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Review of selected North American mitrate stylophorans (Homalozoa: Echinodermata)

by

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CONTENTS

Page

Morphology, Functional Morphology, and Life Habits

Morphology

Systematic Paleontology

Systematics

Class Stylophora

Order Mitrata

Family Placocystitidae

LIST OF ILLUSTRATIONS

LIST OF TABLES

REVIEW OF SELECTED NORTH AMERICAN MITRATE STYLOPHORANS (HOMALOZOA: ECHINODERMATA)

by

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ABSTRACT

This paper reviews most of the North American mitrate stylophoran genera and species that are assigned to two suborders, the Anomalocystitida and the Peltocystida. The Anomalocystitida is herein divided into two long-ranging families, the Anomalocystitidae and the Placocystitidae. The Anomalocystitidae contains mostly North American species (Middle Ordovician–Early Devonian) that are characterized by the proximal carapace margin having three plates, and only very rarely a placocystitid plate. North American species include, within the new subfamily Anomalocystitinae, *Willmanocystis denticulatus* Kolata and Jollie, 1982 (Middle Ordovician), *Kierocystis insertus*, n. gen. and sp. (Middle Ordovician), *Anomalocystites cornutus* Hall, 1859 [= *A. disparilis* Hall, 1859], (Early Devonian); and within the subfamily Enoplourinae, *Enoploura punctata* Bassler, 1932 (Middle Ordovician), *Enoploura balanoides* (Meek, 1872) [= *E. crustacea* (Haeckel, 1896) = *E. wetherbyi* Caster, 1952 = *E. meeki* Caster, 1952] and *Enoploura popei* Caster, 1952 (Late Ordovician). Species assignable to the Placocystitidae are found in North America, Europe, and Australia. They are characterized by the proximal carapace having only two plates in contact with the aulacophore, the **MA** plate consistently excluded, and the placocystitid plate rarely missing. North American forms discussed herein include, within the subfamily Placocystitinae, *Ateleocystites huxleyi* Billings, 1858 (Middle Ordovician), and *Kopficystis kirkfieldi*, n. gen. and sp. (Middle Ordovician). It seems likely that the Southern Hemisphere subfamily Allanicytidiinae branched off from the placocystitids some time in the Early Silurian and persisted until the Early Devonian. The North American representative of the Peltocystida, the kirkocystid *Anatiferocystis spinosa* Ubaghs, 1979 [= *Kirkocystis papillata* (Bassler, 1932)] from the Middle Ordovician of Oklahoma, is represented in Bohemia as well. This genus has a greatly reduced number of plates. The disposition and growth of these plates are discussed herein.

The feeding strategies of mitrates are seen to be different than previously reported. In mitrates, the aulacophore faced into the prevailing current, convex upward, and food was conveyed to the food groove under the dorsally-fused cover plates through the arcuate to chevron-shaped openings between the overlapping set of cover plate pairs. The width of these openings was controlled by the degree of distal aulacophore convexity. Previous representations of feeding figured the distal aulacophore concavely curved over the proximal aulacophore and proximal theca. I see this as a closing mechanism, used under extreme conditions, that resulted in jamming together of the overlapping fused cover plate pairs (the configuration commonly preserved in the fossil record).

Origin of the Anomalocystitida derives from *Reticulocarpos*-like cornutans. It is suggested that the distal marginal plate elements of the theca in the cornute ancestral stock have been lost. Only **M1–M4** thecal marginals are homologous between cornutes and anomalocystitids.

INTRODUCTION

In the years since Caster's seminal 1952 paper on *Enoploura* Wetherby, 1879, which included the first major review of many of the known North American mitrate echinoderms, a great deal of new material and knowledge of stylophorans has come to light. Many new ideas have been presented concerning their classification and how they functioned as animals. Ubaghs (1961 and subsequent publications) pointed out that the tail-like appendage in stylophorans was a feeding organ (aulacophore) and thereby reversed the orientation commonly assumed for these creatures. Haude (1980) modified Ubaghs' aulacophore model in the mitrates by proposing that they pipetted nutrients off the sea floor through an opening in the distal end of the aulacophore. Abundant examples of closed terminal ends of mitrate aulacophores show that view to be untenable. This work supports Ubaghs, with some minor modifications in interpretation of the deployment of the aulacophore as a feeding organ.

Ubaghs' opinion on the location of the mouth and function of the aulacophore is by no means universally accepted. Philip (1979, pp. 458–460), for example, suggests that the distal opening in all homalozoans is the site of both mouth and anus, the gut being U-shaped. Philip reflects the traditional view held by authors prior to Ubaghs' work of 1961. More recent adherents to this model are Kolata and Jollie (1982) and Kolata (1984). In the latter work, Kolata postulates a shallow burrowing habit with the distal (abaulacophoral) end protruding from the substrate along with the articulating distal spines.

Jefferies (1967, 1968a, and subsequent papers) has proposed that the Stylophora are not echinoderms at all, but are more properly placed in the chordates under the subphylum Calcichordata Jefferies, 1967. His views have met with a storm of rebuttal (Jefferies, 1968b, Ubaghs, 1975, Philip, 1979, Chauvel, 1981, Kolata and Jollie, 1982, and Jollie, 1982), in which I concur.

Various aspects of stylophoran evolution are also under debate. I support Ubaghs' view that homalozoans are polyphyletic and that their primary symmetry is nearly, but not truly bilateral. Caster (1968, 1983), on the other hand, strongly suggests that homalozoans are monophyletic and that the ancestral echinodermal radical was triradiate. Using cladistic methods, Paul and Smith (1984, pp. 461–462) would derive the carpoid homalozoans from an Early Cambrian asymmetric solute radical, and by virtue of their methodology argue that the group is monophyletic.

OVERVIEW OF RECUMBENT ECHINODERMS

In this brief introductory look at the homalozoans and other recumbent echinoderm groups (*i.e.*, pleurocystitids and rhipidocystians), I suggest that the overall morphologic similarity displayed by all of these groups is due to convergence brought on by adaptation to similar bottom-living habits. Generally all of these forms have a high degree of thecal streamlining and bilaterality (but rarely are they truly bilateral). In most, a rim of substantial marginal plates surrounds flexible polyplated central surfaces on both inferior and superior surfaces. In some, one or both somatic surfaces are also regularized into rigid surfaces. Ventral or inferior surfaces are commonly concave, with the marginals serving as runners or skids to minimize adhesion to the bottom. In many forms, appendages such as columns, steles, and aulacophores were adapted to serve locomotor functions. These recumbent forms not only exploited a similar food source, but in doing so exercised some degree of vagility in moving from place to place using their elongated appendage, or, minimally, were sufficiently vagile to favorably orient themselves on the sea floor relative to nutrient-bearing currents.

Most of these forms are found in low-energy environments where lime muds to limy shales were deposited, although higher energy environments (*i.e.*, in calcarenites and fine-grained sandstones) are associated with a number of genera. These low-energy environments suggest that stylophorans fed at or very near the water–sediment interface, where nutrients accumulated. Perhaps these organisms are best described as concentrate suspension feeders, utilizing the rich organic concentrates and associated microbiota present in slow current regimes in the first few mm above the water–sediment interface. None of the mentioned recumbent echinoderms appears to have been a true suspension feeder in the "upper" water column. The total range of these recumbent feeders is from Middle Cambrian to Early Pennsylvanian. The greatest diversity, if all recumbent echinoderms are considered together, is in the Middle and Late Ordovician. It should be noted that articulate brachiopods and nestling clams, which derived their food from the same part of the water column, also enjoyed considerable diversity in the Middle and Late Ordovician.

I can only speculate why homalozoans and recumbent blastozoans did not persist higher in the geologic column. They were probably supplanted by more efficient forms or eliminated by durophagous predators (Signor and Brett, 1984), because there is little reason to believe that the physical aspects of this ecologic niche have significantly changed since the Early Paleozoic.

REVIEW OF THE SUBPHYLUM HOMALOZOA

The subphylum Homalozoa Whitehouse, 1941, is an artificial grouping of four morphologically similar classes that ecologically exploited the nutrient-rich layer at and near the water–sediment interface, and perhaps the smaller elements of the closely-adjacent meiofauna. Homalozoans range from the Middle Cambrian to Early Pennsylvanian and manifest their greatest abundance and diversity in Middle and Late Ordovician, at which time recumbent bottom-living echinoderms of the subphylum Blastozoa are also at the acme of their abundance and diversity.

The class Homostelea Gill and Caster, 1960, is made up of a single order, the Cincta Jaekel, 1918, and is limited to the Middle Cambrian of Europe and North Africa.

The class Ctenocystoidea Robison and Sprinkle, 1969, is also limited to the Middle Cambrian of North America, Europe (France and Bohemia), and North Africa, and is the only "carpoid" group without an appendage.

The class Homoiostelea Gill and Caster, 1960, ranges from the Late Cambrian to the Middle Devonian of Europe and North America. Because of their ecological convergence, members of this class show remarkable similarities to some stylophoran genera and to several of the pleurocystitid rhombiferans, such as *Amecystis* Ulrich and Kirk, 1921, and *Pleurocystites* Billings, 1854 (see, *e.g.*, Dehm, 1934).

The class Stylophora Gill and Caster, 1960, ranges from the Middle Cambrian to Early Pennsylvanian and is geographically the most widely-distributed class, being found in North America, Europe, South America, Africa, and Australia. To date, no stylophorans have been reported from the several continental plates that make up Asia. Stylophorans have a long feeding organ, the aulacophore, that in some is strongly homeomorphic with the stem or stele of homoiosteles. This homeomorphy, as discussed below, is probably in part due to the convergence in locomotor function.

THE CLASS HOMOSTELEA

Homosteleans, which are restricted to the Middle Cambrian, are characterized by a thecal margin of large plates, and slightly convex superior and inferior surfaces of smaller plates, presumably forming flexible surfaces. Antipodal to the single appendage, two juxtaposed openings, the mouth and anus, argue for the presence of a U-shaped gut in the living animal. Derstler (written commun., 1986) and Paul (written commun., 1986) have reported that a small structure like an anal pyramid is located near the operculum (over the ?anal opening) in the field of small flexible platelets on the superior surface. The function and frequency of occurrence of this structure is unknown. The short and probably relatively inflexible stele appears to be dimerous; the large dimeres are interpreted to be extensions of the thecal marginal plates. Dorsal and ventral intercalates give the structure a superficially tetramerous appearance. The intercalates along the length of the stele may be homologous with the thecal centralia. Nowhere among recumbent echinoderms is the derivation of the major appendage (stele, column, or aulacophore) from the theca as clear as it is in the Homostelea. The smooth transition from marginal plates to stele plates is reminiscent of some early eocrinoids (see Sprinkle, 1973, pp. 36–40), where the column appears to be differentiated from existing aboral thecal plates (see Ubaghs, 1968b, p. S576).

The primitive deployment of transverse epithecal food grooves on the marginal plates, coupled with the closely positioned mouth and anal openings, suggest an ancestral stemmed form that derived its food from the water column and secondarily became recumbent on the sea bottom, presumably to exploit a richer food source. Only the homosteleans and homoiosteleans offer strong evidence for once having been attached "pelmatozoans" (Ubaghs and Robison, 1985), and as such, free-standing, suspension-feeding echinoderms.

The juxtaposition of the mouth and anus, which is good evidence for a U-shaped gut, and the theca–stele transition are both characteristics of homosteleans that clearly make them different from all other homalozoans. On philosophical grounds, it might be more sensible to place the homosteleans in the Blastozoa Sprinkle, 1973, where transverse ambulacra, (?)anal or (?)gonopore pyramids, transitional plating between theca and column, and essentially undifferentiated columns are more common. However, the lack of exothecal or true epithecal brachioles makes such a reassignment on sound morphological grounds impossible.

THE CLASS CTENOCYSTOIDEA

The Ctenocystoidea are unusual homalozoans that are devoid of any sort of appendage, and their marginal plates do not extend from top to bottom surfaces. Rather, they are laterally sutured, in roughly opposed top and bottom series. Their top and bottom polyplated somatic surfaces are similar, however, to those of other polyplated homalozoans and recumbent blastozoans. The anterior ctenoid structures are unique, but laterally, grooves impressed into the marginals are reminiscent of the lateral food grooves of the Homostelea.

Ubaghs (1975, p. 84) has suggested that this class is closer to the Stylophora than any other class. However, on morphological grounds, there is little evidence for this. One might argue with equal persuasion for phylogenetic closeness to the Homalozoa (both groups have similar lateral food grooves on the marginals) or the rhipidiocystian eocrinoids (both groups have a similar thecal shape, and ctenoid organs may be homologous with brachiole bases); all this, of course, is speculation. Horns on the posterior left side of the marginals may suggest a remnant insert area of a lost appendage. Sprinkle and Robison (1978) have detailed what is known of this group. At this time, ctenocystoids cannot be allied with any other class and their inclusion in the Homalozoa is one of convenience.

Although this class was known until recently only from the Middle Cambrian of North America (Utah and Idaho, *Glossopleura* Zone), it is now known from North Africa (Sprinkle, oral commun., 1985), the Jince Formation of Bohemia (Fatka and Kordule, 1985), Montagne Noire, France (Ubaghs, 1987), and the Coonigan Formation of New South Wales, Australia (Jell, Barrett, and Banks, 1985).

THE CLASS HOMOIOSTELEA

Homoiosteleans commonly bear strong resemblance to the stylophorans because of the similarity of their main appendage and, in some, thecal morphology. In the homoiosteleans the proxistele is fundamentally and commonly an imbricating tetramerous structure that grades into a trimerous or dimerous medial section, the mesistele, which in turn grades into a long dististele that commonly is dimerous, but by intercalation may be superficially trimerous. The close similarity of the homoiostelean stele to the stylophoran aulacophore is probably due to the similarity in locomotor function (*i.e.*, in the wriggling or swimming of the animal, with the appendage posterior). In the homoiosteleans, the stele is a stem: in stylophorans, the aulacophore, a stem-like structure, is also the feeding organ. Juvenile specimens of *Castericystis vali* Ubaghs and Robison, 1985, from the Middle Cambrian of Utah, further suggest this appendage is a stem: they were attached to the substrate at the distal end of the stele. More mature specimens broke loose and then used the stele as a locomotor organ. Despite the numerous superficial similarities between homoiosteleans and stylophorans, nothing suggests that the appendages or the thecal plates can be homologized[1]. The single, anterior, undifferentiated, biserial feeding appendage in homoiosteleans is a true arm, a skeletal extension of the body cavity (Caster, 1968, p. S586); all other recumbent bottom-feeding echinoderms with biserial feeding appendages (*e.g.*, pleurocystitids, rhipidocystians) have brachioles, and with rare exceptions have two or more. Some Ordovician homoiosteleans from North America (*e.g.*, *Iowacystis* Thomas and Ladd, 1926, and *Belemnocystites* Miller and Gurley, 1894) have well-developed marginal and infracentral plates and bear superficial similarities to some mitrate stylophorans and to some pleurocystitid rhombiferans.

THE CLASS STYLOPHORA

The Stylophora, as previously indicated, have an appendage somewhat similar to the stele of the homoiosteleans. Proximally it is tetramerous, abruptly giving way to a basically uniserial cone-shaped section (stylocone) or a section that has flanges (styloids), which in turn grades into an elongate uniserial "tail-like" section. Both the styloid/stylocone and distal section have covering plates. On the styloid/stylocone they are small: on the distal section, they are large, commonly firmly articulated with the basal ossicle, and almost always tightly sutured to each other. In the Stylophora, the appendage is the aulacophore and serves as the feeding structure. The aulacophore (Gr. = groove bearer) is named for the food groove on the superior surface of the ossicles (Ubaghs, 1968a, p. S532). The structure and organization of the aulacophore, while somewhat similar to that of the homoiostelean stele, is unique. No class other than the Stylophora has an exothecal subvective structure with proximodistally tripartite organization, attachment devices for temporary anchoring (spines and flanges on styloids), and a functional mouth located in the structure itself (between the proximal aulacophore and the styloid/stylocone), and that serves as a locomotor organ. Not all authors agree with the functional aspects of this interpretation. Indeed, the subvective nature of the aulacophore is questioned on several fronts (Jefferies, 1967, 1968b; Philip, 1979; Kolata and Jollie, 1982). These authors opt to place the mouth at the opposite end of the theca.

Stylophora have "suffered" more than any other recumbent echinoderm group from interpretation and reinterpretation. This work is no exception, and a revised morphological analysis of the aulacophore, and an overall discussion of the *modus operandi* of the mitrates is presented herein.

Taxonomic Position

Homalozoans are among the most enigmatic of fossils. No homalozoan group has been more variously interpreted than the Stylophora. Because of different interpretations concerning the aulacophore, position of mouth and anus, and identity of superior and inferior surfaces of the theca, many different sets of morphological terms, orientations, and indeed zoological affinities are rooted in the literature. In this paper, I will discuss why I believe the orientation and general functional morphology presented by Ubaghs (1961) are correct. I am especially concerned with the rationale for viewing the multisegmented appendage or aulacophore as subvective and anterior. However, I will modify Ubaghs' views on modes of feeding and locomotion.

Other basic organizational interpretations have fallen into two categories: (1) The mouth and anus are located at the distal opening of the theca, perhaps with an introvert tucked inside and extruded for feeding (Kolata and Jollie, 1982). An extension of this reasoning is that the animal is presumed to have a U-shaped gut (Philip, 1979). (2) These animals are not echinoderms, and should be placed in a subphylum of the Chordata, the Calcichordata (Jefferies: 1967; 1968a; and subsequent papers). In Jefferies' scheme the Mitrates are commonly inverted, relative to "echinoderm" orientation; instead of the aulacophore extending into the substrate as a digging and/or locomotor organ, the flanges on the styloid, in his orientation, are directed away from the substrate, and locomotion is effected by sapping movements of the aulacophore (Jefferies, 1984). Numerous aspects of mitrate morphology indicate, in my opinion, that the convex thecal surface is uppermost and the aulacophore did not "grub" in the substrate. Cornutes in Jefferies' scheme are maintained in their usual top–bottom orientation: the oral end of the animal is opposite (distal) to the appendage (aulacophore). I believe that Jefferies' position has been adequately refuted in the literature by others (Ubaghs, 1975; Philip, 1979; Jollie, 1982; Kolata and Jollie, 1982), and in this paper I will treat stylophorans as echinoderms.

Stylophora must be regarded as Echinodermata because of many of the traits of that phylum which they variously manifest. All have unicrystalline calcium carbonate plates that are infused with stromal cavities. Carlson and Fisher (1981) have shown that in the mitrate *Enoploura* Wetherby, 1879, stereom to which muscles and ligaments were attached is discernible in the articulations of the aulacophore. Also, other features together characteristic of echinoderms in the Stylophora are anal pyramids, sutural pores, articulated

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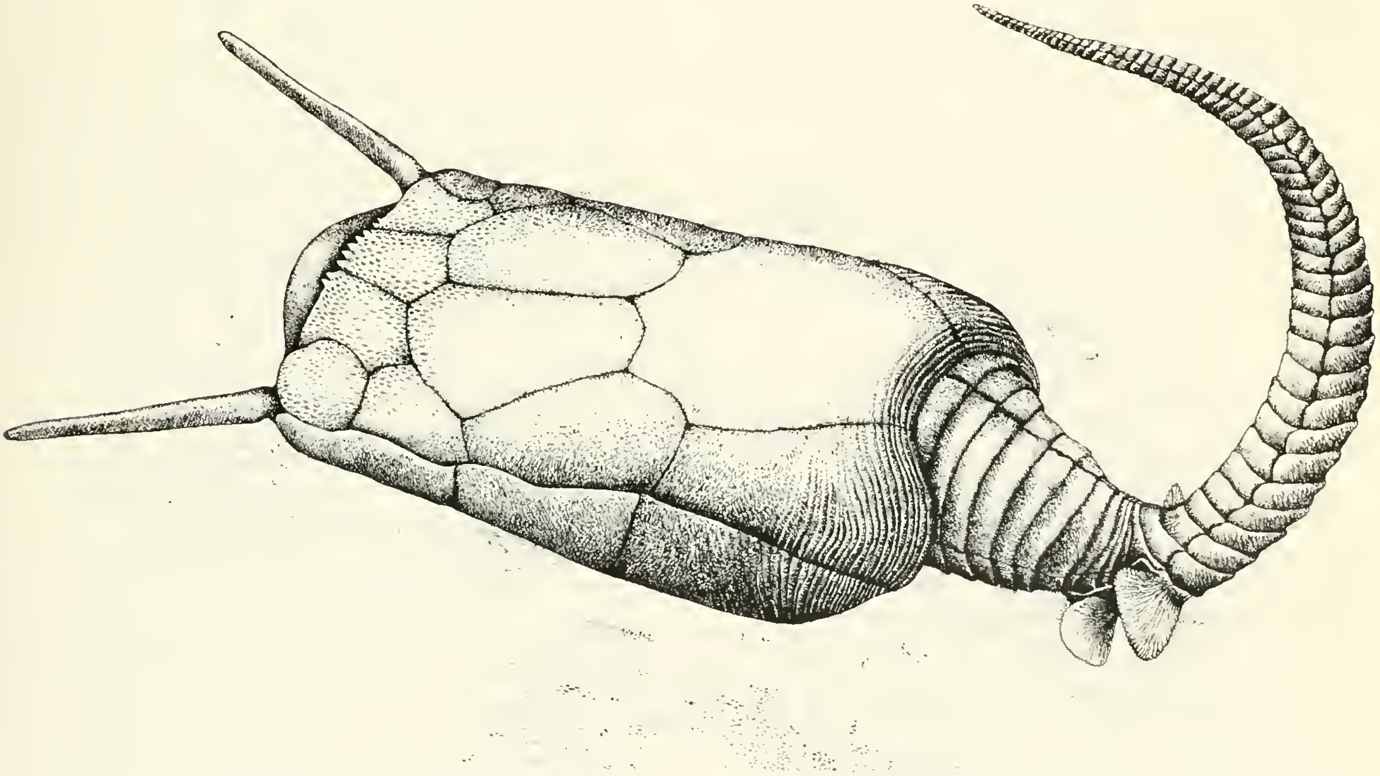
[1] For a dissenting opinion concerning the appendage, see Caster, 1968, p. S582.

spines, and differentiated marginal and somatic plates. Syzygial sutures have been observed in the styloids of *Enoploura*, and pillar structures, similar to those in sand dollars, have been observed on both sides of the distal thecal opening in *Ateleocystites* Billings, 1858 (Kolata and Jollie, 1982) and in *Anomalocystites* Hall, 1858 (herein). Evidence for a water-vascular system in the Stylophora is good. The best evidence is seen in the aulacophore of *Phyllocystis* Thoral, 1935 in the form of parallel grooves and transverse grooves connecting to the main food groove (Ubaghs, 1968a, p. S529; Ubaghs, 1969, pp. 32–36). Similar structures, less well defined, are seen in the aulacophore of *Mitrocystites* Barrande, 1887 (Ubaghs, 1968a, p. S531). In both cases shallow pits at the ends of the transverse grooves would have been sites of the ampullae for the podia. Structures such as cothurnopores and ctenoid organs have been variously interpreted but are probably respiratory. *In toto*, the combination of characteristic echinoderm features seems sufficient to place stylophorans in the Echinodermata.

Morphology, Functional Morphology, and Life Habits

Orientation

The two major morphological parts of a stylophoran are the theca and the aulacophore (Text-fig. 1). The mitrate theca commonly has single or paired movable spines at the opposite end of the theca from the aulacophore. The proximal ends of the theca and of the aulacophore are at their junction: it should be noted that the aulacophore is often inset several segments into the theca. The terms *oral* and *aboral* are not synonymous with *proximal* and *distal*, respectively, with regard to the theca, because the oral opening appears to be at the distal end of the proximal aulacophore. Thus, either on the theca or on the aulacophore, *distal* should be interpreted as away from where the theca and aulacophore join. In this sense it is similar to the proximal plane of "pelmatozoans" except here it is used with a feeding appendage and not with a columnar appendage. The terms *proximal* and *distal* will be used



Text-figure 1.—Reconstruction of *Enoploura popei* in its distressed orientation, with the distal aulacophore reflexed over the proximal aulacophore and proximal end of the theca. This figure is based on UCM 25993 (Pl. 6, figs. 1–3). In this orientation, the cover plates are tightly closed. In many cases, this is the curved condition in which the aulacophore is found in the fossil record. The moveable distal paired spines help buttress the theca and, along with styloid blades, aid in stabilizing the organism in the current, which in this figure moves from lower right to upper left.

herein to avoid confusion. The terms *superior* and *inferior* or *dorsal* and *ventral* are used relative to perceived habitus orientation, and in the strict morphological sense may not be correct.

The theca in most mitrates is convexo-concave or convexoplane: the convex face is invariably superior or dorsal. This orientation is suggested not only by hydrodynamic considerations but because the ventrolateral margins are commonly produced into runners or skids, apparently to minimize adhesion to the substrate. Spines or flanges on the styloid and distal aulacophore for purchase in the substrate always face downward relative to the convex thecal face: thus the food groove faces away from the substrate. The single or paired distal articulating spines helped buttress the animal and served as sensory–tactile structures, analogous to a cat's whisker, when the animal was at rest.

In living and feeding mitrates, the distal aulacophore was bowed upward from the styloid; the distalmost end rested against or was close to the substrate (Parsley and Caster, 1982; Parsley, 1988). Many mitrate specimens have been found with the aulacophore preserved with a concave-upward curvature. This probably was an extreme distress position that was preserved in death. Cornutes, on the other hand, deployed the entire aulacophore parallel to the sea floor (Parsley, 1988).

Morphology

Theca

Almost all mitrates and some cornutes have an essentially bilateral streamlined theca (sagittate outlines are seen in some cornutans [*e.g.*, *Phyllocystis* Thoral, 1935, *Amygdalotheca* Ubaghs, 1969]), but true bilateral plating is rare. Some Silurian (*Tasmanicytidium* Caster, 1983, and *Notocarpos* Philip, 1981) and Devonian (*Allanicytidium* Caster and Gill *in* Ubaghs, 1968a) genera appear bilaterally symmetrical in their plating, but these are rare and restricted to the present-day Southern Hemisphere (the mid-Paleozoic Malvinokaffric Realm). The proximal end of theca is the thickest and most convexly-rounded part of the dorsal theca. Distally the theca thins and the superior surface is flattened. Commonly the greatest width is just distal to the proximal end of the theca. Distal tapering is slight in most mitrates, except for sagittate forms, and most genera have a blunted distal end. The distal aperture includes the anal opening. In some (*e.g.*, *Enoploura* Wetherby, 1879, and *Ateleocystites* Billings, 1858), a distinct lip extends distally from the ventral distal marginals and is commonly cantilevered slightly above the concave ventral surface. In *Anomalocystites* Hall, 1858, the lip is folded back on itself to raise the threshold of the distal opening higher above the substrate.

Some cornutes also have irregularly-shaped thecae (which are commonly outlined by well-defined marginals) that are commonly likened to a medieval boot or shoe. In these cornutes, the marginals have prominent ventral knobs that contact the sea bottom. Genera such as *Cothurnocystis* Bather, 1913, and *Galliaecystis* Ubaghs, 1969, which manifest these features, are considered to have been essentially sessile (Parsley, 1988).

