types. This may be exemplified by *Pyrgocystis,* which does not consistently follow up the line of development operating at increased plasticity of the theca without loss of firmness (29).

A reduction of the ambulacral grooves, brought about in various ways, is a phenomenon met with in several groups of echinoderms. Not so in the Edrioasteroidea. On the contrary, the lengthening of the ambulacral grooves during ontogenetic development is paralleled by a similar trend in phylogeny. This may be correlated with the fact that in the Edrioasteroidea the ambulacral grooves retained their primary function of collecting nourishment and transporting food particles to the mouth. So an extension of the distal part of the ambulacra was an advantage in the economy of the animal, the more so since these organisms were mostly sedentary. In the Edrioasteridae, which were surely not permanently fixed, the ambulacra even passed on to the aboral surface. A similar effect was achieved by branching in the unique genus *Thresherodiscus.*

A limit for extension of the ambulacra in a radial direction was set by the inner zone of the peripheral ring, which in many genera was rigid. In consequence, the ambulacra had to deviate in a tangential direction, thus producing curved structures. The curvature of rays seen in adult specimens may have been initiated well before reaching maturity. An explanation possibly is found in the fact, referred to above, that the peripheral ring is proportionally much broader in young individuals of certain species than in fully grown individuals.

The trend toward enlargement of food-collecting areas is demonstrated by the predominance of curved ambulacra in geologically younger genera. It is true that forms with curved ambulacra are met with even in the Middle Cambrian (e.g., *Walcottidiscus*) and some Ordovician edrioasteroids developed extremely long ambulacra. But until Devonian time there is still a comparatively large number of genera in which the ambulacra are not affected by curving. The following figures support this statement, though available material provides only a narrow basis for generic judgment. Of known pre-Devonian genera, 9 have curved ambulacra out of a total of 17, i.e., 53 percent. Of known post-Silurian genera, 8 have curved ambulacra out of a total of 11, i.e., 73 percent. (No attention has been paid to the fact that, in *Hemicystites*, the ambulacra may tend to curve slightly, and *Thresherodiscus* is left out of account.)

The direction of curvature of the ambulacra is not governed by any apparent trend. It has been pointed out in discussion of ambulacral structures that the primitive condition of ray curvature conjecturally was a contrasolar one. To this one may object that in the oldest genus in which curving of the ambulacra has been observed (viz., *Walcottidiscus*, M.Cam.) one ray, ambulacrum *C*, curves in a solar direction. In view of the very scarce material of Edrioasteroidea obtained from Cambrian strata, however, it may be justified in this case to refer to the incompleteness of the fossil record available for study. In fact, the various types of ambulacral curving are distributed fairly equally, as known now, throughout the stratigraphic column, from Middle Cambrian to Upper Mississippian, as appears from the following survey. (1) All contrasolar: Middle Ordovician *(Lebetodiscus, Lepidoconia)*; Upper Ordovician *(Streptaster)*; Upper Devonian *(Dinocystis)*; Upper Mississippian *(Ulrichidiscus)*. (2) *A, B, D, E* contrasolar, *C* solar: Middle Cambrian *(Walcottidiscus)*; Middle Ordovician *(Bassleridiscus, Carneyella, Isorophus, *Edrioaster bigsbyi)*; Upper Ordovician *(Carneyella, Isorophus)*; Middle Devonian *(Lepidodiscus)*; Upper Devonian *(Lepidodiscus)*; Lower and Upper Mississippian *(Anglidiscus, Lepidodiscus, Discocystis)*. (3) *A, D, E* contrasolar, *B, C* solar: Middle Ordovician *(Isorophusella)*; Lower to Upper Devonian *(Agelacrinites, ?Xenocystites)*; Lower Mississippian *(Agelacrinites)* (4). All solar: Middle Ordovician (*Foerstediscus, Edrioaster* in part); Upper Ordovician (*Foerstediscus, Edrioaster* in part); Upper Devonian *(Cooperidiscus)*.

The structure of the ambulacra also seems not to have changed in a distinct direction. A tendency toward uniseriality of the ambulacral cover plates may have operated during phylogeny of Edrioasteroidea, however. As to the floor plates of the ambulacral grooves, it is difficult to trace a general line in development of their arrangement in the actual fossil material; however, they seem to have progressed from a biserial to uniserial plan, rather than the reverse, in conformity with the cover plates (30).

It should be remarked, finally, that a tendency toward a free-living mode of life is apparent in a few forms (e.g., Edrioasteridae), although this is met with even in some early types (e.g., Stromatocystitidae). CABIBEL, TERMIER & TERMIER (8) have suggested a line of evolution leading from *Stromatocystites* (which they consider an eleutherozoan) through *Eikosacystis* CABIBEL, TERMIER & TERMIER, 1959 (*incertae sedis*) to the Carpoidea Cincta (Trochocystitida), which, too, are thought to have been free-living.

ECOLOGY

Edrioasteroidea lived in various lithotopes, their fossil remains having been met within sandstones (more or less pure, micaceous, calcareous, etc.), shales (sandy, micaceous, calcareous, etc., black, brown, etc.), marls, and limestones. Optimal edaphic conditions apparently prevailed on a calcareous substratum. Sandy bottoms seem not to have appealed to most Edrioasteroidea, since relatively few forms have been found in sandstones (which in part may be due to poorer chances of preservation in this kind of rock). As far as known, only *Stromatocystites* seems to have been restricted to sandy bottoms. This genus may have lived in the intertidal zone. A few genera (e.g., *Pyrgocystis, Edrioaster*) were tolerant of varied lithological characters of the substratum, but the bulk of genera were fairly selective in this respect. Most, if not all, species of Edrioasteroidea had specific demands on the nature of the substratum.

Some edrioasteroids seemingly were attached directly to the indurated bottom surface (18, 36). *Pyrgocystis* mostly may have stuck in soft mud or ooze. In general, however, the Edrioasteroidea were attached to some hard foreign object, preferably the shell of some organism. Most commonly valves of brachiopods (especially *Rafinesquina alternata* where forms contemporaneous with that species are concerned, and in addition *Chonetes, Hebertella, Platystrophia, Spirifer,* etc.) were suited for this purpose. Other examples are afforded by sponges, corals, bryozoans, conulariids, pelecypods, cystoids, and crinoids. Most Maysville (Upper Ordovician) specimens from North America are found on *Rafinesquina alternata* (40), and most *Hemicystites* from Bohemia on conulariids (22). On the whole, all species seem to have been strictly selective in their choice of host. This raises question as to what sort of symbiotic relations existed between the two organisms. The edrioasteroid might be suspected of parasitism, but, as observed by GEKKER (17) in the case of *Cyathocystis plautinae,* which he found both on species of *Heliocrinites* and on the bryozoan *Dianulites (Monticulipora) petropolitanus,* undoubtedly we have to do with commensalism. It is possible also that edrioasteroids were attached to exoskeletons of dead animals, but this probably was not the rule, because it would then have been reasonable to find Edrioasteroidea attached to, for example, trilobites, the exuviae of which were undoubtedly often abundantly available. That they did not attach themselves to living trilobites is easy to realize.

The associated fauna and sediments indicate clearly that the Edrioasteroidea lived in a littoral environment. From comparison with the habitat of pelmatozoans in general we may assume that the water was neither polluted nor turbid.

Most Edrioasteroidea were permanently attached. Others were evidently capable of restricted shifts in position. This must be true for the Edrioasteridae provided with pores between the ambulacral floor plates, in which the presence of a tube-foot-ampulla system is indicated and in which the ambulacra pass on to the marginal area of the aboral surface.

DISTRIBUTION

The Edrioasteroidea range from Lower Cambrian to Mississippian, where they disappear abruptly. They reached a very pronounced acme in the Middle Ordovician and in smaller degree in the Upper Ordovician, as is evident from the graph (Fig. 122) based on the number of genera represented in each division of the geological systems. Another high point, but far less extreme, was attained in the Upper Devonian. The edrioasteroid stock was subjected to severe crises in Late Cambrian and the Late Silurian time. The curves showing number of new genera appearing in each division and the rate of appearance of genera during the several periods mutually conform, on the whole, as shown by the diagram. It is noticeable that, just before becoming extinct, the Edrioasteroidea rose, in a way, to new activity. It should be observed that essentially coincident patterns are obtained in this instance, whether a graph of this kind is based on the stratigraphic range of families, genera, or species. If we construct a curve based on number of species and this curve be resolved into its North American and European components, we find that the maximum development of the Edrioasteroidea in the Middle Ordovician is due almost exclusively to the prolificity of the North American stock, mainly the Hemicystitidae. The second high point of the joint curve transpires as due to an accumulation of the two individual curves, so that for North America alone the high point appears in the Lower Mississippian (no European representatives being known) instead of in the Upper Devonian. Apart from the peaks mentioned, the two curves also show other, minor, differences which indicate that the Edrioasteroidea at various times contributed in a varying degree to the Paleozoic biota of North America on the one hand and Europe on the other.

It is a remarkable fact that Edrioasteroidea have not been recorded so far from any areas outside of North America and Europe[1]. Further, it is striking that forms with a more or less a turret-shaped theca are, on the whole, very scanty in North American deposits. Clearly, this group had an eastern Baltic origin. In spite of the great predominance of ***Hemicystites*** in North America, there is evidence that this type arose in central European seas in Early Ordovician time. Otherwise, the more or less discoidal forms are mainly characteristic of North America, which undoubtedly was the center of evolution and dispersal of the Agelacrinitidae and Stromatocystitidae, since most genera belonging to these families, as well as to Hemicystitidae, are confined to North America. The Edrioasteridae are less significant from a biogeographical point of view (30).

---

[1] Except a unique find in Victoria, Australia, of a form (Upper Silurian?) said to resemble *Cincinnatidiscus* (G. M. Philip, 1963. Austral. Jour. Sci., v. 26, p. 25).

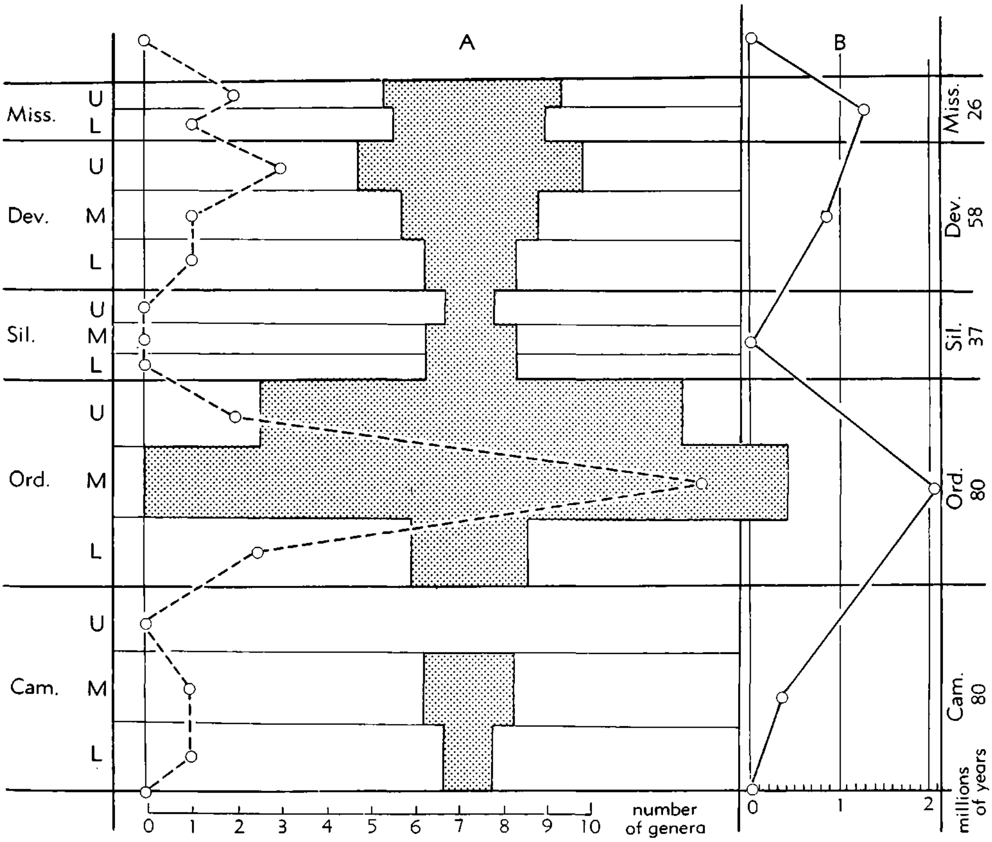


FIG. 122. Stratigraphic distribution of edrioasteroid genera (known to 1963) shown in column A, with broken line indicating appearance of new genera, and origination rate of new genera in 10-million-year intervals, shown in column B (height of systemic divisions plotted proportional to estimated duration of periods but subdivisions within them arbitrarily equal; the diagram was prepared before publication of revised time scale by KULP, 1961) (Regnéll, n).

CLASSIFICATION

In several textbooks and indices (e.g., BASSLER & MOODEY, 1943, 5), the Edrioasteroidea have been ranked as an order of the class Cystoidea. On the other hand, most specialists have credited them with a rank equal to that of the Cystoidea. Undoubtedly, this latter opinion is supported by many features in the structural organization of the Edrioasteroidea, especially the presence of pores between the ambulacral skeletal elements and the absence of skeletal subvective appendages (29).

The current classification of the Edrioasteroidea was established by BASSLER (3, 4) with due attention to proposals made by previous authors. This classification seems to be useful and therefore its essential features have been retained in the present *Treatise,* although other arrangements call for notice. For example, two main divisions might be recognized, one group having pores between the ambulacral floor plates, the other group having none. But how, then, should we classify the Stromatocystitidae and Cyathocystidae, which are insufficiently known in this respect? In my opinion, we lack evidence needed for assigning the families here recognized to units of suprafamilial rank.

For the definition of families, it would be preferable to make consistent use of some one morphological character, or, rather, set of characters, if such were available. Leaving out of account the Edrioasteridae which are known to be characterized, among other features, by pores intervening between the ambulacral floor plates, remaining families are in fact distinguished from each other, mainly on the basis of the structure of the mouth cover. There is no reason why this feature should not be as valid from a taxonomic point of view as any other expression of morphological differentiation. The nature of the oral tegmen demonstrates namely a modification of the ambulacral cover plates resulting in morphologically distinct types of orotegminal construction. One consequence of a classification on this basis is the recognition of two lines of development, parallel in many respects, represented by the Hemicystitidae, on the one hand, and the Agelacrinitidae, on the other.

The behavior of the ambulacra—whether straight or curved and if curved, in what direction—has been deemed to be a feature of importance for discrimination of species, as agreed by previous authors. A variation in the direction of curvature of the ambulacra does exist in some species, but this may be compared with the occasional excess of the normal number of rays, for example. As pointed out above, the ambulacra observed in early growth stages of forms having curved ambulacra in the adult state are not affected either by solar or contrasolar curvature. As noted by BATHER (7, pt. 8), "The distribution, however, being characteristic of species separated by other characters, cannot be fortuitous. There must have been some structures or habit in each species predisposing in turn of the coil in a solar or contrasolar direction."

Outline of Edrioasteroid Classification

[Figures enclosed by parentheses indicate numbers of known genera and subgenera]

Edrioasteroidea *(class)* (27; 1). *L.Cam.-L.Carb. (Miss.).*
- Stromatocystitidae (3). *L.Cam.-U.Dev.*
- Cyathocystidae (2). *?L.Ord., M.Ord.-L.Sil.*
- Hemicystitidae (12; 1). *Ord.-L.Carb.(Miss.).*
- Agelacrinitidae (8). *M.Ord.-L.Carb.(U.Miss.).*
- Edrioasteridae (2). *M.Ord.-U.Dev.*

SYSTEMATIC DESCRIPTIONS

Family STROMATOCYSTITIDAE Bassler, 1936

Mouth surrounded and covered by 4 large imperforate plates and many small ones; theca flexible, subpentagonal or circular, adoral side depressed convex, aboral side slightly concave, enclosing a shallow cavity; interambulacral areas and aboral side mostly composed of polygonal plates; ambulacra 5, narrow, straight or curved, confined to the upper surface; unstalked and unattached. *L.Cam.-U.Dev.*

Stromatocystites POMPECKJ, 1896, p. 505 [**S. pentangularis*; OD] [=*Stromatocystis* BATHER, 1900; *?Cambraster* JAEKEL, 1923]. Theca subpentagonal, reaching about 35 mm. in diam.; skeleton of numerous nonimbricate plates, usually 5- or 6-

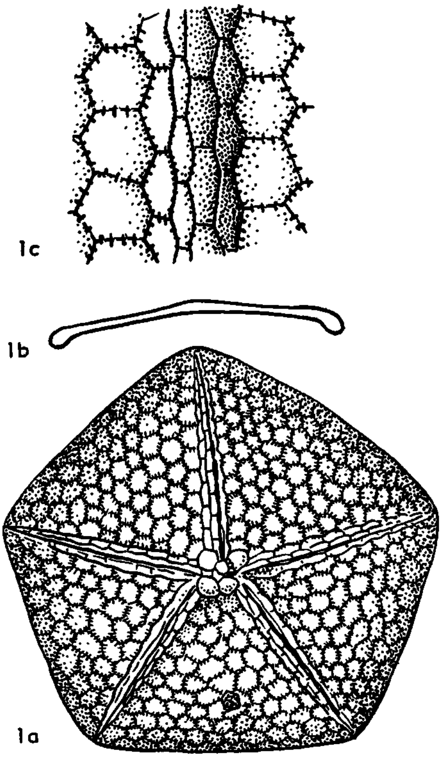


FIG. 123. Stromatocystitidae (p. *U*160-*U*161).

sided (on aboral side larger toward center, which is occupied by a more or less well-defined centrodorsal plate), or indistinctly differentiated and weakly calcified (*S. balticus* JAEKEL, 1899); sutures of interambulacrals crossed by 1 to 3 diploporoid structures, which undoubtedly are places of stroma strands uniting individual plates; ambulacra straight, terminating in angles of theca; ambulacral floor plates in 2 rows of elongate alternating plates; side plates long, about equal in number to floor plates and alternating with them; ambulacral grooves roofed over by small cover plates; anal opening pentagonal, covered by a pyramid of (about 9) small plates (35). *L.Cam.-M. Cam.,* N. Am.(Newf.)-Eu.(Baltic-Czech.-?Fr.).——FIG. 123,*1*. **S. pentangularis,* M.Cam., Czech.; *1a,* adoral side (restored), ×1.5 (6); *1b,* detail of ambulacrum and adjacent plates, ×6; *1c,* median section of theca, ×1.1 (27).

[The name *Cambraster* was introduced by JAEKEL, 1923 (Palaeont. Zeitschr., vol. 5, p. 344), for a fossil from the Middle Cambrian of Hérault, south France, that was considered to be a primitive asterozoan. JAEKEL gave only a very generalized description and no figure. Therefore, the meaning of *Cambraster* remains obscure. Probably it must be looked upon as a *nomen nudum.* Only with great hesitation has it been entered here as a synonym of *Stromatocystites* (cf. REGNÉLL, 29, p. 199, and CABIBEL, TERMIER & TERMIER, 8, p. 284)].

Walcottidiscus BASSLER, 1935, p. 3 [**W. typicalis*; OD]. Theca as in *Stromatocystites* but larger (up to 60 mm.), its edge formed by small imbricate plates; interambulacrals and plates of aboral side polygonal, slightly imbricate; ambulacra more or less curved, *A, B, D, E,* contrasolar, *C,* solar. Insufficiently known (3, 4). *M.Cam.(Burgess Sh.),* Can.(B.C.).

Xenocystites BASSLER, 1936, p. 3 [**X. carteri*; OD]. Theca circular, about 45 mm. in diam.; interambulacral areas and aboral side covered by polygonal and mosaic plates; ambulacra slightly curved, 2 of them probably solar; ambulacral floor plates long, narrow, in single row. Insufficiently known (4). [G. W. SINCLAIR doubts assignment of this genus to Stromatocystitidae, suggesting it may actually belong to *Cooperidiscus* (personal communication).] *U.Dev. (Chemung.),* USA (N.Y.).

Family CYATHOCYSTIDAE Bather, 1899

[=Thecocystidae JAEKEL, 1918, emend. 1927; by error as Cyathothecidae JAEKEL, 1927, in REGNÉLL, 1945]

Adoral face with 5 short, straight ambulacra, which have either a triangular plate between each two ambulacra, adoral surface being surrounded by a border of marginal plates, or are covered by 5 triangular interradial plates; theca saclike, forming a solid mass permanently attached at aboral end to some foreign object; no third aperture observed. *?L.Ord., M.Ord.-L.Sil.*

Cyathocystis F. SCHMIDT, 1879, p. 2 [**C. plautinae*; SD HAECKEL, 1896, p. 115]. Theca up to about 15 mm. high, attached by broad or tapering aboral surface more or less drawn out into rootlike processes; deltoids as in *Cyathotheca* but not covering ambulacra, which are straight, short, broad or comparatively broad, and taper distally; 2 rows of alternating ambulacral cover plates; mouth covered by 5 large plates; anal pyramid of 5 triangular plates located in posterior interradius between deltoid and adjacent marginals; adoral surface bordered by frame of about 40 marginals (4). [A couple of the skeletal elements of the adoral surface recall strongly the conditions in *Stephanocrinus,* possibly affording an example of homeomorphism.] *M.Ord.-U.Ord.,* Eu.(Est.)-N. Am.(Okla.-Tenn.).——FIG. 124,*2*. **C. plautinae,* M.Ord., Est.; *2a,* adoral, ×3; *2b,* lat. view of two specimens attached to bryozoan, ×3 (22).

Cyathotheca JAEKEL, 1927, p. 4 [**C. suecica*; OD]. Theca irregular, goblet-shaped, height up to 8 mm., with irregular or pointed attachment surface; ambulacra apparently very narrow, practically hidden at surface, adoral face covered by very flat pyramid of 5 triangular deltoids (orals),

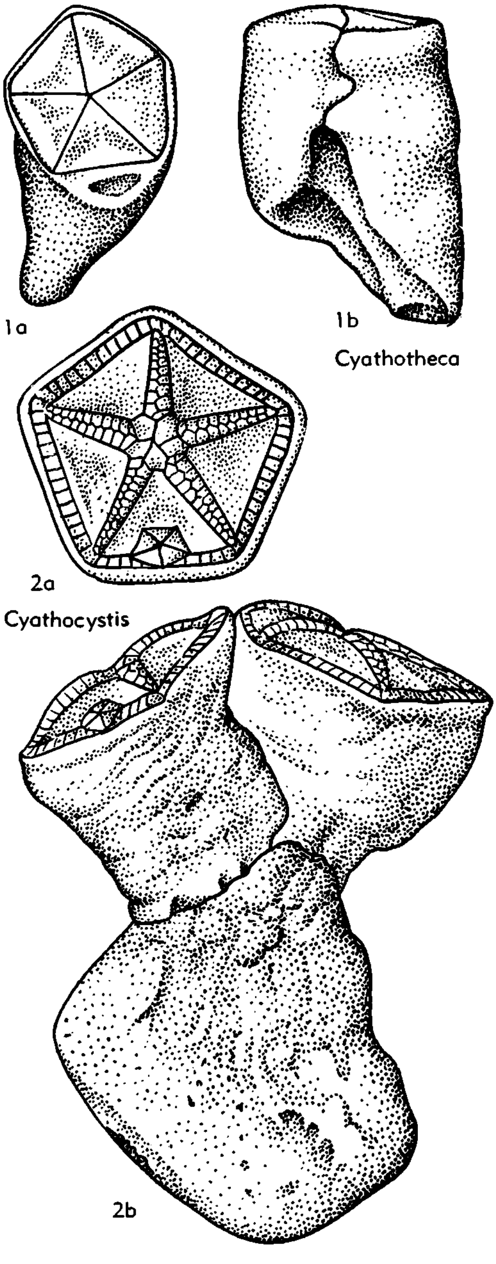


FIG. 124. Cyathocystidae (p. *U*161-*U*162).

behind which is lunate space with anal opening; no marginal plates (29). *?L.Ord., L.Sil.,* Eu. (Swed.-USSR).——FIG. 124,*1*. **C. suecica,* L.Sil., Sweden; *1a,b,* adoral, left lat. views, ×6 (23).

Family HEMICYSTITIDAE Bassler, 1936

Peristome covered by ?3, 4, or more plates, ?3, 4 of which have definite arrangement; 3 meeting in center of peristomial region, 1 lying over posterocentral part of peristome, other 2 with 1 on each side of ambulacrum *A*; theca flat, saclike or turret-shaped, composed of thin plates, attached permanently (or ?temporarily) to some foreign object by greater part of aboral surface; ambulacra normally 5, straight or curved; single row of ambulacral floor plates more or less overlapping proximally. *Ord.-L.Carb. (Miss.).*

Hemicystites HALL, 1852, p. 245 [**H. parasiticus*; OD] [=*Hemicystis* CARPENTER, 1891]. Theca subcircular, depressed or disclike, 5 to 20 mm. in diameter, attached preferably to shells of *Rafinesquina* and other brachiopods, or to cephalopods; thecal plates polygonal, squamose, imbricating, differentiated into larger interambulacrals (mainly increasing in size toward periphery) and zone of smaller marginals; ambulacra 5 or more *(H. multibrachiatus)*, in which rays *B*, *D*, and *E* bifurcate anomalously ("normal" specimens with 5 rays do occur), typically short, broad, in some forms tapering), and straight (or with a tendency to slight solar curvature of *C* and solar or contrasolar curvature of *A* especially); floor plates delicate, probably one for each pair of cover plates; anal pyramid elevated, of triangular plates arranged in regular circle; third aperture near the posterior oral plate (4). [Most prolific of all known edrioasteroid genera.] *Ord.-M.Dev., ?Miss.,* N.Am.-Eu.(Fr.-Czech.).——FIG. 125,*7*; 126,*1*. *H. chapmani* (RAYMOND), M.Ord.(Trenton.), Can. (Ont.); 125,*7*, adoral, view of holotype, ×3(4); 126,*1*, same (reconstr.) ×3(24). [See also Fig. 118,*3*; 120,*5a'*.]

Anglidiscus REGNÉLL, 1950, p. 226 [**Lepidodiscus fistulosus* ANDERSON, 1939, p. 68; OD]. Like *Carneyella,* but theca not attached (at least not permanently); ambulacral cover plates varying in different regions so that proximally only single row present but distally with 2 rows of interlocking plates, those near middle of ambulacrum being broad, wedge-shaped and relatively shorter than regular, pentagonal distal ones; ambulacral floor plates apparently pierced by lateral pores (for tube feet); periproct located farther back; peripheral ring less definite (30). *L.Carb.,* Eu.(Eng.).——FIG. 125,*4*; 126,*2*. **A. fistulosus* (ANDERSON); 125,*4,* adoral view (reconstr.), *ca.* ×5(1); 126,*2*, same, ×5 (24). [See also Fig. 116,*3*; 117, *1,5*; 119,*2*; 120,*5a"*.]

