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PALEOBIOLOGY AND REVISION OF THE ORDOVICIAN ASTERIADINA [ECHINODERMATA: ASTEROIDEA] OF THE CINCINNATI AREA

A dissertation submitted to the

Division of Graduate Studies
of the University of Cincinnati

in partial fulfillment of the
requirements for the degree of

DOCTOR OF PHILOSOPHY

in the Department of Geology
of the Graduate School of Arts and Sciences

1975

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May 13th 19 75

I hereby recommend that the thesis prepared under my supervision by JON WAYNE BRANSTRATOR

entitled PALEOBIOLOGY AND REVISION OF THE ORDOVICIAN ASTERIADINA (ECHINODERMATA: ASTEROIDEA) OF THE CINCINNATI AREA

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

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Madeleine Briskin

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TABLE OF CONTENTS

TEXT-FIGURES AND ILLUSTATIONS

ABSTRACT

Ordovician pustulosid asteroid taxa require re-evaluation because important specimen material from the Cincinnati Area has not been accurately or adequately characterized, nor have taxobases been realistically conceived. Some specimen differences which have been given taxonomic significance by paleontologists are comparable to ontogenic differences or interspecific variations in modern forms. Other specimen attributes which have been overlooked by paleontologists are of at least generic significance among modern forms.

The re-diagnosed Ordovician families Hudsonasteridae Schuchert, Mesopalaeasteridae Schuchert, and Promopalaeasteridae Schuchert are assignable to the forcipulate suborder Asteriadina Perrier, because they possess the preservable attributes of modern representatives of this taxon.

There are two species of Hudsonaster Stürtz in Cincinnati rocks. Hudsonaster simplex (Miller and Dyer) is distinct from Hudsonaster incomptus (Meek) and should be resurrected from synonomy with this latter species.

Mesopalaeaster shaefferi (Hall) is the only species of Mesopalaeasteridae in Cincinnati rocks. Other Cincinnatian species which have been placed in Mesopalaeaster by earlier authors are better accommodated elsewhere because they do not share essential familial characteristics with re-examined M. shaefferi material. Palaeaster spinulosus Miller and Dyer, Palaeaster longibrachiatus Miller, and Palaeaster exculptus Miller are synonyms of Palaeaster shaefferi Hall. They are moved from the Promopalaeasteridae, where they were

placed by Schuchert (1914), to this species in Mesopalaeasteridae.

Promopalaeaster Schuchert is monotypic. Two new genera accommodate the remainder of Cincinnatian Promopalaeasteridae. *Mesopalaeaster proavitus* Schuchert is a synonym of *Palaeaster finei* Ulrich, the type species of *Kenothecaster* gen. n. *Palaeaster magnificus* Miller, *Palaeaster wykoffi* Miller, and *Promopalaeaster bellulus* Schuchert are synonyms of *Kenothecaster miamiensis* (Miller). *Kenothecaster dyeri* (Meek) also belongs in this new genus. *Promopalaeaster prenuntius* Schuchert is the type species of *Neardisaster* gen. n.

I. INTRODUCTION

Strata exposed on the flanks of the Cincinnati Arch have produced most of the Ordovician asteroid species known from North America. Geologically older asteroid specimens are known from elsewhere in North America and Europe, but those of this area are particularly well-preserved and offer excellent data on early asteroid paleobiology. This study deals with the description, illustration, functional anatomy, and taxonomic revision of Ordovician genera from this area which are assignable to Suborder Asteriadina Fisher, 1928.

The fossil forms dealt with in this investigation are removed from the polyphyletic Order Valvatida Perrier, 1884 (where they were placed by The Treatise on Invertebrate Paleontology, Part U) and placed in Order Forcipulatida Perrier, 1884, Suborder Asteriadina. This re-assignment of orders is justified by the close similarity of the fossil forms described herein to modern forcipulatid asteroids of Suborder Asteriadina. This re-assignment extends the range of the Asteriadina from Recent to Middle Ordovician.

Nearly all fossil taxa herein considered have been previously described. Affinities and taxobases have been re-evaluated in light of knowledge obtained from observation of modern species and new observations on the fossil material. There is considerable realignment of taxa. Most formerly recognized species are placed in subjective synonomy with a few early described species by virtue of the fact that their type materials represent, in reality, different ontogenic stages of a few specific entities. Criteria used as bases for synonomizing many named species are herein derived from observations on modern representatives of the Asteriadina and all available and appropriate fossil materials.

The primary aim of this study is the better understanding of early asteroid paleobiology. It differs from earlier investigations on the same or similar material in that it compares the functional anatomies of these early members of the subclass with those of modern forms of known ecologies, ethologies and genetic relationships. Thereby, it is able not only to propose, but to evaluate fossil asteroid taxobases in light of knowledge outside that obtainable directly from the fossils.

There are three major data sources which are useful in determining the paleobiology of fossil asteroids. Only one derives directly from the fossils. The other two, the literature on modern forms, and first-hand observation of modern forms, are indespensible tools in this investigation. The first section of this report is a summary of studies on the body systems found in modern asteroids which are also evidenced in fossilized skeletons of early species, or are necessarily understood in order to reconstruct tenable species models for paleontologic material. It draws heavily on the biological literature in determining the functionality of the characters commonly determinable from fossil material. Where the literature does not provide data necessary for a knowledgable interpretation of these features, it has been necessary to make first-hand observations on living forms. This has been accomplished by dissection of preserved or narcotized specimens and observation of living individuals in their natural habitats or in aquaria.

The approach is functional. It aims to describe morphology in terms of how it serves the individual. Variations in form and function within and between modern taxa receive special attention in order that correlative characters of fossil specimens described in later sections may be viewed in their proper perspectives.

Historical framework. -- Recent investigations have produced extensive information on modern asteroid anatomy, physiology, ethology and ecology. Most fossil asteroid remains, on the other hand, have not been examined since they were originally found or identified. Recent advances in asteroid biology have not yet been applied to these fossil forms. It is an unfortunate fact that few paleontologists who have worked with early asteroid remains have inquired into the biology of living forms as part of their investigations; their works seem to be exercises in descriptive anatomy and nomenclature. There has been a parallel disinterest among asteroid biologists to consider the facts of geological occurrence, morphology and morphological development through time as shown by fossil asteroids. This failure to amalgamate principles and information derived by these separate groups of investigators, both ostensibly interested in the natural history of asteroids, has led to an inadequate comprehension of this long-ranging group. This dilemma is reflected in classification schemes wherein taxa at all levels seldom traverse era boundaries or separate taxa are established for fossil and modern material. One must agree with C. W. Wright's (1967) admonition that the assumed pattern of evolution among the asteroids rests largely on inference and ignorance.

The most comprehensive theory of asteroid origin and evolution thus far conceived does not escape Wright's assessment. H. B. Fell, a neontologist, published his "The Phylogeny of Sea-stars" in 1963. His work considers the living species Platasterias latiradiata Gray to be a bona fide member of the Somasteroidea, a subclass of stelleroids otherwise extinct since the Middle Paleozoic. P. latiradiata's remarkable similarity to luidiaid asteroids further led Fell to conclude that the Luidiidae are the most archaic surviving true asteroids. Consistent with his placement of the Luidiidae within the otherwise Early Paleozoic Order Platyasteridae, he conceived a scheme of stelleroid evolution based on developmental growth gradients. This pattern of evolution necessitates a luidiaid ancestor to all asteroids. Such an ancestor is supposed to have lived at least as far back in geological history as the Early Ordovician. Fell's theory further derives this luidiaid asteroid ancestor from a generalized somasteroid, a condition Fell ascribes to Chinianaster. This latter form, in turn, is suppose to have evolved from a crinoid or a crinoid-like ancestor with biserial brachia. Once the asteroids had evolved to the luidiaid stage, according to Fell's theory, a subsequent astropectenid stage was necessary in the progression to later forms, such as those represented by the earliest known (Middle Ordovician) asteroid fossils.

Important observations on both modern specimen material and the fossil record tend to cast some doubt on Fell's seemingly comprehensive theory of asteroid origin and evolution. Madsen (1966) questioned the inclusion of Chinianaster within the Somasteroidea on the bases of Spencer's (1951) and later investigators' misinterpretations of basic perivascular skeletal anatomy in these forms. Madsen also expressed doubt that *P. latiradiata* is a somasteroid. Blake (1973) examined the critical specimen material of *P. latiradiata* and concluded that the essential features of *Luidia* ossicle morphology are present in the species; that is, interspecific variations in ossicle morphology within *Luidia* exceed those between that genus and *Platasterias*. Blake concludes, with documentation, that *P. latiradiata* belongs within the Luidiidae. This explains its remarkable similarity to other Luidiidae as per Fell's theory. It further casts doubt on the supposition that the species belongs among the somasteroids at all.

Furthermore, Philip (1965) has noted that the earliest somasteroid occurs hundreds of millions of years earlier in the fossil record than does a biserial crinoid likely to be the progenitor to the Somasteroidea as described by Fell. A similar discordance between Fell's theoretical timetable and fossil occurrence becomes apparent as one notes that known Luidiidae range only as far back as the Miocene, and Astropectinidae to the Lower Jurassic. While neither the crinoid or asteroid fossil record can be deemed complete, Fell's theory certainly gains no support from either.

Prior to Fell's theory, paleontologists with an interest in stelleroid origins subscribed either to Bather's (1901) idea that the immediate ancestor to the earliest stelleroid was an unknown, primative edrioasteroid, or to Schuchert's (1915) notion that stelleroids, as first known in the Middle Ordovician, evolved from an earlier, stelleroid-like animal without a preservable skeleton. While neither of these latter theories enjoys corroboration by the fossil record, neither is any less consistent with it than Fell's. All three theories rely on the existance of obscure ancestors which either have not been preserved or have not yet been discovered. Available data which may have some bearing on asteroid origins are available only from modern and fossil specimen material. Clearly, the fossil record and earliest known specimens in each of the stelleroid subclasses must be considered in any investigation of stelleroid origins.

This report does not purport to investigate the origin of the asteroid subclass. It aims, instead, at the better documentation and understanding of some related and associated Ordovician species. It is offered in order that future theories on the genesis of asteroids may consider the facts of morphology and diversification within early representatives of the subclass.

Most contemporary knowledge of Ordovician Asterozoa comes from the comprehensive publications of two authors whose works appeared early in this century. Charles Schuchert's "Revision of Paleozoic Stelleroidea" (1915) offered a compilation of earlier observations by paleontologists on North American forms, as well as some new morphological data on a few taxa. It established a plethora of new Ordovician species from new and previously described materials. It also used many of these new species to characterize the higher taxa proposed a year earlier by Schuchert in "Stelleroidea paleozoica" (1914), a volume of "Fossilium Catalogus".[1] W. K. Spencer's "Monograph of the British

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[1] Schuchert's "Revision" was finished prior to his submission of "Stelleroidea paleozoica" for publication. Unfortunately, however, the descriptive work was published subsequent to the "Fossilium Cata-

logus" listing of taxa. Consequently, the species names he mentioned the first time in "Fossilium Catalogus" stood as nomina nuda until they were made available by description in "Revision".

Palaeozoic Asterozoa" (1914-1940) offers another taxonomic revision, this one based on direct morphological evidence from European, mostly British, specimens. Spencer had the advantage of Schuchert's publications during most of his work, and accommodates the North American forms in his systematics. It is apparent that Spencer did not observe much North American material first-hand, however.

These early monographs dealt mainly with taxonomic revision, but often based such revision upon morphologic and stratigraphic inferences rather than morphologic fact. Such literature development is to be expected in a group, such as the fossil Asteroidea, where specimens are rare, commonly fragmentary, seldom show but a portion of either the dorsal or ventral skeletal surface, and are likely to have been collected by amateurs with little or no regard as to precise stratigraphic occurrence of their "treasures". Since these early works were produced, more specimen material has become available for study. Improved techniques of preparation and documentation have been developed. And, as mentioned above, a voluminous, easily accessible biological literature on modern echinoderms has come into being since most Early Paleozoic asteroid specimens were last examined in detail. This work takes advantage of these improvements. Thereby, it is able to emend and supplement earlier ideas on asteroid paleobiology.

Stratigraphic framework of this investigation. -- The Paleozoic strata exposed in the vicinity of Cincinnati, Ohio compose the North American standard section for the Upper Ordovician. These strata crop out in Ohio, Indiana, and Kentucky on the northern flanks of a NNE trending anticline called the Cincinnati Arch. The Cincinnatian Series is a time-stratigraphic unit and is considered a provincial series of Eastern North America. Lithologically the unit is composed of interstratified limestones and calcareous mudstones and siltstones in the vicinity of Cincinnati. Early geologic reports termed the unit "Hudson River Group" or "Western Hudson River Group" on the basis of its supposed lithologic and faunal similarities to the Hudson River Group of Eastern New York State. Subsequent investigations show that the Upper Ordovician rocks in the Cincinnati area are not closely related in their lithologies or faunas to these latter rocks and the Cincinnatian is now recognized as provincially distinct from them.

Three distinct lithological sub-units may be distinguished within the Cincinnatian type area. A lower unit, composed primarily, but not exclusively, of siltstones and mudstones, has been variously called "Utica Slate", "Utica Shale", "Utica Group", "Eden Shale", "Eden Shales", "Eden Group", "Eden Series", "Latonia Formation" and "Kope Formation". The "Utica" names were applied by early workers who correlated the unit with the lithologic unit of the same name in New York. The "Eden" and "Latonia" names were applied by later workers who considered the rock units to be provincially distinct from those of New York. "Kope" is currently applied to this lower unit by geologists dissatisfied that either "Eden" or "Latonia" are properly defined or distinctive rock-stratigraphic units. Notwithstanding possible shortcomings of the name, the name Eden Shale is herein used in reference to this lower rock unit of the Cincinnatian time-stratigraphic interval. This name is used because the majority of asteroid specimens collected from these rocks carry labels with such a stratum identification. Synonomous terms for this rock unit will be employed, however, when they have been used on authenticated specimen labels. It is both awkward and deceptive to revise specimen labels to conform to current nomenclature unless the precise locality of a specimen's occurrence is known for certain. This is seldom the case in fossil asteroids from Cincinnati. These specimens are commonly labeled only with the vernacular name of their rock units in use at the time of their collection or acquisition into a museum. Because they are the most authentic data on the stratigraphic occurrence of such specimens, these names must be preserved for use in documentative paleontology.

Above the Eden Shales, a middle rock unit composed primarily of limestones and thin, discontinuous interbeds of mudstones and siltstones has been called "Lorraine Group", "Lorraine Beds", "Lorraine Series", "Maysville", "Maysville Group", "Maysville Series", "Maysville Formation", "Maysville Limestone", "Covington Group", "Grant Lake Limestone and Fairview Formation" and "Maysvillian". The "Lorraine" was applied by early workers who correlated the unit with the lithologic unit of the same name in New York State. The "Maysville" and "Covington" names were applied by later workers who considered the rock unit to be provincially distinct from the New York unit. The unit has been divided on lithologic criteria into "Grant Lake Limestone" and "Fairview Formation" by geologists dissatisfied that either "Maysville" or "Covington Group" are properly defined or distinctive rock-stratigraphic names applicable to this middle unit in the type area. For the same reasons expressed above in the discussion of Eden Shale nomenclature, Maysville is used herein to refer to this lithologic unit.

An upper lithologic unit, which is reminicent of the Eden Shale except for the presence of a few more laterally continuous limestones, has been termed "Richmondian", "Richmond Group", "Richmond Series", "Richmond Stage", "Richmond Formation", "Richmond Limestone" and "Bull Fork Formation". The various "Richmond" names have been applied through time to this distinct lithologic unit. The upper part of this section is exposed in the city of Richmond, about sixty miles to the northwest of Cincinnati. Lower parts of the unit are exposed between Cincinnati and Richmond. Latter day geologists, discontented that the "Richmondian" is a properly defined rock-stratigraphic unit, have defined the synonomous "Bull Fork Formation". For the same reasons expressed above in the discussion of Eden Shale and Maysville rock-stratigraphic nomenclature, Richmond is used herein to refer to this lithologic unit.

The abundance and excellence of preservation of the fossils in Cincinnatian rocks has led to a biostratigraphic subdivision of the rocks by most stratigraphers who have worked on them. The "formations" and "members" into which the series has been divided are, in reality, inferred biozones or assemblage zones which have been given geographic rather than paleontologic names. While the placement of a relatively intact fossil starfish within a biozone would have paleoecological significance, this is seldom possible. Nearly all of the relatively intact specimens, and all the critical types, were collected before the utilitarian "formations" and "members" were described; thus they cannot be accompanied by an authentic reference to these biozones. Furthermore, nearly all later collected asteroid specimens have been stratigraphically placed by their collectors in simply the Eden, Maysville or Richmond rock units and references to associated fauna or "formation" and "member" are usually lacking.

Other major stratigraphic problems are introduced by the fact that neither the lithologic, nor the biozone units are well understood in their lateral extensions away from the locality at which each was originally described. It is becoming increasingly apparent that paleoecological examinations coordinating both lithological and paleobiological data will be necessary in constructing a complete, realistic model of these rocks which compose the North American standard for the Upper Ordovician.

Fossilization of asteroids. -- As is the case for most other echinoderms, the ossicular skeleton is the most preservable system in the asteroid body. Fossil specimens from Cincinnati are usually composed of crystalline calcite, which presumably is a replacement of original skeletal high-magnesium calcite. Fine detail is commonly well-preserved.

Several stelleroid characteristics, however, tend to make good asteroid fossils rare. With few exceptions, individual asteroid ossicles are not rigidly fused to adjacent ossicles. Rather, they are loosely joined by interossicular muscles or by common investment in an integument of connective tissue. Any organic decomposition prior to or after the death of an individual increases the possibility of skeletal disarticulation. Such separation of skeletal elements is detrimental to paleobiologic studies in two obvious ways. First, comparison to modern seastars is made more difficult because living forms are nearly always described and understood from whole animals; attempts to establish modern analogs to fossil forms require observation and redescription of modern species in terms of characteristics observable in the usually fragmented remains of fossils. Secondly, the more fractionated a skeleton becomes, the smaller become the individual pieces; such breakage increases surface area and makes these smaller pieces subject to greater chemical corrosion and physical abrasion. They may also be moved by a greater variety of dispersal agents. Potentially preservable features are thus degraded and reconstruction is made more difficult.

The precise conditions to which a potentially preservable asteroid skeleton is subjected determine whether it is preserved at all, and the fineness of the preservation. Little is known of the detailed chemical changes which occur during decay in the geologically more important subaquatic environments, partly because of the difficulty of study under such conditions (Rolfe and Brett, 1969). Plankton and vertebrates (Zangerl and Richardson, 1963) are the only marine organisms which have received much attention in this respect. These studies, however, have generated several principles which may be applied to marine benthonic intertebrates, including asteroids.

It is a general principle of vertebrate actuopalaeontology that articulated fossils of marine animals can result only from their being quickly buried, or from the slow processes of anaerobic decay (Rolfe and Brett, 1969). The former action precludes epifaunal scavengers and subsequent biogenic disarticulation by them; the latter state eliminates all scavengers.[2]

Another principle, borrowed from forensic medicine, is applicable to studies of asteroid preservation. In aerobic benthonic habitats, cellular death of exposed tissues is followed by increased permeability of cellular membranes and consequent rapid loss of soluable substances. In addition to this strictly physical, soft-part degradation, increased membrane permeability leads to microbal invasion and decay of organic materials. The gaseous products of decay tend to decrease environ-

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[2] Dead animals subjected to anaerobic decay are less likely to be disarticulated than those subjected to aerobic decay. There are two reasons for this. Macrofaunal scavengers capable of dismembering marine benthonic animals are aerobic animals; they are not present anaerobic environments. On the microbe scale, anaerobically decaying organisms produce much less gas than those utilizing aerobic respiration. Gas collected in body cavities of decaying organisms tends to make them more bouyant and more easily moved by environmental agents. As a moving, decaying animal's body disintegrates, potentially fossilizable elements are likely to be spread over a wide area, making collection and subsequent reconstruction more difficult than for one which disintegrates in place.

mental pH. The solubility of the already highly soluable high-magnesium calcite skeletal ossicles is increased under this condition. This factor, also, tends to degrade the fossilizable elements of the asteroid theca.

Another factor to consider in any study of skeletal decomposition is the completeness of a skeleton as it is subjected to burial. Under adverse conditions modern seastars autotomize injured or trapped body parts and commonly survive with much less than a whole skeleton. Under conditions of progressive stagnation, starvation or infection, many modern asteroids slough body parts before finally dying. Even rapid burial could not preserve an entire skeleton under these conditions. Blake (1967) considered spine loss among modern asteroids prior to a natural burial and concluded that it is a common occurrence.

Even rapid burial does not guarantee excellent preservation for marine organisms, however. Once buried and dead, an organism is still subject to disarticulation by infaunal organisms. Or, once interred organisms may become secondarily unburied by natural agents and resubjected to epifaunal scavengers. Nor does permanent, rapid burial prevent distortion of organisms with flexible bodies. Most recognized fossil asteroid specimens have been collapsed and distorted either at the time of their burial or during sediment compaction.

Finally, the feeding habits of asteroids themselves make good asteroid fossils unlikely. Although some forms have developed a predaceous habit, nearly all examined modern species are facultative scavengers. There is no documentation in the literature of an obligate predator among the asteroids. Where conditions are suitable for one scavenger, they are suitable for others; the scavenger, itself, is likely to be scavenged after death. Both predaceous and scavenging cannibalism is well known among modern asteroids; it is likely that ancestral forms possessed a similar feeding ethology.

Fortunately, not all asteroid skeletons have been completely disarticulated during preservation or re-esposure. These specimens, although rare, are most readily identifiable because the taxobases for fossils at almost every level of taxonomy have been derived from relative arrangements of ossicles in the theca. These specimens also offer the best opportunity for comparison with modern species of better known systematic affinities, ecologies and ethologies. Unfortunately, such fossil specimens usually show only portions of either the ventral or dorsal surface. Ossicles of fossils are seldom sufficiently fused during preservation to allow specimens to be removed intact from their matrix. Thus, many fossil species are known from a single surface.

II. ACKNOWLEDGEMENTS AND MATERIALS

All fossil material herein evaluated has come from Upper Ordovician strata in the vicinity of Cincinnati, Ohio. Asteroid material from this area has been disseminated to many museums in Eastern United States and Canada. A comprehensive examination of this material has required the cooperation of these museums and their curators. All the following have lent specimens and allowed preparatory improvements where required for study: Bruce M. Bell of New York State Museum, Stig Bergstrom of the Ohio State University (OSU), Thomas Bolton of the Geological Survey of Canada (GSC), Lois J. Campbell of the University of Kentucky Geology Department, Kenneth E. Caster and Richard A. Davis of the University of Cincinnati Museum of Geology (UCGM), Robert Kesling of the University of Michigan Museum of Paleontology (UMPM), Porter Kier of the National Museum of Natural History, formerly United States National Museum (USNM), Bernhard Kummel of the Museum of Comparative Zoology (MCZ), John Monteith of the Royal Ontario Museum (ROM), Norman Newell of the American Museum of Natural History (AMNH), John Pope of Miami University Geology Museum (MUGM), Karl Waage of the Yale Peabody Museum (YPM), and Matthew Nitecki and Eugene Richardson of the Field Museum of Natural History (FMNH). All the above individuals also provided working facilities for the author when he visited their respective museums or institutions.

Part of this work was completed while the author was in residence as the Fenneman Fellow of the Geology Department at the University of Cincinnati. The department provided working facilities, travel monies and photographic supplies. Kenneth E. Caster deserves special thanks for his help and encouragement in this author's asteroid investigations. His instruction, advice and personal library have been invaluable. He helped to make readable prose of this author's Hoosier garble.

Another special thanks is extended to Mr. William H. White, Jr. of Milford, Ohio. This amateur geologist gave freely of his time, effort, experience and specimens. The specimens Mr. White has contributed to the University of Cincinnati Museum of Geology have provided one of the keys to the understanding of ontogeny in early asteroids.

The Geology Department of the University of California at Davis and the Bodega Bay Marine Laboratory of the University of California have provided facilities and modern specimen material for the completion of this project. These facilities include aquaria, access to the Cambridge scanning electron microscope at the Facility for Advanced Instrumentation at Davis and the Digital PDP11 computer of the Davis Geology Department.

Several individuals have provided the author with specimens of modern asteroids which have been useful in his assessment of the paleobiology of the asteroid skeleton. Francisco Ayala of the Genetics Department and James Valentine of the Geology Department at Davis provided abyssal specimens dredged from the San Diego Trough off southern California. Jere Lipps and Thomas Kauffman of the Davis Geology Department allowed the author to examine and identify Antarctic specimens they have collected. Thomas Ronan of the Ecology Group at Davis and the Bodega Marine Laboratory provided fresh specimens of various northern California coastal species.

Supported in part by an NSF summer stipend, the author was able to collect representative asteroids from North Carolina coastal waters as part of a course in Marine Ecology offered by Duke University Marine Laboratories. Dr. I. E. Gray provided invaluable advice and experience in locating the various species.

During a field course in the Florida Keys which was taught by Wayne A. Pryor and supported, in part, by a grant from the Office of the Provost at the University of Cincinnati, the author was able to collect Florida specimens common to several subaquatic environments.

All fossil preparation, data evaluation, photography, scanning electron microscopy, and drafting involved in the preparation of this manuscript were done by the author. He accepts responsibility for errors and misjudgements herein. Lynn Oxley typed the final draft of this manuscript.

III. GENERAL MORPHOLOGY OF ASTEROIDS

General orientation and measurements. -- The asteroid body, or theca, is characterized by a depressed, pentaradial stellate plan with a ventral surface against the substrate and an upwardly facing dorsal surface. Five, occasionally more, arms, or brachia, radiate from the disc, or central portion of the body.

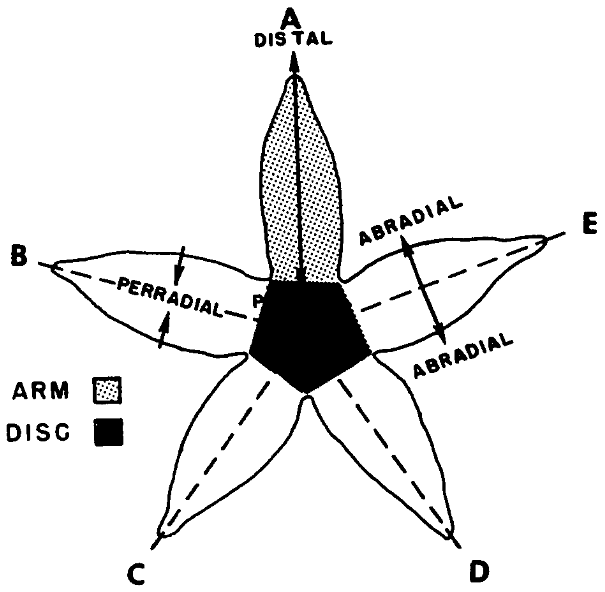
A mouth is located in the center of the ventral surface. The apical field of ossicles occupies the center of the dorsal surface and generally includes the anus. An oral-apical axis of the asterozoan theca passes through the geometric centers of the mouth and the apical field. Proximal and distal indicate respectively toward and way from this axis (Text-figure 1).

A vertical plane longitudinally bisects each brachium from its distal terminus to the oral-apical axis. Perradial indicates a feature on this plane, adradial indicates a feature near or toward this plane, and abradial indicates a position relatively away from it.

Where applicable, the Carpenter System of labeling brachia and interbrachial areas is used herein. This orientation technique can be applied for general purposes when the position of the madreporite, the only preservable surface diversion from otherwise perfect polyradial symmetry, is known. In dorsal aspect, or viewing the theca from above, the madreporite lies in the interradius opposite Brachium A; the remaining arms are alphabetically labeled counterclockwise. Interbrachial areas take the label of their enclosing brachia. In a five-armed asteroid, therefore, the madreporite lies in Interbrachium CD.

Many fossil specimens do not show their madreporites because they

Text-figure 1. -- General orientation terminology of asteroid theca including the Carpenter System of brachial and interbrachial designation. The madreporite is located on the disc in interbrachium CD (dorsal aspect).


A
DISTAL
B
PERRADIAL
P
ABRADIAL
E
ABRADIAL
ARM
DISC
C
D

been lost, have never been exposed from the matrix, or are too obscure to be recognized. Where no other criteria can be used to establish the position of the madreporite or an analygous structure, no thecal orientation technique is applied. It should be emphasized that there appears never to have been cephalization within the asteroid subclass; thus, any such orientation procedure is for descriptive purposes only.

Three measurements are commonly given for an asteroid specimen. The major radius, or brachial length, (R) is the length measurement from the oral-apical axis, along the surface of the animal on the perradial plane, to the arm tip. The minor radius (r) is the shortest possible measurement in each interbrachial area between the oral-apical axis and the margin of the theca. Brachial width (wr) is taken across the brachium from one interbrachial plane to the next. A single value is usually given for each of these parameters of a specimen. It is the mean of the individual measurements of each parameter. As mentioned in the introduction, fossil specimens are usually fragmental or disdorted from their living condition and proportions. This makes it possible to arrive at only approximate values for these parameters in such specimens.

By convention among stelleroid investigators, the length, height, and width of individual body features, such as separate ossicles, features on ossicles or features formed by groups of ossicles or spines, are taken relative to thecal orientation and not necessarily relative to the features themselves. For instance, the width of an ossicle is its maximum horizontal measurement taken normal to a radial axis passing through it; its length is taken along that radial axis;

and its height is taken normal to the horizontal plane. As do the thecal parameters, characteristics of fossil stelleroid ossicles also usually suffer preservational distortion. The same reservations must be applied to measurements of both.

Glossary. -- Several investigators have provided useful glossaries of terms commonly applied to fossil and modern stelleroids. Schuchert (1915) was the first to assemble and publish a uniform, cross-referenced, and exhaustive list of vernacular terms applied to fossil asteroids. His terminology, however, clearly reflects his pedestrian knowledge of modern forms and ontogenic changes within individuals of a species. Spencer and Wright (1965) made the next attempt at a functional glossary. Like Schuchert's, however, it reflects the terminology of paleontologists, with terms such as "odontophore" and "radial" being applied to ossicles which may or may not be homologous to similar ossicles in modern forms.

Blake (1973) amalgamated the important works and terms of earlier investigators of modern and fossil asteroids [notably: Schuchert, Spencer and Wright, Fisher (1911), Verrill (1914), Spencer (1914-1940), Rasmussen (1950), Muller (1953), and Hess (1955)] into an illustrated glossary which includes terms and abbreviations commonly applied to features of individual ossicles of some paxillose genera. When coupled with the general orientation terms and terms applied to non-paxillose asteroids included in the following glossary, it should be useful and necessary to asteroid anatomist, functional morphologists, and taxonomists.

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abactinal. See dorsal.

aboral. See dorsal.

abradial. Refers to a position relatively away from the bisecting vertical axial plane (the perradial plane) of each brachium. Opposite of adradial.

accessory ossicles. All thecal ossicles other than those of the primary skeleton. Accessory ossicles compose the secondary skeleton and intercalate between columns of the primary skeleton.

actinal. See ventral.

adambulacral. An external thecal ossicle of the single primary ossicle column located immediately abradial to each ambulacral ossicle column. Each adambulacral ossicle is adjacent to serial ossicles of the same column, either one (early forms) or two (modern forms) ambulacral ossicles of the adjacent ambulacral column, and ossicles of the adjacent marginal column. Adambulacral ossicles always carry articulating spines or indications thereof.

adaxial. Regular brachial ossicular arrangement where each thecal ossicle is part of a transverse series (row) which includes a single ambulacral ossicle and single ossicles of each successive primary column from adambulacral to median dorsal.

adoral. Toward the center of the mouth opening on the ventral surface. See proximal.

adoral carina. A ridge of paired, adnate adambulacral ossicles of adjacent arms which lies between each mouth-angle ossicle pair and the point where the adambulacral columns diverge onto their respective brachia.

adradial. Refers to a position relatively toward, but not on, the perradial plane of each brachium. Opposite of abradial.

ambitus. The peripheral margin of the theca in plan view.

ambulacral. An ossicle of the paired columns which form the dorsal canopy of the deep groove running the length of the ventral surface of each brachium. These ossicles are bases of attachment for podia and never carry spines. The junction of the paired columns in each brachium defines the perradial plane of each arm.

ambulacral channel. The deepest part of the ambulacral groove. It houses the radial canal and radial nerve of each brachium.

ambulacral groove. Groove running the length of the ventral surface of each brachium.

ampulla. (pl. *ampullae*) The proximal end of the podium which is functional as its fluid reservoir. Internal in all modern asteroids, but possibly external in some primative, early forms.

anus. The opening through which solid waste materials are eliminated. When present in asteroids, it is located near the central dorsal ossicle.

apical. Refers to the geometric center of the dorsal surface. Has been used as a more general term referring to the whole of the dorsal surface.

apical field. All dorsal disc ossicles proximal to the primary circlet.

In cases where the primary circlet is indistinguishable, the term refers to the centrale and the accessory disc ossicles surrounding it.

arm. See brachium.

axial. Refers to radiating grooves formed by fornicated, paired ambulacral columns and running the length of each brachium. Any structure or feature so located may be called an axial feature.

axial skeleton. See perivascular skeleton.

axil. The area of the junction of two brachia at the disc. Area can be subdivided into ventral, lateral, and dorsal areas.

axillary. Any ossicle in an axil; should be used with adjectives to denote specific ossicles (eg. most-proximal inferomarginal axillary).

bivium. The axil with the madreporite and its enclosing brachia (C and D in Carpenter System). Term should be used for orientations purposes only.

body wall. The external integument including an outer epidermis, a middle dermal layer of connective tissue with its endodermal skeleton and associated musculature and the coelomic epithelium.

brachium. (pl. brachia) A radial extension of the asteroid body. Arm.

buccal tube-foot. An adoral podium which functions in food manipulation as it enters the mouth. Buccal podium.

caecal pore. See papular pore.

carina. (pl. carinae) A ridge or flange on an ossicle.

carinal. See median dorsal.

Carpenter System. A simple method of asteroid orientation for descriptive purposes. In dorsal aspect, the madreporite lies in the interradius opposite Brachium A, the remaining arms being alphabetically labeled counterclockwise. The bivium thus includes brachia C and D, and the enclosed interradius CD.

centrale. See centrodorsal.

centrodorsal. A prominent ossicle in the center of the apical field, which is usually obvious on geologically and ontogenically early forms. Marks the center of the primary circlet.

column. A series of brachial ossicles roughly parallel to the longitudinal axis of a brachium. Each member of a column holds a position in a cross-section of the brachium similar to that of other members of the same column at their respective cross-sections.

cryptozonate. General term referring to asteroids in which marginal ossicles are not conspicuously larger than other brachial ossicles.

cupule. A depression in the oral surface of an ambulacral column which housed the proximal end of a podium in an early form which did not possess internal ampullae.

dentition. Crenulations on the dorsal perradial surface of an ambulacral ossicle marking its surface of articulation with its counterpart in the adjacent ambulacral column.

diplacanthid. Possessing two primary spines. Compare with monacanthid and multiacanthid.

disc. General term for central part of the asteroid theca; that part of the body not part of the brachia.

distal. Relatively away from the axis which passes through the center of the mouth opening on the ventral surface and the center of the apical field on the dorsal surface. Radially.

dorsal. The surface of the asteroid theca opposite that possessing the mouth; the aboral, abactinal, apical or top surface. The surface normally exposed to the environment away from the substrate. Surface opposite the ventral surface.

dorsal aspect. View of the theca or some component from above, or as from the dorsal surface toward the ventral surface.

dorsolateral. See interdorsals.

external ossicles. Ossicles exposed at the surface of the theca; those normally visible in non-disarranged specimens.

extrathecal ossicles. Ossicles not invested in the thecal integument, but articulated in or on thecal ossicles by muscles. Collectively, spines, granules, spinelets, and pedicellaria valves.

extravascular skeleton. The non-perivascular skeleton. Thecal ossicles other than those of the mouthframe and ambulacral and adambulacral columns.

fasciole. Ciliated tract between ossicles which functions in the movement of water and particles of food and other detritus.

granule. Extrathecal spherical or subspherical skeletal elements similar in origin to spines.

groove spines. Adambulacral spines involved in covering or manipulating materials within the ambulacral groove. Subadambulacral spines lie immediately abradial to groove spines in many species.

hydrovascular system. See water-vascular system.

inferomarginal. Extravascular, thecal ossicle type always arranged in columns along the edge of the oral surface in most asteroids with obvious primary columns. Although a primary ossicle type, inferomarginals are absent in some forms where their position is held by enlarged adambulacral columns of the perivascular skeleton.

inframarginal. See inferomarginal.

interactinal. See ventral intermediates.

interbrachial. Refers to external or internal thecal ossicles or other features positioned between the brachia.

interdorsals. Accessory ossicles of dorsal body wall located between median dorsal column and more dorsal marginal column on either side. May be adaxially arranged, arranged only relative to other extravascular ossicles, or with no apparent arrangement.

intermarginal. Extravascular accessory ossicles of lateral body wall located between inferomarginal and superomarginal columns. Not present in all asteroids. Term may also refer to the surface of a marginal ossicle facing an ossicle of the adjacent marginal column.

intermediates. See ventral intermediates.

internal ossicles. Ossicles not normally exposed at the surface of the theca. Internal ossicles are visible only in disarranged specimens.

interradial. See interbrachial.

interradius. Refers to a position on or in the disc between brachia.

jaw. A misnomer in the literature for each or all mouth-angle ossicle pairs of an asteroid.

lateral. Marginal surfaces of asteroid brachia and disc which are neither ventral or dorsal. Has no application to specific ossicle columns in asteroids.

lateral aspect. View of the theca, a brachium, or some component thereof from the side.

longitudinal. Refers to any feature, axis or section radiating from the oral-apical axis of an asteroid. When applied to individual ossicles it still refers to that element as oriented on the theca, and not necessarily to the major axis of that ossicle. Contrast with transverse.

madreporite. Porous ossicle occluding the hydropore of asteroids. Normally conspicuous on the dorsal surface of asteroids.

marginals. Collectively, the superomarginal and inferomarginal ossicles. One or both of these series lie along the brachial ambitus of most asteroids.

maw. A feeding vestibule immediately outside the mouthframe of a stomach-everting asteroid formed as the animal closes its brachia about its food and arches up the central portion of its body.

median dorsals. A single, more or less prominent column of external, primary ossicles extending from the primary circlet to the terminal ossicle along the median dorsal surface of each brachium. Other authors have termed these radials or carinals.

monacanthid. Possessing a single primary spine.

mouth. Central, ventral opening serving as entrance to digestive system.

mouth-angle ossicles. Ossicles at proximal end of each adambulacral column. Functions as base for oral spines, insertion ossicle for circumoral muscles, and articulation structure for ambulacral columns and mouthframe. Adnate with mouth-angle ossicle of adjacent brachium. Jaw, tooth, MAP (mouth-angle plate).

mouthframe. All ossicles mechanically involved in asteroid oral skeleton. Includes mouth-angle ossicles, most-proximal ambulacrals, and odontophores.

multiacanthid. Refers to a single ossicle which possesses many primary spines.

obverse. The surface that is opposite to the one currently under discussion.

odontophore. Unpaired, internal primary axillary within mouthframe. Located between distal ends of each mouth-angle ossicle pair. Functions in the opening, or dialation, of the mouth.

oral. Pertains to the mouth opening. Has been unwittingly applied to the whole of the ventral surface by many earlier investigators.

oral intermediate. See ventral intermediate.

ossicle. Any calcified skeletal element, but less commonly applied to spines, granules, spinelets and pedicellaria valves.

ossicle body. Refers to the main, most massive portion of an ossicle, as contrasted with protruding carinae, flanges, bosses or processes.

papula. (pl. papulae) Evagination of coelomic epithelium through a perforation in the remainder of the thecal wall. Coelomic protuberance may be conical, tubular or branced. These are the so-called "skin gills" that function in respiration.

papular pore. Opening in the dorsal, lateral, or ventral thecal wall through which a papula passes or has passed.

paxilla. (pl. paxillae) Extravascular, external ossicle composed of a base, a shaft, and an apical crown. Small spines, or spinelets, articulate in a tuft on the crown.

paxillose. Possessing paxillae.

pedicellaria. (pl. pedicellariae) Minute, sessile or pedunculate, extrathecal accessory, calcareous pincers arising in ossicular excavations, from the ossicle surface, or from the dermal surface of the asteroid theca. Sometimes arising from fleshy integument around spines. May have two, three, and occasionally more valves. These structures have been shown to function in cleansing, food movement, and food capture. Common to modern epifaunal asteroids, but absent in genera which commonly burrow. Valves have not yet been detected in early asteroids.

periproct. See anus.

perivascular ossicles. Ossicles intimately associated with the water-vascular system so as to show reflections of its anatomy in their structure. Includes ossicles of the mouthframe and the ambulacral adambulacral columns. There is always a one-to-one ration between ossicles of a brachial ambulacral column and ossicles of the adjacent adambulacral column.

perivascular skeleton. Collectively the ambulacral, adambulacral and mouthframe ossicles.

perradial. Denotes a position on or in the theca at the bisecting vertical axial plane of each brachium.

perradial aspect. A view from a position on the bisecting vertical axial plane of each brachium.

phanerozonate. Asteroids in which marginal ossicles are conspicuously larger than other brachial ossicles. Compare with cryptozonate.

plate. A flattened, discoid ossicle. Has been used by earlier authors as a synonym for ossicle.

podial basin. An external excavation in, but not a perforation through, an ambulacral column at the junction of each two serial ossicles. In early asteroids these cupules housed podia or ampullae of completely external podia or podia which passed ampullae into the brachial cavity in a position abradial to the ambulacral ossicle columns.

podial pore. A perforation through a column of serially arranged ambulacral ossicles through which a podial ampulla extends. Compare with podial basin.

podium. (pl. podia) One of many exposed, serially arranged, outer extensions of the water-vascular system. Podia protrude from the ambulacral groove in living asteroids. Each connects to the radial vessel by a lateral vessel. Each is composed of a proximal ampulla, and terminates at its outer extremity in an acuminate point, an adhesive pad, or a sucking disc.

primary circlet. A ring of prominent ossicles of the dorsal disc. It is generally around, but is not necessarily adjacent to, a prominent centrodorsal ossicle. It is composed of a radial ossicle in line with the median dorsals of each brachium, a more or less prominent interradial ossicle for each interradial area, and occasionally other secondary intercalating ossicles.

primary skeleton. Ossicles of the thecal columns commonly present in recently metamorphosed, post-larval asteroids. Includes ossicles of the primary circlet, the mouthframe, the centrodorsal, the primary axillaries, ambulacrals, adambulacrals, marginals, median dorsals, and terminals. Secondary skeletal elements develop between the ossicles of the primary skeleton.

proximal. Toward the axis which passes through the center of the mouth opening of the ventral surface and the center of the apical field on the dorsal surface. In the case of individual appendages of the brachia, the term refers to the end or part closest to the theca.

pustule. Small monticule on an ossicle. It does not have a conspicuous central pit. Generally is an articulation process for a minute spine or granule.

pustulose. Possessing pustules and spine-base monticules.

radial. See median dorsal. Also see distal. Also applied to components lying along longitudinal axis of brachia.

radius. See brachium.

ray. See brachium.

radial canals. See radial vessels.

radial vessels. Extensions of the water-vascular system from the ring canal, out the length of each ambulacral channel.

ring canal. Tubular ring of water-vascular system which circles the buccal opening and from which radial vessels radiate into the ambulacral channel of each brachium. Another more or less ossified vessel leads from the ring canal to the madreporite.

row. A transverse or diagonal series of ossicles. Contrast with column.

secondary skeleton. All thecal ossicles other than those of the primary skeleton.

spicules. General collective term for all skeletal elements of unknown affinities. These ossicles are usually small and accessory.

spine. Elongated, extrathecal skeletal element which articulates by means of muscles to a thecal ossicle. May be sharp or blunt, and terete or irregular in cross-section. Granules are similar in origin, but are not elongated.

spinelet. A small, slender spine.

spine-base monticule. A small elevation with a central pit on a thecal ossicle. The structure is the insertion area for muscles controlling the attitude of articulating spines, granules, or spinelets. Also called spine pit. Primary spine pits are larger than secondary spine pits.

stone canal. The ossified canal connecting the madreporite and ring canal in modern asteroids. In some early forms this structure was merely an extension of the madreporite.

subadambulacral spines. Adambulacral spines abradial to the groove spines in many asteroid species.

superoambulacral ossicle. Internal ossicle forming a strut between the endothecal surface of each ambulacral ossicle and an adjacent inferomarginal ossicle. Common in digging asteroids; uncommon in exclusively epifaunal species.

superomarginal. Thecal ossicle of extravascular primary skeletal column lying nearest to the ambitus in dorsal aspect, but not visible in ventral aspect. The more dorsal primary marginal column in phanerozonate forms.

supramarginal. See superomarginal.

tentacle. See podium.

terminal. The most distal median dorsal ossicle on each brachium. Also, the first median dorsal formed in ontogeny. Sometimes called ocular.

theca. The stelleroid body and body wall, including perivascular and extravascular skeletal and integumental tissues. May be divided into arm and disc regions for descriptive purposes.

thecal ossicles. Ossicles invested in the integument. This includes the primary and accessory ossicles, but not spines, granules, etc. which articulate on these ossicles.

tooth. A misnomer for a pair of mouth-angle ossicles. They do not function as masticatory apparatuses.

torus. A single ossicle, commonly carrying one or more spines, orad of mouth-angle ossicle pair in each oral interradius of most early asteroids. Not present in modern asteroids, but present in all ophiuroids.

transverse. Refers to any feature, axis, or section running from one side of a brachium to the other side. When the term is applied to individual ossicles, it still refers to that element as it is oriented in the theca and not, necessarily, to the major axis of that ossicle. Contrast with longitudinal.

transverse vessel. Vessel of the water-vascular system which connects a podium to the radial vessel in its brachium. Also called lateral vessel.

triplacanthid. Refers to a single ossicle, generally an adambulacral, which possesses three primary spines.

trivium. General orientation term referring to theca not part of the bivium. Useful in five-armed asteroids when the position of the madreporite can be determined.

tube foot. See podium.

ventral. Thecal surface possessing the mouth opening. Also called the oral, actinal, abactinal, or bottom surface by other authors. This surface is normally in contact with the substrate. It is the thecal surface opposite to the dorsal surface.

ventral aspect. View of the theca or some component from below, as from the substrate or from the ventral surface toward the dorsal surface.

ventral intermediates. Extravascular, accessory thecal ossicle columns intercalating between adambulacral and inferomarginal comumns in some genera.

water-vascular system. A secondary coelomic system unique to Echinoderms. In asteroids it is composed of all elements of the podia, transverse vessels, radial vessels, ring canal and its extensions, the stone canal and the external madreporite. Known to function in locomotion, food acquisition, excretion, respiration, circulation, phagocytosis, and serological regulation.