Aulacophore

Ubaghs (1961, 1968a) clearly demonstrated (to the satisfaction of most workers) that the distal end of the appendage in the Mitrata and Cornuta was the primary feeding organ. He renamed the entire appendage the *aulacophore* and re-oriented it by rotating it 180° (contrary to the orientation of previous authors), to place it at the anterior end of the animal, in normal, bilaterian mouth-anterior fashion. Several features of the distal aulacophore indicate that it was posterior during locomotion, but its feeding orientation is not as obvious and is open to some speculation. In all stylophorans, the aulacophore is basically the same structure and remains conservatively unchanged in each of the two major orders, the Cornuta and the Mitrata. In each order, a tetramerous proximal aulacophore distally (after six or more segments) abruptly gives way to a stylocone (in cornutes and in a few mitrates) or styloid (in most mitrates), which is made up of fused uniserial ossicles. The styloid/stylocone is derived from the distal aulacophore by fusion of at least three of its most proximal uniserial ossicles. In the mitrate *Enoploura* Wetherby, 1879, the two styloid flanges are lateral extentions of ossicles on either side of the syzygially-fused sutures (Text-figs. 10 and 13), and represent an extreme in styloid development. Each styloid/stylocone ossicle has a pair of small cover plates. The styloid/stylocone grades distally into the distal aulacophore, which is made up of large, articulating, uniserial ossicles. Each ossicle is covered by large paired, distally-overlapping covering plates (Text-fig. 2). The distal aulacophore may be one-and-one-half to two times the length of the theca.

Generally, feeding appendages are considered to be uniserial (in stylophorans, crinoids, and paracrinoids) or biserial (in some advanced crinoids and almost all blastozoans), their covering plates being incidental because of their small size. In the uniserial mitrates, where the cover plates are much larger and do not seem to be erectile, they are instead tightly sutured along the dorsal sagittal axis. Here the distal aulacophore is at least *functionally* a triserial appendage. The cover plates roof over a well-defined food groove that terminates at the junction of the styloid and the proximal aulacophore. The feeding mechanics of the mitrate aulacophore, through the intersegmental arcuate openings made by the overlapping cover plates, is discussed below. Earlier suggestions by Parsley (1980) that the cover plates may have rotated outwards to expose the food groove do not, in light of newer data on the nature of cover plate suturing, seem to be viable as a feeding mechanism. In cornutes, the cover plates open to expose the food groove. This is especially manifest in irregular or asymmetrical forms, which appear to have been sessile (Parsley, 1988).

The stylophoran aulacophore and the homoiostelean stele are very similar. In both, the proximal part of the appendage is tetramerous. In some of the dendrocystitid homiosteleans, the tetrameres secondarily break up into multiplated rings and smaller annulations of platelets (see Caster, 1968, pp. S594– S598). Distally, the stele grades into a dimerous distal stele, commonly through an intermediate area, the mesistele, that necks down and twists. In some genera, large intercalates make this area trimerous. The function of the mesistele seems to have been one of stiffening, to impart more leverage to the flexible dististele. This leverage presumably made locomotion more efficient.

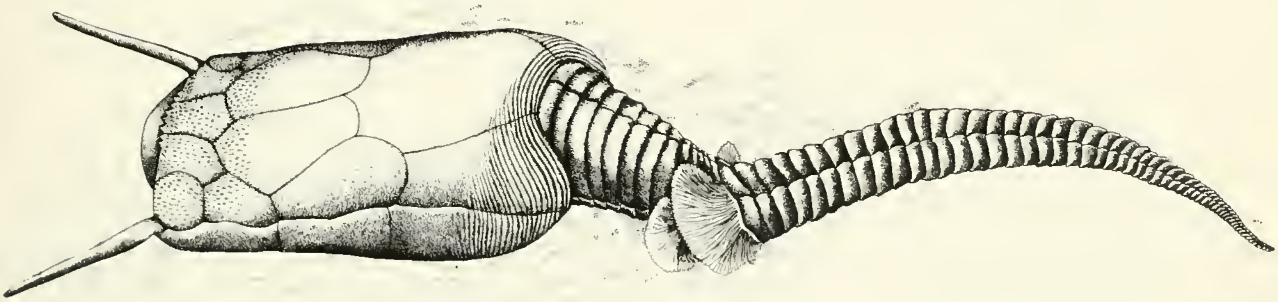
The mesistele–stylocone/styloid and distal stele–distal aulacophore, while they are commonly superficially similar, are basically different structures, and their shared homeomorphy is apparently due to functional convergence.

The adthecal part of the aulacophore structure, the proximal aulacophore, has a very large internal lumen which is continuous with the interior of the theca. The proximal aulacophore extends through, not out from the surface of the marginals as, for example, in most blastozoans, and might best be viewed as a proboscis with the mouth opening at the distal end. The only other bilateral echinoderms with a feeding proboscis that extends through an opening in a rigid theca are the psolid holothurians. Only very rarely [*e.g.*, in *Kierocystis*, n. gen., and possibly in *Allanicytidium* Caster and Gill *in* Ubaghs, 1968a] do superior proximalmost tetrameres of the proximal aulacophore abut against the external surfaces of the marginals, rather than being significantly inset and resting against the apophyses.

The aulacophore apophyses in most stylophorans invariably considerably restrict the openness between theca and aulacophore. The apophyses serve for muscle attachment, and against them the proximalmost platelets of the proximal aulacophore abutted.

The mouth is located at the juncture of the stylocone/styloid and the alimentary canal, which in turn is located at the distal end of the proximal aulacophore. This is suggested by the deeply-incised food groove on the superior face of the styloid, which is closely juxtaposed to the distal elements of the proximal aulacophore. Ingested food was passed under the plating of the proximal aulacophore and into the theca. None of the many specimens, belonging to diverse genera, that have been examined show evidence that the food groove passed over the proximal aulacophore and entered the theca at the juncture with proximal aulacophore.

Extensions of the ambulacra away from the mouth onto exothecal extensions are quite common in the Echinodermata and have occurred independently a number of times. In some, these ambulacral extensions



Text-figure 2.—Reconstruction of *Enoploura popei* in its normal feeding orientation. This figure is based on UCM 25993 (Pl. 6, figs. 1–3). While the styloid and proximalmost distal aulacophore segments bite into the sediment for stability, with additional buttressing from the distal spines, the distal aulacophore curves convexly over the substrate to feed. The openings thus formed between the fused cover plates are chevron-shaped to narrowly hemi-elliptical, but are large enough to admit food particles to the food groove. Current direction is from right to left.

include evaginations of the coelomic tissues as, for example, in crinoids. These are primarily uniserial structures and bear pinnules. Others do not seem to have coelomic evaginations in the exothecal extensions and are biserial (brachioles) and are only rarely "pinnulate". Brachioles are manifest in blastozoans such as rhombiferans, diploporids, and eocrinoids. Rarely, brachioles may be triserial, as seen in the diploporid *Eumorphocystis* Branson and Peck, 1940 (see Parsley, 1982).

The unidirectional extension of the ambulacrum away from the mouth in stylophorans is very primitive and apparently was never part of a more complex arrangement. Indeed this would be nearly impossible, since the mouth opening is on the aulacophore itself, located between the proximal aulacophore and the styloid/stylocone. Recent authors have championed ideas of early primary symmetry in echinoderms; Caster (1968, 1983), Paul and Smith (1984), and Smith (1988) for a triradiate system; Parsley and Mintz (1975), and Parsley (1982) for a transverse–bilateral system. Neither can apply to the Stylophora.

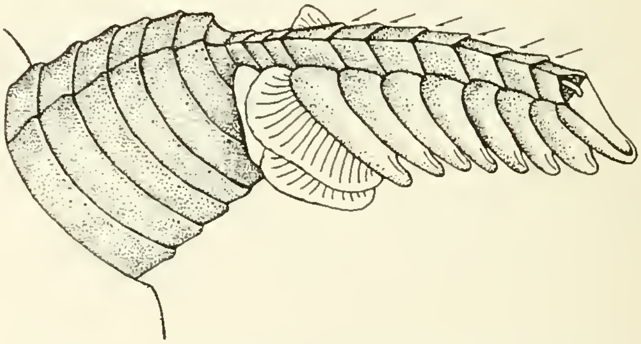
The exothecal extension of coelomic tissue in the Stylophora would have extended into the proximal aulacophore and the proximal end of the stylocone/styloid. The distal aulacophore is a true uniserial structure like the arms of crinoids and paracrinoids, but without evaginations of the coelomic linings extending through the ossicles. Coelomic tissue, including the water-vascular system, may have been developed on the superior surface of the ossicles, where it would have been closely associated with the food groove.

With the overall similarity of the distal aulacophore to other echinoderm feeding appendages, it is hard to imagine that it is anything else. The maintenance in mitrates of a large grooved area on the upper surface of the ventral ossicles, especially in conjunction with the large space formed by roofing over the food groove with very tightly sutured or possibly even fused cover plates suggests primary and continued use of the structure in a subvective role.

I suggest that if the aulacophore were not a feeding structure, selective pressures to enhance locomotion would have reduced the hollowed-out aspect of the structure and in other ways would have modified it for greater strength and flexibility. Rather, it seems that a balance of feeding and locomotor selective pressures was responsible for the conservative morphology of the aulacophore exhibited in both cornutes and mitrates.

Actual function of the distal aulacophore differs somewhat between the Mitrata and the Cornuta. In the cornutes, Ubaghs (1961, 1968a) has conclusively shown that the cover plates opened (apparently in succession from the proximal to the distal end, because of distal overlap) to expose the food groove. Feeding was apparently carried out by the distal aulacophore in the nutrient-rich layer just above the water–sediment interface. The cornute aulacophore, especially as seen in the genus *Phyllocystis* Thoral, 1935, may have had a water-vascular system. Lateral depressions on either side of the food groove are connected to it by short transverse grooves, one set per segment. The geometry of this interconnected groove system is strongly suggestive of a water-vascular system. Ubaghs (1968a) suggested that the lateral depressions were for ampullae, with podia extending from them for feeding purposes. Similar structures suggestive of a water-vascular system have been observed in other cornutes (*e.g.*, *Ceratocystis* Jaekel, 1901), but have been observed only in a single mitrate (*Mitrocystites* Barrande, 1887).

Distal aulacophores in mitrates are commonly segmentally intact, strongly suggesting that the dorsal (sagittal) cover plate suture was very tight, as are the sutures between the cover plates and the ventral ossicle. In conjunction, the distal aulacophore abuts the styloid at a narrow angle to the perpendicular: this angled articulation kept the aulacophore away from the sea floor. Parsley (1980), Parsley and Caster (1982), Sprinkle (1976), Ubaghs (1979), and Carlson and Fisher (1981) have interpreted this, and the concave upper surface of the distal aulacophores that are commonly preserved, to mean that the distal aulacophore was held straight up or curved above the proximal aulacophore and possibly over the proximal theca ("scorpion" configuration). Thus the ossicles would face into the current like the arms of rheophobic crinoids, and feeding would occur in back eddies in the lee of the ossicles. Kolata and Jollie (1982) have pointed out that, indeed, the cover plates could not open and in the *concave*-upward configuration, the cover plates are too tightly



Text-figure 3.—An oblique view of the proximal aulacophore, styloid, and a portion of the distal aulacophore of *Enoploura popei*. By convexly arching the aulacophore ossicles, the fused plate pairs are distally prized open to admit food-laden currents [arrows]. Food moved to the mouth, at the junction of the proximal aulacophore and styloid, *via* ciliary action along the longitudinal food groove.

pinched together to expose the food groove. This seems be the "distressed" pre-mortality position, and that most commonly preserved (Text-fig. 1). This configuration is especially prevalent in Cincinnatian age specimens of *Enoploura*, and is common in other Ordovician mitrates as well. Devonian genera such as *Rhenocystis* Dehm, 1932 (pl. 1, figs. 4–9), *Paranacystis* Caster, 1954a (text-fig. 2; pl. 1, figs. 2, 3, 7, 8; pl. 3, fig. 1) and *Anomalocystites* Hall, 1858 (pl. 1, figs. 6, 7), are also good examples. Suspension feeding by holding the aulacophore aloft in the water column, also would have rendered the animal hydrodynamically unstable. Preliminary results from testing 1:1 scale models of *Enoploura*-like mitrates in a flume clearly suggest that the aulacophore-aloft "scorpion" configuration was stable only when the animal was facing directly into the current. Cross currents, even under 10 cm/sec, would topple the model: by direct inference this configuration seems unlikely in living animals.

Examination of more than a dozen distal aulacophores also shows that the ventral ossicles are commonly strongly denticulate: the proximal ventral ossicles of this series are similar to those of the styloid. These denticulations are curved toward the theca and could have provided additional purchase on the sea bottom. The recurved or undercut flanges allow the aulacophore to bow convexly upward from the styloid to the tip. In doing so, the cover plates were prized open, forcing the distal ends of the cover plate pairs upward, thereby exposing the food groove by creating narrow, arcuate to chevron-shaped openings. By altering the degree of curvature, the openings could be enlarged or diminished. The distal edges of the cover plates served as small scoops directing nutrient-rich waters toward the food groove (Text-figs. 2 and 3). Presumably only small particulate matter would be able to reach the food groove, minimizing clogging problems in this roofed-over system. An analogous scheme of narrow openings allowing size-sorted particles to enter the food conduit area is used by articulate brachiopods.

Feeding close to the water–sediment interface placed the mitrates in the same niche as other recumbent homalozoans and blastozoans. The length of the food groove on the aulacophore, in proportion to thecal size, indicates that the relative size of the feeding area is small. Since these animals are presumed to have been active and would have had moderately high energy-input requirements, the relatively small feeding area of the aulacophore clearly suggests not only that it was efficient, but also that it exploited a nutrient-rich environment. The most available high-nutrient food source would be in the concentrated organic layer just above the water–sediment interface. Feeding, with the aulacophore held in a shallow convex arc would have been far more stable than holding it aloft, directed into the prevailing current. Cornutes also would have fed in the nutrient-rich bottom layer. The erectile cover plates in cornutes suggest that a wider range of size of food particles could be utilized. This seemingly more primitive scheme had the advantage of allowing less selective but more efficient feeding in asymmetrical, essentially sessile cornutes, but they may have lacked the sorting ability to allow continuous feeding in turbid waters. Cornutes may have had to close their cover plates under very turbid conditions, while mitrates would have been able to continue feeding by virtue of the sieving ability of their non-erectile plates.

In mitrates, the very narrow slit in the styloid near the end of the food groove suggests food was probably finely particulate. Fine particulate food was probably more readily digestible and more easily transported down the food groove. If Ubaghs (1961) and Parsley (1988) are correct about the presence of a well-developed water-vascular system in the cornute aulacophore, the sorting and rejection of food particles could have been carried out by action of the podia.

The aulacophore was fully extended during locomotion. The distal overlap of cover plates and their tight sutures on the top and sides of the aulacophore also made it a stronger and more efficient locomotor appendage.

Among most recumbent–vagile Early Paleozoic echinoderms, the theca commonly has one or both thecal faces flexibly polyplated, presumably for respiratory pumping. Parsley (1982; 1988) has suggested that in some forms pumping may also have aided in feeding. In mitrates that have rigid thecae (*e.g.*, *Enoploura* and *Ateleocystites*), the supracentralia have what appear to be muscle scars on their inner faces. These scars are presumed to be part of a muscular system that compressed either or both the gut and surrounding body cavity, to propel water through it (Text-figs. 12, 17). In mitrates, gut pumping may have induced a current inside the roofed-over aulacophore. The pressure differential along the food groove would have created incurrents through the narrow arcuate openings made by the cover plates, and ingestion through the narrow openings may have been a more dynamic process than would one simply powered by ciliary currents.

Parsley (1981, p. K2) has also shown that in life *Enoploura* may have taken refuge under brachiopod shells (*e.g.*, *Rafinesquina* Hall and Clarke, 1892). Several specimens from the Middle Ordovician Lexington Limestone of Kentucky suggest that the theca was under the shell and the aulacophore extended out from beneath it.

The common occurrence of mitrates in fine-grained sandstones and limy shales would indicate that they were not efficient swimmers and/or feeders in higher energy environments. In lower energy environments, more nutrients would accumulate at the water–sediment interface, and aulacophore feeding would be more efficient. Most mitrates and solutes, for that matter, were little more than wrigglers, and were not capable of swift or sustained movement. Lateral overlapping in the inferior, or both superior and inferior, sutures of the proximal aulacophore or stele would permit limited lateral movements in this probably well-muscled area. These lateral movements, translated distally, would have set up propulsive, undulating waves.

Movement and orientation of mitrates can be summarized as follows: (1) The aulacophore was both a feeding and a locomotor organ. (2) While the animal was being propelled by the aulacophore, the distal end of the theca acted as the prow of the animal. The articulated spines may have aided in maneuvering. (3) The styloid blades were primarily for anchoring the animal, and were not the primary locomotor structures. (4) The animal displayed a rheotaxial orientation.

Lastly, it must be stressed that the orientations used herein are functional and perhaps only partly morphological. As is stated elsewhere, it is unwise to attempt to postulate orientation on the basis of inferred larval type [*cf.* Caster's (1952, p. 10, fn. 4) discussion of the basic orientation suggested by Bather (1900), which is primarily based on the embryology of the comatulid crinoid *Antedon* Freminville, 1811]. Morphologically, aulacophore-bearing carpoids can be oriented aulacophore = anterior; aboral theca = posterior. Whether or not the carapace and plastron should be morphologically "dorsal–ventral" or "right–left" is largely speculative.

ORIGINS AND PHYLOGENY OF THE MITRATA

Most of the evidence that mitrates are derived from cornutes is based on homologous elements and on morphological trends. The two groups share a homologous aulacophore and several homologous thecal elements; primarily, the marginal plates. Mitrates appear simpler than their cornute ancestors, with reduced numbers of marginals, fewer centralia, and reduced anal structures. Mitrates show a higher degree of bilaterality (including loss of the cornute zygal or strut), which seems to be related to adaptation for greater mobility.

Since the publication of the *Treatise on Invertebrate Paleontology, Part S* (Ubaghs, 1968a), several new cornute and mitrate genera have been described, and it is now possible to construct a reasonable scenario showing in generalized terms the evolution of some of the early mitrates (anomalocystitids and mitrocystitids) from symmetrical cornutes (Parsley, 1988). The evidence is still too sketchy for meaningful cladistic analysis: a viewpoint that runs counter to that of Jefferies (1981, 1986) and of Jefferies and Lewis (1978). Derivation of an early mitrate from a symmetrical cornute stock involved a number of evolutionary steps. Major changes included relative shortening of the theca, by means of a reduction in the number of distal marginal plates. While there are commonly no more than four paired marginals in a mitrate (possibly up to six pairs in mitrocystitids), there may be up to seven pairs in a symmetrical cornute such as *Amygdalotheca* Ubaghs, 1969. While relative thecal shortening occurs in all mitrates, the mode and manifestation varies with the suborder. In mitrocystitids, marginal plate loss is minimal to none; the distalmost marginals symmetrically move toward and impinge on the anal apparatus. Anomalocystitids commonly have four marginals, the anal apparatus having retreated proximally between the nearly parallel distal marginals. Marginals in lagynocystids are not only reduced in number but are asymmetrically and azygously arranged. The theca in this suborder is also diagonally compressed distally, which is partly responsible for the loss of marginals and centralia. Peltocystids manifest the greatest reduction in marginals and centralia. While not so asymmetrical as lagynocystids, peltocystids also show evidence of distal diagonal compression, and homology of the distal marginals in this suborder is quite problematical.

A development concomitant with distal loss of marginals is that instead of the distalmost single (in peltocystids and lagnocystids) or paired (in anomalocystitids) marginals being lost, a flexible articulation was developed between them (or it) and the adjacent marginal(s), and the distalmost marginal(s) functioned as distal spines. This morphologic deviation was first suggested by Kirk (1911, p. 25).

In the Mitrocystitidae, there are no articulating spines, and marginals **M5/M'5** and **M6/M'6** may be homologous with **M5/M'5** and **M6/M'6** of *Amygdalotheca* Ubaghs, 1969. Distal marginal **M7** may be an intercalate from the infracentralia. If this marginal plate homology is correct, it probably precludes the mitrocystitids from being ancestral to the anomalocystitids, and suggests that they are an independent lineage (Ubaghs, 1968a, p. S545).

Regularization of the centralia seems to have proceeded more rapidly on the inferior than on the superior surface in all mitrates. On the inferior surface in anomalocystitids, for example, a large central plate is partly surrounded by smaller infracentrals (including the anomalocystitid plate). The smaller plates commonly are concentrated along the distal margin. In anomalocystitids, the distal marginal plates (**M5/M'5** and **M6** in the commonly-used numbering system, equivalent to **m5/m'5** and **m6**, herein) do not resemble the proximal and lateral marginals (**M1–M4**) that commonly lie between the superior and inferior surfaces. Distal marginals **m5/m′5** and **m6** are taken to be infracentralia that have regularized and filled the open gap between the distal ends of **M4/M′4**. Originally these "infracentralia" were probably adjacent to the anal apparatus and retreated with the anus as the ancestral stock paedomorphically shortened (see Text-fig. 4).

The only known exception to this pattern among anomalocystitids is in the Early Caradocian genus *Barrandeocarpus* Ubaghs, 1979, where the inferior distal marginals extend distally from **M4/M′4** in a manner suggestive of a continuous marginal series. These plates are labelled **M5/M′5** and **M6** by Ubaghs (1979, pp. 112–119). There are no articulating spines and I assume that they have been lost, or even more likely, were never present. In *Barrandeocarpus*, as in more advanced anomalocystitids, there are three infracentralia including the anomalocystitid plate. I conclude that the inferior distal marginals **m5/m′5** and **m6** in *Barrandeocarpus* have migrated distally to form a rounded distal margin and are *not* homologous with **M5/M′5** and **M6** of cornutes or mitrocystitids.

While mitrates do retain anal-valve structures, these in most cases are considerably reduced in size and complexity from the condition of their cornute ancestors. The degree to which the anal-valve apparatus was retained appears to be directly related to the degree of thecal shortening and simplification. Mitrates with the least anal-valve reduction are the mitrocystitids, which show the least thecal shortening or reduction of centralia. This can be contrasted with genera of the peltocystitid family Kirkocystidae (*Balanocystites* Barrande, 1887, and *Anatiferocystis* Chauvel, 1941), which demonstrate the maximum thecal shortening, and reduction in plate number, and are without a demonstrable anal opening. Anomalocystitids show a reduced, possibly vestigial anal-valve apparatus in Ordovician and Silurian genera, and this structure is lost in Devonian representatives. The only exception to the correlation of thecal shortening and plate loss with anal-valve simplification, is in *Lagynocystis* Jaekel, 1918, in which the size of the anal apparatus, relative to thecal size is considerably greater. Why thecal shortening and simplification of the theca should be related to anal size and complexity is conjectural. If shortening and simplification was a neotenic process then possible reduction of the anal-valve elements may have been involved: but whatever the reason, the phenomenon is clearly present.

The mitrate aulacophore has the same elements as does that of the cornute. Mitrate aulacophores are laterally compressed, and the ventral ossicles of the distal aulacophore are pointed and undercut (especially at the proximal end) for arching and for purchase on the bottom. The ancestral cornute stylocone was modified to form the styloid — a stylocone with spines or flanges for embedment in the substrate.

To construct a scenario for evolving mitrates from symmetrical cornutes requires morphological types, as stated above, that represent a logical or plausible transition. Ubaghs (1968a) noted that this was difficult because some of the then earliest known mitrates (*Peltocystis* Thoral, 1935, and *Chinianocarpos* Ubaghs, 1961, both from the Early Ordovician) were morphologically more advanced than a number of Middle Ordovician genera. Since that time several new genera have been described that allow a plausible scenario to be constructed. The most generalized of the symmetrical cornutes is the Early Ordovician genus *Amygdalotheca* Ubaghs, 1969. It has seven marginals, a short zygal, and an open distal end (the marginals do not join), which is presumably occupied by the anal-valve apparatus. In order for the theca to gain greater rigidity, either the marginals must form a distal closure, forcing the anal apparatus to the distalmost end of the superior surface (a condition seen in the symmetrical cornute *Phyllocystis* Thoral, 1935), or inferior distal centralia must fuse in order to form a cross-bracing series at the distal margin.

It seems most likely, in light of observed morphological patterns, that all mitrates evolved from a distally "open" symmetrical cornute, even though some early mitrates show distal marginals converging toward the anal-valve. An excellent case in point is the mitrocystitids. These show only slight thecal shortening (six marginals), but distally they impinge on the well-developed anal-valve. The anal-valve is partially floored by the distalmost thecal plate (**M7** of Ubaghs, 1968a) which is a marginal infracentral (a condition well illustrated by *Aspidocarpus* Ubaghs, 1979). Mitrocystitids do not have distal movable spines. The marginals, which are equivalent to spines in anomalocystitids and other suborders, are conservatively maintained as marginals. Mitrocystitids appear to be an early mitrate lineage that probably did not give rise to any other mitrate group.

A genus critical to the understanding of the evolution from symmetrical cornutes to mitrates is *Reticulocarpos* Jefferies and Prokop, 1972, from the Early Ordovician of Bohemia. In many ways, it is intermediate between symmetrical cornutes and anomalocystitids. *Reticulocarpos* is probably best considered the most advanced cornute. In *Reticulocarpos*, the zygal is distally shortened and does not attach to a lateral marginal. Respiratory pore structures are greatly reduced and are not arranged in the usual arcuate pattern. Centralia on both faces are enlarged in size and reduced in number. As in *Amygdalotheca* Ubaghs, 1969, the distal end is not continuous with marginals (as in *Phyllocystis* Thoral, 1935), but is open and occupied by centralia. The distal end of the theca is buttressed by a bar extending transversely from **M4** to **M'4** across the carapace and slightly diagonally at the distal ends of these two marginals. Distal to the transverse bar are short marginals **M5/M'5**, which with superior and inferior distal centralia, form the distal margin.

Continued thecal shortening by distal omission of centralia (by paedomorphosis) would result in **M5/M'5** protruding from the end of the theca in descendant forms. As descendant shortening continued, protuberent **M5/M'5** began to articulate flexibly with **M4/M'4** and ultimately they evolved into the articulating spines (Kirk, 1911, p. 25). The distal ends of **M4/M'4** became the terminal stadium in thecal shortening, uniformly marking the distal end of the theca in all anomalocystitids.

The aulacophore of *Reticulocarpos* is also mitrate-like. The styloid and the proximal ossicles of the distal aulacophore are produced into adthecally-curved spines. The cover plates on styloid and distal aulacophore are nonerectile.

The other two suborders, the Lagynocystida and Peltocystida, are markedly shortened in the theca and are laterally and diagonally compressed, thereby eliminating in azygous fashion many marginalia and centralia. Those elements that are still present are difficult to homologize. Peltocystids appeared in the Early Ordovician, and lagynocystids in the Middle Ordovician. Derivation and differentiation of the mitrates can reasonably be placed in the Late Cambrian or earliest Ordovician, and because of the lack of morphological intermediates, the process was apparently quite rapid.