Bassleridiscus FISHER, 1951, p. 691 [**B. mohawkensis*; OD]. Intermediate between *Streptaster* and *Carneyella* in that ambulacra are strongly curved

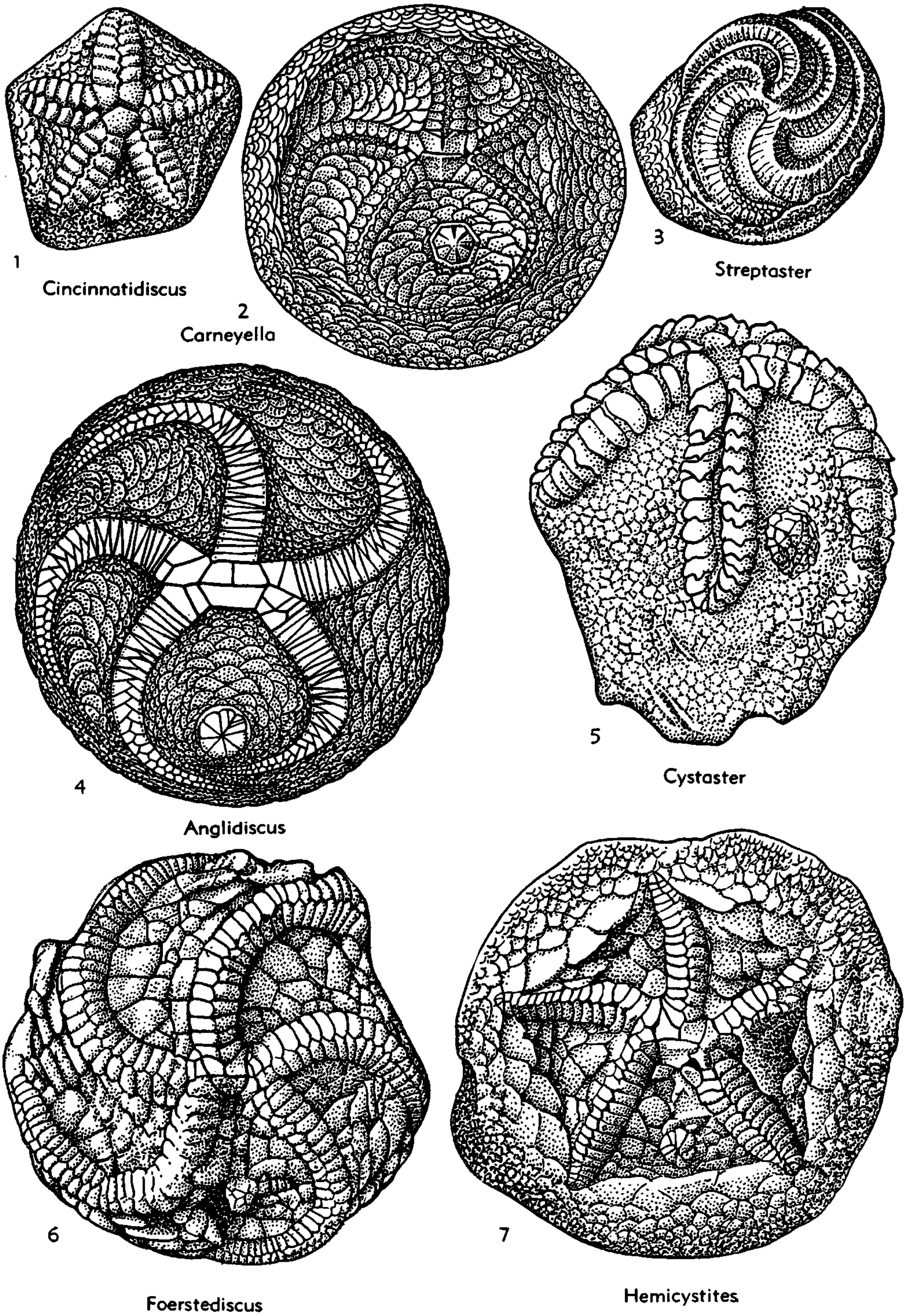
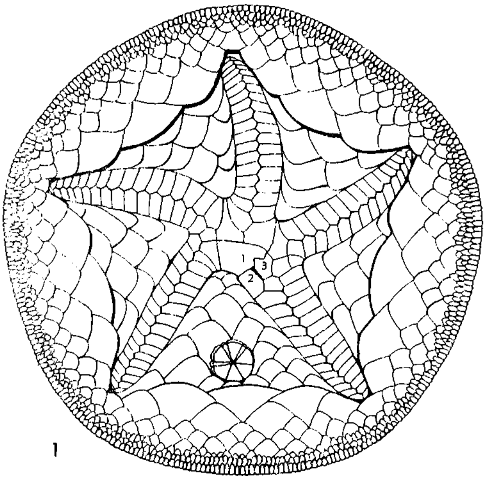
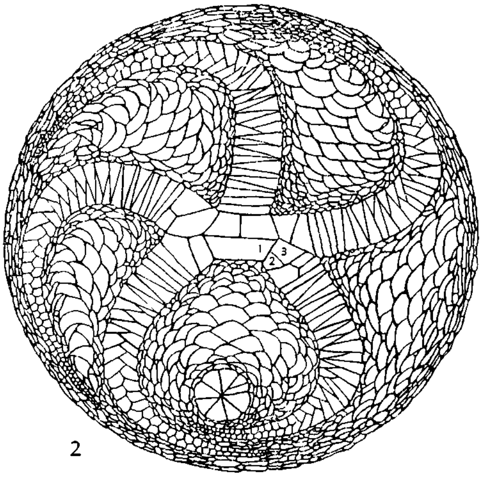


FIG. 125. Hemicystitidae (p. *U*162, *U*165, *U*167).



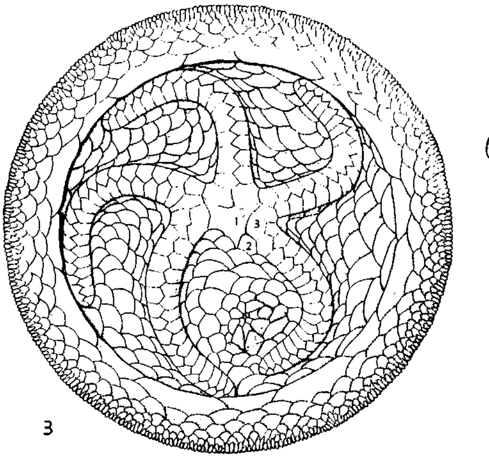
1

Hemicystites



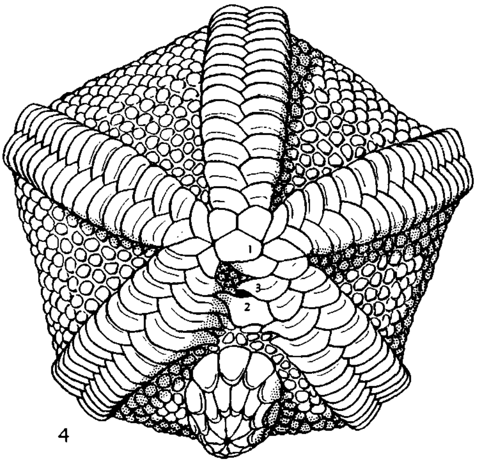
2

Anglidiscus



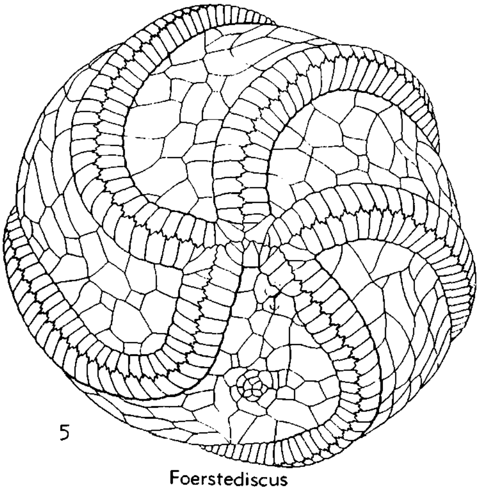
3

Carneyella



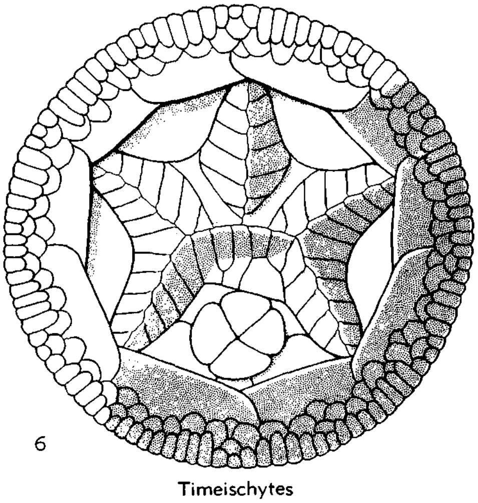
4

Cystaster



5

Foerstediscus



6

Timeischytes

with sharply elevated ambulacral cover plates in 2 rows (as in *Streptaster*), ambulacrum *C* curving in solar direction, other ambulacra in contrasolar direction (as in *Carneyella*); theca depressed saclike, diam. about 15 mm.; interambulacrals small (0.25 to 1 mm.), slightly imbricating, polygonal to circular; ambulacra rather broad and very long, extending to aboral side (15). *M.Ord.(Trenton.),* USA(N.Y.).

Carneyella Foerste, 1916, p. 340 [**Agelacrinus pileus* Hall, 1866, p. 7; OD]. Theca subcircular, typically elevated, saclike, attached by broad basal part, but also forming depressed epizoic discs usually on brachiopods, diameter reaching 30 mm. but usually 15 to 20 mm.; thecal plates more or less imbricating, differentiated into interambulacral fields and marginal zone; ambulacra normally 5, varying in length, curved, ambulacrum *C* solar, others contrasolar, some (as in figured species) with small additional cover plates along mid-line of ambulacra; surface of plates minutely pitted and commonly ornamented with ridges and conspicuous nodes (spiniferous tubercles); anal pyramid of about 7 (or more) triangular pieces (4, 26). *M.Ord.-U.Ord.*, N.Am.——Fig. 125,*2*. *C. cincinnatiensis* (Hall), U.Ord.(Maysvill.), USA (Ohio); adoral view (reconstr.), ×3(20).——Fig. 126,*3*. **C. pileus* (Hall), U.Ord., USA (Ohio); adoral view (reconstr.), ×3 (26). [See also Fig. 112,*2*; 117,*3*; 120,*5a*; 129,*1*,*5*.]

Cincinnatidiscus Bassler, 1935, p. 3 [**Agelacrinus (Hemicystites) stellatus* Hall, 1866, p. 8; OD]. Like *Cystaster* except that the theca is depressed or flat, subpentagonal, up to 10 mm. in diameter, attached by the whole aboral surface, and that the interambulacral plates are squamose, imbricating distinctly, being surrounded by a marginal zone of small nodose plates; casually more than 5 ambulacra (4). *M.Ord.-U.Ord.,* USA(Ky.-Ohio).——Fig. 125,*1*. **C. stellatus* (Hall), U.Ord. (Maysvill.), USA(Ohio); adoral view, ×9 (20).

Cystaster Hall, 1871, p. opp. pl. 6 (as subgenus of *Hemicystites*) [**C. granulatus* (=*Thecocystis sacculus* Jaekel, 1899); OD] [=*Thecocystis* Jaekel, 1899]. Theca saclike (height and width about 6 mm.), attached by aboral surface to some foreign object (or ?free); interambulacrals minute (0.25 mm.), fused, rounded or polygonal, forming mosaic; ambulacra 5, short, straight, with rather coarse, alternating cover plates supported by small side plates; raised anal pyramid composed of about 10 small, elongate, nodose plates (22). *U.Ord.*, USA(Ohio-Ky.).——Fig. 125,*5*; 126,*4*. **C granulatus*, Maysvill., Ohio; 125,*5*, posterolateral view, ×9(22); 126,*4*, adoral view (reconstr.), ×7.5 (24). [See also Fig. 114,*1*; 120,*3a*.]

Foerstediscus Bassler, 1935, p. 6 [**F. grandis*; OD]. Theca depressed to flattened, diameter 6 to 30 mm.; interambulacrals relatively large, polygonal, only slightly imbricating in center, piled up on edge along margin; plates generally smooth; ambulacra 5, short or long, all strongly curved in solar direction, with elongate cover plates; anal pyramid a narrow elevated tube or flat broad area of small plates (4). *M.Ord.-U.Ord.*, USA(Minn.-Ky.)-Can.(Ont.).——Fig. 125,*6*; 126,*5*. *F. splendens* Bassler, M.Ord.(Blackriver.); USA(Minn.); 125,*6*, adoral view of holotype, ×4.5 (4); 126,*5*, same (reconstr.), ×2.2 (24). [See also Fig. 115, *1*; 120,*2b*.]

Lebetodiscus Bather, 1908, p. 543 [**Agelacrinites dicksoni* Billings, 1857, p. 294; OD]. Theca discoidal, up to 24 mm. in diameter, adoral surface convex, aboral surface attached to some foreign body; interambulacral plates large, with slight adoral imbrication or forming mosaic, decreasing in size toward marginal zone of very small plates; ambulacra 5, long, contrasolar, reaching periphery but not passing it; ambulacral cover plates in 2 sets, smaller median ones and larger lateral ones with single large pore between each pair; anal opening large, covered with small plates (28, 41). *M.Ord.*, N.Am.(Can.).——Fig. 127,*4*. **L. dicksoni* (Billings), (Trenton.), Ont.; adoral view, ×2.25 (28). [See also Fig. 117,*4*.]

Lepidoconia Wilson, 1946, p. 21 [**Lebetodiscus loriformis* Raymond, 1915, p. 56; OD] Similar to *Lebetodiscus* but with 5 pores on either side of ambulacral cover plates; theca about 23 mm. in diameter; marginal ring wide; ambulacra curving in a contrasolar direction, long and stout, covering large part of disc surface and rising considerably above it, tip of each ambulacrum touching or nearly touching coil of adjacent one so that interambulacrals have little or no contact with peripheral plates (41). *M.Ord.*; N.Am.(Can.).——Fig. 127,*1*. **L. loriformis*(Raymond), Trenton., Ont.; adoral view; ×2.25(4).

Pyrgocystis Bather, 1915, p. 5 [**P. sardesoni*; OD]. Theca elevated, subcylindrical or polygonal [*P. (Rhenopyrgus?) octogona* R. Richter, 1930], turret-shaped, with subparallel or aborally tapering sides which are curved or nearly straight, composed of scalelike plates that imbricate from below upward, disposed in spirals or columns which inosculate or are separated by grooves; ambulacra 5, restricted to adoral surface, broad and straight; plates of (incompletely known) oral face, as well as free borders of turret plates may bear spines (7, 29). *L.Ord.-M.Dev.*, Eu.-N.Am.

P. (Pyrgocystis). Theca of moderate size (ranging upward to 20 mm. in Ordovician species, 11 mm.

(Facing page.)

Fig. 126. Hemicystitidae, adoral views (reconstr., 24), *1-4* showing posterior orotegminals (numbered 1, 2) and proximal cover plate of *C* ambulacrum (numbered 3), with "third aperture" between them (p. *U*162, *U*165, *U*167).

in Silurian species); basal part of theca developed as sort of ferrule formed by small number of closely amalgamated plates. *L.Ord.-M.Dev.* Eu. (USSR-Norway-Czech.-Br.I.-Gotl.)-N.Am.(USA).——FIG. 127,*2b*. *P.(P.)sulcata* (AURIVILLIUS), Sil.(U.Wenlock), Sweden(Gotl.); long. sec., ×4.7(29). [See also Fig. 113,*2*.]——FIG. 127, *2a*. **P. (P.) sardesoni,* M.Ord. (Blackriver.); USA (Minn.); adoral view, ×5.5(7).

P. (Rhenopyrgus) DEHM, 1961, p. 16 [**P. coronaeformis* RIEVERS, 1961, p. 10; OD]. Theca big (ranging to 95 mm.), widening in adoral

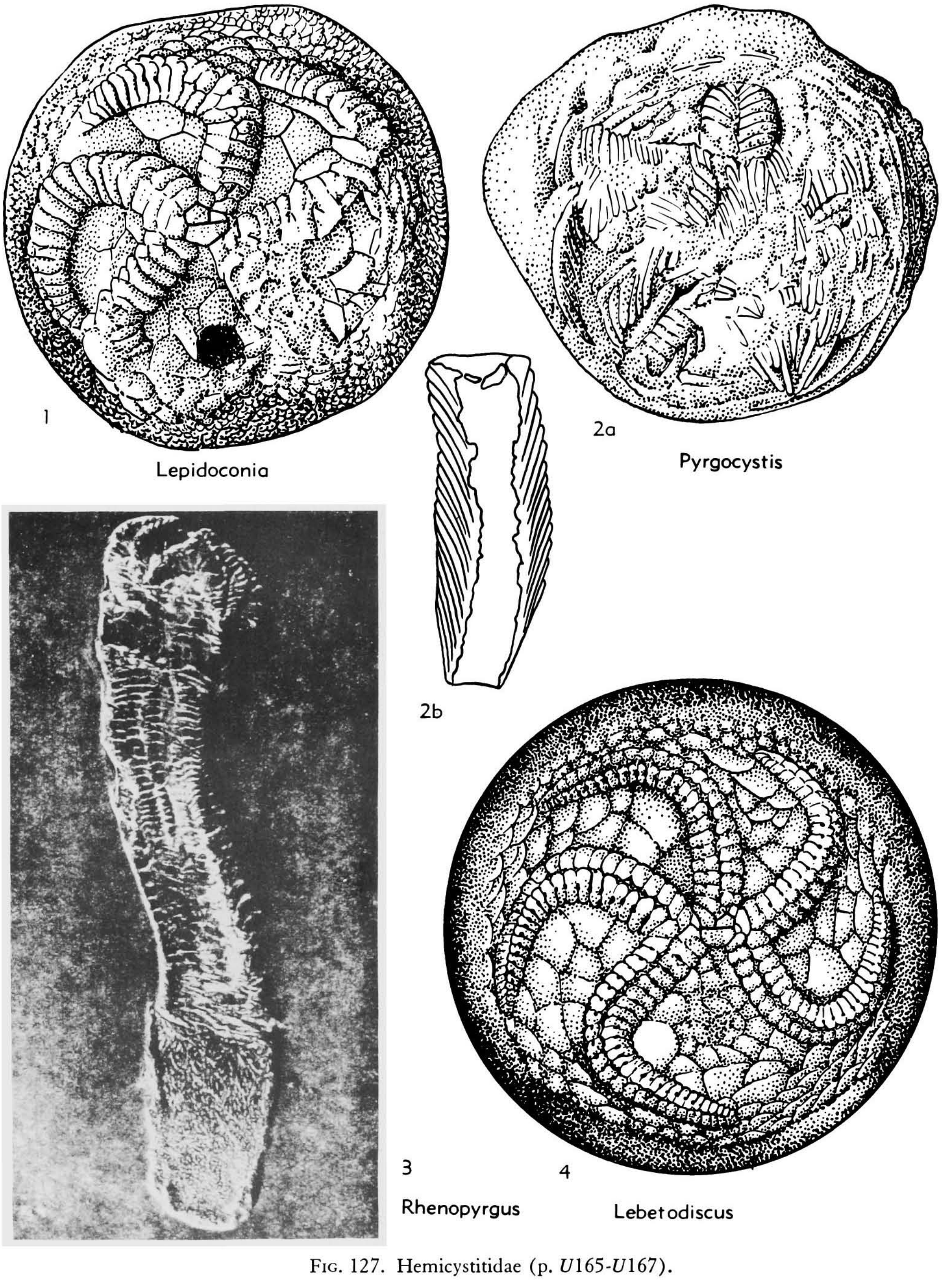


FIG. 127. Hemicystitidae (p. *U*165-*U*167).

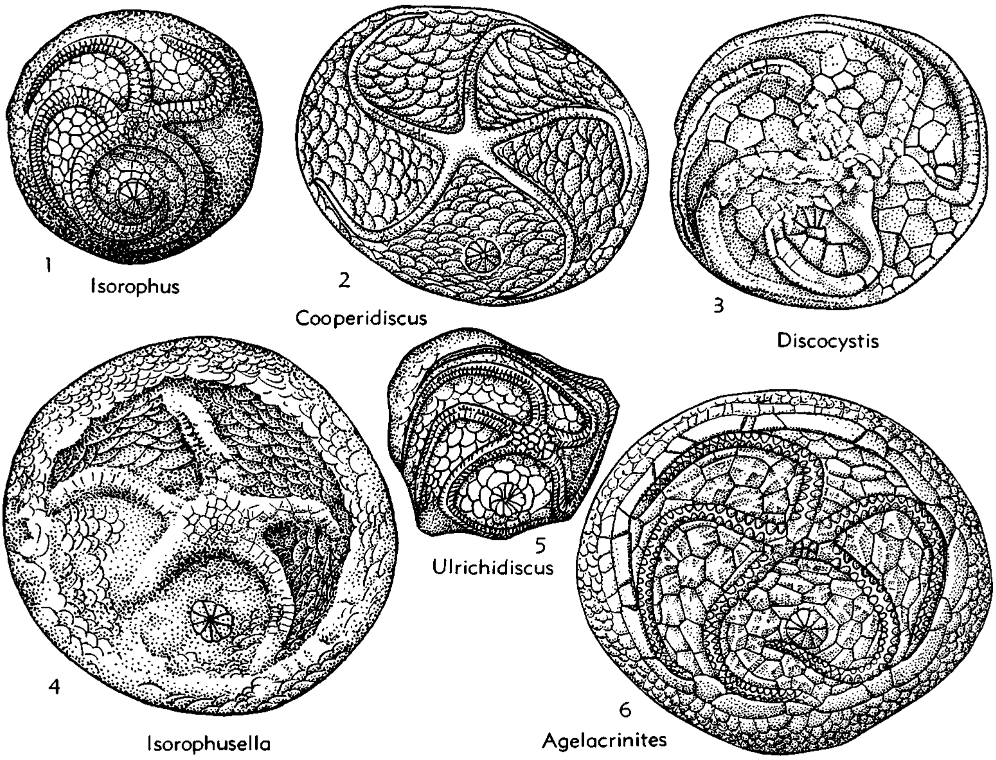


FIG. 128. Agelacrinitidae (p. *U*167-*U*169, *U*171).

direction; basal part of theca saccate, composed of numerous minute plates scattered in coriaceous skin. *L.Dev.*, Eu.(Ger.).——FIG. 127,*3*. *P. (Rhenopyrgus) coronaeformis*; lat. view, ×1 (32).

Streptaster HALL, 1872, p. following pl. 6 (as subgenus of *Agelacrinus*) [**Agelacrinus vorticellatus* HALL, 1866, p. 7; OD]. Like *Carneyella* but ambulacra revolving strongly in contrasolar direction (except solar ambulacrum *C* in *S. reversatus*, which may be a random variation) and composed of highly elevated plates; interambucrals polygonal, small (0.5 to 1 mm. diameter), forming mosaic; ambulacra normally 5, but *S. septembrachiatus* (MILLER & DYER, 1878) having 7 (not constantly); single set of ambulacral cover plates (2 rows), which show pronounced palisade-like elongation in lateral view (16). *U.Ord.*, USA (Ohio-Tenn.-?Ky.).——FIG. 125,*3*. **S. vorticellatus* (HALL), Maysvill., Ohio; adoral view, ×3.75 (20).——FIG. 130,*2*. S. sp., *cf.* **S. vorticellatus* (HALL), Maysvill., Ohio; adoral view (reconstr.), ×6 (24). [See also Fig. 117,*2*; 120,*3b*.]

Timeischytes EHLERS & KESLING, 1958, p. 934 [**T. megapinacotus*; OD]. Similar to *Hemicystites* from which it differs in having several plates in the posterior half of peristome, and in having only one large sublunar or sublinguiform interambulacral in all interambulacra except the posterior one; theca very small (4 to 4.5 mm. in 2 specimens known); anal pyramid proportionally very large, quatrefoliated (13). *M.Dev.*, USA(Mich.).——FIG. 126,*6*. **T. megapinacotus*; adoral view (reconstr.), ×15.5(24). [See also Fig. 120,*5b*.]

Family AGELACRINITIDAE Clarke, 1901

[=Agelacrinidae auctt. *(partim)*]

Theca as in Hemicystitidae except that plates covering mouth are small, numerous, and without any definite order; ambulacra normally 5, more or less curved, rarely branching; ambulacral floor plates in single row, overlapping proximally. *M.Ord.-L. Carb.(U.Miss.).*

Agelacrinites VANUXEM, 1842, p. 158 [**A. hamiltonensis*; OD] [=*Agelacrinus* Roemer, 1851; *Haplocystites* ROEMER, 1855; *Haplocystis, Agelacystis* HAECKEL, 1896]. Theca developed as thin epizoic disc attached by entire aboral surface, chiefly on *Rafinesquina,* subcircular to oval in outline; marginal zone formed by several rows of small plates bordering on ring of tangentially extended submarginal plates (diam., 10 to *ca.* 32 mm.) in single row; interambulacrals typically polygonal, with very slight overlap forming mosaic, sculptured, but in some species smooth and imbricating; ambulacra 5, long, usually narrow, much curved, *A,D,E* contrasolar, *B,C* solar; ambulacral cover plates in double row; anal area circular, covered by about 10 triangular plates regularly arranged in circle located approximately at center of posterior interambulacrum which may

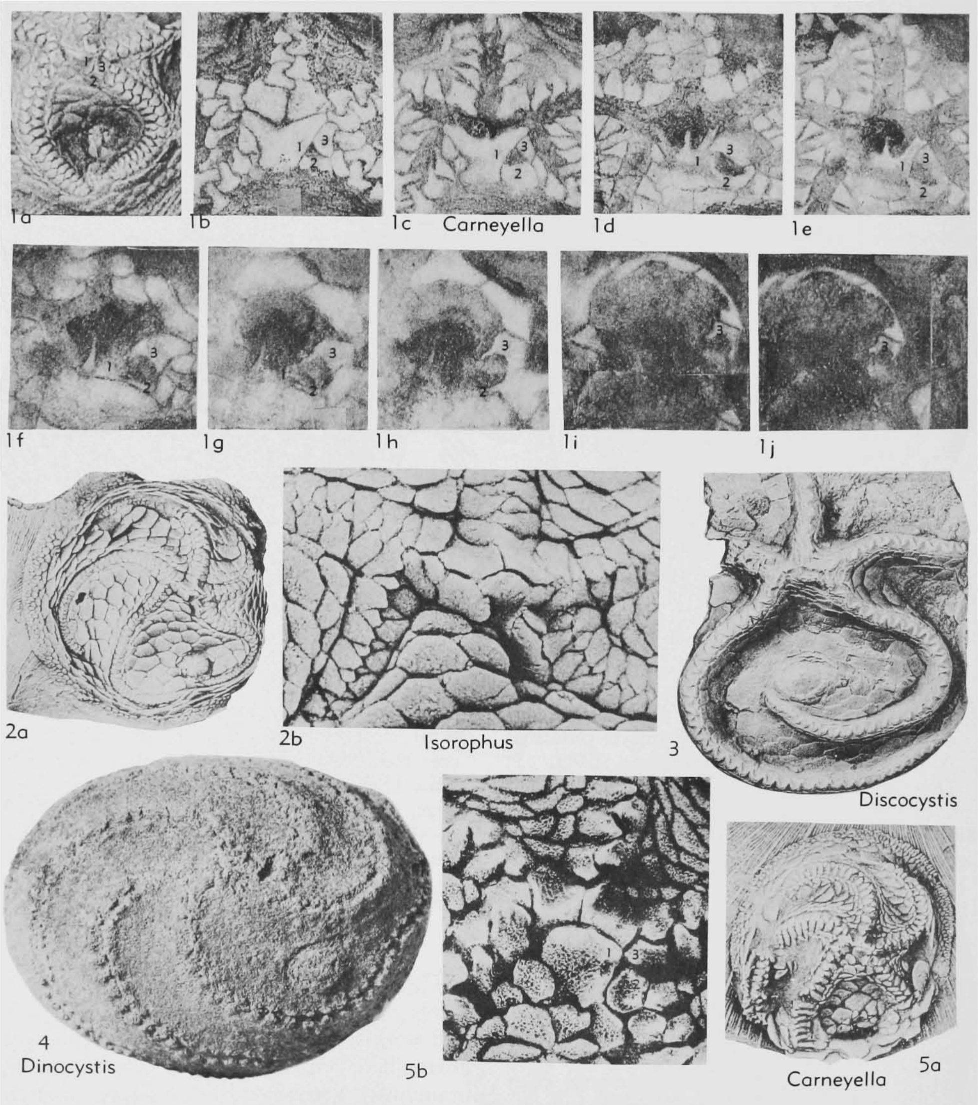


FIG. 129. Adoral views of edrioasteroids.——*1. Carneyella pileus* (HALL), U.Ord., USA(Ohio); *1a,* part of exterior surface, peristomial region (upper central) with posterior orotegminals indicated by numerals 1 and 2, proximal cover plate of *C* ambulacrum by 3, ×3; *1b-j,* photos of tangentially ground sections in succession toward aboral side of skeleton, showing "third aperture" (interpreted by KESLING as hydropore) between posterior orotegminals (numbered 1, 2) and proximal cover plate of *C* ambulacrum *(3),* ×5.5 (26).——*2. Isorophus cincinnatiensis* (ROEMER), U.Ord., USA(Ohio); *2a,* entire specimen, ×1.5; *2b,* peristomial region, ×6 (24).——*3. Discocystis laudoni* BASSLER, L.Miss., USA(Iowa); central and posterior parts of specimen, ×1.5 (24).——*4. Dinocystis barroisi* BATHER, U.Dev., Belg.; all ambulacra curved in contrasolar direction, ×1.5 (Regnéll, n).——*5. Carneyella pileus* (HALL), U.Ord., USA(Ohio); *5a,* entire specimen, ×1.5; *5b,* peristomial region with posterior orotegminals numbered 1,2, and proximal cover plate of *C* ambulacrum, 3, ×6 (24).

be entirely surrounded by ambulacra *C* and *D* (3,4). *L.Dev.-L.Miss.*, N.Am.(N.Y.-Mo.-Iowa-Ont.)-Eu.(Ger.).——FIG. 128,*6*. **A. hamiltonensis*, M.Dev.(Chenango), USA(N.Y.); adoral view, ×2.25(9).——FIG. 130,*6*. *A.* sp., M.Dev.(Traverse), USA(Mich.); adoral view (reconstr.), ×4.5(24). [See also Fig. 120,*4*.]