Arrangement of skeletal elements in asteroids. — The asteriadinid brachial skeleton is built on a framework of five kinds of primary ossicles arranged in nine longitudinal columns. The primary ossicle columns are: one column of median dorsal ossicles along the dorsal perradial surface; two columns of superomarginal ossicles, one on each side of the median dorsal coumn; two columns of inferomarginal ossicles, one beneath each superomarginal column; two columns of adambulacral ossicles, each just adradial to a column of inferomarginals; and two abutting columns of ambulacral ossicles, the ventral abradial ends of which are surmounted on the adambulacral columns. In more complex forms, additional columns of non-primary, accessory ossicles intercalate between median dorsal, superomarginal, inferomarginal, and adambulacral columns. These intercalated columns allow the skeletal framework of the brachia to increase in diameter and flexibility (Verrill, 1914).

The brachial ossicle columns converge at the disc. The skeletal framework of the disc is composed of these proximal brachial ossicle columns, plus additional ossicles functioning ostensibly as space fillers. The ossicles of each median dorsal column commonly continue onto the dorsal surface of the disc where they may become more prominent, do not change in relative size, or become indistinguishable from the other ossicles of the disc. Disc median dorsals in columns of adjacent brachia are separated from one another by ossicles termed centro-interbrachials. Some centro-interbrachials are aligned with the superomarginal columns of the brachia and are termed disc superomarginals, axillary superomarginals, or most-proximal superomarginals, depending on their relative positions and prominence. Likewise there are disc inferomarginals, axillary inferomarginals and most-proximal inferomarginals.

The centrodorsal is usually distinguishable in the center of the apical field by its size and pentaradial symmetry. It is commonly surrounded by numerous smaller ossicles arranged in concentric circlets. The ossicles of these circlets may be regularly aligned with radial or interradial areas and referable as such, or they may be apparently random in arrangement. The centrodorsal and the surrounding circlets of smaller ossicles are collectively termed apical field ossicles. In some species the apical field terminates distally against a prominent ring of enlarged median dorsals and centro-interbrachials called a primary circlet or coronet; in others the apical field may grade imperceptibly into the dorsal brachial ossicles.

The mouthframe of both modern and fossil asteroids is composed of ten spine-bearing mouth-angle ossicles arranged in five interradial pairs, five odontophores distal to these pairs, and ten most-proximal ambulacral ossicles arrange in five radial pairs. These ossicles form a contiguous circlet of ossicles around the mouth opening in the center of the thecal ventral surface. In living animals, muscles between adjacent oral frame ossicles function to change the attitudes of the frame ossicles and to provide flexibility in the size of the frame. These same muscles probably existed in fossil forms.

For purposes of description and functional analysis, it is useful to consider the asteroid skeleton in terms of two sub-units. These are the perivascular skeleton and the extravascular skeleton.

The ossicles of the perivascular skeleton are those intimately associated with the water-vascular system. They reflect something of the anatomy and functionality of this latter system, the details of which are discussed in a later section of this work. Perivascular ossicles include the ambulacrals, the adambulacrals, and the ossicles of the mouthframe including the mouth-angle ossicles, the odontophore, and the madreporite with its stone canal. The ossicles in adjacent ambulacral and adambulacral columns of all asteroid brachia are always present in a one-to-one ratio.

All other thecal ossicles compose the extravascular skeleton. Primary extrathecal ossicles in columns of each bracium also maintain a one-to-one ratio; that is, for each median dorsal, there is a single superomarginal and a single inferomarginal on either side. Intercalating accessory ossicles between these primary columns in more complex forms maintain a regular numerical relationship to them.

The numerical relationship between the ossicles of the perivascular and extravascular skeletons is not commonly one-to-one. This may be evidence that these two sub-units are somewhat independent of one another, and that the herein proposed subdivision of the asteroid skeleton has something more than descriptive significance. Within families, individuals appear to develop characteristic ratios of either one-to-one or greater than on-to-one between perivascular column ossicle number and extravascular column ossicle number. Cincinnatian asteriadinids are divided into three families; individuals in Mesopalaeasteridae maintain a ratio of one-to-one, while Hudsonasteridae and Promopalaeasteridae species possess nearly twice as many ossicles in each perivascular column as in each extravascular colmn.

IV. FUNCTIONAL INTERPRETATION OF PRESERVABLE CHARACTERISTICS

Before any taxonomic revision or paleobiological assessment of fossil asteroids is undertaken, it is wise to observe modern asteroids and search the literature for characteristics which are both preservable and useful in establishing an understanding of individual specimens and the subclass as a whole. Such an investigation should yield information on characteristics which seem to distinguish the various asteroid groups. It should also point out characteristics which should be cautiously utilized as taxobases, as well as those characteristics which are not significant in taxonomic differentiation.

This section considers some preservable aspects of asteroids which are useful in understanding the biology of the animals which possess, or did possess, them. The taxonomic revision of the Cincinnati forms which follows uses the principles elucidated here to reconstruct realistic paleobiological models of the animals represented by the fossils.

The asteroid endoskeleton. -- Many fossil asteroid taxa have been described from observable differences in skeletal remains among fossil specimens. Few paleontologists, however, have assessed the functionality of the skeletal features they employ to differentiate taxa. A review of the skeleton's role in echinoderm and asteroid ways of life necessarily precedes a knowledgeable evaluation of a taxonomy founded on skeletal characteristics.

The ossicular skeleton, held together by short, integumental muscles, provides the structural framework of the asteroid theca. Several other functions, performed by individual skeletal elements, are necessarily understood prior to any accessment of the taxonomic significance of skeletal details. These ossicle characteristics and functions are common to all extant echinoderm classes and can probably be assigned to ossicles of all known fossil groups as well.

As summarized by Raup (1966), the echinoderm skeleton is always composed of calcite ossicles which are mesodermal in origin. The magnesium content of echinoderm calcite is consistently high and is thus comparable to that of coralline algae, calcareous sponges, and octocorals. Chave (1952) documented that echinoderm magnesium is generally in the form of $MgCO_3$ in solid solution wich calcitic $CaCO_3$. In modern echinoderms, the comparative weight percentage of these two skeletal carbonates is a general index to environmental temperature, a higher magnesium content indicating warmer temperatures (Clark, 1911; Chave, 1954a). There appears to be considerable variation in this characteristic among lower taxonomic levels at any given temperature range (Vinogradov, 1953); this suggest that magnesium content is, at least to some degree, under genetic control.

The magnesium content of echinoderm fossils is of little value in taxonomic work because the composition of the original material is difficult to establish. Chave (1954b) documented that the mineralogy of the relatively unstable high-magnesium calcite of echinoderm ossicles nearly always changes either toward pure calcite or dolomite during fossilization.

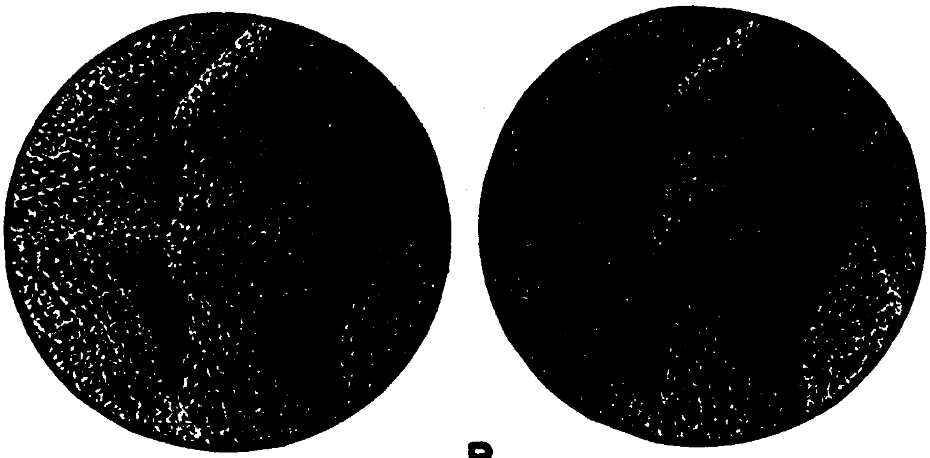
Each echinoderm ossicle is an open meshwork (Text-figure 2) of calcite which grows by accretion and behaves optically as a single crystal. Spaces (stromal canals) within the calcitic stereom of each ossicle are filled with connective tissue (stroma) in the living animal.

Nichols (1962) offered some attractive suggestions as to the function of the fenestrated nature of echinoderm ossicles. He suggested that the stereom structure offers ample opportunity for interossicular muscle fiber attachement, and that the fenestrate nature also results from the need to conserve $CaCO_3$ and to make a strong, light, rigid skeleton. Nichols' suggestions do not explain why entire ossicles are meshworks, whereas muscle attachments are restricted to small areas. Nor do they explain why $CaCO_3$ requires conservation on the part of echinoderms, but apparently not by associated fauna which commonly builds massive, $CaCO_3$ skeletons.

A characteristic of echinoderm ossicles observable on scanning electron photomicrographs of asteroid ossicles deserves mention in regards to Nichols' suggestion that a fenestrate structure offers ample opportunity for interossicular muscle fiber attachment. Text-figure 2B is a stereo-pair photomicrograph of the ventral transverse muscle attachment zone in a specimen of Asterias forbesi (Desor). The fenestrate nature of the individual ossicles is clear, but the muscle attachment area on the surface of each ossicle differs from those areas where there were no muscle attachments (muscle attachment zones enclosed by dashed lines in figure A). Digitate extensions of skeletal material protrude from the ossicle in the muscle areas, whereas there are no such protrusions in other areas. It is suggested that these knobs and bosses increase the surface area contact between muscle fiber and ossicle. Macurda and Meyer (1975) noted similar "stalagmites" in the muscle attachment sites on some modern crinoids and ascribe a similar function to them. In terms of gross ossicular structure, the larger

Text-figure 2. -- Denuded ambulacral ossicles of *Asterias forbesi* showing stereomal meshwork. A. Ventral aspect, transverse ventral muscle insertion areas outlined by hatched lines (HG = hemal groove), X45, B. Stereo-pair photomicrographs of area circled in A (note digitate extensions of meshwork in areas where muscles attach), X80.

A

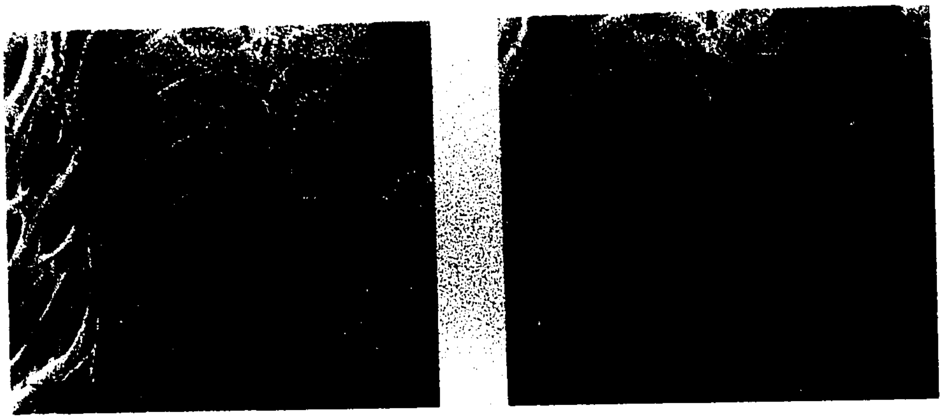


B

interossicular muscles of asteroids commonly attach to bosses, flanges, or in excavations of the ossicular surface (Text-figure 3). These structures also serve to increase surface area contact between muscles and ossicles by providing more ossicle surface area in zones where it is mechanically advantageous. Hence, Nichols' suggestion should not be extended to imply that the holes in the ossicular meshwork are, in themselves, sufficient for all muscle attachment. In fact, Macurda and Meyer (1975) suggest that crinoid muscles do not really penetrate the stereom of crinoid ossicles, but attach to surface structures of the ossicles.

The meshwork structure of echinoderm ossicles makes them less massive than solid ossicles of the same size would be. One line of reasoning, however, may suggest that there is a physiological basis for the fenestrate, rather than solid or hollow, high-magnesium calcite echinoderm ossicle plan. It is commonly known that both calcium and magnesium are essential in the enzymatic control of invertebrate muscle activity. The stereomal-stromal microstructure of echinoderm ossicles provides nearly maximal contact between the chemicals of the skeletal material and the tissue filled stroma. No one seems to have examined the possibility that magnesium and calcium move across the stereomal-stromal interface as a result of a physiological need of interossicular or long body muscles. Gay and Simon (1964) found that excised holothurian muscle contracts irreversibly when bathed in Mg^{++}-free seawater. The presence of magnesium in the echinoderm skeleton could well be a reserve against possible low Mg^{++} conditions deletereous to normal muscle activity.

Text-figure 3. -- SEM stereophotomicrographs of denuded ambulacral ossicle columns of *Asterias forbesi*. This oblique dorsal aspect shows muscle insertion excavation (MIE) for dorsal transverse ambulacral muscles, muscle insertion boss (MIB) for transverse ventral ambulacral muscles, and muscle insertion flange (MIF) for longitudinal ambulacral muscles, X60.



A reasonable argument against this suggestion is the fact that magnesium cations are second only to sodium in abundance in normal seawater, and it is thus unlikely that exclusively marine organisms would ever face a low magnesium concentration in their surroundings. The fact that neither of these points can be effectively argued much further points out that the role skeletal chemistry plays in echinoderm physiology is virtually unexplored.

Another possible function of the ossicle meshwork results from a mineralogic characteristic of crystalline calcite; it is easily cleaved by physical shock. A meshwork dissipates shock by absorbing it in partial failure. A more solid calcitic structure would transmit such energy and is more likely to fail completely.

The replacement of other alteration of skeletal material during fossilization seems to have obliterated direct evidence of fenestrated ossicles in most echinoderm fossils. During the normal processes of fossilization, stromal canals commonly fill with secondary calcite in optical continuity with that of each ossicle. This makes it difficult to isolate and study original skeletal material. Secondary replacement may follow this petrifaction process, thus removing all traces of the original structure except, possibly, the crystalligraphic orientation. Where replacement is not complete, such as in some Paleozoic crinoids (Moore, Jeffords, and Miller, 1968), stereomal characters may be seen in thin-sections of fossils. Macurda (1973) reported such for some Permian blastoid specimens. Caster and Eaton (1956) documented an incidence of preserved stromal filling, rather than preserved stereom, in the Brazilian Lower Dovonian carpoid Paranacystis. In this latter example, limonite (possibly after an iron sulfide) fillings of the stromal canals stand in relief from the rock matrix. The calcareous material of the ossicular stereom has been removed by dissolution at some time subsequent to the filling of the stromal canals by an iron mineral. Spines on a specimen (Plate 18, figure 2c) of Neardisaster prenuntius (Schuchert) from the Ordovician Lexington Limestone near Frankfort, Kentucky also show differential weathering of replaced stereom and stromal filling. All these specimens support the idea that the fenestrate plane of echinoderm ossicles developed early and was maintained throughout the history of the phylum.

Asteroid ossicles also function in ways not as apparent from their composition and microstructure. They are flexibly, but securely, joined by durable, "slow", unstriated muscles into a structure which serves as the supportive frame of the body. Collectively and individually the ossicles fulfill Ramsay's (1957) definition of a skeleton; that is, they compose a device capable of transmitting forces from one part of the body to another.

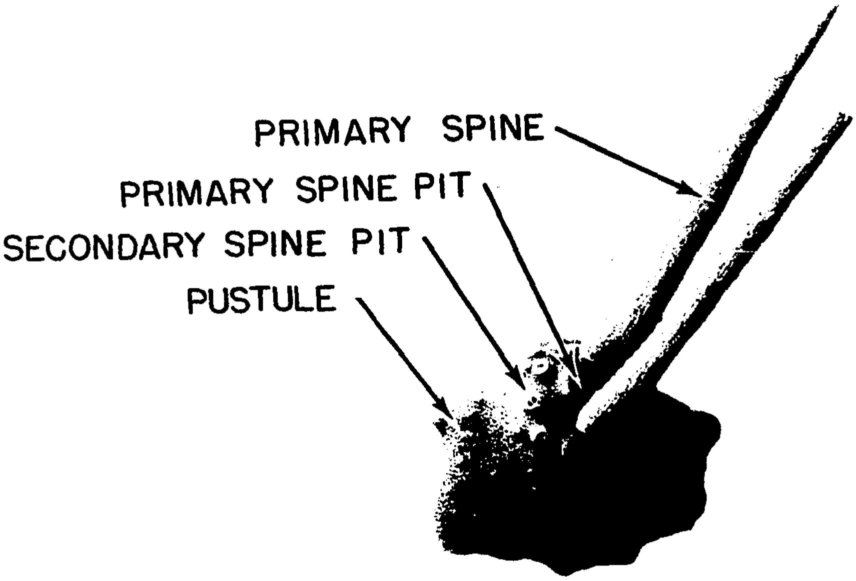
All asteroid ossicles, except the ambulacrals and internal disc ossicles, usually carry articulating spines, spinelets or granules. These extrathecal elements serve to protect respiratory papulae protruding through the skeletal frame. They also serve to channel water currents generated by dermal cilia, hold vela erect, or keep overlying sediment away from the dorsal and lateral body surfaces; their precise function depends on their structure and location on the theca.

For practical reasons, the details of ossicle spinosity are commonly difficult to determine for fossil asteroids. Only from well-exposed ossicle surfaces can precise information on spine arrangement be obtained. The spines are likely to have been removed from these ossicles by weathering, or whatever phenomenon exposed the ossicle surface. Information on spine shape and macrostructure is lacking in such specimens. It is also possible that the spines may not have been preserved with the thecal ossicles. Blake (1967) discussed spine removal by natural processes prior to burial of asteroids, and concluded that it was a common phenomena unless burial was immediate and permanent. It is also possible that spines may be selectively removed during preservation. Quenstedt (1928) suggested that small organisms and fine structures are more easily lost through solution than larger and coarser structures of the same material. This selective removal of fine structures occurs during and after burial because there is more effective solution surface per unit volume in fine structures. The relatively high solubility of high-magnesium calcite in echinoderm skeletons increases this latter possibility.

Fortunately, places where spines articulate on their thecal ossicles are nearly always marked by spine-base monticules, spine pits, or pustules on the ossicles of modern specimens (Text-figure 4). These articulation structures, which reflect the muscle attachments between spines and thecal ossicles, are commonly preserved in fossils, although the spines are not.

Some ideas of spine size and maneuverability can be deduced

Text-figure 4. -- Marginal ossicle of *Nearchaster aciculosus* showing surface features indicative of articulating structures. The largest spines, nominally the primary spines, articulate on large spine-base monticules with central pits. Secondary spines arise on smaller monticule pits, and the smallest spines are mounted on small pustules without pits. The author has searched for similar reflections of the attachment of pedunculated pedicellaria, but has concluded that pedicellaria leave no such indication of their presence. X12.


PRIMARY SPINE
PRIMARY SPINE PIT
SECONDARY SPINE PIT
PUSTULE

from the morphology of these articulation structures. From empirical evidence it can be seen that larger spines articulate on larger and more structurally complicated monticules than do smaller spines or spinelets. This difference between spine-base structures of small and large spines is actually a matter of degree, rather than kind. A centeral pit or groove for articulating muscle attachment is always apparent in the center of a monticule for a spine of large diameter or a small-diameter, long spine. The pustules for small spines do not usually possess such obvious central pits. The shape and attitude of the central pit or groove on a spine-base monticule is useful in determining the plane or planes of movement of the articulating spine. Observations of spine movement by living asteroids in aquaria and subsequent examination of the spine bases to which the observed spines were attached show that a spine which moves in a single plane commonly possesses a basal monticule with a groove, rather than a circular pit. The plane of movement is parallel to the longitudinal axis of the groove in all species examined; these include species of *Pisaster*, *Orthasterias*, *Mediaster*, *Pycnopodia*, *Astropecten*, and *Patiria*. Where the central pit does not appear linear, spine movement is not planar.

The significance of these observations on modern asteroids in a functional interpretation of fossil asteroids is obvious. The size and maneuverability of spines which have been lost from a fossil asteroid specimen can be determined with some degree of accuracy.

Aspects of spinosity must be cautiously applied as taxobases, because some seem to vary widely within species, both throughout ontogeny and in final attainment. Rasmussen (1965) found that within each of three closely related species of Henricia a fairly close correlation exists between mean brachial length and mean spine number on each dorsal, marginal and adambulacral ossicle; mean spine number per ossicle increases with mean brachial length in this genus. The same feature has yet to be examined in other genera. Chia (1966) discussed polymorphism within Leptasterias and showed that three forms formerly regarded as distinct on the bases of color, stoutness, pedicellaria and spine distribution are, in reality, the same species, L. hexactis. He found that these forms naturally intermingle and do not form separate populations. Further, they crossbreed freely and produce fertile offspring. In terms of this discussion, Chia's findings indicate intraspecific variation in overall spinosity in Leptasterias. Variations in spinosity, such as occur in the above two genera, may occur in other asteroids, including fossil forms. Furthermore, the findings of Chia and Rasmussen indicate that spinosity is a difficult characteristic to access for a taxon without observations on a sizable number of individuals.

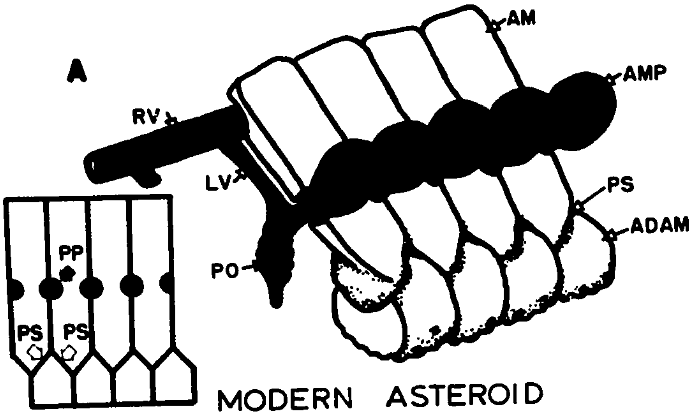
Verrill (1914) suggested that within the Asteriidae, the characteristics of the oral spines commonly offer good specific distinction, and in some cases are at least of generic value. He further adds, however, that in most cases oral spines have not been figured or described with care, and the taxonomic level at which the characteristic is usable is uncertain. Since the Asteriidae comprises mainly our best known and most thoroughly studied genera, it is clear that much more observation and documentation on modern species must occur before spinosity characteristics can be assessed as realistic taxobases on fossil representatives of the subclass.

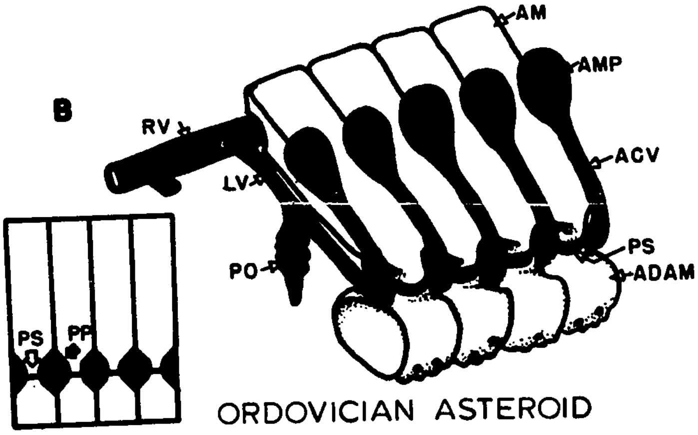
The water-vascular system and perivascular skeleton. -- The water-vascular system of fossil asteroids offered little potential for fossilizaiton. Something of its anatomy and function can be determined, however, from analyses of those preserved skeletal elements which were closely associated with the system during life. These include ambulacral, adambulacral and the mouthframe ossicles. Coupled with information on the system available from modern asteroids, data from these fossil perivascular ossicles provides information about the vascular and respiratory paleobiology of early members of the subclass.

In living asteroids, brachial tube feet, or podia, protrude from ambulacral grooves on the ventral arm surfaces. They are commonly arranged in two, four, or more longitudinal columns in each groove, depending upon the species, the maturity of the individual and their location on the brachium. Depending on the taxon, each tube foot may terminate in a simple point, an adhesive pad, or a sucking disc.

A podium issues from between each two consecutive ambulacral ossicles in the paired ambulacral columns for the length of each arm (Text-figure 5A and Text-figure 6A). Communication with other podia is by means of lateral or transverse vessels which extend from each podium to the brachial radial water vessel located deep

<u>Text-figure 5</u>. -- Perivascular ossicles and associated water-vascular organs of modern (A) and Ordovician (B) asteroid brachia. Each figure shows only the ossicles on one side of the brachium. Ampullar connecting vessel (ACV); adambulacral ossicle (ADAM); ambulacral ossicle (AM); ampulla (AMP); lateral vessel (LV); external podium (PO); podial perforation through perivascular skeleton (PP); perivascular suture (PS); radial water-vascular vessel (RV).


A
AM
AMP
RV
LV
PS
ADAM
PP
PO
PS
PS
MODERN ASTEROID


B
AM
AMP
RV
ACV
LV
PS
ADAM
PO
PS
PP
ORDOVICIAN ASTEROID

Text-figure 6. -- SEM stereophotomicrographs of an excised portion of the ambulacral column of Asterias forbesi (A), X 15, and abutting ambulacral columns of a Cincinnatian promopalaeasterid (B), X 18. Note lack of inter-ambulacral podial perforations and dorsal transverse muscle attachment features in the promoplaeasterid.

A

B

in the ambulacral channel. This radial water vessel is immediately external to the abutting, opposed ambulacral columns. Inside, or above the ambulacral columns, each podium develops into an ampulla.

The histology of the brachial water-vascular system in all types of living echinoderms is known to varying degrees. In all cases, the various vessels and organ walls are composed of an inner epithelium, which is continuous throughout the entire water-vascular system, intermediate layers of connective tissue and muscle, and an external epithelium. The external epithelium of the podia is continuous with that of the covering of the remainder of the body. In ampullated echinoderms, the external epithelium of the internal ampullae is continuous with that of the outer lining of the perivisceral coelom.

Tube feet are used by asteroids for locomotion, digging into or hanging onto the substrate, and food manipulation. They also play an indispensable part in respiration. Farmanfarmaian (1966) noted that echinoderms commonly employ outpouchings of the water-vascular system, such as tube feet in asteroids, as respiratory surfaces and demonstrated (1959) that, in the modern echinoid <u>Strongylocentrotus purpuratus</u>, oxygen traverses the ampullar membrane by diffusion after being transported to ampullae from podia by means of ciliary currents. Although it has not been documented, similarities in histologies suggest that such is probably the case in modern asteroids as well. Meyer (1935) demonstrated that in <u>Asterias rubens</u>, a European species of Asteriadina, approximately ten percent of an animal's total oxygen uptake is accomplished through the podia in each arm. This suggests that in such five-armed asteroids about half of the required oxygen is taken into the theca via the tube feet. Animals without dermal papulae or other ancillary modes of oxygen uptake probably acquire nearly all their oxygen by diffusion from the surrounding seawater into the podia.

Both hemal and water-vascular systems have been rejected by zoologists as effective circulatory systems in echinoids (Farmanfarmaian and Phillips, 1962). Oxygen and nutrients are probably circulated to internal organs by means of the ciliary currents within the perivisceral coelomic fluid (Farmanfarmaian, 1968). That "skin gills", or papulae, are extensions of the coelomic wall of many echinoderms indicates that coelomic fluid is, at least to some degree, involved in gaseous exchange and transport. Thus, in ampullated modern echinoderms, oxygen absorbed by the external podia reaches the circulatory perivisceral fluids by means of the internal ampullae.

The mechanisms of podial extension among modern asteroids are reasonably well understood. Nichols (1969, 1972) and others have presented accounts of podial extension and retraction by asteroids, noting that both the radial canal and ampullae supply and hold fluid for such action.

Three aspects of early asteroid brachia are important to an understanding of their water-vascular system: (1) the nature of the ampullar perforations through the ambulacral columns; (2) the ambulacral-adambulacral junction; and (3) the ability of these early asteroids to rotate abutting ambulacral columns about a common fulcrum and thereby open and close the ambulacral groove.

Uniform as modern asteroids are in possessing ampullar perforations through ambulacral columns near ossicular mid-width (Text-figure 5A), Ordovician members of the subclass passed their ampullae into the theca nearer the abradial termini of these ossicles (Text-figure 5B). No known Ordovician asteriadinid shows any evidence that podial perforations existed between the main ossicle bodies of the brachial ambulacral ossicles. Rather, the ampullae passed from the open ventral groove into the brachia through perforations bounded by four ossicles at the junctions of the ambulacral and adjacent adambulacral columns. In modern asteroids, a much stronger perivascular skeleton as developed with ossicles of the ambulacral column alternate to those of the adjacent adambulacrals. This alternate arrangement precludes the possiblity of podial perforations at the ambulacral-adambulacral junction; the ampullar perforations lie between successive ambulacral ossicles. A very large specimen of Kenothecaster miamiensis(Miller) (Plate 12, figure 2b) shows that some large Ordovician individuals had, in their oral region, buccal podia similar to all podia of modern asteroids where ampullar perforations are located away from the ambulacral-adambulacral junctions. The fact that the most proximal adambulacrals were closely fused with the most proximal ambulacrals in the crowded oral region of large individuals and the need for the ampullar reservoir probably resulted in such a condition.

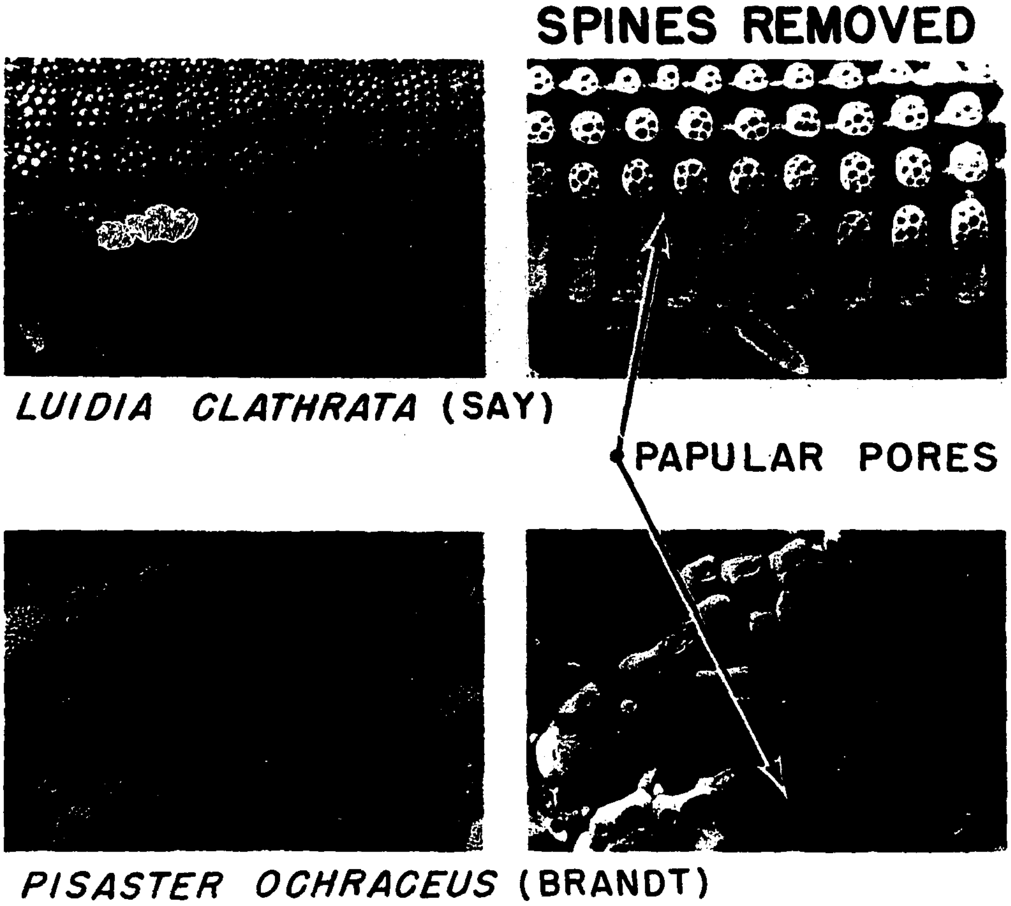
Other than in the ventral buccal area described above, the junction between ambulacral and adambulacral ossicles in Ordovician asteroids appears to have allowed only a slight degree of ambulacral groove closing by the sliding or rotation of adambulacrals on the abradial, ventral end of the ambulacral ossicles. Algor (1971) suggested that the adambulacral ossicles were completely responsible for the closing of the ambulacral groove in many early Paleozoic starfish because he could find no evidence in Petraster speciosus (Miller and Dyer), one of the more common asteroid species of the Richmond rocks to the north and east of Cincinnati, of transverse ventral or dorsal ambulacral muscles to rotate ambulacral ossicles about a common fulcrum and thereby open and close the groove. However, specimen of this species do show a variety of degrees of erection of the ambulacral columns, suggesting that the groove depth was, to some degree, under muscular control. Apparent dentition, which in modern asteroids serves as a hinge about which ossicles rotate under muscular control, is present on the perradial ends of ambulacral ossicles in this species. Such structures are present in all well-preserved Ordovician forms which present appropriate views. Also, many early species, including P. speciosus, show areas on the ventral, perradial ambulacral ossicle surfaces which were likely areas of ventral transverse muscle attachment. Antagonistic dorsal transverse muscles, however, have left no such record of their insertion areas. The maintenance of massive dorsal ossicles by all such early asteroids bespeaks the possibility that the skeletal-muscle system of the dorsal theca performed the flattening of the ambulacral groove accomplished by ambulacral dorsal transverse muscles in modern forms.

In conclusion, the water-vascular system of the Ordovician Asteriadina possessed all the attributes of that of modern members of subclass, except that a longer connective vessel between external podium and internal ampulla was present. This longer connection undoubtedly imposed an inefficiency on the respiratory capabilities of the system which, in turn, may explain the general small size of Ordovician asteroids.

Respiration. -- As indicated and discussed in the previous section, the water-vascular system of asteroids plays an important role in respiration. The remaining gaseous exchange take place through the dermis, or by special external extensions of the coelomic wall termed papulae or "skin gills". These organs protrude between ossicles and into the surrounding seawater. They are protected by spines projecting around them (Text-figure 7). Their internal lumen is continuous with that of the perivisceral coelom and is lined with ciliated coelomic epithelium. In modern paxillose asteroids, the papulae usually emit singly between ossicles and are usually confined to the dorsal surface (Hymen, 1955), but are absent from the central disc and the perradial areas of the bracia. In modern forms with reticulated dorsal skeletons, such as the Asteriidae of the Asteriadina, many papulae protrude from the fleshy area between ossicles and are commonly present on both dorsal and ventral surfaces of individuals.

Papular perforations through the extravascular skeleton are most easily seen in modern species after the protecting spines are removed (Text-figure 7). Ossicles surrounding papular openings in the body wall show, by their arrangement and shape, that such

Text-figure 7. -- Spines in place and removed from dorso-lateral ossicles of examples of paxillose (*Luidia clathrata*) and pustulose (*Pisaster ochraceus*) asteroid species. The papular pores, where outpouchings of the coelomic membrane (papulae) penetrate the remainder of the body wall, show in both examples.


SPINES REMOVED
LUIDIA CLATHRATA (SAY)
PAPULAR PORES
PISASTER OCHRACEUS (BRANDT)

perforations are present. They meet other ossicles with extensions or small accessory ossicles in order to accommodate the papular openings. In asteroids without papulae, or in areas void of papulae on those forms which do possess them, integumental ossicles fit closely together with no sizable holes through the skeletal framework.