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Text-figure 4.—Phylogenetic chart of the Anomalocystitida.

(1) The ancestral stock of the anomalocystitids is probably in the *Reticulocarpos*-like cornutans. *Reticulocarpos* Jefferies and Prokop, 1972 has four pairs of marginals proximal to a transverse "bar" across the carapace that connects **M4** and **M'4**. The distal ends of **M4/M'4** seem to be the distal limit of the theca in most anomalocystitids. Ancestral marginals **M5/M'5** have evolved into the movable distal spines.

(2) *Barrandeocarpus* Ubaghs, 1979 is clearly a placocystitid, but this early form has completly lost, or never had, articulating spines. Distal plastron marginals **m5**, **m6**, **m'5** (M5, M6, M'5 of Ubaghs, 1979, p. 114) extend distally to lengthen the theca.

(3) The basic dichotomy of the families Placocystitidae and Anomalocystitidae apparently occurred by the end of the Early Ordovician, and they retained their characteristic features well into the Early Devonian. In the Anomalocystitidae, all three of the carapace adaulacophorals make up the proximal margin of the carapace. With rare exceptions, taxa within this family lack a placocystitid plate. In taxa within the Placocystitidae, the median aulacophoral (**MA**) plate is invariably excluded from the proximal margin, in some specimens very narrowly. A placocystitid plate is almost always present.

(4) Placocystitid traits are well established in Middle Ordovician genera, but the placocystitid plate is missing in *Kopficystis*, n. gen.

(5) The Allanicytidiinae have a nearly bilaterally symmetrical theca, and while lacking a placocystitid plate, most seem to exclude the **MA** plate from the proximal margin. The assignment of this subfamily to the Placocystitidae is admittedly speculative. All of the representatives of the Allanicytidiinae are restricted to the Malvinokaffric Realm (Australia, Tasmania, and New Zealand). Two possible species, *Placocystis africanus* Reed, 1925 and *Placocystella capensis* Rennie, 1936 are omitted because of the incomplete knowledge of their plate arrangements. Both are from the Early Devonian of South Africa. [see Caster, 1954b]

(6) *Allanicytidium* Caster and Gill *in* Ubaghs, 1968a seems to have its **MA** plate nearly in contact with the proximal margin, but excluded from the proximal aulacophore by apparent incorporation of a pair of upper tetrameres. Details of this area are indistinct, as indicated by photos of Caster's latex casts and his drawings (see Caster, 1983, p. 327).

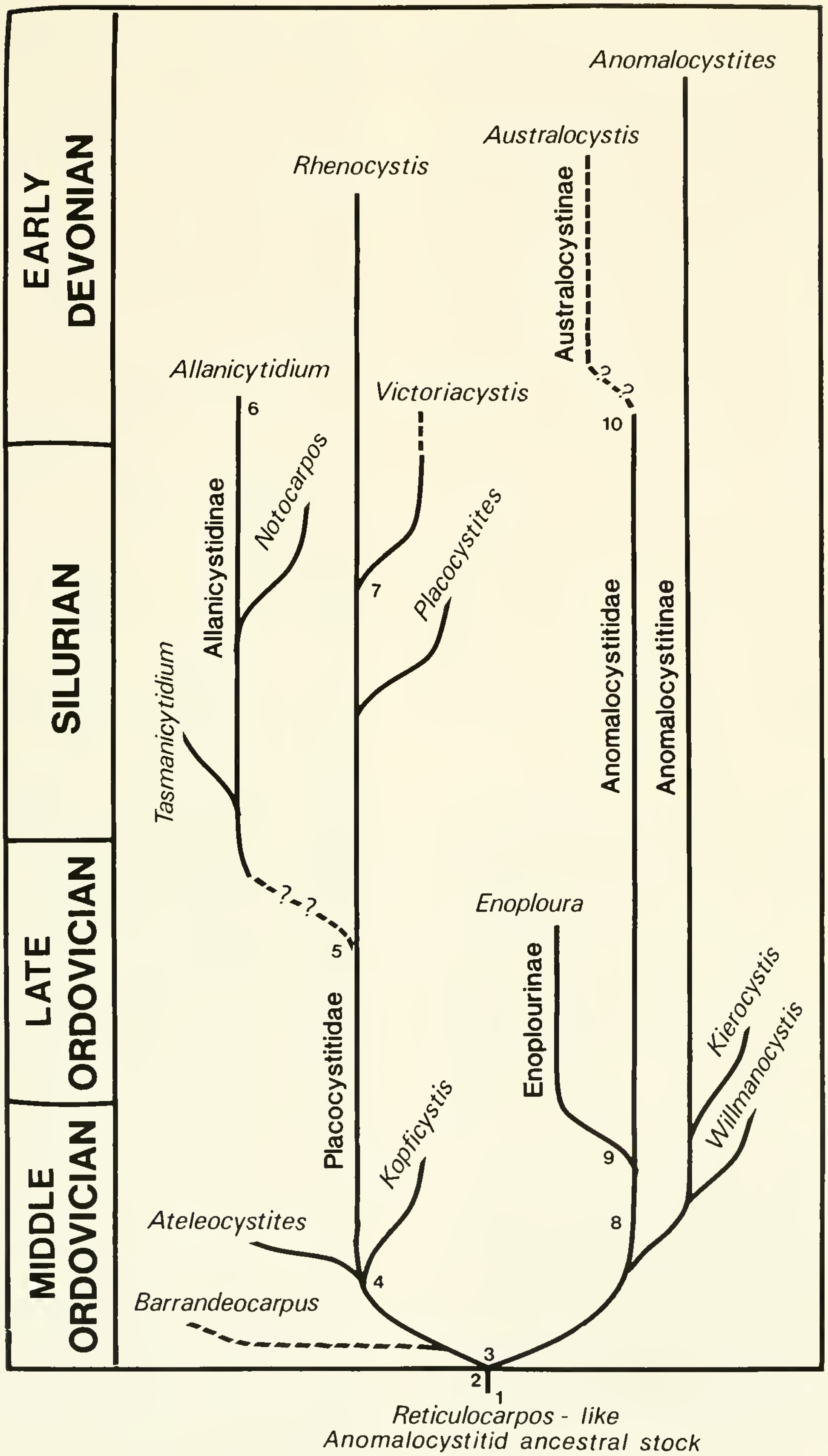
(7) *Victoriacystis* Gill and Caster, 1960 is a placocystitid occurring in the Late Silurian of Victoria, Australia. The presence of undoubted placocystitids in the Malvinokaffric Realm may strengthen the argument for the postulated close relationship of *Victoriacystis* to the Allanicytidiinae.

(8) The Anomalocystitidae and the subfamily Anomalocystitinae are present in the Middle Ordovician. The family group remains as a remarkably conservative taxon until extinction in the Early Devonian. In the Anomalocystitinae, the carapace has at least five arcuate rows of supracentrals.

(9) The Enoplourinae, consisting of the single genus *Enoploura* Wetherby, 1879, ranges from the Middle Ordovician to nearly the end of the Ordovician. In this subfamily, the carapace has undergone considerable reduction in the number of rows and in the number of supracentrals. The **MA** plate dominates the proximal end of the carapace.

(10) The Australocystinae is represented by the single South African genus *Australocystis* Caster, 1954b. Its assignment to the Anomalocystitidae is tentative because the carapace is unknown. The plastron, however, suggests a close relationship with this family. As with the Allanicytidiinae, this Malvinokaffric genus has an enhanced bilateral thecal plate arrangement.

For explanations of plate abbreviations, see Table 1 (foldout inside back cover).


EARLY DEVONIAN
SILURIAN
LATE ORDOVICIAN
MIDDLE ORDOVICIAN
Anomalocystites
Australocystis
Australocystinae
Rhenocystis
Allanicytidium
Victoriacystis
Notocarpos
Allanicystidinae
Placocystites
Tasmanicytidium
Anomalocystitidae
Anomalocystitinae
Enoploura
Enoplourinae
Placocystitidae
Kierocystis
Willmanocystis
Kopficystis
Ateleocystites
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?
Reticulocarpos - like
Anomalocystitid ancestral stock

ton, DC, U. S. A., were unstinting in making the necessary specimens available.

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SYSTEMATIC PALEONTOLOGY

INTRODUCTION

With various and conflicting terminologies used for thecal plates and structures [*e.g.*, Ubaghs, 1968a; Jefferies, 1967 and subsequent papers; Kolata and Guensburg, 1979; and Philip, 1979], it is easy to become confused. I have modified the terminology used by Ubaghs, which stresses the echinodermal affinities of the mitrate stylophorans. While I am in agreement with Ubaghs' (1968a) numbering of most of the marginalia and centralia, I will introduce some new terminology for the centralia, distal inferior (plastron) marginals, and distal superior (carapace) marginals (Text-figs. 5–7).

This study includes all of the North American Mitrata (Middle Ordovician to Early Devonian) with the exception of *Ateleocystites* Billings, 1858 (redescribed by Kolata and Jollie, 1982), *Diamphidiocystis* Kolata and Guensburg, 1979, and *Willmanocystis* Kolata and Jollie, 1982. I will, however, comment on *Ateleocystites* in the discussions of other forms. While some of my terminology and interpretation of life modes differs from that used by Kolata and Guensburg (1979) and Kolata and Jollie (1982), I am in complete agreement with the systematics used therein.

Synonymies used herein tend to be comprehensive and chronicle the taxonomic concept of the genus or species. Listings in various editions of paleontological or stratigraphical treatises are commonly omitted unless the listing has systematic importance.

ABBREVIATIONS OF REPOSITORY INSTITUTIONS

All specimens studied are housed in the following specimen repositories.

AMNH: American Museum of Natural History, New York, NY, U. S. A.
GSC: Geological Survey of Canada, Ottawa, Ontario, Canada.
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, MA, U. S. A.
NYSM: New York State Museum, Albany, NY, U. S. A.
UCB: University of Calfornia, Museum of Paleontology, Berkeley, CA, U. S. A.
UCM: University of Cincinnati, Cincinnati, OH, U. S. A.
USNM: U. S. National Museum of Natural History, Washington, DC, U. S. A.

SYSTEMATICS

Class **STYLOPHORA** Gill and Caster, 1960[2]
Order **MITRATA** Jaekel, 1918
Suborder **ANOMALOCYSTITIDA** Caster, 1952[3]

Diagnosis.—Convexo-concave (or planar) mitrates with rigid bilaterally symmetrical thecae and nearly bilaterally symmetrical plating. Two adaulacophoral marginals, three lateral marginals with paired articulating spines extending from **M4/M'4**. Two or three adaulacophorals on carapace. Aulacophore commonly with well-developed styloid.

Range.—Middle Ordovician–Early Pennsylvanian.

Discussion.—Caster (*in* Gill and Caster, 1960, p. 43, fn. 6; p. 44, fn. 10), calls attention to the fact that he separated the Anomalocystida [*sic*] from the Placocystida [*sic*] on the basis of Schuchert's (1904, p. 206, pl. 40, fig. 5) description of *Anomalocystites cornutus* Hall, 1859, in which he described the arms as flexible structures made up of "about 20 pieces in each column." Schuchert was probably influenced by the fantastic reconstruction of *Placocystis crustacea* Haeckel, 1896 (p. 40, figs. 1, 2) [= *Enoploura balanoides* (Meek, 1872)], in which Haeckel depicted the arms as being flexible and bearing short pinnulations. Examination of the type material of *A. cornutus*, subsequent to exacting preparation by Caster, has led me to conclude that the so-called segmented arm is a fortuitously

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[2] =Subphylum Calcichordata Jefferies, 1967, a subphylum of the Chordata.

[3] *nom. correct.* Ubaghs, 1968a (*pro* Anomalocystida Caster, 1952).

placed, detached distal end of an aulacophore. No evidence of a flexible distal arm as conceived by Haeckel or by Schuchert is present in this or any other mitrate. Inasmuch as the Anomalocystitida are differentiated from the Placocystitida only on the basis of the supposed presence of flexible arms, it follows that the two suborders are synonymous, as has already been suggested by Caster (*in* Gill and Caster, 1960, p. 44, fn. 10). The subordinal name Anomalocystitida is retained herein, as it is by Ubaghs (1968a).

As emended by Ubaghs (1968a), the Anomalocystitidae Bassler, 1938, includes all North American genera currently assigned to the Anomalocystitida (see Caster, 1952) and all genera formerly placed in the Placocystitida by Caster (1952), and Gill and Caster (1960). The latter group is herein recognized as a family. The subfamily Australocystinae Caster, 1954b, raised to family rank by Ubaghs (1968a, p. S561), includes nearly symmetrical forms from the Malvinokaffric Realm that lack anomalocystitid plates. It is retained herein as a subfamily of the Anomalocystitidae. The anomalocystitid family Allanicytidiidae Caster and Gill (*in* Ubaghs, 1968a, pp. S561–S564), revised by Caster (1983), was originally erected for the nearly perfectly bilaterally symmetrical genus *Allanicytidium* Caster and Gill *in* Ubaghs, 1968a, from the Early Devonian of Australia. Two recently described genera, *Notocarpos* Philip, 1981 from the Silurian of Victoria, Australia, and *Tasmanicytidium* Caster, 1983 from the Early Silurian of Tasmania have been added to the Allanicytidiidae. This family has been reduced herein to subfamily rank and included within the Placocystitidae. Taxa within the Allanicytidiinae have considerably reduced numbers of thecal plates; the median adaulacophoral does not contact the proximal margin; the anomalocystitid plate (**Z** plate of Philip in *Notocarpos*) is either present or absent, and commonly there is a well-developed laterally-extended flange on the styloid.

Kolata and Guensburg (1979) erected a new suborder Diamphidiocystida and new family Diamphidiocystidae for the unusual mitrate *Diamphidiocystis* Kolata and Guensburg, 1979, in which the theca is turned into a lateral U shape in plan view, with a single long articulating spine that superfically resembles a cornute thecal spine.

Family **ANOMALOCYSTITIDAE** Bassler, 1938

Diagnosis.—Diagnosis of the family is the same as that of the suborder.

Discussion.—As discussed above, the cornute genus *Reticulocarpos* Jefferies and Prokop, 1972, shows many features intermediate between symmetrical cornutes and anomalocystitids. In *Reticulocarpos*, a transverse bar made up of lateral extensions of **M4/M′4** crosses the superior face near the distal margin. The distalmost marginal plates (**M5/M′5**) extend distally from the joined **M4/M′4** marginals. These distalmost marginal plates are unequal in size and show no sign of movable articulation, and appear to be solidly sutured. However, in my view, they are homologous to the articulating spines in anomalocystitids. In this scheme, the number and disposition of marginal plates in *Reticulocarpos* is consistent with that of the Anomalocystitida.

Subfamily **ANOMALOCYSTITINAE** Bassler, 1938

Diagnosis.—Anomalocystitids with three adaulacophoral plates, two infracentrals (some may have three) including the anomalocystitid plate. Placocystitid plate rarely present. Supracentrals arranged in two or more rows between adaulacophorals and distal marginals.

Range.—Middle Ordovician to Early Devonian.

Discussion.—This subfamily retains what appears to be a primitively large number of supracentrals, but at the same time shows morphologic innovations in other parts of the organism (discussed below). This subfamily probably best exemplifies mosaic evolution within the mitrates. Genera included in this subfamily are *Willmanocystis* Kolata and Jollie, 1982, *Kierocystis*, n. gen., and *Anomalocystites* Hall, 1858.

Genus **ANOMALOCYSTITES** Hall, 1858

Anomalocystites Hall, 1858, p. 279; Hall, 1859, vol. 3, pp. 122, 131; Hall, 1861, pl. 7A, figs. 5–7, pl. 8B, figs. 1–4; Miller, 1889, p. 224 [*pars*]; Bather, 1900, p. 51; Jaekel, 1901, p. 668; Schuchert, 1904, pp. 204–206; Kirk, 1911, pp. 22–26, pl. 3, figs. 9–11; Springer, 1913, pp. 150–151 [*pars*]; Caster, 1952, pp. 20–23; Caster *in* Ubaghs, 1968a, pp. S556–S557, S559; Derstler and Price, 1975, pp. 7–9; Derstler, 1979, p. 102.

Ateleocystites Billings. Woodward, 1871, pp. 71–73 [*pars*]; Woodward, 1880, pp. 194–201 [*pars*].

Anomocystis Hall. Haeckel, 1896, p. 40.

Anomalocystis Hall. Bather, 1889, p. 266 [*non Anomalocystis* Hall. Barrande, 1887, p. 89].

Basslerocystis Caster, 1952, pp. 22–26; Caster *in* Ubaghs, 1968a, pp. S559, S560.

Type Species.—*Anomalocystites cornutus* Hall, 1859.

Diagnosis.[4]—Anomalocystitid with theca subovoid in outline, carapace and lateral surfaces strongly convex, plastron concave with marked lateral runners; proximal and distal carapace margins transversely concave, proximal plastron margin deeply concave. Proximal carapace margin with three adaulacophoral plates, distally followed by four rows of four, five, six, and four plates, respectively; lateral margins comprised of four paired marginals (**M1–M4**), three inferior distal marginals (**m5, m6, m′5**), and two infracentrals, a large

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[4] This diagnosis is based on that of Caster (*in* Ubaghs, 1968a, pp. S556–S557).

central plate, and an anomalocystitid plate. Two small articulating spines on **M4/M'4**. Proximal aulacophore wide, eight or nine segments that imbricate axially on inferior surface; distal aulacophore long and narrow.

Occurrence.—Early Devonian of Maryland, New York, and Pennsylvania.

Discussion.—The two previously-recognized species *A. cornutus* and *A. disparilis* Hall, 1859, are preserved quite differently; the former as moderately complete to partial specimens of original carbonate material. Evidence of some disarticulation by compression is common. Specimens of the latter are only complete to partial thecae that are replaced by silica. Most of the surface detail has been lost and many of the interior features are not distinct. Commonly, specimens recognized as *A. disparilis* are three to four times larger than those recognized as *A. cornutus.*

On the basis of this restudy of the type and other material, there is little reason to separate the two species. Their plate patterns are nearly identical and their minor differences in patterns of the supracentral plates are easily attributable to growth (*i.e.*, size differences).

While these putative species are found in different formations, they are narrowly separated stratigraphically (probably less than 10 m) and given the strong tendency for stasis in the family, I maintain that the two are conspecific and the genus therefore is monotypic.

Although several features of this genus are unique and highly distinctive, it appears to be the end member of a very conservative lineage. The overall proportions of theca to aulacophore, general makeup of the theca and aulacophore, and nature of most of the features on the internal plastron are little changed from Middle Ordovician genera (*e.g.*, *Enoploura* Wetherby, 1879 or *Ateleocystites*).

The distal end of the theca is certainly distinct from that of its forerunners. The two lateral distal carapace marginals fold over to restrict the lateral ends of the distal (anal) opening. Likewise the lip on the inferior distal marginals is folded inwards, moving the inferior threshold higher off the substrate than in earlier genera (*e.g.*, *Enoploura*, [Pl. 2, figs. 3, 7, 14, Pl. 3, figs. 5, 14]). There is no evidence of the small wedge-shaped (?)vestigial anal pyramid plates that are common in older mitrate genera.

At the opposite end of the theca the aulacophore apophyses are perhaps the largest relative to the size of the proximal aulacophore. The deep embayment in the theca for the aulacophore results in the apophyses being deeply curved inferiorly and less so superiorly where the wall curves towards the proximal superior margin. The horns of the apophyses, however, appear to be somewhat reduced (Pl. 2, figs. 4, 9, 10, Pl. 3, figs. 13, 15).

Retention of the multiplated carapace, a primitive trait when compared to Malvinokaffric Realm Silurian and Devonian mitrates (*e.g.*, *Tasmanicytidium*, *Allanicytidium* and *Notocarpos*), and Ordovician Enoplourinae (*e.g.*, *Enoploura*) reinforces the overall conservative nature of North American Anomalocystitidae. Malvinokaffric Realm genera (see, *e.g.*, Caster, 1954b, 1968, and 1983, and Philip, 1981) show a definitive trend toward thecal simplification, especially on the superior (carapace) surface. But in reference to the whole animal, including spines and aulacophore, they too must be considered only moderately different from their North American relatives.

The presence of a placocystitid plate in this subfamily is unusual, just as is its lack in the new genus *Kopficystis* in the Placocystitinae. The placocystitid plate, and the polyplated carapace in *Anomalocystites* which superficially shows resemblance to placocystitids, clearly show the close-knit nature of the Anomalocystitida. The advanced aspects of the distal aperture morphology and the cover plate apparatus of the distal aulacophore are examples of mosaic evolution.

Anomalocystites cornutus Hall, 1859
Plate 1, figures 1–14, Plate 2, figures 1–16,
Plate 3, figures 1–15; Text-figures 5–8

Anomalocystites cornutus Hall, 1859, p. 133; Hall, 1861, pl. 7A, figs. 5–7.

Anomalocystites disparilis Hall, 1859, p. 145; Hall, 1861, pl. 88, figs. 1–4.

Bassleroscystis disparilis (Hall). Caster, 1952, pp. 22, 29, figs. 2e, 2f.

Diagnosis.—Because *A. cornutus* and *A. disparilis* are considered conspecific herein, the genus becomes monotypic. Hence, the diagnoses for genus and species are the same.

Description.—The theca is subovoid in outline with a slightly concave distal carapace margin, resulting in the appearance of having slightly distally directed horns or excrescences. The proximal plastron margin is more deeply indented than the proximal carapace margin (Pl. 2, figs. 12, 16). In profile, the theca is inflated; the carapace gently convex, gradually tapering distally (Pl. 2, figs. 2, 8, 11; Text-fig. 7). The plastron is nearly planar, but the distal end bends upward into the short, nearly vertical distal face; proximally the plastron margin curves gently into the nearly vertical straight proximal margin. In transverse profile, the plastron is centrally planate with the margins sharply curving vertically to form the lateral, runnerlike, inferolateral margins (Pl. 2, figs. 3, 4, 7, 9, 10, 14).

Marginal plates make up the bulk of the inferior and inferolateral surfaces (Pl. 1, figs. 3, 7; Text-fig. 6). Adaulacophoral plates **M1/M'1** are deeply excavated for the reception of the proximal aulacophore, and together they comprise the entire aulacophore embayment (Pl. 1, figs. 3, 7, Pl. 2, fig. 5; Text-fig. 6). Relative to those of most other mitrates, these plates are smaller in size, due primarily to their excavate nature. Lateral to **M1/M'1** are **M2/M'2**, which on the plastron are subarcuate in outline and unlike **M1/M'1**, which do not extend onto the lateral faces, have the greatest lateral expression of any of the marginals, in lateral view commonly displaying a subpentagonal outline (Text-figs. 6, 7). Marginals **M3/M'3** are subrectangular on the plastron and subpentagonal on the lateral faces. They are nearly as long as the **M2/M'2** laterals. On the distal margins are **M4/M'4**. These are the smallest of the marginals and are the most complex in form, being developed on the distal margin as well as inferiorly and laterally. The distal end of each plate is produced obliquely towards the carapace, and extending out from this surface are the spine bases. Each spine base is composed of a rounded ridge that parallels the distal wall of the carapace. They each truncate near the distal inferolateral margin and each is surrounded by a U-shaped muscle pit (Pl. 2, figs. 3, 7, Pl. 3, fig. 5). The entire articulatory apparatus is located on **M4/M'4**, and does not extend onto adjacent plates.

The inferior distal margin is made up of three subrectangular to subpentagonal plates, **m5**, **m6**, and **m'5**, which vary slightly in outline and relative length from one specimen to another. Together they form a slightly convex distal margin of the plastron.

The rest of the plastron is made up of two infracentrals that together occupy a roughly pentagonal area on the distal half of the theca. The larger infracentral is commonly pentagonal, although irregularly so; the smaller anomalocystitid plate is located at the distal left of the pentagonal area, abutting against **M'4** and **m'5**, and is commonly pentagonal in outline (Pl. 1, figs. 3, 7; Text-fig. 6).

On the superior surface, the carapace is made up of 27 plates arranged in distally concave arcuate rows. The three adaulacophoral plates are relatively small, compared to earlier mitrates. The central plate is subhexagonal, and the two lateral plates are irregularly pentagonal (Pl. 1, figs. 4, 14; Text-fig. 5).

Distal to the adaulacophorals is the first of four arcuate rows of polygonal supracentrals. This first series is commonly made up of four plates with the lateral plates being the largest of all supracentrals. In the sagittal axis of this series most specimens commonly are weathered, and plate material is commonly missing. At least one specimen (Pl. 1, fig. 14) clearly shows a placocystitid plate in this position, and since the placocystitid plate is commonly thin, it probably explains why this plate is seldom seen (also see Jefferies, 1984, pp. 310, 311, fig. 9).

The next arcuate row is made up of five slightly smaller plates with the median and admedian plates being the largest. The lateral plates, however, are only slightly reduced. These plates are all irregularly hexagonal in outline. The next series is made up of six, again slightly smaller, but nearly equisized plates. Most are hexagonal, but tend to be somewhat irregular in facet length. The final series consists of only four supracentrals that are all of unequal size, and most are hexagonal.

The distal carapace marginal plates commonly form a shallow concave margin with the lateralmost plates projecting distally to form low rounded horns (Pl. 2, figs. 1, 16; Text-fig. 5). These same outer lateral distal carapace plates are geniculated, folding inward to reduce the size of the lateral opening and to define it as an oval to squared–oval opening. The other three carapace marginals are small, nearly equal in size, and pentagonal. This series extends distally farther than the inferior lip and as such gives the distal opening the aspect of being slightly recessed. This feature may be unique among mitrates, but preservation among some Devonian Malvinokaffric Realm mitrates precludes a more definite statement.

With the material at hand, little can be determined of the inner surfaces of the carapace plates. What can be seen on the floor of the plastron suggests the overall structure is very similar to that of *Enoploura* Wetherby, 1879, or *Ateleocystites* Billings, 1858. A prominent diagonally-trending septum extends from the proximal left area of the plastron to the distal right corner, where it terminates at the outer margin of what appears to be one of a pair of distal muscle pits (Pl. 1, fig. 2, Pl. 3, figs. 4, 7, 9, 13; Text-fig. 8). The spur (the pointed peak on the septum) stands quite high and is located about one-third the length of the large infracentral, measured from its proximal margin. A prominent triangular field of convexly-curved thickened stereom (typical of mitrates) extends from the aulacophore insert margin to the spur on the transverse septum.

Prominent pits, probably for muscle attachment, are located on **m5** and **m'5** and extend and open onto the adjacent **M4/M'4** marginals. These pits are especially noticeable due to the thickening of the adjacent plate material, which is actually the thickened area where the plates bend slightly to form the up-stepped distal margin (Text-fig. 8). If the walls of the pits are projected through the walls of **M4/M'4**, they coincide with the muscle pits of the movable spines. The pits are, in part, diagonally roofed over by pillars (*apophyses* of Kolata and Jollie, 1982, pp. 643, 646, fig. 4-A) that extend from **m5/m'5** to the interior surfaces of the geniculated lateral distal carapace plates. The suture is located near the middle of the pillars and appears to be similar to the irregular sutures in the pillars of sand dollars.