Cooperidiscus BASSLER, 1935, p. 8 [**Lepidodiscus alleganius* CLARKE, 1901, p. 194; OD]. Theca semiglobose, diameter about 40 mm., not attached, even temporarily; interambulacrals strongly imbricating; ambulacra 5, long, very narrow, strongly curved, all solar; ambulacral cover plates in double row; anal pyramid distinct, composed of 10 triangular plates in circle located near posterior margin (3). *U.Dev.*, USA(N.Y.-Pa.). —— FIG. 128,*2*. **C. alleganius*(CLARKE), Chemung., USA (N.Y.); adoral view, ×1.5 (9).

Discocystis GREGORY, 1897, p. 131 [**Agelacrinus kaskaskiensis* HALL, 1858, p. 696 (=*Echinodiscus optatus* WORTHEN & MILLER, 1883); OD] [=*Echinodiscus* WORTHEN & MILLER, 1883 (*non* LESKE, 1778, *nec* D'ORBIGNY, 1854, STÜRTZ, 1900); *Ageladiscus* S. A. MILLER, 1897]. Theca subcircular in outline, diameter to at least 30 mm., somewhat saclike, attached by central part of aboral side, with many rows of closely imbricated marginal plates; interambulacrals polygonal, forming mosaic; ambulacra normally 5, long, narrow, with strong curvature directed as in *Isorophus*; ambulacral cover plates in double row or forming cyclic pattern on each side of zigzag perradial line, with each cycle composed of 6 plates (e.g., *D. laudoni* BASSLER, 1936); periproct encircled by ambulacra *C* and *D*, anal pyramid distinct, composed of 7 or 8 triangular plates in circle located relatively near oral field (4, 12). [EHLERS & KESLING (12) have suggested that *Discocystis* might be a junior synonym of *Lepidodiscus* on evidence of the remarkable resemblance in shape and cyclic arrangement of the ambulacral cover plates in *D. laudoni* BASSLER, 1936, and *Lepidodiscus squamosus* (MEEK & WORTHEN, 1868).] *Miss.*, USA(Ala.-Ky.-Ill.-Mo.-Iowa).——FIG. 128,*3*. **D. kaskaskiensis*(HALL), U.Miss.(Chester), Ala.; adoral view, ×2(4).——FIG. 130,*5*. *D. laudoni* BASSLER, L.Miss. (Kinderhook.), USA(Iowa); adoral view (reconstr.), ×1.8 (24). [See also Fig. 113,*3*; 120,*6a*; 129,*3*.]

Isorophus FOERSTE, 1916, p. 340 [**Agelacrinus cincinnatiensis* ROEMER, 1851, p. 372; OD]. Theca circular in outline, diameter 8 to 40 mm., attached by entire aboral surface to *Rafinesquina* and other shells, disc-shaped to hemispherical, usually bordered by wide peripheral ring; interambulacrals scalelike, imbricating or nearly forming mosaic; ambulacra 5, almost straight to strongly curved, ambulacrum *C* solar, others contrasolar, relatively short and broad in most species; extra series of ambulacral cover plates commonly present between usual pair of rows; anal pyramid well defined, composed of 6 to 12 plates, in some specimens surrounded by zone of small plates, in species with curved rays periproct encircled by ambulacra *C* and *D* (4, 26, 30). [As illustrated by ROEMER (1851, pl. 5, fig. 3), curvature of the ambulacra is opposite to the true direction, owing to reversal of the image by the camera lucida used.] *M.Ord.-U.Ord.*, USA(N.Y.-Ky.-Tenn.-Ohio-Ind.).——FIG. 128,*1*; 130,*1*. **I. cincinnatiensis* (ROEMER), U. Ord. (Maysvill.), Ohio; 128,*1*, adoral view, ×1.5 (4); 130,*1*, same (reconstr.), ×2.4 (26). [See also Fig. 121; 129,*2*.]

Isorophusella BASSLER, 1935, p. 5 [**Lebetodiscus inconditus* RAYMOND, 1915, p. 61; OD]. Theca circular in outline, diameter up to 20 mm., slightly convex, resting on or attached by entire aboral surface to a hard substratum; with broad border of closely imbricating plates which decrease in size toward periphery; interambulacrals scalelike, strongly imbricating; ambulacra 5, short and stout, curving slightly in same direction as in *Agelacrinites*; median cover plates commonly present; oral area broad; anal pyramid distinct but almost flat, composed of about 10 elongate triangular plates arranged in circle located approximately at center of posterior interambulacrum (3, 4). *M.Ord.*, Can.(Ont.-Que.).——FIG. 128,*4*. **I. incondita* (RAYMOND), Trenton, Que.; adoral view, ×3 (3).

Lepidodiscus MEEK & WORTHEN, 1868, p. 357 [**Agelacrinites (Lepidodiscus) squamosus*; OD]. Theca subcircular or oval in outline, diameter 7 to 25 mm. in most species but 45 mm. in type-species, depressed, mostly with flat marginal rim by which it was attached to hard objects; interambulacrals strongly imbricating, with granular ornamentation in some species; ambulacra normally 5 (except for some specimens of *L. lebouri* SLADEN), long, narrow, much curved in same direction as in *Isorophus*, more seldom relatively short and broad; in *L. squamosus* ambulacral cover plates of one side are divided from those on other by prominent zigzag perradial line and are disposed in regular cycles of 6 throughout most of ambulacrum; ambulacral cover plates of other species arranged in double row, in some bordered by series of small side plates; anal pyramid distinct, composed of 9 to 15 triangular plates, usually not surrounded by ring of small plates, located near posterior margin and encircled by ambulacra *C* and *D* (4, 25, 30). *M.Dev.-U.Miss.*, N. Am. (N.Y.-Pa.-Mich.-Ind.)-Eu. (Eng.-USSR). [EHLERS & KESLING (12) have expressed doubt that many species assigned for the present to *Lepidodiscus* are correctly classified.]——FIG. 130, *4*. **L. squamosus* (MEEK & WORTHEN), L.Miss. (Keokuk), USA(Ind.); adoral view (reconstr.), ×1.5 (24). [See also Fig. 114,*2*; 120,*6a'*.]

Thresherodiscus FOERSTE, 1914, p. 433 [**T. ramosus*; OD]. Theca discoid, with gently convex adoral surface, diameter about 16 mm.; interambulacrals large, squamose, imbricating in central region, decreasing in size distally so as to

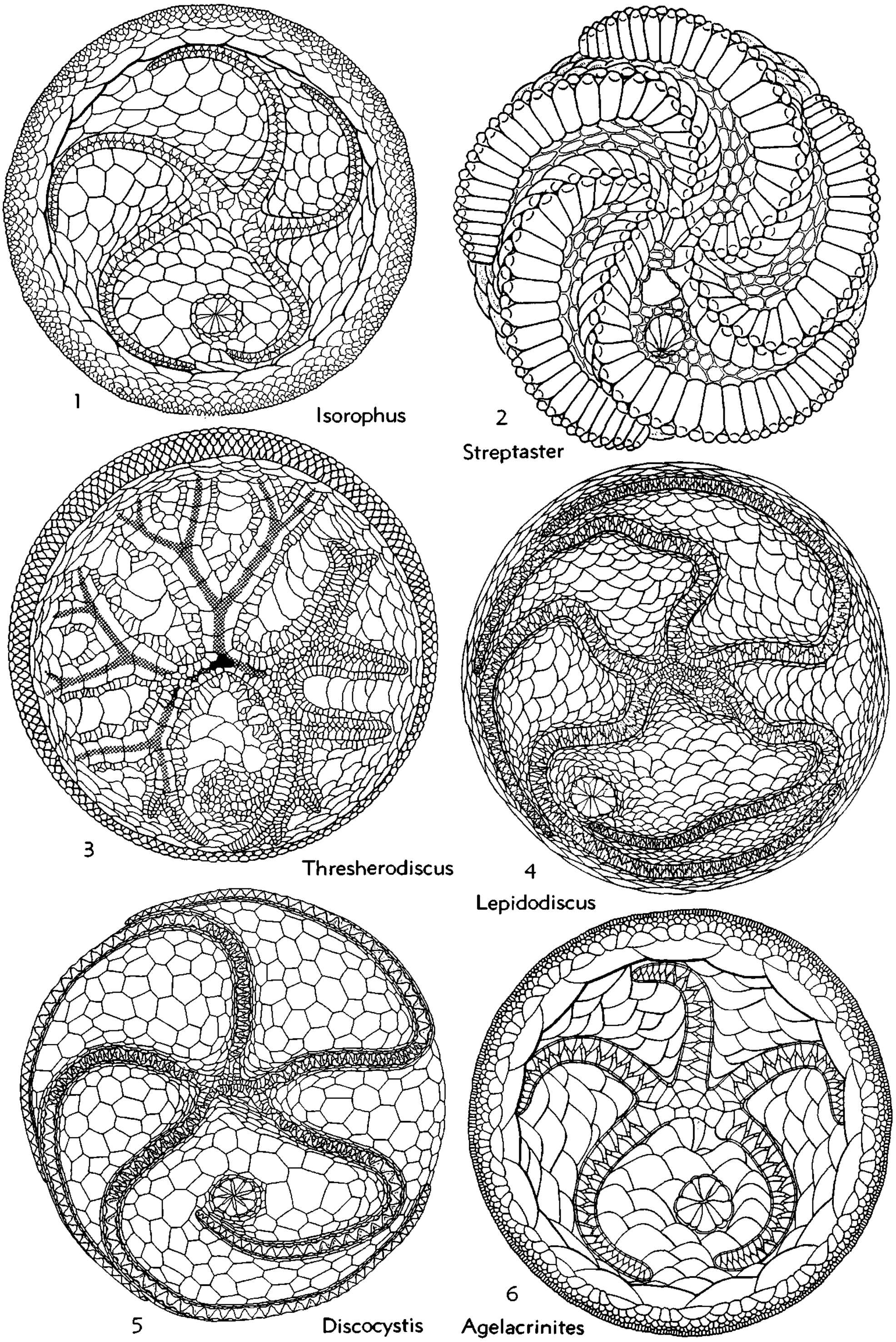


FIG. 130. Hemicystitidae (2); Agelacrinitidae *(1,3-6)*, adoral views (reconstr.) (p. *U*167-*U*169, *U*171).

merge with much smaller plates of marginal zone; ambulacra 5, rather broad, of pronounced trimerous origin, branching dichotomously with bifurcations of 1st, 2nd, and probably 3rd order; ambulacral cover plates in 2 sets consisting of very small median ones and much larger lateral ones; periproct unknown (16). *M.Ord.*, Can. (Ont.).——Fig. 130,*3*. **T. ramosus*, Trenton.; adoral view of holotype (reconstr.), ×4 (24). [See also Fig. 112,*1*; 120,*2a*.]

Ulrichidiscus Bassler, 1935, p. 8 [**Agelacrinus pulaskiensis* Miller & Gurley, 1894, p. 16; OD]. Theca semiglobose, diameter about 26 mm.; interambulacrals relatively large, polygonal, slightly imbricating; ambulacra 5, narrow but well defined, very long, all strongly curving in contrasolar direction; anal pyramid well defined, composed of many long triangular plates in circle (3). *U.Miss.*, N.Am.(USA).——Fig. 128,*5*. **U. pulaskiensis* (Miller & Gurley), Chester., Ky.; adoral view, ×1 (3).

Family EDRIOASTERIDAE Bather, 1898

Theca shaped like tam-o'-shanter, not permanently attached; central part of aboral surface excavated, covered by flexible integument; interambulacrals polygonal, forming mosaic, continuous with those of aboral face; ambulacra 5, very long, strongly curved, passing on to aboral surface; ambulacral floor plates in double rows of alternating plates that meet along zigzag median suture, with pores between floor plates and each cover plate corresponding in position with a floor plate; third aperture located in posterior interambulacrum. *M.Ord.-U.Dev.*

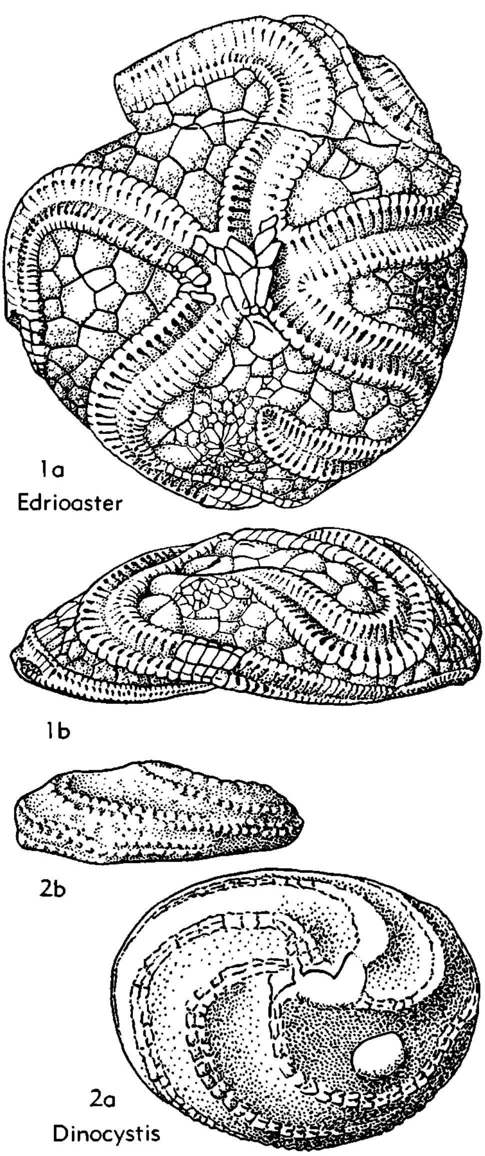


Fig. 131. Edrioasteridae (p. *U*171-*U*172).

Edrioaster Billings, 1858, p. 82 [**Cyclaster bigsbyi* Billings, 1857, p. 293; OD] [=*Cyclaster* Billings, 1857 (*non* Cotteau, 1856; *nec* Mallory, 1904); *Aesiocystites* Miller & Gurley, 1894; *Edriocystis* Haeckel, 1896; *Aesiocystis* Bather, 1900]. Theca subcircular to subpentagonal, diameter 14 to 50 mm., height 0.25 to 0.5 of width; interambulacrals generally more or less pustulose or granulose, separated from central aboral region by frame of stouter plates; peripheral plates of aboral face variable in size but not minute but central plates minute and tending to imbricate; ambulacra comparatively broad, raised or not raised above the general surface, *A, B, D, E* curving in a contrasolar direction, *C* in solar direction (type-species only), or all curving solarly; small median cover plates may be present; peristome covered by solid tegmen of plates serially homologous with ambulacral cover plates; anus well defined, covered by variable number of irregular plates (7). [Forms in which all of the ambulacra curve in a solar direction possibly should be separated generically from *Edrioaster*.] *M.Ord., ?U. Ord.,* N. Am. (Ont.-Que.-Ky.-Mich.-Minn.-N. Y.)-Eu.(N.Wales).——Fig. 131,*1*. **E. bigsbyi* (Billings), M.Ord.(Trenton.), Ont.; *1a,b*, adoral, post. views, ×1.7 (7, pt. 4). [See also Fig. 111; 113,*1*; 115,2; 116,*1,4*; 118,*1*; 119,*1,3*; 120,*1*.]

Dinocystis Bather, 1898, p. 547 [**D. barroisi*; OD]. Theca elliptical in outline, diameter to about 40 mm., like *Edrioaster* but with frame on aboral surface slighter and surrounding region composed of thin flexible integument containing narrow imbricating plates; ambulacra narrow, all curving strongly in a contrasolar direction (7). *U.Dev.*, Eu.(Belg.).——Fig. 131,*2*. **D. barroisi*, Famenn.; 131,*2a*, oral, ×1 (Regnéll, n); 131,*2b*, ant., ×1.2 (7, pt. 1).

REFERENCES

Anderson, F. W.

(1) 1939, *Lepidodiscus fistulosus sp. nov. from Lower Carboniferous rocks, Northumberland:* Great Britain, Geol. Survey, Bull. 1, p. 67-81, pl. 5, text-fig. 1-10.

Aurivillius, C. W. S.

(2) 1892, *Über einige ober-silurische Cirripeden aus Gotland:* [K.] Svenska. Vetenskaps-akad., Handl., Bihang, ser. 4, v. 18, pt. 3, p. 1-24, pl. 1.

Bassler, R. S.

(3) 1935, *The classification of the Edrioasteroidea:* Smithsonian Misc. Coll., v. 93, pt. 8, p. 1-11, pl. 1.

(4) 1936, *New species of American Edrioasteroidea:* Same, v. 95, pt. 6, p. 1-33, pl. 1-7.

———, & Moodey, M. W.

(5) 1943, *Bibliographic and faunal index of Paleozoic pelmatozoan echinoderms:* Geol. Soc. America, Spec. Paper 45, vi+734 p.

Bather, F. A.

(6) 1900, *The Echinoderma* (with contributions by J. W. Gregory and E. S. Goodrich): in Lankester, E. R., A Treatise on Zoology, v. 3, viii+344 p., 309 text-fig., A. & C. Black (London).

(7) 1915, *Studies in Edrioasteroidea, 1-9:* reprinted, with additions, from Geol. Mag. for 1898, 1899, 1900, 1908, 1914, 1915, The Author (Wimbledon).

Cabibel, Jaques, Termier, Henri, & Termier, Geneviève

(8) 1959, *Les échinodermes mésocambriens de la Montagne Noire (Sud de la France):* Ann. Paléontologie, v. 44 (1958), p. 279-294, pl. 6-7, text-fig. 1-10.

Clarke, J. M.

(9) 1901, *New Agelacrinites:* New York State Museum, Ann. Rept. 55 (Bull. 49), p. 182-198, pl. 10, text-fig. 1-7.

Cuénot, Lucien

(10) 1948, *Anatomie, éthologie et systématique des échinodermes:* in Traité de zoologie, Grassé, P.-P (ed.), v. 11, p. 3-272, text-fig. 1-312, Masson (Paris).

Dehm, Richard

(11) 1961, *Über Pyrgocystis (Rhenopyrgus nov. subgen.) coronaeformis Rievers aus dem rheinischen Unter-Devon:* Bayer. Staats-sammlung Paleont. Hist. Geol., Mitteil., v. 1, p. 13-17.

Ehlers, G. M., & Kesling, R. V.

(12) 1958, *Cyclic pattern of ambulacral covering plates in Discocystis laudoni and its taxonomic implication:* Michigan Univ., Museum Paleontology, Contrib., v. 14, no. 15, p. 265-276, pl. 1-3.

(13) 1958, *Timeischytes, a new genus of hemicystitid edrioasteroid from the Middle Devonian Four Mile Dam Limestone of Michigan:* Jour. Paleontology, v. 32, p. 933-936, pl. 121, text-fig. 1.

Fay, R. O.

(14) 1962, *Edrioblastoidea, a new class of Echinodermata:* Jour. Paleontology, v. 36, p. 201-205, pl. 34, text-fig. 1-3.

Fisher, D. W.

(15) 1951, *A new edrioasteroid from the Middle Ordovician of New York:* Jour. Paleontology, v. 25, p. 691-693, text-fig. 1-2.

Foerste, A. F.

(16) 1914, *Notes on Agelacrinidae and Lepadocystinae, with descriptions of Thresherodiscus and Brockocystis:* Denison Univ. Sci. Lab., Bull. 17, p. 399-487, pl. 1-6, text-fig. 1-8.

Gekker [Hecker], R. F.

(17) 1928, *Paläobiologische Betrachtungen an untersilurischen Invertebraten. I:* Ann. Soc. Paléont. Russie, v. 7, p. 47-86, pl. 3-4, text-fig. 1-3.

(18) 1940, *Agelacrinites aus dem Devon der russischen Tafel:* Acad. Sci. URSS, Inst. Paléont., Travaux, v. 9, pt. 4, p. 83-104, pl. 11-12, text-fig. 1-3.

Gislén, Torsten

(19) 1930, *Affinities between the Echinodermata Enteropneusta, and Chordonia:* Zool. Bidrag. Uppsala, 12, p. 199-304, text-fig. 1-46.

Hall, James

(20) 1872, *Description of new species of Crinoidea and other fossils from strata of the age of the Hudson River Group and Trenton Limestone:* New York State Museum, 24th Ann. Rept., p. 205-224, pl. 5-8, text-fig. 1-3.

Harker, Peter

(21) 1953, *A new edrioasteroid from the Carboniferous of Alberta:* Jour. Paleontology, v. 27, p. 288-289, text-fig. 1.

Jaekel, Otto

(22) 1899, *Stammesgeschichte der Pelmatozoen. 1. Thecoidea and Cystoidea:* x + 442 p., 18 pl., 88 text-fig.

(23) 1927, *Cyathotheca suecica n. g., n. sp., eine Thecoidee des schwedischen Ordoviciums:* K. Svenska. Vetenskapsakad., Arkiv Zool., v. 19A, pt. 5, p. 1-5, pl. 1.

Kesling, R. V.

(24) 1960, *Hydropores in edrioasteroids:* Michigan Univ., Museum Paleontology, Contrib., v. 15, no. 8, p. 139-192, pl. 1-13, text-fig. 1-14.

———, & Ehlers, G. M.

(25) 1958, *The edrioasteroid Lepidodiscus squamosus (Meek & Worthen):* Jour. Paleontology, v. 32, p. 923-932, pl. 119-120, text-fig. 1.

———, & Mintz, L. W.

(26) 1960, *Internal structures in two edrioasteroid species, Isorophus cincinnatiensis (Roemer) and Carneyella pilea (Hall):* Michigan Univ., Museum Paleontology, Contrib., v. 15, no. 14, p. 315-348, pl. 1-9, text-fig. 1-4.

Pompeckj, J. F.

(27) 1896, *Die Fauna des Cambrium von Tejřovic und Skrej in Böhmen:* K.-K. Geol. Reichsanst. Wien, Jahrb., v. 45 (1895), p. 495-614, pl. 13-17, text-fig. 1.

Raymond, P. E.

(28) 1921, *A contribution to the description of the fauna of the Trenton Group:* Canada, Geol. Survey, Dept. Min. & Res., Museum Bull. 31, p. 1-64, pl. 1-10.

Regnéll, Gerhard

(29) 1945, *Non-crinoid Pelmatozoa from the Paleozoic of Sweden:* Lunds Geol.-Min. Inst., Meddel. 108, p. i-viii+1-255, pl. 1-15, text-fig. 1-30.

(30) 1950, *"Agelacrinites" ephraemovianus Bogolubov and "Lepidodiscus" fistulosus Anderson:* K. Fysiogr. Sällsk. Lund Förhandl., v. 20, pt. 20, p. 218-237, text-fig. 1-2.

(31) 1960, *Données concernant le développement ontogénétique des pelmatozoaires du Paléozoïque (échinodermes):* Soc. Géol. France, Bull., ser. 7, v. 1 (1959), p. 773-783, text-fig. 1-6.

Rievers, Johannes

(32) 1961, *Eine neue Pyrgocystis (Echinod., Edrioasteroidea) aus den Bundenbacher Dachschiefern (Devon):* Bayer. Staatssammlung Paleont. Hist. Geol., Mitteil., v. 1, p. 9-11, pl. 2.

Rösler, Artur

(33) 1953, *Agelacrinites taunicus n. sp. (Edrioaster.) aus dem Unterdevon von Mensfelden (Blatt Limburg, Lahn). Mit Bemerkungen zu Agelacrinites? rhenanus (F. Roemer) und einer Übersicht über die Funde von nichtcrinoiden Pelmatozoen im rheinischen Unterdevon:* Hess. Landesamt Bodenf., Notizbl., v. 81, p. 69-74, pl. 3.

Schmidt, Friedrich

(34) 1879, *Ueber Cyathocystis Plautinae, eine neue Cystideenform aus Reval:* Russische-Kaiserl. Min. Gesell., Verhandl., ser. 2, v. 15, p. 1-7, text-fig. 1-3. [The entire volume was published in 1880, as given on the title-page, but separate of the present paper appeared in October 1879 (*fide* O. Jaekel, 1899, p. 439).]

Schuchert, Charles

(35) 1919, *A Lower Cambrian edrioasterid:* Smithsonian Misc. Coll., v. 70, pt. 1, p. 1-8, pl. 1, text-fig. 1.

Sinclair, G. W.

(36) 1951, *Three notes on Ordovician agelacrinitids:* (unpublished manuscript).

Spencer, W. K.

(37) 1904, *On the structure and affinities of Palaeodiscus and Agelacrinus:* Royal Soc. London, Proc., v. 74, p. 31-46, pl. 1, text-fig. 1-12.

(38) 1938, *Some aspects of evolution in Echinodermata:* Evolution, essays presented to E. S. Goodrich, p. 287-303, pl. 1-2.

Strimple, H. L., & Graffham, A. A.

(39) 1955, *A new species of Cyathocystis:* Washington Acad. Sci., Jour., v. 45, p. 353-355.

Williams, S. R.

(40) 1918, *Concerning the structure of Agelacrinites and Streptaster, Edrioasteroidea of the Richmond and Maysville divisions of the Ordovician:* Ohio Jour. Sci., v. 19, p. 59-86, pl. 1-9.

Wilson, Alice E.

(41) 1946, *Echinodermata of the Ottawa Formation of the Otawa-St. Lawrence Lowland:* Canada, Geol. Survey, Dept. Min. & Res., Bull. 4, p. i-v + 1-61, pl. 1-6, text-fig. 1-2.

OPHIOCISTIOIDS

By Georges Ubaghs

[Université de Liège]

[The author expresses sincere thanks to R. C. Moore for an excellent translation of his French typescript. Also, he acknowledges with great appreciation aid given to him by officers of the British Museum (Natural History) and the Oxford University Museum in making available for study by him various type-specimens and other ophiocistioid materials contained in their collections.]

CONTENTS

INTRODUCTION

Ophiocistioids, named from the Greek words *ophis* ("snake") and *kiste* ("box"), are a small group of pentaradiate free-moving echinoderms known only as fossils in Paleozoic strata. Their body may be entirely enclosed, except for the peristome, by a test composed of plates like that of echinoids, or it may be covered by plates on one side only, the other being protected by an integument that is little calcified if at all. A resemblance to echinoids does not include the mode of union of the test plates, for in the ophiocistioid *Sollasina,* at least, junction of the plates seems to differ from that observed in echinoids. Ophiocistioids have no arms comparable to those of asterozoans and crinoids or brachioles like those of cystoids. Instead, they bear hollow tubular organs with a cover of small imbricated plates, and despite their relatively large size, these organs are interpreted to be ambulacral tube feet.

The test has an oral surface, on which the animal rests or travels about, and an aboral surface. One is approximately equal to the other in area, but otherwise the two surfaces are quite dissimilar. Plates of the aboral surface are irregularly disposed in some ophiocistioids, whereas they exhibit a more or less definite radial arrangement in others. The anus is located on this surface or at its edge in genera represented by specimens with the anal vent preserved. At the center of the oral surface is the mouth, equipped with a masticatory apparatus consisting of five interradially placed jaws, each of which is composed of two pieces. The buccal apparatus is surrounded by a flexible peristomial membrane not unlike that of echinoids. Beyond the peristomial area, the oral surface is divided into five large ambulacral tracts and five narrow interambulacral ones. No ambulacral grooves are present. The ambulacra terminate at the border of the test without extending onto the aboral surface. Each ambulacral tract contains three columns of plates, one perradial and the other adradial. A single pore for each ambulacral tube foot is located at the intersection of adradial and perradial plate pairs. One of the oral interrays in two genera contains a madreporite associated with one or several orifices interpreted as gonopores. In another genus a single orifice on the aboral surface is possibly a gonopore, or hydropore, or combined gonopore-hydropore.