From this discussion it may be concluded that an opening through the extravascular skeleton of an asteroid probably accommodated a respiratory papula when the animal was alive. Papulae appear to be supplemental structures developed by asteroids to augment the gaseous exchanges accomplished in large part by the water-vascular system.

Several questions must be answered before taxonomic or paleoecological interpretations may be made for the abundance of papular openings in fossil specimens. It must be determined if increased papular number or size on some members of a species necessarily correlates with oxygen availability in their habitats. Preliminary qualitative results from modern Pisaster ochraceus specimens from high-oxygen and lower oxygen habitats indicates that asteroids from high-oxygen habitats possess less papular area than those from lower oxygen areas. It has yet to be determined if this tendency is more genetically or environmentally controlled. The importance of the dermal papulae in functions other than oxygen exchange must also be determined. As discussed in the following section, phagocytic coelomocytes appear to exit from the asteroid body through the papular openings. Carbon dioxide and other waste gases are also lost to the environment through the papulae. The environmental factors effecting these functions must be determined for asteroids as a whole.

The asteroid hemal system. -- The asteroid hemal system is a plexus of intercommunicating channels in connective tissue. The hemal channels lack epithelial walls (Grasse, Poisson, and Tuzet, 1961), although they are enclosed within coelomic lacunae or channels (Hyman, 1955). The hemal system is commonly referred to as a blood system in asteroids and other echinoderms, although there is no evidence that its fluids actually circulate or are chemically distinct from those of the coeloms.

The axial gland appears to be an enlarged portion of the hemal system in all echinoderms except the holothuroids where it is lacking. Gemmill (1919) noted a pulsation of this gland in young ophiuroids and echinoids and ascribed a pumping or "heart" function to it. Boolootian and Campbell (1964) described a series of contractile compartments within the axial gland, noted the interconnection of the hemal, perivisceral coelom, and water-vascular systems at the axial gland, and suggested that the pulsations within the axial gland serve to transfer fluids between these three systems and to create a one-way circulation within the hemal system. Burton (1964), however, noted only a flow and ebb movement of hemal fluids and ascribed only a local mixing capability to the hemal system. Farmanfarmaian (1968) presented experimental evidence that neither the axial gland or the hemal system plays a significant role in respiration in modern adult echinoids. Hyman (1955) suggests that the axial gland played a greater role in hemal circulation in the past than it does in modern forms. She notes that hearts are usually enclosed in a coelomic cavity and the axial gland of echinoderms is enclosed within the axial sinus, implying that the axial gland is the remnant of an echinoderm heart. There is no paleontologic or zoologic evidence to confirm or deny this hypothesis.

Parker and Cole (1940) point out that there seems to be so much free communication between surrounding seawater and coelomic and hemal fluids that there is little chemical difference between them. Binyon (1972) and Boolootian and Campbell (1964) also made this observation. Subtle differences in potassium concentration do occur within the body fluids of some echinoderm individuals. Watér-vascular system fluid commonly contains more potassium than does perivisceral fluid, which in turn has a greater concentration of this ion than the surrounding seawater (Robertson, 1949). The significance of this potassium gradient has not been explored. The differences in potassium concentration in the respective coelomic systems becomes more intriguing if true confluence of liquids is accomplished at the axial organ as noted by a number of investigators.

Endean (1966) reports that the same kinds of coelomocytes occur in fluids of the hemal channels, the perivisceral cavities, ambulacral vessels and among the body tissues. While the general origins, functions and fates of most of these independently motile cells are unknown, some are known to be phagocytes. This coelomocyte type, which is notably abundant in modern asteroids, ingests particulate matter and moves out the asteroid body via the dermal papulae (Durham, 1887), the madreporite, or the alimentary canal (Liston, 1930).

Since these coelomocytes are not unique to the hemal system, however, it cannot be ascribed an important role as a coelomocyte reservoir or vector system unless it can be documented by a future investigator that coelomocytes are concentrated there or that blocking the hemal system disrupts coelomocyte motility.

Because of its location within coelomic channels, the greater part of the asteroid hemal system does not reflect in the skeletal ossicles. It is, thus, unlikely to leave a fossil record. No worker, however, has considered the reflection of the hemal system in the brachial axial ossicles where there is close contact between hemal channels and skeleton. Cuénot (1887) described and illustrated the paths of hemal channels on the ventral surface of modern asteroid brachia, but did not explore their reflection in the skeleton. Blake (1973) noted an "oral groove" on each ambulacral ossicle extending abradially from the ventral transverse muscle scar, but did not relate it to function or to the hemal system. Neither Schuchert (1915) or Spencer (1913-1940) considered or mentioned the hemal system or its skeletal impressions in their monumental monographas on paleozoic stelleroids. Müller (1953) figured the hemal groove on the ventral transverse ridge of a <u>Metopaster poulsenii</u> Neilsen ambulacral, but did not label or discuss it.

Close examination of the ventral surface of many modern asteroids' ambulacral ossicles reveals grooves in the surface which carry the hemal channels of the living animal.[3] Where preservation is

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adequate, these hemal grooves may also be seen on some fossil Promopalaeasteridae (Plate 15, figure 1a).

The significance of these hemal grooves in both fossil and modern species is difficult to determine, since there is no agreement as to the function of the system to which they belong. All that can be offered here is that specimens of Promopalaeasteridae clearly possessed a hemal system and that its proporations and location on the ventral surface of the ambulacral ossicles seem to correspond to those of modern Asteriidae.

No author has examined the precise histological composition of the soft parts occupying the hemal grooves in various modern taxa. Such a study would be of significance in documenting the paleobiology of fossil asteroids now that the grooves have been recognized in early fossil specimens.

Growth in asteroids. -- Growth is progressive development. It is manifested in asteroids, as in most other animals, by a gradual increase in size and the attainment of characteristics common to normally developed older individuals.

The size of an asteroid may be measured or given in several ways, depending upon the purpose and requirements of the investigation. Mean brachial length (R) is the most commonly used indicator of size among zoologists and paleontologists. Diameter and longest distance between any two arm tips are two other indicators of size

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[3] These hemal grooves in Asterias forbesi are clearly visible along the ridges of the transverse carinae in Text-figure 2.

which have been used occasionally by zoologists. For paleontologists, however, whose specimen material is usually somewhat fragmentary, obtaining the latter two measurements usually involves an extrapolation which seems only to compound errors in already tenuously conceived measurements. Feder (1970) suggested that net weight is a more reliable indicator of individual size than brachial length, because he noted that his consecutive measurements of brachial length in a specimen of Pisaster ochraceus varied more than eighteen percent. In another section of the same paper, however, he notes that a specimen's net weight may increase as much as thirty-four percent during the spawning season. As an asteroid swells with gametes, no major skeletal changes occur, other than a slight spreading apart of the dorsal brachial ossicles. It is clear that for paleontological studies net weight is impossible to obtain, and radial length is the more dependable indicator of size that can be obtained from a variety of specimens. This author has found that methodical measurement of brachial length in living and preserved specimens of several species, including P. ochraceus, reduces differences between consecutive measurements to about five percent. All that is required for this accuracy are a flexible ruler and consistency of measuring procedure.

Mead (1900, 1901) established, with documentation, several important principles in regards to asteroid growth and maturity. He found that, contrary to the conclusions of A. Agassiz (1877), size is not a reliable indicator of age in asteroids. Food availability and suitability determine the size attained and rate of growth of an individual. Furthermore, sexual maturity seems to be a function of size and not age. Mead found that most individuals of A. forbesi, the asteriadinid from which he obtained nearly all his data, achieve sexual maturity when they achieve a particular size, whether this is during their first year or later.

Galtsoff and Loosanoff (1939) arrived at many of the same conclusions as did Mead, with their work on the same species. Their data is more exhaustive, however, and offers important information in regards to ecological range and size distribution of this carnivorous species. Distribtuion and individual size is influenced primarily by the availability of appropriate food; where food is abundant, asteroid density is highest and mean individual size is greatest. Overall, however, about 70 percent of the individuals obtained in sampling grabs are of medium size; that is, when a number of specimens are collected in any one area at one time, most are neither extremely small or large individuals as compared with the remainder of the sample. Samples from different areas may be expected to show some variation in mean individual size because larger individuals are concentrated in some areas due to an abundance of food. Paine (1974) has confirmed this phenomena in Pisaster ochraceus and has even found a correlation between mean asteroid size and mean prey size in a given area. These findings may explain why all fossil specimens known from each multi-occurrence situation are of approximately the same size.

Paine (1969) suggests that Pisaster individuals have a seasonal migration, spending the winter months in the subtidal and summer months in the intertidal zones. Should there be a concomitant difference in mean individual size in this asteriadinid, or any other migratory species, there is the possibility of the selective preservation of the winter size class, since preservation potential is somewhat higher in the subtital. Galtsoff and Loosanoff, on the other hand, report the absence of seasonal migrations in A. forbesi. Preservational bias, in this case, may be introduced if appropriate food (and thus larger individuals) are concentrated in areas of higher preservation potential.

Few kinds of changes, other than a general increase in size, which take place in the asteroid skeleton as it grows have been well documented. Yet, understanding these changes is important to paleontologists who must be able to recognize developmental stages of species as such, and not relegate them to separate taxa. For example, without verification that such characters had real systematic significance among the asteroids, Schuchert used total number of adambulacral ossicles in each column and the number of adambulacral pairs involved in the adoral carinae as diagnostic characteristics of some of his "species" of Promopalaeaster. As indicated by the following data, both of these characters change during the ontogeny of asteroid species. To be meaningful, any reference to them must be given in terms of animal size. It is not unusual to find fossil asteroid species which have been distinguished from their contemporaries solely on the basis of characteristics which, in modern species, demonstrably change during ontogeny. The validity of some of these Ordovician species is challenged in the systematic sections which follow in this report.

Nearly all available information on asteroid ontogeny has precipitated from embryological studies. Asteroids offer excellent materials for the study of larval ontogeny and for years have been the subjects of numerous investigations. By convention among embryologists, however, the end of echinoderm larval development is signaled by the origin of the first skeletal ossicles. Only a few embryologists have continued their investigations of developing asteroids into those stages with hard, preservable parts. Fewkes (1889) examined the developing stages of *Asterias vulgaris* Sladen and documented the time and position of primary ossicle first occurrence. Gemmill (1914) did the same for *Asterina rubens* Linné and Ludwig (1882) for *Asterina gibbosa* (Pennant), but each of these latter studies dealt only with soft-part development. Gordon (1929) traced the very early hard-part development of *Leptasterias* and contrasted development in the genus with that in genera investigated by Fewkes, Gemmill and Ludwig. None of these studies has generated information directly applicable to paleontologic material because the ontogenically least developed fossil asteroid known is more mature than any specimens these authors describe.

Birkeland, Chia and Strathmann (1971) offered data on substratum selection, timing of metamorphosis and growth rates in juvenile and adult *Mediater aequalis* Stimpton, but stopped short of morphological documentation useful to skeletal ontogenists. Using weight gain, Feder (1970) documented growth rates for *P. ochraceus* under natural and aquarium conditions. Neither of these articles make allusion to growth characteristics readily usable by paleontologists. In fact, any study of ossicular development from early junvenile through geratic stages seems to be completely wanting in the zoological literature.

Rasmussen (1965) obtained some useful results concerning the gross structure of three species of Henricia. While his findings within this genus cannot be extended to all genera, they make known some kinds of growth phenomena possible within the subclass. He found, from quantitative data, that mean spine number per ossicle on inferomarginal, superomarginal and adambulacral ossicles increases with mean brachial length. His data also indicates that although R/r generally increases during growth, there is much variation within species, especially in larger specimens. There is also considerable overlap between species. He attributes these phenomena, in part, to seasonal differences in gonad development. This results in differences in disc, but not brachial length, measurements. In fossils, however, the reliability of r measurements as indicators of animal size or proportions should be suspect. Distortion occurring during or after burial may drastically alter this parameter in forms without rigid skeletons. Brachial length may also be altered somewhat, but the firmness with which consecutive ambulacral and adambulacral ossicles are held together by interossicular muscles somewhat reduces such preservational distortion.

Other changes occurring during asteroid growth may be deduced from observations on suites of modern species. Understanding these phenomena requires only some general knowledge on the mechanisms of asteroid growth.

First, ossicles of a growing asteroid remain contiguous during thecal enlargement. This is necessary to keep short muscles between adjacent ossicles.[4] As the theca enlarges, close contact between ossicles is maintained either by the increase in size of the ossicles already present, or the addition of new ossicles between formerly adjacent ones. Both phenomena are generally occurring in an asteroid skeleton whenever growth is taking place.

As radial length increases in an asteroid, new ossicles are added to each brachial column. Primary column ossicles are added only in an area just proximal to the enlarged, most-distal median dorsal (terminal) ossicle of each brachium.

New columns of secondary brachial ossicles are added in generative zones between pre-existing columns as brachia increase in diameter. The location of these zones depends on taxon and the type of secondary ossicle being added. In asteroids with non-reticular extrathecal skeletons, these zones occur in longitudinal bands at the edges of the ossicle field being generated. In reticulated asteroids,

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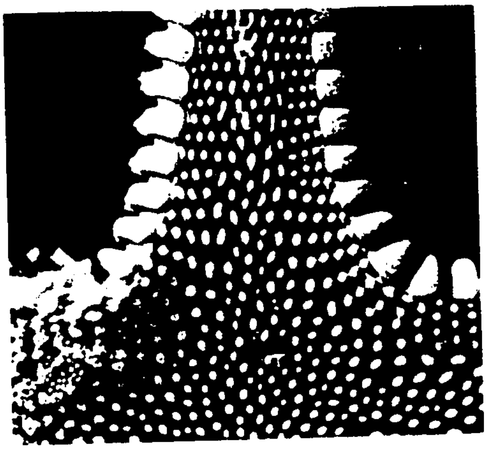
[4] Asteroids possess short muscles between their thecal ossicles. Morphological and physiological short muscles are not fast muscles, but they are usually quite strong and always very durable. Free-living, non-testaceous marine epifauna must be either quick or strong to survive. Asteroids are slow movers, but they are strong and durable.

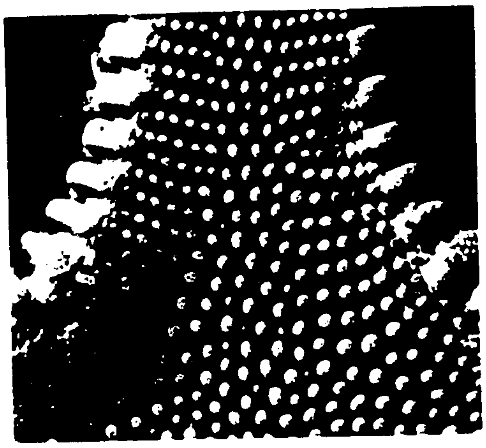
articulation of new secondary ossicles does not appear to be limited to specific zones. Verrill (1914) has argued that increase in ossicle column number not only increases internal brachial volume for the accommodation of gastric caecae and gonads, but it also provides for greater arm flexibility than would be possible with simple enlargement of ossicles already present. He considered this character an important development in the evolution of the Asteriidae. Other groups of asteroids, however, practice this method of brachial volume increase as well. Most paxillose forms, typified by Astropecten californicus Fisher (Text-figure 8) also grow in this manner. It is noteworthy that many such asteroids possess rigid, rather than flexible brachia. Scatter diagrams (Text-figure 9C) show that there is a greater rate of increase of interdorsal ossicle number proximally than distally in this latter species. This is probably because arm widths become suddenly greater at the brachial bases in this species; the interdorsals must become more numerous to maintain a flexible dorsal skeleton. Heddle (1967) has proven the absolute necessity of a flexible dorsal skeleton in the astropectinid life style. While the arms of these asteroids do not flex from side to side, it is necessary that the dorsal surface remain flexible because it is thrown into plicated folds as the animal digs into the substrate.

Another scatter diagram (Text-figure 9A) indicates that there is not a perfectly linear relationship between radial length and number of ossicles in each perivascular or extravascular column. This is readily explained by two factors. First, as mentioned

Text-figure 8. -- Dorsal aspect of interdorsal ossicles of the modern paxillose species Astropecten californicus. The spinelets have been removed to show thecal ossicles. Specimen A (R = 22 mm.) shows fewer columns of interdorsals at the arm base that specimen B (R = 36 mm.). Note also that the larger specimen possesses larger ossicles in comparable thecal areas.

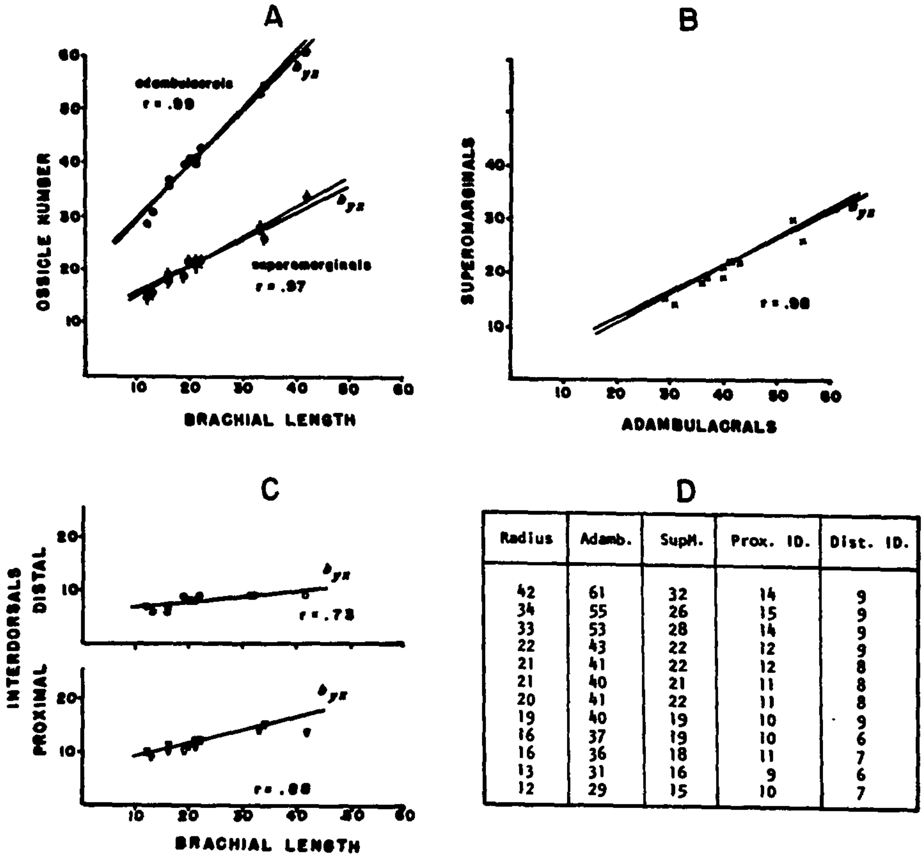


A



B

Text-figure 9. -- Scatter diagrams of data obtained from a sample of *Astropecten californicus* Fisher from a dredge haul off Santa Catalina Island, California (*A*) Adambulacral (perivascular) and superomarginal (extravascular) number plotted against brachial length. Both calculated regression lines drawn in; regression of ossicle number axis on length axis labeled b_{yx}; r = coefficient of correlation. (*B*) Superomarginal number compared with adambulacral number; abbreviations same as for *A*. (C) Interdorsal column number at arm base (proximal) and at mid-length plotted against brachial length; same abbreviations. (D) data. Increased size clearly indicates increases in ossicle numbers.



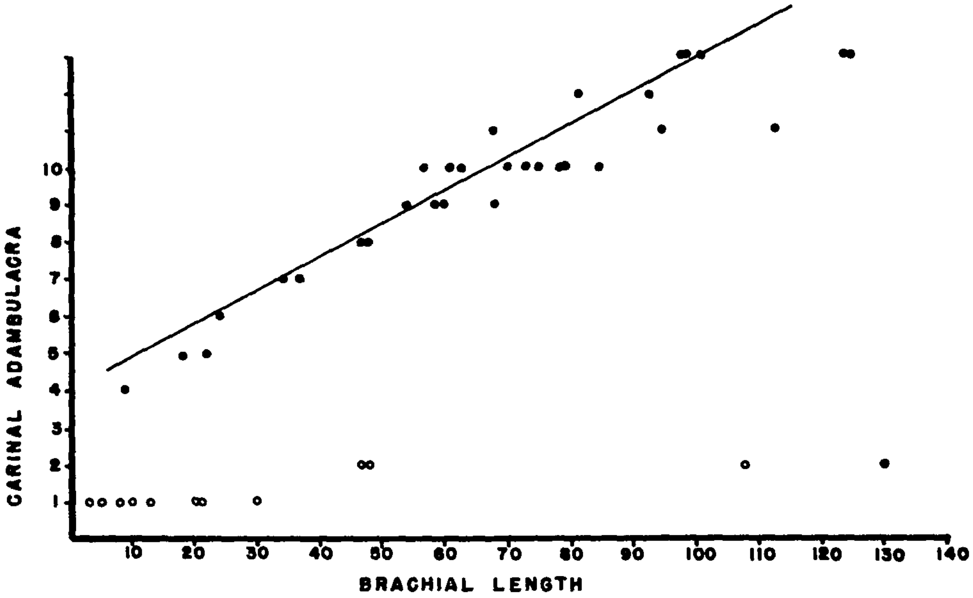
Radius	Adamb.	SupM.	Prox. ID.	Dist. ID.
42	61	32	14	9
34	55	26	15	9
33	53	28	14	9
22	43	22	12	9
21	41	22	12	8
21	40	21	11	8
20	41	22	11	8
19	40	19	10	9
16	37	19	10	6
16	36	18	11	7
13	31	16	9	6
12	29	15	10	7

above, preexisting ossicles generally grow allometrically as the animal grows. Next, there may well be some geratic modification. In the largest individuals, column ossicle number increase does not maintain its established rate relative to brachial length increase.

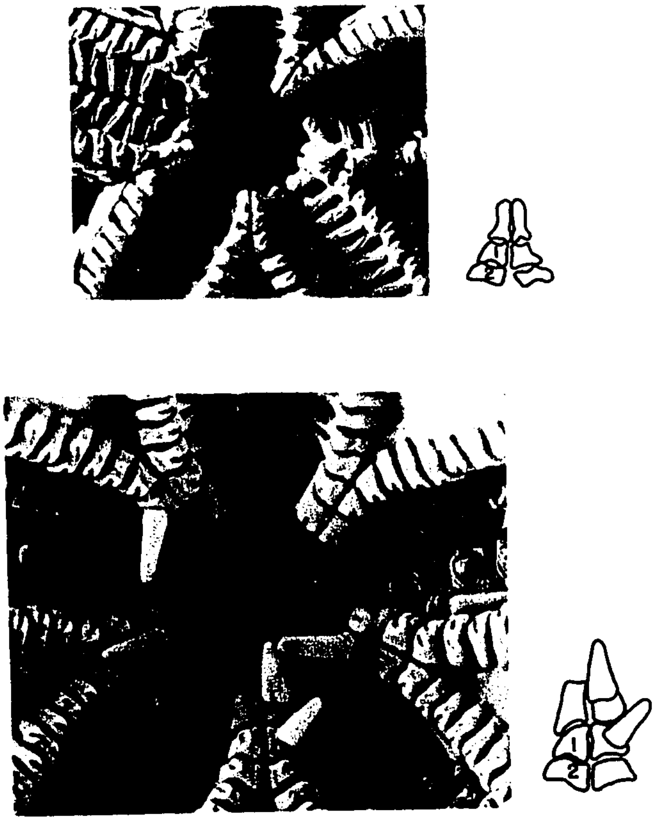
There also appears to a relationship betwen perivascular column ossicle number and extravascular column ossicle number; as one increases, so does the other (Text-figure 9B). When plotted against the brachial length, these individual increases are seen not to occur at the same rate (Text-figure 9A). Again, the slope of the relationship in larger individuals appears to differ from that in smaller individuals. Therefore, it is impossible to characterize the species examined in terms of a single, simple expression which defines the numerical relationship between perivascular and extracular column ossicle number, because this changes during ontogeny. Many such expressions are necessary to charactrize a species in all stages of individual development. A notable exception to this, of course, would be a taxon in which there is a consistent one-to-one (adaxial) ratio between perivascular column ossicle number and extra-vascular column ossicle number. As described in a following section, this occurs and is a diagnostic characteristic of Ordovician Mesopalaeasteridae.

Graphic evidence from data obtained from _P. ochraceus_ (Text-figure 10) and illustrative evidence from _Asterias forbesi_ (Text-figure 11) prove that, at least among some asteriadinid species, adambulacral ossicle pairs involved in adoral carinae increase in number as animal size increases. The pattern of points in Text-

Text-figure 10. -- Scatter diagram showing near linear relationship between mean number of adambulacral ossicle pairs involved in the adoral carinae of two species and their brachial lengths. Solid circles represent individuals of *Pisaster ochraceus*; hollow circles represent *Orthasterias kohleri*. The calculated regression line is shown for *Pisaster*.


CARINAL ADAMBULACRA
1
2
3
4
5
6
7
8
9
10
BRACHIAL LENGTH
10
20
30
40
50
60
70
80
90
100
110
120
130
140

Text-figure 11. -- Oral ossicles (ventral aspect) of a small (R = 6 mm.) and a larger (R = 36 mm.) specimen of the same species. Adoral carinae of smaller (upper) specimen composed of adnate first adambulacral pairs only. Carinae of bottom specimen involves first and second adambulacral pairs.



ASTERIAS FORBESI (DESOR)

figure 10 indicates a near linear relationship between these two parameters in P. ochraceus. Another species in another genus is also shown on the same graph. Orthasterias kohleri never develops long adoral carinae. It is interesting to note that these parameters in two other species of Pisaster fall within the pattern established for P. ochraceus. All three species of Pisaster and O. kohleri have somewhat overlapping ecological ranges. From this evidence it appears that the differences in the slope of data plotted in Text-figure 10 is at least of generic significance. Further research on this problem is currently in progress by the author.

Several principles in regard to adoral carinae are adhered to in the taxonomy of Ordovician asteroids considered herein. The number of adambulacral ossicle pairs in an adoral carina is, in itself, useless as a realistic taxobasis. The number of adnate adambulacral pairs in individual carinae depends on the size of the individual as well as its taxon. Within asteroid species there seems to be a close relationship between brachial length and number of adnate adoral carinal ossicle pairs. A sizeable deviation from this linear relationship probably indicates at least generic differences between specimens.

The principles of asteroid growth discussed above must be taken into account in the paleobiological re-evaluation of Cincinnatian asteriadinids. Taxonomic revision, in light of these principles, must synonomize species which can be morphologically distinguished only on the bases of characters which are likely to be mere ontogenic differences.

Feeding ethology and form. -- Various authors have compiled information from the literature or added new data on food resources and feeding habits of modern asteroids. Hyman (1955) and Feder and Christensen (1966) have reviewed the literature and published sizable accounts of known or implied food sources of various species. Carey (1972) added considerable information on the stomach contents of sublittoral, bathyal, and abyssal asteroids to the end of establishing a correlation between food resources and habitat depth. More direct data on asteroid feeding was offered by Mauzey, Birkeland and Dayton (1968) as they reported on an extensive series of direct observations by SCUBA divers on asteroid feeding. Rasmussen (1965) reviewed the literature on the feeding habits of Henricia Gray and documented that some members of the genus practice suspension feeding, at least to some degree. He failed, however, to relate the suspension feeding habit to any preservable skeletal feature.

It is usually possible to classify a species' feeding ethology into either stomach-everting or wholistic swallowing. Some genera, such as Patiria, practice both types of feeding, although individuals ingest only small food particles and most commonly practice typical stomach-everting. Other genera, such as Henricia, have species which practice suspension feeding in addition to the usual stomach-everting. Most genera, however, seem to be restricted to a particular feeding type; it is noteworthy that their skeletal structure reflects their feeding ethology.

Only a few authors have shown an interest in skeletal form and feeding ethology in asteroids. Spencer (1922) contrasted the structure of the ophiuroid mouthframe with that of the asteroids. He found an important correlation between the stomach-everting feeding habit of some asteroids and body form. He noted that modern asteroids with so-called "ambulacral" mouthframes[5] are stomach-everters. He suggested that asteroids with an ambulacral mouthframe possess a fixed mouth aperature size and, thus, must extrude their stomachs if they are to take advantage of large food particles. Spencer further noted that this type of asteroid typically has especially large digestive glands, a character which he believed complemented the practice of extrathecal digestion.

Much digestion is accomplished outside the body by stomach-everters. Digestive fluids are secreted from the everted cardiac stomach when it comes in close contact with potential food. Only digested nutrients and minute particles of food are taken into the theca. There they are routed from the proximal pyloric stomach to the pyloric caecae. These latter organs are what Spencer referred to as "digestive glands". They are located in the dorsal part of the perivisceral coelom of each arm (Meglitsch, 1967).

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[5] The relative prominence of the mouth-angle ossicle pairs and the most-proximal ambulacral ossicle pairs in a specimen has been the basis of its mouthframe being termed "adambulacral" or ambulacral". In most conventional taxonomic schemes, mouthframe types is used as an ordinal taxobasis.

A stomach-everter must maintain close contact between the walls of its cardiac stomach and the food it is digesting, because digestion is accomplished at the interface between food and stomach, and not in a "pool" of digestive fluids (Anderson, 1966). In modern asteroids this close contact is accomplished by means of suckered tube feet holding the food close to the oral area. An important relationship exists between the number of podial columns on a brachium and feeding habits. All Asteriidae possessing four columns or more of tube feet per brachium practice the stomach-everting feeding habits of Pisaster, Asterias and Evasterias (Feder and Christensen, 1966). These animals grasp their prey firmly with their suckered podia arch over it, and insert their stomachs through any gape in their prey's defenses. Tensional force exerted by means of the many rows of attached, suckered podia is used where necessary to achieve a gape suitable for stomach insertion. The usual prey is bivalves, although these animals also remove sessile organisms such as tubiculous annelids, barnacles, chitons and limpets from their substrates, press them against their oral areas and consume them. This author has been unable to find evidence, either in the literature or in the field, that any asteroid with more than two podial columns in each brachium is not primarily a stomach-everting feeder. There are asteroids, such as Patiria, Dermasterias, Mediaster and Psilaster, which sometimes evert their stomachs, but possess only two podial columns in each brachium, and others with two podial columns which never evert their stomachs; thus, two columns is not indicative of a particular feeding ethology.

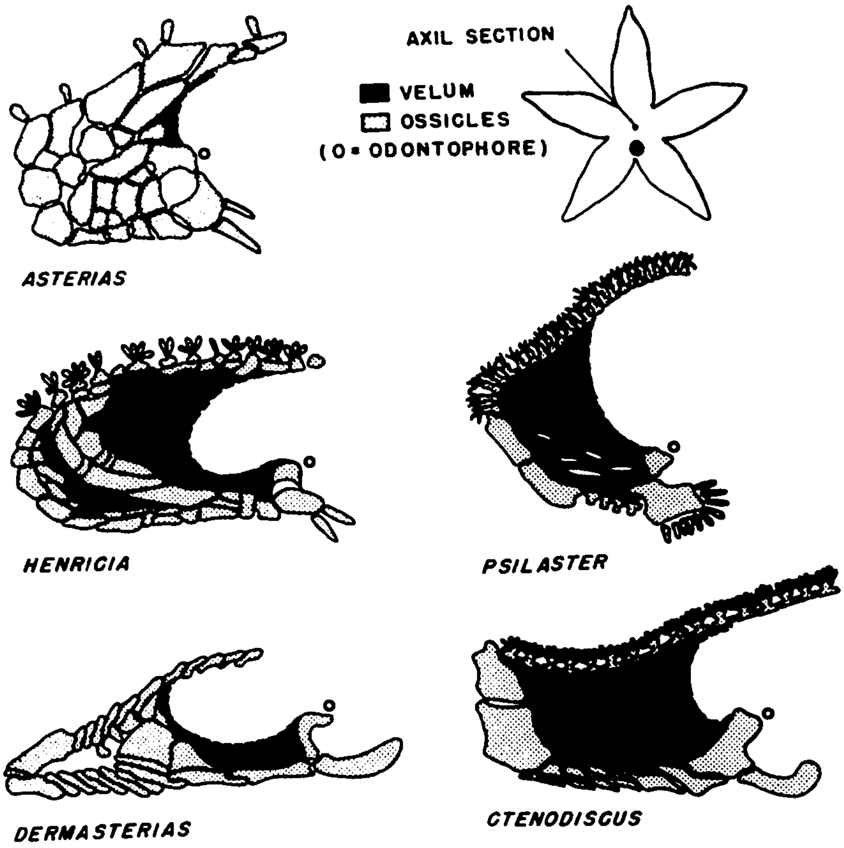
Four or more podial columns in each brachium, on the other hand, seem to be indicative of the stomach-everting habit in an asteroid.

Although not previously noted as such, another potentially preservable skeletal character proves useful in determining the feeding ethology of modern asteroids. This characteristic, commonly inferable for fossil species, is the degree to which the interradial septal ossicles occlude the internal disc (Text-figure 12). Viguiér (1878) figured this area of the skeleton for many of the species he examined, but did not make the connection between feeding habit and form. A thorough understanding of how interradial skeletal structure correlates with mode of feeding requires an understanding of the functions of the various mouthframe ossicles.

An odontophore is located between and slightly dorsal and distal to the paired mouth-angle ossicles in each oral interradius. It may be visible on the ventral surface of the animal and carry articulating spines, as in the less complex Ordovician forms, or it may be entirely internal as in the Promopalaeasteridae and most modern species. It is connected by separate muscles to the internal surfaces of each of the paired mouth-angle ossicles in its interradius. The distal end is always connected to ossicles of the adjacent marginal frame either by a long muscle or by a train of ossicles connected by short muscles.

In modern asteroids and the Promopalaeasteridae among Cincinnati forms, the proximal wings of each odontophore contact the distal dorsal surfaces of the adjacent mouth-angle ossicles (Plate 13, figures 3 a,b). The main body of the ossicle lies between the most-

Text-figure 12. — Interbrachial occlusion in some modern asteroids. Explanation in text.


AXIL SECTION
■ VELUM
☐ OSSICLES
(O = ODONTOPHORE)
O
ASTERIAS
HENRICIA
PSILASTER
DERMASTERIAS
CTENODISCUS

proximal buccal podial perforations through the adjacent ambulacral columns. This first podial perforation occurs on either side of the ambulacral tract as a result of the apparent fusion of the most-proximal two ambulacral ossicles in each column.

The first two ambulacral ossicles of other Cincinnatian asteriadinid families do not appear to have been fused, but no known specimen offers absolute proof of this. The same positional relationships exist among the odontophore and the adjacent mouth-angle ossicles and most-proximal ambulacrals, however. A long muscle connects the odontophore to the adjacent ventral interbrachials, marginal frame and interbrachial dorsal ossicles in modern asteroids, such as Astropecten and Ctenodiscus, which swallow their prey whole or practice mud swallowing. This muscle lies close to the body wall, commonly as part of a soft septum which divides the disc volume into five sections, each openly confluent with the internal cavity of one of the brachia. The skeletal structure is entirely peripheral; that is, it does not, itself, participate in the subdivision of the internal disc volume.

Asteroids, such as Asterias, which always practice extrathecal digestion by means of stomach eversion, maintain heavily ossified connections between the odontophore and the dorsal interbrachials. These internal interbrachial ossicles are connected by muscles capable of shortening the entire occluding structure by pulling the individual ossicles closer together. This pulls the odontophore distally, or dorso-distally, and pulls the ventral surface closer to the dorsal surface. Spencer (1922) noted that this former action serves to open the mouthframe. The latter action effectively decreases the volume of the visceral cavity.

How these two basic plans of organization make possible the feeding mechanisms of the individuals which possess them is clear. Asteroids which ingest food cannot occlude their food vestibule with relatively rigid and massive skeletal structures between ventral and dorsal surfaces. Some mechanism, however, must be maintained to assist in opening the oral frame; such is the function of the long muscle adnate to the body wall in most wholistic swallowers. Asteroids which evert their stomachs exclusively in feeding need not maintain a large, unobstructed vestibule between ventral and dorsal surfaces in the oral area. These animals must, however, maintain a mechanism for opening their mouth and some mechanism for stomach eversion. The dorso-distal movement of the odontophore by means of its muscular connection to the train of interbrachial ossicles provides the former capability. The same strong connection between ventral and dorsal surfaces allows a forceful reduction body cavity volume by bringing dorsal and ventral body walls closer together. This increases internal hydrostatic pressure which pushes the stomach out of the mouthframe.

Animals, such as Henricia and Dermasterias, which are not wholely dependent on one or the other modes of feeding possess interbrachial structures which can accommodate both feeding styles. The internal vestibules are not wholely occluded with skeletonized septa, yet there is some ossified structure in each interbrachium which allows the utilization of short, durable muscles to forcibly evert the stomach.

The degree to which the interbrachial areas of the disc were occluded in fossil forms should be determinable from specimens which show sections through the interbrachial areas, or from reasonably complete specimens which show some collapse of the dorsal skeleton into the disc area during or after burial. In the latter cases, animals without ossified interbrachial septa collapse interadially, while animals with strongly ossified interbrachial septa do not so collapse.

Using the above established criteria, Cincinnati Asteriadina seem to have been stomach-everters, because all specimens which show appropriate aspects seem to show occluded interbrachial septa.

Burrowing asteroids and Cincinnati "Asteriacites". -- The paleobiology of burrowing fossil stelleroids is better understood when the incidence and role of burrowing in modern echinoderms are explored. Negative phototropism and positive geotropism are the two most commonly given reasons in the literature for echinoderm burrowing. Crozier (1915) concluded that burrowing in the holothurian Holothuria surinamensis Ludwig, is a negative phototropism because the species is found on the substrate at night, but burrows during the daylight hours, and more deeply during daylight low tides. A positive geotropism is usually given by authors to explain burrowing by spatangoid and clypeasteroid echinoids, but Binyon (1972) points out that the experimental proof is wanting.

The burrowing habit is not especially widespread in ophiuroids or asteroids (Reese, 1966). Binyon (1972) claims that the ophiuroid

Amphiura chiajae digs in response to its negative phototropism. Some species of the asteroid genus Luidia and most species of Astropecten move with a diurnal rhythm, living part of the day just beneath the surface of the sand in relatively shallow water. Burla et al. (1972) documented that Astropecten aranciacus (Linne) is a nocturnal Mediterranian species which forages at night, but remains buried during the day. Mori and Matutani (1952) found that A. polyacanthus Muller and Troschel moves out of the substrate twice daily, once in low-intensity morning light and once in low-intensity evening light. Specimens continue such movement when experimentally isolated in total darkness; this indicates the presence of a circadian rhythm. Thus, the timing of this movement may have been fixed within the species in direct response to some stimulus other than light, such as the presence of a predator or potential prey species whose own movements are influnced by the availability of light. Mori and Matutani also documented that the time this asteroid spends in activity of the surface is longer in animals which have been deprived of food; this suggests that feeding is accomplished while out of the substrate in this burrowing species. This can be contrasted with the holothurian behavior observed by Reese (1966) in which feeding nearly always occurs as specimens burrow. Pisaster brevispinus (Stimpson) is an asteroid which digs only in response to the occurrence of a prey bivalve beneath the substrate surface. This species is able to locate itself over its prey and dig down to it. Smith (1961), who first reported digging behavior in this species, does not consider its activity as true burrowing, because after the seastar has its prey, it returns immediately to the surface before consuming it. P. brevispinus is thus an epifaunal animal which ventures into the substrate; it does not use the substrate as a domicile. It appears, therefore, that regardless of the initiating stimuli involved, truly burrowing asteroids (by definition) utilize the substrate primarily as a place of refuge, rather than as a hunting or feeding ground.

The role of Cincinnatian Asteriadina in the origin of stellate cubichnia found in Maysville and Richmond strata can now be explored. Osgood (1970) has cautioned that extreme care must be exercised in making specific assignments as to the subclass which produced these obviously stelleroid traces, but suggests that traces found in the Cincinnati Area were formed by an asteroid, "possibly Promopalaeaster Schuchert (1914), which is a Maysville and Richmond form and is of the same general size and shape as Asteriacites stelliforme".

Miller and Dyer (1878) supposed that their trace fossil Heliophycus stelliforme from Maysville rocks in Cincinnati represents the impression of a stemless, star-like plant. J. F. James (1885) recognized the trace as having been formed by an asteroid such as Palaeaster[6],

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[6] Palaeaster Hall was the generic name of all known Cincinnatian species in James' time. This includes those species later included by Schuchert in his genus Promopalaeaster.

that striations on the radial extensions of the stellate, convex hyporeliefs represented imperfect impressions of ventral ossicles. Seilacher (1954) documented, through experiments with modern asteroids, that such rugosities reflect the activities of the tube feet. He placed *H. stelliforme* in synonomy with *Asteriacites lumbricalis* Schlotheim, cubichnia Seilacher attributed to ophiuroid burrowing activity. Osgood (1970) accepted Seilacher's interpretation concerning the tube feet markings but preferred not to attribute the Cincinnatian traces he called *Asteriacites stelliforme* (Miller and Dyer) to an ophiuroid origin. He felt this trace sufficiently different from *A. lumbricalis* and *A. quinquefolius* (Quenstedt, 1876), the trace species which Seilacher promotes as having an asteroid origin, to be retained as a separate ichnological species. According to Osgood, *A. stelliforme* has broader arms that *A. lumbricalis*, and chevron-shape straiae on its arms. This latter species does not appear to possess any distinctive, uniform arm prosopon. *A. quinquefolius* has even broader arms, and tube feet markings have a "shaggy" appearance.