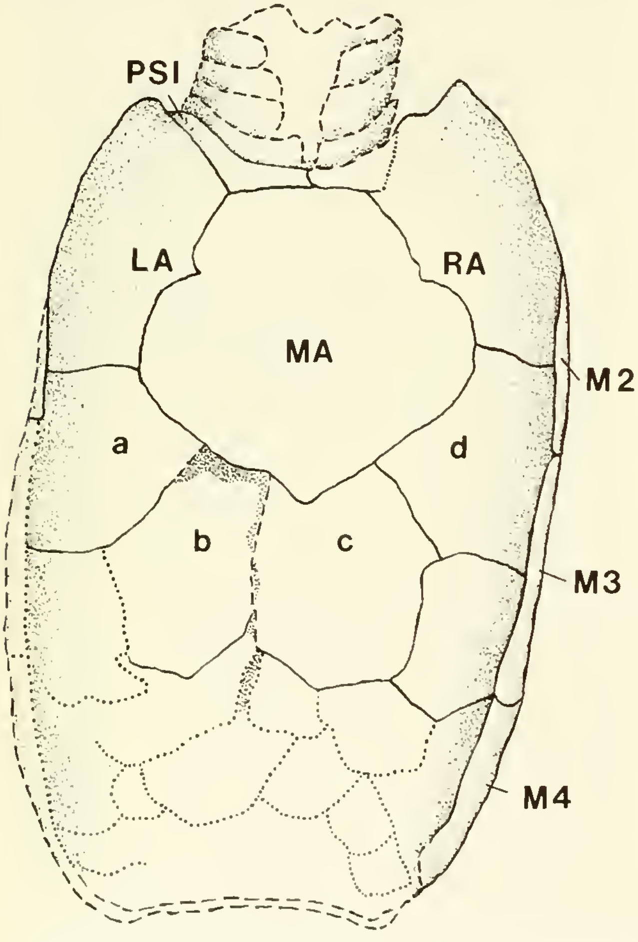
Aulacophore apophyses, horns and other elements of the aulacophore articulating apparatus are not well preserved, but overall appear to differ little from those structures in earlier mitrates. Perhaps the most significant difference between *Anomalocystites* and older anomalocystitid genera is the reduction in the number of segments of the proximal aulacophore to only eight or nine (Pl. 1, figs. 1–4). Judging from the aulacophore insert area of the theca, the proximal aulacophore was greatly inflated, but had a significant taper toward the styloid (Pl. 1, figs. 7, 8). This tetramerous structure has sutures in the axial plane and medially along the lateral faces; all sutures abut smoothly, except on the inferior surface where they alternately imbricate to give the structure added flexibility (Pl. 1, fig. 3).

The styloid, like that of all anomalocystitids, is made up of three segments. So far as can be determined, the styloid blades are not greatly extended as in *Enoploura*, but are only slightly protuberant, as in *Ateleocystites* (see Kolata and Jollie, 1982, p. 642). The nature of the styloid covering plates, the articulation between styloid and distal aulacophore, and the angle of insertion of the distal aulacophore into the styloid, are all unknown.

Distal aulacophores are known from only a few specimens (Pl. 1, figs. 2, 5–9, 14). They are virtually the same as those of earlier anomalocystitids. Several differences, however, are worth noting. The inferior spines are not as pronounced as in earlier forms and thereby give the inferior faces of the ossicle a more externally-rounded appearance. The covering plates are not as extensively overlapped and the portion that overlaps the adjacent distal plate appears to sit in a recess or depression. Also, the covering plates are not as large and produce a lower vault over the food groove than in Ordovician and Silurian genera. The overall length of the distal aulacophore appears to be about the same, relative to thecal length, as that of *Enoploura* or *Ateleocystites*.

Occurrence.—Manlius Formation, Olney Member, Saltsburg quarries, Dayville, New York (Localities A and C); also, from an unknown locality "Lower Helderberg, Litchfield, New York" (Locality B), [*A. cornutus*]; Ridgely Formation, Cumberland, Maryland (Locality D), and Ridgely, West Virginia; Shriver Formation, Curtin, Pennsylvania: Early Devonian (see Derstler and Price, 1975, Derstler, 1979).

Types.—Syntypes: AMNH 2288[5], Locality A. Hypotypes: NYSM 15010, 15011, Locality A. UCB D-1875, Locality A. UCM 46044, Locality B. USNM 35078[6], Locality C. USNM 35079, Locality C. USNM 33661A–33661G, Locality D. AMNH 2720, Locality D.



Text-figure 9.—Carapace of *Kierocystis insertus*. This figure is based on USNM 42166 (Pl. 4, figs. 10, 12). The paired plates between the proximal aulacophore and the adorals are the proximal aulacophore insert plates (**PSI**).

For explanations of plate abbreviations, see Table 1 (foldout inside back cover).

Genus **KIEROCYSTIS**, new genus

Type species.—*Kierocystis insertus*, n. sp.

Remarks.—Because this genus is monotypic, it follows that its diagnosis, description, and occurrence will be the same as for the species.

Kierocystis insertus, new species
Plate 4, figures 10–12; Text-figure 9

Diagnosis.—Anomalocystitids with small, triangular, proximal aulacophore insert (**PSI**) plates inserted between right and left adaulacophorals and median adaulacophoral plates.

Occurrence.—The single known specimen is from the Curdsville Limestone Member of the Lexington Limestone, Middle Ordovician (Trentonian), Curdsville, Mercer County, Kentucky (Locality G).

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[5] four specimens on a small slab. Because each specimen shows different aspects of the morphology of *A. cornutus*, it seems advisable to me *not* to designate a lectotype.

[6] four carapace specimens and several aulacophores on a small slab.

Type.—Holotype: USNM 42166, Locality G.

Description.—The most striking feature of this new species, and its principal taxonomic trait, is the presence of two small, triangular plates inserted into the proximal margin of the carapace (Pl. 4, fig. 12; Text-fig. 9). These proximal aulacophore insert plates (**PSI**) were probably derived from the dorsal meres of the proximal segment of the proximal aulacophore. The maximum extension of these plates into the theca occurs at the **RA/MA** and **LA/MA** sutures. The **PSI** plates abut medially and exclude the **MA** plate from the proximal margin. Curvature of the **PSI** plates laterally exceeds that of **RA** and **LA** so that the lateral ends hang free of the theca and articulate in an apparently normal fashion with the superior meres of the distally-adjacent, proximal aulacophore segment.

Aside from the incorporation of the **PSI** plates into the theca and the slight modification in outline of plates adjacent to them, especially the **MA** plate, the shapes and positions of the rest of the plates seem to be fairly typical of *Anomalocystites* Hall, 1858: the median adaulacophoral plate (**MA**) is shaped more like that of *Enoploura* Wetherby, 1879. There is no evidence of the infolded distal lip seen in *Anomalocystites*. Because of preservation, the number of supracentrals is not possible to determine, but the number and arrangement appear to be similar to those of *Anomalocystites*.

Discussion.—Some illustrations of *Placocystites* de Koninck, 1869 (Woodward, 1871, p. 72; Haeckel, 1896, pl. 2, fig. 12) show a pair of **PSI**-like plates inserted into the dorsal stele embayment. Woodward (1880, p. 196) called them "narrow basals". Jefferies (1984) and Jefferies and Lewis (1978) refer to this area as the posterior surface ("p. sf."). The excellent photo illustrations of *Placocystites forbesianus* de Koninck, 1869, in Jefferies and Lewis (1978) clearly indicate that **PSI**-like plates may also be present, but whether they are truly inserted plates, or whether it is an area that simply displays a different ornament pattern, is unknown. The presence of **PSI**-like plates in *Placocystites* demonstrates possible morphologic convergence with *Kierocystis*, n. gen. However, the general supracentral plate pattern of the carapace clearly supports the assignment of *Kierocystis* to the Anomalocystitinae.

As is a normal trait for this subfamily, the carapace embayment for the proximal aulacophore is unusually pronounced. The proximal end of the carapace also lacks the usual transverse, ridgelike ornament common to many species of anomalocystitids.

Aside from the incorporation into the theca of the dorsal meres of the first proximal segment of the aulacophore, the remaining proximal aulacophore segments are in every way typical of other anomalocystitids. The sagittal area of the proximal aulacophore of the holotype of *Kierocystis insertus*, n. sp., has been so fractured that its internal, distally imbricate nature is exposed. Externally, the meres are distally tightly telescoped over one another. The styloid and distal aulacophore are absent in this monotypic genus.

The conservative morphology seen in this subfamily is striking. *Anomalocystites* (Early Devonian) and *Kierocystis* (Middle Ordovician) are very similar overall.

Subfamily **ENOPLOURINAE** Caster, 1952

Diagnosis[7].—Anomalocystitids that have three adaulacophorals, three infracentrals, and lack a placocystitid plate. Commonly a single arcuate row of supracentrals between adaulacophorals and distal carapace marginals.

Discussion.—This monotypic subfamily of the Anomalocystitidae is based on *Enoploura*, which in thecal characteristics is distinct from other genera in the family because of the decreased rows and numbers of supracentralia. Caster (1952) originally placed *Ateleocystites* Billings, 1858, in this subfamily, but its clearcut placocystitid traits place it outside the family group. Kolata and Jollie (1982), in their emendation of the subfamily, included *Willmanocystis* Kolata and Jollie, 1982 within it. The current definition of the subfamily suggests *Willmanocystis* should be placed in the subfamily Anomalocystitinae, because of its more abundant rows and greater number of supracentralia.

Genus **ENOPLOURA** Wetherby, 1879[8]

Anomalocystites Hall. Meek, 1872, p. 423, 424 [*pars*]; Meek, 1873, pp. 41–44, pl. 3*bis*, figs. 6a–c [*pars*]; Miller, 1889, p. 224 [*pars*]; Springer, 1913, pp. 150–151 [*pars*]; [*non Anomalocystites* Hall, 1858].

Enoploura Wetherby, 1879, pp. 162–166, pl. 7, figs. 1a–g [as a crustacean]; Jaekel, 1901, p. 668; Bather, 1900, p. 51; Caster, 1952, pp. 9–56, pl. 1–4; Ubaghs, 1968a, p. S560.

Ateleocystites Billings. Woodward, 1880, pp. 193–201 [*pars*]; Bassler, 1915, p. 88 [*pars*] [*non Ateleocystites* Billings, 1858].

Placocystis [*sic*] de Koninck. Haeckel, 1896, pp. 39, 40 [*pars*] [*non Placocystites* de Koninck, 1869].

Type species.—*Anomalocystites* (*Ateleocystites*?) *balanoides* Meek, 1872.

Diagnosis.—Theca subrectangular in outline, depressed, gently convexo-concave. Superior surface (carpace) with three large adaulacophorals; six smaller, arcuately-arranged supracentrals; five distal carapace marginals, the central three bearing distally-directed fixed spines. Inferior face (plastron) with three infracentrals; three distal plastron marginals that together form an up-stepped, distally-produced, arcuate lip. Articulated spines about one-half length of theca long; spines articulate on a well-defined mamelon in vertical groove on distal ends of **M4/M'4**. Proximal aulacop-

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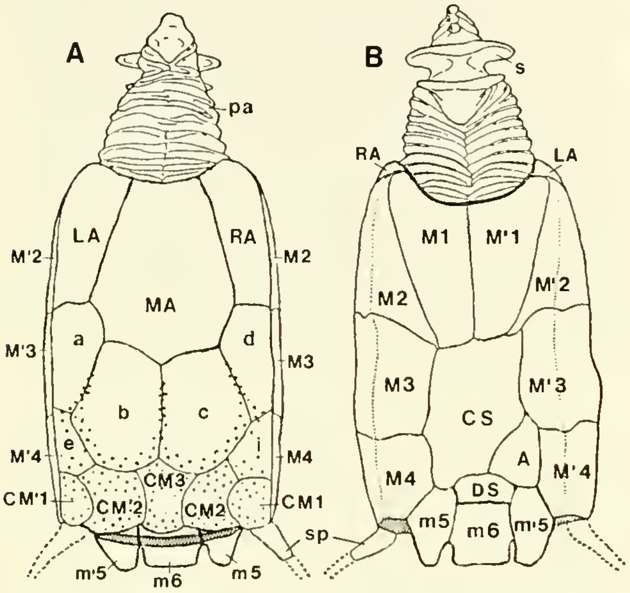
[7] modified from Kolata and Jollie, 1982, p. 649.

[8] emended.

hore with about 11 segments; styloid robust, some species with extended rounded flanges; distal aulacophore with from 20 to more than 40 segments, and proximal segments markedly spinose.

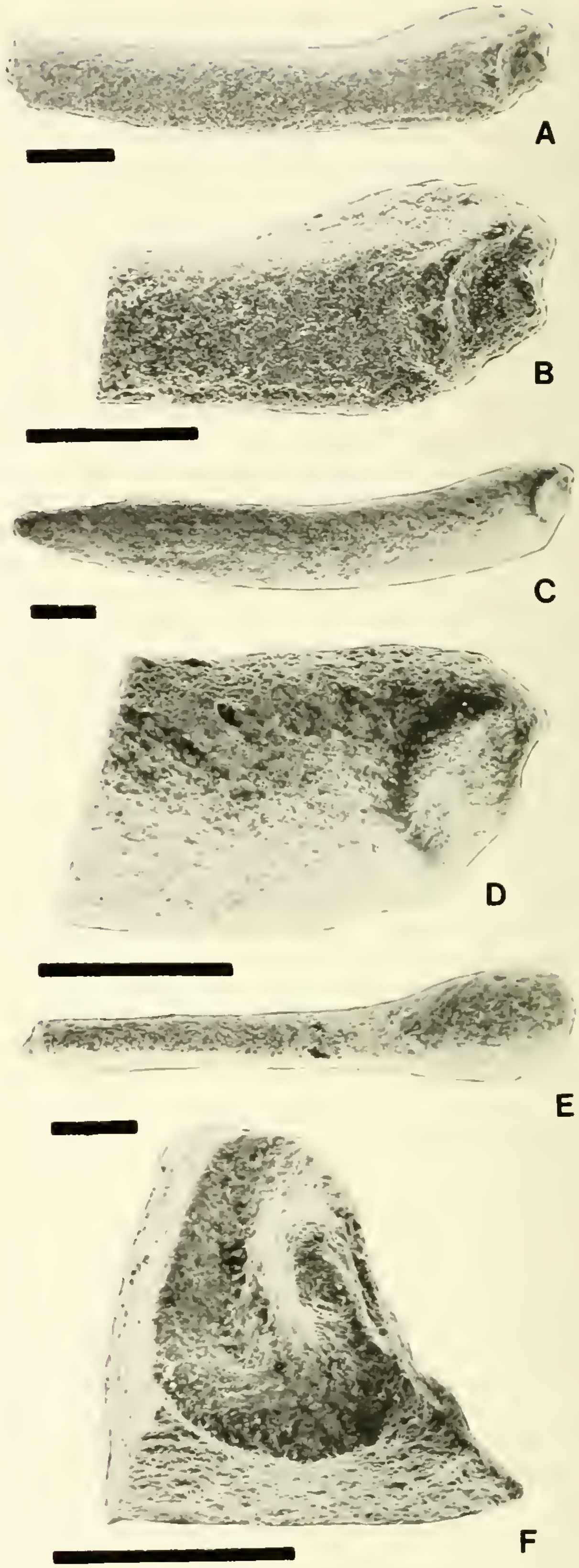
Occurrence.—Middle Ordovician: Trentonian of Tennessee and Kentucky. Late Ordovician: Edenian of Tennessee; Cincinnatian of Ohio, Kentucky, and Indiana.

Discussion.—Caster's (1952) extensive paper on this genus eliminates the need for detailed description of the thecal plating (see Text-fig. 10). However, since that work, new aspects of the morphology have become known. I will concentrate on these new findings in the



Text-figure 10.—Carapace (**A**) and plastron (**B**) of *Enoploura popei*. This figure is based on UCM 25993 (Pl. 6, figs. 1, 3). On the aulacophore: **pa** = proximal aulacophore; s = styloid.

For explanations of other plate abbreviations, see Table 1 (foldout inside back cover).



Text-figure 11.—Articulating spines and articulating surface on **M4/M'5** of *Enoploura popei*. Scale bar in all figures is 1 mm long. **A**, **B**, adsagittal (inside) side of a right spine. Note the articulating socket which abuts the mamelon and the bounding arcuate muscle ridge (Text-fig. 11F); **C**, **D**, absagittal views of a left spine, showing muscle ridge and pit. Presumably these pits were for attachment of muscles antagonistic to those on the opposite lateral surface. Muscles attached on this side would pull the spine laterally outward: those on the opposite surface would pull the spines laterally toward the sagittal plane; **E**, top view of a spine. The thickened end is the top side of the articulating area. Note how it would cover much of the articulating area; **F**, articulating area on an **M4** plate. The raised boss is the mamelon. The spine would articulate between the mamelon and the left margin of the slightly-depressed articulating area (as viewed). All photos were taken on an Amray 1700 S.E.M. at a power setting of 30 kv.

For explanations of plate abbreviations, see Table 1 (foldout inside back cover).

following detailed discussion on the morphology of the genus.

The new information comes from: (1) restudy of the hitherto poorly-known Edenian forms; (2) new articulated Cincinnatian specimens; and (3) several thousand disarticulated plates of *Enoploura* now in the University of Cincinnati Museum.

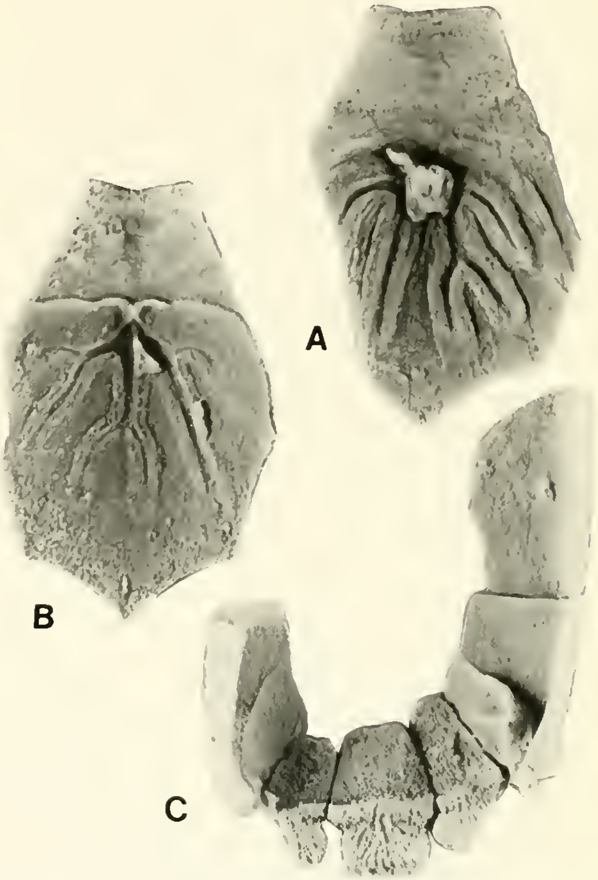
Theca.—Several important aspects of thecal morphology have hitherto been unknown or have not been discussed in the literature. The distal margin of many mitrates, including *Enoploura*, is commonly not preserved, or is badly crushed and incomplete. With the exception of several Edenian specimens [figured by Bassler (1932, pl. 18, fig. 9), but the distal margins not discussed], all specimens previously illustrated in the literature fail to show the lower, distally-protuding, rounded lip of the distal marginals **m5**, **m6**, **m′5**. The lip extends from the upper portion of the transverse ridge, so that when one of these plates is viewed laterally, the lip is cantilevered above and out from the plastron surface. On **m6**, the lip portion of the plate is not as wide as the thecal portion at the transverse ridge, thereby creating slight gaps between **m6** and **m5/m′5**. The lateral edges of the lip portion are slightly indented, but are parallel to the sagittal plane.

The adjacent marginals **m5** and **m′5** are also divided into thecal and lip portions, but not as distinctly, due to the lateral reduction in height and width of the transverse ridge. The shorter lip portion is angled toward the **m6** lip and apparently in some individuals not only fills the indented portion of **m6**, but slightly underlies it as well (Text-figs. 10, 12C).

The serrate transverse ridge developed on the internal faces of the inferior distal marginals (Pl. 5, figs. 1, 3, 10) is matched by a similar serrate ridge developed on the interior of at least three distal carapace marginal plates: **CM2**, **CM3**, **CM′2**. These opposed ridges form a transverse wall across the central portion of the distal aperture, but apparently it is not complete laterally. It is not known whether the serrations mesh, forming a solid wall, or are opposed, and result in a perforated structure. The latter case seems more likely when the venations discussed below are considered.

The serrations on the transverse ridges appear to be the remnants of the anal pyramid system. These serrations appear to be platelets of the ancestral anal pyramid, which are clearly seen in earlier mitrates (see *Mitrocystites* Barrande, 1887, or *Mitrocystella* Jaekel, 1901, where the anal pyramid is frequently preserved more or less intact). These platelets appear to be fused to the adjacent thecal plate(s) and show little tendency to be displaced. The degree to which these triangular platelets function in *Enoploura* is unknown, but the redeployment of these anal platelets along transverse ridges, rather than in an anal pyramid configuration, may be concomitant with the development of some sort of cloacal arrangement situated proximal to them.

In disarticulated Cincinnatian specimens of *Enoploura*, the lip is traversed by a fine, diverging "vein" or groove system that originates at the serrate transverse ridge (wall), each trunk or groove in line with a depression or serration on the top of the ridge (Text-fig. 12C). The venations are more prominent on the **m6** lip than on the adjacent **m5** and **m′5** marginals, where the serrations on the transverse ridge are correspondingly less developed. The serrate ridge on the inner face of the **CM3** plate may be homologous or



Text-figure 12.—Internal features of *Enoploura popei*. **A**, **B**, internal markings on the median adaulacophoral (**MA**) plate. These markings are, putatively, scars of muscles used in anal–cloacal pumping, which served primarily for respiration; **C**, partial reconstruction of lateral marginal plates and distal marginal plates (**m5**, **m6**, **m′5**). Note the veinlike pattern on the lip extending out from, and included on the transverse ridge marking the end of the distal body cavity. The internal ridges on the distalmost marginals (**M4–M′4**) are of uncertain function. It is suggested that they are muscle attachment ridges to impart control on the opening and closing of the presumed distal anal–cloacal structure.

For explanations of plate abbreviations, see Table 1 (foldout inside back cover).

analogous with the internal foldings of this plate in *Mitrocystites* (see Pl. 5, figs. 1, 7, 8).

The distal ends of the marginals **M4** and **M'4** are flared along their outside lateral and ventral edges into rounded ridges and produce an expanded articulatory area for the movable spines (Text-fig. 11F). These two ridges meet at nearly a right angle in the inferolateral portion of the **M4/M'4** distal face, and both ridges are in contact with a third diagonally-sloping ridge that completes the enclosure of the triangular articulatory area. The boss or mamelon, on which the spines articulate, is part of this sloping ridge, and is located halfway between the superior and inferior thecal faces. The outside lateral wall or ridge of the articulatory area seems to serve as a "bumper" to limit the range of lateral movement of the spines. It probably functioned as a seat of muscle attachment for the spines as well. When articulated specimens are viewed dorsally, the spines seem to articulate in a simple groove. The mamelon is slightly indented into the articulatory area from the diagonal ridge. In outline, the mamelon is elongate oval, with the long axis parallel to the adjacent sloping ridge. In profile, its articulatory surface is evenly rounded.

Articulatory surfaces on the spines are considerably more complex than those on the marginals. The spines are differentiable into right and left on the basis of these surfaces. Each process has a pair of lateral, inferoproximal hollows, the greater indentation being the acetabulum, which articulates against the outer–lateral surface of the mamelon. The outside and smaller inferoproximal embayment is probably a seat of attachment for muscles that extended from the embayment to the raised wall of the articulatory area (Text-figs. 11A–D). Between the two embayments at the extreme proximal end of the spine is a suboval pit with its long axis parallel to the extensiplane. It seems likely that it was filled with cartilage or flesh, which ensured smooth movement against the rounded embayment of the thecal articulatory groove. The detail of this articulatory area has been observed only on recently-discovered disarticulated specimens of Cincinnatian age.

Spines of *Enoploura* distal to the proximal articulatory area show a consistent morphology. In profile, they are slightly bowed ventrally (Text-fig. 11C). Distally they are compressed and somewhat bladelike; proximally, adjacent to the articulatory area, the shaft is nearly terete (Text-fig. 11E). The upper surface of the most proximal part of the shaft is broad and rounded, effectively concealing the complex articulatory apparatus in the few known specimens that preserve the spine in place. The length of a spine is roughly half that of the theca to which it is attached (Pl. 5, fig. 9). Ornament consists of very fine reticulate ridges that are parallel or subparallel to the length of the spine. Commonly the ornament is hidden by fine-grained sediment or is altered to a fine, pustulose texture due to impressions from the matrix.

The marginals **M4** and **M'4** are externally evenly paired, but on the interior inferior surfaces they are curiously unpaired (Text-fig. 12C). On the floor of the right marginal **M4** is an elevated, subquadrate area that is bounded on the outside–lateral and distal sides by sharply elevated ridges. The outside–lateral ridge is higher, commonly with two cusps. In some specimens, the cusps are slightly bent over the raised area. Commonly this area is bisected by a third ridge that extends diagonally toward the distal margin, from the juncture of the two previously-mentioned ridges to the **M4–m5** suture. Marginal **M'4** does not have an elevated area, but the same general area is differentiated by a low ridge (Text-fig. 12C). The function of these areas is not completely understood, but they were at least partially for muscle attachment.

