PALEOENVIRONMENTAL ANALYSIS OF THE UPPER SILURIAN CALLOCYSTITIDAE (CYSTOIDEA, RHOMBIFERA) IN THE CENTRAL APPALACHIANS

A Thesis Submitted
to the Temple University Graduate Board

---

in Partial Fullfiment
of the Requirement for the Degree

MASTER OF ARTS

---

by

David Charles Stephenson

December 1974

DEPARTMENT COPY

PALEOENVIRONMENTAL ANALYSIS OF THE UPPER SILURIAN CALLOCYSTITIDAE (CYSTOIDEA, RHOMBIFERA) IN THE CENTRAL APPALACHIANS

A Thesis Submitted
to the Temple University Graduate Board

---

in Partial Fullfiment
of the Requirement for the Degree

MASTER OF ARTS

---

by

David Charles Stephenson

December 1974

DEPARTMENT COPY

PALEOENVIRONMENTAL ANALYSIS OF THE UPPER SILURIAN CALLOCYSTITIDAE (CYSTOIDEA, RHOMBIFERA) IN THE CENTRAL APPALACHIANS

by

David Charles Stephenson

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Arts
at Temple University

December, 1974

Dec. 19, 1974 Peter W. Goodwin for E. J. Anderson (on leave)

Dr. Edwin J. Anderson, Advisor
Assistant Professor of Geology

Abstract

The dominantly transgressive Upper Silurian interval of the Keyser Limestone (U. Sil. - L. Dev.) in the central Appalachians has yielded the most diverse fauna of rhombiferan cystoids found in any single formation in North America. All forms are members of the Callocystitidae, a diverse family of the Glyptocystitida. Nine lithofacies are recognized within this stratigraphic interval, representing all major epeiric sea environments from supratidal through shallow shelf below wave base. Identification of cystoid genera and species by disarticulated part studies (comparison of isolated plates to the corresponding element on whole thecae of known taxa) demonstrates their restriction to three discrete assemblages on the open shelf.

Cystoid bearing lithofacies represent a contemporaneous and laterally coexisting sequence of skeletal sands and silt which include: 1. well sorted calcarenite (both biosparudite and biosparite), 2. poorly sorted biosparite, 3. open shelf (fossiliferous) calcisiltite. Maximum cystoid diversity is recorded in the calcisiltite, diminishing progressively in coarser shoreward calcarenites. Callocystitid distribution is suggested to have been primarily depth controlled. These cystoids were intolerant of turbid water, high sedimentation rate and of high energy nearshore sands and infirm mud bottoms.

A new genus Laosacystis monterey is described and assigned to the subfamily Staurocystinae on the basis of its four protuberant ambulacra.

Acknowledgements

I am indebted to many persons for their help during the course of this study. Foremost, I would like to thank Dr. E. J. Anderson, thesis advisor, and Dr. P. W. Goodwin for their guidance, suggestions and assistance in the field. The aid of Dr. C. R. C. Paul and Dr. J. K. Adams, who critically reviewed the manuscript, is gratefully acknowledged. Dr. P. M. Kier generously loaned cystoid specimens from the collection of the National Museum in Washington, D. C.

Financial support was provided by the Geology Department of Temple University in the form of a teaching assistantship. Field work during the summer of 1972 was aided by a Temple University Research Fellowship and in 1973 by a Sigma Xi Grant-in-Aid-of-Research.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

I. INTRODUCTION

The Crinozoa are complex invertebrates that exhibit a diversity of structure and form. It is well known that the dissociated segments (ossicles) of their skeleton are a primary constituent of numerous Paleozoic marine deposits. This is in strong contrast to the general scarcity of fairly complete thecae, usually needed for identification. The apparent environmental preference of many taxa for at least moderate current agitation coupled with the lack of a firm bond between skeletal parts accounts for this discrepancy. The utility of the Crinozoa in stratigraphic and environmental reconstruction is therefore severely limited in contrast to their potential value and abundance.