DEVELOPMENT OF KNOWLEDGE

Ophiocistioids were first differentiated from other echinoderms by Sollas (15) in 1899 when he proposed recognition of them as an order named Ophiocistia in the class

Ophiuroidea. In 1912 SOLLAS & SOLLAS (16) elevated the group to class rank, even though up to that time it included only three Silurian species from Great Britain. These are now judged to represent three monotypic genera: *Eucladia* WOODWARD, 1869; *Euthemon* SOLLAS, 1899; *Sollasina* FEDOTOV, 1926. In 1930 RICHTER (13) introduced the name *Rhenosquama* for organic remains from the Middle Devonian of Germany which he interpreted as ambulacral tube feet of an otherwise unknown ophiocistioid. The assignment of *Rhenosquama* to the ophiocistioids is by no means certain, however. In 1938 and 1940 GEKKER (6, 7) described certain fossils from the Lower Ordovician (Skiddavian) in the vicinity of Leningrad. Earlier, JAEKEL (1901, 1918) and BATHER (1913) had considered these fossils to be thecas of the fantastic *Rhipidocystis* JAEKEL, 1901. GEKKER concluded that in reality they are fragments of the test of a quite different organism, which he named *Volchovia* and classified among the ophiocistioids even though it differs greatly from typical ophiocistioids from the British Silurian. Subsequently, *Volchovia* has been discovered in Lower Ordovician rocks of Norway (REGNÉLL, 12) and in Upper Ordovician deposits of Ohio (POPE, 1960). Finally, a fossil from the Lower Devonian (Helderberg) of New York which SCHUCHERT (1915) described as *Eucladia? beecheri* and attributed (14) doubtfully to the ophiocistioids, is an enigmatic form impossible to classify in the state of present knowledge.

Owing to the strange features and rarity of ophiocistioids, interpretation of these echinoderms has been very difficult. Only a single specimen of *Eucladia* and one of *Euthemon* are known. Other genera are represented by a mere handful of specimens including fragments. First descriptions (WOODWARD, 18; GREGORY, 8) are partly erroneous. SOLLAS (15) may be credited with having shown accurately the structure of most typical genera and BATHER (1,2) with having been first to indicate that the tubular appendages of these forms are not arms but equivalents of the tube feet found in other echinoderms. More recently, FEDOTOV (4), GEKKER (7), and REGNÉLL (12) have contributed important new information concerning the morphology of ophiocistioids and discussion of their systematic position has been published, especially by FEDOTOV (4, 5), REGNÉLL (12), and UBAGHS (17).

For many years the ophiocistioids were placed among the ophiuroids, as suggested by their name, or in a separate group allied to the Ophiuroidea. At present they are accorded the rank of a distinct class, coordinate taxonomically with the Stelleroidea, Echinoidea, and Holothuroidea, for example. This is the view adopted by SOLLAS & SOLLAS (16), FEDOTOV (4, 5), RICHTER (13), GEKKER (6, 7), REGNÉLL (12) and a majority of modern treatises and manuals. Although they have been almost universally considered as Eleutherozoa, MATSUMOTO placed them in his subphylum Crinozoa, corresponding to Pelmatozoa less Edrioasteroidea. FELL (1963) has assigned them to the Echinozoa, and this classification is accepted in the *Treatise*.

MORPHOLOGY

GENERAL FORM AND SIZE

In outline the theca of ophiocistioids may be elliptical *(Sollasina),* suboval *(Volchovia),* subpentagonal *(Euthemon),* or faintly pentalobate *(Eucladia).* The border is sinuous and somewhat angulated in *Volchovia* but evenly regular in other genera.

The test bears no arms or rays corresponding to those of starfishes or crinoids, and, as previously noted, its downwardly directed oral surface with central mouth is very unlike the opposite aboral surface on the upper side. The oral surface of *Eucladia* (Fig. 132) and *Euthemon* (Fig. 133) is flat or gently convex medially but progressively curved upward near the border so as to grade into the unknown, probably arched aboral surface. In *Sollasina* (Fig. 134) both surfaces of all observed specimens are crushed, yet position of the appendages suggests that the theca in undistorted condition was low dome-shaped. The central part of the aboral side of *Volchovia* has the form of a moderately ele-

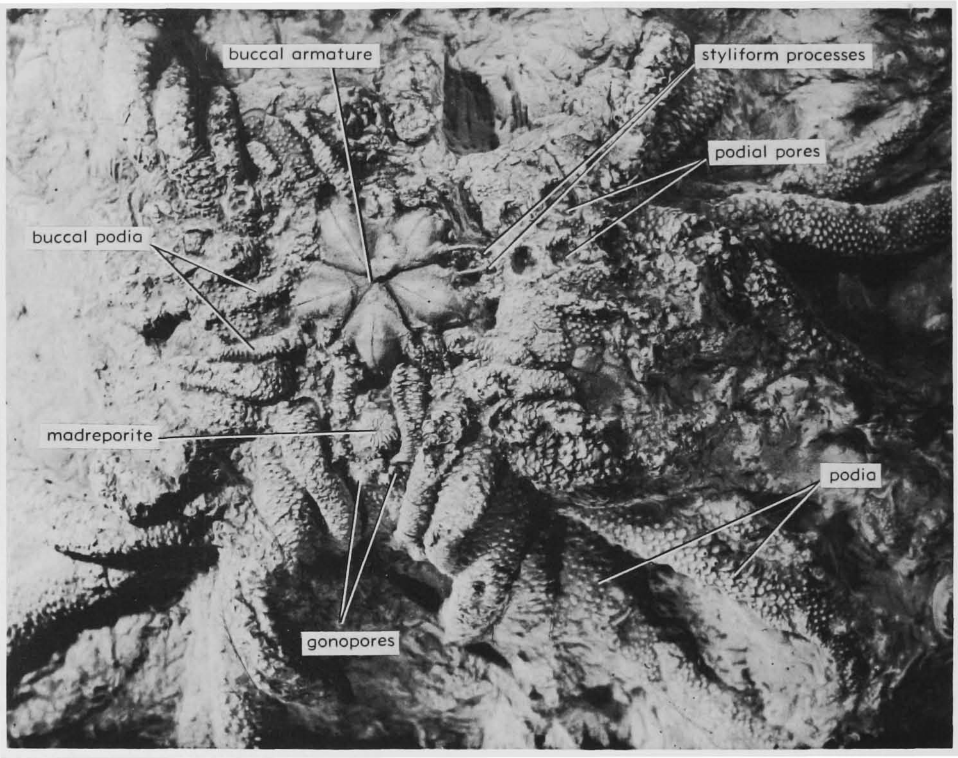


FIG. 132. *Eucladia johnsoni* WOODWARD, U.Sil.(L.Ludlov.), Eng.; part of oral surface showing morphological features, ×1.3 (Ubaghs, n).

vated mound which grades peripherally into very gently sloping, nearly flat marginal areas (Fig. 135). The sharply defined border of the theca is indented by angular embayments between the several pointed extensions of its circumference. The oral surface, not observed in this genus, is doubtless flat or concave. The theca of *Rhenosquama* is entirely unknown.

The size of tests belonging to ophiocistioids is small to modest, as shown by following measurements: *Euthemon,* diameter 7 or 8 mm.; *Sollasina,* length 30 mm., width 20 mm., *Eucladia,* length 50 mm., width 40 mm.; *Volchovia,* maximum diameter, 90 mm.

SYMMETRY

The oral surface of all genera in which it is known exhibits pentaradiate symmetry. This is marked by (1) distribution of plates in five radial and five interradial areas, (2) distribution of tube feet in five groups, and (3) presence of a buccal armature composed of five pairs of interradially disposed plates. A tendency toward pentaradiate symmetry appears also in the arrangement of aboral plates in *Volchovia,* but as noted later, this symmetry is far from perfect.

Orientation of the test can be determined in various ophiocistioids belonging to dif-

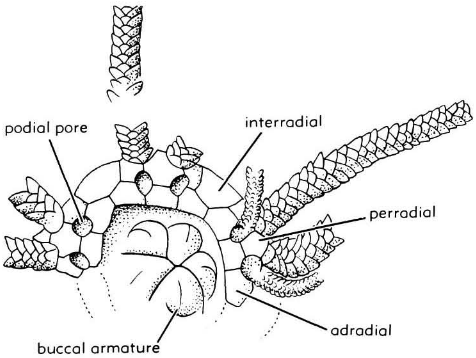


FIG. 133. *Euthemon igerna* SOLLAS, U.Sil. (Wenlock.), Eng.; adoral side, ×3.5 (4).

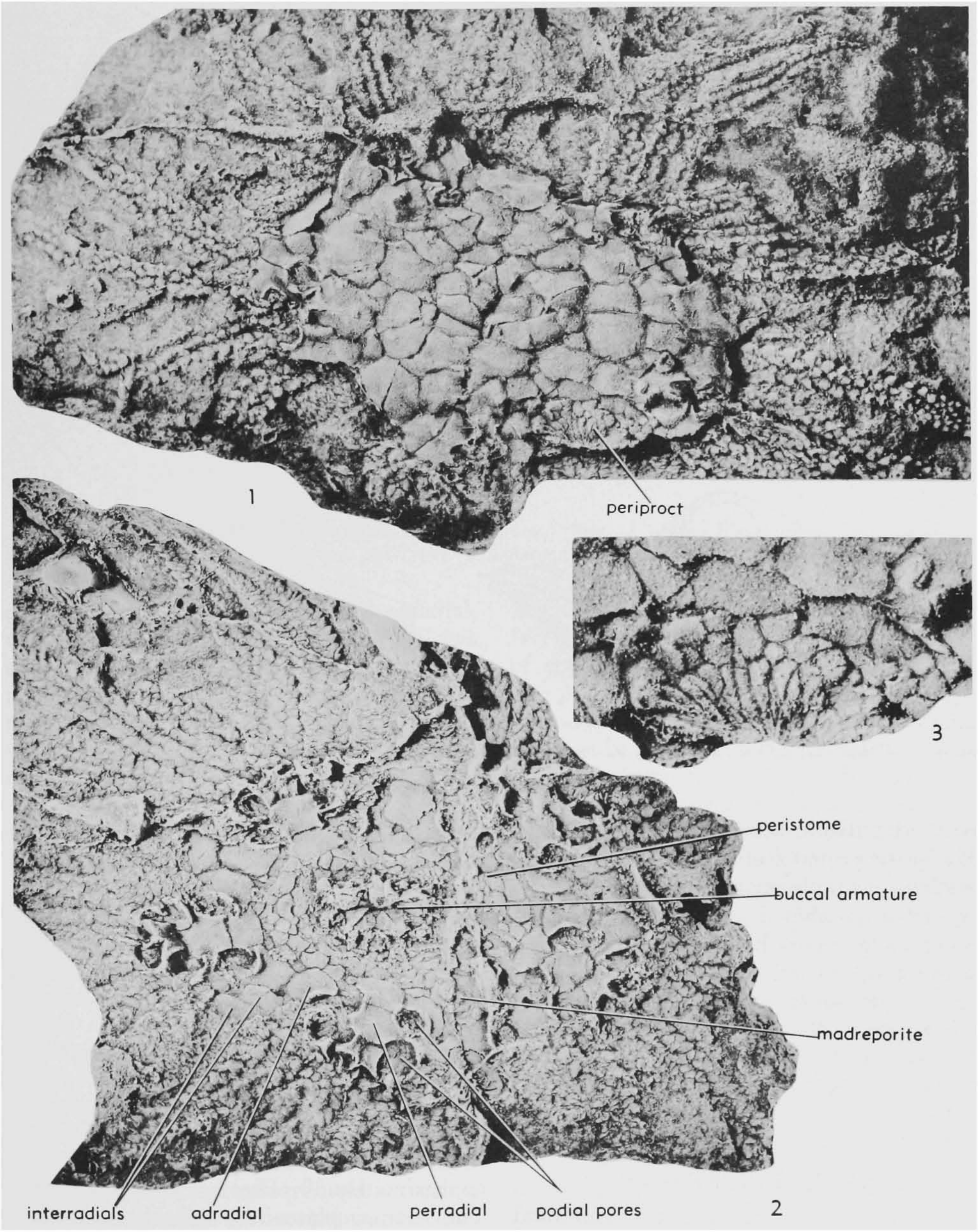


FIG. 134. *Sollasina woodwardi* (SOLLAS), U.Sil.(L.Ludlov.), Eng.; *1,2,* aboral and oral sides, ×2; *3,* periproct, ×15 (all Ubaghs, n).

ferent genera. In *Eucladia* (Fig. 132) and *Sollasina* (Fig. 134,*2*) the presence of a madreporite accompanied by one or more perforated tubercles (?gonopores) in an interray of the oral surface serves to identify this interray as *CD,* in terms of the Carpenter system. Moreover, some specimens of *Sollasina* (Fig. 134,*1,3*) show presence of the periproct on the aboral side of the test adjacent to the border and located in this interray or one next to it (decision as to which being difficult). The *CD* inter-

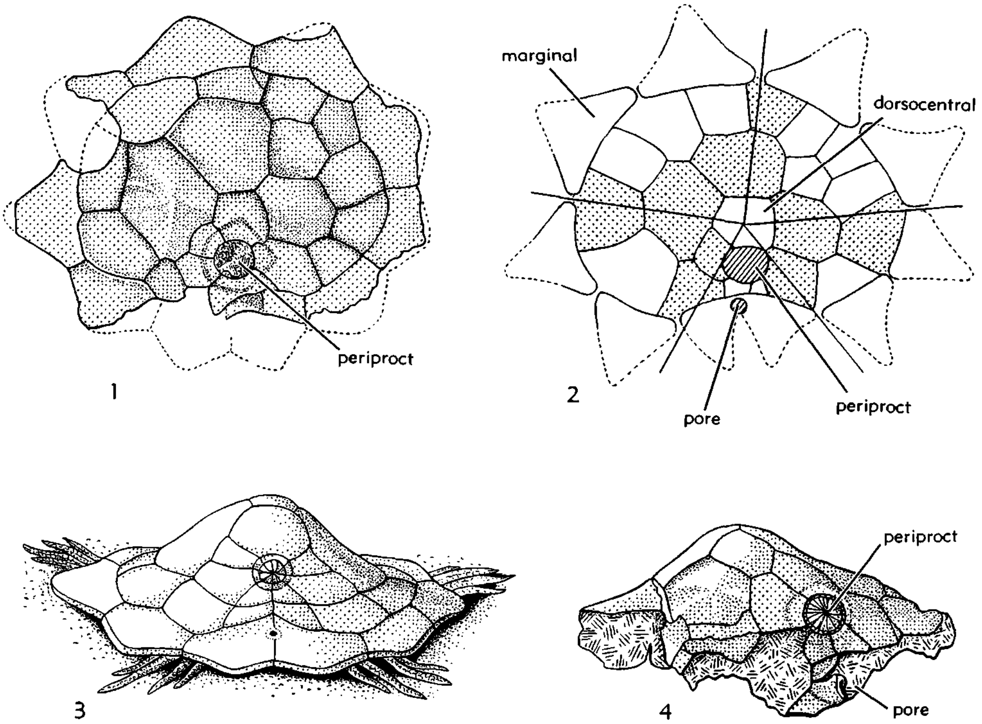


FIG. 135. *Volchovia*, L.Ord., Eu.; *1-3, V. mobilis* GEKKER, USSR (7); *4, V. norvegica* REGNÉLL, Norway (12); all ×1.

ray is identifiable also in *Volchovia* (Fig. 135) by the presence of an orifice previously mentioned as probably a gonopore or hydropore or a combined gonopore-hydropore; this opening occurs between two marginal plates on the aboral surface. The anus occurs in the same interray approximately midway between the supposed gonopore and the summit of the theca. The major axis of the test is perpendicular to the *CD* interradius in *Volchovia* and oblique to it in *Sollasina.*

ABORAL SURFACE

The upper surface of the theca is known only in *Sollasina* and *Volchovia.*

In *Sollasina* many irregular polygonal or rounded plates form the aboral surface (Fig. 134,*1*). The plates are thin and do not exceed 5 mm. in diameter. Their surface is smooth or covered by very minute scattered granules. Arrangement of the aboral plates seems to fit no determinable pattern, and no sign of an apical system resembling that of echinoids and many starfishes can be discerned. The small plates probably overlapped one another when the animals were alive, but the extent of their overlap clearly has been increased by post-mortem flattening of the test found in all specimens studied. An anal pyramid, described below, occurs between two groups of tube feet on a certain part of the margin.

In *Volchovia* the aboral surface, evidently rigid, is composed of large plates (Fig. 135). A flat framework formed by ten pentagonal or subtrigonal plates surrounds a central dome, composed of 20 to approximately 30 plates in different species. The dome plates are arranged in an outer, submarginal circle and an inner central area. REGNÉLL (12) has shown that the placement of aboral plates indicates a degree of pentaradiate symmetry, and evidence previously noted (location of periproct and ?gonopore) permits determination of the *CD* interray. Inasmuch as the two marginal plates adjoining the supposed gonopore belong to this interray, it is reasonable to conclude that the eight

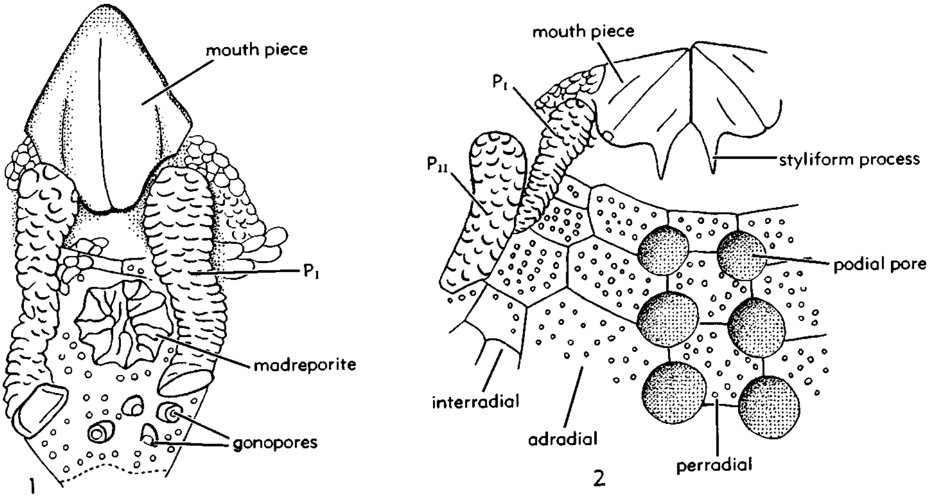


FIG. 136. *Eucladia johnsoni* WOODWARD, U.Sil.(L.Ludlov.), Eng.; *1,* part of *B* ray and *BC* interray, ×2 (4); *2,* part of *CD* interray, ×2.7 (4). [Explanation: PI, PII, 1st, 2nd pairs of podia.]

other marginal plates also are interradial, each interray having two such plates. Plates of the central region seemingly include (1) a "dorsocentral" located between the geometrical center of the test and the periproct, (2) a ring of five "radial" plates, which, in company with the first-mentioned element, form a kind of apical system, and (3) another circle of plates which in each ray contains a supplementary "radial" and in each interray one or more "interradials." The rays and interrays thus defined differ from one another, for plates of the *C* and *D* rays are smaller than those of other rays, which also are distinctly longer than the *C* and *D* rays. In *V. norvegica* the *D* ray contains only a single "radial," whereas in *V. mobilis* the *C* ray has three such plates. The "radials" and "interradials" are dissimilar in shape and size and the latter vary in number from one interray to another. These inequalities are distributed in such a way as to indicate a tendency toward acquisition of bilateral symmetry with respect to an anteroposterior axis (through *A* ray and *CD* interray).

ORAL SURFACE

The lower surface of the theca is known in *Eucladia, Sollasina,* and *Euthemon,* but unobserved in any specimen of *Volchovia,* doubtless owing to absence or very weak development of an oral skeleton in this genus.

The three genera in which the oral surface has been studied show that this part of the ophiocistioid theca consists of central peristome, described subsequently, and surrounding plates divisible into five radial or ambulacral tracts and five interradial or interambulacral tracts. The radial tracts are large, and as previously stated, contain a median column of perradial plates and two lateral columns of adradial plates (Fig. 134, *2,3*; 136,*1*). The interradial tracts are narrow, consisting of few plates disposed in single columns. The radial areas are pierced by double rows of simple circular orifices (ambulacral or tube-feet pores) with thickened borders, each pore being adjoined by two perradial and two adradial plates. In addition, an unpaired orifice occurs at the aboral extremity of each ambulacrum; it is adjoined by two plates, which in *Sollasina* are adradials but in other genera undetermined. In living ophiocistioids this orifice must have been located at the margin of the theca, but in fossils it is near the edge of the aboral side owing to compression which the specimens have undergone. From each orifice, including the unpaired terminal one of each ambulacrum, arises one of the tubular organs with scaly skeletal cover which is inferred to be a tube foot.

Around the peristome of *Sollasina,* and probably of *Euthemon* also, is a circle of 15 or 16 plates, of which five are perradial, ten adradial, and presumably one in addition with madreporite and gonopore. In *Eucladia* the 15 radial plates are accompanied by five interradial plates, making 20 in all. The radial tracts of *Eucladia* contain seven plates in each column, whereas in *Euthemon* these are reduced to three. *Sollasina* has three plates in each perradial column and four in each adradial column. Five or six plates occur in each interradial area of *Eucladia,* two in *Sollasina,* and a single one in *Euthemon.*

The pores of each ambulacral area are placed opposite one another or in slightly alternating position (e.g., *Eucladia,* Fig. 136,*2*). Those of the pair farthest from the peristome are closely adjoined, with only a thin calcareous partition between them, and accordingly, the perradial plate in this position has a cruciform outline.

TUBE FEET

The nature of relationships to the theca of appendages distributed along the ambulacral areas proves that these organs, in spite of their appearance and considerable size, are homologous with the ambulacral tube feet or podia of other echinoderms. Each is cylindrical, undivided, and hollow, and probably was flexible in the living animal. A skeletal cover consists of minute scalelike calcareous plates with imbricate arrangement, overlap being directed toward the distal extremity. Since the presence of such organs is unknown in *Volchovia,* its tube feet may have been naked or protected only by a very weak skeleton.

In *Eucladia,* the first pair of podial appendages, nearest to the mouth, are much smaller than others, with length of approximately 9 mm. and diameter of 2 mm. (Fig. 132; 136,*2*; 137,*3*). They are distinguished otherwise in being associated closely with the jaw plates and in forming part of the peristomial area; thus they have been termed buccal tentacles. Their imbricated cover of very minute plates extends to a distal flattened expansion that possibly denotes a sucker. These podia are comparable to the oral tube feet of stelleroids. Equivalent tube feet of *Sollasina* are too poorly preserved for description but their existence seems to be indicated by depressions corresponding to their insertions and by rows of tiny plates apparently belonging to them (Fig. 137,*1*). No trace of buccal tube feet is discernible in the single available specimen of *Euthemon.*

Other ambulacral tube feet are close together in slightly alternating position in *Eucladia* (Fig. 132), which has five pairs in each ray, though some rays show the presence of an additional single tube foot which may correspond to the unpaired tentacle of *Sollasina* noted subsequently. The diameter and length of the tube foot appendages increase toward the periphery of the theca, largest ones having a length of approximately 40 mm. and a diameter up to 6 mm. Their surface is completely covered by small shingled plates which overlap distally and are divisible into two groups. A set of larger, more salient cover plates ends distally in a conical point. Another set consists of much smaller, less salient plates which terminate in a gently rounded extremity. The distal end of these tube feet is not well preserved and therefore of an uncertain nature.

The tube feet of *Sollasina* other than those associated with the buccal apparatus number seven in each ray: three pairs in opposed positions and an unpaired terminal tentacle in perradial position at the extreme edge of the theca. The two proximal tube feet differ from others in their smaller size —length approximately 12 mm. and diameter 2 mm.—and in their extremely numerous, densely crowded, and strongly imbricated thin cover plates. Remaining tube feet and the unpaired tentacle resemble one another in consisting of tubes approximately 25 mm. in length and 3 mm. in diameter at the base. They end in points. Their skeleton consists of small imbricate plates arranged in more or less even longitudinal rows. Distally there are four rows: median aboral, median oral, and two lateral. Toward the base of the appendage the number of rows increases to six or more, with supplementary much smaller plates intercalated between them. All these plates have rhomboid outlines. The largest are patelliform, with an excentrically pointed distal apex. In the view of Nichols (11), pores probably existed between these plates, serving for passage to papillae like those of modern crinoids and ophiuroids.

In *Euthemon* only two pairs of tube feet are present in each ray (Fig. 133).

Those next to the mouth are smallest, with length not more than 5 mm., and they are covered with greatly crowded, very thin calcareous scales. The distal pair of tube feet in each ray attain a length of 12 or 13 mm. and diameter of 1.5 mm. or a little more. Their skeleton consists of four rows of plates, dorsal, ventral, two lateral, resembling in structure the arms of ophiuroids.

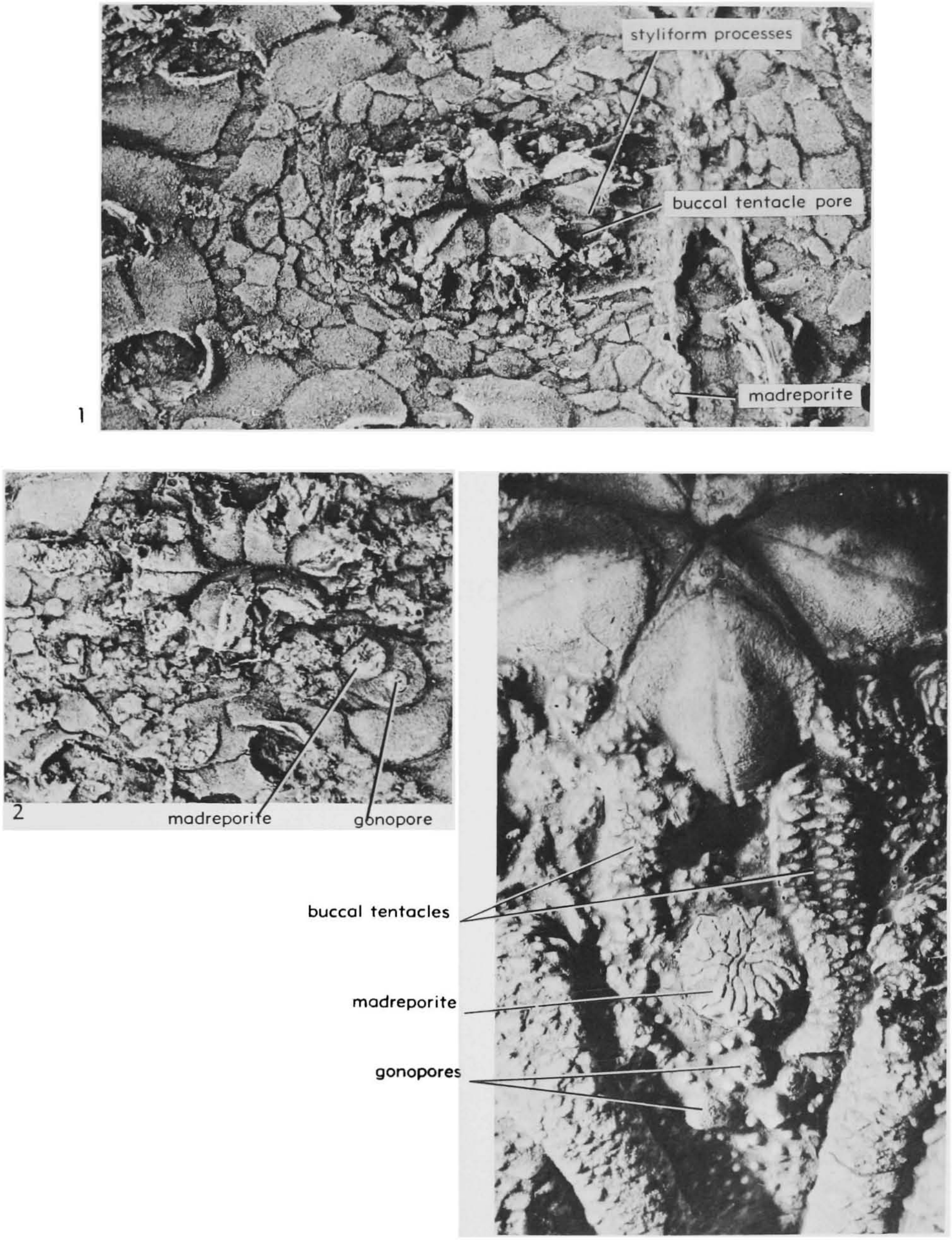


FIG. 137. *Sollasina* and *Eucladia,* U.Sil.(L.Ludlov.), Eng.; *1,2, S. woodwardi* (SOLLAS), features of oral side, ×5; *3, E. johnsoni* WOODWARD, part of oral side, ×5 (all Ubaghs, n).