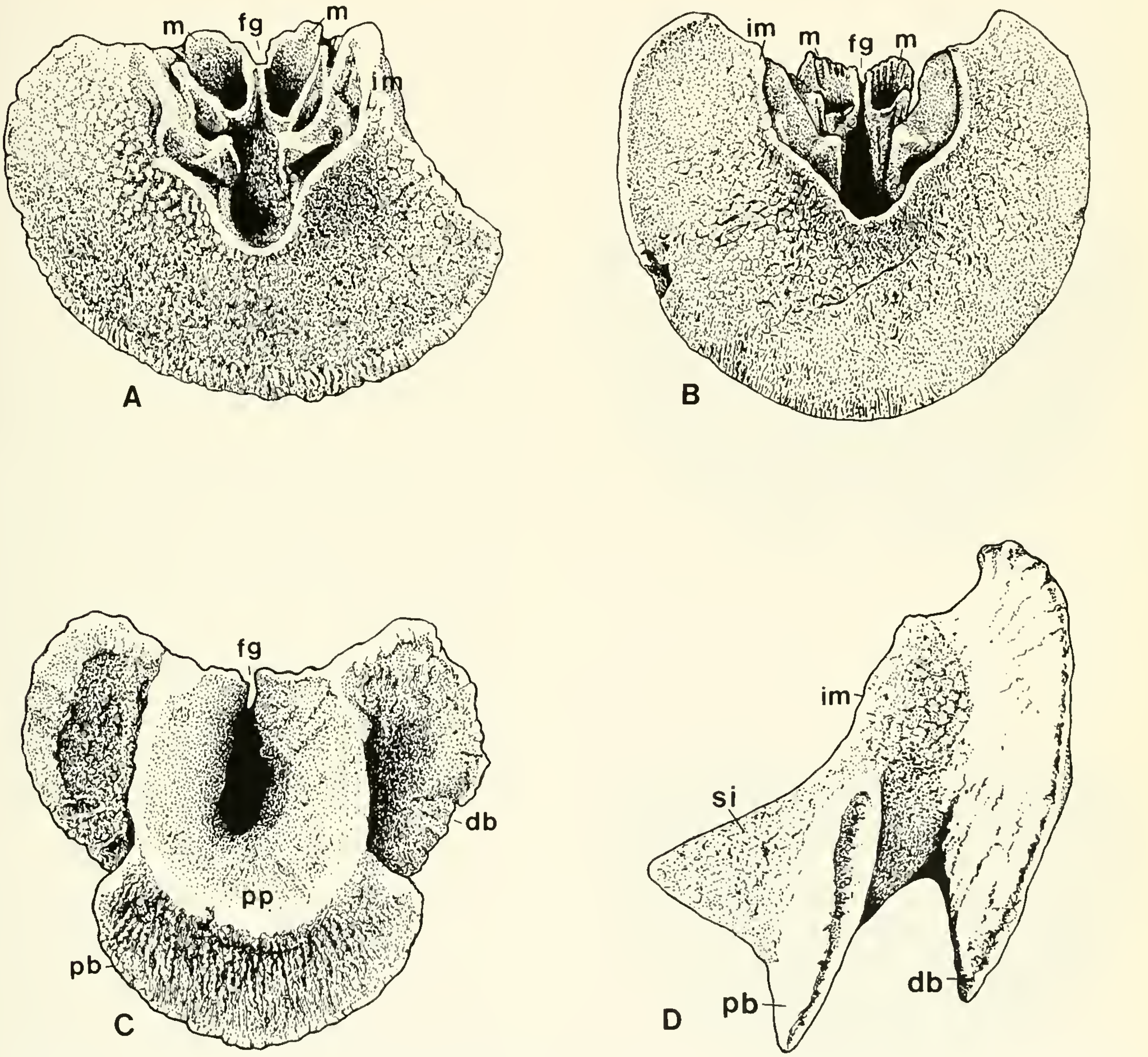
Sagittally adjacent to the spine articulatory areas is a sharply-incised, squared embayment that receives a squared boss or peg located on the outside angled edge of **m5** and **m'5** (Text-fig. 12C). This peg is located on the edge of the thecal portion of the plate and does not extend onto the lip. This angular articulation greatly strengthens the distal edge of the theca, and the portion of the peg protruding out of the squared embayment may also serve for muscle attachment. Pegs on **m5** and **m'5** seem to be equal in size.

Protruding from the distal carapace marginal plates **CM2**, **CM'2**, and **CM3** are distally-directed, short spines that extend out over the lip (Pl. 5, fig. 9; Text-fig. 17B) on the inferior surface. These spines are frequently broken off: in life they would have helped protect the distal, anal opening. On the proximal margin of the theca, Caster (1952, p. 12) described small, triangular "interbasal plates" (**ib**) intercalating between the **M1/M'1** and **M2/M'2** marginals. These so-called **ib** plates are now seen to be simply prosopon features defined by ridges on the **M1/M'1** marginals.

Internally the **M1** marginals are greatly modified. Extending from the inner margin of the aulacophore embayment is an internal wall, the aulacophore apophyses, which slopes distally from the plastron and abuts, but does not fuse with the inner surface of the carapace (*i.e.*, against the **RA**, **MA**, and **LA** plates). In their overall appearance, the aulacophore apophyses seem similar to those of *Anomalocystites disparilis* Hall, 1859 (see Kirk, 1911, pl. 3, fig. 11), *Placocystites forbesianus* de Koninck, 1869 (see Ubaghs, 1968a, p. 522, fig. 4), and *Ateleocystites guttenbergensis* Kolata and Jollie, 1982 (pl. 2, figs. 11, 13). Commonly this partition is only slightly thinner than the normal plate thickness. The apophyses are equal in size and are divided by the common suture between the marginals **M1/M'1**. Near the carapace there is a horizontally-directed, sagittally-centered, oval foramen in the apophyses. This is apparantly the only avenue of communication between the aulacophore and the theca. Most of the outer periphery of the apophyses is bordered by a sharply defined ridge. It is just inside this ridge and against the apophyseal wall that the first elements of the proximal aulacophore abut. The ridge probably served as an anchoring collar between the aulacophore and theca.

Aulacophore.—As in all Stylophora, the aulacophore of *Enoploura* is divisible into three basic parts: (1) a tetramerous proximal aulacophore, the ossicles of which dovetail inferosagittally, more or less evenly abut superosagittally, and evenly abut in the plane of extension; (2) an intermediate zone, the styloid, made up of three uniserial segments, and produced into the two blades or flanges for purchase into the substrate; (3) a multisegmented, uniserial, distal aulacophore, which consists of sharply-keeled ossicles, each with a large, evenly paired set of covering plates (Pl. 6, figs. 4, 5; Text-figs. 1–3).

Enoploura has about 11 complete segments in the

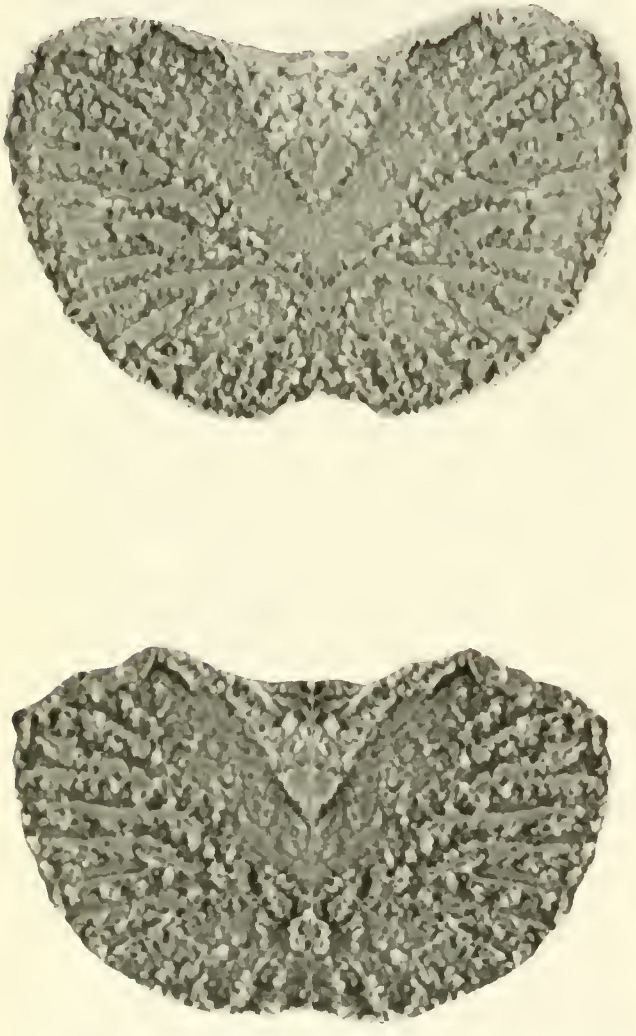


Text-figure 13.—Detail of the styloid of *Enoploura popei*. These figures are based on UCM 46049 (Pl. 6, figs. 6, 8, 11, and 9, respectively). **A**, **B**, distal views with distal aulacophore insert area; **C**, proximal view, showing the proximal aulacophore insert area; **D**, lateral view of the styloid. **db** = distal blade of the styloid; **fg** = food groove; **im** = insert margin; **m** = muscle pit; **pb** = proximal blade of the styloid; **pp** = proximal pit; **si** = styloid insert area (part of the styloid that displaces ventral tetrameres of the proximal aulacophores).

For explanations of other plate abbreviations, see Table 1 (foldout inside back cover).

proximal aulacophore. Adjacent to the styloid there are several segments that do not meet inferosagittally; they are pushed aside by the proximal process of the styloid (Pl. 6, fig. 2). Overlap of the inferior meres in each segment at the sagittal plane is slight. This is in contrast to the tetramerous solutan proxistele where the overlapping, both superior and inferior, is more extensive. The lateral sutures in *Enoploura* are very tightly ankylosed, as is the dorsal sagittal suture, but in the latter case the suture is recessed in a shallow groove (Pl. 6, fig. 12). In adult specimens, the cross-sectional outline of the proximal aulacophore is a slightly depressed oval, while in juveniles it tends to be circular.

Distal to the proximal stele is the three-segment styloid, which has flanges paralleling the inner sutures between the first and second, and between the second and third ossicles. Flanges show definite specific variations. In the Cincinnatian species *E. popei* Caster, 1952, they are broadly-rounded transversely and inferiorly (Pl. 6, figs. 9, 11; Text-figs. 13A–D), but in other Cincinnatian species and in Trentonian and Edenian forms, they are less transversely-expanded and more acuminate inferiorly (Pl. 4, fig. 6, Pl. 5, figs. 1, 5, Pl. 6, figs. 10, 13). The styloid also includes two pairs of covering plates that convexly arch over the longitudinally-short superior extremity of the distal blade (Pl. 4, fig. 6, Pl. 6, fig. 1).



Text-figure 14.—Transverse cross-sections of the distal styloid blade of *Enoploura popei*. Both figures are mirror-image reconstructions generated by duplicating a single half-image in reverse. Note the "canal" systems in the syzygial suture system.

In *E. popei*, the morphology of the styloid blades is easily observed (Pl. 6, figs. 1–3, 6–9, 11; Text-fig. 13). In this species, the styloid blades are dissimilar in size and outline. The distal blade is larger, hemispherical in outline, and dorsally capped by the covering plates. The smaller proximal blade is situated in a more inferior position and is quadrate in outline. This blade underlies that portion of the styloid that protrudes into the inferior distal portion of the proximal aulacophore and is without covering plates. On both blades the distal faces are generally gently convex. The proximal face of the distal blade is slightly concave to moderately convex, while the proximal face of the proximal blade is planar to markedly convex. The differences in curvature on both blades is a function of size; smaller specimens have blades with more surface curvature, but as they grow they tend to become flatter on both surfaces. Subradial ridges composed of pustules are present, especially near the periphery of the proximal faces of both blades. Similar ornament is present on the distal faces, except the ridges are commonly less distinct and the pustulose ridges tend to anastomose.

The three segments that comprise the styloid are markedly unequal in length; the proximal and medial segments comprise most of the total length, while the distal segment is restricted to the distal portions of the distal blade and the distal aulacophore insert area. Only two pairs of covering plates have been detected and they are supra-oral in position, belonging to the medial and distal segments. They seem to be non-erectile and are greatly reduced in length. The pair for the proximal segment is apparently lost due to insertion into the proximal aulacophore.

In the planes of the sutures in *E. popei* is a radiate "canal" system that underlies the radiate prosopon (Text-fig. 14). These "canals" are commonly seen as lines of greenish-black pyrite, which commonly weathers into red ferric compounds near the periphery of the blade. There are 40 to 60 of them in the distal blade and about half as many in the proximal blade. Their function is unknown; perhaps they were sensory in nature. Connection between this system and the internal cavities (*i.e.*, in the aulacophore insert area or in the protruding portion that extends into the proximal aulacophore) has not been observed, but it does seem likely. This system, when viewed between the thecal plates by serial sectioning, appears to be similar to syzygial suturing, although this condition has independently evolved within the mitrates. On the distal face of the distal blade is the indented insert area for the distal aulacophore. This area is subogival in outline and is bordered by a low ridge (Pl. 6, figs. 6–8; Text-figs. 13A, B). Medially, in the insert area, is a flat-sided cavity that extends ventrally into a well-rounded muscle pit. Superior to this cavity are the two, stepwise-arranged, flat-topped, paired seats for the remnant covering plates.

The proximal end of the insert area is defined by a pair of muscle pits on elevated column-like bases, separated along the sagittal axis by a very thin septum (Pl. 6, figs. 6–8; Text-figs. 13A, B). The septum ends near the superior margin and the medial indentation probably marks the course of the food groove. Each muscle pit is transversely ovoid. The distal walls of the pits are lower and concave, while the proximal walls are considerably elevated and convex.

The dorsal muscle pits are situated on pier-like bases that have migrated upward during ontogeny due to peripheral growth, and in larger specimens the bases are, as expected, more highly developed. The dorsal muscle pits are located in the second or middle of the three segments. Between the bases of the muscle pits and the distal end of the distal aulacophore insert area are paired "septa" that extend parallel to the suture toward the midline. These "septa" appear to be part of the distalmost segment and probably served as abutments for the proximalmost ossicle of the distal aulacophore. The upper parts of these abutment plates may also have provided muscle attachment to the distal aulacophore.

The two distal styloid segments also share the ventral muscle pit that occupies the bottom of the distal aulacophore insert area. This deep rounded pit allowed the distal aulacophore to move up and down in the medial plane. Muscle(s) extending from the inferior pit would have probably attached close to the top of the ossicle and the contraction of this and the two superior muscles would have elevated the aulacophore with the lower parts of the abutment plates serving as the fulcrum.

Proximal to the proximal wall of the insert area, the inferior styloid section slopes toward the midline and comprises that part of the styloid which inserts into the proximal aulacophore. In profile, this portion of the styloid is concave superiorly and gently convex inferiorly (Pl. 6, fig. 9; Text-fig. 13D). On the superior margin of this spoonlike protrusion is the narrow medial slit which, as indicated above, is probably for the passage of the food groove. Most of the large hollow space enclosed by the spoonlike protrusion was probably for muscle attachments and enclosure of other organ systems associated with feeding (*i.e.*, (?) water-vascular, nervous, and associated coelomic cavities) (Pl. 6, fig. 11; Text-fig. 13C). No trace of water-vascular apparatus is found in the styloid interior or on the distal aulacophore of this genus.

The two non-erectile covering plates situated over the distal styloid blade are supra-oral. The mouth was situated at the termination of the food groove, which was located between the superior muscle pits. In the proximal insert area of the styloid, the food conduit is internal and extends under the superior meres of the proximal aulacophore and into the theca. Speculation by some authors that the mouth, or orifice to the interior, lay between the theca and superior meres of the proximal aulacophore is not tenable in *Enoploura* or any other observed genus. The very tight suturing in this area precludes the possibility of such an orifice in this position. In all known specimens, the length of the distal aulacophore exceeds that of the theca. It tapers very gently to an acute and apparently very flexible terminus. Throughout its length, it is consistently uniserial. Ossicle and cover plates present a teardrop-shaped cross-section. The V-shaped or keeled ossicle, like those in other mitrates and in the Cornuta, lacks an internal lumen.

The transverse sutures between the ossicles bisect the sutural flanges that extend inferiorly and inferolaterally. These flanges are developed to a much lesser degree than in the styloid. Especially prominent are proximally-directed sutural cusps, which are best developed on the ossicles adjacent to the styloid.

Evenly paired over each ventral ossicle is a pair of covering plates that are nearly as tall as the underlying ossicle and distally overlap the covering plates on the adjacent distal segment. The gently concave articulatory bases fit evenly along the correspondingly convex dorsal surfaces of the ossicles.

The distally-overlapping cover plates meet in a straight, very tight suture along the superior midline. The tightness of the suturing is attested to by the fact that in known specimens, cover plates are rarely separated from their opposed basal ossicles. There is no evidence that the cover plates were erectile or capable of rotation.

Most specimens have between 30 and 40 segments (Pl. 6, figs. 4, 5, 10) in the distal aulacophore. In specimens of Cincinnatian age, the distal aulacophore of *Enoploura* inserts into the specialized insert area of the styloid at an angle of approximately 55° to the horizontal. The nature of the articulatory surfaces indicates, however, that the distal aulacophore could be straightened in this location. Trentonian and Edenian forms do not seem to have this initial insertion angle with the distal segment of the styloid, and probably this lack of insert angularity is a more primitive condition.

Functional considerations.—While much of this section applies to many other mitrates as well, the detailed knowledge of the nature of the styloid and spine articulation in *Enoploura* makes this the appropriate place for this discussion.

The three segments of the styloid are joined by coarse syzygial sutures between the middle and end members. The sutural portions of these segments are produced into the flanges that anchor into the substrate. The stromal openings in the sutures are large enough to make up, in effect, a radiating "canal" system. The ends of these "canals" appear slightly bulbous and the tissue in them may have served as sediment chemoreceptors and/or as an orientating sensory device. The canals terminate internally near the food groove, and it is assumed connected with axial nerve trunks.

The principal direction of active locomotion was with the distal end of the theca foremost. The prowlike character of the protruding, cantilevered lip, the ventrally-arched runnerlike articulating spines, and the distally-directed spines on the **CM3** plate all point to this interpretation. The hydrofoil profile of *Enoploura* would have acted as a laminar-flow wing and would have provided lift while the animal was swimming or sculling along. Lift would also be generated while the animal was at rest: water flowed over the theca in the opposite direction (*i.e.*, proximally to distally while the animal faced into the current). While this might induce less stability due to hydrodynamic lift, it may, in part, indicate the selective value of the counteracting large styloid blades. The animal may have ratcheted for short distances across the sea floor using the styloid (*cf.* Caster, 1952, pl. 42) and the large spines on the proximal ossicles of the distal aulacophore, to adjust its orientation relative to currents.

Orientation of the mamelon and acetabulum on the spine strongly suggests that the thecal spines moved parallel or nearly parallel to the substrate. Movement probably extended from an outward position of approximately 30° to the sagittal plane to an inward and slightly upward (as evidenced by the inclined articulatory boss) position of the same magnitude, and totaling about 60° of movement. These must be considered as maximum values; movement was, most likely, commonly through a smaller angular distance. Inward swing probably extended only slightly inside the lateral marginal plane and total outward movement was probably not more than 20°. Some authors have speculated that the spines may have served as struts to hold the theca off the sea floor (see, *e.g.*, Caster, Dalvé, and Pope, 1955). Dehm (1934, p. 29), on the other hand, postulated that the fine spines of the mitrate *Rhenocystis* Dehm, 1932, were too delicate and attenuate to serve as struts to elevate the animal above the substrate. The articulatory apparatus of the spines on *Enoploura* strongly indicates that vertical movement that would lift the animal off the substrate was improbable. Considering the general similarity of all anomalocystitid spines in size, shape, and area of articulation, these structures most likely all had a similar horizontal mode of movement and served as buttresses to hold the animal stable while feeding.

Enoploura punctata Bassler, 1932

Plate 4, figures 5–9, Plate 5, figures 1–5, 8, 10,
Plate 6, figures 10, 13; Text-figures 15, 16

Enopleura [*sic*] *punctata* Bassler, 1932, p. 218, pl. 18. fig. 9; Bassler, 1935, p. 406.
Enoploura punctata (Bassler) [*sic*]. Bassler, 1943, p. 157.

Diagnosis.—Theca commonly, but not invariably, relatively wider than Late Ordovician species; carapace ornament scaly punctate; distal lip thick, spines thick, apparently straight, terete. Styloid blades not greatly expanded.

Occurrence.—Trentonian, Cannon Limestone, known from a single locality 0.5 mi north-northeast of Pulaski, Tennessee. Guensburg (oral commun., 1987) feels certain that the material is from the base of the Catheys Limestone, *Costellaria* beds (Edenian), at the same geographical locality, and is not from the Cannon Limestone as originally described (Locality F).

Types.—Syntypes[9]: USNM 91854, Locality F. Topotypes/hypotypes: USNM 91854[10], Locality F.

Morphological discussion.—The dorsal theca differs little in plate configuration from younger Cincinnatian age species except that the plates commonly are wider and result in a relatively broader theca. Ornament on the carapace is made up of deep punctae uniformly spread across the plates. This pattern, as the species name implies, is characteristic of the species. Most specimens are so weathered that coarser stromal patterns in the punctae can be seen. As is typical in most mitrates, a band of small, transverse, aborally-overlapping ridges extends across the distal end of the carapace (see Caster, 1952, p. 13).

The plastron is known from a single specimen (Pl. 5, fig. 8), which does not significantly differ from that of other species of *Enoploura* (Text-fig. 16).

The arcuate lip on the distal end of the theca is

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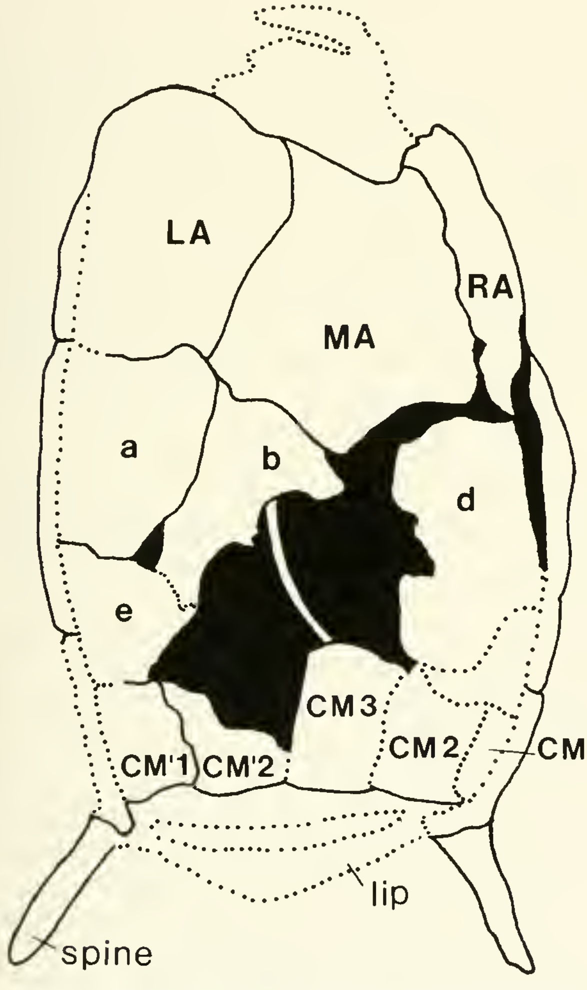
[9] The four syntypes consist of three variously preserved carapaces and a laterally crushed proximal aulacophore, styloid, and proximal segments of a distal aulacophore, all on a small slab. It seems inadvisable to me to select a lectotype.

[10] nine specimens collected at the same time and place by Bassler; mostly carapaces, but one plastron and fragments of the aulacophore are also preserved. All specimens are USNM 91854.

thicker than that found on *E. popei* Caster, 1952, from the Cincinnatian, which probably accounts for its preservation, and in *E. punctata*, the radiating venation system on the lip has not been observed (Pl. 4, fig. 5; Text-fig. 15).

Proximal to the distal margin of the lip, the transverse serrate marginal ridge is well-developed on several specimens. Its greatest elevation is medial on the median marginal plate **m6** and slopes laterally to the floor of the theca on marginal plates **m5** and **m′5**. On marginals **m5** and **m′5**, there is a shallow depression between the end of the transverse marginal ridge and the distal–lateral corner of **M4–M′4**, where the spine articulation is located. Probably there was a pair of aboral openings on either side of the transverse ridge, as indicated by the depressions that served as avenues for muscles between the thecal interior and the spines, as well as serving as the anal opening of the gut. That the anus probably opened through the right aperture is suggested by the fact that the diagonal ridge, or septum (Ubaghs, 1968a, p. S528) (Pl. 4, fig. 5, Pl. 5, fig. 4), a probable secretion of the gut-support mesentery, extends directly to it.

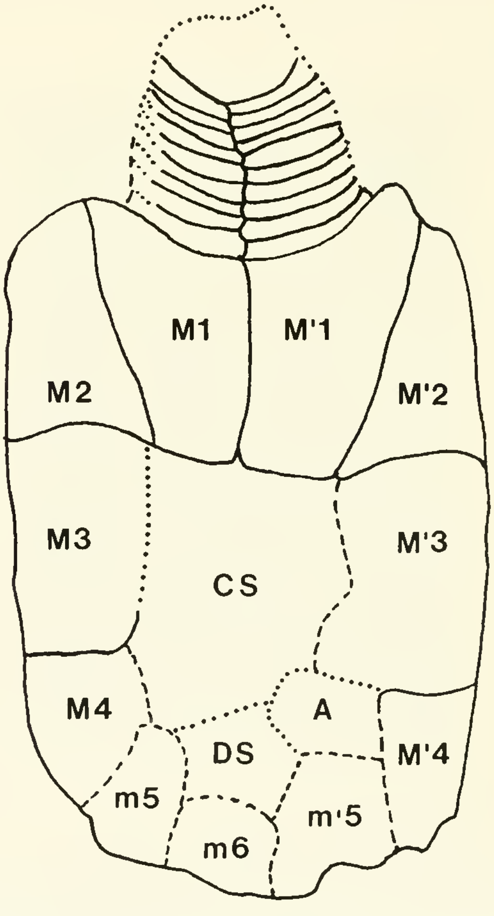


Text-figure 15.—Carapace of *Enoploura punctata*. This figure is based on USNM 91856 (Pl. 4, fig. 5). Note that the spines are more massive and terete than the thinner, blade-like spines of *Enoploura popei*. Also, note that the distal lip is more robust than that in *Enoploura popei*.

For explanations of plate abbreviations, see Table 1 (foldout inside back cover).

Spine sockets are not so well defined as in some younger species, but there seems to be little difference in their basic configuration. Spines are apparently terete throughout and show little, if any, of the distal compression seen in Cincinnatian species. Total relative length of the spines is not known; there is no assurance that the distal ends of any of the preserved spines are present. Those that are preserved appear to be unusually short (Pl. 4, figs. 5, 8, 9, Pl. 5, figs. 1, 3, Pl. 6, fig. 10).

The proximal aulacophore is made up of about 10 or 11 segments, of which three or four are hidden by the carapace, but their inferior tetrameres are exposed in the plastron embayment. The proximal aulacophore



Text-figure 16.—Plastron of *Enoploura punctata*. This figure is based on USNM 91854 (Pl. 5, fig. 8). Morphologic details of the external distal end of the plastron are poorly known.

For explanations of plate abbreviations, see Table 1 (foldout inside back cover).

is completely typical of the genus (see Caster, 1952, p. 14). The styloid of *E. punctata* is similar to that of *E. balanoides* (Meek, 1872). The blades do not extend out as far, nor are they as rounded as those in *E. popei.* They are more acutely rounded inferiorly, resulting in a plowshare-like outline (Pl. 4, figs. 7, 8, Pl. 5, fig. 1).

Two pairs of covering plates above the distal styloid blade are larger than those in *E. popei* and less constricted dorsally, due to the flatter insertion angle of the distal aulacophore into the styloid (Pl. 4, fig. 7). In *E. popei*, the angle of insertion is such that the proximal pair of covering plates on the distal aulacophore is almost in contact with the superior meres of the distal proximal aulacophore segment; the superior ends of the covering plates are nearly crowded out.

Preservation of the styloid of *E. punctata* shows none of the syzygial suturing that is present between the styloid elements in disarticulated specimens of *E. popei.*

The distal aulacophore, as in other species of *Enoploura*, consists of a keel-shaped basal series with a pair of covering plates over each ossicle. Narrow sutural flanges on the proximal end of the distal aulacophore are especially prominent.