Cystoids, an extinct class of Crinizoa, achieved maximum diversity in the Ordovician Period. Although cystoids seldom figured as dominant members of benthic communities, when conditions were favorable, they did occur in considerable numbers. Their distribution in Upper Silurian strata of the Appalachian Basin testifies that they were very sensitive to a number of environmental and biologic controls and may be used as sensitive paleoecological indicators in Lower Paleozoic marine strata.

This thesis has three objectives:

1. To demonstrate the taxonomic relationship between isolated plates on limestone slabs to known taxa

represented by complete cystoid thecae.

2. To interpret the environments of limestones containing the isolated plates in the Keyser Formation using biologic and sedimentologic evidence and to demonstrate the habitat preferences and environmental limitations of the Keyser cystoids.

3. To define cystoid communities and relate them to specific environments and patterns of environmental fluctuation in the Keyser.

II. PREVIOUS WORK ON THE PALEOECOLOGY OF CYSTOIDS

Early work on the Cystoidea was predominantly taxonomic (see Bather, 1900; Jaekel, 1918; Bassler & Moodey, 1943, Kesling, 1967). A search through the literature reveals a minimum of recorded observations on paleoecology and most of these are brief comments mentioned in the course of systematic descriptions. Although modern specialists are primarily concerned with additions to and revisions of existing taxonomy, a few have expanded their inquiry into the field of functional morphological interpretation of specific skeletal structures. The work of Paul (1967b,1968, 1972) on the respiratory function of dipores and rhombs is exemplary in this respect.

With the exception of Paul's work, published information on the paleoecology of cystoids is of little consequence. Kesling (1967) in a review of cystoid paleoecology explained that a comprehensive treatment of the subject cannot be accomplished because, "occurrences are not generally reported with details of the burial attitude, associated fauna, lithology of the enclosing strata, or distribution through a sequence of beds."

Perhaps the major deterrent to ecologic analysis of the Cystoidea as well as other Crinozoa is the rapid postmortem disintegration of the skeletal components. Thecal plates and stem ossicles are loosely articulated and held in place by ligament strands and muscle tissue. Upon death, ligaments and muscle tissue rapidly disintegrate by oxidation and biological attack leaving a mass of disarticulated parts. Even minor current agitation would rapidly accelerate this process. Cain (1968) using specimens of Andedon bifida, an extant comatulid crinoid, found that within two days of death, in completely static sea water, "specimens had collapsed into a mass of isolated fragments, even under anaerobic conditions". He concluded that well preserved crinoid remains are due to instant burial by rapid sedimentation or by sinking of the animal into semi-liquid mud upon death. Similar results were obtained by Meyer (1971).

Several publications in the past decade have made major contributions toward a general understanding of cystoid paleoecology. Although these publications are primarily concerned with taxonomy, each has a few paragraphs devoted to ecological considerations. Their conclusions are made possible by exceptional preservation of several individuals of a single species or museum collections representing numerous species over a rather restricted stratigraphic interval.

Kesling and Mintz (1961), reporting on the Upper Ordovician callocystitid Lepadocystis moorei, described several slabs representing a biocoenose (in place community) containing a gregarious population of Lepadocystis and including numerous ramose bryozoa, small pedunculid brachiopods, edrioasteroids, and other filter feeders that "together formed a living filter carpeting a part of the seafloor". They noted that all animals in this association were microphagous and concluded that "the ideal circumstance for providing microscopic detritus in great quantities would be an eddy in relatively shallow water near a low land mass so that only fine calcareous mud was being deposited and that at a slow rate". They placed particular emphasis on the terminal attachment processes of the cystoids which are preserved on complete specimens, since Lepadocystis is the first published report of a cystoid with an undoubtedly attached stem. Permanent attachment was accomplished by expansion of the distal-most stem ossicles which cemented this part of the stem to a firm substrate and allowed it to conform to the object to which attachment was made. Attachment was secured to the branches of ramose bryozoa. In some specimens, the lower part of the stem was wrapped around a bryozoan branch in a prehensile fashion. Kesling and Mintz theorize that the function of the terminal process was to secure permanent fixation and raise the theca in an upright position a considerable distance off the sea floor allowing the flexible upper section of the stem "to seek out the most advantageous position for its theca within the hemisphere of action to which it restricted itself by fixation", while at the same time elevating the feeding apparatus above competing filter feeders.