Finally, the tube feet of *Rhenosquama*—assuming that this genus belongs with the ophiocistioids—are covered by imbricated plates which are all of similar nature. They are arranged in longitudinal and transverse rows, those of the latter alternating with one another in adjacent rows. Since four plates occur in each transverse row, their alternating placement produces eight longitudinal rows. The small arcuate plates have a small median point distally.

PERISTOME

The peristome occupies the center of the oral surface. It is circular or subcircular in outline as seen in *Eucladia* and *Euthemon* but is clearly elliptical in *Sollasina.* Its diameter equals 0.4 to 0.5 that of the test in *Eucladia* and *Euthemon,* respectively, and its longer axis in *Sollasina* is equal to, or slightly greater than, one-half that of the test.

A pentagonal rosette *(Eucladia, Euthemon)* or elliptical apparatus *(Sollasina)* at the center of the peristome is formed by five strong jaws, each of which is rhomboid in outline and located interradially (Fig. 132, 133, 136, 137). Each jaw consists of two pieces united along the interray axes. The adradial edge of each piece projects aborally in a styliform process, between which and the body of the jaw is a rather small podial pore. Whether the process is actually a separate ossicle is difficult to determine. The presence of the pore is firmly established in *Eucladia,* probable in *Sollasina* (Fig. 137,1), and possible but uncertain in *Euthemon.*

A flexible membrane extending from the buccal apparatus to borders of the peristome is very wide in *Sollasina* but much narrower in *Eucladia* and *Euthemon.* It is well preserved in the first-mentioned genus, where the membrane is reinforced by a pavement of many polygonal small plates arranged irregularly (Fig. 134,*2*; 137,*1*).

PERIPROCT

A periproct has been observed only in *Volchovia* and *Sollasina.*

In *Volchovia* (Fig. 135) the periproct consists of a cone composed of some 20 cuneiform plates surrounded by a circle of very small plates. It covers a rounded vent on the aboral surface located in the *CD* interray just behind the dorsocentral.

In *Sollasina* (Fig. 134,*1,3*) the periproct also is found on the aboral side but in marginal position close to one of the two extremities of the test. It is located in an interray doubtfully identified as *CD.* Narrow and elongate small plates form a pyramid, at the base of which irregularly polygonal small plates constitute a transition to other plates of the aboral surface.

MADREPORITE

One of the interrays of the oral surface bears a madreporite not far from the edge of the peristome, according to observations of *Eucladia* and *Sollasina.*

In *Eucladia* (Fig. 136,*2*, 137,*3*) it is found on the second plate of the *CD* interray, proceeding distally from the peristome. Edges of the madreporite, which has a diameter of 4 mm., are indented and its surface bears several irregularly forked grooves, reminiscent of the meandriform pattern of the madreporite in living asteroids.

The madreporite of *Sollasina* (Fig. 137,*2*) occurs on a special plate located between the peristome border and adjacent adradial plates of the *CD* interray. It consists of a small truncate cone, 1.2 mm. in diameter at the base, with a low, probably perforate summit.

GONOPORES

On the interradial plate which next follows that bearing the madreporite in *Eucladia* four prominent papillae with hollows filled by sediment may be observed (Fig. 136,*2*; 137,*3*). In *Sollasina* the cone interpreted as a madreporite is accompanied on the same plate by a large, seemingly perforated tubercle (Fig. 137,*2*). The papillae and tubercle probably represent genital pores. GEKKER (6, 7) has recorded the presence behind the periproct of *Volchovia* of a second orifice, located between the two posterior marginals (Fig. 135). This opening may be a gonopore, hydropore, or gonopore-hydropore (REGNÉLL, 12).

MODE OF LIFE

Ophiocistioids were free-moving echinoderms, as demonstrated by the absence of a stem or other means of fixation, by lack of ambulacral furrows, by the development of enormous tube feet, by the aboral location of the anus, and by the seemingly masticatory buccal apparatus. Almost certainly these animals rested and moved about on their oral surface. The extraordinary size of the ambulacral tube feet and their superficial resemblance, in *Euthemon* at least, to the arms of ophiuroids suggests that ophiocistioids belonged to the vagile benthos. This may not apply to *Volchovia,* however, for its form and weak development of an adoral skeleton denote a passive existence, possibly like that of patelloid gastropods or such ophiuroids as *Astrophiura,* which in resting position attach themselves by the ventral surface to hard surfaces so that the whole body acts as a cupping glass (REGNÉLL, 12).

The structural diversity of the podia even in a single individual evidently reflects differences of function. The buccal tentacles, smaller than others, possibly were sensory organs mainly, like the buccal podia of sea urchins used for exploring the sea bottom over which the animal crawls. Other tube feet may have served as locomotory organs, aiding also in grasping prey and in pushing it to the mouth. FEDOTOV (4) judged that the podia of *Euthemon* and *Sollasina* provided creeping movement like the arms of ophiuroids, whereas those of *Eucladia* behaved like the ambulacral tube feet of asteroids. That the podia were very mobile is indicated by the highly varied positions in which they are found in fossils. Perhaps the importance of their activities is related to dimensions of the madreporite (REGNÉLL, 12).

Finally, respiration of these animals may be explained very possibly by the presence of papillae which extended out between scales of the skeletal cover of their tube feet (NICHOLS, 11).

SYSTEMATIC POSITION

The body of ophiocistioids has often been compared, as by BATHER (1, 2), to the central disc of ophiuroids. In line with this concept, developed by FEDOTOV (4, 5), the perradial and adradial plates of ophiocistioids are judged respectively homologous to orals and laterals in the ophiuroid arm, and interradial plates would correspond to the skeletal pavement of interbrachial areas in ophiuroids. Since the ophiocistioids lacked arms, however, comparison can be made only with proximal segments of the rays incorporated in the disc of ophiuroids.

These resemblances are balanced by countervailing differences. Whereas interradial areas are narrow and radial areas wide in ophiocistioids, the opposite is true of ophiuroids. The ambulacral pores of ophiocistioids are not found on a level with plates postulated as corresponding to the ventrals and laterals of ophiuroids, but instead, each occurs at the junction of two perradial and two adradial plates. Moreover, the perradials of ophiocistioids cannot be homologous with oral plates of ophiuroid arms, since the latter certainly are a secondary development produced late in the history of the group—consequently, without possible genetic relationship to ophiocistioid perradials. Such resemblance as appears between the disc of ophiuroids and the body of ophiocistioids therefore seems to be of superficial nature, pertaining to some aspects only, and even this disappears when comparison is extended to the archaic ophiuroids, which ought to be most similar to ophiocistioids if truly they were derived from ophiuroids.

REGNÉLL (12) is the one who has shown that the disposition of plates on the aboral surface of *Volchovia* offers analogies with the apical skeletal organization of very young ophiuroids and of some adult ophiuroids, such as *Astrophiura.* In each of these the apical system is predominantly composed of radial elements. However, in addition to question as to placement of *Volchovia* as an ophiocistioid (NICHOLS, 11), the nature of the apical system in this genus can hardly denote more than topographic similarities to the system of ophiuroids, since similar morphogenetic potentialities in this part of the body tend to be manifested in almost all echinoderm groups.

Furthermore, various other characters serve to distinguish the ophiocistioids from ophiuroids and from stelleroids generally. Among these are (1) entire absence of arms in ophiocistioids and of any structure allowing supposition that growth of the body at any stage was dominated by five divergent radial axes; (2) the presence in ophiocistioids of a well-developed aboral anus protected by a pyramid of small plates, which probably is a fundamental character of the group strikingly in contrast to the absence of such an orifice in ophiuroids, archaic asteroids, and somasteroids; (3) nature of the ophiocistioid buccal apparatus, which is very unlike that of stelleroids and differs from these in lacking any feature suggestive of its derivation by a transformation of primary ossicles belonging to the rays; and (4) the probable presence in ophiocistioids of an unpaired interradial gonad, a character that allies them with archaic pelmatozoans or holothuroids much more than with stelleroids.

If the ophiocistioids thus differ in numerous ways from asterozoans, resembling them only superficially, various characters typical of echinoids are not to be overlooked. Both assemblages possess a cap- or dome-shaped test formed of plates that enclose the entire body, except for the peristomial region, and this test, lacking arms, is divided on the oral side at least into five ambulacral areas and five intervening interambulacral areas. The buccal apparatus of ophiocistioids is closely analogous to that of echinoids in its seemingly different origin from the ray skeleton, its association with a peristomial membrane inlaid by small plates, and its structure and probable function as a masticatory mechanism. The presence of a well-developed periproct and its resemblance to the anal pyramid of archaic urchins such as *Aulechinus* and *Ectinechinus* is also an echinoid character, for the existence of a periproct on the test is one of the fundamental features of these echinoderms that dates from their origin. Interradial areas consisting of a single column of plates in each tract are restricted to the echinoid *Bothriocidaris*. Finally, if it is true that only a single gonad existed in ophiocistioids, this character perhaps is matched in certain archaic echinoids which possessed only one genital plate.

Evidently, such similarities do not imply direct parentage bonds, for they could have been acquired independently. As a matter of fact, other morphological aspects indicate that the ophiocistioids are far removed from echinoids. Especially important among these is division into ambulacral and interambulacral areas only on the lower side of the body, structure of the ophiocistioid ambulacrum, the gigantic size and distinctive construction of the ambulacral tube feet, the eccentric and even marginal location of the periproct, the oral placement of the madreporite and gonopores, the nature of the madreporite in closely resembling that of asteroids, the absence of any apical system, at least in most typical forms —all these characters suffice to show that ophiocistioids cannot be closely allied to echinoids.

The presence of certain features suggestive of archaic pelmatozoans also characterizes the morphology of ophiocistioids. Such features include structure and position of the anal pyramid, close association of the mouth with the madreporite and genital pores, and the probable existence of a single gonad.

Finally, Fedotov (4, 5) has emphasized general resemblances of the ophiocistioids to very young stelleroids and echinoids, in which the discoid body exhibits equally well-developed oral and aboral faces and bears some relatively very large podia. Ultimately, the stelleroids develop arms and acquire the star-shaped outline that characterizes them. Among echinoids, the oral part of the body undergoes enormous expansion, as result of which the aboral part becomes reduced to a very restricted area at the summit of the test. The interbrachial areas of ophiuroids expand mostly in adoral directions so as to modify profoundly the oral side of the disc. The ophiocistioids appear to have become fixed in their evolution at the stage when the disc, devoid of arms but provided with podia of considerable size in relation to the body, had developed subequal oral and aboral sides. Their unpaired gonad corresponds to the primary gonad of stelleroids and echinoids, which developed subsequently into five pairs of distinctive genital organs. Interpretable as a juvenile character are the large dimensions of the terminal tentacle, which are somewhat comparable to the primary podia of echinoderm larvae. The remarkable resemblance of ophiocistioids to some Recent echinoderms shortly after metamorphosis is perhaps the most typical feature of their organization.

In conclusion, it is obvious that ophiocistioids cannot be assigned to any class of living echinoderms. They comprise an extinct, entirely separate class of unknown origin, but on the whole seeming to offer greater similarities to echinoids than to stelleroids.

SYSTEMATIC DESCRIPTIONS

Class OPHIOCISTIOIDEA Sollas, 1899

[*nom. correct.* UBAGHS, 1953 (*pro* class Ophiocistia SOLLAS & SOLLAS, 1912, *nom. transl. ex* order Ophiocistia SOLLAS, 1899)] [=class Ophiocista MATSUMOTO, 1929 (*nom. null.*); Ophiocistioïdes LAMEERE, 1931 (*nom. neg.*); class Ophiocystia MOORE, LALICKER & FISCHER, 1952 (*nom. null.*)]

Unattached pentaradiate echinoderms with more or less depressed dome-shaped body entirely covered by plated test or with cover of plates on one side only, lacking arms or comparable projections; center of oral face occupied by peristome with buccal apparatus consisting of 5 interradially disposed jaws, each consisting of 2 pieces; remainder of oral surface divided into 5 large ambulacral tracts composed of 3 plate columns (1 perradial, 2 adradial) and 5 narrow interradial tracts composed of a single plate column; ambulacra confined to oral face; ambulacral pores simple, each located at junction of 2 perradial and 2 adradial plates; podia of relatively enormous size, covered by imbricated plates; periproct aboral, eccentric or marginal; madreporite and gonopores in same interray, typically on oral face. *L.Ord.-U.Sil., ?M.Dev.*

Family EUCLADIIDAE Gregory, 1896

[=Eucladidae SOLLAS, 1899 (*nom. null.*)]

Test subpentalobate; peristome rather restricted, surrounded by ring of 20 plates (5 perradial, 10 adradial, 5 interradial); ambulacra with at least 7 plates in perradial or adradial columns and 6 pairs of slightly alternating podia, plus unpaired terminal tentacle, most proximal pair of podia reduced in size and placed in peristomial area, others increasingly large toward periphery of test; interambulacra with 5 or 6 plates in single column; strong buccal apparatus occupying nearly entire peristome; madreporite well developed, with branched grooves, located in adoral interray that also contains several gonopores. *U.Sil.*

Eucladia WOODWARD, 1869 [**E. johnsoni*; OD]. Characters of family. *U.Sil.(L.Ludlov.),* Eu.(Eng.).——FIG. 132; 136; 137,*3*. **E. johnsoni*; 132, part of oral surface, ×1.3 (Ubaghs, n); 136,*1*, part of *B* ray and *BC* interray, ×2 (4); 136,*2*, part of *CD* interray, ×2.7 (4); 137,*3*, part of oral side, ×5 (Ubaghs, n).

Family SOLLASINIDAE Fedotov, 1926

Well-developed peristome surrounded by ring of 15 (or 16) plates comprising 5 perradials, 10 adradials, and possibly additional plate bearing madreporite and gonopore; podia located opposite one another, ending in point and covered by small plates arranged typically in longitudinal rows, podia next to buccal tentacles (if present) unlike all others. *U.Sil.*

Sollasina FEDOTOV, 1926 [**Eucladia woodwardi* SOLLAS, 1899; OD]. Test elliptical in outline; aboral surface covered by irregular plates; oral surface with 3 perradials and 2 rows of 4 adradials in each ambulacrum, which bears pair of ?buccal podia, 3 other pairs, and terminal tentacle identical with adjacent podia; each interambulacral tract with 2 interradials; elliptical peristome with relatively small oval buccal apparatus surrounded by membrane reinforced by minute irregular plates; periproct with anal pyramid dorsomarginal; madreporite and gonopore on single plate in interray at border of peristome. *U.Sil. (L.Ludlov.),* Eu.(Eng.).——FIG. 134; 137,*1,2*; 138. **S. woodwardi* (SOLLAS); 134,*1,2,* aboral and oral sides, ×2 (Ubaghs, n); 134,*3*, periproct, ×5 (Ubaghs, n); 137,*1,2*, buccal apparatus, peristome, madreporite, and gonopores, ×5 (Ubaghs, n); 138, ambulacral tube feet, ×5, ×10 (Ubaghs, n).

Euthemon SOLLAS, 1899 [**E. igerna*; OD]. Test rounded, each ambulacrum with 3 perradials and

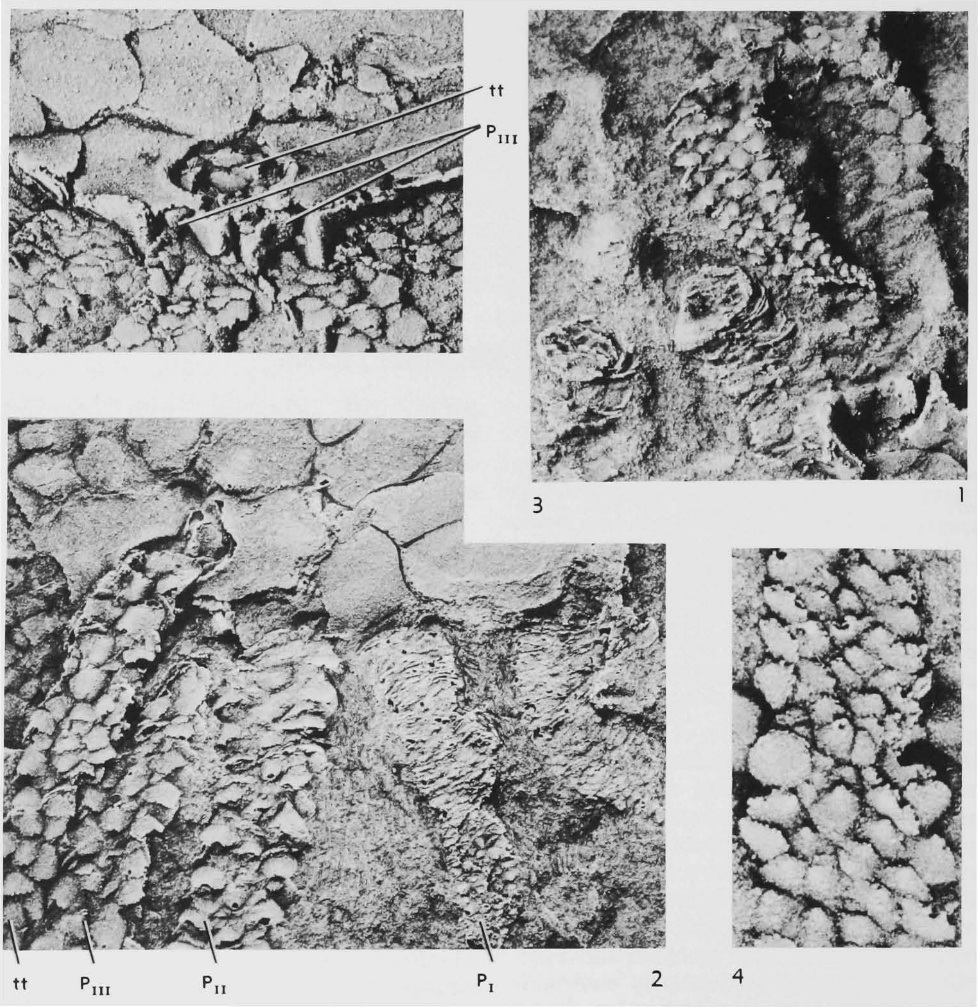


FIG. 138. *Sollasina woodwardi* (SOLLAS), U.Sil.(L.Ludlov.), Eng., ambulacral podia and pores; *1,* unpaired pore for terminal tentacle and paired pores for 3rd podial pair, ×5; *2,* part of surface showing terminal and associated paired podia, ×5; *3,* first pair of podia (at left) and one of following pair, ×5; *4,* part of podium, ×10 (all Ubaghs, n). [Explanation: P_I, P_{II}, P_{III}, 1st, 2nd, 3rd pairs of podia; *tt,* terminal tentacle.]

?3 adradials adjoined by 2 pairs of podia, small near peristome, other pair very large; interambulacral areas containing single interradial; buccal apparatus large, strong. *U.Sil.(Wenlock.),* Eu.(Eng.).——FIG. 133. **E. igerna*; oral side, ×3.5 (4).

Family VOLCHOVIIDAE Gekker, 1938

Body oval dome-shaped; aboral face of test showing 10 subpentagonal or subtriangular marginals which form flattened border with indentations on outer side, central area composed of 20 to 30 plates well uparched medially; anal pyramid excentrically placed in *CD* interray with single pore interpreted as gonopore, hydropore, or gonopore-hydropore in same interray nearer margin; oral surface and podia unknown. *L.Ord.-U.Ord.*

Volchovia GEKKER, 1938 [**V. mobilis*; SD GEKKER, 1940]. Characters of family. [Genus differs from others referred to class much more than these differ from one another; therefore its assignment to the ophiocistioids is not entirely firm.] *L.Ord.-U. Ord.,* Eu. (USSR-Norway)-N. Am. (Ohio).——FIG. 135,*1-3*. **V. mobilis,* L.Ord., USSR; *1,* aboral view; *2,* plate diagram; *3,* oblique post. view (reconstr.); all ×1 (7).——FIG. 135,*4*. *V. norvegica* REGNÉLL, L.Ord., Norway; post. view from slightly left of *CD* interray, ×1 (12).

?Family RHENOSQUAMIDAE R. Richter, 1930

Organs doubtfully identified as ophiocistioid podia terminating distally in point, covered by mutually similar scales arranged in transverse rows of alternately placed plates so as to produce 8 longitudinal rows. *M.Dev.*

The inclusion of this taxon and its single presently known genus among the ophiocistioids is reasonable but decidedly open to question.

Rhenosquama R. RICHTER, 1930 [**R. westfalica*; OD, M]. Characters of family. *M.Dev.(Couvin.)*, Eu.(Ger.).——FIG. 139,*1*. **R. westfalica,* Eifel; impressions of ?podia, ×3 (13).

FIG. 139. *Rhenosquama westfalica* R. RICHTER, M. Dev., Ger.; impressions of ?podia, ×3 (13).

REFERENCES

Bather, F. A.

(1) 1907, *A guide to the fossil invertebrate animals in the department of geology and paleontology in the British Museum (Natural History):* 182 p., 7 pl., 96 text-fig. (London).

(2) 1910, *Echinoderma,* in Encyclopaedia Britannica: Edit. 11, v. 8, p. 871-882, Univ. Press (Cambridge, Eng.).

Cuénot, Lucien

(3) 1948, *Ophiocistia:* in Traité de Zoologie (P.-P. Grassé, ed.), v. 11, p. 270-272, text-fig. 310-312, Masson (Paris).

Fedotov, D. M.

(4) 1926, *The plan of structure and systematic status of the Ophiocistia (Echinoderma):* Zool. Soc. London, Proc., p. 1147-1157, pl. 1-2.

(5) 1928, *Ueber die Beziehungen der Echinodermenklassen zueinander:* Zool. Lab. Sevastopolsk. Biol. Sta., Akad. Nauk SSSR, Travaux, ser. 2, v. 12, p. 31-94.

Gekker [Hecker], R. F.

(6) 1938, *A new member of the class Ophiocistia Sollas (Volchovia n.g.) from the Ordovician of Leningrad province and changes in the diagnosis of this class:* Acad. Sci. URSS, Compte Rendus (Doklady), new ser., v. 19, p. 425-427, 1 text-fig.

(7) 1940, *Carpoidea, Eocrinoidea und Ophiocistia des Ordoviziums des Leningrader Gebietes und Estlands:* Acad. Sci. URSS, Inst. Paléont., Travaux, v. 9, p. 5-82, pl. 1-10.

Gregory, J. W.

(8) 1897, *On the classification of the Palaeozoic echinoderms of the group Ophiuroidea:* Zool. Soc. London, Proc. (1896), p. 1028-1044.

Lameere, Aug.

(9) 1931, *Précis de zoologie:* v. 2, 456 p., Univ. Inst. Geol. Torley Rousseau (Bruxelles).

Matsumoto, Hikoshichirô

(10) 1929, *Outline of a classification of Echinodermata:* Tohoku Univ., Sci. Rept., ser. 2 (Geol.), v. 13, no. 2, p. 27-33.

Nichols, David

(11) 1962, *Echinoderms:* 200 p., 26 text-fig., Hutchinson Univ. Library (London).

Regnéll, Gerhard

(12) 1948, *Echinoderms (Hydrophoridea, Ophiocistia) from the Ordovician (Upper Skiddavian, 3Cβ of the Oslo Region:* Norsk Geol. Tidsskrift, v. 27, p. 14-58, pl. 1-2.

Richter, Rudolf

(13) 1930, *Schuppenröhren als Anzeiger von zwei im deutschen Devon neuen Echinodermen-Gruppen (Edrioasteroidea Billings und Ophiocistia Sollas?):* Senckenbergiana, v. 12, p. 279-304.

Schuchert, Charles

(14) 1915, *Revision of Paleozoic Stelleroidea with special reference to North American Asteroidea:* U.S. Natl. Museum, Bull. 88, 311 p., 38 pl., 41 text-fig.

Sollas, W. J.

(15) 1899, *Fossils in the University Museum, Oxford: I. On Silurian Echinoidea and Ophiuroidea:* Geol. Soc. London, Quart. Jour., v. 55, p. 692-715, text-fig.

———, & Sollas, I. B. J.

(16) 1912, *Lapworthura: a typical brittle-star of the Silurian age:* Royal Soc. London, Philos. Trans., ser. B, v. 202, p. 213-232, pl. 9-10. text-fig. 1-5.

Ubaghs, Georges

(17) 1953, *Classe des ophiocistioïdes (Ophiocistioidea):* in Traité de Paléontologie, Piveteau, Jean (Ed.), v. 3, p. 843-856, text-fig. 1-7, Masson & Cie (Paris).

Woodward, Henry

(18) 1869, *On Eucladia, a new genus of Ophiuridae, from the Upper Silurian, Dudley:* Geol. Mag., dec. 1, v. 6, p. 241-245, pl. 8.

CYCLOCYSTOIDS

By Robert V. Kesling

[Paleontological Museum, University of Michigan]

CONTENTS

INTRODUCTION

The cyclocystoids are an enigmatic group of Paleozoic fossils, most of which are known primarily from the well-preserved ring of submarginal plates. They are small disc-shaped objects, apparently without columns and attached by the flat aboral side. Central covering layers, called discs, of both oral and aboral sides, seem to have been weakly calcified. Food-gathering structures are also inadequately represented. Nevertheless, the Cyclocystoidea are extinct echinoderms, which authors generally have classed as Pelmatozoa, considered by some to be related more closely to Cystoidea than to other classes. In the *Treatise,* however, they are transferred to the subphylum Echinozoa.

Although Cyclocystoidea range from Middle Ordovician to Middle Devonian, relatively few specimens are known. This scanty record may be due in part to their small size and poor preservation, but mostly it may be attributed to lack of interest in fossils so imperfectly understood and to consequent perfunctory collecting.

Classification is deficient for two reasons. First, paucity of the record does not reveal much of the diversity that probably existed in the taxon. Second, essential systems of the animal cannot be discerned in sufficient detail to permit clear recognition of differences. Only one genus, *Cyclocystoides,* is accepted by all workers on the group. And this is perhaps a matter of nomenclatorial necessity, rather than taxonomic conviction.

Certain characteristics of cyclocystoids invite comparison with other ancient echinoderms. The discoid shape and the marginal ring of tiny plates forming a "shagreen," imbricating and partly embedded in a flexible integument, are remarkably like those in edrioasteroids. The facets lying within the submarginal ring, small tubercles with surrounding grooves, resemble the brachiole facets of cystoids. The sharp differentiation of oral and aboral surfaces and the ramification of the ambulacral system are more nearly like those in crinoids.

Differences, however, set the cyclocystoids apart as a class discrete from any of these groups. Multiple branching of the ambulacral system is unknown in edrioasteroids; the flattened shape is foreign to cystoids; and the flat aboral (dorsal) surface is unlike that in crinoids. Other points of dissimilarity could be mentioned. Despite our ignorance of parts of their morphology, we can clearly separate cyclocystoids from other echinoderms.

PREVIOUS STUDIES

Contributions to the knowledge of cyclocystoids are few. They are marked by tentative interpretations and confessions of doubt. The first published account of which I know was made by JAMES HALL in FOSTER & WHITNEY's *Report of the Geology of the Lake Superior Land District* (1851). HALL briefly described a specimen from the Escanaba region of Michigan and concluded, "This curious body is evidently Crinoidean. . . . It is possible that it may be the elevated marginal ring of some one of the sessile Crinoids. . . ." In 1858, J. W. SALTER & ELKANAH BILLINGS named *Cyclocystoides* and presented a remarkably good analysis of its organization. They distinguished the "integument of the upper side" from the "integument of the under side," and accurately described the ring of submarginal plates (which they called "marginal plates") as bearing a channel with "marginal excavations" and "connected with the interior by small pores penetrating through the marginal plates." Incorrectly, I believe, they regarded a dissociated tubelike fossil as a part of *Cyclocystoides,* but on the whole their account is more lucid than several which appeared more than half a century later. SALTER & BILLINGS thought that "regarding the affinities of the fossils, the choice seems to be between Star-fishes and Cystideae"; they also compared *Cyclocystoides* with *Amygdalocystites,* now regarded as a paracrinoid.

HALL (8) figured an oral disc with an eccentric oval opening, which he interpreted as the mouth. In a modified version of this figure, F. A. BATHER (1) called this opening the "supposed region of anus." Although incontestable evidence on the location and nature of the anal opening has not yet been offered, I am inclined to agree with BATHER.

S. A. MILLER & C. B. DYER (12) confirmed the presence of ducts or pores through plates of the submarginal ring. In 1882, MILLER created the family Cyclocystoididae, without pertinent distinctions from other families. In 1895, MILLER & W. F. E. GURLEY erected the order Cyclocystoidea, more or less as a convenience in directing attention to the singular features of *Cyclocystoides.* BATHER (1) discussed the genus in his chapter on Edrioasteroidea, stating that it "probably belongs to this class, though not to any of the recognized families." This concept of diverse forms in the edrioasteroids reflects BATHER's conviction that the "Edrioasteroidea are alone among Pelmatozoa in presenting a type of ambulacrum from which the holothurian, stellerid, and echinoid types may readily be derived."