Covering plates on the distal aulacophore are relatively larger than those of *E. popei*, and tend to display a greater degree of distal overlapping. Raised muscle ridges on the distal margins of these plates tend to be larger than on Cincinnatian species (Pl. 4, fig. 6).

The total number of segments in *E. punctata* is unknown; no example of a complete distal aulacophore is extant. When one compares a nearly complete aulacophore of *E. punctata* (Pl. 5, fig. 5, Pl. 6, fig. 10) to that of specifically indeterminate Cincinnatian age specimens of the same genus (Pl. 6, figs. 4, 5), the total number of segments in both cases is commonly 30 to 40 and may be as high as 50. Species of *Enoploura* of Cincinnatian age have a thicker, more robust, distal aulacophore.

Discussion.—Bassler (1932), p. 218, 219) briefly described and figured this species, "which is distinguished from other members of this genus by its punctate surface." Bassler (1935, pp. 403, 406) briefly redescribed the species, explaining that this was necessary under the new, post-1930 rules of zoological nomenclature, in order to validate this and other taxa proposed as new in his 1932 publication. The original description was minimally adequate, and the 1935 publication did little to improve it: *E. punctata* was described as follows:

"This well marked cystid is distinguished from the genotype, *E. balanoides* (Meek), by its flattened theca and specially by its highly punctate surface."

In both descriptions, Bassler misspelled the generic name, introducing the *nomen imperfectum*, *Enopleura.*

The flattened theca is partly due to preservation, although these relatively broad specimens probably did have a flatter carapace than most of the Cincinnatian species.

Enoploura balanoides (Meek, 1872)
Plate 4, figures 1–4

Anomalocystites (*Ateleocystites*?) *balanoides* Meek, 1872, pp. 423, 424; Meek, 1873, p. 41–44, pl. 3*bis*, figs. 6a–c.

Enoploura balanoides (Meek). Wetherby, 1879, pt. 1, p. 163; pt. 2, pl. 7, figs. 1d–g; Bather, 1900, p. 51; Bassler and Moodey, 1943, p. 157; Caster, 1952, pp. 28, 30, pl. 2, figs. 7–9.

Ateleocystites balanoides (Meek). Woodward, 1880, p. 198, pl. 6 figs. 6–15; Bassler, 1915, p. 88.

Anomalocystites balanoides (Meek). Miller, 1889, p. 224, fig. 247.

Placocystis crustacea Haeckel, 1896, pp. 39, 40, pl. 2, figs. 5, 6, 7, text-figs. 1, 2,

Enoploura crustacea (Haeckel). Bather, 1900, p. 51; Caster, 1952, pp. 30–32, pl. 2, figs. 1–6.

Enoploura wetherbyi Caster, 1952, pp. 32–33, pl. 2, figs. 10–12.

Enoploura meeki Caster, 1952, p. 39. pl. 4, figs. 1–3.

Diagnosis.—*Enoploura* with smooth carapace except for cuesta-like ridges on adaulacophoral carapace plates and marginals, styloid blades plowshare-shaped.

Occurrence.—Maysvillian and Cincinnatian: Cincinnati, Ohio and vicinity (Localities E and Q [Locality Q, identified by Caster (1952) is that of the holotype of *Enoploura balanoides*, which is presumed lost]).

Types[11].—Holotype: The holotype specimen of *Enoploura balanoides* (Meek, 1872), is presumed lost. It is from the Fairview Formation, Cincinnati, Ohio (see Caster, 1952, pp. 28, 30). UCM 37296 [holotype of *E. crustacea* (Haeckel, 1896)], Locality E. UCM 31309, Locality L.

Description.—The type species varies from other species by surface markings and by the paired plowshare-like blades rather than a rounded pair of styloid blades (*e.g.*, as in *E. popei*). In all other respects the description under the generic heading holds for this species.

Discussion.—The genus *Enoploura* was based on incomplete specimens of *E. balanoides*, which consist of the proximal half of the theca, with or without an attached partial to complete proximal aulacophore. In one specimen the styloid appears to be intact and is of a size and configuration similar to that of *Ateleocystites* Billings, 1858, or *Anomalocystites* Hall, 1858 (see Wetherby, 1879, pl. 7, figs. 1a–g).

The holotype specimen of *Enoploura crustacea* (Haeckel) was lost for many years; in the 1960's, it was located and is now in the collections of the University of Cincinnati. This original specimen of Wetherby was given a new species name by Haeckel and placed in

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[11] *E. meeki* Caster, 1952, and *E. wetherbyi* Caster, 1952, are regarded as synonyms of *E. balanoides*: each is represented by a single incomplete specimen (see Caster, 1952).

the genus *Placocystis* [*sic*]. Haeckel felt it was sufficiently different from Meek's holotype (which is only a proximal end of a theca) to warrant a new species assignment. Caster (1952) removed a second specimen illustrated by Wetherby (1879, pl. 7, figs. 1, 1a, 1b) and established *Enoploura wetherbyi*. This specimen with the styloid and several segments of the distal aulacophore intact and attached to a distally incomplete theca was originally placed in the Crustacea by Wetherby. This mistaken assignment brought disparaging remarks by Woodward (1880) [see Caster, 1952, p. 33].

Enoploura crustacea, *Enoploura wetherbyi*, and *Enoploura meeki*, each of which is known only by a partial (proximal) theca with few or no aulacophore segments attached, are all late Richmondian in age and are herein considered conspecific with *E. balanoides*. *Enoploura balanoides* is also probably Maysvillian in age, although the data on the stratigraphic placement of the holotype are obscure (see Caster, 1952, p. 30).

Other than the priority established by *E. balanoides*, the validity of any of these synonymized species is questionable. Together, all of them easily fit within the range of variability now known for the clearly-recognizable species *E. punctata* (Edenian) or *E. popei* (Cincinnatian). *E. balanoides* is coeval with *E. popei*, but with the synonymized forms extends farther up the section. In the Cincinnatian, two species of *Enoploura* are now recognized: *E. popei*, with large, rounded styloid flanges (Maysvillian), and *E. balanoides*, with plowshare-like flanges (Maysvillian and Richmondian).

Enoploura cf. **E. balanoides** (Meek, 1872)
Plate 5, figures 6, 7, Plate 6, figure 12

Occurrence.—Maysvillian: Cincinnati, Ohio (Locality Q) and Camden, Ohio (Locality L).

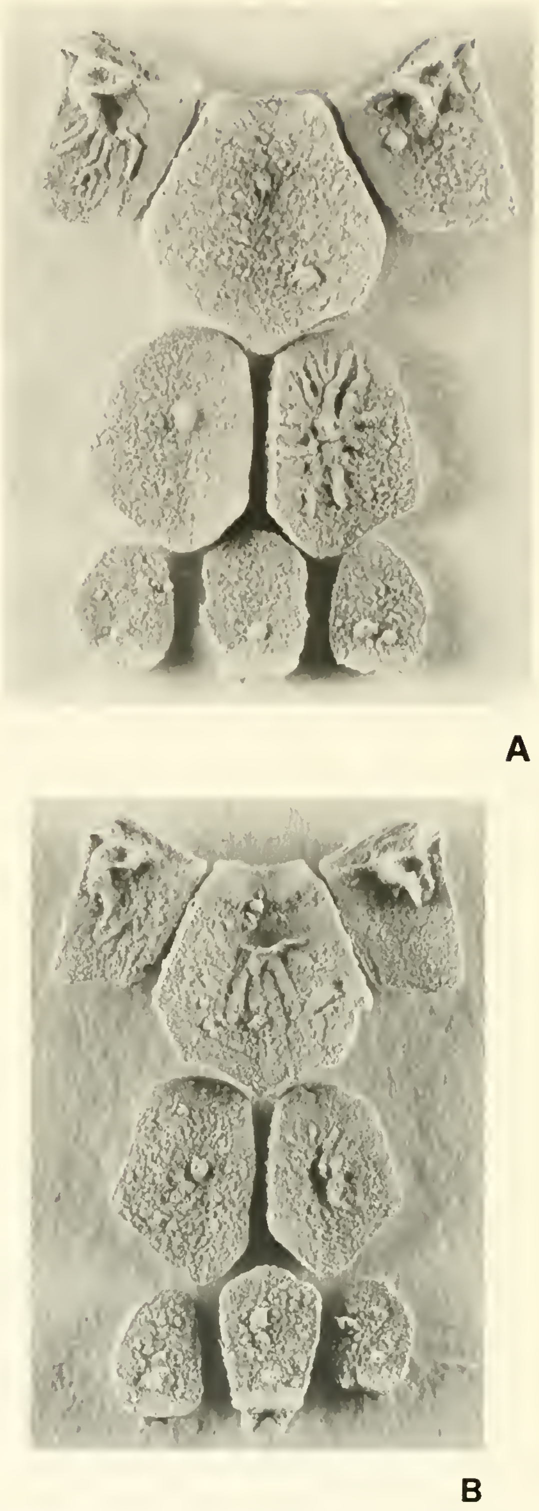
Types.—UCM 46045, 46046 (Locality Q); UCM 31309 (Locality L).

Discussion.—The proximal aulacophore of *E. balanoides*, with its plowshare-like styloid, is usually narrower, rounder, and more tapered than the proximal aulacophore of *E. popei*. The incomplete specimens included under *Enoploura* cf. *E. balanoides* are tentatively placed here due to the nature of their proximal aulacophores. Because the proximal aulacophore is easily deformed, this method of assigning specimens to species is tenuous and not reliable as a taxobasis.

Enoploura popei Caster, 1952
Plate 6, figures 1–3, 6–9, 11;
Text-figures 1–3, 10–14, 17

Enoploura popei Caster, 1952, pp. 34–39, pl. 1, figs. 1–6, pl. 3, figs. 1–6, pl. 4, figs. 4–8, text-fig. 1.

Diagnosis.—*Enoploura* with large rounded styloid



Text-figure 17.—A, B, partial reconstructions of the internal surface of the carapace of *Enoploura popei*, using disarticulated plates. Markings on these plates are highly variable and presumably represent muscle and tissue attachment sites. The large ridges on the **LA** and **RA** plates probably served for proximal aulacophore anchoring, and/or muscle attachments. Note the well-developed, distally-directed spines on the carapace marginals (**CM2**, **CM3**, **CM'2**).

For explanations of plate abbreviations, see Table 1 (foldout inside back cover).

blades, distal marginal carapace plates with punctate prosopon.

Occurrence.—Late Ordovician (Maysvillian), vicinity of Cincinnati, Ohio (Localities I and K).

Types.—Holotype: UCM 25993, Locality I. Hypotypes: UCM 46049, Locality K.

Discussion.—The general aspects of this species have been described above under the generic heading. The distinguishing characters of the species are given in the diagnosis.

In addition to the known articulated specimens, which include complete thecae, spines, and nearly complete aulacophores, thousands of disarticulated plates and spines are known. These come from Boudinot Avenue in Cincinnati, and were collected by J. Stocker and W. Deak, amateur paleontologists. Their collections of these plates are now in the collections of the University of Cincinnati. Also in the University collections are similar, but commonly less well-preserved plates from St. Marys, Indiana. The plates from the latter locality appear to be from about the same horizon as those from Boudinot Avenue. These give us a good picture of the internal plate anatomy of this genus, which is quite similar to that of other anomalocystitids. The most important variable appears to be the branching pattern on the internal surface of the **MA** plate (Text-figs. 12A, 12B, 17A, 17B).

Enoploura cf. **E. popei** Caster, 1952
Plate 5, figures 9, 11

cf. *Enoploura popei* Caster, 1952, pp. 34–39, pl. 1, figs. 1–6, pl. 3, figs. 1–6, pl. 4, figs. 4–8, text-fig. 1.

Occurrence.—Late Ordovician Whitewater Formation (Locality H) and Waynesville Formation (Locality P), southern Indiana.

Discussion.—Proximal aulacophores of *E. popei* tend to be broader, and more oval than circular in cross-section, and are less tapered than those of *E. balanoides*. This more robust nature is probably due to the larger and more rounded styloid blades. The poorly preserved specimens included under *Enoploura* cf. *E. popei* appear to have remnants of *E. popei*-like proximal aulacophores. As with *E. balanoides*, this method of assigning specimens to this species is very tentative due to the deformable nature of the proximal aulacophore.

Family **PLACOCYSTITIDAE** Caster, 1952[12]
Subfamily **PLACOCYSTITINAE** Caster, 1952[13]

Diagnosis.—Anomalocystitids with one to three infracentrals, four or five rows of more or less symmetrically-arranged supracentralia, median adaulacophoral (**MA**) plate does not reach superior proximal margin, sagittally-placed placocystitid plate commonly present, rarely missing.

Discussion.—Caster (1952, p. 27) defined this subfamily, in part, as having one or two somatic plates on the plastron, a symmetrically-arranged carapace with four or five rows of centralia, and a sagittally-placed placocystitid plate.

Kolata and Jollie (1982) modified the definition to include *Ateleocystites* Billings, 1858 (Caradocian–Trentonian of eastern North America) and *Barrandeocarpus* Ubaghs, 1979 (Early Caradocian of Bohemia), each of which have three infracentrals. More importantly, they recognized the subfamilial characteristic that only two superior (left and right) adaulacophoral plates form the proximal margin. The median adaulacophoral plate is excluded, in some specimens quite narrowly, from contact with the proximal aulacophore. This characteristic, which might seem to be a minor morphological variable, is nevertheless consistent throughout the range of the subfamily (Middle Ordovician–Early Devonian).

In *Placocystites forbesianus* de Koninck, 1869, the **P** or placocystitid plate (Caster, 1952) or the **xi** plate (Jefferies, 1984) has been observed in juveniles to be large and variable relative to the size of the carapace. As Jefferies (1984) observed, while the location of the plate center remains relatively the same, the adjacent lateral somatics gradually surround it and it becomes relatively reduced in size. In more mature specimens, the greatly-reduced plate, in terms of the area exposed to the interior of the theca, evenly flares out (as seen in its broad funnel-shaped cross-section) over the adjacent plates and results in a rounded plate outline on the outer surface. Because the plate overrides the adjacent centralia and thins considerably near its periphery, a relatively minor amount of surface erosion and/or solution can significantly reduce the size of this plate. The shape of the **P** plate is apparently determined neither by abutting against adjacent plates, nor by forming at a triple junction (Jefferies 1984, pp. 308–311; text-figs. 9, 10). Rather, the mode of emplacement is either by reduction through resorption and surrounding by adjacent centralia, or possibly by secondary resorption and subsequent redeposition. Neither case has been observed. However, Jefferies' evidence for the former case is highly compelling.

The closely-related new genus, *Kopficystis*, does not show signs of this ontogenetic sequence (*i.e.*, the **P** plate is apparently missing, which could be due to juvenile resorption). The area of the carapace where the **P** plate occurs appears to be a zone of considerable stereom secretion/?resorption activity in mitrates, even in non-placocystitids, because a small placocystitid-like plate

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[12] =Placocystidae Caster, 1952 (*nom. correct.* Gill and Caster, 1960).

[13] =Placocystinae Caster, 1952 (*nom. correct.* Gill and Caster, 1960).

has been observed in some specimens of *Anomalocystites.*

The genera *Placocystites* de Koninck, 1869, *Rhenocystis* Dehm, 1932, *Barrandeocarpus* Ubaghs, 1979, and *Ateleocystites* Billings 1858, easily fit into this subfamily. *Kopficystis*, n. gen., very closely resembles *Rhenocystis* in its general outline, number of plate series on the carapace, and configuration of the superior proximal theca. It differs in that no placocystitid plate is present in this monotypic genus. As previously indicated, it seems advisable to slightly expand the definition of this subfamily rather than to create a new one to receive this single genus. Inclusion of *Ateleocystites*, *Barrandeocarpus*, and *Kopficystis* in the Placocystitinae extends the range of the subfamily from Late Silurian–Early Devonian downward to the Middle Ordovician.

Genus **KOPFICYSTIS**, new genus

Type species.—*Kopficystis kirkfieldi*, n. sp.

Remarks.—Since this genus is monotypic, it follows that diagnosis, description, and occurrence of this new genus are the same as those for the species.

Kopficystis kirkfieldi, new species

Plate 7, figure 10; Text-figure 18

Diagnosis.—Placocystitid with median adaulacophoral plate exserted from adoral margin; no **P** plate; at least five transverse series of supracentralia.

Occurrence.—Middle Ordovician (Trentonian), Kirkfield, Ontario (Locality O).

Type.—Holotype: USNM 116408, Locality O.

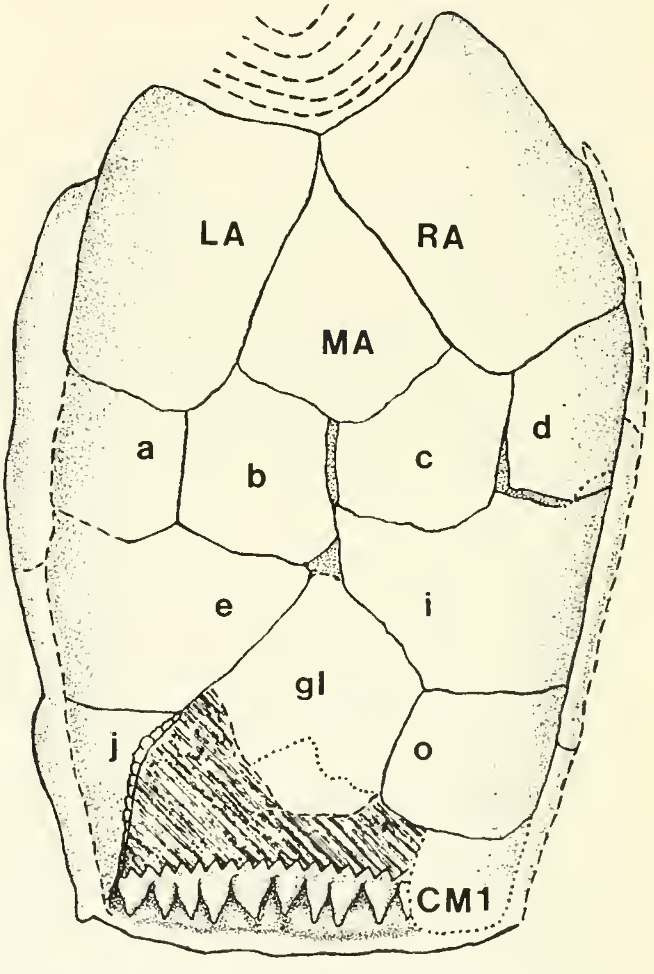
Description.—What is known of this new taxon is derived from a single specimen that shows the nearly complete but distally weathered superior surface (carapace) of the theca. Thecal sockets for the articulating distal spines are present, but the spines themselves are missing. A poorly-preserved portion of an apparently typical mitrate proximal aulacophore is present.

In outline and general plate arrangement, *Kopficystis kirkfieldi*, n. sp., bears a strong resemblance to the Devonian genus *Rhenocystis* Dehm, 1932. There is no evidence of any transverse ornament ridges, especially on the adaulacophorals, that are so common on taxa included in the Anomalocystitida; instead, the surface is covered with even, fine-grained, pustules.

The aulacophore embayment is broad, as in *Enoploura*, but the median adaulacophoral (**MA**) plate is narrowly excluded from the margin, which is wholly made up of right and left adaulacophoral plates (**RA** and **LA**). Both the right and left adaulacophoral plates are broad at the expense of the quadrangular median adaulacophoral plate (Pl. 7, fig. 10; Text-fig. 18).

Distal to the adaulacophoral series are four subequal median supracentrals (**a**–**d**) in a transverse series across the theca: their disposition is typical within the Placocystitinae.

Distal to this transverse series of supracentrals is a pair of large, subpentagonal supracentral plates (**e**, **i**) that extend almost to the middle of the theca. These subpentagonal plates are most atypical of anomalocystitids, and their size and shape must be regarded as generic characters. The marginal positions of these plates correspond to the area covered by supracentrals **e** and **i** of *Anomalocystites* . Whether there is any homology between these two genera which are in different families, with respect to these plates, is conjectural. Discussion and identification of the supracentralia in *Kopficystis* is, however, compared to the position of supracentralia in *Anomalocystites*.



Text-figure 18.—Carapace of *Kopficystis kirkfieldi*, n. gen. and sp. This figure is based on USNM 116408 (Pl. 7, fig. 10). The **MA** plate is slightly excluded from the aulacophoral margin. Plates covering the distal half of the carapace either represent composites of smaller plates or are enlarged plates that have crowded out adjacent supracentral plates. For example, plate **gl** occupies the same space as plates **g** and **l** in *Anomalocystites cornutus*.

For explanations of plate abbreviations, see Table 1 (foldout inside back cover).

Distal to **e** and **i** are two marginal supracentrals, **j** and **o**, which are irregularly-square in outline. The left plate, **j**, is poorly preserved and largely missing. Between **e/j** and **i/o** is a large pentagonal "central–dorsal" (**gl**) plate that extends from a sutured contact with **b** distally beyond **j** and **o** to contact the distal carapace marginal series. The "central–dorsal" plate is so named because it occupies the space of the midplates of the second and third rows of supracentrals in *Anomalocystites*.

Partial remains of the right distal carapace marginal (**CM1**) indicate a similar outline to that of the adjacent **o** plate. The rest of the distal carapace marginals are not preserved.

Anal valve platelets are visible at the distal end of the carapace: normally they would be covered by the distal carapace marginals. They appear to be better developed than in either *Enoploura* Wetherby, 1879, or *Ateleocystites* Billings, 1858.

Articulatory sockets for spines located on the aboral ends **M4** and **M'4** are similar to those of *Enoploura*.

Discussion.—Despite the incompleteness of the holotype of the type and only known species, there is enough to see the striking resemblance to the placocystitid carapace (*cf. Rhenocystis* or *Placocystites* de Koninck, 1869) in the number and arrangement of the plates. *Kopficystis* lacks the typical placocystitid (**P**) plate, which is diagnostic of the placocystitids.

It also appears, but with no great degree of certainty, that the carapace distal margin consists of three plates. This number is typical in the Placocystitinae (except in *Ateleocystites*, which apparently has four), while in the Enoplourinae this margin is composed of five plates.

Genus **ATELEOCYSTITES** Billings, 1858

Ateleocystites Billings, 1858, pp. 72–73, fig. 4; Zittel, 1879, p. 413(*pars*); Woodward, 1880, pp. 194–201, pl. 6(*pars*); Kirk, 1911, pp. 22–23; Bassler, 1915, p. 88; Jaekel, 1918, p. 122; Wilson, 1946, pp. 7, 8, pl. 2, figs. 1–4; Caster, 1952, pp. 17–21, 27–29, figs. 2A, 2B; Gill and Caster, 1960, pp. 44, 45; Regnéll, 1960, pp. 166, 167; Kolata and Jollie, 1982, pp. 640–649, pl. 1, figs. 1–16, pl. 2, text-figs. 3–9.

non Placocystites de Koninck, 1869. Woodward and Billings *in* Woodward, 1871, pp. 71, 72.

non Anomalocystites (*Ateleocystites*?) Meek, 1872, pp. 423, 424; Meek, 1873, pp. 41–44, pl. 3*bis*, figs. 6a–c [= *Enoploura balanoides* (Meek). Caster, 1952, p. 28].

Anomalocystites Hall. Miller, 1889, pp. 224, 226(*pars*); Springer, 1913, p. 150(*pars*).

non Atelocystites Haeckel, 1896, pp. 41–43, pl. 2, figs. 10–12. [= *Placocystites*, *fide* Regnéll, 1945, p. 197.]

Atelecystis Billings. Bather, 1900, p. 51.

[?] *Ateleocystites* Lindström, *non* Billings. Regnéll, 1945, pp. 196–197. [= *Placocystites fide* Regnéll, 1945, p. 197, fn. 7]

Type species.—*Ateleocystites huxleyi* Billings, 1858.

Diagnosis.—Placocystitinae with well developed transverse distally pseudo-imbricating ornament ridges on **M1/M'1** and **M2/M'2**; placocystitid plate prominent, **MA** plate excluded from adaulacophoral margin.

Occurrence.—Type species known from three Trentonian age localities: ?Hull Beds, Ottawa Limestone, Brigham Quarry, near Hull, Quebec (Locality R); Ottawa Limestone, Hull Beds, locality unknown (Locality S); and Martinsburg Formation, Swatara Gap, Lebanon County, Pennsylvania (Locality T). One and possibly two other species are known from the Glens Falls Formation, Trenton Falls, New York (Locality M), and from the Guttenberg Formation, upper Mississippi River Valley: Middle Ordovician.

Discussion.—Kolata and Jollie (1982) clearly demonstrated that *Ateleocystites* is properly included in the anomalocystitid subfamily Placocystitinae. The two features diagnostic of the subfamily, the exclusion of the **MA** plate from the adaulacophore margin, and the presence of a placocystitid plate are both present in this genus.

Most of the type specimens of *A. huxleyi* Billings, 1858, from Quebec are plastrons, and only a single specimen displays a poorly-preserved proximal carapace. Previous to this report, the complete carapace of *Ateleocystites* was known only in *A. guttenbergensis* Kolata and Jollie, 1982. Fortuitous preservation of specimens of *Ateleocystites* from the Glens Falls Limestone locality at Trenton Falls, New York, has resulted in mostly plastrons being represented. For years it was thought these undescribed specimens were referable to *Enoploura*. Recent discovery of several carapaces in the collections of the MCZ unquestionably places these specimens in *Ateleocystites*: they are referred, with some degree of certainty, to the type species, *A. huxleyi*.

Specimens collected in Swatara Gap, in the uppermost Martinsburg Formation (*Climacograptus spiniferus* Zone), Lebanon County, Pennsylvania, are morphologically very close if not identical to the type species, *A. huxleyi*, and may even be conspecific with *A. guttenbergensis* (Derstler, written commun., 1984). Kolata and Jollie (1982, p. 648) point out, however, that there is an extra supracentral, directly distal to the **P** plate in the specimen from Swatara Gap. In *A. guttenbergensis*, the spines of the styloid and adjacent ossicles of the distal aulacophore are especially prominent. Kolata (written commun., 1987) reports that in subsequent finds of *A. guttenbergensis*, the theca may reach lengths of 2.5 cm, certainly the largest size yet reported for this genus. The degree to which the observed differences between *A. huxleyi* and *A. guttenbergensis* represent intra- or interspecies variability is open to question, and the specimens from the Glens Falls Limestone are of little help in this matter. There is no need to redescribe this genus: Kolata and Jollie (1982) have given an excellent picture of its characteristics. I will, however, illustrate herein new specimens of *A.* cf. *A. huxleyi* from the Glens Falls Limestone, Trenton Falls, New York.

Ateleocystites huxleyi Billings, 1858

Ateleocystites huxleyi Billings, 1858, pp. 72–74, fig. 4; Woodward, 1871, pp. 71–73; Woodward, 1880, pp. 193–201, pl. 6, fig. 1; Bassler, 1915, p. 88; Wilson, 1946, pp. 7, 8, pl. 2, figs. 1–4; Caster, 1952, p. 29, fig. 29, figs. 2A, 2B; Kolata and Jollie, 1982, pp. 640, 648; [*non* Lindström, 1888 (*ref.* Regnéll, 1945, pp. 196, 197 [= *Placocystites* aff. *forbesianus fide* Gislén *in* Regnéll, 1945, fn. 7, p. 197])].