Koch and Strimple (1968) described numerous specimens of Adocetocystis williamsi, a callocystitid and a close relative of Tetracystis chrysalis found in the Upper Silurian portion of the Keyser Formation. Adocetocystis with more abundant edrioasteroids, were the dominant members of a thriving biocoenose in the Upper Devonian of Iowa. Sub-dominant members of the fauna include auloporoid, tabulate and rugose corals, worm tubes and subspherical stromatoporoids. All specimens are contained on rock slabs, the upper surfaces of which may have as many as 125 edrioasteroids on a 4 X 4 surface. Many of the cystoids are preserved attached by expansion of the distal stem ossicles. A conspicuous zone of pyrite impregnation and evidence of current scour led Koch and Strimple to conclude that during the development of the community, the water was shallow and subjected to at least moderate current or eddy activity implying that a dense fauna dominated by microphageous filter feeders would only have been able to thrive in areas where food was abundantly and consistently in suspension.

The comprehensive treatment of the Silurian Cystoidea of the British Isles by Paul (1967b) is of particular interest to this study since two genera, Pseudocrinites and Tetracystis, described from the Middle Silurian Wenlock Limestone Formation are also found in the Upper Silurian Keyser Formation. Paul commented that although information on the stratigraphic distribution of the Silurian species is limited, they appear to have had a "very restricted distribution in shallow water", as indicated by associated brachiopod assemblages analagous to shallow water brachiopod communities established by Ziegler (1965) from the Lower Silurian of Wales.

Many of the Wenlock specimens are preserved in excellent condition on the upper surfaces of calcarenite slabs covered with a "thin veneer of shale". Paul recognized that the excellent state of preservation almost certainly indicates the contemporaneous echinoderm fauna was exterminated and rapidly buried by a sudden mud influx. One exceptional specimen of <u>Pseudocrinites</u> <u>bifasciatus</u> displays a complete stem ending in a terminal attachment process similar to that described by Kesling and Mintz (1961) for <u>Lepadocystis moorei</u>.

III. PREVIOUS WORK ON THE STRATIGRAPHIC SETTING OF THE KEYSER

The name Keyser Limestone was proposed by Ulrich (1911) and first fully described and initially recognized as a member of the Helderberg Formation by C.K. Swartz (1913). Exposures near Keyser, West Virginia were designated as the type section. F.M. Swartz (1929) raised the Helderberg to group status and established the Keyser as a formation within the Helderberg. Recent work, primarily based on brachiopod range zonation,has assigned an Upper Silurian age (Cayugan Group) to the lower Keyser (Boucot and Johnson, 1967; Bowen, 1967; Head, 1969). The Silurian-Devonian boundary is currently placed near the top of the lower limestone member (Byers Island). For a review of the distribution of the formation, general lithologic variation and the establishment of faunal zones and subzones, see Bowen, 1967; and Head, 1969.

The Keyser outcrop belt (fig. 1) extends from southern Virginia and strikes northeast through eastern West Virginia, Maryland and most of central Pennsylvania. Thickness varies from over three hundred feet near Great Cacapon, Maryland, to less than one hundred feet in central Pennsylvania.

The Keyser is currently divided into five lithologically distinct members (fig. 2). Stratigraphically, the lowest member is the Byers Island (Head, 1969) dominantly composed of biomicrites with a nodular texture and variably restricted