An important point which seems to have escaped previous investigators must be emphasized here. That is, whatever the precise morphology of the podial traces, the outer-most (lowest) surface of a complete convex hyporelief shows marks made by a stelleroid at the bottom of its dig. They are marks of interring activity or activity associated with clearing material from beneath the body. Podial features within the hyporelief, whether exposed by cross-sectioning or spalling, are marks left by the organism exhuming itself. When a body fossil is not located at the bottom of stelleroid cubichnia, both kinds of digging activity must have occurred.[7]

Osgood appears to have been the last investigator to examine Cincinnatian _Asteriacites_, and his work is the most comprehensive on these trace-fossils. He recognizes two forms of striae on the three reported specimens. The type specimen (Harvard Botanical Museum no. 3175) from Maysville rocks in Cincinnati and the specimen from the Corryville Shale "Member" of the McMillan "Formation" at Stonelick Creek east of Milford, Ohio (UCGM no. 37599) possess

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[7] Little literature is available on the methods used by burrowing stelleroids to exhume themselves from their burrows. Forms with rigid bodies, such as is the case for most recognized burrowers, may reverse the action of their podia, or make strike off obliquely toward the surface. In addition to these methods, pliably bodied forms may alternate upward digging of the brachia with flexing the body upwards, as Smith reports of _Pisaster brevispinus_. Unless the substrate recently disturbed as the asteroid interred itself offers less resistence to the exhuming animal than the surrounding substrate, there seems no reason why a stelleroid should follow precisely this former path to the surface. If a stelleroid does change its course from its interring path, "digging in" and "digging out" burrows with distinctive characteristics are possible for each burrowing species.

chevron-like striae on their arms. The apex of each chevron is on the midline and points proximally. Osgood analogizes these striae with those on Rusophycus (interpreted as trilobite cubichnium), but reasoned that a digging stelleroid has to make its interring strokes from midline to margin in order to remove sediment from beneath its body, rather than toward the midline and to the rear as in Rusophycus. This functional model for a digging asteroid is substantiated by Heddle's (1967) observations of Astropecten irregularis, one of the many sand-dwelling asteroids with biserial, non-suckered podia. Heddle shows that in the interring action of this species, the tube feet of each side of the arm are protracted and bent laterally outwards from the midline. They are then withdrawn from their lateral positions and the cycle is repeated. Smith (1961) reports that Pisaster brevispinus digs bivalve prey from gravel and coarse sand by pushing sediment distally with its tube feet, rather than laterally as do the truly burrowing asteroids. This species has suckered, quadriserial podia, but Smith emphasizes that suckers are not used to grasp sediment particles and that the podia experienced difficulty in moving fine particles.

A specimen (UCGM no. 37674) of A. stelliforme of uncertain stratigraphic placement or locality does not possess chevron-shape striae. Rather, striae run transversely across each arm from margin to margin. Each striation is noticably wider and more prominent than those of the other known Cincinnatian specimens.

The two types of tube feet striations common to the Cincinnati specimens and the analogous "shaggy" markings on A. quinquefolius indicate differences in digging ethology among their respective excavators. These differences may, but do not necessarily, indicate that distinct asteroid taxa made each trace type. Such digging behavior differences could be due to differences in substrate firmness, direction of digging, or behavioral variations within the same species.

Osgood was correct in his suggestion that *Promopalaeaster* specimens of appropriate sizes to have made *A. stelliforme* are known from Maysville and Richmond rocks. Such is also the case, however, for a number of ophiuroids and species of *Mesopalaeaster*, *Salteraster* and *Lanthanaster*.

Shape is also useful in the search for diggers of *A. stelliforme*. Seilacher (1953) models the origin of stellate cubichnia of various shapes formed by both asteroids and ophiuroids. He suggests that broad-armed cubichnia can be formed by both asteroids (which typically possess broad brachia) and ophiuroids which wriggle their narrow brachia in a horizontal plane as they dig, thus producing arm depressions in the sediment which are broader than their brachia. An interring ophiuroid, digging in such a manner, could not have produced *A. stelliforme*. Such brachial movement would frequently displace an organism's axial plane, and thus disrupt the formation of regular chevron-shaped striae. At least the specimens of *A. stelliforme* with chevron-shaped striae reflect their excavators proportions more faithfully than could be supposed from Seilacher's models.

No available evidence precludes the possibility that the other Cincinnati specimen, with its same general proportions, but longer and broader striae not arranged in chevrons, was formed by an opiuroid interring or exhuming itself in the wriggling manner described above. The tube feet of ophiuroids are usually thinner, but no less extensible, than those of asteroids, even though there are no intrabrachial ampullae in the former subclass. Nichols (1972) recently concluded that ophiuroid radial vessels and proximal portions of ophiurod tube feet function, in part, as fluid reservoirs analogous to the intrabrachial amplullae of asteroids; a large or bulbous ampulla, therefore, is not required as part of a podium capable of great extension or diameter. Ophiuroids present in Cincinnatian strata have open radial channels, a fact which may support the extension of Nichols' conclusions to these species and to stellate cubichnia with long, transversely disposed striae which are not arranged in chevrons. It is also possible, however, that this third Cincinnatian specimen does not show the bottom-most part of the burrow, but rather represents a section through an exhuming burrow of the same species which formed the two traces with chevron-shaped striae.

A third burrow type, A. quinquefolius, has not yet been found in the Cincinnatian. From Seilacher's photograph (1953, pl. 10, fig. 1a) it is clear that the "shaggy" appearance of this species results from fillings of depressions caused by tube feet being pushed into, rather than dragged across, the substrate. The long axes of the impressions lie longitudinally on the arms, indicating that, in their roles as sediment movers, the tube feet moved material proximally or distally. This is similar to the digging behavior in

P. brevispinus, the bivalve-digging modern asteroid. Thus, it may not be incidental that the *A. quinquefolius* trace figured by Seilacher is on the holotype slab of the bivalve cubichnia *Pelecypodichnus amydgaloides* Seilacher.

Three major forms of *Asteriacites* have herein been discussed and functional models have been proposed for an interpretation of each. Characteristics of Asteriadina known to occur in Cincinnatian strata must now be compared with these models in order to determine if the Cincinnati traces could possibly have been formed by members of this suborder.

The temporally unique characteristic of *Promopalaeaster* was its quadriserial podial condition. Unfortunately, burrow structures comparable to those known from fossil traces have not been reported for any modern asteroid with quadriserial podia. Thus, the influence of the quadriserial podial condition on stelleroid burrows is not known from data. Some inferences may be made, however. This author considers the podial condition of *Promopalaeaster* to be an adaptation for increasing respiratory surface area and ability to hold potentially motile prey to its buccal area by means of additional rows of suckered tube feet. Evidence presented elsewhere herein supports these conclusions. Suckered podia also permit asteroids to move and climb on substrates with firm, irregular surfaces. Such is the usual habitat of modern asteroids with such podial arrangement. Most reported burrowing asteroids (Text-figure 13) live in or on soft substrates and possess biserial, nonsuckered podia. The Cincinnati *Asteriacites* are found in calcareous mudstones generally believed to have been

Text-figure 13. -- Burrowing and digging asteroids reported in the zoological literature or observed by the author.

SPECIES	PODIAL COLUMNS	PODIAL TERMINUS	SUBSTRATE	PAXILLAE	REFERENCES
Astropecten araniacus (Linné)	2	pointed	sand, silt	yes	Burla, et. al., 1972
Astropecten polyacanthus Müller & Troschel	2	pointed	sand, silt	yes	Mori & Matutani, 1952
Astropecten marginatus	2	pointed	sand, silt	yes	Kenk, 1944
Luidia clathrata (Say)	2	pointed	sand, silt	yes	Author
Psilaster charcoti (Koehler)	2	pointed	sand, silt	yes	Author
Pisaster brevispinus (Stimpson)	4	suckers	rock, gravel	no	Smith, 1961

a soft bottom during sedimentation. Thus, if the podial condition of Promopalaeasteridae is correctly assessed here, individuals of this family were not adapted to the substrate common to Asteriacites. It is unlikely that Cincinnati stelleroid cubichnia were formed by species of Promopalaeasteridae.

Cincinnatian specimens belonging to Mesopalaeasteridae are also of an appropriate size and shape to have produced the burrows in question. And, as documented in the following section, they possessed biserial podia for their arm lengths. This latter condition is similar to that of bona fide modern asteroid burrowers. But Mesopalaeaster was a stomach everter; this habit is uncommon in burrowing asteroids. Furthermore, Spencer (1922) observed that asteroids which spend much time within the substrate possess paxillar dorsal ossicles. The absence of this ossicle type in any Cincinnatian asteriadinid is evidence that none were burrowers, and are thus not responsible for A. stelliforme.

On the basis of the evidence presented from modern asteroids, other genera known from Cincinnati have attributes which make them likely to be responsible for stelleroid burrows there. Both Salteraster Sturtz and Lanthanaster Branstrator have appropriate shapes, sizes and podial arrangements. In addition, Salteraster is known to range throughout the Cincinnatian, and possesses distinctive, well-developed paxillae.

V. TAXOBASES IN THE ORDOVICIAN ASTERIADINA

In light of the voluminous taxonomic literature on modern asteroids, it would seem an easy task to establish taxobases for fossil species by using the same criteria employed by zoologists for modern forms. Unfortunately, many of the "heavily weighted" zoological taxobases are not preservable, thus they are not available in the taxonomic evaluation of fossils. Others require fine preservation with little or no thecal distortion in order to be observed; few fossil asteroid specimens faithfully preserve structural details or proportions of the animals they represent.

One strategy for building a realistic classification for fossil asteroids is to assess modern asteroid taxa for characteristics commonly determinable from fossils, and use these same characteristics at similar taxonomic levels in constructing a taxonomy for the fossil forms. The levels at which particular preservable characteristics are utilized as taxobases in this report on Ordovician Asteriadina conform to the levels at which the same specimen attributes are employed by zoologists in classifying modern representatives of the suborder. These characteristics and levels were determined during a survey of various classifications of modern Asteriadina, most notably those of Fisher (1928, 1930) and Verrill (1914). Fisher's taxonomy seems to be the most comprehensive, to date, for the suborder because it considers species from the widest geographic and ecologic ranges. Subsequent evaluation of parts of Fisther's taxonomy, in the form of comparative physiological, anatomical and behavioral investigations of individuals in taxa included therein by such investigators as Chia (1966), Feder (1959), Christensen (1957), MacGinitie and MacGinitie (1949) and Paine (1966, 1969), seem to confirm the cohesiveness of its taxa.

This investigation, after Fisher, consistently employs the following preservable charcteristics at their respective taxonomic levels:

Family:
1. Type and arrangement of accessory ossicles in adult individuals.
2. Numerical relationship between ossicles in perivascular and extravascular columns.
3. Prominence of mouth-angle ossicles.
4. Arrangement of adambulacral spines.
5. Modifications of podial arrangements and number of podial columns on each brachium.

Genus:
1. Structural pattern of dorsal skeleton.
2. Papular development and abundance.
3. Development of adoral carinae in adults.
4. Number of adambulacral spines.

Species:
1. Shape and spination of primary ossicles.
2. Structural details of dorsal spines and granules.
3. Structural details of adambulacral spines.

VI. SYSTEMATIC PALEONTOLOGY OF CINCINNATIAN ASTERIADINA

Order FORCIPULATIDA Perrier, 1884

Suborder ASTERIADINA Fisher, 1928

1928 Suborder Asteriadina Fisher, W. K., p. 3.

1951 Suborder Pustulosa Spencer, W. K. [partim], p. 122.

1966 Suborder Pustulosina Spencer, Spencer, W. K., and Wright, C. W. [partim], p. 48.

1969 Suborder Bimarginalina Kesling, R. V. [partim], p. 366.

Diagnosis. -- Spinose, non-paxillose, asteroids with spines mounted on pustules. Median dorsal, superomarginal, and inferomarginal ossicle columns prominent over entire brachial length during early or all stages of post-larval ontogeny. Dorsal and dorsolateral skeleton usually composed of lobed ossicles imbricated in longitudinal columns, and transverse series of primary or primary and accessory ossicles, or primary and accessory ossicles linked into a regular or irregular reticulum. Dorsal and dorsolateral papular openings through the skeletal wall always present in adults. Ambulacral and adambulacral ossicles usually compressed in adults; relatively short and wide. Accommodations for four or more columns of podia tending to develop in each brachial groove.

Synonomic Discussion. -- Fisher (1928) erected Suborder Asteriadina to accommodate all modern asteroids with forcipulate pedicellaria, except those he included in his new Suborder Brisingina. This latter taxon is composed of Cenozoic and recent forms from the deep-sea which have a distinctive, ophiuroid-like body shape. The two suborders appear to have little in common, except pedicellaria type.

Spencer (1951) attempted to devise a higher taxonomic system which would be useful in the classification of Paleozoic asteroids. The characteristics of pedicellaria, employed by neontologists, are useless in paleontology; pedicellaria have yet to be discovered in fossil asteroids. Spencer utilized features of relative prominence and arrangement of perivasuclar skeletal elements, some of which are visible on nearly every fossil seastar. As helpful as Spencer's classification would seem to be to paleontologists, it possesses several shortcomings which make it unacceptable. First, it is still not easy to apply to the majority of fossils because it requires that specimens be relatively undistorted from their living shapes. As noted earlier, asteroid fossils usually suffer considerable distortion and fragmentation during preservation and emergence. Furthermore, erecting separate classification systems for fossil and modern asteroids is a move away from increased comprehension of the subclass. Spencer's classification contained an order, Phanerozonida Sladen, which could, conceivably, accommodate the majority of modern asteroids, but he erected under it only a single suborder, Pustulosa, to accommodate five fossil families. One of these, Petrasteridae Spencer, is a paxillose family, and is clearly not closely related to other families he includes in Pustulosa. These other families are Hudsonasteridae Schuchert, Promopalaeasteridae Schuchert, Palaeasteridae Schuchert, and Xenasteridae Schoendorf.

The Treatise (Spencer and Wright, 1966) correctly removes Petrasteridae to the Paxillosida, but places remaining families of

Spencer's Pustulosa, plus the monomarginate, monotypic family Neopalaeasteridae, in the Order Valvatida Perrier; it does this with no explanation. This unfortunate arrangement should not, perhaps, be surprising because Valvata, as a suborder of Order Phanerozonia, seems to have been used by numerous authors (Fisher, 1911; Verrill, 1914; Hymen, 1955) as a polyphyletic taxon to accommodate all non-benthopectinid phanerozonates with suckered podia. On the basis of the known characteristics of the fossil material at the time of the Treatise's publication, there can be no other reason for placing Hudsonasteridae, Promopalaeasteridae, Palaeasteridae and Xenasteridae in Order Valvatida.

Kesling (1969) elevated Spencer's Pustulosina to Order Pustulosida. He then erected two new suborders, Bimarginalina and Monomarginalina, to separate the order into fossil seastars with two prominent columns of marginals for the entire lengths of their brachia (Palaeasteridae, Hudonastericae, Mesopalaeasteridae, Xenasteridae, Promopalaeasteridae, Eoactinidae, Stauranderasteridae) and fossil forms bearing only one entire column of marginals (Neopalaeasteridae and Monasteridae). Kesling's ordinal characterization, however, does not allow the inclusion of the Promopalaeasteridae, because it specifies that axillaries, or first inferomarginals, be associated with each pair of mouth-angle ossicles. This is not the case in adult specimens of Promopalaeasteridae. This ordinal feature seems to have been included in order that Eoactinidae could be included in Pustulosida. Although specimens of this latter family are not well-known, they seem to have no other relationship to other of Spencer's Pustulosina. Kesling places Eoactinidae in his Bimarginalina, yet specimens show no superomarginals and only single pairs of most-proximal inferomarginals. As they are currently comprehended, eoactinid specimens are not closely related to the hudsonasterids, mesopalaeasterids, or promopalaeasterids. This author is unable to comment on Kesling's inclusion of the Stauranderasteridae in the same suborder as Hudsonasteridae, Mesopalaeasteridae, and Promopalaeasteridae because he has not examined appropriate specimen material of the former family.

Family HUDSONASTERIDAE Schuchert, 1914

1914 Hudsonasteridae Schuchert, Charles [*partim*], p. 6.

1915 Hudsonasteridae Schuchert, Charles [*partim*], p. 53.

1916 Hudsonasteridae Schuchert, Spencer, W. K. [*partim*], p. 68.

1922 Hudsonasteridae Schuchert, Raymond, P. E. [*partim*], p. 169.

1952 Protopalaeasteridae Rasmussen, H. W. [*partim*], p. 23.

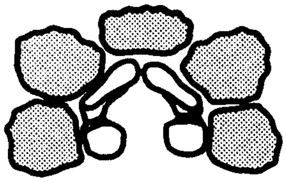
1966 Hudsonasteridae Schuchert, Spencer, W. K., and Wright, C. W. [*partim*], p. 50.

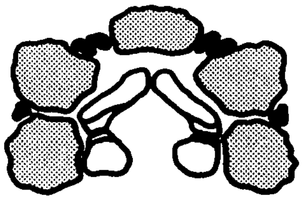
1969 Hudsonasteridae Schuchert, Kesling, R. V. [*partim*], p. 366.

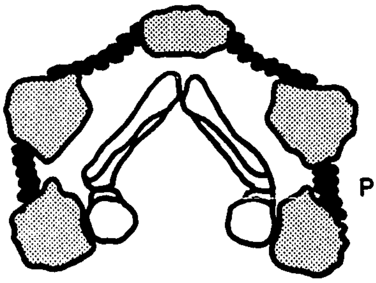
Diagnosis. -- Asteriadina without accessory ossicles intercalated between columns of primary ossicles (Text-figure 14). Ratio between numbers of ossicles in perivascular and extravascular ossicle columns is 2:1 or nearly so. Mouth-angle ossicles usually small throughout life, only slightly more prominent than adjacent adambulacrals. Adambulacral spines in vertical, pectinate series. Podial basins monoserial.

Synonomic discussion. -- Adult members of this family resemble, to some degree, early developmental stages of individuals belonging to

Text-figure 14. -- Comparative diagrammatic brachial cross-sections of individuals with mature ossicle complements in three Asteriadina families represented in Cincinnatian rocks. Perivascular ossicles not stippled, extravascular primary ossicles lightly stippled, and intercalating accessory ossicles black.


HUDSONASTERIDAE


MESOPALAEASTERIDAE


PROMOPALAEASTERIDAE

Mesopalaeasteridae and Promopalaeasteridae. Mesopalaeasteridae individuals, however, maintain a perivascular column ossicle number identical to the ossicle number in each extravascular column. Promopalaeasteridae specimens, on the other hand, differ from hudsonasterids in that individuals tend to develop intercalating interdorsal and intermarginal columns and axial intermarginals become occluded from the ambitus early in ontogeny. These latter phenomena occur, but at a later ontogenic stage, in the Mesopalaeasteridae as well. The failure of earlier paleontologists to recognize these attributes as useful in separating fossils into families has led to several classifications with polyphyletic groupings of genera and species.

Schuchert (1914) erected Hudsonasteridae to include Hudsonaster Stürtz and Siluraster Jaekel. Schuchert added five additional species to Sturtz's type species to compose a more comprehensive genus. Of these, only the type species, Palaeasterina rugosus Billings, and Palaeaster incomptus Meek, Protopalaeaster narrawayi Hudson and Asterias matutina Hall can justifiably remain. To these species this report adds Palaeaster simplex Miller and Dyer, which it resurrects from Schuchert's synonomy with Palaeaster incomptus. The European species Hudsonaster batheri Schuchert clearly belongs in Mesopalaeasteridae. Hudsonaster milleri Schuchert is in such poor state of preservation that it cannot be assigned, with confidence to Asteriadina. The Bohemian genus Siluraster remains unsatisfactorily characterized and diagnosed, but seems, from Jaekel's line-drawings of the type species, to belong in the Mesopalaeasteridae.

In terms of family-group designation, Schuchert 1915 reiterates

Schuchert 1914.

Spencer (1915) seems to have accepted Schuchert's assignment of species to Hudsonaster, but added three new genera, Girvanaster, Belaster and Coccaster, to the Hudsonasteridae. Evidence from his work indicates that his assignment of Girvanaster and Coccaster to this family is warranted, but Belaster ordovicus shows the mesopalaeasterid ossicle ratios and clearly does not belong in Hudsonasteridae.

Raymond (1922) erected Macroporaster to accommodate Palaeaster matutina (Hall) and his new species, Macroporaster nylanderi. He listed his new genus and those included by Spencer, plus Siluraster in the Hudsonasteridae. As mentioned above, this investigation rejects Belaster and Siluraster as hudsonasterids.

Rasmussen (1952) refers to the Hudsonasteridae, as conceived by Raymond, as "Protopalaeasteridae". He does not explain his action. Schuchert's name has priority.

Spencer and Wright (1966) included, in three subfamilies, the genera earlier authors had placed in Hudsonasteridae. Siluraster is given its own new subfamily as is Coccaster. Belaster is erroneously placed in synonomy with Protopalaeaster in the Hudsonasterinae with Hudsonaster, Girvanaster and Macroporaster. The Treatise notes that Protopalaeasteridae Rasmussen, 1962 [actually 1952] is synonomous with Hudsonasteridae.

Kesling (1969) included Hudsonasteridae in his list of families belonging in his new Suborder Bimarginalina (See synonomic discussion under Asteriadina).

Genus *Hudsonaster* Sturtz, 1900

1854	[*non*] *Palaeasterina* McCoy, F., p. 59.
1857	*Paleasterina* McCoy, Billings, Elkanah [*partim*], p. 290.
1858	*Palaeasterina* McCoy, Billings, Elkanah [*partim*], p. 76.
1863	*Palasterina* McCoy, Wright, T. [*partim*], p. 26.
1900	*Hudsonaster* Sturtz, B., p. 206, 218, 224-225.
1914	*Hudsonaster* Sturtz, Schuchert, Charles [*partim*], p. 21.
1915	*Hudsonaster* Sturtz, Schuchert, Charles [*partim*], p. 53-57.
1916	*Hudsonaster* Sturtz, Spencer, W. K. [*partim*], p. 77.
1922	*Hudsonaster* Sturtz, Raymond, P. E., p. 169.
1928	*Hudsonaster* Sturtz, Sardeson, F. W. [*partim*], p. 109.
1966	*Hudsonaster* Sturtz, Spencer, W. K., and Wright, C. W., p. 50, fig. 47 (4 a-b).

Diagnosis. --Hudsonasteridae with blocky, non-overlapping, compressed ambulacral ossicles without longitudinal flanges for articulation with successive ambulacrals. Brachia rapidly tapering from wide bases.

Type species. -- *Palaeasterina rugosus* Billings, 1857, by original designation of Sturtz, 1900.

Discussion. -- Asteroids of the genus *Hudsonaster* are heavily plated, five-rayed; they possess relatively short, acuminate brachia and single axillary inferomarginals against which the mouth-angle ossicles abut. The axillary inferomarginal is on the ambitus throughout ontogeny. The brachial skeleton is composed of nine columns of primary ossicles without intercalating secondary ossicles.

Successive ambulacral ossicles abut, but do not overlap. They possess no proximal or distal flanges or grooves for articulation with successive ossicles. Ampullar perforations, if present, at ambulacral-adambulacral column junctions. Ampullae may have been accommodated entirely within excavations (between transverse ridges) in the oral surfaces of the ambulacral columns.

The dorsal surface of the theca may possess small, spherical or stellate, superficial extrathecal ossicles not arranged in columns so as to intercalate between the primary ossicles. All well-preserved, external thecal ossicles possess a prosopon of small, contiguous or separated, spine-base monticules or pustules; these pustules carried spines or granules articulated upon them in the living animal. Some spine-base structures still have spines attached to them in well-preserved and finely exhumed specimens.

The most-proximal ambulacral ossicles are composed of fused first and second ambulacrals in each column, but are not noticably larger than adjacent ambulacrals. The mouth-angle ossicles are only slightly larger than the adjacent adambulacrals.

The madreporite is usually dorsolateral, between proximal flanges of the two most-proximal (axillary) superomarginals of the bivial interbrachial area. Its surface relief is variable, being flat, concave, or convex, depending on taxon.

<u>Species</u>. -- This investigation recognizes three species of <u>Hudsonaster</u> from North America. In addition to the type species, there are <u>Hudsonaster incomptus</u> (Meek, 1872) and <u>Hudsonaster simplex</u> (Miller and Dyer, 1878). Although the type species is not known from the Cincinnati Area, it is described here in detail for purposes of

comparison with the two species known from Cincinnati rocks.

Hudsonaster rugosus (Billings, 1858).

Plate 1

Text-figure 15A

1857 *Palaeasterina rugosus* Billings, Elkanah, p. 291.

1858 *Palasterina rugosa* Billings, Billings, Elkanah, p. 77, pl. 9, fig. 2 a-c.

1863 *Palasterina rugosa* Billings, Wright, T., p. 27.

1900 *Hudsonaster* (*Palasterina*) *rugosum* (Billings), [chart] Sturtz, B., p. 206; as *Palasterina rugosa* Billings, p. 218; as *Hudsonaster* (*Palasterina*) *rugosa* (Billings), p. 224; as *Hudsonaster* (*Palaster*) *rugosa* (Billings), p. 225.

1914 *Hudsonaster rugosus* (Billings), Schuchert, Charles, p. 21-22.

1915 *Hudsonaster rugosus* (Billings), Schuchert, Charles, p. 55-56, 64-65, pl. 3, fig. 1.

1922 *Palaeasterina rugosa* Billings, Raymond, P. E., p. 166, pl. 3.

1928 *Hudsonaster rugosus* (Billings), Sardeson, F., p. 109-110.

1928 [*non*] *Hudsonaster rugosus* (Billings), Twenhofel, W. H., p. 141, pl. 4.

1966 *Palaeasterina rugosa* (Billings), Spencer, W. K., and Wright, C. W., p. 50.

Diagnosis. -- *Hudsonaster* with primary axis of axillary superomarginals nearly vertical and most prominent lobe on ossicle ventral of ossicle body (Text-figure 15A). Dorsal extrathecal ossicles granular and small.

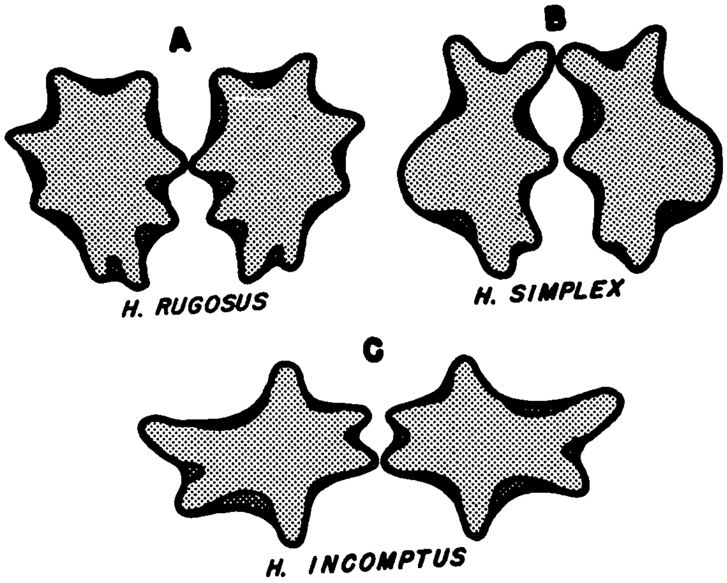
Primary type material and locality. -- The holotype and a single paratype, CGS nos. 1999 and 1999a, were found in the Vauréal Formation [= English Head], Upper Ordovician; Carleton Point, Anticosti Island, Quebec, Canada.

Occurrence. -- The type materials are the only reported specimens. Two specimens erroneously assigned to this species (YPM nos. 20491A and 20491B) by Twenhofel (1928) belong within the Mesopalaeasteridae.

Description. -- The holotype is relatively large and the brachia are short and broad (Plate 1, figure 1a); R = 24 mm., r = 9 mm., and wr = 12 mm.

Varying views of several ambulacral ossicles are now visible on the holotype (Plate 1, figures 1 c-d). The ossicles are two to three times as wide as long, and about as thick as long. The dorsal (internal) surface as a broad, lengthwise sulcus. The ventral (external) surface has a ridge, hereafter termed the elongate or transverse ridge, which runs parallel to the long axis of the ossicle and abuts adradially against the vertex of a V-shaped ridge. The distal branch of the V-shaped ridge is interrupted close to the elongate ridge by a transverse furrow. This furrow was a passage for the lateral vessel which joined the podium to the radial water-vascular vessel (Refer to Text-figure 5). The ridges on the ventral surface of the ambulacral columns define the podial basins. The elongate ridges bisect the ventral surfaces of the ambulacral ossicles in the holotype; this suggests that the podial basins were shared equally

Text-figure 15. -- Axillary superomarginals of species of *Hudsonaster*. Proximal is toward the top of the page in each case. A. *H. rugosus*; B. *H. simplex*; C. *H. incomptus*.


A
B
H. RUGOSUS
H. SIMPLEX
C
H. INCOMPTUS

by successive ambulacral ambulacral ossicles. Abradially the elongate ridge gains greater relief from the general surface of the ossicle. The most abradial portion of the ossicle is the abradial expansion of the ridge, making the ossicle acuminate at that end. The proximal and distal margins of the ossicle are slightly excavate for the insertion of voluminous interossicular muscles, but no articulating grooves or flanges are apparent. The ventral surface of each ambulacral is excavated adradial to the V-shaped ridge; this is the site of insertion of the ventral transverse ambulacral muscles. The perradial portion of this excavation presumably housed the radial water vessel and the radial nerve when the animal was alive.

The adambulacral ossicles are not exposed well on either specimen, but something of their structure and arrangement may be determined. Where they show through the disarranged distal skeleton of the holotype they are slightly wider than long. From the ventral aspect of the paratype it is clear that proximal adambulacrals maintain this same proportion. The dorsal surfaces of these ossicles carry an abradial sub-trigonal area where they were in contact with the adjacent inferomarginals, a slight central depression, and adradial, transverse ridge with an ovate, concave summit (Plate 1, figure 1f). The ossicles each articulated with a single ambulacral ossicle by means of this ridge structure. The adradial edge of the ovate ridge of an adambulacral ossicle is at the adradial end of the ossicle. Thus, the adambulacral ossicle columns extended only slightly under the abradial ends of the ambulacral ossicles, making it necessary for the brachium to be only slightly flattened in order for the ambulacral groove to be opened. Conversely, unless the animal could produce an acute angle between opposing ambulacral columns, it could not close the ambulacral groove by means of the adambulacral ossicles. Since the paratype shows the proximal portions of opposing adambulacral columns adjacent to one another, it must be assumed that H. rugosus could erect its ambulacral columns into an acute ridge. The earlier interpretation that part of the perradial end of each ambulacral ossicle was in insertion area for ventral transverse muscles is thus given more support.

Slight excavations in the proximal and distal surfaces of the adambulacral ossicles were, as in the case of the ambulacrals, accommodations for interossicular muscles. No adambulacral spines, or spine-base structures, are visible on either specimen of H. rugosus. The shapes of the ossicles, especially the proximal ones of the paratype, indicate that they carried vertically pectinate series of spines. The pectinate series of the more distal ossicles were probably multiple and the spines were probably smaller, as in other species of Hudsonaster.

In plan view the proximal inferomarginals of H. rugosus are elongated normal to the perradial plane. The reverse is true for the distal ossicles in the same columns. Height is always the greatest dimension of brachial inferomarginals. They are abradially broadly rounded (Plate 1, figures 1b, 2b) and have a dorsal and abradial lobe. The dorsal lobe ascends to meet a prominent ventral lobe of the overlying superomarginal. The abradial ridge is beveled at its ventral edge and the adjacent adambulacral ossicles fit against the beveled surface. The proximal and distal surfaces of the inferomarginals are excavated for the accommodation of interossicular muscles. The prosopon of the exposed surfaces of the ossicles is of contiguous monticules, each covered by smaller, low, perforate spine-base structures. These latter structures indicate that spines or granules were present on the inferomarginals of the living animal.

The numerical relationship between the inferomarginals and the adambulacrals of H. rugosus can be deduced from the size relationships of the two types of adjacent ossicles at similar proximo-distal positions on the brachia, or the paratype can be consulted for the proximal relationship. Both lines of evidence indicate that there are about two adambulacrals for each inferomarginal.

The ventral axil of each pair of brachia is formed by a single axillary inferomarginal. It displays a prosopon similar to that of the other inferomarginals proving that the axillary was on the ambitus of the living animal. The axillary is noticably larger than the adjacent inferomarginals. It has a broad, V-shaped ridge on its dorsal surface (Plate 1, figure 1b) as evidenced from a well-displayed ossicle of the holotype. The paratype retains two axillary inferomarginals which appear to have been similar to those described for the holotype.

The distal superomarginals are indistinguishable from adjacent inferomarginals in form. Both are rhombus-like with flattened proximal and distal angles. Proximally, however, the superomarginals become wider and acquire a hexagonally lobate plan. The most proximal, non-axillary superomarginals are quite elongated and are concave on their proximal and distal surfaces in plan view. They are about as massive as adjacent inferomarginals. Where preserved, the prosopon of the superomarginals is similar to that of the inferomarginals.

The axillary superomarginals are the largest ossicles of H. rugosus. Each of two, large, mirrored ossicles in each axil possesses a relatively long, slightly bifurcated, distal acuminate lobe which descends to meet one of the arms of the V-shaped ridge of the axillary inferomarginal. Six additional lobes of each axillary superomarginal radiate to meet lobes of adjacent ossicles. The prosopon, where preserved, is similar to that of the other superomarginals.

The median dorsal ossicles are slightly smaller than adjacent superomarginals. They are rhombus-shaped and proximal ones are wider than long. Distal median dorsals are longer than wide. The proximal and distal angles of the rhombs are flattened or excavated to accommodate interossicular muscles. Although somewhat abraded, some median dorsals retain a prosopon similar to that of the other external thecal ossicles.

The most-proximal median dorsal of each brachium is large, proximally the widest, and has six lobes, two of them on the perradial plane. The interbrachials of the dorsal disc surface are also widest proximally, but they possess seven lobes each. There is one proximal and two distal lobes on this latter ossicle type.

Neither the holotype nor the paratype possesses a madreporite. It is possible to discern the former location of the madreporite of the holotype, however. It was located between the ossicle bodies of the two axillary superomarginals in one of the axils as evidenced from a difference in shape of the two enclosing ossicles from that of the others of the specimen.

The apical field of the holotype has collapsed, as seems to have happended in most hudsonasterid specimens. The ossicles appear to have been large, however (Plate 1, figure 1a).

The paratype of *H. rugosus* displays part of the mouthframe, but it is disarranged and incomplete. The mouth-angle ossicles are not noticably enlarged, but they are slightly larger than the adjacent adambulacral ossicles. The apparent great distance between the mouth-angle ossicles and their axillary inferomarginals (Plate 1, figure 2a) is due to distortion, because the adambulacrals, which normally lie close to the axillary, are also some distance from it.

Small accessory ossicles are present on the surface of the primary ossicles of the holotype (Plate 1, figures 1 a-b, e). They are very small, randomly dispersed and acutely lobate.

Synonomic discussion. -- Since the species is known only from the holotype and a single paratype, the synonomy is self-explanatory.

Hudsonaster incomptus (Meek, 1872).

Plate 2

Text-figures 15C, 16

1872 *Palaeaster incomptus* Meek, F. B., p. 275-276.

1873 *Palaeaster incomptus* Meek, Meek, F. B., p. 64, pl. 4, figs. 5 a-b.

1914 *Hudsonaster incomptus* (Meek), Schuchert, Charles [*partim*], p. 21.

1915 *Hudsonaster incomptus* (Meek), Schucert, Charles [*partim*],

p. 55, 61.

1966 [non] Hudsonaster incomptus (Meek), Spencer, W. K., and Wright, C. W., p. 50, fig. 47 (4 a-b).

Diagnosis. -- Hudsonaster with primary axis of axillary superomarginals nearly horizontal, the most prominent lobes being themselves horizontal. Dorsal extrathecal ossicles spherical and of variable sizes; proximally they overlie the junctions between successive median dorsals, but do not articulate between primary ossicle columns.

Primary type material and locality. -- The holotype (MCZ no. 471) is accompanied with no more complete description than "Cincinnati Group, Cincinnati, Ohio". The specimen was collected by C. B. Dyer who commonly failed to record precise locality or stratigraphic data for his many excellent echinoderm fossils now in various North American museums.

Other known specimens. -- Another specimen, YPM no. 14778, was collected from Richmond rocks in Madison, Jefferson County, Indiana. Two additional unnumbered specimens labeled "Hudsonaster, Jefferson County, Indiana; J. Braun" are in the same museum. The precise locality or strata from which these specimens were collected is unknown.

Description. -- All known specimens are near the size of the holotype; R = 11 mm., r = 6 mm., wr = 6 mm. The holotype is the least fragmented specimen, thus its proportions most faithfully preserve those of the living animal. This specimen also best preserves the interossicular arrangements of ossicles.

The ambulacral ossicles are similar to those of H. rugosus. They have the same broad, dorsal proximo-distal sulcus, the same proportions in their ventral ridges, and lack flanges and grooves for articulation with successive ossicles. Perradially, proximally, and distally the ossicles are flattened or excavated for interossicular muscle attachment, but the ossicles do not appear to be as high (thick) as those of the type species. Where several successive ambulacral ossicles can be seen adjacent to one another, there are no interossicular passages for ampullae between ambulacrals.

The dorsal surfaces of the adambulacral ossicles are similar to those of H. rugosus. Where they are exposed through the somewhat separated dorsal ossicles of the holotype, however, the elongate ridges seem neither proportionally as wide, nor to have concave summits. The connection between ambulacral and adambulacral columns was probably not as strong in this species as in H. rugosus.

No specimen provides clear data on the nature of the adambulacral spinosity. The adambulacrals maintain about a two to one ratio to the inferomarginal ossicles and are wider than long. Their shape can be ascertained through the slumped extravascular skeleton of Brachium A of the holotype. Most short, wide asteroid adambulacral ossicles carry an armature of spines in a vertically pectinate series.

The inferomarginals are pyriform in lateral aspect. In plan view they maintain the same proportions for the brachial length as do those of H. rugosus. They are also broadly rounded abradially, but their dorsal and perradial lobes, or articulation processes, are more extreme than those of the former species. These longer processes on the marginal ossicles allowed a more open skeleton. Thus, larger papular areas were possible than in H. rugosus. The inferomarginals are pustulose on their exposed surfaces, but not to the degree of the former species (Plate 2, figure 1e).

There is a single axillary inferomarginal in each axil of H. incomptus. Some of these ossicles display an external prosopon similar to that of the other inferomarginals. Usually, however, slumping of the skeletal frame has made the axillary inferomarginals appear not to be marginal because the more distal marginals appear to enclose them. This is a preservational feature, however, because the DE interbrachial area of the holotype maintains its axial inferomarginal on the ambitus. The typical surface prosopon of each axillary further indicates that the axillary inferomarginals were marginal in the living animals. The ventral expression of the axillary inferomarginals is unknown for H. incomptus.

The form and arrangement of the superomarginals, with the exception of the axillaries, are similar to those of H. rugosus. The ossicles are somewhat more erect than those of the former species. This latter characteristic produces larger dermal areas between ossicle columns (Plate 2, figures 1 a-b). The pustular prosopon is concentrated along the outer ridges of these ossicles, further indicating that the ossicles were upright during life. This ossicle arrangement probably allowed more lateral brachial flexure than the more blocky arrangement of H. rugosus. The granular accessory ossicles aided in producing an armature protective of these dermal areas.

The axillary superomarginals of H. incomptus are considerably wider than long (Plate 2, figures 1a, 1e, 2a). This feature provides the most obvious basis for distinguishing the species from others of the genus (Text-figure 15C). Each ossicle possess five main lobes, the one extending toward the opposite axial superomarginal being terminally bifid. A single, non-bifurcating lobe on each ossicle descends ventrally to articulate with the axillary inferomarginal. Spine-base pustules cover the external surfaces of these superomarginals, but a row of relatively large spine-base features, along a transossicular ridge, is most obvious (Plate 2, figure 1e), and it is another distinctive characteristic of this species.

The median dorsals of this species are similar in shape and proportions to those of _H_. _rugosus_.

The most-proximal median dorsal does not possess the proximal lobe which is apparent in the type species and on more distal ossicles of the same column. It is not as wide as the next few more distal median dorsals of the same column due to its lack of long lateral lobes. Its lobes are broadly rounded both laterally and distally (Plate 2, figure 1b). The prosopon is the same as on the remainder of the dorsal ossicles.

The remaining median dorsals possess proximal and distal acuminate lobes and long lateral lobes. They are notably tumescent in lateral profile. Both the tumescence and the prominence of the lobes diminish distally.

Small, rounded grains are situated over the juncture between successive proximal arm and disc median dorsals (Plate 2, figure 1b). There are other smaller granules lateral to these accessory ossicles.

Both well-preserved specimens retain their madreporites, but that of the holotype is better preserved. It is ovate, tumescent, and marked with radiating, incised, bifurcating striae. It is situated between the proximal lobes of a pair of axillary superomarginals.