Anomalocystites huxleyi (Billings). Miller, 1889, pp. 224, 226.

Ateleocystis huxleyi (Billings). Haeckel, 1896, p. 41.

Atelecystis huxleyi (Billings). Bather, 1900, p. 51.

Diagnosis.—*Ateleocystites* with well developed transverse distally pseudo-imbricating ornament ridges on **M1/M'1** and **M2/M'2**; placocystitid plate well developed.

Occurrence.—Hull Beds, Ottawa Limestone, Brigham Quarry, near Hull, Quebec (Locality R); an unknown locality, Hull Beds, presumably close to the former site (Locality S); and Martinsburg Formation, Swatara Gap, Lebanon County, Pennsylvania: Middle Ordovician (Locality T).

Types.—Holotype: GSC 1392, paratypes GSC 1392 a-h, Brigham Quarry, Hull Beds, Ottawa Limestone, near Hull, Quebec (Locality R). Hypotypes: MCZ 1063, MCZ 2064, USNM 93348 and USNM 401499, Locality M.

Discussion.—The type species *A. huxleyi*, and *A. guttenbergensis* may be conspecific. The question will be settled by obtaining topotypes of *A. huxleyi* with the carapace intact. Until then, the excellent descriptions of *A. guttenbergensis* by Kolata and Jollie will for practical purposes more than suffice for a detailed explanation of morphology.

In describing the type material, Billings (1858, pp. 72, 73, fig. 4) originally figured a comb-like structure traversing the aboral end of the theca, which he suggested to be "the marginal ambulacral ossicula of the ordinary Cystitidae." On further examination of Billings' lectotype, Wilson (1946, p. 7) noted that this structure is "a piece of plate half buried in the matrix", and it is recognized herein as internal corrugations related to the transverse ridge of the distal carapace marginals. Wilson added that "another specimen . . . shows another and perhaps truer branching arrangement of the pinnules." This paralectotype specimen displays a bundle of spicular material aboral to the **m6** marginal. It seems to be nothing more than extraneous organic carbonate material and is not like any structure known in the mitrates.

Ateleocystites cf. **A. huxleyi** Billings, 1858
Plate 7, figures 1–4

Occurrence.—Glens Falls Formation, Trenton Falls, New York: Middle Ordovician (Locality M).

Types.—The four specimens figured are MCZ 1063, MCZ 2064, USNM 93348, and USNM 401499.

Discussion.—For a number of years, specimens labeled *Enoploura* in the USNM and other collections have been known, but were unfigured in earlier works because of their incomplete nature and because of some uncertainty as to their correct generic assignment. Recently, incomplete specimens with well-preserved carapaces were discovered in the collections of the MCZ. The presence of a placocystitid plate, the exclusion of the **MA** plate from the proximal carapace margin, and the distinctive ornament on the adaulacophoral plates demonstrate that these specimens are truly assignable to *Ateleocystites*. They seem to be quite close to the type species, *A. huxleyi*.

Several specimens show rather complete aulacophores. They are long, fully extended, and not reflexed back toward the theca as is typical with anomalocystitids, especially specimens preserved in younger strata. Also, the number of distal aulacophore segments in these specimens is estimated at between 25 and 30. In *A. guttenbergensis*, Kolata and Jollie estimate there are 35 to 40 segments in the distal aulacophore. In both species, counts were estimated on nearly complete distal aulacophores. However, the thecal size in the illustrated examples of *A. guttenbergensis* appears to be about one-half that of *A.* cf. *A. huxleyi*. As in *Enoploura*, the number of distal aulacophore segments seems variable, and the number of segments alone probably is not of taxonomic significance.

Suborder **PELTOCYSTIDA** Jefferies and Lewis, 1978

Diagnosis.—Mitrates with an asymmetrical theca, number of thecal plates reduced, two especially large adaulacophorals, these in some genera considerably overlapped along superior sagittal axis: single tapering, slightly sigmoidal articulating spine on right distal end of theca: aulacophore long, ossicles of proximal segments of distal aulacophore especially spinose.

Discussion.—Jefferies and Lewis (1978, p. 422) removed the superficially-similar peltocystids from the Lagynocystida because of the lack of common morphological traits. *Lagynocystis* Jaekel, 1918, has a hollow articulating spine on left side of the theca and three adaulacophorals on the superior surface. The proximal aulacophore is quite different from that of the Peltocystida, and the styloid is considerably more denticulate (see Jefferies and Lewis, 1978, p. 422). The Peltocystida do not have internal ctenoid organs, which are a diagnostic feature of *Lagynocystis*, and the proximal plates on the superior surface of peltocystids are large and paired.

This suborder is now divided into two families, the Peltocystidae and the Kirkocystidae. The Peltocystidae is characterized by the single genus *Peltocystis* Thoral, 1935 from the Early Ordovician of France. Asymmetry in the marginals and intracentrals is marked in *Peltocystis*, and reversal of the basic asymmetrical plate order (see Ubaghs, 1968a, p. S500; Ubaghs, 1969, p. 82) is also evident. The single sigmoidal articulating spine, large adaulacophorals, and similar aulacophore seem sufficient to demonstrate close relationship to the other peltocystid family, the Kirkocystidae.

The Kirkocystidae, with two genera, represents the end-point in the reduction in number of thecal plates in the Mitrata. In *Anatiferocystis* Chauvel, 1941, adaulacophorals are the dominant plates and make up most of the theca. Marginals **M1/M'1** are extremely asymmetrical and are completely restricted to the inferior surface. A large distal marginal flap on the infradistal end completes the theca, except for a narrowly-exposed infraplate (probably an ingressed marginal), adjacent to the right adaulacophoral, which bears the single, articulating, sigmoidal spine. *Balanocystites* Barrande, 1887 is quite similar to *Anatiferocystis*, but does vary slightly (see Ubaghs, 1968a, pp. S555, S557; Jefferies, 1981, p. 374).

Family **KIRKOCYSTIDAE** Caster, 1952

Diagnosis.[14]—Theca convexoplanar, asymmetrical, composed of only two adaulacophorals, two marginals (**M1, M'1**), one subanal, and in some an internal marginal (**?M5** or **?M'4**) with articulating distal spine; adaulacophorals convex, elongate, subequal, very large, covering entire superior face and large part of inferior face; **M1** and **M'1** reduced, **M1** smaller than **M'1**, **M'1** extends distally to subanal, which is inserted between distal lateral inferior margins of adaulacophorals; proximal region of aulacophore composed of four tetramerous segments; styloid and following distal aulacophore ossicles inferiorly spinose.

Occurrence.—Kirkocystids are found in the Middle Ordovician of North America (Oklahoma) and Europe (Bohemia). Recently a probable kirkocystid of Morrowan (Pennsylvanian) age was uncovered in the Gene Autry Shale Member of the Golf Course Formation in southern Oklahoma. This specimen is the youngest known mitrate and extends the upper range of this group by about 70 million years (Frest, Kolata, and Mapes, 1985).

Discussion.—The Kirkocystidae are probably derived from the Early Ordovician genus *Peltocystis* Thoral, 1935, or a *Peltocystis*-like ancestor. Features such as the very similar aulacophores, sinuous single articulated aboral spine, large paired adaulacophorals, and distally-extended **M'1** on the inferior surface all suggest close affinities. The probability that the spine-bearing plate in *Anatiferocystis* is an ingressed marginal in contact with **M'1** further supports this close relationship.

Marginal plates present in a *Peltocystis*-like ancestor, other than **M1** and **M'1**, may also be fused within the adaulacophoral plates along the inferolateral ridges, but their presence is doubtful. Both superior and inferior centralia, probably present in the ancestral stock, have been lost in the Kirkocystidae, nor are they added during ontogeny. The greatly reduced number of thecal plates, and the ingression of **M'4** or **M5** suggests a paedomorphic mode in the derivation of the kirkocystid from the peltocystid theca (*i.e.*, many distal plates present in ancestral stock are omitted, just as they are, but to a lesser degree, in the evolution of the anomalocystitids). The streamlining and reduced size of the kirkocystid theca, the powerfully-constructed proximal aulacophore, and the long distal aulacophore indicate adaptation to a more mobile mode of life.

Genus **ANATIFEROCYSTIS** Chauvel, 1941

Lagynocystis Jaekel. Chauvel, 1937 [*pars*], p. 3.
Anatiferocystis Chauvel, 1941, pp. 206–210; Ubaghs, 1968a, S555; Ubaghs, 1979, pp. 107–111, fig. 4.
Enoploura? Wetherby. Bassler, 1943 [*pars*], p. 695, pl. 1, figs. 3–5.
Kirkocystis Bassler, 1950, p. 277, p. 275, figs. 15, 16.

Type species.—*Anatiferocystis barrandei* Chauvel, 1941.

Diagnosis.[15]—Theca convexoplanar, asymmetrical, tapering distally, made up of six plates: two adaulacophorals, two marginals (**M1, M'1**); distal marginal (**M'4** or **M5**) with spine articulation, plate almost completely internal except for narrow exposure adjacent to subanal, and inclined, distally situated subanal; sutures between adaulacophorals commonly overlapped.

Discussion.—The study of European species of *Anatiferocystis*, *A. barrandei* (the type species), and *A. spinosa*, has been primarily by use of latex rubber molds and casts. Principal details of the thecae in both seem much the same as in the North American species *A. papillata* (Bassler, 1943), which is preserved as original calcite material. *A. spinosa* Ubaghs, 1979, preserves considerable aulacophore detail and some detail of the articulating spine. Spines with their articulating surfaces are now known in *A. papillata*. Careful comparison of the external features of *A. papillata* and *A. spinosa* indicate that the two species, which appear to be coeval, are also conspecific.

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[14] modified from Ubaghs, 1968a, S555.

[15] modified from Ubaghs, 1979, p. 107.

Anatiferocystis papillata (Bassler, 1943)

Plate 7, figures 5–9, 11–13, Plate 8, figures 1–11;
Text-figures 19, 20

Enopleura? [*sic*] *papillata* Bassler, 1943, p. 695, pl. 1, figs. 3–5.
Kirkocystis papillata (Bassler). Bassler, 1950, p. 277, figs. 15, 16.
Anatiferocystis papillata (Bassler). Ubaghs, 1968a, p. S555; Parsley, 1982, p. 323.
Anatiferocystis spinosa Ubaghs, 1979, pp. 107–111, fig. 4.

Diagnosis.[16]—*Anatiferocystis* with theca covered with numerous posteriorly-inclined small triangular spines.

Occurrence.—Letna Formation (Early Caradocian), Haj near Zahořany, Bohemia, Czechoslovakia; Pooleville Member, Bromide Formation (Blackriveran), Criner Hills, Oklahoma (see Parsley, 1982, p. 323) [Locality N], Benbolt Formation (Blackriveran), eastern Tennessee (Broadhead, written commun., 1986).

Types.—Hypotypes: UCM 46036-46043, USNM 401450-401451, Locality N.

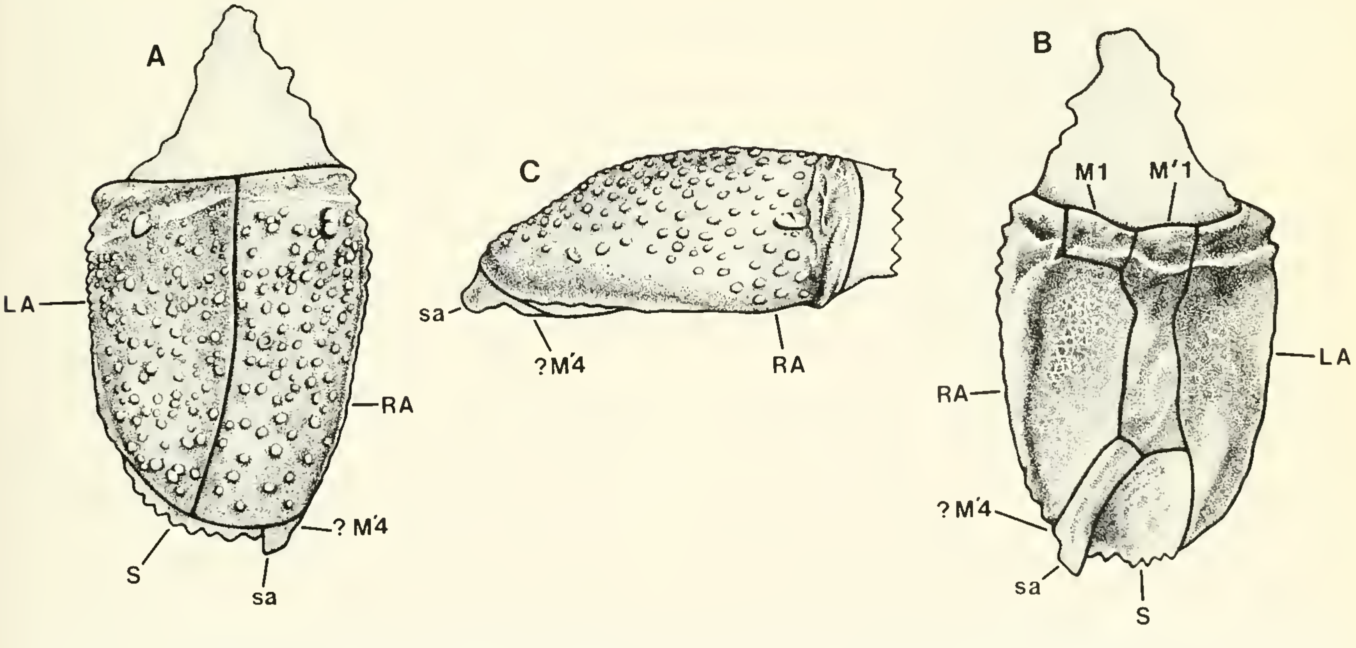
Description.—The superior surface (carapace) of the theca is convex, and the inferior surface (plastron) is slightly concave to planar (Pl. 7, figs. 5, 6, 9, 11, 12; Pl. 8, figs. 1–8, 11). The sides and carapace gently taper distally to the asymmetrically-blunted end (Pl. 7, figs. 7, 8; Text-fig. 19C). The theca is almost entirely made up of the paired adaulacophoral plates. Both adaulacophorals are reflexed into an inferolateral ridge at the proximal end of theca, which becomes diagonally lateral distally (Pl. 7, figs. 6, 12, Pl. 8, figs. 3, 7, 11). The suture between the adaulacophorals is considerably overlapped on the carapace; commonly the right adaulacophoral overlaps the left at a ratio of about 2:1. There is little thinning of the plates along this suture. Hence, the suture is marked by a step on the carapace surface (Pl. 7, figs. 9, 11; Pl. 8, figs. 1, 2, 4, 6).

On the plastron, marginals **M1**, **M′1** form the inferior proximal margin. **M1** is small, rectangular, and is developed only as part of the marginal rim. **M′1** extends distally as a narrow band between adaulacophorals to the subanal (Text-fig. 19); and the adaulacophorals may overlap the lateral surfaces of **M′1** so that the plate seems inset into the plastron surface.

Between the right adaulacophoral and the subanal is a narrow, slightly arcuate plate that commonly appears to be set slightly on edge. This is the external exposure of a larger ingressed marginal plate that extends from the right distal margin, proximally to the midline of the theca, where it terminates against the distal extremity of **M′1**. At the distal margin of this plate is a short peglike extension with a terminal articulatory surface for a moveable spine (Pl. 7, fig. 7, Pl. 8, figs. 7, 11). For reasons given below, this plate is presumed to be homologous with **M′4** or **M5**. (Text-figs. 19, 20).

Serial sectioning shows that the septum extends from the apophyses, across the interior of the right adambulacral to its termination, apparently under the spine boss on **M′4** or **M′5**.

Proximally the variably-shaped subanal is hinged against the left adaulacophoral, **M′1** and **M′4** or **M5**. The plate seems tightly sutured but probably could



Text-figure 19.—Carapace and plastron of *Anatiferocystis papillata* (Bassler). This figure is based on UCM 46036 (Pl. 7, figs. 5–7). **A**, superior (carapace) surface; **B**, inferior surface (plastron); **C**, right lateral view. S = subanal plate; sa = spine attachment base.
For explanations of other plate abbreviations, see Table 1 (foldout inside back cover).

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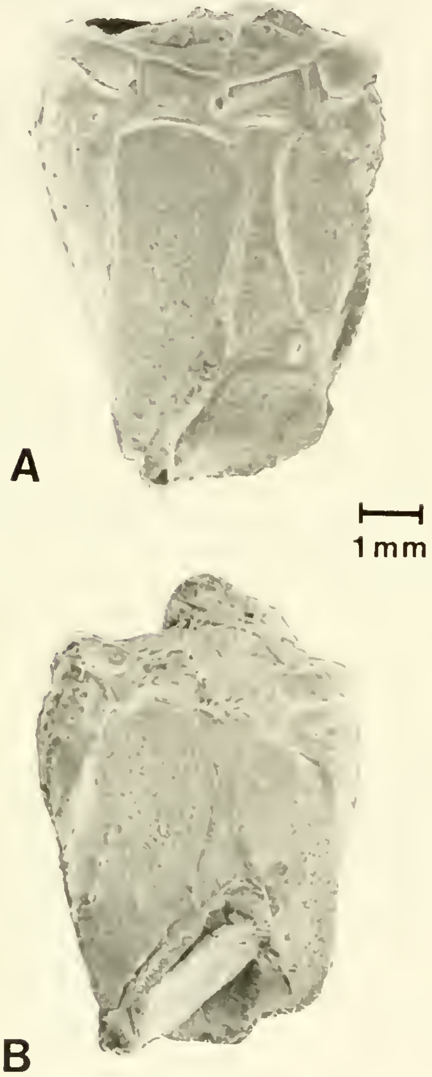
[16] Translated from Ubaghs, 1979, p. 108.

open sufficiently to allow for passage of fecal material (Pl. 7, fig. 6; Pl. 8, fig. 7; Text-figs. 19, 20). The distal edge of the subanal is denticulate (seen only in well-preserved specimens).

The lateral and inferior aulacophoral rim is equipped with ridges and shallow pits, which probably served for muscle attachment. Adaulacophorals have a raised triangular area on the outer inferolateral corner of the theca. The central part of this area is roundly excavated with the deepest part adjacent to the juxtaposed marginals. Marginals **M1/M′1** are similarly raised in narrow rectangular fields adjacent to the aulacophore insert area and are similarly roundly excavated (Pl. 7, figs. 12, 13, Pl. 8, figs. 3, 7). These depressed areas superficially resemble scutelae (normally internal structures), and probably served a similar function (*i.e.*, aulacophore muscle attachment). A broad low ridge on the proximal ends of the adaulacophorals may also have served for muscle attachment.



Text-figure 20.—*Anatiferocystis papillata* (Bassler). S.E.M. photographs of plastrons, showing the nature of ?**M′4** and its spine base. **A**, Undisturbed plastron showing plate sutures. UCM 46047. **B**, Plastron with subanal displaced to an on-edge position. ?**M′4** is more clearly seen as being ingressed at a low angle into the theca. UCM 46048. Photos taken on an Amray 1700 S.E.M. at a power setting of 30 kv.

For explanations of plate abbreviations, see Table 1 (foldout inside back cover).

The surfaces of the superior and lateral faces are covered with short, distally-inclined, triangular denticles (see Ubaghs, 1979, pp. 108–110, fig. 4e). They are concentrated along the proximal–lateral margins where the distal cant is especially prominent, but are otherwise evenly distributed over the superior surface. Denticles are present on the plastron but are restricted to the adaulacophoral plates, especially the left. They are more symmetrical than those on the carapace and without distal cant. The epistereom is quite thin on all of the plates and slight surface erosion exposes the coarser stroma in the interior of the plates.

The aulacophore insertion area is large and encompasses nearly the total width and height of the theca. Into this cavity the proximal aulacophore is tightly inserted (Pl. 8, fig. 9). Apophyses have not been observed. The proximal aulacophore is made up of four tetramerous segments that sharply taper toward the styloid. In cross-section, it is an inflated oval; the lateral margins are sharply angled, the superior and inferior faces flatly and evenly curved. The edges of the segments are slightly thickened and fluted. The styloid is poorly known, but is significantly narrower than the proximal aulacophore. There appear to be two inferiorly-directed spines, connected by a narrow septum on the inferior surface.

Distal aulacophores, known only from Bohemian specimens, are made up of from 40 to more than 45 segments. Each segment consists of an ossicle with paired dorsal covering plates. Covering plates overlap the proximal part of each distal cover plate pair. The proximal ossicles are produced into sharp styloid-like flanges, presumably to grip the substrate.

Total length of the aulacophore exceeds three times that of the theca and in terms of the ratio of length of aulacophore to length of theca, is the longest aulacophore known in the Mitrata (see Ubaghs, 1979, pp. 109, figs. 4a–d, f, g, 110).

The distal articulating spine is thin, slightly curved, and gently tapering from its thickened basal area. It is about one-half the length of the theca and is apparently curved toward the sagittal axis (Pl. 8, fig. 10).

Discussion.—Derivation of these unusual kirkocystid genera (*Anatiferocystis* Chauvel, 1941, and *Balanocystites* Barrande, 1887), is clearly the result of reduction in the number of thecal plates from a more abundantly-plated ancestor. The large paired adaulacophorals on the superior thecal surface are distinctive in all genera in this suborder. In kirkocystids, distal centralia in ancestral forms have been eliminated by the distal extension of this large plate pair. Similarly the lack of marginal plates, almost certainly present in the ancestral stock, is difficult to explain. They have either been excluded, with the exception of **M1**, **M'1**, and the ingressed marginal **M'4** or **M5**, or they may be fused into the theca (primarily on the lateral and inferior faces of the theca). This fusion, if true, would have occurred along with the development of the reflexed lateral–ventral ridge, which in some specimens appears to be a very tightly ankylosed suture. If homologies with *Peltocystis* Thoral, 1935, are valid, **M2**, **M3**, and **M4** on the right side, and **M'2** and **M'3** on the left may be retained in the theca, fused to their adjacent adaulacophorals or, perhaps, some of the elements may be incorporated, and others omitted. However, I suspect that with the exception of **M1**, **M'1**, and the ingressed marginal, all of the marginals have been excluded in the phylogeny of the kirkocystid lineage. Discovery of intermediate forms would probably throw light on this matter.

The ingressed marginal is called **M'4** or **M5** because it has the spine base and is tentatively assumed to be homologous with the spine base-bearing **M'4** or **M5** plate in *Peltocystis*. **M4/M'4** plates are commonly the moveable spine-bearing plates among mitrates. If **M5** of *Peltocystis* (as designated by Ubaghs, 1969, p. 82) is in reality **M'4**, then the relationship of marginal plate to articulated spine remains constant. The markedly asymmetric nature of the marginal thecal plates in *Peltocystis* suggests this interpretation is correct. Whether or not the ingressed spine-bearing marginal in *Anatiferocystis* is homologous to **M'4** or to **M5** of *Peltocystis* is speculative.

The subanal is commonly oblique to the sagittal axis and at best was capable of limited opening, enough to allow for the passage of fecal material. Similar subanal plates in *Balanocystites* and *Chinianocarpos* Ubaghs, 1961, also appear to be tightly sutured, and at best were capable of limited movement. This would seem to refute Philip's (1979, p. 468) opinion that mitrates possessed U-shaped guts, with mouth opening and anus at the distal end of the theca. Feeding at this end of theca, involving movements of the subanal plate in these genera, would appear to have been difficult and unlikely. In *Chinianocarpos*, mouth and anus would have had to open into the substrate. There is no evidence that mitrates were ever deposit feeders.

Overlap of the adaulacophorals on the superior surface is considerable, with the right adaulacophoral overlapping the left with a ratio of about 2:1 (Pl. 8, figs. 2, 6). There may be a tendency in this suborder toward minor reversals in right–left thecal symmetry, which may be related to asymmetry of infracentral plastron plates seen in *Peltocystis* (see Ubaghs, 1968a, p. S500; Ubaghs, 1969, pp. 82–84). No apparent reason or cause for the reversal of overlap in *Anatiferocystis* seems apparent. The consistent overlap ratio seen in specimens from various localities does suggest, however, uniform genetic control.

Life habits of *Anatiferocystis* probably differ slightly from those of the anomalocystitids and most of the other mitrates as well. The small, compact, streamlined theca and unusually long aulacophore suggest a more mobile organism. Undulations of the aulacophore probably originated in the proximal aulacophore and were translated through the styloid to the laterally-compressed distal aulacophore. Several simultaneous waves may have been possible, thus allowing the animal to swim with a minimum of thecal yawing. Undulations would have propelled the animal, theca end first, in tadpole fashion above the bottom. The streamlined hydrofoil shape of the theca would provide lift and the diagonal lateral ridges would have served as hydrofoils to keep the distal end horizontal or facing slightly upward while the aulacophore was sculling. Likewise, the single articulating spine may have in part had a hydrofoil function, as well as serving as a buttress while the animal was at rest.

The sharp ventral spines on the distal aulacophore (see Ubaghs, 1979, p. 109, figs. 4b, d, f) would seem to indicate that the aulacophore stretched out along the bottom, taking in nutrients just above the water–sediment interface. If the aulacophore faced into a current, as the moveable spine and curvature of the aulacophore ossicle spines suggests that it did, then the slightly-arched aulacophore would have effectively trapped food particles moving just off the bottom: the method of feeding suggested for all other Mitrata.

APPENDIX

Collecting Localities

A.—"Jerusalum Hill"[17]. Manlius Formation, Olney Member, Saltsburg quarries, Dayville, New York.

B.—Unknown locality, Lower Helderberg, Litchfield, New York[18].

C.—Manlius Formation, Olney Member, Saltsburg quarries, Days Corner, Herkimer Co., New York.

D.—Ridgely Formation, Cumberland, Maryland[19].

E.—Whitewater or Saluda formations, Richmondian, Oxford, Ohio.

F.—Cannon Limestone, 0.5 mi[20] north-north-east of Pulaski, Tennessee [label reads 1.5 miles], Bassler, 1932. Guensburg (written commun., 1987) feels certain that this material is from the lower part of the Catheys Formation (Edenian).

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[17] this locality may no longer be extant.

[18] information from museum label.

[19] see Derstler and Price (1975), Derstler (1979).

[20] label reads 1.5 miles; Guensburg (written commun., 1987) feels certain that this material is from the lower part of the Catheys Formation (Edenian).

G.—Curdsville Member, Lexington Limestone, Curdsville, Mercer Co., Kentucky[21].

H.—Whitewater Formation, in road cut south of Liberty, Indiana.

I.—Grant Lake Formation, Corryville Member, Stonelick Creek, Clermont Co., Ohio.

J.—Grand Lake Formation, Warren Co., Ohio.

K.—Bull Fork Formation, Boudinot Ave, Cincinnati, Ohio.

L.—Elkhorn or Whitewater formations, one mile northeast of Camden, Ohio, on Seven Mile Creek, parallel to main highway[22]

M.—Glens Falls Limestone, Trenton Falls, New York.

N.—Upper Pooleville Member, Bromide Formation, Criner Hills, Carter Co., Oklahoma. All specimens are from Rock Crossing (Sprinkle, 1982).