P. E. RAYMOND (14) believed that he could discern small plates covering the facet-bearing channel, or circular canal, in the distal part of the submarginal plates, redescribing and refiguring one of SALTER & BILLINGS' specimens. He paid special attention to the oral disc, and distinguished five main ridges that by successive bifurcations lead to the submarginal ring. Regarding the ambulacral system, he wrote, "These ridges probably cover ducts which lead from the [submarginal] plate to the centre, and the inference might be that through them, food, in water, was carried from the series of collecting basins in the outer circular canal to the mouth, which would be central and beneath the plates of the disk." Concerning the affinities of *Cyclocystoides,* RAYMOND's contribution was less significant. He thought the animal might be a "free Cystidean or Edrioasteroid," "highly specialized root of a free crinoid," or "it is even possible, if one is sufficiently imaginative, to think of this disk as a swimming organ, the method of propulsion being on the same principle as in some of the cephalopods."

In his comprehensive review and revision of the Pelmatozoa, OTTO JAEKEL (9) ignored *Cyclocystoides.*

A. F. FOERSTE (5) assigned the Cyclocystoididae to the Edrioasteroidea, and distinguished two new genera, *Narrawayella* and *Savagella,* and an unnamed genus exemplified by *Cyclocystoides illinoisensis* MILLER & GURLEY, in addition to the type genus. As discussed later, FOERSTE'S new genera have not been awarded general acceptance.

FOERSTE (6) also gave particular attention to *Cyclocystoides huronensis* BILLINGS, in which he described "spout-like appendages" at the border of the submarginal and marginal rings, equal in number to the facets in the channel of the submarginal ring. He described an unnamed species from Tennessee as having marginal plates sloping outward, and went on to say, "This outward sloping of the marginal plates is so frequent in *Cyclocystoides* as to suggest that these plates could be moved at will, either so as to slope inward, thus covering the outer margin of the submarginal ring of plates, or so as to slope outward, exposing the margin." On the basis of this account, FOERSTE has been credited with support of SALTER & BILLINGS' (17) and RAYMOND'S (14) contention of plates covering the circular channel in which the facets are located. No author has elaborated on these plates, and no convincing figures have been given to support this very important consideration. Inadvertently, FOERSTE seems to have mistaken the collapsed oral disc for the ventral side of the aboral disc in his figure of *C. huronensis* (6, pl. 6, fig. 3). Ten years later, this figure was copied by BEGG (2, pl. 9, fig. 7), who relied heavily on it for certain aspects of orientation; as a result, parts of BEGG'S descriptions are rather confused.

In 1926, E. MALLIEUX reported the occurrence of cyclocystoids in the Devonian of the Ardennes in Belgium, thus greatly extending the known geologic range.

BEGG (2) compared *Cyclocystoides* with the carpoid *Cothurnocystis,* referring to the oral disc as the "lower plate" and the aboral disc as the "upper plate" but describing the submarginal ring as "beyond the spoon-shaped depressions [facets], and sloping downward and outward." At least part of the oral-aboral confusion was undoubtedly occasioned by the preservation of many of his specimens as external molds; yet some of SALTER & BILLINGS' original specimens were similarly preserved, and I am unable to follow some of BEGG'S comparisons.

HERTHA SIEVERTS (later SIEVERTS-DORECK) in the same and the following years reviewed BEGG'S article. She further proposed that the facets were places for attachment of brachioles.

GERHARD REGNÉLL (15) reviewed assignments of *Cyclocystoides* and described two species from Gotland in considerable detail. Concerning facets, he stated, "The mamillary elevations cannot have been facets of brachioles, as supported by SIEVERTS 1934, nor is there anything to indicate that they are bases of spines. Both theories are made impossible by the fact that the canal, in which they are located, was evidently roofed over by small movable plates." Recently, REGNÉLL (16) seems to have changed his mind, for he wrote, "In the opinion of the present writer, *Cyclocystoides* differs so radically from the edrioasteroids that an attribution to that class is definitely not advisable. . . . The theca of the edrioasteroids is not differentiated into a dorsal and a ventral disk; the ambulacral coverplates are invariably biserial; the ambulacral system is never tetraradiate; brachioles do not occur in edrioasteroids." The implication is clear that *Cyclocystoides* does possess brachioles.

REGNÉLL (1948) presented a table of occurrences of known species of *Cyclocystoides* both geographically and geologically. He emphasized the North American origin, the early migration to Britain, the Silurian spread to Gotland, and the final appearance in the Devonian of Belgium.

SIEVERTS-DORECK (20) gave an excellent summary of previously described specimens and analysis of morphology, revising ordinal, familial, and generic diagnoses, and describing a new Devonian species in minute detail. Unquestionably, her work is the best founded, most penetrating, and concise of all that have appeared.

To date, many morphological features which one would expect in these fossils have not been substantiated. The peristome and periproct are known only from poorly preserved, inconclusive evidence. The hydropore is not represented by any preserved structures in the circumoral region, where logically it would be expected. Nothing of the gonopore has been found, nor has any suggestion of its nature been made. It would be very helpful to know if the channel in the submarginal plates is roofed by movable plates, as suggested by RAYMOND (14), or bears brachioles, as suggested by SIEVERTS-DORECK (20).

MORPHOLOGY

GENERAL ORGANIZATION

The cyclocystoid bears at least superficial resemblances to the edrioasteroid. Both of these echinoderms, now referred to the Echinozoa, are disc-shaped and both acquire rigidity from peripheral rather than central elements.

The cyclocystoid theca was somewhat like a thin, inflated drum. The **submarginal ring** of stout plates formed relatively rigid sides, the **oral disc** arched across one side (Fig. 140) and the **aboral disc** extended across the opposite side (Fig. 141) like a drumhead. Although the two discs are collapsed in the fossil state and lie in close proximity, presumably space between them accommodated soft organs of the living animal. The oral disc appears to have had greater flexibility or elasticity than the aboral disc, at least in some species. Possibly, it took on the shape of a blister, expanding in response to internal pressure (Fig. 142).

The submarginal ring is made up of numerous thick, complex plates, which have surfaces exposed on both oral and aboral sides of the theca (Fig. 140-142). Aborally, the submarginal plates appear as truncated wedges; orally, in many species they have distal beveled or concave surfaces that together constitute a circular **channel.** In the channel, each plate bears one of three **facets,** presumably for attachment of brachioles. In forms having a well-developed channel, the proximal part of the submarginal plate is elevated, overhanging, and flat-topped. Grooves lead from the facets to ducts or pores penetrating the proximal part of the plate, and these in turn connect wih enclosed passageways just under the surface of the oral disc. These structures—facets, grooves, ducts, and passageways—are considered to be elements of the ambulacral system. The passageways proximally unite as they approach the center of the oral disc, and are properly regarded as **ambulacral grooves.**

Surrounding the submarginal ring and forming the border of the cyclocystoid is the **marginal ring,** a band of small imbricating platelets that were probably embedded in flexible integument (Fig. 140, 141).

Orientation of the cyclocystoid is only inferred. Most paleontologists believe that the oral disc, which contains the hidden ambulacral grooves leading to the mouth, was uppermost, and that the more rigid, flat, aboral disc, which possesses no essential openings, was lowermost in the living animal. Thus, brachioles (or whatever other kind of food-gathering structures were present at the ends of the ambulacral conduits) were on the upper side. The cyclocystoid probably remained attached to the sea bottom in limpet fashion, creating suction under its aboral disc by muscular contraction of the marginal ring. Other aspects of orientation and application of Carpenter letters to the rays have been presented by MOORE & FELL (p. *U*119).

ORAL DISC

The oral disc has two significant characteristics—it contains a complicated ambulacral system and it undoubtedly possessed great elasticity. This is an unusual combination in pelmatozoans but not unexpected in echinozoans. The edrioasteroids, in which some degree of flexibility is indicated by the imbrication of interambulacral plates in many species, seem also to have had limited expansion of the flooring and covering plates of the ambulacra.

On the oral surface, which is the one commonly exposed in a well-preserved

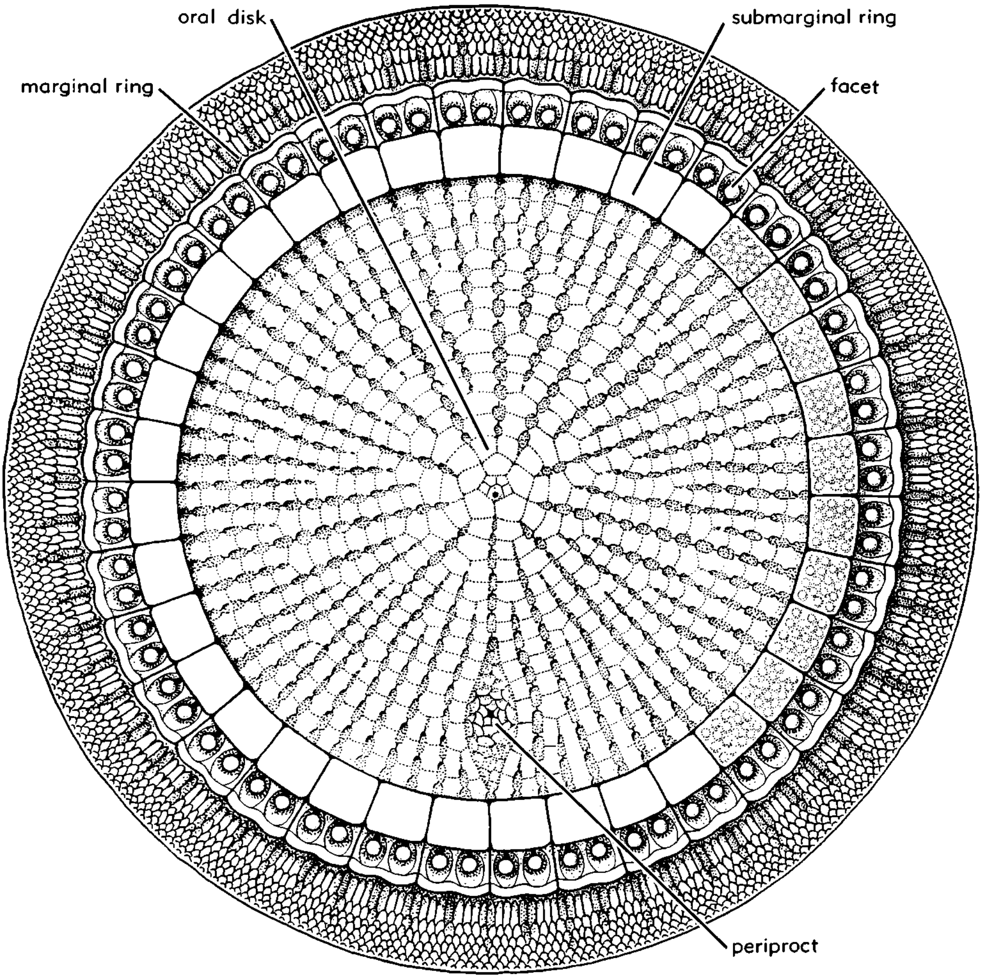


FIG. 140. Hypothetical reconstruction of oral side of *Cyclocystoides halli* BILLINGS, ×4.5 (Kesling, n).

specimen, the dominant feature of the disc is a set of low ridges which bifurcate successively from the center and radiate to the surrounding submarginal ring. This system of branching was well described by RAYMOND (14), "Upon analysis, it is seen that there are one or two ridges in front of each of the submarginal plates, and that each two adjacent ridges quickly unite to form a single ridge. Two of the ridges thus formed unite a little nearer the centre and are joined quite close to the centre by another long ridge formed from four shorter ones." SIEVERTS-DORECK (20) was particularly concerned as to whether the branching was isotomous or heterotomous; unfortunately, so few specimens show the complete pattern that the branching cannot be determined for all species or its taxonomic value tested.

Some details of the plates are not clear, for they are thin and their edges are not sharply delineated, as emphasized by SIEVERTS-DORECK (20). This condition of the plates is much like that in Recent holothurians, and supports the hypothesis that the plates of the oral disc may have been embedded within an integument. At any rate, a sharp difference distinguishes plates of the oral disc and those of the submarginal ring. In his description of *Cyclocystoides halli,* BILLINGS (in SALTER & BILLINGS,

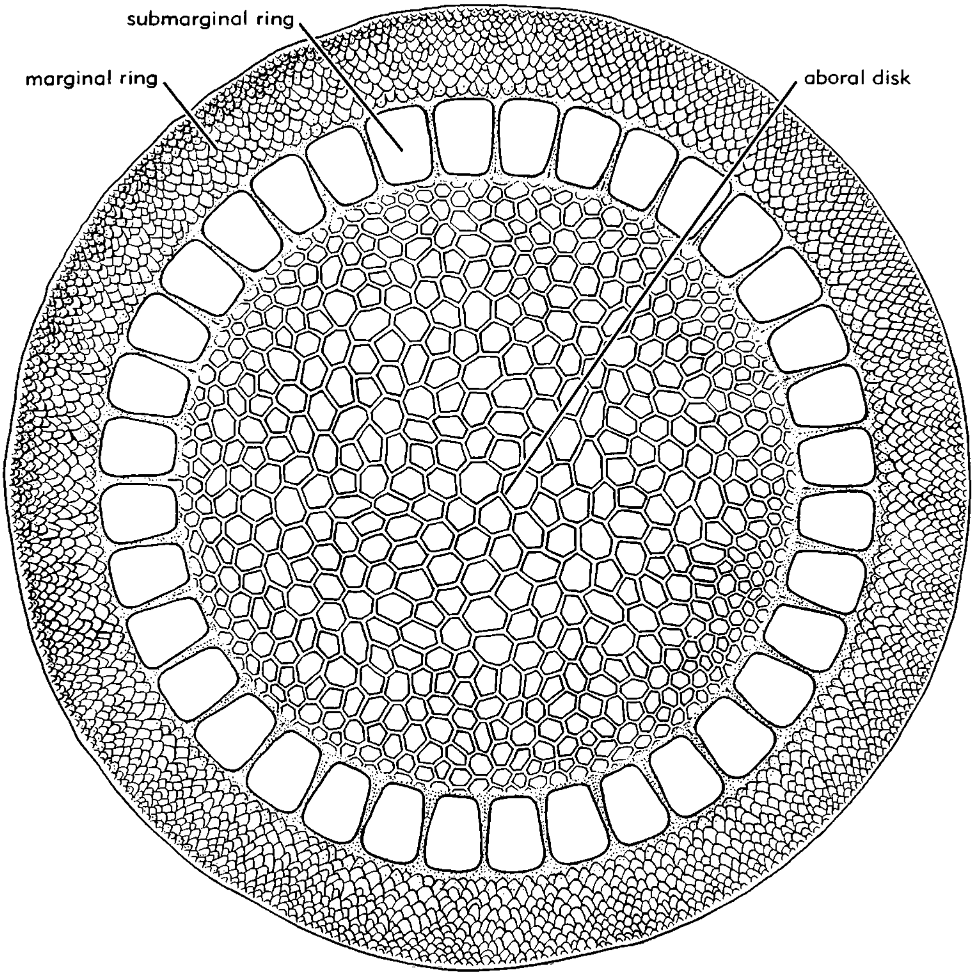


FIG. 141. Hypothetical reconstruction of aboral side of *Cyclocystoides halli* BILLINGS, ×4.5 (Kesling, n).

17) early established that "the integument of the upper side, supposed to be the side on which the marginal plates are excavated, is connected to the inner edge of those plates [submarginal ring] and does not extend over them." This relationship of oral disc and submarginal ring has been confirmed in other species. REGNÉLL (15) reported that in *C. lindstroemi* "the inner margin of the ossicles [submarginal plates] overlap slightly the adjacent rays of the central disk."

The number of ridges at the periphery of the oral disc was at first thought to equal the number of submarginal plates. With respect to *Cyclocystoides davisii,* SALTER (in SALTER & BILLINGS, 17) said, "This species shows the complete surface, on which about as many radiations mark the margin as there are ossicles." In *C. decussatus,* BEGG (2) stated, "The submarginal area is composed of thirty-two plates or ossicles, corresponding to an equal number of rays on the central disc." It seems plausible, however, to assume that all species were constructed similar to *C. devonicus.* In that species, as described by SIEVERTS-DORECK (20) each facet is aligned with a duct through the proximal, elevated part of the submarginal plate and each duct leads to an ambulacral groove. Thus, the peripheral number of ridges equals the number of facets, rather than the number of submarginal plates.

As SIEVERTS-DORECK (20) has pointed out, the plates composing the ridges are

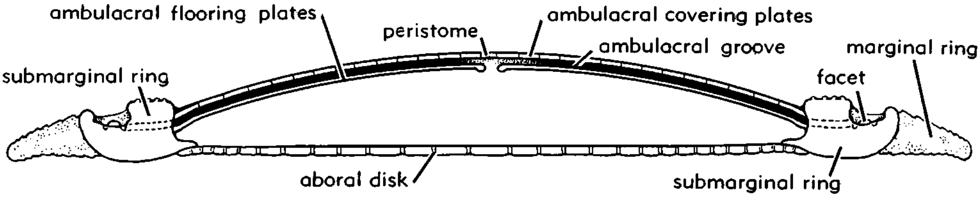


FIG. 142. Hypothetical cross section of *Cyclocystoides halli* BILLINGS, ×4.5 (Kesling, n).

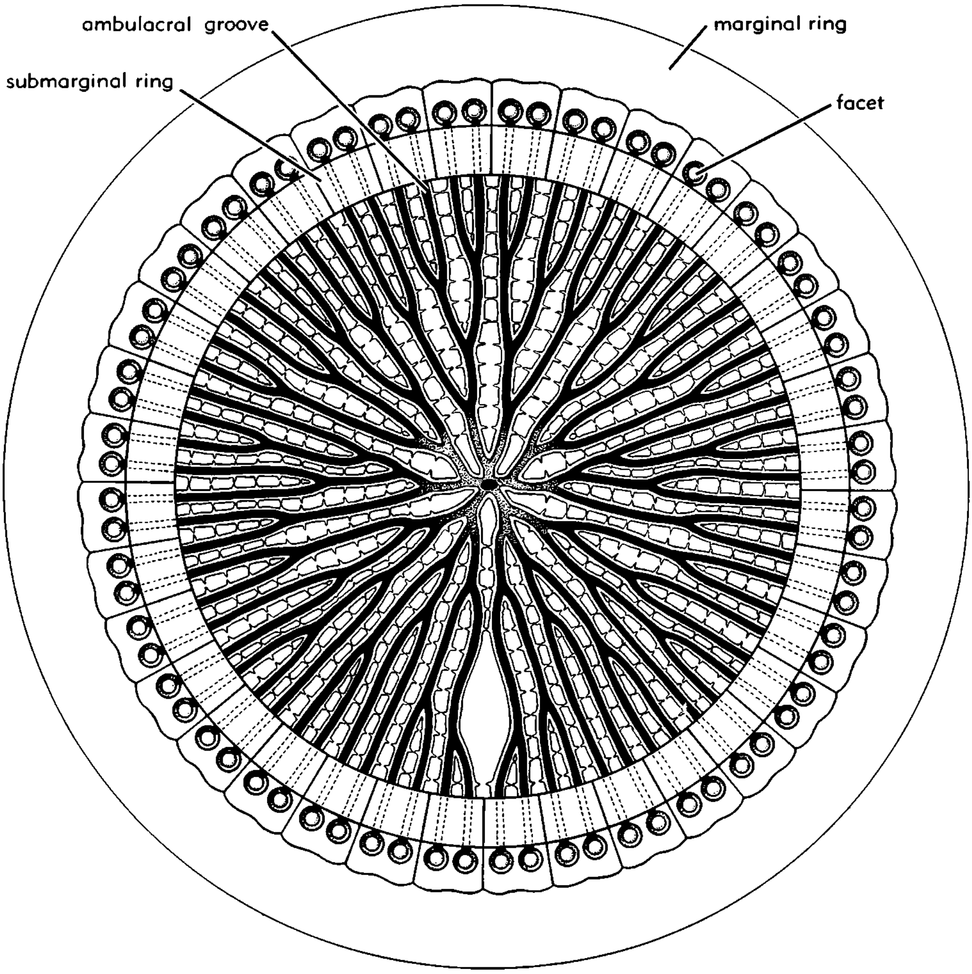


FIG. 143. Hypothetical reconstruction of *Cyclocystoides halli* BILLINGS as viewed orally, ×4.5; ambulacral covering plates removed to show ambulacral grooves (black) (Kesling, n).

uniserial and serve to cover the ambulacral grooves or ducts. Thus, they are **ambulacral covering plates,** fulfilling the same protective function as the biserial covering plates in cystoids. The outer surface of the ambulacral covering plates may vary from one species to another. Those in *Cyclocystoides devonicus* were said by SIEVERTS-DORECK (20) to be somewhat papillate or tuberculate. REGNÉLL (15) stated that "each ray is divided medially by a faint groove . . ." but added, "The rays seem to have been solid." Begg (2) described *C. decussatus* thus: "Each ray is probably divided medially, for the greater part of its length, by a thin narrow longitudinal ridge." From the sides of each ambulacral covering plate, one or possibly more lateral processes extend to meet similar processes on plates of the adjacent ridge or row, at least in *C. decussatus, C. lindstroemi,* and *C. devonicus.* These processes taper distally, so that they resemble spines. Those of most plates seem to be set directly opposite, but some variations have been reported. Together, the ridges and lateral procsses give the outer surface of the oral disc a reticulate appearance, the ridges being radial and the processes being more or less concentric (Fig. 140).

Little is known about the junctions of the ambulacral plates in each row. Foerste (6) stated that in *C. illinoisensis* Miller & Gurley, "the ventral or upper disk consists of numerous scutellate plates imbricating toward the centre of the disk." No other author has suggested imbrication in these plates, and one may question whether Foerste's specimen was normally preserved.

Between distal parts of adjacent ridges and extending proximally until the ridges join (Fig. 140) is a narrow band of small plates, the **interambulacrals.** Although edges of these plates, like those of the adjoining ambulacral covering plates, are poorly defined, it appears that these interambulacrals are uniserial. They are set somewhat below the general level of ambulacral plates and their sutures may be hidden by spinose processes of the latter.

Neither ambulacral covering plates nor intervening interambulacrals have any pores through them, insofar as known. They seem to have provided a plated cover, ribbed like an umbrella, over soft parts of the animal.

As Regnéll (15) and Sieverts-Doreck (20) have stressed, the oral disc is composed of more than one layer of plates. To enclose the ambulacral grooves, troughlike **ambulacral flooring plates** are attached under the **ambulacral covering plates** (Fig. 143). In *Cyclocystoides devonicus* no divisions of these flooring plates have been discerned, perhaps because they were composed of continuous, weakly calcified sections of the integument. In this species Sieverts-Doreck (20) reported that the flooring plates were supplied with lateral processes like those of the overlying covering plates.

The actual number of ambulacra in the circumoral region may not have been the same in all cyclocystoids. In *Cyclocystoides davisii,* Salter (in Salter & Billings, 17) said, "The center of the flat disk is occupied by a star of about eight narrow rays." In *C. decussatus,* Begg (2) described the central area as having "four rays in the form of a St. Andrews' Cross." Raymond (14) stated that in *C. huronensis* Billings "only 5 branches reach the centre." Sieverts-Doreck (20) also discerned 5 ambulacra in *C. devonicus,* originating at the center of the oral disc.

The oral region is poorly known, primarily because the plates there are small, thin, and fragile. In my reconstruction (Fig. 140) I have supposed that tiny plates in interambulacral positions covered the peristome, more or less corresponding to those of certain cystoids.

The eccentric space between two ambulacral ridges figured by Hall (8) and supposed by him to be the mouth can scarcely be interpreted thus, inasmuch as it is removed from the place where the ambulacra converge. Instead, as Bather (1) suggested, it is probably the periproct. No anal pyramid has been discovered in cyclocystoids, and the anus may have been surrounded by tiny plates no larger or thicker than the ambulacral covering plates and interambulacrals.

ABORAL DISC

Underlying the body of the animal, on the aboral or dorsal side of the theca, the aboral disc is a circular layer of plates filling the space wtihin the submarginal ring (Fig. 141). In *Cyclocystoides lindstroemi,* Regnéll (15) determined from cross sections that the aboral inner edge of each submarginal plate extends as two lappets on the oral side of the aboral disc, so that on the aboral (or basal) surface of the theca, the aboral disc overlaps the border of the submarginal ring.

Most writers who have commented upon the matter agree that the aboral disc had greater strength and rigidity than the oral disc. In some cyclocystoids, the plates of this disc are definitely thicker and have better-defined edges than those of the oral disc above.

The plates in the aboral disc are of two kinds. Some cyclocystoids (e.g., *Cyclocystoides wrighti* Begg, *C. halli* Billings) have plates in a mosaic; others (e.g., *C. devonicus* Sieverts-Doreck) have them imbricating in a radial arrangement. As Sieverts-Doreck (20) believed, mosaic plates probably made a stronger, less flexible layer than did imbricating plates. In both kinds the size of plates decreases away from the center.

The imbricating plates are interpreted to have an arrangement corresponding to the branching of the ambulacra in the oral disc. They seem to have been at least partly embedded in integument, so that the structure is somewhat indistinct. Nevertheless, Sieverts-Doreck (20) discerned certain features in *C. devonicus*; she reported that the aboral disc is marked by strong radial ridges, which in places are not in contact but are separated by radial grooves. Around a small central area that cannot be deciphered, five plates appear in the shape of a pentagon. One row of plates that could be traced without interruption to the margin of the aboral disc contains 11 to 13 plates. She distinguished two kinds of plates in the aboral disc; (1) those in elevated rows, each subquadrate or elongate oval to rounded pentagonal or hexagonal in outline, with nodose or tuberculate surface, many of the corners depressed, numerous plates broader distally than proximally, lateral processes extending to processes of adjacent plate rows like those of oral disc, at many places the plates imbricating toward the margin, and (2) elongate oval, rather flat plates corresponding to the interambulacrals of the oral disc. A small structure near the center in an interambulacral plate was questionably called a hydropore by Sieverts-Doreck, but this location would indeed seem impossible for intake of water.

Some kind of central structure was previously indicated by Raymond (14) who said that in *C. halli* the center of the aboral disc contained "a minute opening, surrounded by an elevated ring of 5 plates. . . ." He added, "The remainder of the disk is covered by small plates which seem to be arranged in a somewhat radial fashion, with larger plates towards the centre and very small ones at the outer margin. Adjoining the sub-marginal ring, there seem to be two very small plates in front of each sub-marginal plate. These small plates do not make a solid covering, but have large pores between them. Around the small mound which resembles an anal pyramid, there are five small, deep depressions, which may indicate the main trunks of the sinuses which extend beneath the integument." It is possible, of course, that the minute central opening and the pores near the submarginal ring were features of preservation in the specimen studied by Raymond.

The aboral disc in an unnamed species from Tennessee was described by Foerste (6) in somewhat different terms. He stated, "The dorsal [aboral] disk within the submarginal circle consists of numerous erect plates, like fence-palings in form, which incline inward sufficiently to be said to imbricate in that direction. The height of these more central plates is such as to have produced a strong support though still permitting a certain amount of flexibility." It would clarify several points of structure if authors prepared high-quality photographs or accurate drawings to show how plates fit together.

The mosaic type of aboral plates is best exemplified by *Cyclocystoides wrighti*, as illustrated by Begg (3), in which rather close-fitting plates constitute a pavement. Such an arrangement is indicated in the reconstruction shown in Figure 141.

It might be well to point out that of approximately 21 valid scientific names for cyclocystoids, only six have been applied to fossils for which both oral and aboral sides are known. This helps to explain some of the difficulties in attempting to compare the opposite sides of the same specimen. No evidence has been presented as to whether the imbricating type of aboral plates duplicate the exact pattern of ambulacra in the oral disc or whether they follow a general plan of branching from five central stems.

SUBMARGINAL RING

Because the submarginal ring of plates is the best-preserved part of the cyclocystoid, it has received exceptional attention in definition of species—undue attention in my opinion. According to Sievert-Doreck's (20) summary, three species are each known from one specimen showing only the oral side of the submarginal ring, and five species are each known from one specimen showing only the aboral side of the submarginal ring.

Because plates of the submarginal ring are exceptionally thick, they have been referred to as "ossicles" by several authors (Table 1). They extend from one side to the other of the theca, being exposed on both oral and aboral sides (Fig. 140-142). Although not absolutely rigid, they were evidently attached firmly to one another and provided the frame for maintaining the shape of the theca.