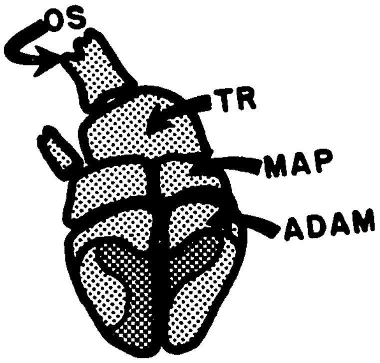
The apical field of the holotype has collapsed into the body cavity beneath it and requires some reconstruction prior to description. The other available specimens of H. incomptus show some apical field ossicles, but they are more disarranged than those of the holotype. The central dorsal is slightly larger than the other ossicles of the apical field. It is tumescent and pentagonal in plan. The other ten apical field ossicles appear to be hexagonal in plan. All have the usual pustulose prosopon.

As in H. rugosus, the centro-interbrachials lie between and slightly distal to the most-proximal median dorsals. These ossicles are not saggitate in plan in this species, however. Rather, they appear to be wide, and somewhat reminiscent of the axial superomarginals just distal to them. They are slightly larger than the adjacent most-proximal median dorsals.

Details of the mouthframe are not available from the holotype. The dorsal ossicle of YPM no. 14778, on the other hand, are sufficiently separated due to slumping to reveal the dorsal aspects of some oral ossicles (Plate 2, figures 2 a-b). A set of mouth-angle ossicles, complete with a spinose (one spine still present) torus is visible in one of the interbrachial areas. The torus is reniform and relatively larger than that of H. simplex. A pair of adambulacral ossicles lies between the axial inferomarginal and the mouth-angle ossicles of each interbrachium (Text-figure 16).

Synonomic discussion -- Meek (1972) established the species with

Text-figure 16. -- Oral ossicles of Hudsonaster incomptus in dorsal aspect (YPM no. 14778). Darkly shaded area insertion area for interossicular muscles between axial inferomarginals and adambulacrals (figured). Oral spine (OS); torus (TR); mouth-angle ossicle (MAP); adambulacral ossicle (ADAM). X 60.


OS
TR
MAP
ADAM

a very detailed description. He erroneously interpreted the thanatocoenosic condition of the holotype, the only specimen of the species he knew. He wrote that the specimen is fastened to a coral which grew over the asteroid as it laid dead on the sea floor. His evidence for this conclusion was that the specimen was attached by its entire ventral side to the "coral" (a bryozoan). Meek was apparently under the impression that H. incomptus lived with its oral surface up while being attached to the substrate by its dorsal surface. It is more realistic to assume that the asteroid was trapped against the bryozoan as it crawled upon it. Asteroids decompose and disarticulate much too quickly to be overgrown by a coral (or bryozoan).

Meek did not figure this species until his 1873 publication. His figures, however, do not relay accurately the nature of the madreporite, which he figured enlarged, nor the slumped condition of the specimen.

Schuchert referred to his previously completed, but subsequently published, "Revision" when he compiled his 1914 listing in Fossilium Catalogus. From his 1915 report it is clear that he considered all Cincinnati specimens of Hudsonaster to belong to H. incomptus. Only one specimen known to him, the holotype of the species, actually belongs to H. incomptus. The present study assigns the remainder of the Cincinnatian hudsonasterids known to Schuchert to H. simplex. Schuchert placed this latter species in synonomy with H. incomptus.

Some confusion has been added to the literature by Schuchert's method of determining characteristics for some of the species he redescribed in 1915. This seems to stem from his failure to critically examine type material. He clearly states his reasoning and the procedure he used. They have been the source of misunderstanding by subsequent workers who have also failed to examine the pertinent type material: "This species [H. rugosus] is undoubtedly congeneric with Palaeaster incomptus, a form fully described in this work from the actinal [ventral] and abactinal [dorsal] sides, and is therefore taken as the genotype for the above generic definition." Schuchert then figured (Bulletin 88, Plate 6) two specimens herein considered to be H. simplex, and he labeled them as H. incomptus.

Spencer and Wright (1966) redrafted Schuchert's figures and propagated his misconceptions.

Hudsonaster simplex (Miller and Dyer, 1878)

Plates 3-4

1878	Palaeaster simplex Miller, S. A., and Dyer, C. B., p. 29, pl. 1, fig. 6.
1889	Palaeaster simplex Miller, Miller, S. A., p. 266, fig. 380.
1914	Hudsonaster incomptus (Meek), Schuchert, Charles [partim], p. 21.
1915	Hudsonaster incomptus (Meek), Schuchert, Charles [partim], p. 55, 61.
1966	Hudsonaster incomptus (Meek), Spencer, W. K., and Wright, C. W. [partim], p. 50.

Diagnosis. -- Hudsonaster with primary axis of axillary superomarginals nearly vertical, and most prominent ossicle lobe bifid and dorsal of ossicle body. Dorsal extrathecal ossicles unknown, probably small spines or granules. Mouth-angle ossicles adnate to axillary inferomarginals.

Primary type material and locality. -- The holotype (FMNH University of Chicago Faber Collection no. 8830) is from near Raysville, Ohio and was found "in the upper part of the Cincinnati Group". The exact locality and stratum of occurrence are unknown. In 1878, Raysville was a small village near the modern village of Lytle in northeastern Warren County. Ordovician strata exposed in the vicinity are exclusively Richmondian. It may be safely concluded that the specimen was found in Richmond rock.

Other known specimens. -- Now that the nature of the H. incomptus holotype is known to be different from that of Miller and Dyer's Palaeaster simplex, it becomes necessary to determine the specific affinities of the specimens Schuchert included in his too comprehensive H. incomptus. These specimens cannot all be divided between these two species, however; some are developmental stages of a promopalaeasterid (refer to following section on Promopalaeasteridae). The following specimens may be assigned to H. simplex: USNM no. 40882[8] from Richmond rocks in the vicinity of Waynesville, Warren

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[8] Schuchert (1915, p. 62) identified four specimens in USNM no. 40882 in the Harris Collection as Hudsonaster incomptus. There are currently six specimens filed under that number in the Springer Room. One specimen is in a small box with a label in Schuchert's handwriting saying, "a different species from others in tray". This work considers that specimen, which is the only one in the lot free of its matrix, along with four other large individuals in the tray, to be specimens

of H. simplex. The smallest specimen in the lot was the basis of Schuchert's diagram (1915, Plate 6, figure 1) which he thought characterized the ventral aspect of H. incomptus. The enlarged mouth-angle ossicles and the axillary inferomarginal ossicles isolated from the ambitus suggest that this specimen is not a hudsonasterid, but rather a developmental stage of a promopalaeasterid, probably Kenothecaster miamiensis (Miller).

County, Ohio; USNM no. 60616 from Maysville rocks on Vine Street Hill in Cincinnati; FMNH no. A 166 of unknown occurrence; ROM no. 961 HR (Walker Collection) form an unknown locality and stratum in Cincinnati; UCGM no. 40756 (Plate 3, figure 5) from the Elkhorn "Formation" at Weisburg, Indiana; a specimen from Richmond rock collected about two miles north of Germantown, Montgomery County, Ohio, a latex mold of which is UCGM no. 40760 (Plate 3, figures 3 a-b; Plate 4, figure 1); a MUGM specimen (Plate 3, figure 4) without an acquisition number and with no locality information; and YPM no. 14772 (Plate 3, figure 2) from Richmond rocks in Madison, Jefferson county, Indiana.

Description. -- The holotype (Plate 3, figure 1) has the following measurements: R = 19 mm., r = 7 mm., wr = 7 mm. Other recognized specimens range down to a radial length of 8 mm. (ROM no. 691 HR). Ossicular and thecal proportions are maintained by all specimens. Some specimens show preservational distortion resulting from flattening, or depression. This makes brachia appear wider than in other specimens of the same size. Compare figures 1 and 3a of Plate 4.

As is characteristic of the genus, successive ambulacral ossicles do not overlap. They possess slightly excavated proximal and distal faces which accommodated large interossicular muscles between successive ossicles.

The ventral and lateral surfaces of the adambulacral ossicles are best exposed on the holotype. The approximate one-to-two ratio between inferomarginal and adambulacral ossicles is clear in this specimen. The axillary inferomarginal, however, has six adambulacral ossicles, in addition to the mouth-angle ossicles, bordering it. The adambulacrals are wide and short for the length of each brachium. Subadambulacral and groove spine-base structures are well-preserved on the holotype (Plate 3, figure 1). A single, vertical, pectinate series of broadly based spines arose from the ventral and perradial margins of each adambulacral ossicle. Some of these spines are preserved in the groove of the holotype. They are short and possess longitudinal striae.

The ventral and lateral aspects of the inferomarginals also show well on the holotype. The lateral margins of the ossicles are broadly rounded with a slight median ridge. Although massive, the ossicles are strongly excavated on their proximal and distal margins for interossicular muscles. The ossicles remain slightly separated, as was probably their condition in life, providing space for the slight movement of one ossicle relative to adjacent ones. A prosopon of relatively high and discrete spine-base structures marks the external surfaces of the ossicles. All these spine-base structures are of approximately the same size on each inferomarginal, but they become progressively smaller toward the end of each arm.

The lateral margins of the axillary inferomarginals of all recognized specimens maintain the prosopon of the remaining inferomarginals. There is no tendency for the axillaries to become occluded from the interbrachial margins as the sizes of the individuals increase. This suggests that they are marginal throughout life.

In specimens preserving the proportions of the living animal, such as the free USNM no. 40882 specimen (Plate 4, figures 2 a-b), superomarginal columns directly overlie inferomarginal columns and converging lobes from the ossicles of both columns converge. These lobes are more prominent in larger individuals; this makes the dermal areas between marginal columns relatively larger in larger individuals. This, in turn, provides for increased dermal respiration area in larger individuals where volume is disproportionately increasing over thecal surface area. Since no hudsonasterid increased podial column number, the other method of increasing respiratory surface among asteroids, this relative increase in dermal area with increased size, was necessary in progressively larger individuals.

The superomarginals are wide and short. They have excavated proximal and distal faces, and are slightly overlapping, distal ossicle upon more proximal. The overlapping progressively disappears in the more distal portions of the superomarginal columns of *H. simplex*. A prominent lobe on each superomarginal reaches adradially toward a single median dorsal ossicle. The prominence of this ridge, as those between marginals, increases with specimen size. The prosopon of the superomarginals and the median dorsals is similar to that of the inferomarginals.

The shape of the axillary superomarginals is useful in distinguishing this species from others in the genus when comparative dorsal aspects are available. The major axis of the ossicle is vertical and the most prominent lobe from the ossicle body is dorsal. As opposed to those of *H. incomptus*, the axillary superomarginals of this species do not possess some spine base pustules which are more prominent than others; all are of about the same size.

There are no prominent accessory ossicles preserved on the dorsum of any member of this species. A few small granules are present on a few specimens, however.

The median dorsals of this species become wider than long on the disc, but not on the brachia. This characteristic (Plate 4, figure 3b) distinguishes this species from others in the genus.

The madreporite of *H. simplex* is quite different from that of *H. incomptus*. In this species it is polygonal or T-shaped and slightly concave, conforming to the hollow at the junction of the bivial axillary superomarginals. In the former species it is ovate, convex, and located entirely proximal to the junction between axillary inferomarginals.

The apical field of *H. simplex* is similar to that of others in the genus. It has collapsed into the body cavity beneath it in all specimens. The *Treatise* (p. 18) suggests that the apical field of the Hudsonasteridae could be raised as a "protrusible cone", a structure allegedly functional in respiration. In fact, it further uses this supposed structure in characterizing the Hudsonasterinae

(p. 50). Examination of specimens of H. simplex reveals that this structure is built in a way which prohibits its protrusion. The most-proximal median dorsals overlie distal flanges of centro-interbrachial ossicles, prohibiting their upward rotation (Plate 3, figure 3b). The ossicles within the apical field are massive and closely fitting. A respiratory apparatus would be expected to have less massive ossicles which permit as much interossicular dermal exposure as possible; such is the case in all modern asteroids with protrusible cones. It is also noteworthy that only paxillose modern asteroids which commonly burrow possess the ability to erect their dorsal integument.

A small specimen (Plate 3, figure 2) shows that the internal, proximal ends of the centro-interbrachials each has an enlarged apex which was possibly a site of attachment for muscles leading to the interbrachial oral frame. This arrangement could allow the forceful collapse of dorsal disc wall so as to evert the stomach by means of hydrostatic pressure. A similar mechanism is used by modern asteroids which evert their stomachs. This interpretation changes the significance of the so-called "protrusible cone" of these early forms. Rather than indicating a respiratory adaptation, it suggests the presence of stomach-everting in these primitive forms.

The known mouthframe of H. simplex is composed of small mouth-angle ossicles adjacent to the axillary inferomarginals (Plate 4, figures 1, 2; Plate 4, figures 4 a-b). A small, reniform torus lies proximal to and partially enveloped by each pair of mouth-angle ossicles. The most-proximal ambulacral ossicles are long (Plate 4, figure 4b).

Synonomic discussion. -- Miller and Dyer (1978) established their then monotypic species as a *Palaeaster* with several noteworthy comments. They noted that the ambulacral groove of the holotype was quite narrow, but erroneously surmised that each groove contained but a single column of ambulacral ossicles. The broken tips of three arms of the holotype show that the species is typical of all stelleroids in that it possesses opposing biserial columns of ambulacral ossicles. Miller and Dyer admit no real observation of the ambulacral condition of the specimen with the following interesting statement (p. 29), "The dorsal surface, madreporiform tubercle, and outer limits of the rays unknown, and likewise the ambulacral ossicles, though some small pieces of crinoidal matter in one of the rays may represent some of them." There is no "crinoidal matter" in any of the brachial grooves.

Miller refigured *P. simplex* in 1889, but erroneously attributed the species name only to himself. His refiguring of the holotype was less accurate in detail than the original diagram.

Schuchert (1914, 1915) placed *H. simplex* in synonomy with *H. incomptus*. He claimed to have seen the holotype of the former species and noted that it was the same species as four USNM no. 40883 specimens, "known to be *H. incomptus* (Meek)". Schuchert does not claim to have observed the holotype of *H. incomptus*, however, and his description of that species was obviously made from observations of the USNM no. 40883 specimens. These latter specimens are, as he indicated, the same species as the *Palaeaster simplex* holotype, but none are correctly referable to *H. incomptus*.

Spencer and Wright (1966) refigured the illustrations originally published by Schuchert (1915, Plate 6, figures 1-2) as *Treatise* figure 47, number 4 a-b. As stated in an earlier footnote, the first of these illustrations is based upon an immature promopalaeasterid specimen and cannot be included in this species.

Family MESOPALAEASTERIDAE Schuchert, 1914

1914 Mesopalaeasterinae Schuchert, Charles [*partim*], p. 3.
1915 Mesopalaeasterinae Schuchert, Charles [*partim*], p. 74.
1916 Hudsonasteridae Schuchert, Spencer, W. K. [*partim*], p. 68-69.
Mesopalaeasterinae Schuchert, Spencer, W. K. [*partim*], p. 79-80.
1934 Hudsonasteridae [Schuchert], Spencer, W. K., and Groom, Theodore [*partim*], p. 233.
1966 Mesopalaeasteridae Schuchert, Spencer, W. K., and Wright, C. W. [*partim*], p. 51.

Diagnosis. -- Asteriadina with a few columns of accessory ossicles intercalating between inferomarginal, superomarginal and median dorsal primary columns, at least in adult stages. Ratio between the numbers of ossicles in adjacent perivascular and extravascular column 1:1. Mouth-angle ossicles long, much larger than adjacent adambulacrals. Subadambulacral spines in each brachial adambulacral ossicle in a horizontal pectinate series. Podial basins monoserial for length of brachia.

Synonomic discussion. -- Members of this family possess the same kinds of ossicles as the neantic stages of individuals belonging to

Promopalaeasteridae (Text-figure 14). Juvenile stages have the same kinds of ossicles as adults of Hudsonasteridae. The diagnostic characteristics listed above, however, serve to distinguish all but very small specimens displaying only dorsal aspects. These latter asteriadinids are difficult to place in their proper family unless they can be associated with a sequence of growth stages.

Schuchert (1914) erected Mesopalaeasterinae as a subfamily of his new family Promopalaeasteridae. He intended (1915, p. 74) the subfamily to accommodate the species he considered the more primitive members of his Promopalaeasteridae. It was his idea that mesopalaeasterid species were evolutionarily intermediate between Hudsonaster and Promopalaeaster. The diagnostic characteristics he offered for the subfamily, however, do not distinguish mesopalaeasterids from neantic individuals assignable to Promopalaeasteridae. Further, he was unaware of the importance of ossicle ratios in separating these fossil families. Subsequent authors who have not examined important specimen material have not recognized the true nature of the species involved.

Spencer (1916), because he was not aware of the precise nature of the species Schuchert assigned to Mesopalaeaster, included his new genus and species Belaster ordovicus in the Hudsonasteridae. Spencer's figures (1916, Plate 3, figures 3-4) show that his new species possesses the essential generic characters of Mesopalaeaster; mouth-angle ossicle proportions, adambulacral-inferomarginal ratio, and adambulacral spination are all correct. The lack of interdorsal and intermarginal intercalary ossicles may well be explained by the small size of the individual he figures.

Spencer recognized the probable polyphyletic nature of Schuchert's Mesopalaeasterinae on the basis of the latter author's figures and descriptions. Being unaware of the essential features of *Mesopaleaster shaefferi*, he retained the British species Schuchert placed in the Mesopalaeasterinae in that subfamily, but erected a new genus, *Caractacaster*, for it. His figures of *C. caractaci* (Gregory), the type species of *Caractacaster* (1916, Plate 2, figure 4; Plate 3, figure 1), show that individuals of the species possess the essential nature of *Palaeaster niagarensis* Hall, but not of *Mesopalaeaster*. Two other new species described by Spencer, *M. complicatus* and *M. primus*, cannot be allied with the *Mesopalaeaster* type species. These specimens show indications of being juvenile promopalaeasterids.

Spencer and Wright (1966) elevated Schuchert's Mesopalaeasterinae to family rank and included within it a polyphyletic association of genera. No species therein contained seems to be at all similar or closely related to the type species of *Mesopalaeaster*.[9]

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[9] In searching the literature, this author was unable to find a publication corresponding to the author citation given by the *Treatise* for *Arisaigaster* Spencer, 1953. Correspondence with Mr. C. W. Wright has revealed that the genus was not actually published prior to its appearance in the *Treatise*. The name is available, however, because the *Treatise* description satisfies all requirements for a published genus. The proper citation of this genus is, therefore, "*Arisaigaster*

Spencer and Wright, 1966".

Genus *Mesopalaeaster* Schuchert, 1914

1914 *Mesopalaeaster* Schuchert, Charles [*partim*], p. 24.

1915 *Mesopalaeaster* Schuchert, Charles [*partim*], p. 74-77.

1916 *Belaster* Spencer, W. K., p. 73.

Mesopalaeaster Schuchert, Spencer, W. K. [*partim*], p. 84.

1934 *Siluraster*[Jaekel], Spencer, W. K., and Groom, Theodore, p. 233.

Belaster Spencer, Spencer, W. K., and Groom, Theodore, p. 233.

1966 *Mesopalaeaster* Schuchert, Spencer, W. K., and Wright, C. W. [*partim*], p. 51.

Diagnosis. -- There is a single genus in Mesopalaeasteridae; see family diagnosis above. All other genera which have been assigned to this family by other authors cannot, in light of new diagnostic characterization of the family, be accommodated therein.

Type species. -- *Palaeaster shaefferi* Hall, 1868, by original designation of Schuchert, 1914.

Discussion. -- Asteroids of the genus *Mesopalaeaster* are heavily plated and five-rayed. Adults possess long brachia with parallel margins. Single axillary inferomarginals are marginal only in young specimens; they tend to become occluded from the ambitus by more distal inferomarginal pairs as individuals increase in size. Long mouth-angle ossicles abut the single axillary in each buccal interbrachial area. There are nine columns of primary ossicles with secondary intercalating ossicles in papular areas between marginal and marginal and median dorsal columns in adult individuals.

Ambulacral ossicles slightly overlap the next more distal ones for the lengths of the brachia (Plate 6, figure 3; Plate 7, figures 1 a-b, 2a, 2c). Large ampullar perforations occur at adambulacral-ambulacral column junctions, each pore bordered by two adambulacral and two ambulacral ossicles. The elongate ridges on the ventral surfaces of the ambulacral ossicles do not allow alternate directions on the proximal brachia; podial arrangement was biserial as in the Hudsonasteridae.

External ossicle have a prosopon of small and medium-sized, discrete, spine-base structures. Each such monticule commonly has a central pit.

The mouth-angle ossicles are at least twice as long as adjacent adambulacrals (Plate 5, figures 3, 6; Plate 6, figures 1a, 1d, 4) in all known ontogenic stages.

The madreporite of the genus is known only from MCZ no. 478 (Plate 7, figures 2b, 2d). It is ovate in plan, slightly convex, and marked with relatively few, coarse striae, not all of which reach the geometric center of the exposed surface. Furthermore, the striae are not bifurcated on the known ossicle.

<u>Synonomic Discussion</u>. -- This genus has been used, since its erection by Schuchert in 1914, as a catch-all for numerous poorly preserved or otherwise difficult to examine specimens of unknown affinities. It was erected to accommodate those Paleozoic species Schuchert considered intermediate in form between <u>Hudsonaster</u> and <u>Promopalaeaster</u>.

Within it he placed fifteen species, eight of them so poorly known that he included them provisionally. Of the four Cincinnatian species he assigned to the genus with confidence, only the type species can remain. Palaeaster finei Ulrich, 1879 and Mesopalaeaster proavitus Schuchert, 1915 are included in a later section as developmental stages of a promopalaeasterid. Mesopalaeaster intermedius Schuchert, 1915 is a lanthanasterid [= Lanthanaster cruciformis Branstrator, 1972].

Discussion of other references in the generic synonomy of Mesopalaeaster are considered above in the familial synonomic discussion.

Mesopalaeaster shaefferi (Hall, 1878)

Plates 5-7

Text-figures 14, 17

1868 Palaeaster shaefferi Hall, James, p. 284, pl. 9, fig. 1.

1878 Palaeaster spinulosus Miller, S. A., and Dyer, C. B., p. 32, pl. 2, figs. 12 a-b.

Palaeaster longibrachiatus Miller, S. A., p. 102, pl. 3, fig. 4.

1881 Palaeaster exculptus Miller, S. A., p. 69, pl. 1, fig. 1.

1914 Mesopalaeaster shaefferi (Hall), Schuchert, Charles, p. 24.

Promopalaeaster exculptus (Miller), Schuchert, Charles, p. 33.

Promopalaeaster spinulosus (Miller and Dyer), Schuchert, Charles, p. 34.

1915 Mesopalaeaster shafferi (Hall), Schuchert, Charles [partim], p. 77-79, pl. 8, fig. 2, [non] fig. 1.

Promopalaeaster exculptus (Miller), Schuchert, Charles, p. 117-118, pl. 18, fig. 7, pl. 20, fig. 2.

Promopalaeaster spinulosus (Miller and Dyer), Schuchert, Charles, p. 115-117, pl. 16, fig. 2, pl. 17, figs. 1-2, pl. 18, figs. 1-3.

1916 Mesopalaeaster shafferi (Hall), Spencer, W. K., p. 80, 84, 98.

Promopalaeaster spinulosus (Miller and Dyer), Spencer, W. K., p. 99.

Promopalaeaster exsculptus [Miller], Spencer, W. K., p. 99.

1966 Mesopalaeaster shafferi (Hall), Spencer, W. K., and Wright, C. W. [partim], p. 51, fig. 49 (2b), [non] fig. 49 (2a).

Diagnosis. -- The genus and family are represented by a single recognized species. Until other species are recognized, the diagnostic characters of the family serve to diagnose this species.

Primary type material and locality. -- The holotype is AMNH no. 1195. Hall (1868, p. 284) writes that the specimen came from "shales of the Hudson-river group, Cincinnati, Ohio. From Mr. D. H. Shaeffer". No more exact locality information is available from labels currently with the specimen. Fauna associated with the specimen on the same, small slab does not seem to be useful in determining stratigraphic occurrence. Schuchert (1915, p. 79), without explanation, suggests that the specimen occurred "probably in the Maysville formation".

Other known specimens. -- Several other specimens have been assigned to M. shaefferi. Schuchert (1915) listed five specimens in addition to the holotype: USNM no. 60605, from Maysville rocks on Vine Street Hill in Cincinnati; FNMH no. 9568 (Faber Collection), from Maysville rocks in Cincinnati; USNM no. 59391, from Richmond rocks near Waynesville, Warren County, Ohio; USNM no. 23540, from the Utica shales near Rome, New York and YPM no. 13180, from Maysville rocks in Cincinnati. Of these specimens, however, only the last may be assigned with certainty to this species. The states of preservation of the other specimens prohibit even their familiar placement. The following well-preserved specimens may be added to this species: YPM no. 13180A (Plate 5, figures 5a, 5b), from Maysville rocks in Cincinnati; USNM no. 60621 (Plate 5, figures 4a, 4b), from Maysville Bellevue "Member" rocks on Rohs Hill [= Bald Knob] in Cincinnati; MCZ no. 478, the holotype of *Palaeaster spinulosus* Miller and Dyer, claimed by S. A. Miller and C. B. Dyer (the latter of whom collected the specimen) to have come from Cincinnati, but subsequently by Schuchert (1915, p. 116) to have come from Richmond rocks at "some locality considerably to the north of Cincinnati"[10]; USNM no. 40881, the holotype of *Palaeaster longibrachiatus* Miller, from the Richmondian near Clarksville, Clinton County, Ohio (Plate 5, figure 2); and USNM no. 60608, the holotype of *Palaeaster exculptus* Miller (Plate 5, figure 3; Plate 6, figure 3), from Richmond rocks near Waynesville, Warren County, Ohio.

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[10] Schuchert synonomized *Palaeaster longibrachiatus* Miller, 1878, which is known to have come from Richmond rocks near Clarksville, Clinton County, Ohio, with *P. spinulosus*.

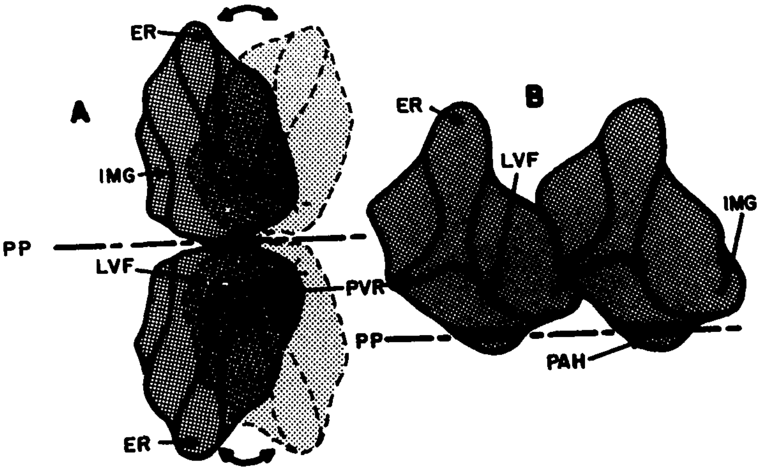
Description. -- the holotype has the following measurements: R = 21 mm., r = 6 mm., wr = 5-7 mm. Other specimens from which radial length can be accurately determined range from 20 mm. to 38 mm. Proportions of both ossicles and thecae are maintained by all known examples of the species.

Ambulacral ossicles are long, moderately wide, but not as thick as the ambulacrals of Hudsonaster. The details of ambulacral ossicle structure are best seen on USNM no. 60608 (Plate 7, figures 1 a-b) where the ambulacral grooves are wide open and the skeleton is slightly disarticulated. The elongate ridge of each ambulacral lies slightly diagonally on the ventral surface of the ossicle, the adradial end being more proximal for the entire arm length than the broader, higher abradial end. The proximal branch of the adradial V-shaped ridge is more prominent than the distal, which is interrupted close to the elongate ridge by the lateral podial vessel furrow. The ridges on the ventral surface of the ambulacral columns define biserially arranged podial basins for the entire brachial lengths. The podial basins are shared equally by successive ambulacral ossicles. In ventral aspect, the proximal edge of each ambulacral ossicle overlies the distal edge of the next more distal ambulacral ossicle. Interossicular musculature was accommodated in an elongate groove parallel to the ossicular width on the distal edge of each ambulacral. The nature of this muscle insertion area on the proximal edge of each ambulacral is unknown, because no ossicle appears to have been overturned to expose the appropriate ossicular aspect. For a similar reason, the nature of the dorsal (internal) ossicular surface is unknown from any specimen. Ambulacral ossicles of adjacent columns did not broadly abut with each other along the perradial plane. Rather, each ambulacral ossicle tapered slightly to a narrowly rounded perradial hinge and contacted its paired ossicle of the adjacent column for less than its entire width. This type of hinge structure (Text-figure 17) allowed horizontal as well as vertical flexure at each perradial ossicle junction, and permitted great flexibility of the brachia. In the disc area, the lengths of the hinges increase; this decreased horizontal movability of the ambulacral ossicles. Less flexibility was required here.

The adambulacral ossicles of M. shaefferi are well displayed by a number of specimens. They are obviously quite different in some respects from those of other Cincinnatian asteriadinids. Unlike those of the husonasterids and promopalaeasterids, those of this family are longer than wide for the length of each brachium. Furthermore, the adambulacral spines of each ossicle are arranged in a horizontally pectinate series (Plate 6, figure 2a; Plate 7, figure 2a). The obviously weak articulation between opposing ambulacral ossicles, as described above, suggests that members of this group were not accomplished grapplers, but preferred more quiescent prey or were strict scavengers.

As in other Ordovician Asteriadina, each adambulacral ossicle contacted a single ambulacral ossicle at the column junctions. The large, ovate opening occurring at the junction of each two adjacent adambulacrals and their respective ambulacral ossicles is indisputable evidence that podial ampullae perforated the skeleton and became internal

Text-figure 17. -- Morphology and movement of ambulacral ossicles of *Mesopalaeaster shaefferi*. A. Ventral aspect of two ambulacral ossicles abutting along perradial palne (PP). Because perradial ambulacral hinge (PAH) is not as wide as individual ossicles, abradial ends of ossicles could swing proximally and distally, as well as up and down. Elongate ridge (ER); interossicular muscle groove between successive ambulacrals (IMG); lateral hydrovascular vessel furrow (LVF); proximal V-shaped ridge (PVR). B. Perradial aspect of two successive ambulacral ossicles (proximal to left).


A
ER
IMG
PP
LVF
PVR
ER
B
ER
LVF
IMG
PP
PAH

in Ordovician asteriadinids (Plate 7, figure 1a). Homologous structures exist in both the hudsonasterids and promopalaeasterids.

No intercalary ossicles separate adambulacral ossicles from the adjacent inferomarginals in Mesopalaeasteridae.

The pustulose brachial inferomarginals of *M. shaefferi* are distally longer than wide in ventral aspect. The proximal-most one or two (depending on individual size) are wider than long. Axillary inferomarginals number three or five in the known specimens; larger specimens possess more axillary inferomarginals. Successive ossicles fit closely along their edges, but the usual muscle excavations in proximal and distal surfaces are present in the inferomarginals (Plate 5, figure 3; Plate 7, figure 2c).

As indicated above, a diagnostic characteristic of the Mesopalaeasteridae is the exact or near one-to-one ratio between the number of ossicles in each primary perivascular and extravascular column. The advantage of this adaxial ossicular arrangement becomes clear as one observes modern asteroids, such as *Henricia*, *Ctenaster*, and *Luidia*, which possess it. These animals, whether common to firm (*Henricia*) or soft (*Ctenaster*, *Luidia*) substrates erect very small spines along the margins of their adambulacral and marginal ossicles to form small enclosed passageways, termed cribriform organs, along the edges of their lateral and ventral ossicles. Cilia-driven water currents within these passageways move particulate matter, including potential food, from the dorsal surface, around the margins of the brachia, and into the food groove. Once in the groove, detrital particles are moved aborally and eventually reach the mouth. Food particles are digested in the stomach and non-digestibles either eliminated by way of the mouth opening, or through an anus. The adaxial ossicular arrangement in Mesopalaeaster permits the formation of such passageways. It may be an adaptation toward detrital feeding. As in the non-paxillose, epifaunal, modern genus Henricia, the detrital feeding mechanism was probably supplemental to scavenging or weak predation.

Broadly rounded ossicle lobes arising from the dorsal proximal and distal edges of each successive pair of inferomarginals align with and internally meet a ventral lobe of a superomarginal ossicle (Plate 5, figure 5a). Some well-preserved specimens show that the species possessed a single column of biserially arranged intermarginal ossicles (Plate 7, figure 2b) over this junction of marginal ossicles. Each biserial pair is composed of a larger, more distal and external pustulose ossicle, and a smaller, more proximal and internal ossicle. Both ossicles carried spines. These intermarginal ossicles have excavated margins to accommodate papular extensions between them. The presence of these ossicles allowed flexibility in this area of the skeleton. The spines on them offered protection for the respiratory papulae in this thin area of the body wall.

In addition to the ventral extensions of the superomarginal ossicles mentioned above, each also has an adradial and proximal lobe. The proximal lobe slightly overlies the next more proximal superomarginal. The adradial lobe meets an abradial lobe from its adaxially arranged median dorsal where arm diameter is small. Where brachial diameter is large, each adradial lobe is connected to its corresponding median dorsal by means of intermediate, biserial interdorsal ossicle pairs. Both the superomarginals and interdorsals possess the usual pustulose prosopon, suggesting the former presence of a coat of small spines. Each of these ossicles of _M_. _shaefferi_, however, possesses one relatively large spine-base pustule with smaller ones surrounding it. This central spine-base structure probably held a longer or broader spine. Excavated margins on the interdorsal ossicles indicate the presence of respiratory papulae through most of the dorsal surface area of each brachium in the living animal. The dorsal spines provided protection for these papulae.

The median dorsals of _M_. _shaefferi_ are larger than the flanking interdorsals. They are also more bilaterally symmetrical with prominent ossicle lobes proximally, distally and laterally. They are wider than long for the length of the brachia. Like the other dorsal ossicles, each possesses a prominent central spine-base structure with smaller ones surrounding it.

The holotype (Plate 5, figure 1; Plate 6, figure 1) presents a ventral aspect. To confirm the dorsal aspects of the species represented by it, it was necessary to remove a portion of one brachium (which had been removed sometime earlier, but never described). It is shown in lateral and dorsal aspect on Plate 6, figures 1 b-c. The dorsal arm structure of the holotype confirms that described above from other specimens. USNM no. 60621 shows the same ossicles (Plate 6, figure 2b) in a specimen which has been flattened during preservation.

Because only one recognized specimen of *M. shaefferi* shows the ossicles of the apical field, all information of the apical field must come from it. Disarrangement of the specimen allows no reliable information which may be utilized in a reconstruction. There seems to be no apical coronet, as in the hudsonasteridae; rather, all ossicles appear to be of about the same size (Plate 7, figure 2d). Only the madreporite and the superomarginals appear distinctly large. The excavated nature of the ossicle margins for the accommodation of dermal papulae is continued onto the disc and into the apical field, as is the characteristic of a single prominent spine surrounded by smaller spines on each ossicle.

The mouth-angle ossicles of this species are notably large (Plate 6, figures 1d, 3, 4). As indicated in the introduction, large mouth-angle ossicles, as carriers of more numerous oral spines than smaller mouth-angle ossicles, are usually a characteristic of a scavenging or detrital-feeding asteroid, rather than an actively predaceous one. This characteristic of *M. shaefferi* corroborates the feeding model proposed for the species.

There does not seem to have been extrathecal accessory ossicles other than spines already mentioned in this species. As in other Ordovician asteroids from Cincinnati, however, preservation does not seem to have been sufficiently fine to preserve pedicellaria, should they have been present.

Synonomic Discussion. -- James Hall (1868) described the species from a single specimen and place it in *Palaeaster*. His original spelling of the species name was *P. shaefferi*; its respelling by Schuchert

(1915, p. 77) to P. shafferi is an unjustified emendation.

The three species described by S. A. Miller, namely P. spinulosus, P. longibrachiatus, and P. exculptus, are herein considered subjective synonyms of P. shaefferi Hall.

Schuchert (1914) established Mesopalaeaster with P. shaefferi as its type species, He synonomized P. spinulosus and P. longibrachiatus, but placed both in his new genus Promopalaeaster. In 1915, he explained his action and noted the similarity between these latter two species and P. exculptus, but left all three species in Promopalaeaster.

Spencer (1916) obviously utilized Schuchert's 1915 publication as the source of data for his characterization of Miller's three species. Following Schuchert, he placed them in Promopalaester. His emendation of P. exculptus to P. exsculptus is, however, an unjustified emendation.

Spencer and Wright (1966) also used Schuchert's work as their primary source of information on M. shaefferi. They refigured Schuchert's figure of a specimen erroneously identified as M. shaefferi.

Family PROMOPALAEASTERIDAE Schuchert, 1914

1914	Promopalaeasteridae Schuchert, Charles [partim], p. 6.
1915	Promopalaeasteridae Schuchert, Charles [partim], p. 73-74.
1916	Promopalaeasteridae Schuchert, Spencer, W. K. [partim], p. 78-79.
1966	Mesopalaeasteridae Schuchert, Spencer, W. K., and Wright, C. W. [partim], p. 51.
	Promopalaesteridae Schuchert, Spencer, W. K., and Wright,

C. W. [partim], p. 53.

Diagnosis. -- Asteriadina with accessory ossicles intercalating between inferomarginal, superomarginal and median dorsal primary columns (Text-figure 14); few columns in juveniles, many in adults. Ratio between the numbers of ossicles in a perivascular column and an extravascular primary column greater than 1:1; usually nearer 2:1. Mouth-angle ossicles prominent in juvenile individuals, becoming less prominent in adults. Adambulacral spines on each brachial adambulacral ossicle arranged in a vertical, pectinate series composed of two or more spines. Podial basins biserial on small individuals, becoming quadriserial proximally on larger individuals.

Discussion. -- Schuchert (1914) erected Promopalaeasteridae to accommodate his three new subfamilies, Mesopalaeasterinae, Promopalaeasterinae, and Anorthasterinae, and to provide a taxon to distinguish these three subfamilies, which he considered closely related, from other forms he included in his new superfamily Promopalaeasteriacea. He explained this in his 1915 contribution.

On the basis of information acquired from the re-examination of the original specimen material and observations on specimens collected subsequent to Schuchert's work, the present investigation proposes a taxonomic reorganization of the specimens Schuchert included in his Promopalaeasteridae. Some species originally included are herein removed or synonomized with others. Two new genera must be erected.

The Treatise elevates Schuchert's Mesopalaeasterinae to family rank, but includes it and several other families, including Hudsonasteridae, in its newly elevated superfamily Palaeasteracea. This investigation does not so relate the Mesopalaeasteridae and the Hudsonasteridae. The *Treatise* includes *Promopalaeaster* Schuchert, *Anorthaster* Schuchert, and ?*Kyraster* Lehmann in its Promopalaeasteridae. *Anorthaster* was erected by Schuchert on the characteristics of a specimen which resulted from preservational or preparational damage. It is conceptually invalid. ?*Kyraster* is a questionable genus of the German Lower Devonian, based on a very poorly preserved specimen. There seems no reason to include ?*Kyraster* in the Promopalaeasteridae.

Genus *Promopalaeaster* Schuchert, 1914

1914 *Promopalaeaster* Schuchert, Charles [*partim*], p. 33-34.
1915 *Promopalaeaster* Schuchert, Charles [*partim*], p. 102-106.
1916 *Promopalaeaster* Schuchert, Spencer, W. K. [*partim*], p. 91-92.
1957 *Promopalaeaster* Schuchert, Cramer, H. R. [*partim*], p. 903, [*non*] pl. 108, figs. 3, 4.
1966 *Promopalaeaster* Schuchert, Spencer, W. K., and Wright, C. W. [*partim*], p. 53.

Diagnosis. -- Promopalaeasteridae with extravascular skeleton of massive, abutting primary and secondary ossicles. Papulae present, but not numerous; emitting at junctions of dorsal and lateral ossicles which are not strongly modified for their passage through the body wall. Adoral carinae poorly developed in the moderately large (R = 44 mm.) specimen. Two primary spines in well-defined, vertical series on each proximal adambulacral ossicle; distal adambulacrals with a few moderate-sized spines among numerous smaller ones.

Type species. -- *Palaeaster speciosus* Meek, 1872 [= *Palaeaster granulosus* Meek, 1872, (*non* Hall, 1868)] by original designation of

Schuchert, 1914.

Discussion. -- Asteroids of the genus *Promopalaeaster* possess numerous gibbous dorsal ossicles and are five-rayed. The only known specimen has slightly petalloid, broadly acuminate brachia. A single axillary is occluded from the margin by two pairs of adjacent axillary inferomarginals, but was presumably marginal at an earlier ontogenic stage. Mouth-angle ossicles are separated from the unpaired axillary in each axil by one pair of adnate adambulacrals forming a very short adoral carina. There are nine columns of primary brachial ossicles with single rows of interdorsals and double rows of intermarginals exposed between the median dorsal and superomarginals columns and between the marginal columns, respectively.

Since *Promopalaeaster* is known from a single specimen, a detailed description of the specimen typifying both the genus and species follows under the description of the species. The generic characters of this specimen are summarized in the diagnosis above.