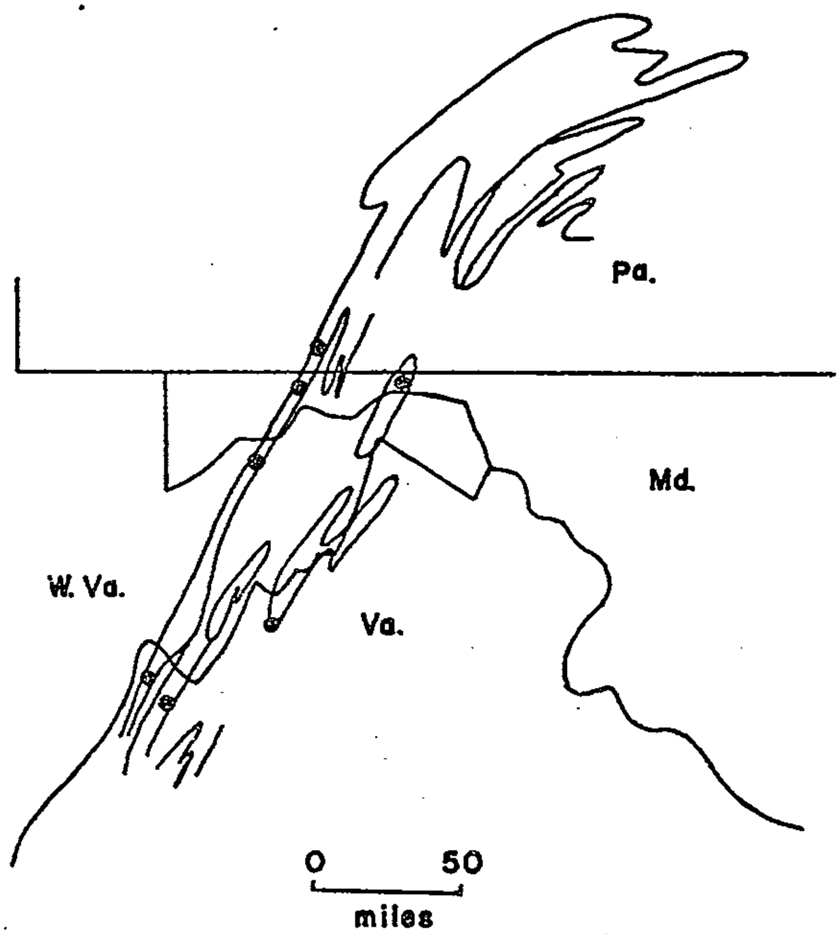


Figure 1. Generalized outcrop belt of the Keyser Formation. Dots represent sampling localities.