The shape of each submarginal plate in radial cross section is not the same in all species. Foerste (5) attached considerable importance to this feature in erecting *Narrawayella* and *Savagella.* According to his classification, *Cyclocystoides s.s.* (exemplified by *C. anteceptus* Hall, *C. halli* Billings, *C. bellulus* Miller & Dyer, and others) has submarginal plates with the proximal half strongly elevated above the distal half, *Narrawayella* (exemplified by *C. cincinnatiensis* Miller & Faber, *C. nitidus*

Table 1. *Morphological Terms Used by Various Authors for Cyclocystoidea.*

	Oral Disc	Aboral Disc	Submarginal Ring	Marginal Ring	Facets	Channel	Ambulacral Grooves
Salter & Billings, 1858	Integument of the upper side	"Underside (at least the flatter and less ornamented side)"	Marginal ossicles	Marginal plating; plated integument	"Circular pit with a tubercle in it"	Tubular channel	"Small pores penetrating through marginal plates," connecting channel with the interior
Bather, 1900	Ventral membrane	Dorsal membrane	Ring of stout ossicles	Border of smaller plates			
Raymond, 1913	Upper side	Lower side	Submarginal ring	"Narrow band . . . of imbricating plates . . . 'shagreen' border"	Spoon-shaped depressions	Circular canal	"Sinuses which extend beneath integument"; "probably pores through plates"
Foerste, 1924	Ventral disc; upper disc	Dorsal disc; lower disc	Submarginal ring	Marginal zone of very small plates; marginal plates	"Oval depressions occupied by corresponding oval elevations"	Outer, lower part of plates	
Begg, 1934	Central disc: lower plate	Upper plate	Submarginal area; ring of ossicles	Marginal zone; "sinuous threads or possibly . . . imbricating plates"	Spoon-shaped depressions	Canal	"Ducts beneath the surface of the disc"
Regnéll, 1945	Central disc	Lower plate	Submarginal area; submarginal ossicles	Marginal zone	Mamillary elevations	Canal	"Ducts penetrate the vaults radially to open on the—likewise excavated—inner side of the ossicles"
Sieverts-Doreck, 1951	Ventral-Scheibe	Dorsal-Scheibe	Submarginal Ring	Randsaum	Warzenförmige Höcker	Platform; ?Ring-Kanal *or* Höhlung	Ambulakral-System; "Strahlen"

Faber, and *C. mundulus* Miller & Dyer) lacks depressions in the distal halves of the plates, *Savagella* (with type-species *C. ornatus* Savage) shows subtriangular cross sections with a steep inner face on the submarginal ring, and an unnamed genus represented by *C. illinoisensis* has submarginal plates with a "flattened elliptical form" in cross section. Sieverts-Doreck (20) described *C. devonicus* as lacking deep depressions in the distal parts of the plates.

The oral side of the submarginal plates is more complex than the aboral side. The sides of each plate converge slightly toward the center of the oral disc, so that adjacent plates have nearly parallel sides. On external molds, the spaces between plates are filled with matrix, which takes the form of radial partitions; this is the preservation in many specimens, the whole of the plates having been dissolved away. The oral part of the submarginal plates is divided into two parts: (1) proximal elevated part, forming a prominent ring, and (2) distal part bearing facets (Fig. 140). The division between the two parts is sharp, tending to be emphasized by the overhanging edge of the proximal part, so that Hall (8) concluded that two circles of plates were present. However, as convincingly shown by Regnéll (15) in cross sections, only one circle or ring of plates exists.

In many species, the proximal part of each submarginal plate is elevated as a subquadrate block. The oral surface is variously ornamented. Most species bear numerous low tubercles or papillae (e.g., *Cyclocystoides salteri* Hall, *C. halli* Billings, *C. magnus* Miller & Dyer, *C. decussatus* Begg, *C. lindstroemi* Regnéll, and *C. devonicus* Sieverts-Doreck); one has radial grooves dividing the surface into four or five low ribs (*C. ornatus* Savage); another was described by Begg (3) as having little round punctae *(C. wrighti)*; and still another was said by Foerste (5) to be "coarsely pitted" (*C. cincinnatiensis* Miller & Faber). The ornamented part overhangs both the outer plates of the oral disc on the proximal side and the edge of the rest of the submarginal plates on the distal side in *C. lindstroemi* and probably in some other species, but not in *C. devonicus* and some of the species referred to by Foerste (5).

The distal part of the oral side of submarginal plates bear **facets,** small circular to elliptical elevations (Fig. 140). No plate is known which lacks a facet, some plates having only one facet, and some as many as four. In some specimens, each of the plates has two facets. Whether this constancy of facet-to-plate relationship is a character of species or of maturity has not been proved. In *C. halli* and *C. lindstroemi,* facets lie in a circular trough called the **channel.** In *C. devonicus,* however, they are on the shallowly excavated, beveled edge of the plate, called by Sieverts-Doreck (20) the **platform.** Those facets within a channel are surrounded by some kind of depression. *C. halli* was described by Billings (in Salter & Billings, 17) as having the outer half of each submarginal plate "deeply excavate, smooth, divided by a radiating ridge into two shovel-shaped portions, which at their inner base are each deepened into a circular pit, with a tubercle in it." Other authors (Table 1) have referred to similar areas surrounding facets as "spoon-shaped depressions." Even in *C. devonicus* (see Fig. 147,*1-2*), external molds show that the facets are in shallow excavations.

Lack of a well-incised channel in *Cyclocystoides devonicus* led Sieverts-Doreck (20) to postulate that parts of submarginal plates under the facets were hollow and that a channel was a secondary feature caused by collapse of the facet-bearing section. She concluded that the channel was not connected with the ambulacral system. The regularity of the channel in specimens of *C. halli* illustrated by Salter & Billings (17) and by Raymond (14), and the lack of any cavities shown in the cross section of *C. lindstroemi* illustrated by Regnéll (15) raises considerable doubt about her interpretation. Sieverts-Doreck stated, however (my translation), "Should my interpretation not prove correct, then there exists a conspicuous contrast between those species of *Cyclocystoides* which possess a peripheral ring-canal and those which lack it."

Insofar as known, facets are invariably aligned with radial ducts or holes through the proximal part of the submarginal plate. These ducts appear to connect with the ambulacral grooves. Authors agree that food entered the ambulacral system through the channel or platform of the submarginal plates. The presence of "small pores" leading from the channel to the interior of the theca and perforating the submarginal plates was made part of the definition of *Cyclocystoides* by SALTER & BILLINGS (17). REGNÉLL (15) found a groove in *C. lindstroemi* leading from the facet to the duct, but in *C. insularis* he failed to find such a groove.

One of the unsolved problems of cyclocystoids concerns the function of covering plates over the channel, if indeed they exist. Supposition that the channel was covered by movable plates originated with SALTER & BILLINGS (17), who based their interpretation on small isolated plates in the channel of one or two submarginal plates. From his study of the same specimen, RAYMOND (14) also concluded that the channel was roofed over by small plates. FOERSTE (6) described some curious structures just outside the submarginal ring as "spout-like appendages," and proposed that these could be moved at will to enclose or expose the depressions containing the facets. The illustrations of these structures are not sufficiently distinct to show the details of their configuration; possibly, they could be fractured outer edges of spoon-shaped depressions, which in *C. lindstroemi* form an elevated rim.

The general resemblance of the ambulacral system in cyclocystoids to that in cystoids supports their assignment to the Crinozoa, rather than Echinozoa. In cystoids and blastoids, food was gathered by brachioles; in crinoids, the ambulacral system was further branched outside the calyx and food was gathered by pinnules on the arms. Only in edrioasteroids was food gathered directly into the ambulacral grooves. Enclosure of ambulacral grooves in cyclocystoids seems irrefutable evidence that food entered from the channel, specifically at the facets. The form of the facets is strikingly like that in cystoids. It is difficult to conceive of brachioles sufficiently developed to gather adequate food and still so small as to be retractable beneath covering plates of the channel.

Perhaps an alternative interpretation will explain both the small plates and the facets. In some species the facets are not in contact with the ducts, but set a short distance away from the openings. Possibly, small plates served as ambulacral covering plates over this part of the ambulacral system. There is no reason to deny that small plates may have also covered parts of the channel between facets. As pointed out later, the complexity of the submarginal plates may be regarded as evidence of their having evolved by fusion of several plates.

On the sides of the submarginal plates—the surfaces facing the adjacent plates—the oral margin is marked by striae normal to the edge. These have been interpreted as scars of ligaments which bound the plates of the submarginal ring together and yet allowed appreciable flexibility. These markings are prominent on some cyclocystoids, but have not been found in others.

On the aboral side of the theca, the exposed part of the submarginal ring has less radial extent than that on the oral side. Each submarginal plate is slightly convex and trapezoidal in outline. The plates are in contact or nearly in contact only at their distal corners; sides of adjacent plates diverge toward the center of the theca (Fig. 141). As illustrated by REGNÉLL (15), each submarginal plate in *C. lindstroemi* has two lappets concealed by the aboral disc along its proximal edge; probably, some such arrangement was present in other species.

MARGINAL RING

Around the periphery of the theca, the cyclocystoid has a ring of imbricating plates remarkably similar to that present in several edrioasteroids. On both oral and aboral sides, plates decrease in size toward the outside edge. Apparently, they were embedded in a thick integument which formed a seal against the bottom and enabled the cyclocystoid to hold fast by suction. No evidence has been presented to indicate whether the marginal ring was composed of two layers or one. For it to have functioned in attachment, much of it must have consisted of muscles.

AMBULACRA

The ambulacral system began, I believe, with brachioles set in a circle in the distal part of the submarginal ring. Fossils show only the facets (Fig. 143), on which I presume brachioles articulated. From the facets in some species, a groove leads to the duct perforating the proximal part of the submarginal plate. Undoubtedly, this groove was provided with some kind of covering plates. In species which show no such groove, some sort of enclosed passageway probably led from the facet to the duct.

Ducts are said to have a funnel-like adit from the channel. SIEVERTS-DORECK (20) found that in submarginal plates having three ducts, the central one is truly radial and the lateral ducts converge somewhat proximally. Each duct connects with one of the ambulacral grooves under the surface of the oral disc. By successive convergences, the number of ambulacral grooves is reduced to only four or five at the mouth.

UNSUBSTANTIATED AND UNKNOWN STRUCTURES

In this category must be listed the hydropore, gonopore, periproct, and brachioles, structures which might be expected in a pelmatozoan, but not brachioles in an echinozoan. The space between ambulacra noted by HALL (8) and interpreted by BATHER (1) as the anus, very likely was occupied by small, rather undifferentiated plates of the periproct. In comparison with pelmatozoans, one would expect the hydropore and gonopore to be present on the oral side of the theca, probably in the circumoral region.

GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO CYCLOCYSTOIDEA

Relative importance of terms is indicated by the type in which they appear: first rank by boldface capital letters, second rank by boldface small letters, and third rank (including obsolete terms, terms having cross references, and synonyms) by italic small letters.

aboral. Located away from mouth; used to refer to flat side presumed to have been base of animal; from inferred position of mouth in center of one side, aboral is same as dorsal on cyclocystoids.

ABORAL DISC. Subcircular section of integument and associated plates stretched across dorsal side of submarginal ring, more or less like a drumhead, also known as dorsal disc. Plates within aboral disc may be rather firmly set as a mosaic or flexibly arranged in imbrication, in latter arrangement showing radial symmetry similar to that in oral disc.

ambulacral covering plates. Small plates, probably uniserial, roofing over ambulacral grooves and embedded in integument of oral disc; in at least some species, each plate had lateral processes extending to similar processes on the adjacent ambulacral branch, forming a reticulation to strengthen the disc.

ambulacral flooring plates. Small plates or fused plates serving as internal walls of enclosed ambulacral grooves, trough-shaped and joined by their edges to ambulacral covering plates.

ambulacral groove. Any of branched passageways through which food was conveyed from channel to mouth, aborally bounded by ambulacral flooring plates and orally bounded by ambulacral covering plates; presumably, ambulacral grooves led adorally from brachioles; technically, ducts or perforations through submarginal plates are parts of ambulacral grooves.

AMBULACRUM. Structure in which food was conveyed to mouth, normally applied to one of major structures and all its branches, so that most cyclocystoids may be said to have five ambulacra.

border. See marginal ring.

brachiole. Inferred erect structure by which food was gathered and transmitted to ambulacrum, although none have been found, presence of brachioles is strongly indicated by form of facets in channel of submarginal ring; presumably, these structures were very similar to those in cystoids.

canal. See channel.

central disc. See oral disc.

CHANNEL. Distal part of submarginal ring, bearing facets, in most cyclocystoids troughlike. Varying degrees of indentation exist; if the facet-bearing surface is very shallow, or if it is more or less expressed as a beveled border of the submarginal ring, it is called a platform.

channel covering plate. One of supposed series of plates roofing over channel in some species; existence of covering plates suggested by disarranged small plates in channel of one of type specimens of *Cyclocystoides halli* described by SALTER & BILLINGS (17), who said in their definition of the genus, "Those [oval excavations], in perfect specimens, are covered over by minute polygonal plates, thus forming a tubular channel around the whole animal." From restudy of this specimen, RAYMOND (14) also thought the channel was covered by small plates. Evidence for a continuous roof, which would enclose the facets and make brachioles ineffective, is far from convincing.

covering plate. See ambulacral covering plate, channel covering plate.

dorsal. Located away from mouth; in cyclocystoids synonymous with aboral.

dorsal disc. See aboral disc.

dorsal membrane. See aboral disc.

duct. Perforation through proximal part of submarginal plate, radially aligned with facet and forming part of ambulacral groove.

FACET. Small protuberance, circular or oval, set within channel and connected with ambulacral system. Probably, facets served for attachment of brachioles, like those in cystoids; each facet surrounded by moatlike groove in some species, whole lying within spoon-shaped depression in channel.

hydropore. Small opening very near center of oral disc whereby water was admitted to water-vascular system. Preservation very poor, but hydropore strongly suggested in specimen described and figured by SIEVERTS-DORECK (20), in which it is in interambulacral position.

imbricating. Overlapping, like shingles; applicable to plates in marginal ring and, in some species, to plates in aboral disc.

integument. Supposed exterior layer of tissue in cyclocystoids which secreted plates and probably formed leathery "skin" encasing plates of certain parts; poorly-preserved edges of ambulacral covering plates suggest that much of thickness of oral disc was made up of integument.

interambulacral. One of small plates between ambulacral covering plates, uniserial insofar as known.

lower plate. Used by BEGG (2) for oral disc.

mammillary elevation. See facet.

MARGINAL RING. Distal part of cyclocystoid, bordering submarginal ring, composed of small imbricating plates that distally decrease in size. Marginal ring forming part of oral and aboral surfaces; whether made of one or two layers is not clear.

marginal zone. See marginal ring.

mosaic. Arrangement of plates more or less in plane, not imbricating and presumably rather rigid; plates of aboral disc in some species disposed as mosaic, in other species imbricating.

mouth. Presumed aperture through which food entered body from ambulacra, situated at center of oral disc, probably covered by small peristomial plates as in cystoids.

ORAL DISC. Subcircular section of integument and associated plates extending across center of oral side and attached to inner surface of submarginal ring, also known as ventral disc; in ambulacral positions, oral disc consists of two layers: ambulacral covering plates and ambulacral flooring plates; in interambulacral positions, disc consists only of interambulacrals. Presumably, mouth was in center of oral disc and anus was offset to one side. In known species, ambulacral covering plates give disc a reticulate appearance, with radial elements made of multiple branching of ridgelike ambulacra and concentric elements made of lateral spinose processes.

ossicle. See submarginal plate.

periproct. Presumed circumanal area in oral disc.

plate. Any calcareous secretion, normally flat, in cyclocystoids.

platform. See channel.

SUBMARGINAL PLATE. One of thick plates in submarginal ring, exposed on both oral and aboral sides of theca, in many specimens, only submarginal plates preserved; on oral side, distal part of plate bears facets and proximal part is elevated as part of thick rim around oral disc, each submarginal plate perforated by radial ducts leading from facets to ambulacral grooves in oral disc; on aboral side, each plate expressed as truncated wedge diverging proximally from adjacent plate. Because of thick form, submarginal plates called ossicles by many workers.

SUBMARGINAL RING. Prominent ring of submarginal plates, most conspicuous and best-preserved feature of cyclocystoids.

THECA. Enclosure of plates and integument in which body of cyclocystoid was housed; generally applied to all fossilized parts.

upper plate. Used by BEGG (2) for aboral disc.

ventral. Located toward mouth, in cyclocystoids synonymous with oral.

ventral disk. See oral disc.

ventral membrane. See oral disc.

ONTOGENY

Practically nothing is known about ontogeny of cyclocystoids, but REGNÉLL (15) and SIEVERTS-DORECK (20) have suspected that the number of submarginal plates increases with size and age in each species, and that several of the "species" based solely on number of submarginal plates may represent growth stages of a single species. The latter author also directed attention to a specimen with one submarginal plate having the shape of a thin wedge, as though it were being intercalated into the ring. If plates were added during ontogeny, the process was intimately correlated with branching of the ambulacra, so that the ambulacral grooves joined to the ducts through the submarginal plates.

COMPARISON WITH PELMATOZOANS

Several students of cyclocystoids have been puzzled by the circular, rather than radial, terminus of the ambulacral system and by the great thickness of the submarginal plates, extending from oral to aboral sides of the theca. These have been regarded as anomalous characters in a pelmatozoan.

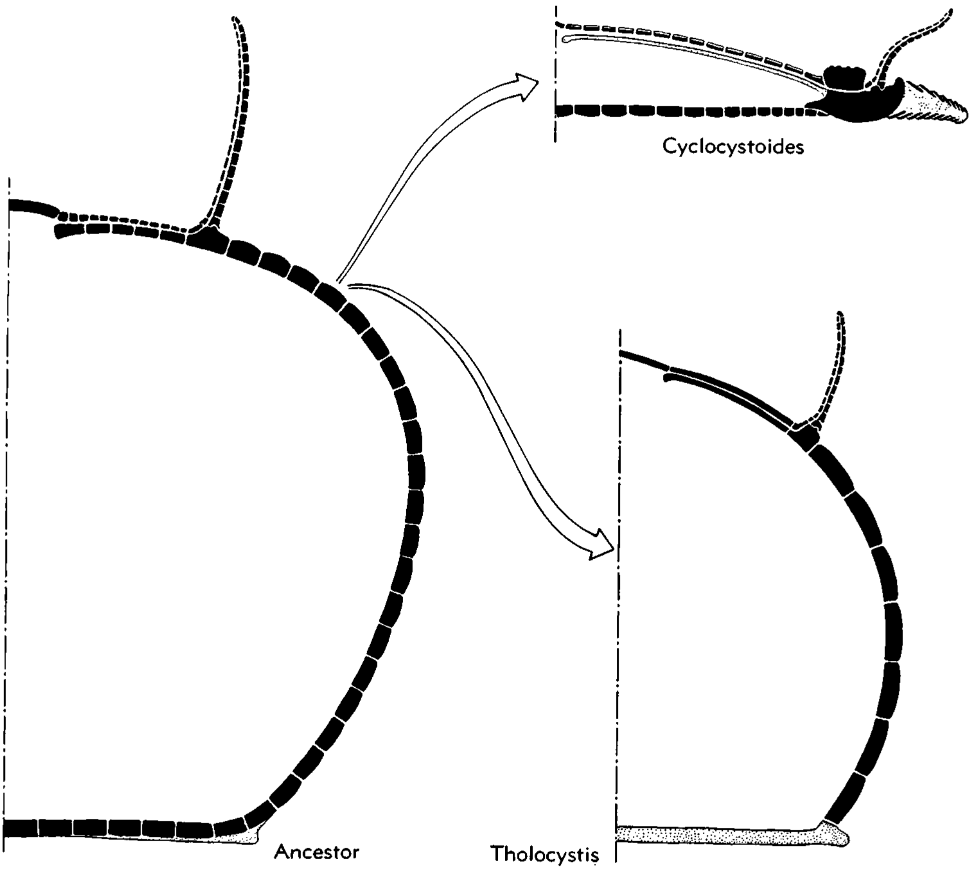


FIG. 144. Hypothetical vertical cross sections of halves of thecae, showing inferred derivation of *Cyclocystoides* and *Tholocystis* from a diplopore-bearing cystoid ancestor. Plates shown in solid black, integument stippled.

Although certain diplopore-bearing cystoids do not duplicate those unusual features they show exceptional similarities. The genus most closely reflecting cyclocystoid organization is *Tholocystis,* of the order Diploporita, superfamily Sphaeronitida, and family Sphaeronitidae (Fig. 144). This cystoid was described by CHAUVEL (4) as shaped like a kettle, with large, orderly disposed radials, orals, and peristomial covering plates corresponding to the lid of the kettle. The broad base of *Tholocystis,* known only from its impression, was probably composed mostly of integument and was called by CHAUVEL the "sole." It is of special interest that *Tholocystis* has (1) branched ambulacra leading to brachioles arranged in a broad-angled pentagram, more or less a circle except for the reentrants necessary for the radials, (2) brachiole facets borne on quadrangular plates, or "adambulacrals," which are thicker than other plates, and (3) a large circular base that was flexible. Presumably, the ambulacral grooves across the oral region were covered by sutures between adjacent oral plates or by small covering plates which left no record.

Cyclocystoides may have descended from a pelmatozoan not very different from *Tholocystis.* The aboral disc and marginal ring of cyclocystoids seem analogous with the base or "sole" of *Tholocystis* and the facet-bearing part of the submarginal ring with the thick quadrangular plates. The ducts through the submarginal plates are novel features for pelmatozoans, but they may have originated by fusion of other plates; their function, protection and enclosure of the ambulacral groove, suggests that the part of the submarginal plate oral to the ducts may have been derived from ambulacral covering plates and that the part aboral to the ducts may have been modified from ambulacral flooring plates. Obviously, *Cyclocystoides* did not attain the exceptional symmetry of *Tholocystis,* and the outer part of its base became more differentiated.

Both *Tholocystis* and *Cyclocystoides* appeared in Middle Ordovician time. The oldest known relative of *Tholocystis* is *Sphaeronites,* from Lower Ordovician strata. Even this genus, however, shows specialization of structures in the circumoral region; the theca is more or less round and attached by the basal surface, which in many specimens retains the imprint of objects to which it was fastened. The Cambrian ancestor of both *Sphaeronites* and *Tholocystis* probably had a theca composed of numerous plates, none of which was highly specialized; such a primitive diploporitan cystoid is conjectured as the possible ancestor of both *Tholocystis* and *Cyclocystoides* (Fig. 144). Whereas no diplopores have been observed in plates of *Cyclocystoides,* integument in which plates of the oral disc are embedded may have fulfilled the same function as diplopores. At any rate, strongest similarities to cyclocystoids occur in this group of sphaeronitid cystoids.

According to this hypothesis, the cyclocystoid is a derivative of the Diploporita in which the theca has undergone extreme oral-aboral compression, the oral region has greatly expanded without plate specialization, submarginal plates have resulted from fusion of "adambulacrals" with proximally adjacent ambulacral flooring and covering plates, the aboral side of the theca has been greatly extended, diplopores have degenerated, and brachioles have migrated outward, assuming circular distribution.

PALEOECOLOGY

Very little can be deduced from occurrences of cyclocystoids. None have been found attached to other organisms. Many have been reported in association with other marine animals, such as corals, brachiopods, and trilobites. No reason exists to suspect that cyclocystoids were not free-living, normal marine creatures.

Because cyclocystoids have been discovered in several kinds of sedimentary strata, it seems likely that they inhabited a variety of depths and thrived under a range of current conditions.

	N. AMERICA	ENGLAND	SCOTLAND	GOTLAND	BELGIUM
Middle Devonian					sp. SIEVERTS-DORECK
Lower Devonian					sp. MAILLIEUX *devonicus* SIEVERTS-DORECK
Ludlovian					
Wenlockian				*insularis* REGNÉLL *lindstroemi* REGNÉLL	
Llandoverian	*ornatus* SAVAGE *huronensis* BILLINGS *illinoisensis* M.&G.	*davisii* SALTER (MS)			
Ashgillian	*cincinnatiensis* M.&F. *minor* MILLER & DYER *mundulus* M.&D. *nitidus* FABER *parvus* M.&D. *bellulus* M.&D. *magnus* M.&D.		*decussatus* BEGG *wrighti* BEGG		
Caradocian	*salteri* HALL	*caractaci* SALTER *marstoni* SALTER (MS)			
Trenton	*raymondi* FOERSTE *anteceptus* HALL *salteri* HALL *halli* BILLINGS *billingsi* WILSON				

FIG. 145. Stratigraphic and geographic distribution of *Cyclocystoides* (modified from Regnéll, 1948).

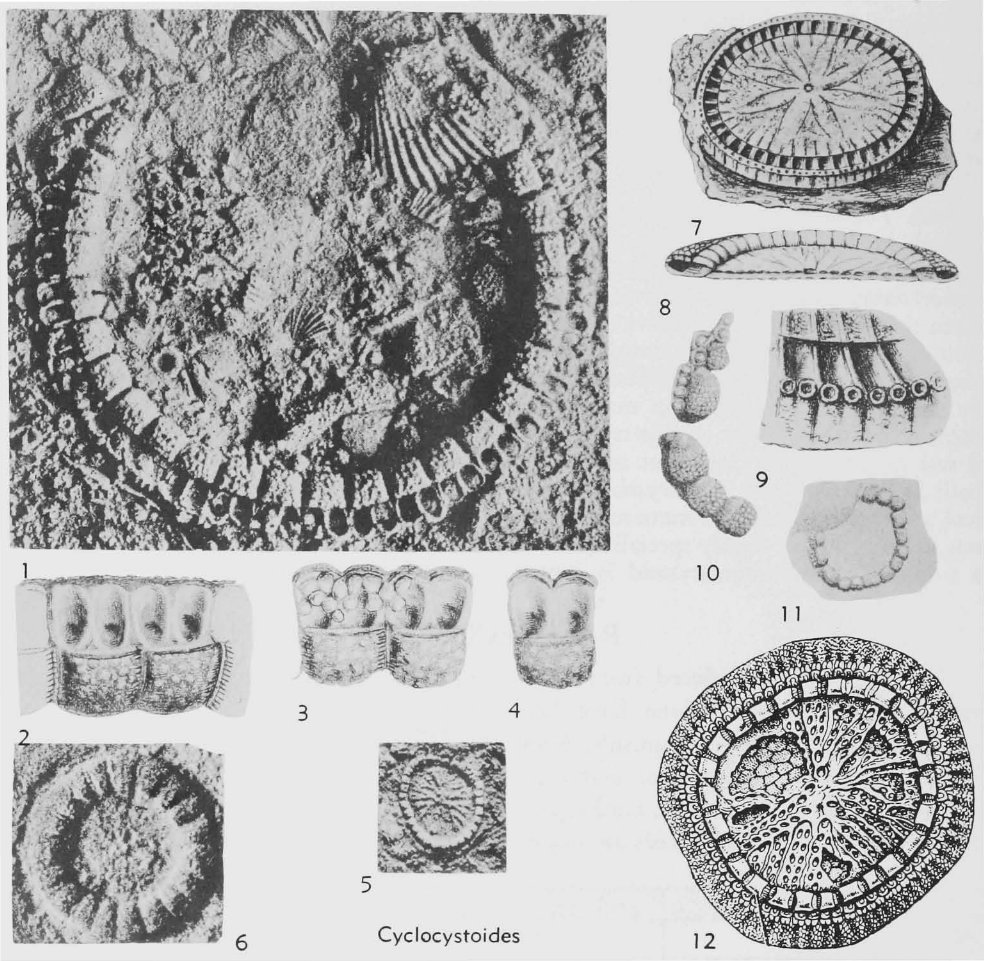


FIG. 146. Cyclocystoididae (p. *U*206-*U*209).

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION

The paleontological record of cyclocystoids is fragmentary and interrupted. Nevertheless, the distribution compiled by REGNÉLL (1948) is essentially unaltered today, and probably is nearly correct.

As shown here (Fig. 145), Cyclocystoidea seem to have originated in North America. The oldest known species is *Cyclocystoides billingsi* WILSON (1946), from late Blackriveran or early Trentonian deposits in the St. Lawrence Lowland of Canada. The genus persisted in eastern North America until Early Silurian time; the last survivor on this continent seems to have been *C. illinoisensis* MILLER & GURLEY (1895), in the Girardeau Limestone of Illinois.