Synonomic discussion. -- Schuchert (1914) erected *Promopalaeaster* to accommodate ten Middle and Upper Ordovician species. A revision of the genus is necessary because the characteristics Schuchert employed (1915) to define the genus and differentiate its species cannot stand up to paleobiologic scrutiny. Such characteristics cannot be used in a taxonomic separation of modern asteroids. Furthermore, they are useless in defining and differentiating taxonomic entities when applied to the larger number of fossil specimens now available. In terms of the taxobases proposed herein, the monotypic type species Schuchert chose for *Promopalaeaster* is not generically allied to other recognizable species of Promopalaeasteridae. Two new genera must be erected to accommodate the diversity of forms properly assigned to the family. Some other species which Schuchert included in *Promopalaeaster* must be removed from the family.

The reassignment of species Schuchert aligned under *Promopalaeaster* is as follows: *Palaeaster speciosus* Meek remains as the type species; *Palaeaster wykoffi* Miller and Gurley, *Palaeaster magnificus* Miller, and *Promopalaeaster bellulus* Schuchert become junior synonyms of *Kenothecaster* gen. n. *miamiensis* (Miller); *Palaeaster dyeri* Meek becomes *Kenothecaster dyeri* (Meek); *Palaeaster exculptus* Miller and *Palaeaster spinulosus* Miller and Dyer become junior synonyms of *Mesopalaeaster shaefferi* (Hall); *Palaeaster wilsoni* Raymond becomes a junior synonym of *Salteraster huxleyi* (Billings); *Promopalaeaster prenuntius* Schuchert becomes *Neardisaster* gen. n. *prenuntius* (Schuchert); and *Palaeaster granulosus* Hall is a name which cannot be ascribed to any specimen.[11]

Spencer (1916) referred his readers to Schuchert's work for an authoritative characterization of *Promopalaeaster*. His main concern

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[11] The type and only known specimen is lost as reported by Schuchert. It was never figured. The characterization of the species offered by Hall does not fit any known specimen from the Cincinnati area. This author has made an exhaustive search for the lost holotype, but could not find it in the collection of any major North American museum.

was the refutation of Schuchert's supposed evolutionary sequence of *Hudsonaster* to *Mesopalaeaster* to *Promopalaeaster*, rather than generic diagnosis or characterization of American forms. He suggests, however, that there are, in reality, fewer forms of *Promopalaeaster* in North American strata than Schuchert's list of species would indicate. The present work agrees with his latter contention.

Cramer (1957) quoted, as a description of *Promopalaeaster*, the characterization of Promopalaeasterinae which Spencer, in turn, quoted from Schuchert. With the following statements, he then placed his new Martinsburg Shale species *Promopalaeaster pricei* in that genus:

> "There is little doubt that the specimen described in this article is of this genus [*Promopalaeaster*]. The odontophore and any other plates which may be in the axillary region, except the adambulacrals, of which there are two pairs, are absent. This is typical in the echinoderm integumental structure. The specimen described has six interbrachial marginals, all spinose. There are only two rows of proximal podial openings."

The interbrachial marginals which Cramer mentions are not arranged similar to those of the promopalaeasterids. The fact that his specimen possesses only two rows of proximal podial basins is a hint that it is not a promopalaeasterid. Additional specimens of this species were, for a short while, in the hands of Dr. Horace G. Richards of the Philadelphia Academy of Natural Sciences. Prior to the time the specimen material was reclaimed by its amateur collector, this author was permitted to make latex pulls of the material. These peels (UCGM no. 40761) make it clear that Cramer's species is generically allied to Petraster speciosus (Miller and Dyer). It is not a promopalaeasterid.

The Treatise characterizes the genus as possessing the familial characteristics of Promopalaeasteridae Schuchert. These are, "arms fused at base and generally more or less cylindrical; ambulacrals compressed and proximally in 4 rows; adambulacrals broad." The genus, as revised herein, is less comprehensive than that of the Treatise.

The familial characterization offered by the Treatise is somewhat misleading. "Ambulacrals" is used, in the same sentence, to refer to both the ambulacral ossicles and the podia. In the Promopalaeasteridae the ambulacral ossicles are typically wide and short (compressed), and the podia, but not the ambulacral ossicles, are arranged in four rows in the proximal brachia of ephebic and older specimens. There is no asteroid which possesses more than two columns of ambulacral ossicles in each brachium.

Promopalaeaster speciosus (Meek, 1872)

Plate 8

Text-figure 18

1868 [non]Palaeaster granulosa Hall, James, p. 285.

1872 Palaeaster granulosus Hall, Meek, F. B., p. 277.

Palaeaster speciosus Meek, F. B., p. 277.

1873 ? Palaeaster granulosus Hall, Meek, F. B., p. 60-61, pl. 4, figs. 3 a-c.

Palaeaster speciosus Meek, Meek, F. B., p. 61, pl. 4, figs. 3 a-c.

1914 Promopalaeaster speciosus (Meek), Schuchert, Charles [partim], p. 34.

1915 Promopalaeaster speciosus (Meek), Schuchert, Charles [partim], p. 109-112, pl. 14, figs. 3-4, pl. 15, figs. 1-4.

Diagnosis. -- The genus, as revised herein, is monotypic. Until other species are recognized, the diagnostic characters of the genus serve to diagnose the species.

Primary type material and locality. -- Labels with the monotypic holotype (MCZ no. 22, Dyer Collection) authenticate only that it is from Cincinnati, Ohio. No more accurate stratigraphic or locality data is available from the specimen or Meek's publications, although Schuchert (1915, p. 110-111) states unequivocally that the specimen was collected "in the Maysvillian at Cincinnati, Ohio". Although there is no reason to doubt this latter information, its authenticity cannot be documented and it must be regarded as an inference on Schuchert's part.

Description. -- The specimen has the following measurements: R = 44 mm., r = 13 mm., wr = 17 mm. The specimen is free from its matrix and both dorsal and ventral aspects are available from it. Two, nearly complete, adjacent brachia meet at their bases in an acute angle (Plate 8, figures 1 a-b). Each arm tapers slowly to a broadly acuminate tip. The ambulacral groove of one arm is open and has been cleaned of its matrix.

Each ambulacral ossicle is high, short and wide, with a prominent ventral carina. Adradial nodes on the ventral carinae are prominent, forming a deep ambulacral channel in at least the distal two-thirds of the ambulacral groove (nodes not exposed proximally on specimen). On the distal half of each brachium the ventral carinae are straight and form two columns of podial basins in the ambulacral groove. On the proximal half they lie alternately diagonal on the ambulacral ossicle bodies and form four longitudinal columns of podial basins. Dentition marks abutting surfaces between opposite ambulacral ossicles of adjacent columns. Contact with adjacent adambulacral ossicles is by means of a prominent abradial flange on the ventral carina.

The distal edge and most of the ossicle body of each ambulacral ossicle overlies the proximal portion of the next more distal ossicle. In longitudinal section, the ossicle body of each ambulacral ossicle does not lie in or near a horizontal plane, but rather in an oblique plane inclined approximately forty-five degrees to the horizontal. A similar condition is shown by modern representatives of the Asteriadina.

Distal adambulacral ossicles of _P_. _speciosus_ have numerous small, undifferentiated groove and subadambulacral spines (Plate 8, figures 1e, 1g). Proximally, a vertically pectinate series of more prominent primary spine-base structures becomes apparent, but numerous smaller spine-base structures still mark the ossicle surface (Plate 8, figure 1h). Two large, primary adambulacral spine-base pustules mark the surfaces of the most proximal two or three adambulacrals. A few large, smooth, adambulacral groove spines remain articulated to their respective ossicles in the proximal parts of the ambulacral grooves. As is characteristic of the family, individual adambulacral ossicles are short and wide, although the difference between these two parameters lessens in distal ossicles.

No intercalary ossicles separate adambulacral ossicles from adjacent inferomarginals in any species assigned to Promopalaeasteridae.

The pustulose brachial inferomarginals are wider than long for lengths of the arms. In specimens the size of the holotype, there are two adnate pairs of axillary inferomarginals, in addition to a single, unpaired axillary which is not the functional odontophore. The functional odontophore is internal in the Promopalaeasteridae. The references by earlier authors to the single, unpaired axillary in P. speciosus as an odontophore are in error.

The prosopon of the inferomarginal ossicles is of small spines on minute, perforate, spine-base pustules. One spine-base structure on some inferomarginal ossicles is notably larger than the others. These enlarged pustules probably carried a larger spine than the other pustules. Individual inferomarginal ossicles are large. There are fewer inferomarginals ossicles than adambulacrals in adjacent columns. There are no obvious lateral flanges or surface carinae, indicating that successive ossicles fit closely and that large papulae were not present adjacent to the inferomarginal columns.

The intermarginal ossicles of P. speciosus maintain the same prosopon as the inferomarginals and are nearly equal in size to adjacent ossicles of this latter type on the more distal portions of the brachia (Plate 8, figures 1 e-g). Close examination reveals that the intermarginal ossicles are arranged in series composed of two subseries. A small, more internal subseries intercalates between each subseries of larger intermarginal ossicles (Plate 8, figures 1f, 1g). There is one of these paired series for each inferomarginal and corresponding superomarginal on each brachium lateral surface. As in Mesopalaeaster, these ossicles provided an armored, flexible body wall between the marginal columns. When compared with the intermarginals of other promopalaeasterid species, however, these ossicles of P. speciosus are relatively massive and carried many more spines. Although papulae obviously emitted from the intermarginal area, there was not a great deal of ossicle modification to accommodate them.

The superomarginals of P. speciosus are slightly more prominent than the adjacent intermarginals. They maintain the charateristic multi-pustulose prosopon of the extrathecal ossicles, although these ossicles do not seem to possess the single enlarged spine-base structure typical of the ossicles in other columns. The ossicles are wider than long for the length of the brachia. They each have a flange which underlies the more dorsal ossicles of the corresponding intermarginal series. There does not appear to be a corresponding flange protruding adradially beneath the interdorsal columns.

Like the intermarginals, the interdorsals of P. speciosus are relatively massive and carry many more spines than similar ossicles of other promopalaeasterids. Abradial interdorsals are at least as prominent as adjacent superomarginals (Plate 8, figures 1c, 1f). The ossicles are only slightly excavated at their margins for the accommodation of dermal papulae. Furthermore, the paired subseries arrangement common to the interdorsals of other promopalaeasterids and the intermarginals of all promopalaeasterids does not occur in

P. speciosus (Text-figure 18).

Median dorsals are the largest ossicles on the dorsal surface of this species (Plate 8, figure 1b). They are multipustulose and usually have one or more primary spine-base structures surrounded by smaller perforate pustules. The enlarged terminal ossicle of the median dorsal column (Plate 8, figure 1d) is maintained by one of the two brachia of the holotype. Modern asteroids which possess large terminal ossicles as adults usually possess them throughout ontogeny.

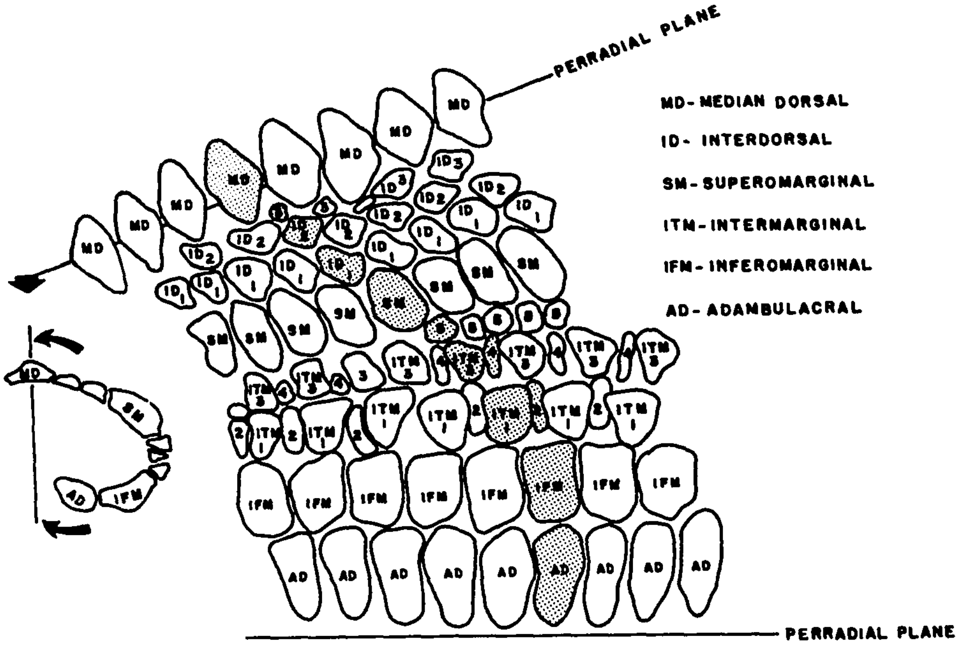
The madreporite is unknown.

Most of the apical field ossicles of this species are obscurred by a hard matrix and cannot be observed. Near the center of the field, however, the matrix has been removed. The ossicles of this area possess the prosopon of the median dorsals and are as large and tumid as these latter ossicles. Exact arrangement cannot be determined.

There is a short adoral carina (Plate 8, figure 1h) composed of a single pair of adambulacral ossicles in each oral axillary area of the holotype. Mouth-angle ossicles with prominent oral spines mounted on high, prominent spine-base structures show on the holotype. Smaller pustules occur between the primary oral spine-base structures on the ventral surfaces of the ossicles. The presence or absence of a torus cannot be verified.

Synonomic discussion. -- The species had a somewhat confusing beginning because it was proposed provisionally by Meek, 1872. In a footnote under the description of his new species _Palaeaster incomptus_, Meek indecisively described a specimen which "presents

Text-figure 18. -- External ossicles of Promopalaeaster speciosus. Brachial portion flattened to show ossicle row arrangement (one row shaded). Note double subseries in intermarginal columns, but single series in interdorsal columns of this specimen. Small diagram on left shows approximate columnar orientation about perradial plane prior to diagrammatic flattening.


PERRADIAL PLANE
MD- MEDIAN DORSAL
ID- INTERDORSAL
SM- SUPEROMARGINAL
ITM- INTERMARGINAL
IFM- INFEROMARGINAL
AD- ADAMBULACRAL
MD
ID
SM
ITM
IFM
AD
PERRADIAL PLANE

many features indicating close relations to *Palaeaster granulosus* of Hall". Meek further describes the specimen and then writes, "If this should prove to be a new species, I would propose to call it *Palaeaster speciosus*." He redescribed the same specimen in 1873 under "*Palaeaster granulosus*, Hall?" and reiterates his provisional assignment of the specimen to a new species.

Schuchert (1914, 1915) accepted Meek's provisionally proposed name for the specimen, which he (Schuchert) considered distinct from Hall's species.[12] He included *Asterias antiquata* Locke, 1848 in his specific synonmy. This latter species is another poorly characterized species with a misplaced holotype. It cannot, with certainty, be synonomized with *P. speciosus*.

Kenothecaster gen. n.

1868-1914	*Palaeaster* of Authors [*partim*]
1914	*Mesopalaeaster* Schuchert, Charles [*partim*], p. 24.
	Promopalaeaster Schuchert, Charles [*partim*], p. 33-34.
	Anorthaster Schuchert, Charles, p. 11.
1915	*Mesopalaeaster* Schuchert, Charles [*partim*], p. 74-77.
	Promopalaeaster Schuchert, Charles [*partim*], p. 102-106.
	Anorthaster Schuchert, Charles, p. 125-126.
1966	*Promopalaeaster* Schuchert, Spencer, W. K., and Wright,

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[12] As indicated above, Hall's species was never figured and the holotype had been lost prior to Schuchert's investigations. Verification that the two species are distinct is unlikely ever to be possible.

C. W. [partim], p. 53, [non] fig. 50 (2 a-b).

Anorthaster Schuchert, Spencer, W. K., and Wright, C. W., p. 53.

Diagnosis. -- Promopaleasteridae with extravascular skeleton of abutting and overlapping, finger-like accessory ossicles which serve to allow passage of numerous, large papular structures through the skeletonized lateral and dorsal body wall. Interdorsal and intermarginal ossicle columns arranged in biserial lateral or transverse rows. Adoral carinae developed in ephebic and geratic individuals; generally composed of at least two pairs of adnate adambulacral ossicles in each oral interradius. Adambulacral spines in well-developed, polyacanthate, vertically pectinate series in ephebic and older individuals. Most distal adambulacrals may have numerous, undifferentiated and unaligned spines.

Type species. -- Palaeaster finei Ulrich, 1879.

Etymology of new name. -- Greek kenos, empty; Greek theke, a case or box (a term commonly applied to echinoderm bodies); Greek aster, a star or starfish. The name refers to the fact established herein that these animals were stomach-everting feeders and, thus, did not take large quantities of food into their thecae.

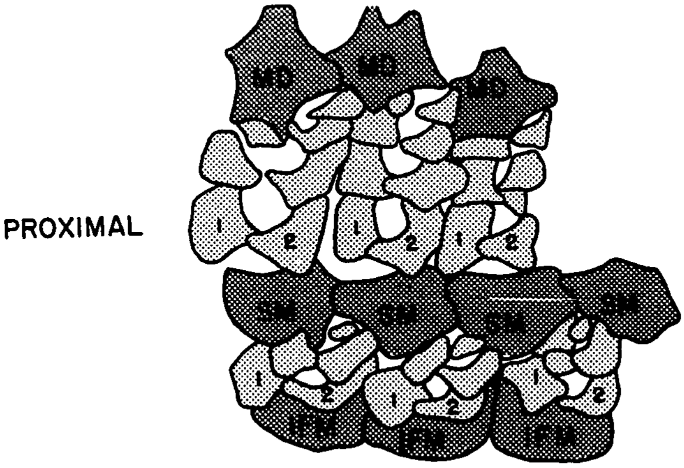
Discussion. -- Asteroids of the genus Kenothecaster possess numerous columns of intermarginal and interdorsal ossicles as adults. These ossicles are arranged in double subseries between each superomarginal and its corresponding median dorsal or inferomarginal (Text-figure 19). Specimens possess slightly petalloid to straight-sided brachia, depending on ontogenic development and species. An unpaired, most-proximal axillary may or may not be present on the thecal surface, depending upon the ontogenic development of the individual (and visibility also dependent on the degree of distortion which occurred during preservation). The most-proximal inferomarginal axillary tends to become internal in larger individuals. Larger individuals also tend to develop more pairs of axillary inferomarginals than smaller individuals; these may number from one to four pairs in each axil.

The adoral carinae are well-developed in most specimens of this genus. As in the modern genera *Pisaster* and *Asterias*, this characteristic is probably a modification suiting its possessor to a stomach-everting, predaceous feeding habit. Such an oral structure and feeding habit usually accompany a very flexible skeleton and four columns of podia in modern asteroids. These two characteristics are also shared by *Kenothecaster* species.

There are usually numerous primary spines arranged in a pectinate, vertical series on each proximal and brachial mid-length adambulacral ossicle of this genus. Distal adambulacrals do not have such vertical series of primary spines. The change in adambulacral spination occurs distal to the transition from two to four distinct columns of podial basins.

Synonomic Discussion. -- Prior to Schuchert's investigations most fossil asteroid species described from the Cincinnati area were assigned to Hall's genus *Palaeaster*. Schuchert erected three new genera to accommodate most Ordovician forms from the Cincinnati area formerly assigned to *Palaeaster*. Believing that he had established a nomen-

Text-figure 19. -- Flattened brachial portion of *Kenothecaster finei* (UMGM no. 6230) showing double subseries of interdorsal and intermarginal ossicles characteristic of the genus. Abbreviations as in Text-figure 18. Dark stipple = primary ossicle columns.


MD
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clatorial groundwork, he supposed that his genera and species were probably too comprehensive (1915, p. 10) and left it to the future student to "separate and reject". The present investigation agrees that Schucert's genera were too comprehensive. It synonomizes many of the species he recognized, however. This indicates that the asteroid subclass is represented in Cincinnatian strata by a few, distinct forms, rather than the plethora of species recognized by Schuchert and earlier workers.

Promopalaeaster has already been reduced to a single specimen. *Kenothecaster* is herein erected to accommodate a sequence of closely related species, most specimens of which were assigned to *Promopalaeaster* by Schuchert, but which differ at the generic level from *P. speciosus*. Schuchert included some additional specimens now placed in *Kenothecaster* in *Mesopalaeaster* and *Anorthaster*.

Kenothecaster finei (Ulrich, 1879)

Plates 9-11

Text-figure 19.

1879	*Palaeaster finei* Ulrich, E. O., p. 19, pl. 7, figs. 15 a-b.
1914	*Mesopalaeaster finei* (Ulrich), Schuchert, Charles, p. 25.
1915	*Mesopalaeaster finei* (Ulrich), Schuchert, Charles, p. 81-82, pl. 7, fig. 5, pl. 9, fig. 5.
	Mesopalaeaster proavitus Schuchert, Charles, p. 83-84.

Diagnosis. — *Kenothecaster* with brachial superomarginals noticably more prominent than adjacent accessory ossicles; each superomarginal with a thin, proximal flange that overlaps the next more proximal superomarginal. Ossicle prosopon generally of small, contiguous, perforate spine-base structures. Small articulating spines produced a monotonous armature, except for one enlarged spine on each non-axillary inferomarginal in all but the smallest specimens. Subadambulacral spines long, thin, terete and acuminate. Groove spines similar, but shorter.

Primary type material and occurrence. -- The type materials of both Palaeaster finei Ulrich and Mesopalaeaster proavitus Schuchert are suites of specimens (= cotype suites). Lectotypes and paralectotypes must be designated for each species even though M. proavitus is herein considered in subjective synonomy.

The lectotype of Palaeaster finei is fixed herein as the specimen figured on Plate 9, figures 1 a-b. It is from Ulrich cotypes (USNM no. 60604) and has been circled on its slab by this author to distinguish it from the other specimens in the suite which become paralectotypes. Material which may have been part of Ulrich's original suite is catalogued under YPM no. 14779, but because of this uncertainty, this latter material is specifically excluded from paralectotype designation. No specimens known to this author correspond to the drawn figures published by Ulrich when he described the species.

The largest fragment (Plate 9, figures 2a, 2d) of the Mesopalaeaster proavitus syntypes (FMNH no. 54069, Walker Collection) is herein fixed as the lectotype of the species; the remainder of the fragments under that museum number become paralectotypes. M. proavitus has not been previously figured.

Ulrich's specimens represent immature individuals from the Eden Shale in eastern Cincinnati. Schuchert's more mature specimens came from the same rock unit across the Ohio River in Covington, Kentucky. Mr. William H. White Jr. of Milford, Ohio found a number of well-preserved, small specimens representing a range of early juvenile ontogenic stages. Mr. White's specimens (Plate 11) came from the Eden Shale at Beechmond and Elstun Avenues in eastern Cincinnati. They have been donated to the University of Cincinnati Museum of Paleontology (UCGM nos. 40371-40383). A fragment (USNM no. 92613) of what would be the largest known indiviudal of this species (Plate 10, figure 1) comes from an unknown stratum in Covington, Kentucky. The largest specimen in a suite of materials from an unknown locality in Cincinnati (AMNH no. 1196) also represents a large individual and displays well the generic and specific characteristics of large individuals of the species (Plate 10, figures 3 a-d). UCGM no. 40758 (Winnes' Collection) was collected near Augusta, Bracken County, Kentucky.

<u>Description</u>. -- The generic description and the species diagnosis serve to describe and distinguish <u>K</u>. <u>finei</u> from other Cincinnatian Asteriadina. Some important information on ontogeny in early asteroids is made available by the numerous known specimens of this species. Utilizing the principle established by neontologists that asteroid size is a reliable indicator of maturity, changes occurring during the maturation of <u>K</u>. <u>finei</u> can be documented by assembling some specimens in a sequence of growth stages. Individual specimens are placed in the sequence on the basis of their radial length. Mr. White's Elstun Avenue specimens range in radial length from 1.5 mm. to about 8 mm. The type suite of the species contains specimens ranging in radial

length from about 6 mm. to 11 mm. The lectotype of M. proavitus, which belongs to this species, has a radial length of about 18 mm. A specimen in the Museum of Paleontology at the University of Michigan (no. 6230) has a radial length of about 20 mm. UCGM no. 40758 has a radial length of about 25 mm., and the largest nearly complete specimen (AMNH no. 1196) has a radial length of nearly 30 mm.

Some facts on early asteroid developmental ontogeny are available from these specimens. The adaxial or non-adaxial relationship between perivascular and extravascular ossicles is apparent from the smallest of juvenile growth stages. The adambulacrals of K. finei are more numerous than adjacent inferomarginals throughout ontogeny. Mouth-angle ossicles establish a size relationship to adjacent adambulacrals early in ontogeny (Plate 11, figures 1b, 2a) and maintain it throughout the growth of the individual (Plate 9, figures 1b, 2d); the mouth-angle ossicles in all specimens of K. finei are about three times as large as adjacent adambulacral ossicles. The adoral carinae do not develop in K. finei until after individuals reach a radial length of at least 20 mm. Unpaired axillaries become progressively more isolated from the lateral margin of the theca. In this species they are isolated from the ambitus by the time the radial length is 6 mm. (Plate 11, figures 1b, 2a; Plate 9, figure 2d; Plate 10, figure 3b); the first paired axillaries are no longer on the abmitus at radial length 18 mm. The youngest specimens (R = less than 3 mm; Plate 11, figures 1, 5, 6) do not show interdorsal or intermarginal accessory ossicles in this species; both kinds of ossicles are present by R = 5 mm. (Plate 11, figures 2b, 3-4). These specimens also show that an increase in brachial diameter is accompanied by increases in both size and number of accessory ossicles. There do not seem to be radical changes in the kind and pattern of spinosity throughout ontogeny in K. *finei*. Apical field ossicles are few in young specimens, but become more numerous as disc size increases. Extravascular primary ossicles change in relative prominence on the proximal portions of the brachia; in this species, median dorsals and superomarginals become increasingly difficult to distinguish from adjacent accessory ossicles, and brachial inferomarginals enlarge on the proximal portions of the brachia of larger individuals. These ontogenic characteristics exemplify the kinds of morphological changes which may occur within a species as it grows. They have not been previously documented in either modern or fossil taxa.

UCGM no. 40758 (Winnes Collection) is preserved in such a way that it displays the dorsal (internal) aspect of its oral frame (Plate 9, figure 3). It confirms the suggestion made earlier in this study that at least this species of the family was a stomach-everting feeder. The large functional odontophores which are firmly attached to the lateral and dorsal body wall and occlude the interbrachial disc area are direct evidence of this feeding habit in modern and, by interpretation, fossil asteroids. It is noteworthy that these V-shaped structures are the true odontophores in the Promopalaeasteridae. Earlier paleontologists have erroneously labeled the single, unpaired inferomarginal axillary in the ventral interbrachial area as the odontophore of this and similar genera.

Synonomic discussion. -- Ulrich accurately and exhaustively described the materials in the type suite, but neither he nor Schuchert seemed to consider the possibility that the specimens represented small individuals of a species which achieved a larger size. Both authors described the species as one of small individuals.

Schuchert placed the species in his comprehensive genus Mesopalaeaster ostensibly on the basis of its interbrachial structure, although he admitted (1915, p. 82) that he was not able to positively ascertain the composition of the interbrachial area. He noted that the differences between this species and Mesopalaeaster proavitus (herein synonomized) are not great, and the Ulrich's species is smaller, has fewer ossicles in each of its columns, more prominent axillary inferomarginals, and was found at a lower geological horizon. The first three of these differences are demonstrably ontogenic, rather than systematic differences. The uncertain stratigraphic occurrence of the M. proavitus specimens makes Schuchert's stratigraphic differentiation of dubious value.

Kenothecaster dyeri (Meek, 1872)

Plates 12; 13 figs. 1 a-b, 2 a-b.

1872	Palaeaster? dyeri Meek, F. B., p. 257.
1873	Palaeaster? dyeri Meek, Meek, F. B., p. 59-60, pl. 4, figs. 2 a-f.
1914	Promopalaeaster dyeri (Meek), Schuchert, Charles, p. 33.
1915	Promopalaeaster dyeri (Meek), Schuchert, Charles, p. 120-122, pl. 18, fig. 8, pl. 20, figs. 3-6, pl. 25, fig. 1.

Diagnosis. -- Kenothecaster with exposed portion of the superomarginals nearly the same small size as adjacent accessory ossicles; successive superomarginals not closely spaced. Dorsal skeleton more open than others of the genus. Each dorsal ossicle has a single, large, spine-base structure to which articulated a short, broad spine. Numerous smaller pustules surrounding the primary one carried similar, but smaller spines. Usual armature of interomarginls is of small, thin, terete, acuminate spines, except for one, rarely two, long, broad clavate spines which articulate on large, obvious spine pits. Subadambulacral and groove spines, similar to those of _K_. _finei_, except groove spines are relatively longer in this species.

Primary type material and occurrence. -- The holotype (MCZ no. 469, Dyer Collection) came from Maysville rocks, "about one hundred feet below the tops of the hills" (Meek, 1872) in Cincinnati. Meek described the species from a single specimen.

Description. -- The above generic description and species diagnosis serve to characterize this species. Meek's specimen (Plate 12) is fragmentary, but quite large (R = about 75 mm.). Most of the dorsal surface is obscured by the disarranged spines of the specimen. Where the dorsal ossicles show, they are distinctive in that they possess a well-developed primary spine-base pustule surrounded by several smaller pustules. A smaller specimen (UCGM no. 1455) from the Mt. Hope "Member" of the Fairview "Formation" does not show these primary spine-base pustules as prominently as the holotype (Plate 13, figure 2b). The dorsal ossicles of this smaller specimen are better exposed and preserved, however, and they reveal that there are many more secondary spines around the primary spine of each dorsal ossicle than has been supposed from the exposed dorsal ossicles of the holotype.

Another Maysville specimen from Cincinnati (UCGM no. 40395) shows an intermediate stage of development and preservation of spines on the dorsal ossicles. Although only a single axil, the size of this latter specimen is obviously between that of the smaller and larger specimens already described.

UCGM no. 40395 shows a large odontophore (Plate 13, figure 1b) and some structural details of the mouth-angle ossicles and the most-proximal adambulacral ossicles (Plate 13, figure 1a). The other two specimens also show that the most-proximal ambulacrals are relatively longer than more distal pairs. As indicated in the introduction, these long, most-proximal ambulacrals correlate with the stomach-everting habit in asteroids.

Synonomic discussion. -- Meek first described the species as *Palaeaster? dyeri* in 1872. At that time he noted the openness of the dorsal skeleton and supposed it possible that the species is actually a *Petraster*, because illustrations of the previously described *Palaeaster* species showed close-fitting dorsal ossicles. In 1873 he explained that there may be a few ossicles between the proximal adambulacral columns and their respective inferomarginal columns. This latter condition he knew to be an essential characteristic of *Petraster*. Schuchert (1914) correctly determined that the ossicles Meek considered intercalary between adambulacral and inferomarginal columns are actually inferomarginal themselves. Meek had misidentified the primary columns on the specimen. Schuchert (1914, 1915) included the species in his comprehensive genus *Promopalaeaster*.

Kenothecaster miamiensis (Miller, 1880).

Plates 13 figs. 3, 4; 14-17.

Text-figure 20.

1880 *Palaeaster miamiensis* Miller, S. A., p. 143, pl. 4, fig. 3.

1884 *Palaeaster magnificus* Miller, S. A., p. 16, pl. 4, figs. 3, 3a.

1897 *Palaeaster wykoffi* Miller, S. A., and Gurley, W. F., p. 46, pl. 3, fig. 27.

1914 *Anorthaster miamiensis* (Miller), Schuchert, Charles, p. 11.

Promopalaeaster magnificus (Miller), Schuchert, Charles, p. 33.

Promopalaeaster wykoffi (Miller and Gurley), Schuchert, Charles, p. 34.

1915 *Promopalaeaster bellulus* Schuchert, Charles, p. 113-115, pl. 15, figs. 6-8, pl. 16, fig. 1, pl. 18, figs. 4-5.

Promopalaeaster wykoffi (Miller and Gurley), Schuchert, Charles, p. 119-120, pl. 18, fig. 6, pl. 19, fig. 2.

Promopalaeaster magnificus (Miller), Schuchert, Charles [*partim*], p. 122-125, pl. 21, fig. 1., pl. 22, fig. 1, pl. 23, figs. 1-3.

Anorthaster miamiensis (Miller), Schuchert, Charles, p. 127-128, pl. 13, fig. 4, pl. 20, fig. 1.

1966 *Promopalaeaster bellulus* Schuchert, Spencer, W. K., and Wright, C. W., p. 23.

Promopalaeaster magnificus (Miller), Spencer, W. K., and Wright, C. W., p. 53, fig. 50 (2 a-b).

Anorthaster miamiensis (Miller), Spencer, W. K., and Wright, C. W., p. 53.

Diagnosis. -- *Kenothecaster* with tumid brachial and disc superomarginal ossicles which are noticably more prominent than adjacent accessory ossicles. Interdorsal ossicle prosopon of small, contiguous pustules, one of which is enlarged on each ossicle. Inferomarginal ossicles on small and medium size specimens without prominent spines or large spine-base pustules; enlarged inferomarginal spines on large pustules present on large (R = 150 mm.) specimens only. Subadambulacral and groove spines terete, clavate and broadly acuminate, except some proximal subadambulacral spines which tend to become spatulate. All spines on each adambulacral ossicle of about the same size.

Primary type material and occurrence. -- The holotype of K. miamiensis (USNM no. 40880) is from Richmond rocks near Waynesville, Warren County, Ohio. The specimen is badly abraded and presents a ventral aspect of a small (R = 23 mm.) specimen. Miller (1880) described the species from this single specimen.

Description. -- Known specimens of this species range in size from a radial length of about 20 mm. to more than 150 mm.

Ambulacral ossicles are typically short and quite wide in this species. They become wider as the animals increase in radial length. They are always widest where the brachia meet the disc and taper gradually to the terminus of the arm, and more abruptly to the most proximal, longest pair (Plate 13, figure no. 4 ; Plate 14, figure 2c; Plate 17, figure 2a). The ventral elongated ridges of the ambulacral ossicles in each groove produce four columns of podial basins for part of the brachial length. The percentage of the groove occupied by these four columns is greater in larger individuals. The tips of the brachia always maintain some biserial podial basins, however

(Plate 15, figure 2a; Plate 16, figure 1b).

A large specimen (FMNH no. 10981, Gurley Collection) which shows details of the oral ambulacrals offers some important information on the evolution of the internal ampullar condition common to modern asteroids, but rarely found in Ordovician specimens. A few proximal ampullae have perforated the ambulacral columns adradial of the adambulacral-ambulacral ossicle column junction (Plate 17, figure 2b). This modification in this large (R = more than 75 mm.) specimen is the only incidence of the modern ampullar perforation condition in the Ordovician Asteriadina. It is probably significant that it occurs in a large individual in conjunction with the buccal podia. Fell (1963) stated, without explanation, that the small openings between successive distal ambulacrals of Platasterias indicate that the perforate ambulacral condition arose distally in the stelleroid class. This is contrary to what appears to be the case among the Asteriadina as evidenced by this specimen of Kenothecaster.

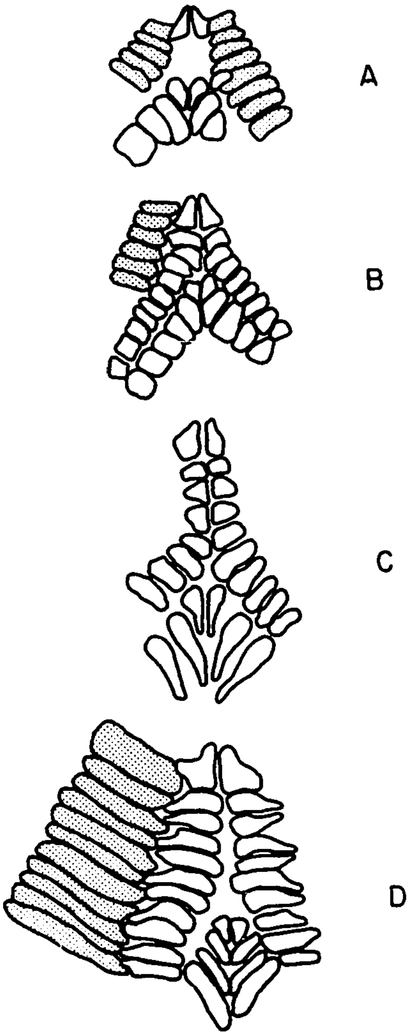
Adambulacral ossicles are short and wide (Plate 14, figure 3a; Plate 15, figure 1a; Plate 16, figure 3). Where visible, all except the most distal (Plate 16, figure 1b) have, or show indications of having, a single vertical column of subadambulacral and groove spines (Plate 16, figure 3) all of which seem to have been about the same length (Plate 17, figures 1 a-b). Some of the most-proximal subadambulacral spines tend to become flattened and spatulate (Plate 14, figure 3b). A few small pustules on the abradial ventral surfaces of the axillary adambulacral ossicles suggest the former presence of additional, small spines on that surface (Plate 16, figure 2d).

Individuals of K. miamiensis do not develop large inferomarginal spines until they are large. The largest known specimen of this species (MUGM no. 6809) is the only one showing such distinctive spines (Plate 17, figure 1a). Large inferomarginal spines or spine-base pustules are typical of all sizes of individuals of the other two species herein assigned to this genus.

The arrangement of the axillary inferomarginals in Kenothecaster varies with the size of the individual. Larger individuals possess more axillary inferomarginals (Plate 17, figure 2a) than smaller ones Plate 14, figure 2b). Progressively lengthening adoral carinae parallel the increasing numbers of axillary inferomarginals in progressively larger individuals. These phenomena are illustrated in Text-figure 20 which shows tracings, to scale, of progressively larger specimens of K. miamiensis. Earlier authors, failing to correlate axial structure with size of individuals, have named and distinguished three species, Palaeaster magnificus Miller, Palaeaster wykoffi Miller and Gurley, and Promopalaeaster bellulus Schuchert, chiefly on differences in axillary inferomarginal number and adoral carina length in the type material of each. It now appears that all these species are junior synonyms of Palaeaster miamiensis Miller because each represents a stage of development of this species.

The intermarginal and interdorsal ossicles of K. miamiensis are arranged in a double subseries (Plate 15, figures 2 b-c; Plate 16, figures 2 a-c; Plate 17, figures 1c, 3 a-b). The holotype of P. magnificus (Plate 15, figure 2 a-c) shows this characteristic well.

Text-figure 20. -- Ontogenic development in axils of *Kenothecaster miamiensis* as shown by the type materials of A. *Palaeaster miamiensis* Miller; B. *Palaeaster wykoffi* Miller and Gurley; C, *Promopalaeaster bellulus* Schuchert; and D. *Palaeaster magnificus* Miller. All but *P. bellulus* have been somewhat flattened during preservation. Ambulacral ossicles stippled. All diagrams X 2.5


A
B
C
D

This specimen also shows the prominence of the primary ossicle columns on the brachia, as does an isolated axil (Plate 15, figure 1b) catalogued under the same museum number. Another specimen with the same museum number shows that this species possessed acuminate arm tips which are composed essentially of primary ossicles (Plate 16, figures 1 a-b). It also shows that the dorsal ossicles were generated along both edges of the interdorsal ossicle field in these forms. Dorsal aspects of other specimens confirm this.

In addition to their externally exposed surfaces, the superomarginals of this species have long flanges or trails which are normally obscurred by overlying accessory ossicles. A specimen collected by Mrs. Elizabeth Dalvé from the Waynesville "Formation" at the Boudinot Avenue site in Cincinnati shows these characteristics well. Although only the proximal portion of a single brachium, this specimen also shows well the double subseries of intermarginal accessory ossicles common to promopalaeasterids (Plate 17, figures 3 a-b).

The median dorsals of _K_. _miamiensis_ are more tumid than adjacent interdorsals and may be traced onto the disc in well preserved specimens (Plate 16, figure 2b). There they seem to melt into the hodgepodge of small and large, tumid ossicles composing the dorsal skeleton of the disc. No specimen preserved the apical field of this species well enough for accurate description. It can only be described as complex and composed of many ossicles where it can be seen on a rather large (R = more than 67 mm.) specimen.

The madreporite is nearly on the ambitus of the dorsal surface. It is relatively large compared to that of other species (Plate 16, figure 2e). The madreporite of UCGM no. 1459 is shown to be more than just a surface plate (Plate 14, figure 1). It has a long, solid extension which must have reached nearly to the circumoral water-vascular ring in the living animal. This ossicle extension does not appear to have had a main canal from its outer surface to its inner end. It must have possessed a complex of small tubules or lacunae which permitted communication between the circumoral ring and the exterior. In modern asteroids this massive structure has been replaced by a thinner, usually flexible, convoluted tube which is usually invested with granules or small plates of skeletal calcite. Why this "stone canal" of modern asteroids has skeletal material in its structure has never been satisfactorily answered by biologists. It is interesting that early Asteriadina possessed a heavily calcified homologue of the stone canal.