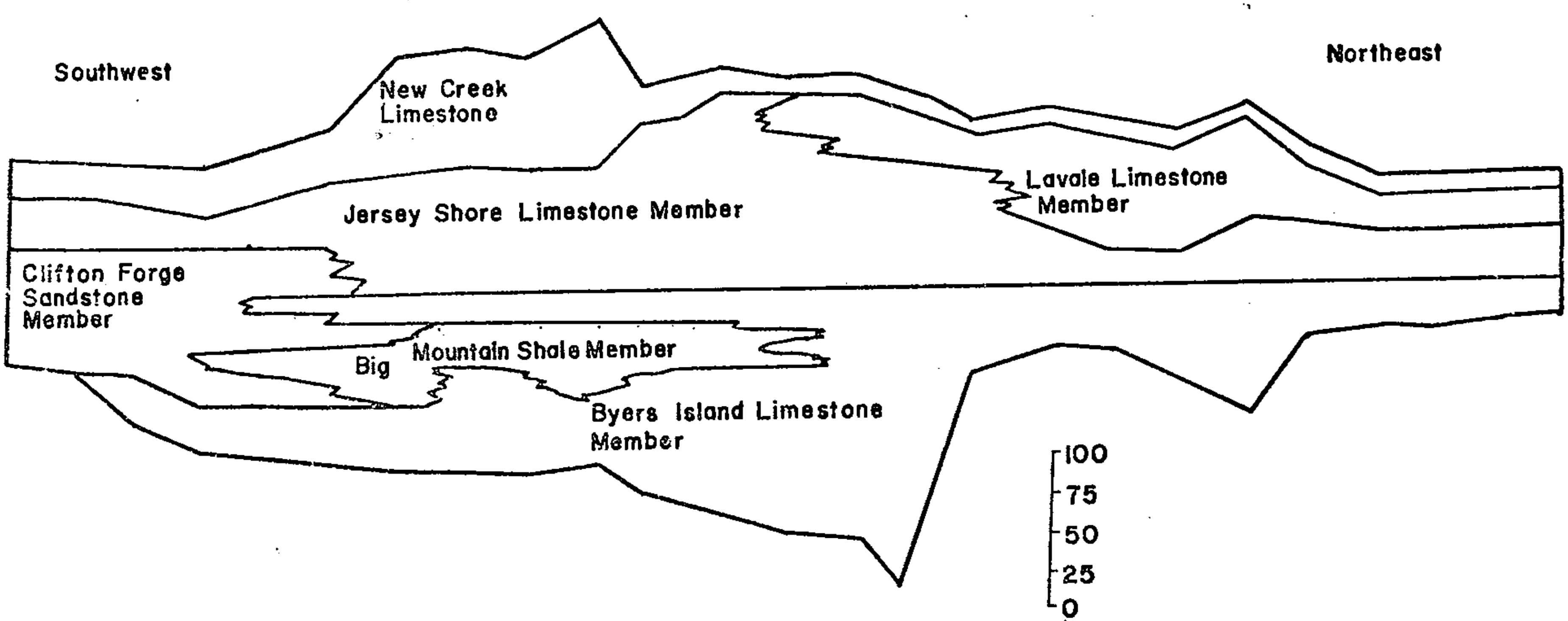


Figure 2. Stratigraphic cross-section of the Keyser Formation

fauna and calcarenites with a more diverse fauna. Thinly laminated, mud cracked and unfossiliferous dolomitic limestones of the Tonoloway Formation underly the Byers Island. Usually clasts of the Tonoloway are incorporated into the nodular beds at the base of the Byers Island indicating an erosional contact. Occasionally calcarenite beds constitute the basal Keyser. To the south, the Byers Island grades up into the Big Mountain Shale Member and the Clifton Forge Sandstone Member (Swartz, 1929), both of which represent terrigenous influxes from the southeast. The next highest subunit stratigraphically is the Jersey Shore Member (Head, 1969), which may be traced along the entire length of the outcrop belt. The Jersey Shore contains a variety of lithologies but is dominated by calcarenites, calcisiltites and coral-stromatoporoid biostromes.

The LaVale Member (Head, 1969) overlies, and to the south grades laterally into, the Jersey Shore Member. It contains the most restricted fauna of the five Keyser members and is readily distinguished lithologically by a predominance of laminated dolomitic limestones and banded lime mudstones. In the northern half of the outcrop belt the upper contact of the Keyser is quite distinct. Thinly laminated and banded limestone beds of the upper LaVale Member are overlain by well-sorted and massive crinoidal biosparites of the New Creek Formation, usually in erosional contact. South of

Keyser, West Virginia, the LaVale grades laterally into the Jersey Shore. The more fossiliferous and lithologically variable nature of the Jersey Shore somewhat obscures the Keyser's upper contact with New Creek calcarenites at some localities compared with points further north (Bowen, 1967). However, due to the lithologic homogeneity of the New Creek Formation, the contact is usually apparent.

Lithofacies within the five Keyser members are indicative of depositional environments ranging from supratidal through shallow restricted subtidal to offshore open shelf. Their thicknesses, spatial arrangement and similarity to better understood units further north (Helderberg Group of New York State), suggests that the deposition of facies during Keyser time can be best explained by the epeiric model of basin sedimentation (Shaw, 1964; Irwin, 1965; Laporte, 1969; Anderson, 1971).