The first migration of *Cyclocystoides* occurred in the Caradocian, when it reached England. There it persisted into the Llandoverian. The genus continued to move northward and eastward, reaching Scotland in Ashgillian time, Gotland in Wenlockian time, and Belgium in the Early Devonian. The final stand of *Cyclocystoides* was in Belgium and the Rhineland, where it is present in Lower and Middle Devonian strata.

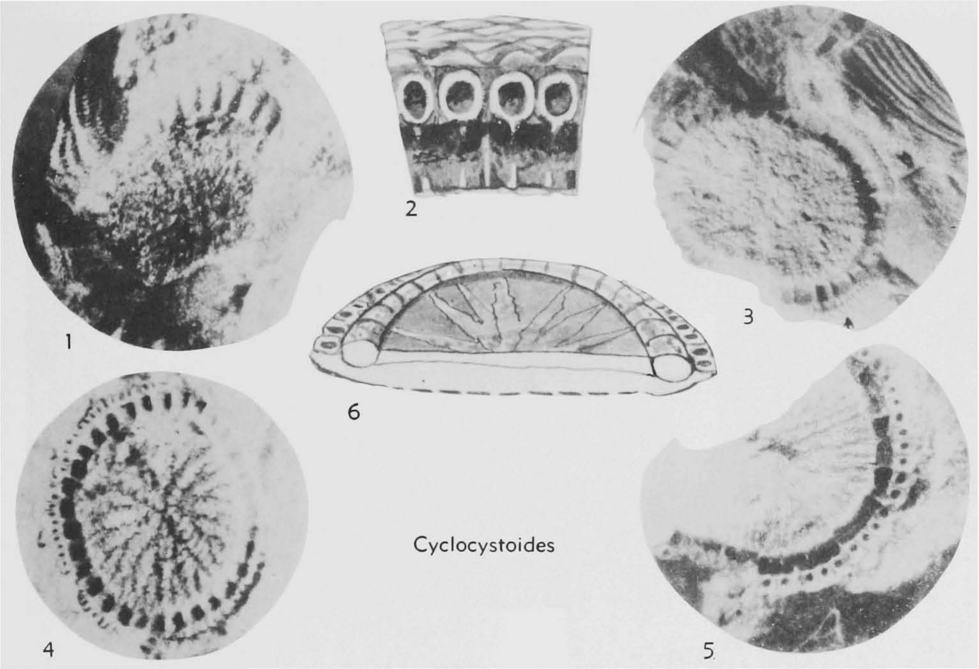


FIG. 147. Cyclocystoididae (p. *U*206-*U*209).

CLASSIFICATION

Admittedly, classification of cyclocystoids is unsatisfactory. Fragmentary nature of most fossils rules out an assessment of characteristics. Whereas workers are aware of variations in plate arrangement in the aboral disc, number and shape of plates in the submarginal ring, depth and form of the channel, number and shape of facets, and ornamentation of submarginal plates, it has been impossible to establish the association of these variations. Many species are known only from one side.

Genera were set up by FOERSTE (5) primarily on shape of submarginal plates in cross section. He distinguished *Narrawayella,* which lacks depressions in the distal halves of the plates, and *Savagella,* which is subtriangular in section, from *Cyclocystoides s.s.,* which has the proximal part strongly elevated and block-shaped. REGNÉLL (15) thought that *Narrawayella* might prove to be a valid genus, but expressed doubt about *Savagella.* SIEVERTS-DORECK (20) placed both of FOERSTE's genera in synonymy with *Cyclocystoides.*

Probably, the cyclocystoids with mosaic plates in the aboral disc are generically different from those with imbricating plates. And forms with deeply excavated channels may prove distinct from those with shallow "platforms." Until the association of characteristics in each species is discovered, it seems best to put all forms into one genus.

SYSTEMATIC DESCRIPTIONS

Class CYCLOCYSTOIDEA Miller & Gurley, 1895

[*nom. transl.* KESLING, herein (*ex* order Cyclocystoidea MILLER & GURLEY, 1895, p. 61)]

Small, disc-shaped echinoderms, lacking columns of any kind, probably attached by suction on nearly flat aboral side. Theca composed of numerous calcareous plates, distinctly separated into central oral and aboral discs, submarginal ring, and marginal ring. Submarginal ring of thick plates, exposed on both oral and aboral surfaces of theca, forming stout frame for attachment of thin oral and aboral discs. Oral disc cir-

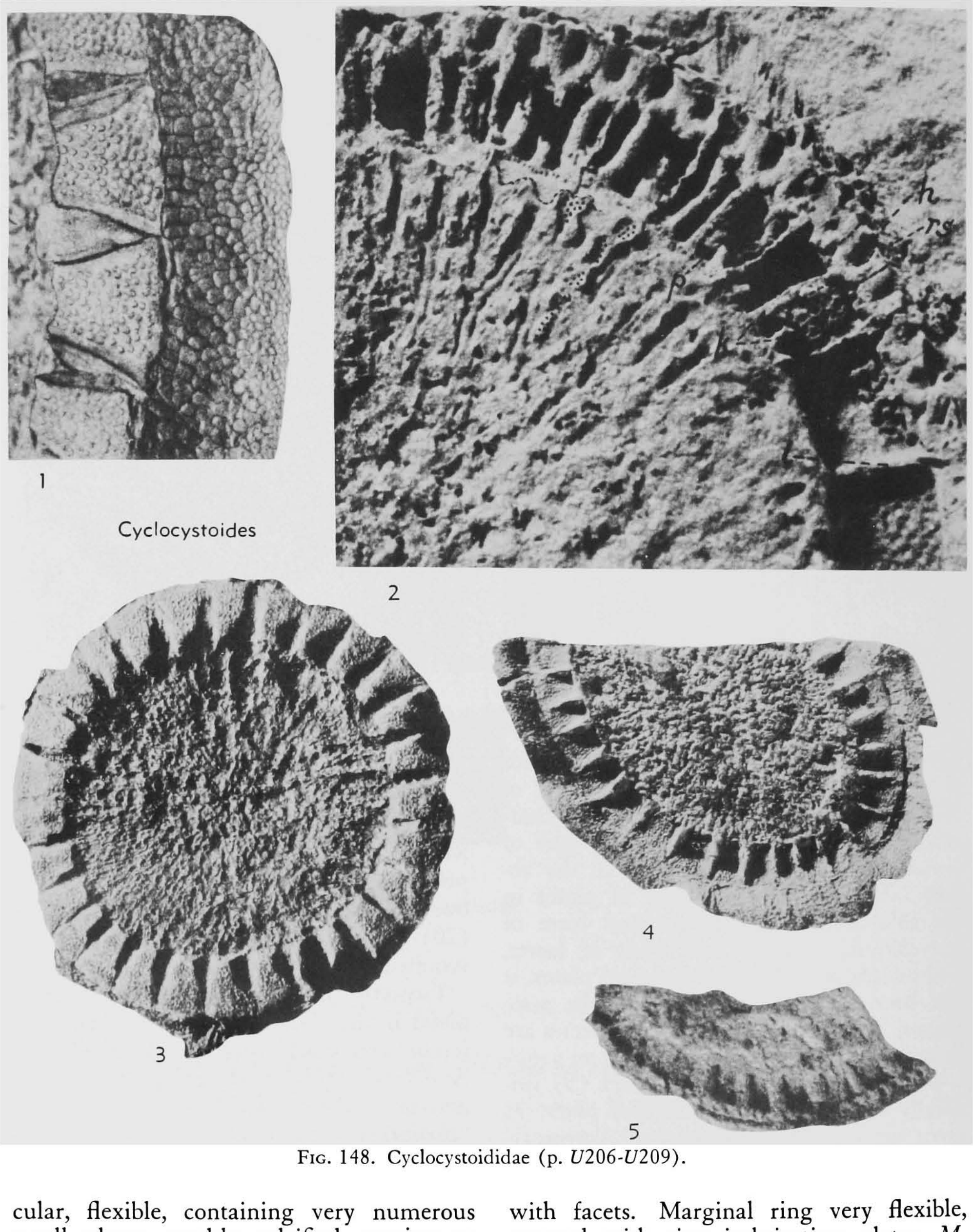


FIG. 148. Cyclocystoididae (p. U206-U209).

cular, flexible, containing very numerous small plates, weakly calcified, serving to cover soft parts of animal and incorporating radiating, multiply branched, enclosed ambulacra. Aboral disc less flexible than oral disc, serving as floor under body. Submarginal plates complex; proximal part of each plate radially perforated; distal part bearing facets on oral surface. Perforation connected with ambulacral passageways and aligned with facets. Marginal ring very flexible, covered with tiny imbricating plates. *M. Ord.-M.Dev.*

Family CYCLOCYSTOIDIDAE

S. A. Miller, 1882

[Cyclocystoididae S. A. MILLER, 1882, p. 223]

Characters of class. *M.Ord.-M.Dev.*

Cyclocystoides SALTER & BILLINGS, 1858, p. 86 [**C. halli* BILLINGS, 1858; OD] [=*Narrawayella*

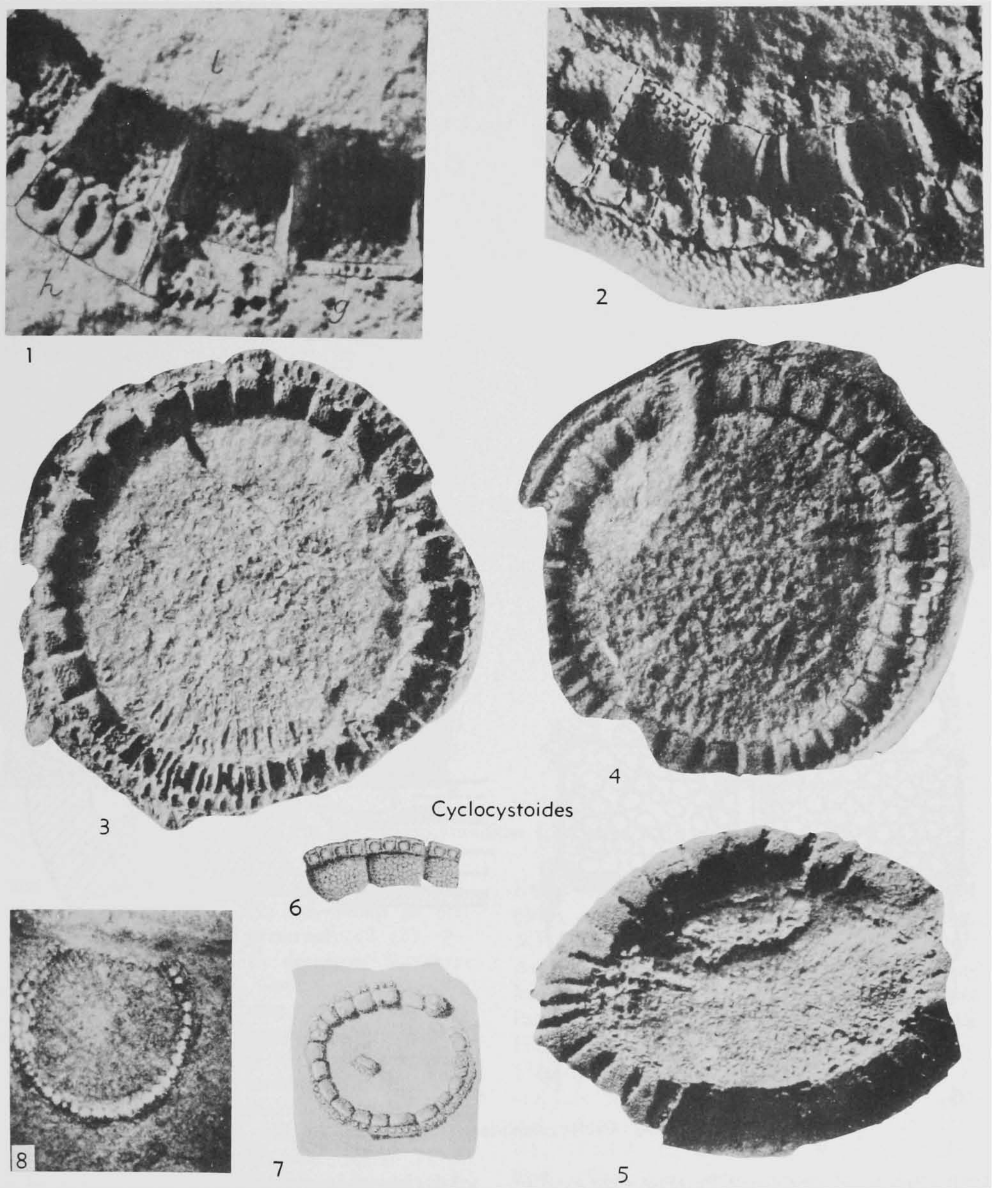


FIG. 149. Cyclocystoididae (p. *U*206-*U*209).

FOERSTE, 1920, p. 59 (type, *Cyclocystoides cincinnatiensis* MILLER & FABER, 1892, p. 84; OD); *Savagella* FOERSTE, 1920, p. 61 (type, *Cyclocystoides ornatus* SAVAGE, 1917, p. 265; OD)]. Oral disc with 4 or 5 ambulacra, each branched several times from circumoral region to periphery, covering most of disc except small area presumed to be periproct. Ambulacra enclosed between flooring plates and covering plates, those of adjacent branches separated by small interambulacral plates. Aboral disc containing plates disposed in either mosaic or imbricating radial pattern. Submarginal plates with shape of truncated wedges, joined together by ligaments, in cross section subtriangular, elliptical, or subquadrate; distal part of oral surface deeply excavate to form circular troughlike channel or shallowly depressed to form platform, each plate bearing 1 to 4 facets, which are radially aligned with perforations through proximal parts of submarginal plates, leading to ambulacral passageways in oral disc. Hydropore, gonopore, and brachioles not known. *M.Ord.-M.Dev.*, N.Am.(Ill.-

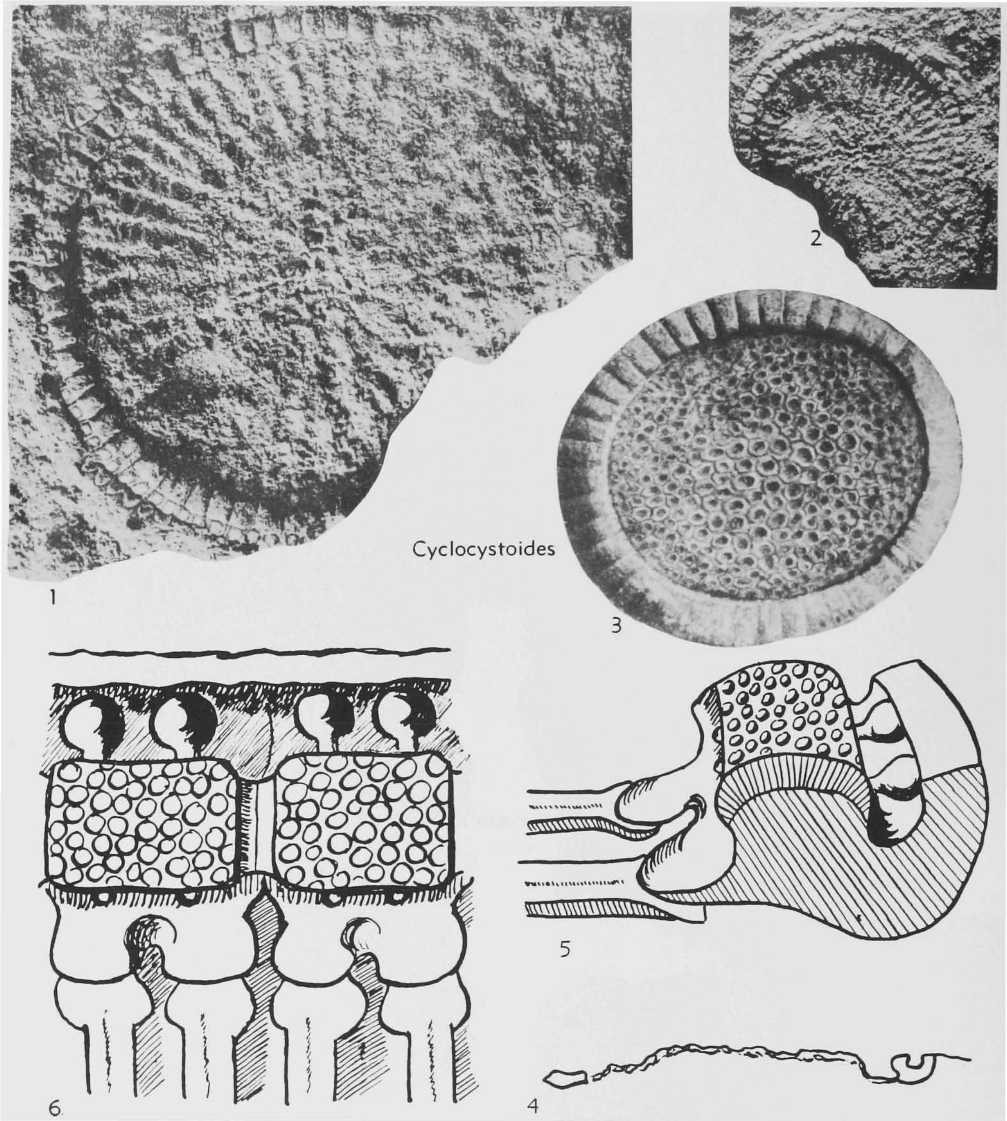


FIG. 150. Cyclocystoididae (p. *U*206-*U*209).

Mich.-Ohio-N. Y.-Ont.-Que.)-Eu.(Eng.-Scot.-Gotl.-Belg.-Ger.).——FIG. 146,*1-5*; 147,*6*. **C. halli,* M. Ord.(Trenton.), Can.(Ottawa); 146,*1*, oral side of ring of submarginal plates, 2 spoon-shaped depressions on each plate, vertical marginal plates, ×3 (14); 146,*2-4*, oral side of marginal plates, enlarged (17); 146, *5*, oral view, ×0.2 (14); 147,*6*, oblique view of half of theca (reconstr.), "drawing copied from Salter & Billings, 1858. Here the authors err in showing, by dotted line, the upper plate passing under the lower plate" (Begg has made his correction in this drawing), mag. unknown (2).——FIG. 146,*6*. *C. raymondi* FOERSTE, M.Ord.(Trenton.), Can.; aboral side, ×3.5 (14, wherein this fig. called *C. halli*).——FIG. 146,*10-11*. *C. bellulus* MILLER & DYER, U. Ord., Ohio; *10*, oral side of submarginal plates, enlarged; *11*, oral side, submarginal plates, ×1 (12).——FIG. 146,*7-9*. *C. davisii* SALTER, L.Sil. (Llandover.), S.Wales; *7*, mold of specimen with perfect margin, ×1; *8*, ideal section of *Cyclocystoides,* mag. unknown; *9*, mold of part of margin, enlarged (17).——FIG. 146,*12*. *C. salteri* HALL, M.Ord.(Trenton.), USA(N.Y.); oral side, ×2 (21).——FIG. 147,*1-5*. *C. decussatus* BEGG, U. Ord.(Ashgill.), Scot.; *1*, aboral side, ×2; *2*, drawing of mold of part of marginal and submarginal rings with spoon-shaped depressions, casts of pores,

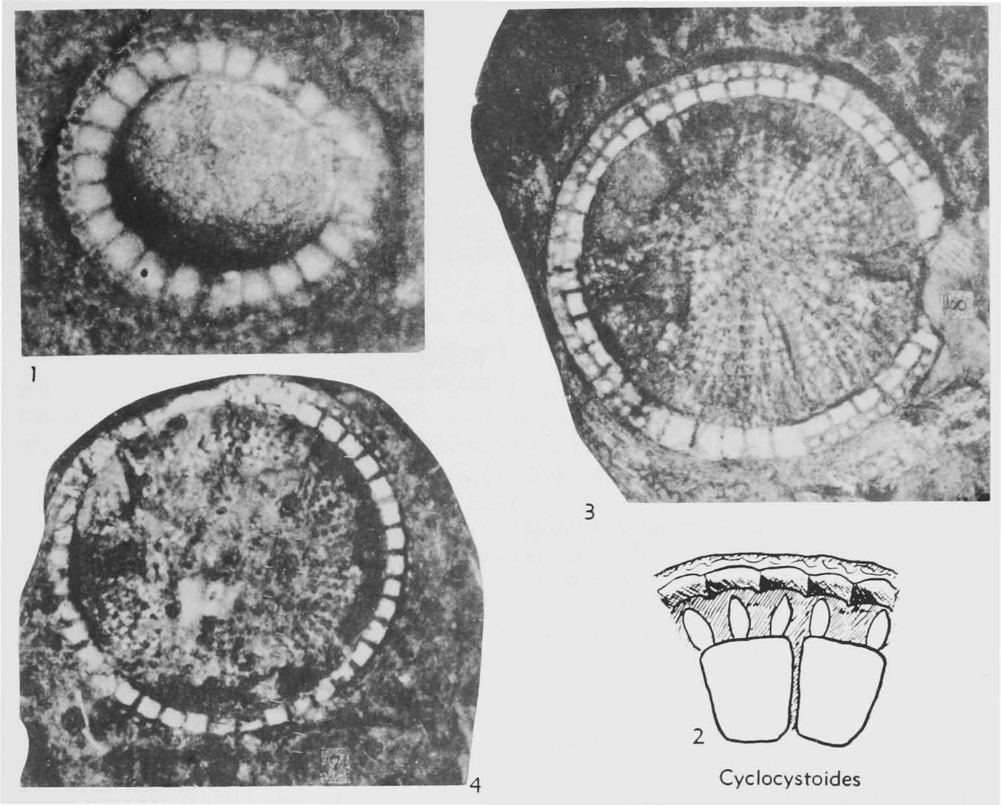


FIG. 151. Cyclocystoididae (p. *U*206-*U*209).

and filling of spaces between submarginal plates, enlarged; *3*, oral side, ×2; *4,5*, molds of oral sides, marginal rings not preserved ×2 (2).——FIG. 148,*1-5*; 149, *1-5*. *C. devonicus* SIEVERTS-DORECK; 148,*1-4*, M.Dev., Ger.(Westphalia); 148, *1*, aboral side, marginal ring, ×6; 148,*2*, mold seen aborally, ×6; 148,*3*, cast of aboral side, ×2; 148,*4*, mold of aboral side, ×2; 148,*5*, upper L. Dev., Ger.(Rhine Prov.); mold of oral side, ×2; 149,*1-3*, M.Dev.(Westphalia); molds of oral sides, ×6, ×5, ×2; 149,*4*, L.Dev., Belg. (Ardennes); mold of oral side, ×2.5; 149,*5*, L.Dev., Ger.(Rhine Prov.); cast of aboral side, ×2 (20).——FIG. 149,*8*. *C. billingsi* WILSON, M. Ord.(Blackriv.-Trenton.), Can.(Ottawa); oral side, ×1 (22).——FIG. 149,*6-7*. *C. magnus* MILLER & DYER, U.Ord., Ohio; *6*, oral side, submarginal plates, enlarged; *7*, oral side, submarginal ring, ×1 (12).——FIG. 150,*3*. *C. wrighti* BEGG, U.Ord. Ashgill.), Girvan, Scot.; aboral side, magn. unknown (20).——FIG. 150,*1-2*. *C. huronensis* BILLINGS, U.Ord.(Richmond.), Rabbit Is., Lake Huron; oral sides, ×2.5 (6), ×1 (20).——FIG. 151,*1-2*. *C. insularis* REGNÉLL, U.Sil., Gotl.; *1*, oral side, ×1; *2*, drawing of oral side of marginal and submarginal plates, ×8 (15).——FIG. 150, *4-6*; 151,*3-4*. *C. lindstroemi* REGNÉLL, U.Sil., Gotl.; 150,*4*, cross section, ×1; 150,*5*, lat., isolated submarginal plate and part of aboral disc, ×8; 150,*6*, oral side of 2 submarginal plates, ×8; 151,*3-4*, oral sides, ×1 (15).

REFERENCES

Bather, F. A.

(1) 1900, *The Edrioasteroida,* in E. R. LANKESTER (ed.), A Treatise on Zoology, Pt. III, The Echinoderma (by F. A. BATHER, J. W. GREGORY, and E. S. GOODRICH), p. 205-16, 8 text-fig., Adam & Charles Black (London).

Begg, J. L.

(2) 1934, *Notes on Cyclocystoides:* Geol. Mag., v. 71, no. 839, p. 220-24, pl. 11.

(3) 1940(1939), *On the genus Cyclocystoides, with a description of a new species from the Ashgillian of Girvan:* Geol. Soc. Glasgow, Trans., v. 20, pt. 1, p. 21-28, pl. 1.

Chauvel, Jean

(4) 1941, *Recherches sur les Cystoïdes et les Carpoïdes Armoricains:* Soc. Géol. et Mineral. Bretagne, Mém. v. 5, p. 1-286, pl. 1-7.

Foerste, A. F.

(5) 1920, *Racine and Cedarville cystids and blastoids with notes on other echinoderms:* Ohio Jour. Sci., v. 21, no. 2, p. 33-78, 4 pl., 4 text-fig.

(6) 1924, *Upper Ordovician faunas of Ontario and Quebec:* Canada, Geol. Survey, Dept. Mines, Mem. 138 (Geol. Ser. No. 121), iv+255 p., 46 pl., 14 text-fig.

Hall, James

(7) 1851, in J. W. Foster & J. D. Whitney, *Report of the geology of the Lake Superior Land District, Pt. II, The iron region:* U.S. 32nd Congress Spec. Session, Sen. Ex. Doc. 4, p. 203-31.

(8) 1872, *Description of new species of Crinoidea and other fossils from strata of the age of the Hudson-River Group and Trenton Limestone:* N.Y. State Museum Nat. History, 24th Ann. Rept. (also N.Y. State Cab. Nat. History, advance sheets 20th Rept., 1866), p. 205-24, pl. 5-8, 3 text-fig.

Jaekel, Otto

(9) 1918, *Phylogenie und System der Pelmatozoen:* Paläont. Zeitschr., v. 3, no. 1, p. 1-128, 114 text-fig.

Kesling, R. V.

(10) 1963, *Morphology and relationships of Cyclocystoides:* Univ. Michigan, Museum Paleontology, Contrib., v. 18, no. 9, p. 157-176, 5 text-fig.

Miller, S. A.

(11) 1882, *Descriptions of three new orders and four new families, in the Class Echinodermata, and eight new species from the Silurian and Devonian formations:* Cincinnati Soc. Nat. History, Jour., v. 5, p. 221-31, pl. 9.

———, & Dyer, C. B.

(12) 1878, *Contributions to Palaeontology:* Cincinnati Soc. Nat. History, Jour., v. 1, no. 1, p. 24-39.

———, & Gurley, W. F. E.

(13) 1895, *Description of new species of Palaeozoic Echinodermata:* Illinois State Museum Nat. History, Bull. 6, 62 p., pl.1-5.

Raymond, P. E.

(14) 1913, *Notes on Cyclocystoides:* Canada, Geol. Survey, Dept. Mines, Victoria Mem. Museum, Bull. 1, p. 23-32, pl. 3 (fig. 1-4), text-fig. 2-3.

Regnéll, Gerhard

(15) 1945, *Non-crinoid Pelmatozoa from the Paleozoic of Sweden:* Lunds Geol.-Mineral Inst., Medd., no. 108, viii+255 p., 15 pl., 30 text-fig.

(16) 1960, *"Intermediate" forms in early Paleozoic echinoderms:* Internatl. Geol. Congress, Rept. 21st Sess., pt. 22, p. 71-80.

Salter, J. W., & Billings, Elkanah

(17) 1858, *On Cyclocystoides, a new genus of Echinodermata from the Lower and Middle Silurian rocks:* Canada, Geol. Survey, Figs. and Descr. Canadian Organic Remains, Decade 3, p. 86-90, pl. 10 bis.

Sieverts [Sieverts-Doreck], Hertha

(18) 1935, *Begg, James L. "On the genus Cyclocystoides (Review):* Neues Jahrb. Mineral., Geol., & Paläont., 1934, p. 975.

(19) 1935, *Begg, J. L. "On the genus Cyclocystoides" (Review):* Zentralblatt, Mineral., Geol., & Paläont., Abt. B: Palaeont. v. 6, no. 1, p. 46 (entry 134).

(20) 1951, *Über Cyclocystoides Salter & Billings und eine neue Art aus dem belgischen und rheinischen Devon:* Senckenbergiana, v. 32, no. 1/4, p. 9-30, 2 pl., 3 text-fig.

ADDITIONAL SOURCES OF ILLUSTRATIONS

(21) **Piveteau, Jean,** 1953

(22) **Wilson, Alice,** 1946