The mouthframe of K. miamiensis is characteristic of the various species in the genus. It has long most-proximal ambulacral ossicles which may be seen to contact the mouth-angle ossicles of each interbrachium (Plate 13, figure no. 4). This is the arrangement in both modern and these fossil Asteriadina. The large odontophores also contact the internal surfaces of the mouth-angle ossicles and are closely associated with interbrachial ossicles which served to connect them to the dorsolateral body wall. Tori (Plate 14, figure 3b) are sometimes preserved in this species. These latter structures carry oral spines and are located just orad of each mouth-angle ossicle pair. Modern asteroids to not possess these structures, but all modern and fossil ophuroids do. In modern orphiuroids, these structures are usually considered to be an aid to mastication, since the digestive glands are poorly developed in individuals of that subclass. Their role in these early asteroids is problematical because, from all other indications, these animals possessed well-developed digestive glands. Spencer has assigned a possible "trap" function to similar structures with multiple oral spines in some fossil ophiuroids. This latter interpretation would corroborate the model proposed for these fossil Asteriadina, wherein food is necessarily held against the buccal opening.

Synonomic discussion. -- Due to the poor preservation of the material available to Miller (1880) for the description of his monotypic species _P. miamiensis_, he, and later Schuchert, misunderstood the specimen and erroneously characterized the species it represents. The specimen is a ventral aspect from which nearly all traces of the adambulacral and mouth-angle ossicles have been removed. Both authors confounded the true inferomarginals with adambulacral ossicles and described the former as adambulacrals. Subsequent preparation of the specimen has revealed a few remaining fragments of adambulacral ossicles (Plate 14, figures 2 a-b, d). Had either author been aware of the persistent one-to-one ratio between the ossicles in brachial perivascular columns in asteroids, he may well have realized from the ambulacral ossicles present on the specimen that the true adambulacral ossicles had been removed. Both authors further described the true superomarginal ossicle columns as inferomarginals. This latter error resulted from the original misidentification of the true inferomarginal columns. Since nearly all traces of the intermarginal ossicles have also been abraded from the specimen, there was little evidence, other than that already suggested, to intimate that the original interpretations of the specimen were incorrect. Schuchert (1914) erected a new genus, *Anorthaster*, and a new subfamily to accommodate this specimen and its erroneous interpretation. He maintained the subfamily within his Promopalaeasteridae because he felt that " This species has a general resemblance to some of the *Promopalaeasters*, particularly *P. bellulus* and *P. wykoffi*, but the peculiar arrangement of the axillary and interbrachial adambulacral plates will distinguish it not only from them but from all other Ordovicic asterids," (1915, p. 128). Anortheasterinae and its nominate genus are herein rejected because they were founded on erroneous concepts.

Miller (1884) described *Palaeaster magnificus* as a new species on the basis of its arrangement of dorsal ossicles. He knew nothing, of course, of the arrangement of the dorsal ossicles of *P. miamiensis* which he had described earlier from a specimen showing a ventral aspect. His erroneous characterization of that earlier species made his fairly accurate characterization of the ventral surface of this latter species seem to be one of a distinct species.

Schuchert (1915) placed *P. magnificus* as his new genus *Promopalaeaster*. He expanded Miller's description of the species and contrasted it with some other *Promopalaeaster* species on the basis of its dorsal structure, the number of axillary inferomarginals in the specimens he examined, the size of its ossicles, and its dorsal spination. Notably, he did not contrast it with *P. wykoffi*, P.

miamiensis, or his new species Promopalaeaster bellulus.

Miller and Gurley (1897) described Palaeaster wykoffi, but did not contrast it with any other species or offer information on its diagnostic characters. Schuchert (1915) placed the species in his Promopalaeaster, but contrasted the species only with P. exculptus [= Mesopalaeaster shaefferi]. He noted the shorter adoral carinae in this latter species.

Spencer and Wright (1966) redrafted two of Schuchert's figures of P. magnificus and figured them under that name.

Genus Neardisaster gen. n.

1914 Promopalaeaster Schuchert, Charles [partim], p. 34.

1915 Promopalaeaster Schuchert, Charles [partim], p. 102-106.

Diagnosis. -- Promopalaeasteridae not developing adoral carinae. Mouth-angle ossicles remain adnate to unpaired axillary inferomarginal in each ventral axillary area. Most proximal two pairs of adambulacral ossicles adradial of mouth-angle ossicles in each oral area. Extravascular skeleton similar Promopalaeaster. Adambulacral ossicles multiacanthid.

Type species. -- Promopalaeaster prenuntius Schuchert, 1915.

Etymology of new name. -- Greek ne, poetic particle used as a prefix meaning not; Greek ardis, a point; Greek aster, a star or starfish. The name refers to the absence of adoral carinae; oral angles are rounded, rather than pointed, in this genus.

Discussion. -- This taxon is erected for two specimens which differ from other promopalaeasteridae in the Cincinnati area in characteristics employed as generic taxobases. The differences are summarized

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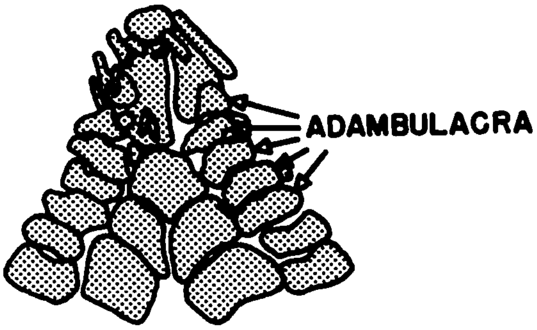
Text-figure 21. -- An oral axillary of *Neardisaster prenuntius* showing distinctive arrangement of proximal adambulacral ossicles. Note absence of adoral corina. X 7.


ADAMBULACRA

in the above diagnosis.

The most important difference between this genus and others in the Promopalaeasteridae is the arrangement of the proximal adambulacral ossicles as shown on the moderately large (R = about 35 mm.) holotype of the type species (Text-figure 21) (Plate 18, figures 1 a-b). There is no suggestion of adoral carinae. Other species in the family which are otherwise similarly developed show at least rudiments of such structure at similar body sizes. Very small specimens of Kenothecaster finei (Plate 9, figure 2d) show a similar oral adambulacral development, but a specimen of the same size as the Neardisaster prenuntius holotype (AMNH no. 1196) possesses a definite adoral carina.

Synonomic discussion. -- Schuchert (1914, 1915) placed the type species of the new genus in his comprehensive genus Promopalaeaster. It is removed from this latter genus on the basis of the characteristics listed in the above diagnosis.

Neardisaster prenuntius (Schuchert, 1915)

Plate 18

Text-figure 21.

1914 Promopalaeaster prenuntius Schuchert, Charles [nomen nudum], p. 34.

1915 Promopalaeaster prenuntius Schuchert, Charles, p. 107-108, pl. 13, fig. 3, pl. 15, fig. 5.

1916 Promopalaeaster prenuntius Schuchert, Spencer, W. K., p. 98.

Diagnosis. -- The genus is monotypic. Until other species are recognized, the diagnostic characteristics of the genus serve to diagnose the species.

Primary type material and locality. -- The holotype (UK no. 403) is from "Trenton" rocks [probably Lexington Limestone] near Frankfort, Kentucky. The exact collecting locality is unknown.

Description. -- The radial length of the holotype is about 35 mm. The specimen presents an oral aspect of the disc and proximal portions of the brachia (Plate 18, figure 1a). One brachium is folded under in such a way that the distal portion of its dorsal surface is visible (Plate 18, figure 1a, 1c).

Ambulacral ossicles are typical of those of the family. Only the disc ambulacral ossicles define four podial basin columns on each brachium.

Adambulacral ossicles are short and wide, as on the other promopalaeasterids. Three or more, longitudinally striated (Plate 18, figure 2) adambulacral spines arranged in a vertically pectinate series protrude into the groove from each adambulacral ossicle. These spines appear to have been long, although each one still preserved on the holotype and another specimen (YPM no. 3405) has been broken (Plate 18, figures 2 a-d).

Intermarginals are similar in shape to those of *Mesopalaeaster* (Plate 18, figure 2d). Each had two or more long spines similar to those of the adambulacral ossicles.

Intermarginals as prominent as adjacent superomarginals. Each carried at least one long spine and several smaller ones. The longer spines of the intermarginals and superomarginals, where preserved (Plate 18, figures 2 a-b), are only slightly smaller than the larger inferomarginal spines.

The interdorsal ossicles are similar to those of *Promopalaeaster*. They do not seem to be strongly modified to accommodate the passage of papulae. They are not arranged in the biserial rows typical of *Kenothecaster*. Their armor of spines becomes progressively finer toward the median dorsal column, the ossicles of which are only slightly more prominent than the adjacent interdorsal ossicles. The median dorsals are covered with numerous small, spine-base structures which indicate the former presence of small spines.

The madreporite and apical field of the species are unknown.

One or two pairs of axillary inferomarginals isolate the unpaired axillary inferomarginal in each axil from the ambitus (Plate 18, figures 1 a-b). This unpaired axillary is adjacent to the mouth-angle ossicles. The first pairs of adambulacral ossicles lie adradial of the mouth-angle ossicles, rather than distal to it as in similar sized specimens of other promopalaeasterids (Text-figure 21). This latter feature is common to much smaller specimens of other species in the family.

Synonomic discussion. -- Schuchert listed the species under his genus *Promopalaeaster* in his 1914 publication, but did not adequately characterize it until 1915. He noted that the species, which he knew only from the holotype, was similar in some ways to *P. speciosus*. His diagnosis of the species was given only in terms of its comparison with this latter species. He distinguished *P. prenuntius* by its "smaller size, less pustulose ornamentation of the plates, and the lower position in the geological column." While size and geological occurrence are, in themselves, inadequate characteristics with which to diagnose taxa, both may be useful in identifying taxa when compared to the other coordinate characteristics he mentions. In closing, he suggests that _P. prenuntius_ is the ancestor of _P. speciosus_.

Spencer (1916) comments only that Schuchert regards this species to be ancestrial to _P. speciosus_.

VII TAXONOMIC CONCLUSIONS

1. The re-diagnosed Ordovician families Hudsonasteridae Schuchert, Mesopalaeasteridae Schuchert, and Promopalaeasteridae Schuchert are assignable to the forcipulate suborder Asteriadina Perrier, because they possess the preservable attributes of modern representatives of this taxon.
2. *Hudsonaster simplex* (Miller and Dyer) is morphologically distinct from *Hudsonaster incomptus* (Meek) and should be removed from synonomy with this latter species as suggested by Schuchert (1914). *Hudsonaster rugosus* (Billings) is the type species of *Hudsonaster*. It is distinct from the above named Cincinnati species.
3. *Mesopalaeaster shaefferi* (Hall) is the only species of Mesopalaeasteridae in Cincinnati rocks. Other Cincinnatian species which have been placed in *Mesopalaeaster* by earlier authors cannot be so accommodated, because they do not share essential familial characteristics with specimens of *M. shaefferi*. The following species are synonomous with *Palaeaster shaefferi* Hall: *Palaeaster spinulosus* Miller and Dyer, *Palaeaster longibrachiatus* Miller, and *Palaeaster exculptus* Miller. Schuchert (1914) erroneously referred these latter species to *Promopalaeaster*.
4. *Promopalaeaster* Schuchert is monotypic. Only the type specimen, *Palaeaster speciosus* Meek, can be retained in this genus.
5. *Kenothecaster* gen. n. is erected to accommodate species of

Promopalaeasteridae which differ from *Promopalaeaster speciosus* in possessing biserial transverse or diagnonal rows of interdorsal accessory ossicles and polyacanthate adambulacral ossicles. Members of this new genus are similar to the specimen of *Promopalaeaster* in that they develop adoral carinae.

6. *Kenothecaster finei* (Ulrich) is the type species of the new genus *Kenothecaster*. *Mesopalaeaster proavitus* Schuchert is a junior synonym of *Palaeaster finei* Ulrich.
7. *Palaeaster dyeri* Meek should be assigned to *Kenothecaster*.
8. *Palaeaster miamiensis* Miller should be assigned to *Kenothecaster*. It is a senior synonym of *Palaeaster magnificus* Miller, *Palaeaster wykoffi* Miller, and *Promopalaeaster bellulus* Schuchert.
9. *Neardisaster* gen. n. is erected for *Promopalaeaster prenuntius* Schuchert, a pre-cincinnatian promopalaeasterid which does not appear to develop the adoral carina typical of other members of the family.
10. The asteroid subclass is represented in Cincinnatian strata by a few distinct forms, rather than the plethora of species named by Schuchert and earlier investigators.

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IX. PLATES

EXPLANATION OF PLATE I

Figure   Page

1 a-f. Hudsonaster rugosus (Billings)

Holotype; Upper member [= English Head] Vauréal Formation, Upper Ordovician; Anticosti Island, Quebec, Canada; CGS no. 1999.

a. Dorsal aspect; X 2 130

b. Lateral aspect of slightly disarranged axial area showing shape and prosopon of inferomarginal and superomarginal ossicles; X 5 .... 127, 128

c. Ventral and slightly distal aspect of an ambulacral ossicle showing abradial extension of transverse ridge (top of photograph), prominent cross-ridge, interruption in distal cross-ridge for accomodation of transverse podial vessel, and adradial depression for ambulacral channel; this ossicle may be seen between the two lower brachia in figure 1a; X 35 123

d. Dorsal (left side of photograph) and distal (right) aspects of two ambulacral ossicles of somewhat disarranged lower left brachial terminus in figure 1a; distal view shows lack of interambulacral articulating flanges and height of transverse ridge (perradial end at top, venter to right); X 25 123

e. Granules on dorsal ossicles; X 48 130

f. Dorsal, perradial aspect of an adambulacral ossicle located near the end of lower left brachium of figure 1a; note adradial (bottom) flange which met the ambulacral ossicle; X 40 126

2 a-b. Hudsonaster rugosus (Billings).

Paratype; Vauréal Formation, Upper Ordovician; Anticosti Island, Quebec, Canada; CGS no. 1999a.

a. Ventral aspect (photograph through xylol to increase contrast between calcitic specimen and matrix); note mouth-angle ossicles adjacent to marginal axillary and non-adaxial relationship between adambulacrals and inferomarginals; X 2 130

b. Dorsal aspect (through xylol); specimen slightly distorted so as to show one set (on left ambitus) of brachial inferomarginals in addition to the three columns of dorsal ossicles; ossicle surfaces abraded; X 2 127

PLATE I

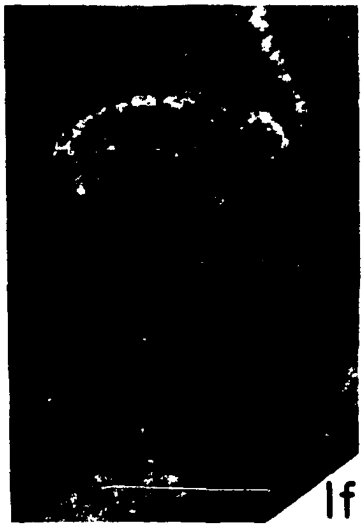

1a


1b


1c


1d


1e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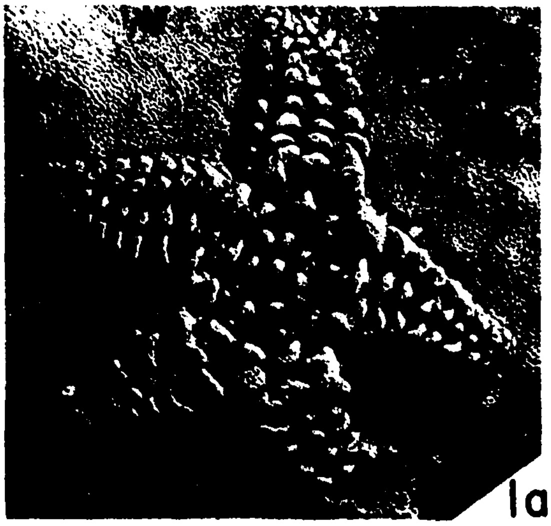
2a


2b

EXPLANATION OF PLATE 2

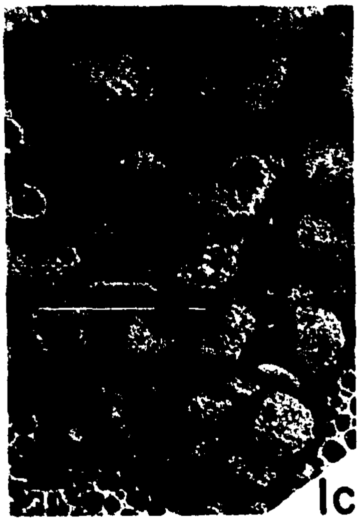
Figure		Page
1 a-e.	Hudsonaster incomptus (Hall).	
	Holotype; "Cincinnati Group.....Cincinnati, Ohio; MCZ no. 471.	
	a. Dorsal aspect; X 3	133
	b. Proximal median dorsal with extrathecal granules located between successive ossicles on proximal portion of Brachium B; X 11	133, 134
	c. Distal portion of Brachium A showing an overturned displaced ambulacral ossicle in series with median dorsal ossicles; X 12	131
	d. Enlarged ambulacral ossicle described in 1c; X 70	131
	e. Bivial axil showing madreporite and prosopon of surrounding ossicles; note large spine-base structures and shape of superomarginals; X 9	133, 134
2 a-b.	Hudsonaster incomptus (Hall).	
	Madison, Jefferson Co., Indiana; probably Richmond rocks; YPM no. 14778.	
	a. Dorsal aspect of the slumped specimen; X 5	133, 135
	b. Dorsal aspect of mouth-angle ossicles, torus, oral spine and adambulacrals (compare with Text-figure 16, p. 136; X 35	135

PLATE 2


1a


2a


1b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EXPLANATION OF PLATE 3

Figure — Page

1. *Hudsonaster simplex* (Miller and Dyer).

Holotype; "upper part of the Cincinnati Group" near Raysville [= Lytle], Warren Co., Ohio; FMNH no. 8830 (Faber Collection); ventral aspect of proximal brachium showing spine-base structures of inferomarginals and adambulacrals, small mouth-angle ossicles with torus still present on one pair, and non-adaxial relationship between adambulacral and inferomarginals; X 8 .... 141, 142

2. *Hudsonaster simplex* (Miller and Dyer).

Richmond rocks; Madison, Jefferson Co., Indiana; YPM no. 14772; oral area of small specimen showing characteristic mouth-angle ossicles and inner aspects of enlarged centro-interbrachials above most of them; X 12 .... 141, 145

3 a-b. *Hudsonaster simplex* (Miller and Dyer).

Richmond rocks; two miles north of Germantown, Montgomery Co., Ohio; specimen in the private collection of Mrs. C. A. Dickie of Cincinnati; rubber pull and plaster cast of the specimen is UCGM no. 40760.

a. Dorsal aspect of entire specimen; X 3 141

b. Enlargement of apical field; X 9 141

4. *Hudsonaster simplex* (Miller and Dyer).

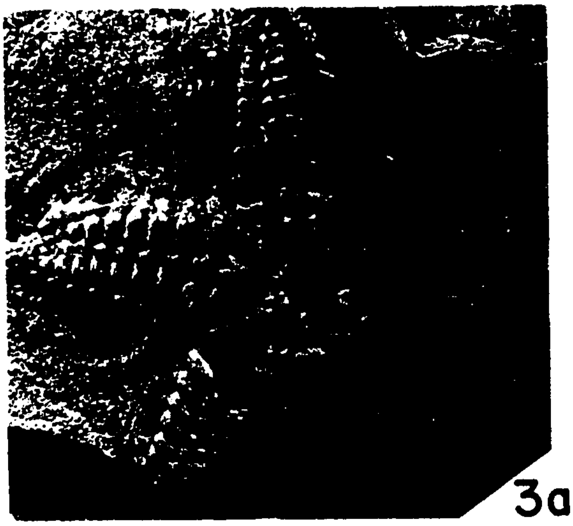
No locality information; MUGM specimen (no number);
X 9 141

5. Hudsonaster simplex (Miller and Dyer).
Elkhorn "Formation", Richmond rocks; Weisburg, Dearborn Co., Indiana; from float at bottom of third large railroad cut south of Weisburn crossing; a small specimen nestled inside the pedicle valve of Platystrophia specimen; specimen shows diagnostic shape of proximal superomarginals; UCGM no. 40756; X 8 141

PLATE 3


1


2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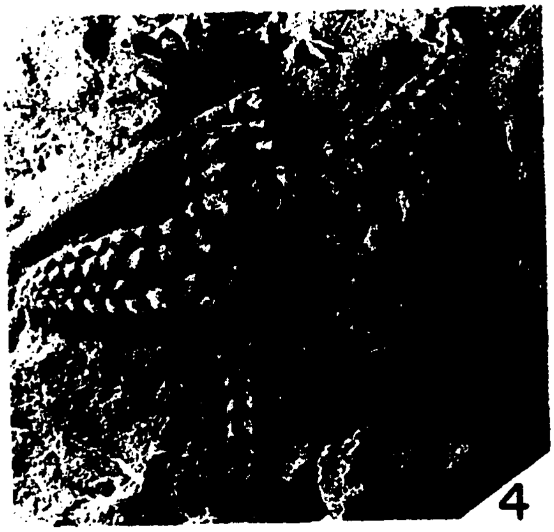
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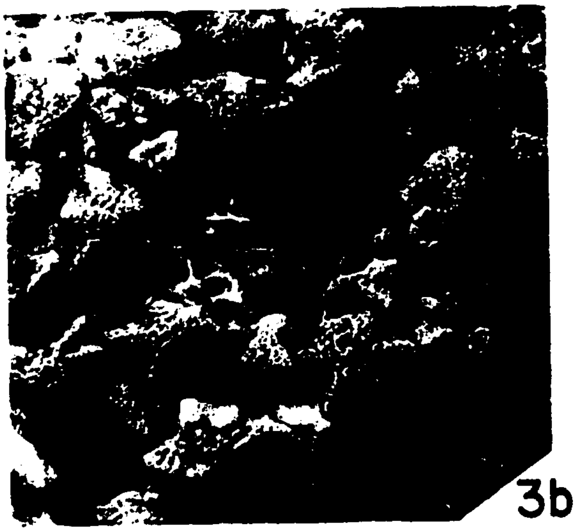
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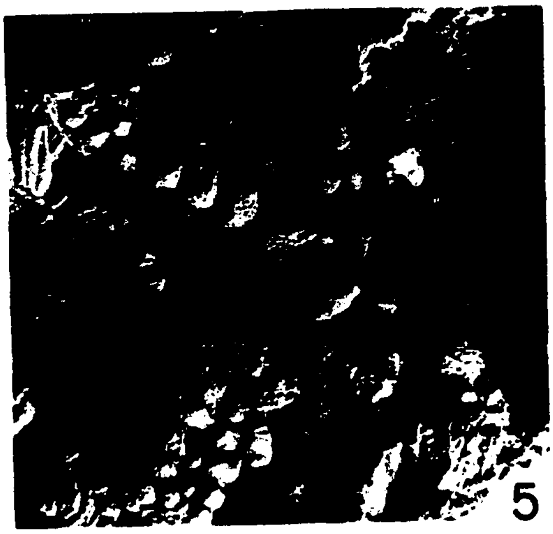
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EXPLANATION OF PLATE 4

Figure | Page

1. *Hudsonaster simplex* (Miller and Dyer).
Same specimen as Pl. 3, figs. 3 a-b; (through xylol);
X 3 .... 141, 145

2 a-b. *Hudsonaster simplex* (Miller and Dyer).
Richmond rock; near Waynesville, Warren Co., Ohio; smallest and only free specimen in lot of six specimens catalogued under USNM no. 40882.

a. Dorsal aspect (through xylol) showing characteristic shape of axial superomarginals of the species; note that brachia have not collapsed and probably maintain approximate living arrangement; X 7 143

b. Ventral aspect (through xylol) showing nonadaxial ossicle relationship; X 7 143

3 a-b. *Hudsonaster simplex* (Miller and Dyer).
Richmond rock; near Waynesville, Warren Co., Ohio; largest specimen showing dorsal aspect in lot of six specimens catalogued under USNM no. 40882.

a. Overall aspect (through xylol) showing preservational splaying of ossicle columns due to flattening (compare with 1a); X 3 141

b. Enlargement of apical field (through xylol) showing primary circlet around relatively large central dorsal ossicle; X 9 144

4 a-b. Hudsonaster simplex (Miller and Dyer).

Richmond rock; near Waynesville, Warren Co., Ohio; largest specimen showing ventral aspect in lot of six specimens catalogued under USNM no. 40882.

a. Overall aspect (through xylol) showing effects of preservational splaying on ossicle columns; the bottom arm is less distorted than the truncated arm, resulting in the latter of these being wider at its base; X 3 145

b. Oral region (through xylol) showing small mouth-angle ossicles adnate to axillary inferomarginals (some fractured); X 9 145

PLATE 4

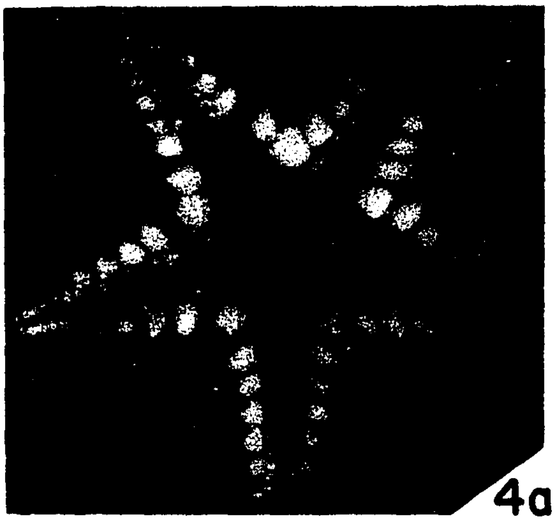

1


2a


2b


3a


3b


4a


4b

EXPLANATION FOR PLATE 5

Figure | Page

1. Mesopalaeaster shaefferi (Hall).

   Holotype; " ...shales of the Hudson River Group in Cincinnati, Ohio." Exact locality and strata unknown; AMNH no. 1195; ventral aspect showing perfect adaxial relationship between Adambulacrals and inferomarginals on several brachia; X 2 .... 151, 161

2. Mesopalaeaster shaefferi (Hall).

   Holotype of Palaeaster longibrachiatus Miller; " ... upper part of Cincinnati Group [= Richmond rock] near Clarksville [Clinton Co.], Ohio."; USNM no. 40881; Ventral aspect of largest known specimen (R = 38 mm.) of species, but specimen maintains unique adaxial relationship characteristic of this Cincinnatian species; X 1 154

3. Mesopalaeaster shaefferi (Hall).

   Holotype of Palaeaster exculptus Miller; "...upper part of Hudson River Group [Richmond rock] near Waynesville [Warren Co.], Ohio; USNM no. 60608; ventral aspect of an interbrachial area showing prosopon of marginal ossicles; X 4 .... 151, 154

4 a-b. Mesopalaeaster shaefferi (Hall).

   "....Maysville beds of Rohs Hill [Bald Knob] in Cincinnati [Hamilton Co.], Ohio." (Schuchert, 1915, p. 125); USNM no. 60621.

   a. Ventral aspect of distal portion of a splayed brachium showing characteristic adambulacral shape and spine arrangement; X 4 154

b. Dorsal aspect showing slight development of intermarginal and interdorsal ossicle columns; X 4 154

5 a-b. Mesopalaeaster shaefferi (Hall).

Maysville rock; Cincinnati, Hamilton Co., Ohio; YPM no. 13180A.

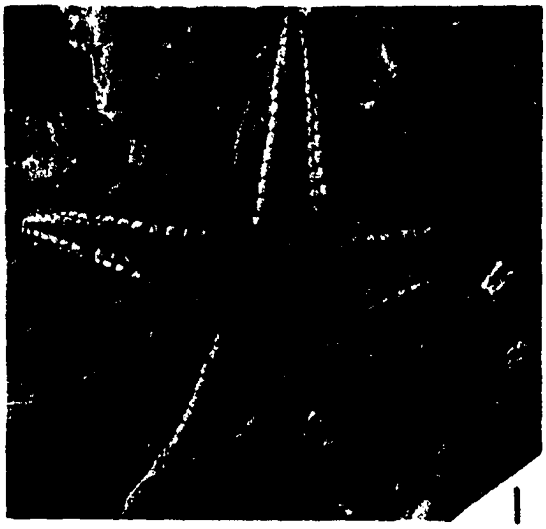
a. Lateral aspect (distal to left) of a brachium with most proximal intermarginals removed exposing the openings between primary ossicles; X 5 .... 154, 160

b. Slightly more dorsal aspect than in 5a showing characteristic weak development of interdorsals; X 5 154

6. Mesopalaeaster shaefferi (Hall).

"... Maysville formation on the hills back of Cincinnati [Hamilton Co., Ohio]." (Schuchert, 1915 p. 79); YPM no. 13180; ventral aspect showing characteristically long mouth-angle ossicles, interbrachial areas, and adaxial relationship of ossicles; X 3 151

PLATE 5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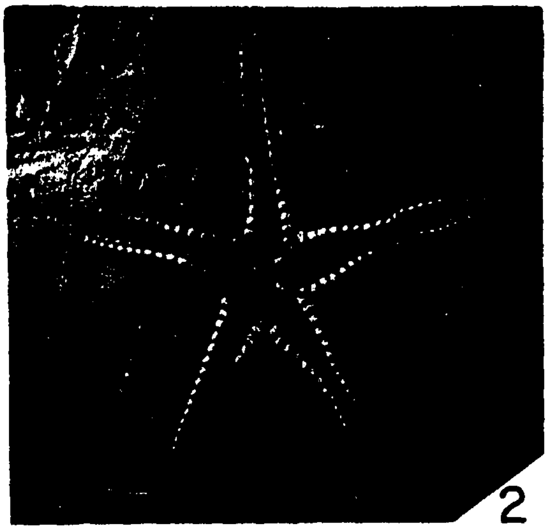
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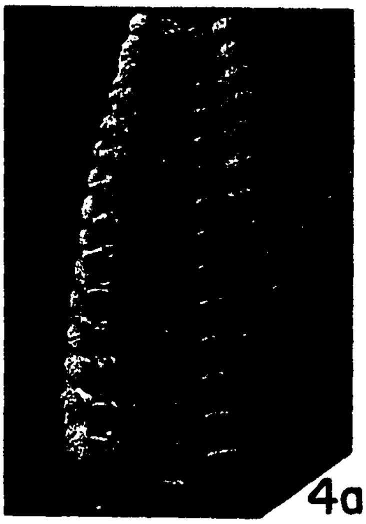
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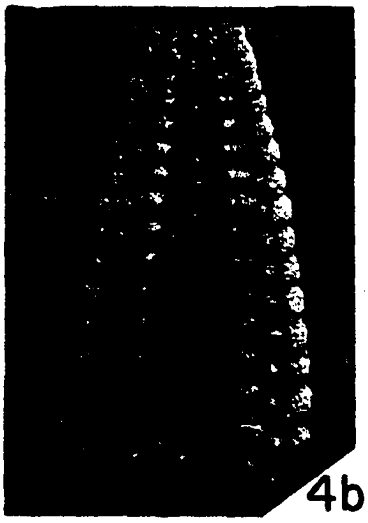
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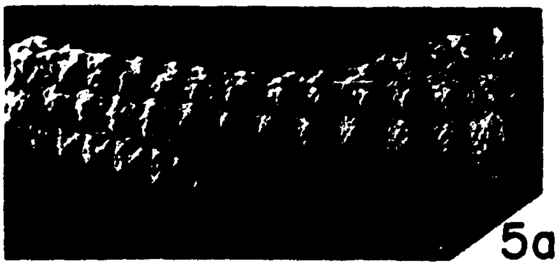
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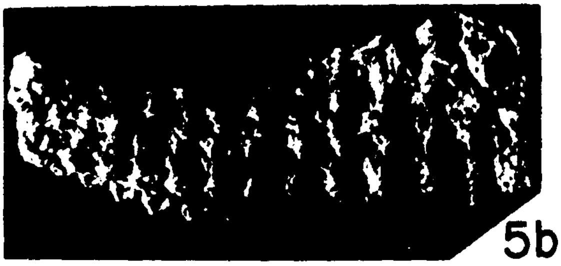

5b


6

EXPLANATION FOR PLATE 6

Figure		Page
1 a-d.	Mesopalaeaster shaefferi (Hall). Holotype; refer to data for AMNH no. 1195 (Pl. 5, fig. 1).	
	a. Ventral aspect (through xylol) showing adaxial ossicle relationship in all brachia; X 2	151, 161
	b. Lateral aspect (through xylol) of lower left brachium of fig. 1a showing intermarginal development; X 5	161
	c. Dorsal aspect (through xylol) of lower left brachium of fig. 1a showing interdorsal development; X 5 .	161
	d. An arm base and two interbrachial areas (through xylol) showing long mouth-angle ossicles, unpaired axillary inferomarginal and adaxial ossicle arrangement; X 6	151, 162
2 a-b.	Mesopalaeaster shaefferi (Hall). Refer to data for USNM no. 60621 (Pl. 5, figs. 4 a-b).	
	a. Ventral aspect (through xylol); note elongated pits of adambulacral spine-base structures; X 4	156
	b. Dorsal aspect (through xylol); note spine-base pits on superomarginals and inferomarginals (compare with prosopon shown in Pl. 5, fig. 3); X 4	160, 161
3.	Mesopalaeaster shaefferi (Hall). Entire ventral aspect of USNM no. 60608 (Pl. 5, fig. 3); X 1.3	151, 154

4. <u>Mesopalaeaster</u> <u>shaefferi</u> (Hall).

Refer to data for YPM no. 13180 (Pl. 5, fig. 6)

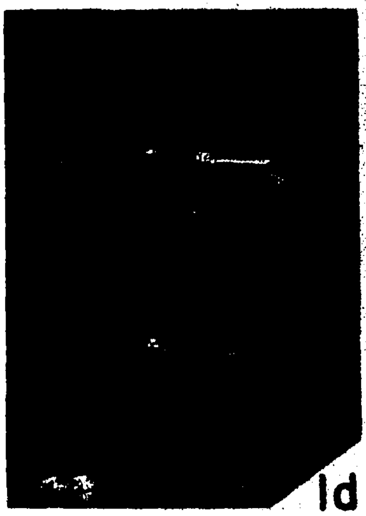
(through xylol); X 3 151

PLATE 6


1a


1b


1c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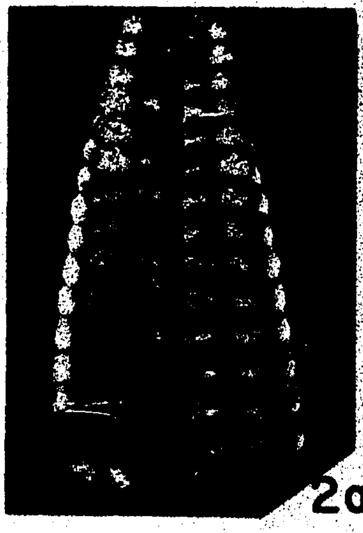
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4

EXPLANATION FOR PLATE 7

Figure Page

1 a-b. *Mesopalaeaster shaefferi* (Hall).

Refer to data for USNM no. 60608 (Pl. 5, fig. 3).

a. View across ambulacral groove (proximal to left) at adambulacrals (top) and ambulacrals (bottom); note podial perforations at column junction; these ossicles located on left side of upper brachium in Pl. 6, fig. 3; X 16 .... 151, 155

b. Perradial end of ambulacral ossicle (proximal to right) showing articulation structure (refer to Text-fig. 17); this ossicle located near arm base on right side of upper brachium in Pl. 6, fig. 3; X 25 .... 151, 155

2 a-d. *Mesopalaeaster shaefferi* (Hall).