O.—Kirkfield Limestone, Kirkfield, Ontario.

P.—Waynesville Formation, along railroad cut number 13, lower ⅓, SE¼, Sec. 8, T. 6 N., R. 2 W., Suman 7½' Quadrangle. near Weisberg, Indiana.

Q.—Fairview Formation?, Cincinnati, Ohio[23].

R.—Hull Beds, Ottawa Limestone, Brigham Quarry, near Hull, Quebec.

S.—Unknown locality, Hull Beds, Ottawa Limestone, presumably close to Brigham Quarry, near Hull, Quebec.

T.—Martinsburg Formation, Swatara Gap, Lebanon County, Pennsylvania: Middle Ordovician.

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[21] information from museum label.

[22] information from museum label.

[23] information from museum label.

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EXPLANATION OF PLATE 1

Figure Page

1–14. ***Anomalocystites cornutus*** Hall 20

1–4. ANMH 2288 [syntypes], Locality A. 1, disturbed specimen, mostly the carapace and proximal aulacophore, ×2.5; 2, eroded specimen showing interior of the plastron [Note the transverse ridge, part of one movable spine attached, proximal aulacophore, and part of the distal aulacophore-covering plates.], ×2.5; 3, plastron with proximal aulacophore and attached eroded styloid, ×3.0; 4, carapace with proximal aulacophore and part of distal aulacophore attached, ×3.0.

5. NYSM 15010, partial carapace with most of aulacophore intact and attached, ×2.5, Locality A.

6. USNM 35079, poorly-preserved theca with proximal and distal aulacophore attached, ×3.0, Locality C.

7. UCM 46044, plastron with proximal aulacophore, ×2.0, Locality B.

8. NYSM 15011, plastron with proximal and most of the ventral distal aulacophore exposed, ×2.5, Locality A.

9. USNM 35078, lateral view of the styloid and adjacent distal aulacophore segments [Other aulacophore segments are in the upper part of the figure.], ×0.5, Locality C.

10. UCB D-1875, eroded specimen, (mostly) interior of plastron exposed, distal marginals of carapace are intact, ×3.0, Locality A.

11–14. USNM 35078, 11, carapace with eroded proximal aulacophore, ×3.0; 12, incomplete carapace with proximal aulacophore and twisted styloid attached, ×4.0; 13, eroded and distorted carapace [Note the displaced distal end of the distal aulacophore resting on the specimen.], ×4.0; 14, proximal end of carapace with distorted proximal aulacophore and twisted distal aulacophore attached [Note the rarely-preserved placocystitid plate.], ×3.0, Locality C.

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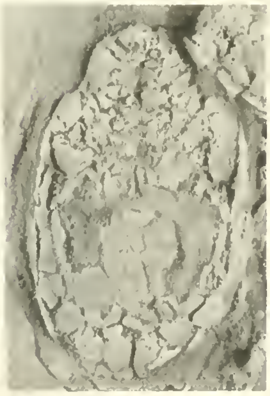

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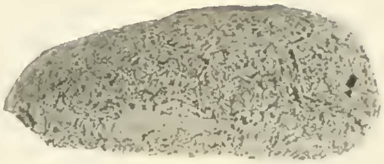
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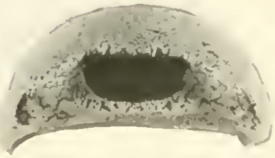
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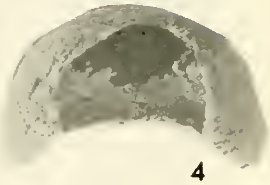
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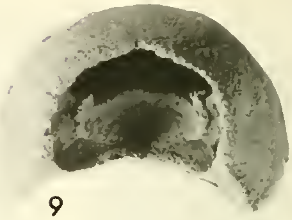
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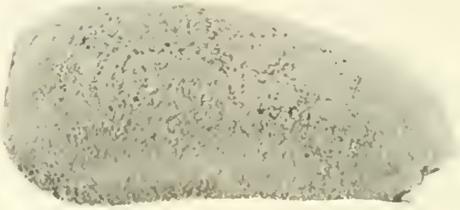
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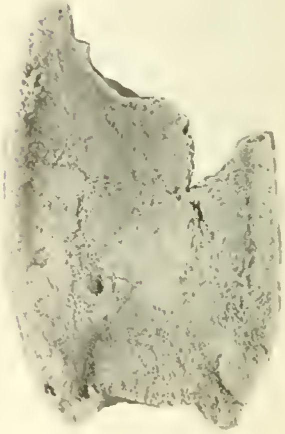
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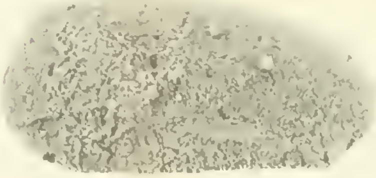
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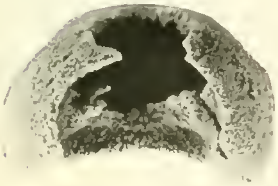
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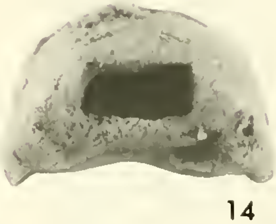
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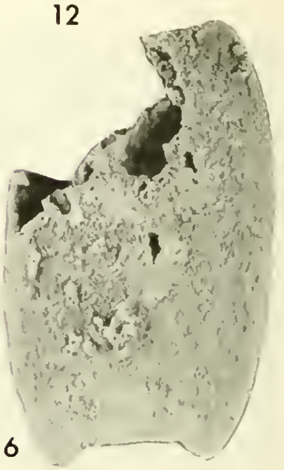
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EXPLANATION OF PLATE 2

Figure Page

1–16. ***Anomalocystites cornutus*** Hall 20

All specimens from Locality D.

1–5. USNM 33661A, carapace, left lateral, distal, proximal, and plastron views of a nearly complete theca, ×2.0.

6–9. USNM 33661B, plastron, distal, proximal, and right lateral views of a nearly complete theca [Note the well-developed "runners" or skids and the beveled lip at the distal end of the theca in figure 6; the well-preserved spine bases and inset anal opening in figure 7; and the attachment area for the proximal aulacophore in figure 9.], ×2.0.

10, 11, 13, 15. USNM 33661D, proximal, right lateral, carapace, and plastron views of a theca damaged in the proximal carapace area, ×2.0.

12, 14, 16. USNM 33661C, plastron, distal, and carapace views of a proximally incomplete theca [Note the rectangular inset anal opening in figure 14.], ×2.0.

EXPLANATION OF PLATE 3

Figure		Page
1–15.	***Anomalocystites cornutus*** Hall	20

All specimens from Locality D.

1, 3. USNM 33661E, carapace and plastron views of a nearly complete theca (except for the proximal area of the carapace) [Theca is slightly skewed.], ×2.0.

2. USNM 3366C, left lateral view of a carapace, ×2.0.

4–7. USNM 33661F, (mostly) internal plastron, distal, external plastron, and oblique internal plastron views of an incomplete theca [Note in figures 4 and 7, the transverse ridge, muscle pits, and aboral platform, and in figure 7, the fractured echinoid-like pillars adjacent to the anal opening.], ×2.0.

8, 10. USNM 33661G, carapace and plastron views of a nearly complete but skewed theca, ×2.0.

9, 11–15. AMNH 2720, (mostly) internal plastron, left lateral, right lateral, proximal to distal oblique view of the internal plastron, distal, and proximal views of an incomplete theca with most of the carapace missing [Note the well-developed transverse ridge and echinoid-like pillars adjacent to the muscle pits and distal aperture.], ×2.0.


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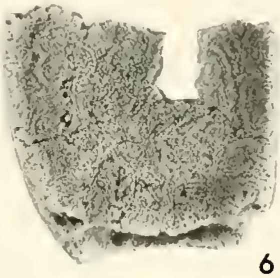
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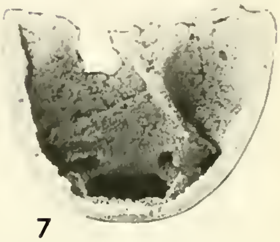
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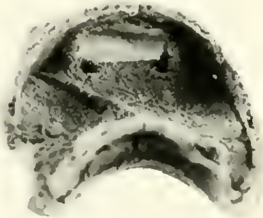
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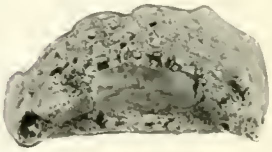
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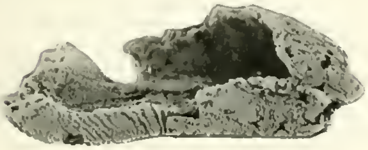
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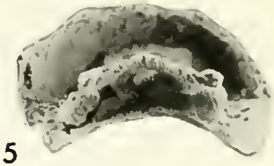
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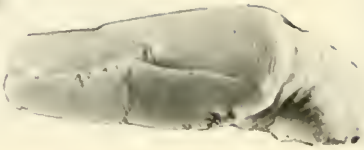
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Explanation of Plate 4

Figure Page

1–4. ***Enoploura balanoides*** (Meek) 32

UCM 37296. Holotype of *Enoploura crustacea* Haeckel, 1896, carapace, right lateral, left lateral, and plastron views of a nearly complete theca with attached proximal aulacophore, ×2.25, Locality E.

5–9. ***Enoploura punctata*** Bassler 30

All specimens are syntypes (USNM 91856), from Locality F.

5. Carapace with articulating spines and distorted proximal aulacophore attached [Note the transverse ridge on the internal surface of the plastron exposed by erosion of the carapace plates.], ×3.0.
6. Lateral view of a deformed proximal aulacophore, eroded styloid, and proximal segments of the distal aulacophore, ×5.0.
7. Nearly complete carapace with the attached poorly-preserved proximal aulacophore and part of the distal aulacophore, ×2.75.
8. Carapace with the internal surface exposed; the distorted proximal aulacophore is also exposed [Part of the right articulated spine is also present.], ×3.5.
9. Slightly distorted carapace with the movable spines articulated; proximal aulacophore incomplete and distorted [This specimen has been considerably prepared since its first illustration by Bassler (1932, p. 18, figure 9, lowermost specimen).], ×3.5.

10–12. ***Kierocystis insertus***, new genus and species 22

USNM 42166 (holotype), from Locality G.

10. Carapace with incomplete proximal aulacophore and discontinuous distal aulacophore, ×3.0.
11. Poorly-preserved and incomplete plastron with proximal aulacophore, eroded styloid, and several segments of the distal aulacophore attached, ×3.0.
12. Proximal area showing the proximalmost upper tetrameres of the proximal aulacophore inserted into the carapace, ×5.0.

Explanation of Plate 5

Figure Page

1–5, 8, 10. ***Enoploura punctata*** Bassler 30

1–5. All specimens from Locality F. 1, USNM 91854, theca with (mostly) internal surface of the plastron exposed, proximal aulacophore, styloid, and short section of distal aulacophore attached and deformed, ×4.0; 2, USNM 91854, deformed theca, carapace exposed, proximal aulacophore attached, and deformed, ×3.5; 3, USNM 91854 (syntype: see Bassler, 1932, p. 18, figure 9, specimen on upper right), weathered carapace with part of the internal surface of the plastron exposed, ×3.5; 4, USNM 91854, eroded carapace showing part of the tranverse ridge on the internal surface of the plastron, proximal aulacophore, and several segments of the distal aulacophore attached, ×4.0; 5, USNM 91854, deformed proximal aulacophore, eroded styloid, and nearly complete ventral distal aulacophore, ×3.0.

8. USNM 91854, plastron and attached proximal aulacophore, ×4.0, Locality F.

10. USNM 91854, distal end of plastron (lip) with denticulate platelets which are probably functional or vestigial anal-pyramid plates [Note adjacent proximal part of the articulated spine with stereom structure preserved.], ×7.5, Locality F.

6, 7. ***Enoploura*** cf. ***E. balanoides*** (Meek) 33

Both specimens ×3.0, from Locality Q.

6. UCM 46045, proximal carapace with proximal aulacophore and several segments of the distal aulacophore attached.

7. UCM 46046, eroded plastron with proximal aulacophore, eroded styloid, and several distal aulacophore ossicles attached.

9, 11. ***Enoploura*** cf. ***E. popei*** Caster 34

9. UCM 43378, eroded carapace with paired spines nearly articulated [Note spines on distal marginal plates of carapace. Stereom structures are visible on most of the plates. This specimen is unusually large for a mitrate.], ×2.0, Locality H.

11. USNM 145586, carapace with attached poorly-preserved proximal aulacophore and part of the distal aulacophore, ×2.5, Locality P.

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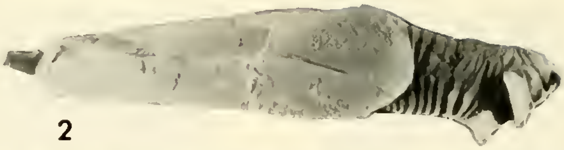

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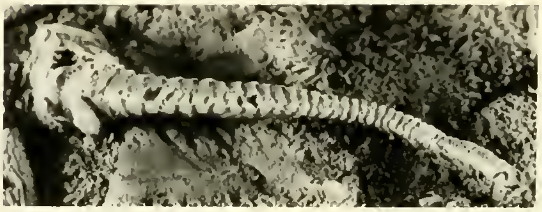

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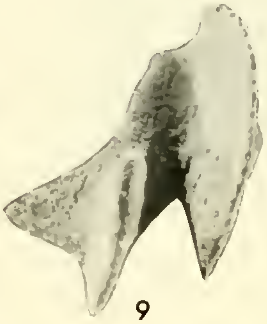

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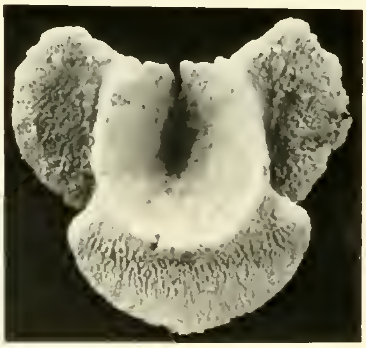

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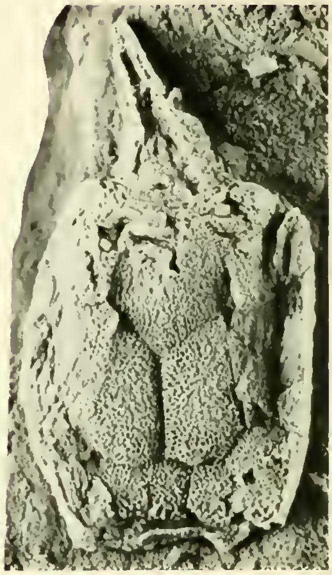

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EXPLANATION OF PLATE 6

Figure — Page

1–3, 6–9, 11. ***Enoploura popei*** Caster 33

1–3. UCM 25993 (holotype), carapace, left lateral, and plastron views [Theca is slightly distorted with the proximal part of the right spine proximal aulacophore, well-defined styloid, and several proximal elements of the distal aulacophore attached.], ×2.0, Locality I.

6–8. UCM 46049, distal ends of distalmost styloid blades [Note the deep muscle pits and narrow slit for the food groove.], ×3.0, Locality K.

9. UCM 46049, lateral view of a styloid that is composed of three fused ossicles, ×6.0, Locality K.

11. UCM 46049, proximal end of styloid blade [The deep pit is continuous with the lumen of the proximal aulacophore.], ×3.0, Locality K.

4, 5. ***Enoploura*** species 32

USNM 40704, lateral and ventral views of a nearly complete aulacophore [Distal aulacophore appears to be preserved in the feeding position.], ×3.0, Locality J.

10, 13. ***Enoploura punctata*** Bassler 30

Both specimens are USNM 91854, ×3.0, Locality F.

10. Incomplete carapace with a spine and most of the aulacophore attached.

13. Eroded carapace with eroded proximal aulacophore and eroded proximal segments of distal aulacophore.

12. ***Enoploura*** cf. ***E. balanoides*** (Meek) 33

UCM 31309, proximal aulacophore with partal styloid blade and poorly-preserved distal aulacophore segments attached, ×3.0, Locality L.

EXPLANATION OF PLATE 7

Figure Page

1–4. ***Ateleocystites*** cf. ***A. huxleyi*** Billings 37

1. MCZ 1063, incomplete and eroded carapace with an attached distorted proximal aulacophore and the proximal half, or so, of the distal aulacophore, ×4.0, Locality M.
2. MCZ 2064, proximal carapace with the proximal aulacophore and several poorly-preserved distal aulacophore segments attached [Note the well-preserved placocystitid plate.], ×4.0, Locality M.
3. USNM 93348, incomplete plastron with poorly-preserved proximal aulacophore and styloid; distal aulacophore essentially complete, ×2.5, Locality M.
4. USNM 401499, distally-incomplete plastron, proximal aulacophore, weathered styloid, and part of the distal aulacophore, ×2.0, Locality M.

5–9, 11–13. ***Anatiferocystis papillata*** (Bassler) 39

5–7. UCM 46036, carapace, plastron, and right lateral views of a theca with distorted and displaced proximal aulacophore [Note the spine base for the single articulating spine in figure 6.], ×4.5, Locality N.

8. UCM 46037, right lateral view of a theca, ×4.5.

9, 13. UCM 46039, carapace and incomplete plastron views of a theca with an incomplete proximal aulacophore attached, ×4.5, Locality N.

11, 12. UCM 46038, carapace and plastron views of a theca [Note the axial displacements of the plates of the plastron.], ×5.0, Locality N.

10. **Kopficystis kirkfieldi**, new genus and species 35

USNM 116408 (holotype), slightly distorted carapace with an incomplete distal aulacophore attached [Note the anal-pyramid platelets at the distal end of the theca exposed by erosion of the overlying CM series.], ×4.5, Locality O.


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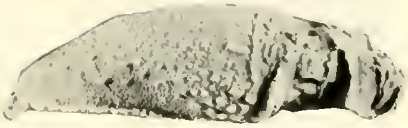
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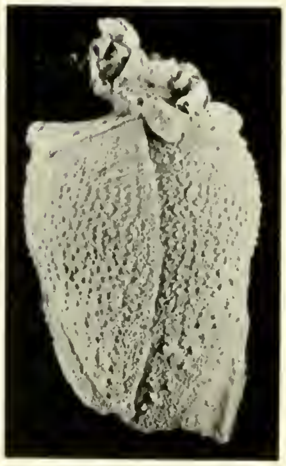
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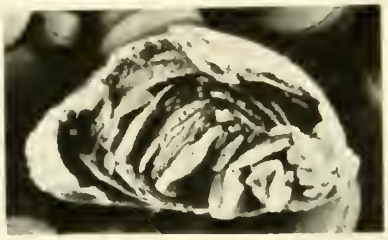

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EXPLANATION OF PLATE 8

Figure Page

1–11. ***Anatiferocystis papillata*** (Bassler) 39

1, 3. UCM 46037, carapace and disturbed plastron of a theca with remnants of the proximal aulacophore attached, ×4.5, Locality N.

2. UCM 46040, carapace of a theca, ×5, Locality N.

4, 5. UCM 46041, carapace and plastron of a distally-incomplete theca [The incomplete distorted proximal aulacophore is attached.], ×4.5, Locality N.

6, 7. USNM 401450, well-preserved carapace and plastron of a theca [Note the protruded subanal plate and spine base.], ×4.5, Locality N.

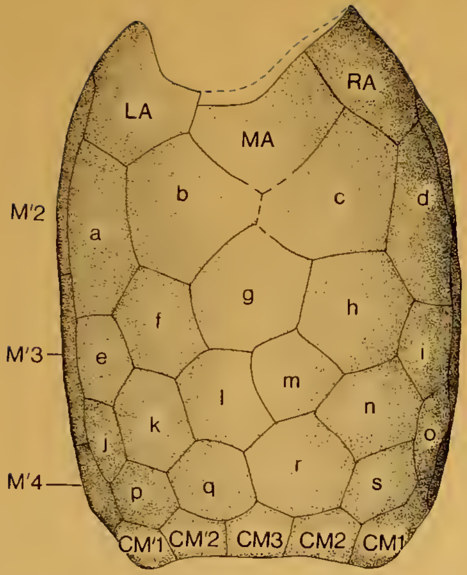
8, 11. USNM 401451, carapace and plastron of a theca [Note the well-defined spine base at end of plastron.], ×5.0, Locality N.

9. UCM 46042, proximal view of a theca with attached distorted proximal aulacophore, ×6.0, Locality N.

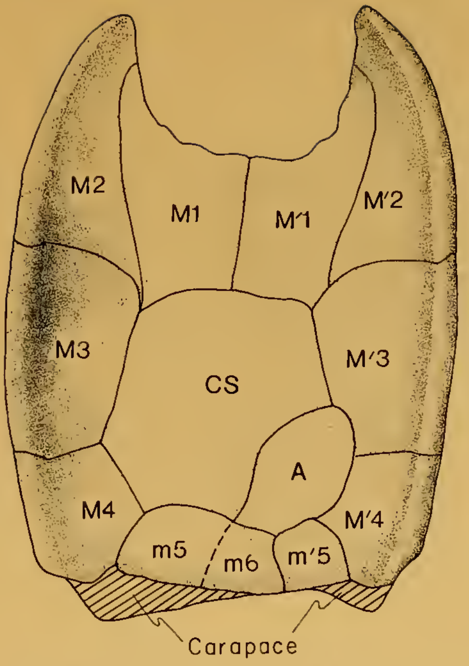
10. UCM 46043, theca with articulated spine lying across it [Note the stereom structure of the spine.], ×5.0, Locality N.

INDEX

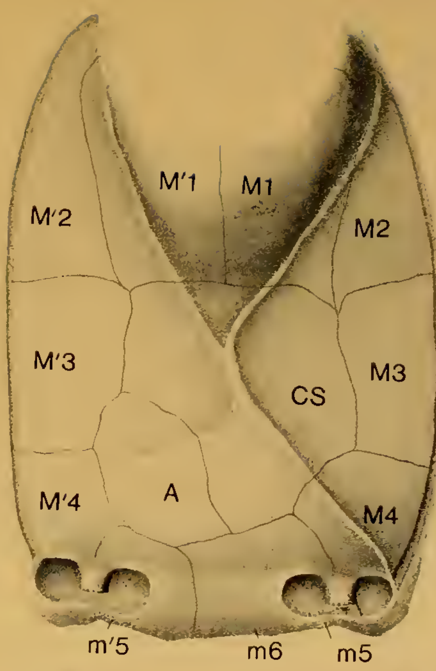
Note: Page numbers are in light face; plate numbers are in **bold face** type; the page numbers on which principal discussions occur are in italics; **B** indicates the foldout inside the back cover.



Text-figure 5.—Carapace detail of *Anomalocystites cornutus.* This figure is based on USNM 33661A (Pl. 2, fig. 1).



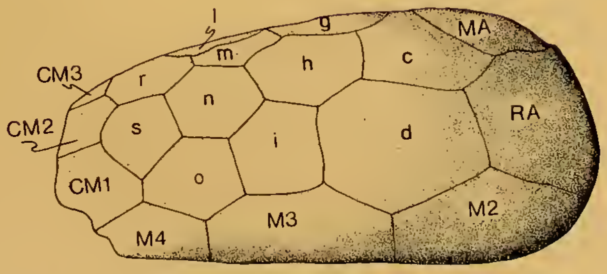
Text-figure 6.—Plastron detail of *Anomolocystites cornutus.* This figure is based on USNM 33661A (Pl. 2, fig. 5).



Text-figure 8.—Internal plastron surface of *Anomalocystites cornutus.* This figure is a composite based on USNM 33661F and AMNH 2720 (Pl. 3, figs. 4, 7, 9, 13). Extending from **M'1** to the muscle pit in **M4** is the diagonally-transverse septum. Triangular area developed mostly on **M'1–M1** is the raised (thickened) oral field. The triangular area developed on **m'5, m6, m5,** A, and **CS** is the thickened distal field. Between **M'4–m'5** and **M4–m5** are the muscle pits. These pits probably contained muscles that moved the spines toward the sagittal plane and (probably) muscles that were part of the anal sphincter system. Overlayering of plate material to form the walls and deepen the muscle pits has obscured the plate sutures. Narrow inner marginal grooves run the length of the theca from the muscle pits to the extremities of **M2–M'2.**

Table 1.—Explanations of plate abbreviations used in this paper.

A:	anomalocystitid plate
a-s:	supracentral plates
CM1-CM2:	carapace marginal plates (right side)
CM'1-CM'2:	carapace marginal plates (left side)
CM3, CM'3:	carapace marginal plate (sagittal)
CS:	central infracentral plate
DS:	distal infracentral plate
LA:	left adaulacophoral plate
MA:	median adaulacophoral plate
M1-M5:	marginal plates (right side)
M'1-M'5:	marginal plates (left side)
m5:	plastron distal–marginal plate (right side)
m'5:	plastron distal–marginal plate (left side)
m6, m'6:	plastron distal–marginal plate (sagittal)
RA:	right adaulacophoral plate



Text-figure 7.—Lateral view of *Anomalocystites cornutus.* This figure is based on USNM 33661A (Pl. 2, fig. 2).

PREPARATION OF MANUSCRIPTS

Bulletins of American Paleontology usually comprises two or more separate monographs in two volumes each year. This series is a publication outlet for significant longer paleontological monographs for which high quality photographic illustrations and the large quarto format are a requisite.

Manuscripts submitted for publication in this monograph series must be typewritten, and double-spaced *throughout* (including direct quotations and references). All manuscripts should contain a table of contents, lists of text-figures and (or) tables, and a short, informative abstract that includes names of all new taxa. Format should follow that of recent numbers in the series. All measurements must be stated in the metric system, alone or in addition to the English system equivalent. The maximum dimensions for photographic plates are 178 mm × 229 mm (7″ × 9″; outlined on this page). Single-page text-figures should be drafted for reproduction as single column (82 mm; 3¼″) or full page (178 mm; 7″) width, but arrangements can be made to publish text-figures that must be larger. Any lettering in illustrations should follow the recommendations of Collinson (1962).

Authors must provide three (3) copies of the text and accompanying illustrative material. The text and line-drawings may be reproduced xerographically, but glossy prints at publication scale must be supplied for all half-tone illustrations and photographic plates. These prints should be identified clearly on the back.

All dated text-citations must be referenced. Additional references may be listed separately if their importance can be demonstrated by a short general comment, or individual annotations. Referenced publication titles must be spelled out in their entirety. Citations of illustrations within the monograph bear initial capitals (*e.g.*, Plate, Text-figure), but citations of illustrations in other articles appear in lower-case letters (*e.g.*, plate, text-figure).

Original plate photomounts should have oversize cardboard backing and strong tracing paper overlays. These photomounts should be retained by the author until the manuscript has been formally accepted for publication. Explanations of text-figures should be interleaved on separate numbered pages within the text, and the approximate position of the text-figure in the text should be indicated. Explanations of plates follow the Bibliography.

Authors are requested to enclose $10 with each manuscript submitted, to cover costs of postage during the review process.

Collinson, J.

1962. *Size of lettering for text-figures.* Journal of Paleontology, vol. 36, p. 1402.