Holotype of *Palaeaster spinulosus* Miller and Dyer; stratum unknown; Cincinnati, Hamilton Co., Ohio: MCZ no. 478.

a. View across ambulacral groove of ambulacrals, adambulacrals, and pustulose inferomarginals; note horizontal pectinate series of groove spines on each adambulacral (compare with spine-pits in USNM no. 60621, Pl. 6, fig. 2a); compare ambulacral morphology with USNM no. 60608, fig. 1a (above); X 4.5 .... 151, 156

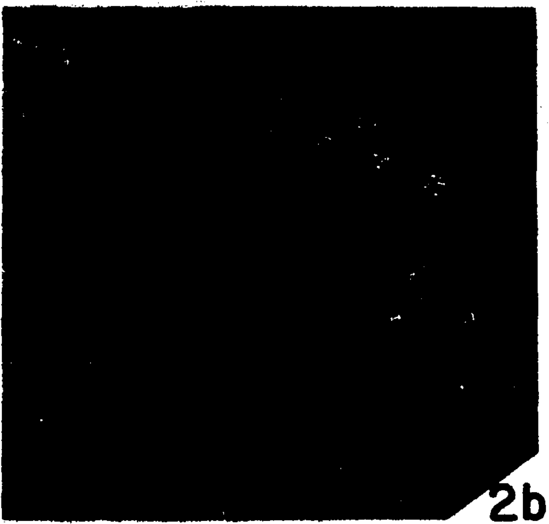
b. Dorsal aspect of brachium showing disarranged ossicles with well-preserved prosopon; note slight

PLATE 7


1a


1b


2a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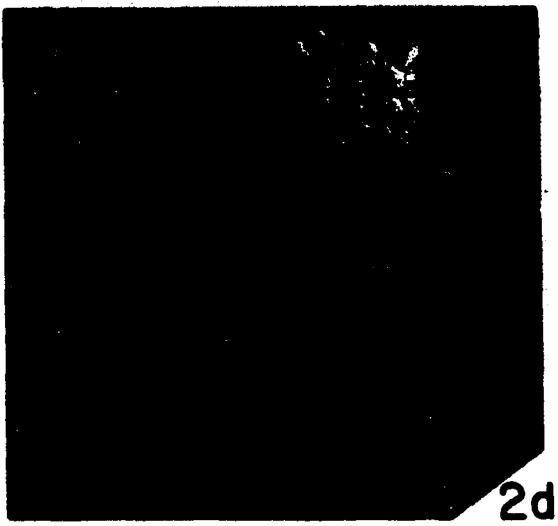
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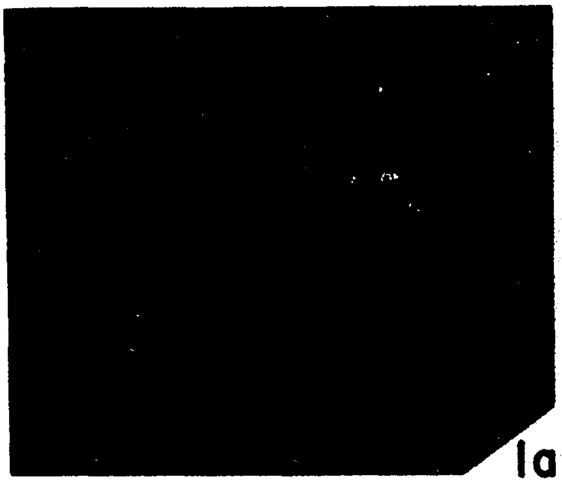
EXPLANATION OF PLATE 8

Figure		Page
1 a-h.	Promopalaeaster speciosus (Meek). Holotype; "Cincinnati Group, Cincinnati [Hamilton Co.], Ohio"; exact locality unknown; MCZ no. 22.	
	a. Ventral aspect showing non-adaxial condition, large mouth-angle ossicles, and alternating proximal ambulacral ridges; note presence of large groove spines on some proximal ambulacrals; X 1.2	171
	b. Dorsal aspect; note variation in arm tip shape; X 1.2	170, 174
	c. Enlargement of dorsum of lower right brachium of fig. 1b showing proxopons of ossicles; note single interdorsal series; X 4.3	173
	d. Distal aspect of left brachium of fig. 1b showing enlarged terminal ossicle and arm tip composed essentially of primary ossicles; X 7	174
	e. Ventral aspect of left brachium of fig. 1b showing slightly differentiated spine-base structures of distal adambulacral ossicles; a few, small spines are present in the groove; X 7	171, 172
	f. Lateral aspect of brachium showing monoserial interdorsals and biserial intermarginals; X 3	172, 173
	g. Ventrolateral aspect of a brachium; X 3	171, 172
	h. Interbrachial area showing adambulacrals and inferomarginals; X 5	171, 174

PLATE 8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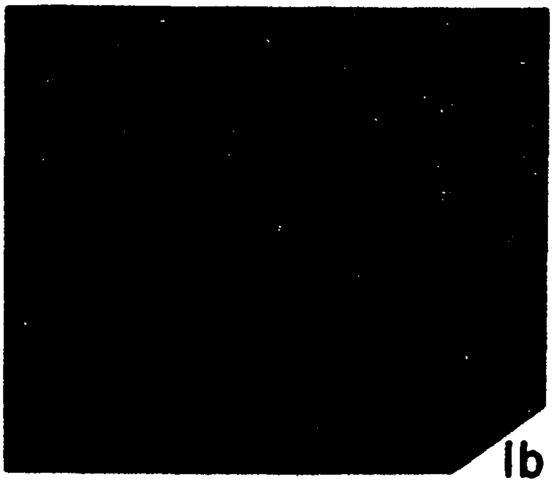
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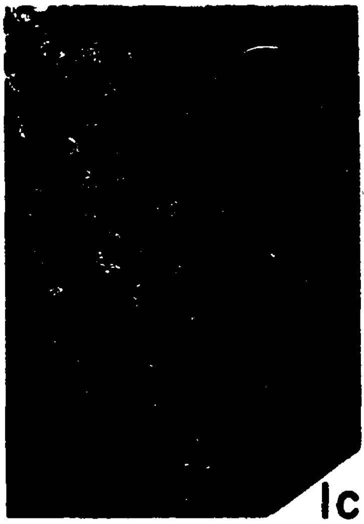
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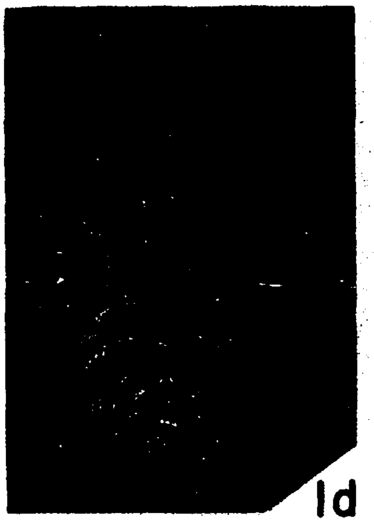
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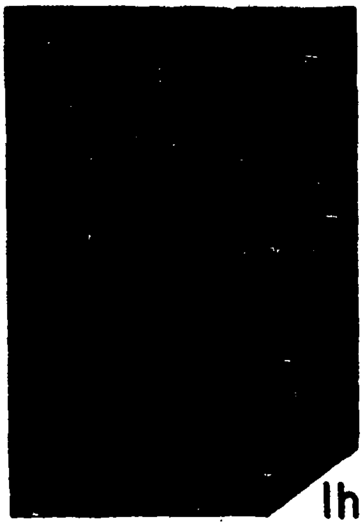
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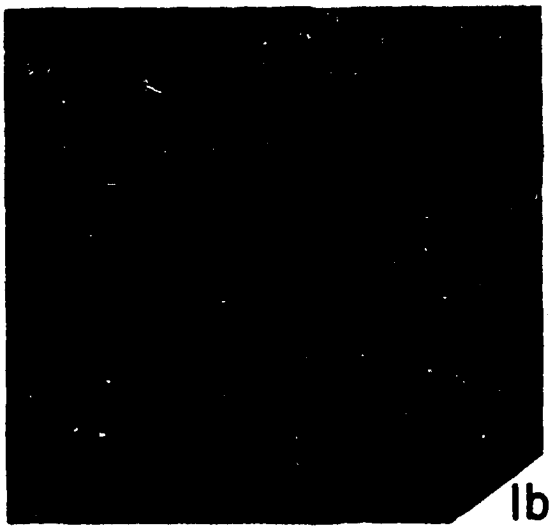
EXPLANATION FOR PLATE 9

Figure		Page
1 a-b.	Kenothecaster finei (Ulrich). Lectotype (designated herein); "...Utica Slate [Eden Shale] that is exposed near low water mark in the Ohio River, at Cincinnati [Hamilton Co.], Ohio"; exact locality unknown; USNM no. 60604.	
	a. Overall view of lectotype which presents a ventral aspect; X 6.2	183
	b. Mouth-angle ossicles adnate to axillary inferomarginal; note absence of adoral carina in this small specimen; X 22	183, 185
2 a-d.	Kenothecaster finei (Ulrich). Cotypes of Mesopalaeaster proavitus Schuchert; "... Eden shale exposed back of Covington [Campbell Co.], Kentucky, at a horizon about 100 feet above low water in the Ohio River"; exact locality is unknown; FMNH no. 54069 (Herzer Coll.).	
	a. Lectotype (designated herein) of Mesopalaeaster proavitus Schuchert; X 4	183
	b. Lectoparatype (herein) of M. proavitus Schuchert; ventral aspect showing adambulacral, ambulacral and prosopon characteristis; X 6	183
	c. Obverse of specimen shown in fig. 2b; X 6	183
	d. Ventral interbrachial area of lectotype; X 10 .	183, 185
3.	Kenothecaster finei (Ulrich). Precise locality and stratum unknown; only label information is Route 8, near Augusta, Kentucky; X 4 .	184, 186

PLATE 9


1a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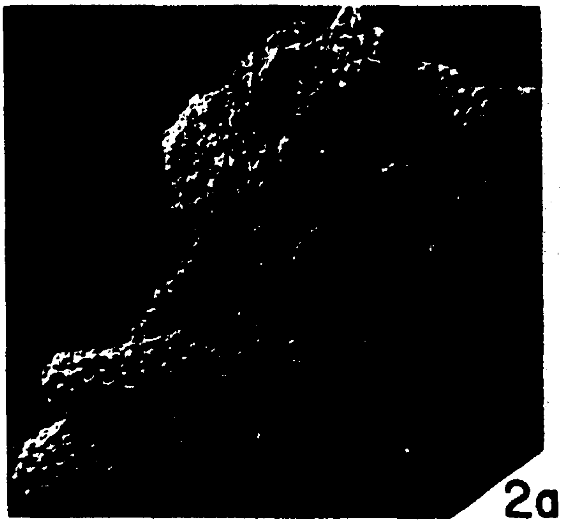
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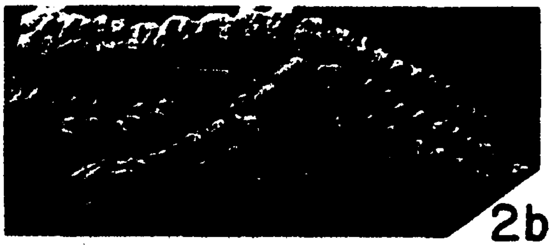
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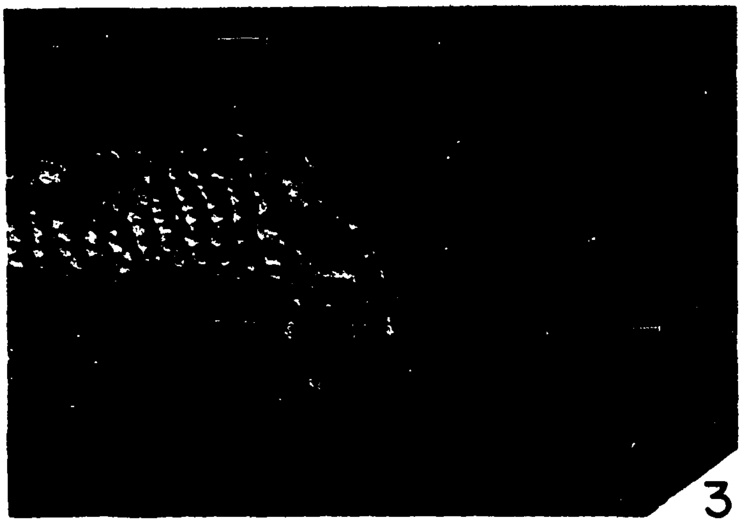
2c


2d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EXPLANATION FOR PLATE 10

Figure		Page
1.	Kenothecaster finei (Ulrich). Cincinnatian; stratum unknown; Covington, Campbell Co., Kentucky; USNM no. 92613; fragment of largest known individual of species; note small groove spines; note ambulacral dentition; X 15	184
2 a-b.	Kenothecaster finei (Ulrich). Stratum unknown; Cincinnati [Hamilton Co.], Ohio; UMPM no. 6230.	
	a. Dorsal aspect of disc showing biserial arrangement of dorsal accessory ossicles; note tumid madreporite; X 5	185
	b. Dorsolateral aspect of brachium showing biseries of both interdorsal and intermarginal ossicles; note prosopon on all dorsal ossicles; X 11	185
3 a-d.	Kenothecaster finei (Ulrich). Labeled, "Western Hudson River Group, Cincinnati [Hamilton Co.], Ohio"; exact locality and stratum unknown; largest specimen catalogued under AMNH no. 1196.	
	a. Ventral aspect; X 2	184
	b. Interbrachial area showing several axillary inferomarginals and short adoral carina; X 6	184, 185
	c. Intermarginal ossicles (bottom of photograph is proximal; X 9	184

PLATE 10


1

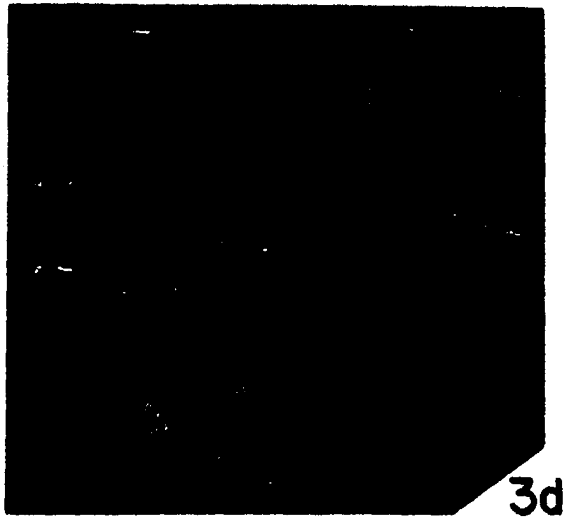

2a


2b


3a


3b


3c


3d

EXPLANATION FOR PLATE 11

Figure — Page

1 a-b. *Kenothecaster finei* (Ulrich).

Economy "Member" of Eden Shale; Beechmont and Elstun Avenues in eastern Cincinnati, Hamilton Co., Ohio; R = 3 mm.; UCGM no. 40375.

a. Dorsal aspect (through xylol) showing lack of dorsal accessory ossicles in smallest specimens; X 10 .... 184, 185

b. Ventral aspect (through xylol) showing relatively large mouth-angle ossicles adjacent to unpaired axillary on the ambitus; X 10 .... 184, 185

2 a-b. *Kenothecaster finei* (Ulrich).

Another juvenile from same locality; R = 5 mm.; UCGM no. 40371.

a. Ventral aspect (through xylol) showing more ossicles in columns than above specimen, and unpaired axillaries more occluded from margin by next successive pair of inferomarginals; X 6 . 184, 185

b. Dorsal aspect showing development of a few interdorsal ossicles; X 6 184

3. *Kenothecaster finei* (Ulrich).

Juvenile from same locality; R = 4 mm.; UCGM no. 40381. Dorsal aspect of specimen showing intermediate stage of development between UCPM nos. 40375 and 40371; note presence of only two interdorsal accessory ossicles on left side of brachium; X 12 184

4. Kenothecaster finei (Ulrich).

Same locality; fragment of largest individual; R = about 8 mm.; UCGM no. 40382a. Note multiple columns of interdorsals and intermarginals and relative relative reduction in size of terminal ossicle; X 9 ....

5. Kenothecaster finei (Ulrich).

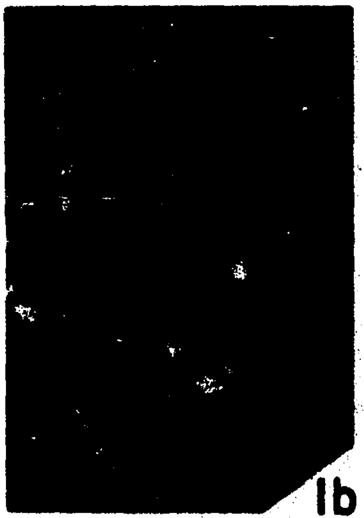
Juvenile from same locality; R = 2 mm.; UCGM no. 40378. Note numerous long, dorsal spines still preserved with specimen; X 19 ....

6. Kenothecaster finei (Ulrich).

Juvenile from same locality; R = 3 mm.; UCGM no. 40378. Note pustulose dorsal prosopon; X 15 ......

PLATE 11


1a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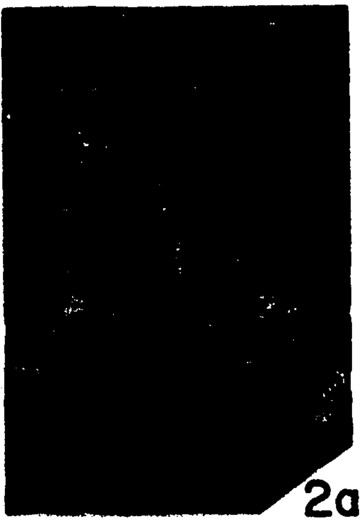
2a


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2b


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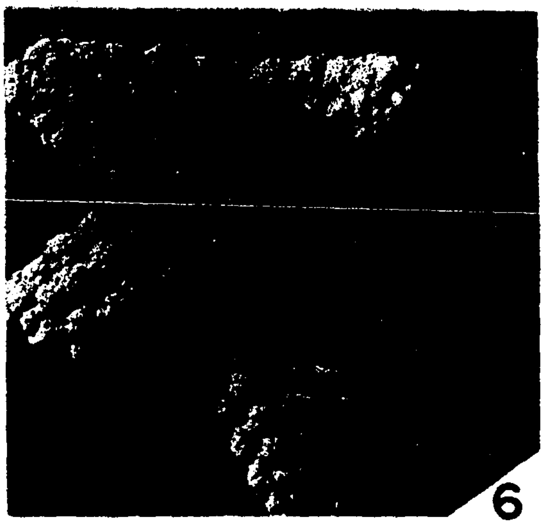

6

EXPLANATION FOR PLATE 12

Figure | Page

1 a-f. *Kenothecaster dyeri* (Meek).

Holotype; "...Lower Silurian [Upper Ordovician] from the horizon of about one hundred feet below the tops of the hills [= Maysville rock] at Cincinnati [Hamilton Co.], Ohio." MCZ no. 469 (Dyer Collection).

a. Ventral aspect of oral area; note wide most-proximal ambulacrals and large, acuminately clavate groove spines; X 4 188

b. Mouth-angle ossicles, proximal adambulacral pair in an adoral carina, and adjacent proximal ambulacral ossicles; note dentition on perradial ends of ambulacral ossicles; X 10 188

c. Ventral aspect; X 1 188

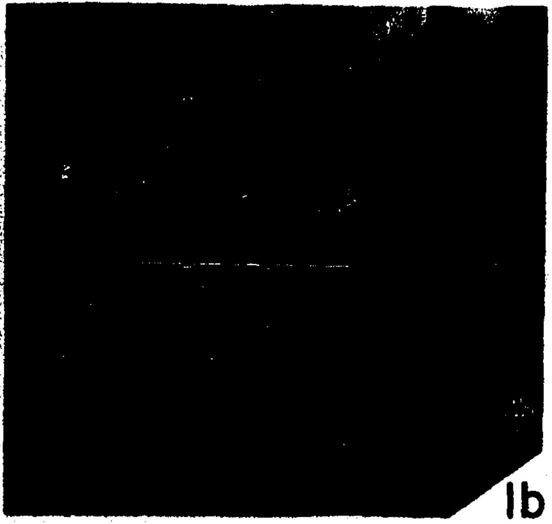
d. Proximal lower left brachium in fig. 1c showing large spine-base structures on inferomarginals; X 3 188

e. Dorsal aspect; X 1 188

f. Lateral aspect of lobate madreporite; X 4 188

PLATE 12


1a


1b


1c


1d


1e

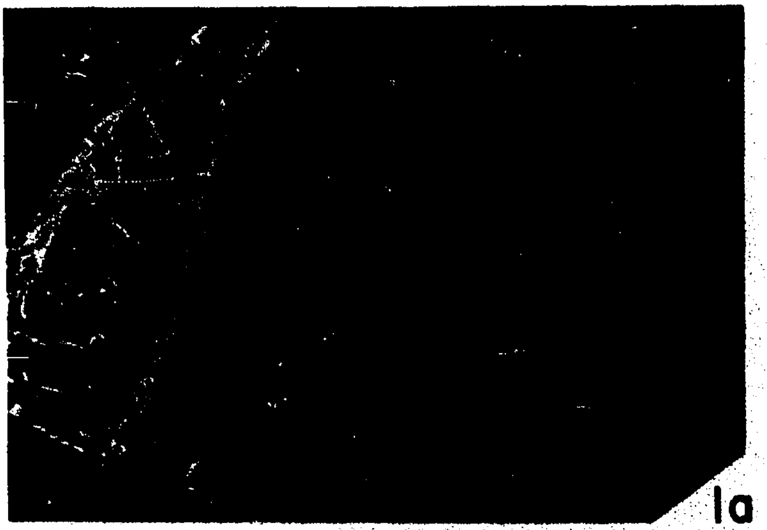

1f

EXPLANATION FOR PLATE 13

Figure		Page
1 a-b.	Kenothecaster dyeri (Meek). Maysville rock; Cincinnati, Hamilton Co., Ohio; more exact data not available; UCGM no. 40,395.	
	a. Ventral aspect showing well-developed adoral carina, prosopons of adambulacrals and inferomarginals, a torus, and details of proximal ambulacral ossicles; X 3.5	189
	b. Dorsal aspect showing small size of proximal accessory and primary ossicles; note top of odontophore protruding through dorsal (top of photograph) body wall; X 3.5	189
2 a-b.	Kenothecaster dyeri (Meek). Mt. Hope "Member" of Fairview "Formation" [Maysville rock]; Cincinnati, Hamilton Co., Ohio; UCGM no. 1455.	
	a. Ventral aspect showing relatively large subadambulacral spines; X 3	188
	b. Dorsal aspect showing enlarged central spine-base structure on some interdorsal ossicles; X 3	188
3.	Kenothecaster miamiensis (Miller). Holotype of Palaeaster wykoffi Miller and Gurley; Richmond rocks; "near Madison [Jefferson Co.], Indiana"; FMNH no. 6066 (Gurley Coll.). Ventral aspect showing characteristic ambulacral ridges of species; X 2	200

4. Kenothecaster miamiensis (Miller).
Cincinnatian; exact locality and stratum unknown; UCGM no. 1459. Internal aspect of the ossicles of the oral frame and the proximal ambulacral ossicles of two brachia. Note V-shaped odontophores, wide most-proximal ambulacrals, and occlusion of internal interbrachial areas by interbrachial thecal ossicles; X 6 .... 191, 197

PLATE 13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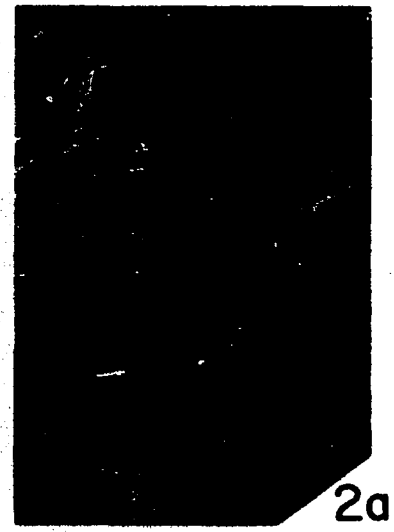
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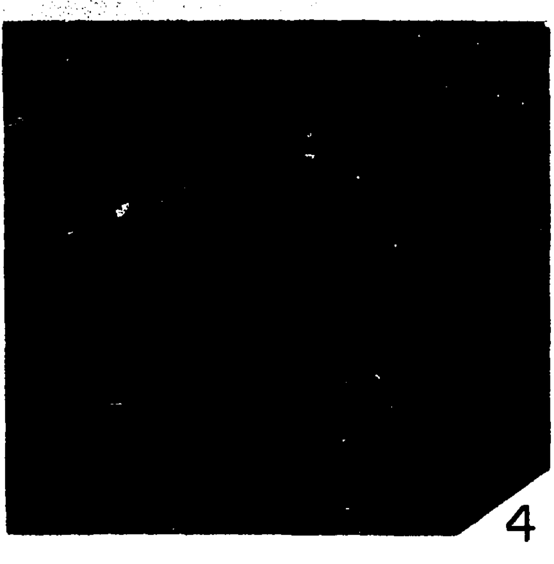

4

EXPLANATION OF PLATE 14

Figure		Page
1.	Kenothecaster miamiensis (Miller). Refer to data for UCGM no. 1459 (Pl. 13, figs. 3 a-b). Madreporite of specimen showing long, solidly ossified extension to circumoral water-vascular vessel; X 15	197
2 a-d.	Kenothecaster miamiensis (Miller). Holotype; "..upper part of the Cincinnati Group [Richmond rocks] near Waynesville [Warren Co.], Ohio; precise locality and stratum unknown; USNM no. 40880.	
	a. Distal end (through xylol) of lower right brachium shown in fig. 2c; note eight or nine adambulacral ossicles overlying ambulacral ossicles at arm tip; X 9	198
	b. Interbrachial area (through xylol) showing remnants of two adoral carina pairs between mouth-angle ossicles and axillary inferomarginals; X 8	193
	c. Overall aspect (through xylol); X 1.8	191
	d. Oral area showing remnants of mouth-angle ossicles and a few fragments of adambulacral ossicles; X 5	198
3 a-b.	Kenothecaster miamiensis (Miller). Holotype of Promopalaeaster bellulus Schuchert; "... Waynesville beds of the Richmondian"; precise locality and strata unknown, but probably near Waynesville,	

Warren Co., Ohio; USNM no. 40879.

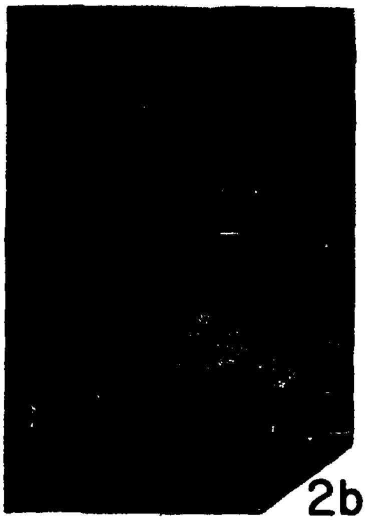
a. Overall aspect in typical Waynesville fauna; X 1.2 .. 192

b. An adoral carina showing adnate carinal adambulacrals; note torus and subadambulacral spine shape in upper groove; X 6.2 .... 192, 197

PLATE 14


1


2a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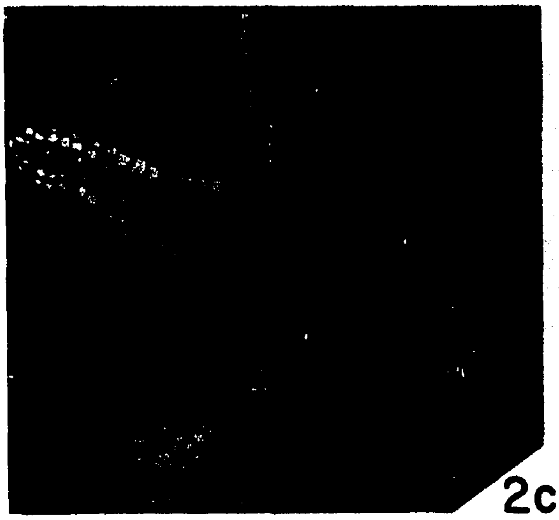
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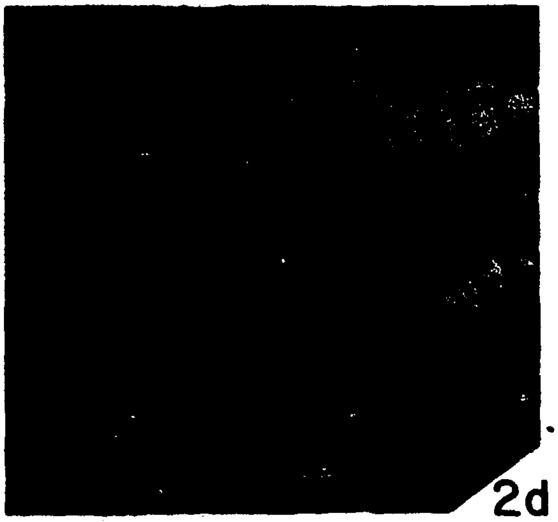

2d


3a


3b

EXPLANATION OF PLATE 15

Figure | Page

1 a-b. *Kenothecaster miamiensis* (Miller).

Paratype of *Palaeaster magnificus* Miller; "...upper part of Hudson River Group [Richmond rocks] of Waynesville [Warren Co.], Ohio; specific locality data unavailable"; USNM no. 40883 [part].

a. Ventral aspect of a large interbrachial area showing adoral carina, geratic development of inferomarginals and details of ambulacral ossicle structure; note hemal channels along transverse ridges on ambulacrals; X 3 192

b. Dorsal aspect showing lack of podial perforations between successive ambulacrals and prominent proximal superomarginals; X 3 196

2 a-c. *Kenothecaster miamiensis* (Miller).

Holotype of *Palaeaster magnificus* Miller; refer to data for USNM no. 40883 (paratype) in figs. 1 a-b; USNM no. 40883 [part].

a. Ventral aspect; X 1 192

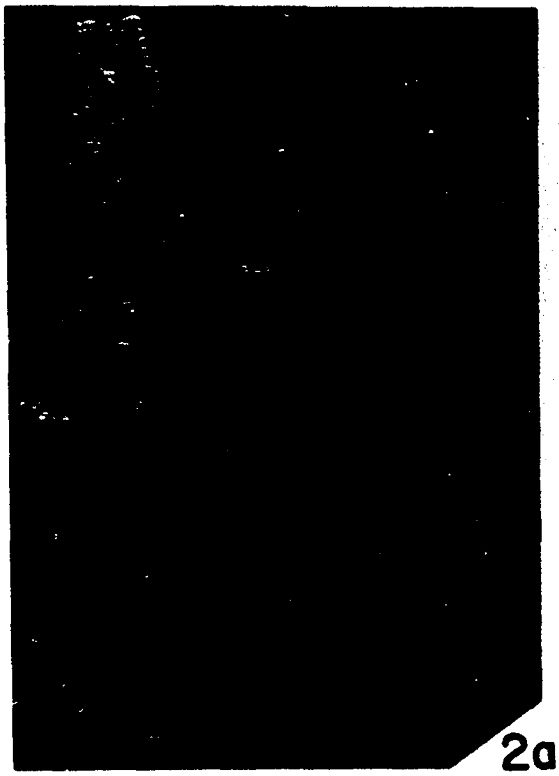
b. Dorsal aspect; X 1 193

c. Lateral aspect of distal portion of lower left brachium in fig. 2b; not biserial arrangement of both accessory ossicle types; X 7 193

PLATE 15


1a


1b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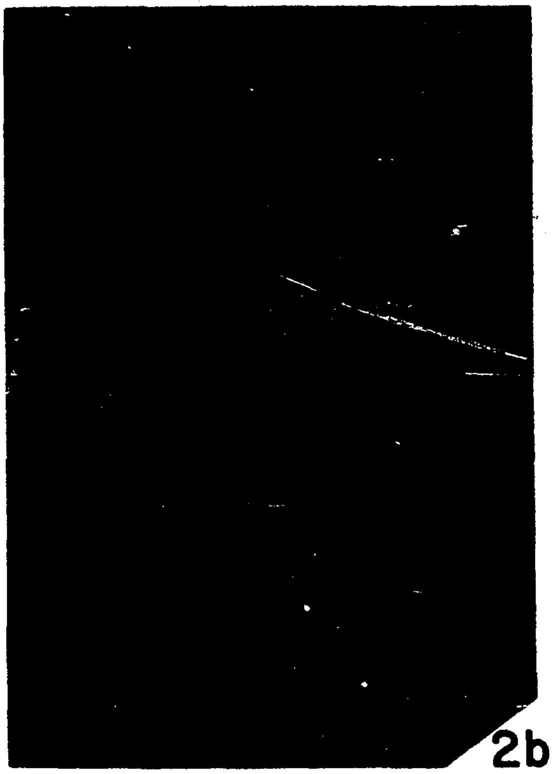

2b

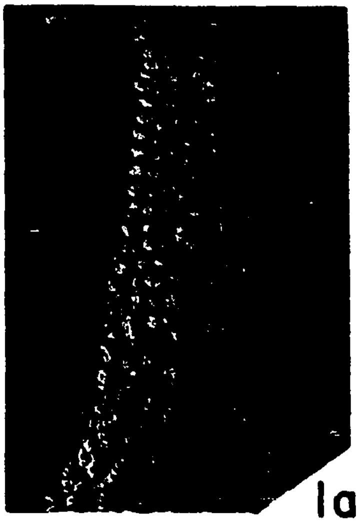

2c

EXPLANATION FOR PLATE 16

Figure		Page
1 a-b.	Kenothecaster miamiensis (Miller). Paratype of Palaeaster magnificus Miller; refer to data for USNM no. 40883 (paratype) in Pl. 15, figs. 1 a-b; USNM no. 40883 [part].	
	a. Dorsal aspect of brachium tip; note decrease in accessory ossicle column number toward terminus; X 3.5	196
	b. Ventral aspect of brachium tip; note preservational calcitic overgrowths on adambulacral ossicles; X 3.5	192, 196
2 a-e.	Kenothecaster miamiensis (Miller). Holotype of Palaeaster magnificus Miller; refer to data for USNM no. 40883 in Pl. 15, figs 2 a-c; USNM no. 40883 [part].	
	a. Dorsal aspect of brachium near tip (lower left brachium in Pl. 15, fig 2b); X 3	193
	b. Dorsal aspect of disc; X 2	193, 196
	c. Dorsal aspect of brachium just distal to mid-length (upper brachium in Pl. 15, fig. 2b); note prominence of primary ossicle columns and biserial arrangement of interdorsals; X 6	193
	d. Ventral aspect of interbrachial area showing slightly irregular development of axillary inferomarginals; X 4	192
	e. Lateral view of madreporite; X 4	196

3. <u>Kenothecaster</u> <u>miamiensis</u> (Miller).
Richmond rocks; near Versailles, Ripley Co., Indiana; exact locality unknown; FMNH no. 10983 (Gurley Coll.). Note alternating ambulacral ridges and spine-base pits for vertically pectinate series of subadambulacral and groove spines; X 10 192

PLATE 16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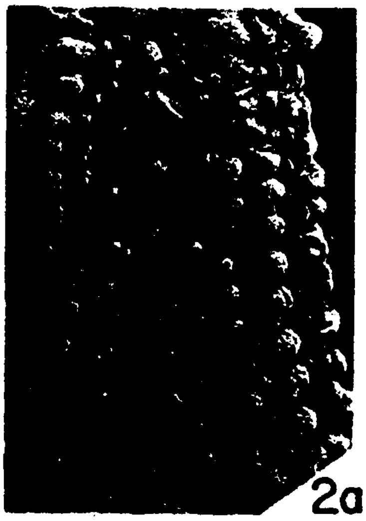
1b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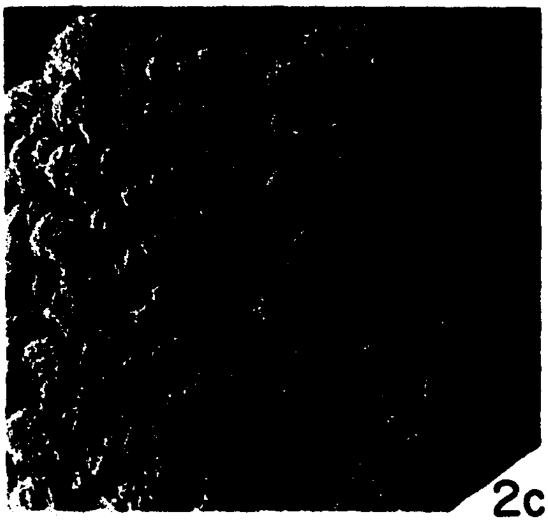
2b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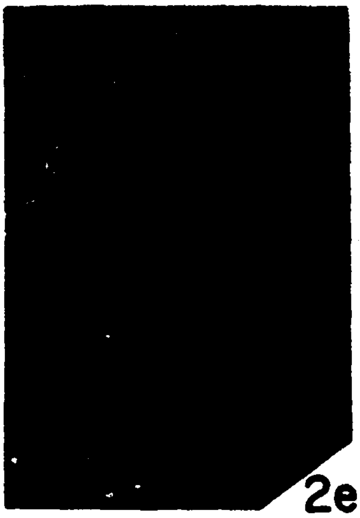

2e


3

EXPLANATION FOR PLATE 17

Figure		Page
1 a-c.	Kenothecaster miamiensis (Miller). Liberty "Formation" (Richmond rock); Hueston Woods St. Pk., Preble Co., Ohio, SW 1/4, Sect. 34. T6N, R1E, on 7.5 min. College Corner (1961) Quad., about 600 feet up a small streambed leading from the southwest into Acton Lake, elevation 880 ft; MUGM no. 6809.	
	a. Ventral aspect of large (R = more than 150 mm.) specimen showing geratic development of large inferomarginal spines and strongly overlapping ambulacral ossicles (upper brachium); X 0.5 ...	192, 193
	b. Proximal inferomarginal and adambulacral spines; X 2.5 ...	192
	c. Dorsal aspect of longest brachium showing numerous interdorsal ossicle columns; X 2. ...	193
2 a-b.	Kenothecaster miamiensis (Miller). Richmond rocks; Jefferson Co., Indiana; exact locality unknown; FMNH no. 10981 (Gurley Coll.).	
	a. Over ventral aspect of large (R = more than 75 mm.) specimen showing well-developed adoral carinae and axillary areas; x 1 ...	191, 193
	b. View across an ambulacral groove at a mouth-angle ossicle and adjacent adambulacrals and ambulacrals showing interambulacral podial perforation between more proximal ossicles; X 10 ...	192

3 a-b. Kenothecaster miamiensis (Miller).

Richmond rocks; Clarksville "Member" of Waynesville "Formation"; Boudinot Avenue at Westwood-Northern Blvd. in Cincinnati, Hamilton Co., Ohio; UCGM no. 40755 (Dalvé Coll.).

a. Dorsolateral aspect of brachium (proximal to right) showing extensions of superomarginals which are usually hidden by accessory ossicles in other specimens of this species; X 6 .... 193, 196

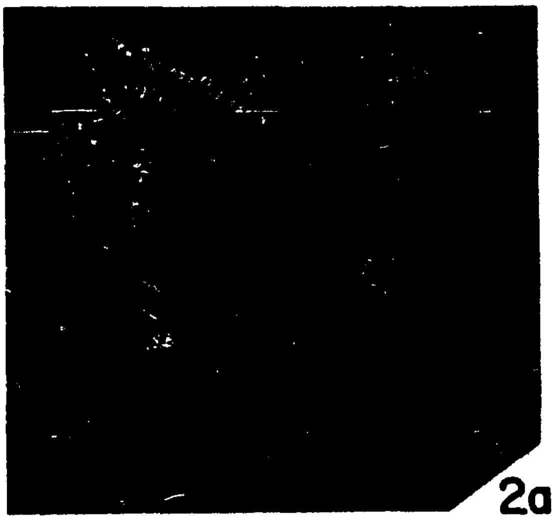
b. Lateral aspect (proximal to left) showing biserial arrangement of intermarginal ossicles, and adambulacral spines; X 6 .... 193, 196

PLATE 17


1a


1b


1c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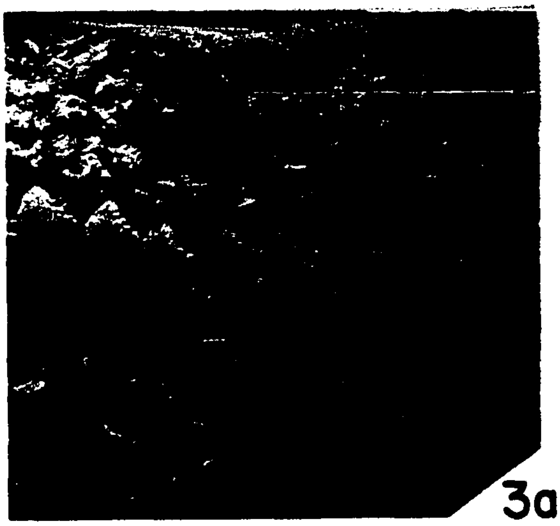
2b


3a


3b

EXPLANATION OF PLATE 18

Figure Page

1 a-c. Neardisaster prenuntius (Schuchert).

Holotype; Champlainian Lexington Limestone; near Frankfort, Franklin Co., Kentucky; exact locality unknown; UK no. 403.

a. Overall ventral aspect of finely recrystallized and slightly etched specimen; note slight development of alternating proximal ambulacral ridges; X 2 .... 203, 204

b. Ventral interbrachial area showing complete lack of adoral carina in this medium-size (R = more than 35 mm.) specimen; compare with Text-fig. 21, p. 199; X 7 .... 203, 205

c. Dorsal aspect of arm which is folded under overturned theca; X 9 204

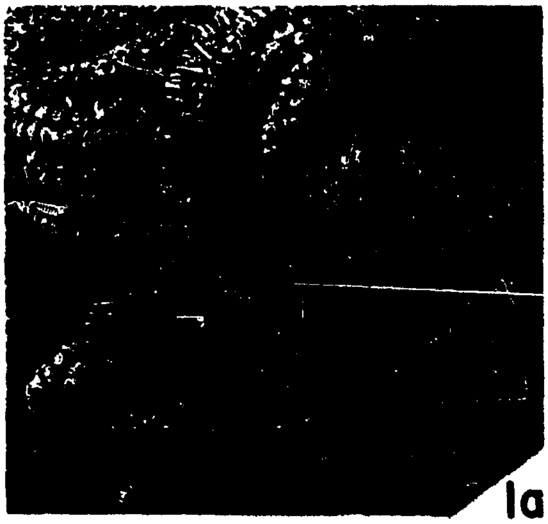
2 a-d. Neardisaster prenuntius (Schuchert).

Champlainian Lexington Limestone; near Frankfort, Franklin Co., Kentucky; exact locality unknown; YPM no. 3405.

a. Lateral aspect of a brachium showing rotund dorsal accessory ossicles and long spines of more abradial columns; X 5 204

b. Lateral aspect of obserse side of brachium shown in fig. 2a; note papular perforations in interdorsal ossicular field and the decrease in size of interdorsal spines near median dorsals; X 4 204

PLATE 18



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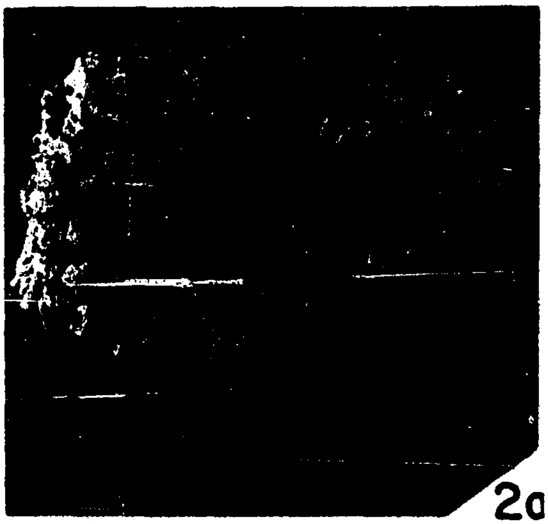

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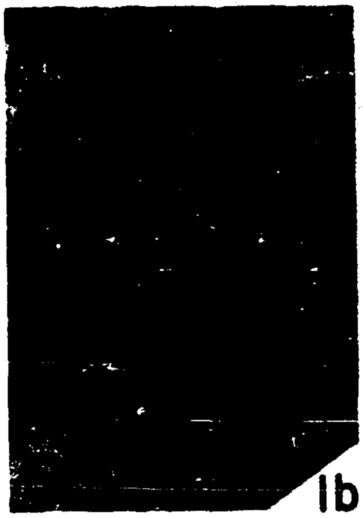
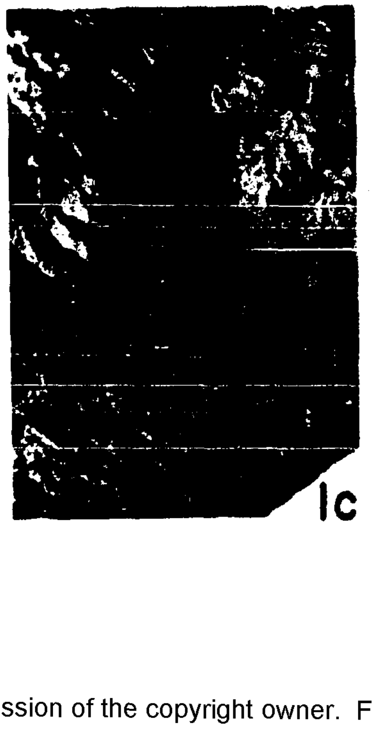


1b

2b

2c



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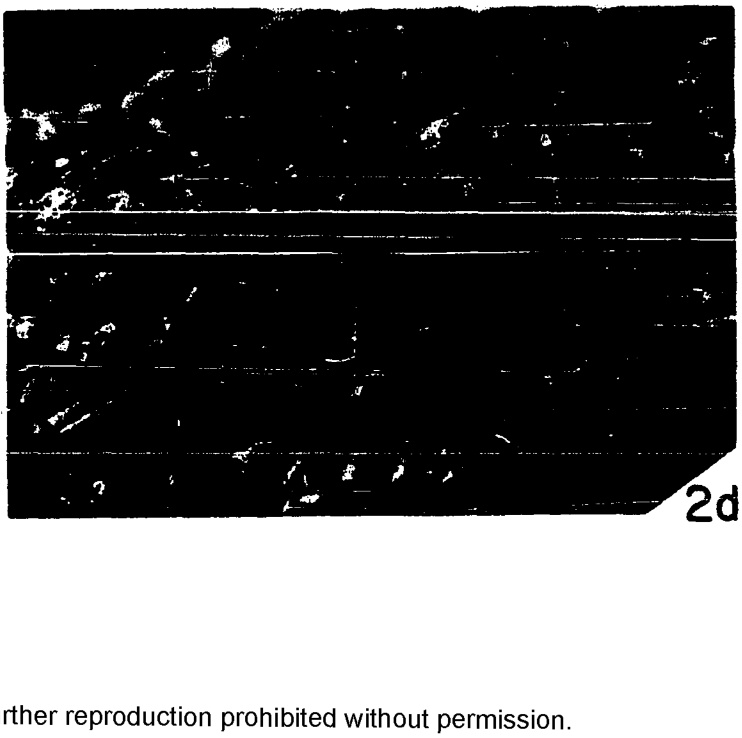

2d