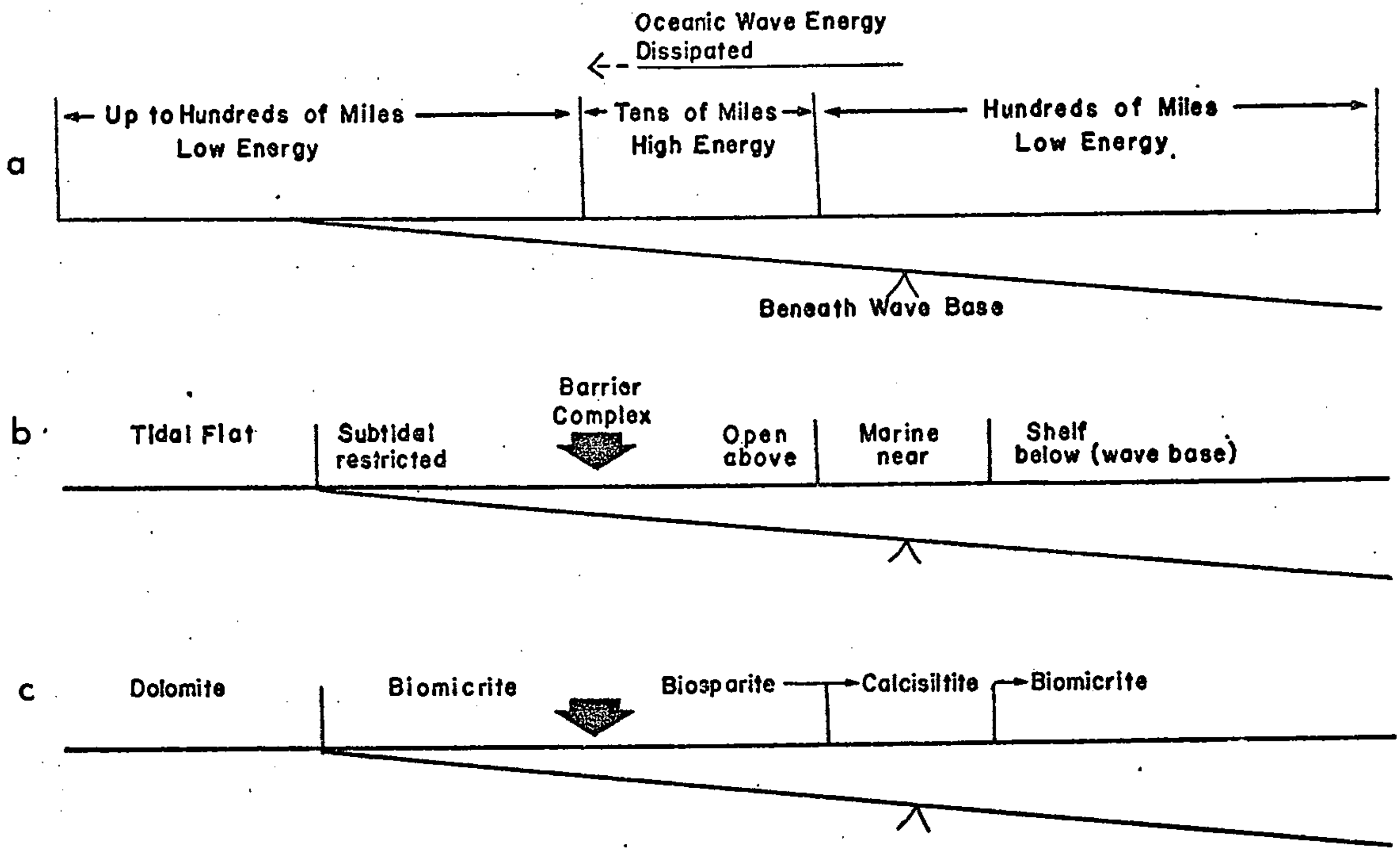
Basin borders for Keyser time are characterized by a stable structural area to the west and to the east, a tectonically active land area with higher relief (fig. 4). Alling and Briggs (1961) have demonstrated that the sedimentary framework for Upper Silurian Cayugan rocks was in large part controlled by the disposition and growth of Niagran reef platforms. Reef rocks, dominantly coral-stromatoporoid bioherms, can be traced almost completely around the Michigan Basin eastward into New York State and southwesterly along the eastern Ohio Border into Virginia. This southwesterly extension forms the western border of

Figure 3. The epeiric model of basin sedimentation.

a. Section showing energy zones (after Shaw, 1964; Irwin, 1965).

b. Section showing the sequence of environments (after Anderson, 1971b).

c. The distribution of carbonate sediments (after Laporte, 1969).


Oceanic Wave Energy Dissipated
a
Up to Hundreds of Miles
Low Energy
Tens of Miles
High Energy
Hundreds of Miles
Low Energy
Beneath Wave Base
b
Tidal Flat
Subtidal restricted
Barrier Complex
Open above
Marine near
Shelf below (wave base)
c
Dolomite
Biomicrite
Biosparite
Calcisiltite
Biomicrite

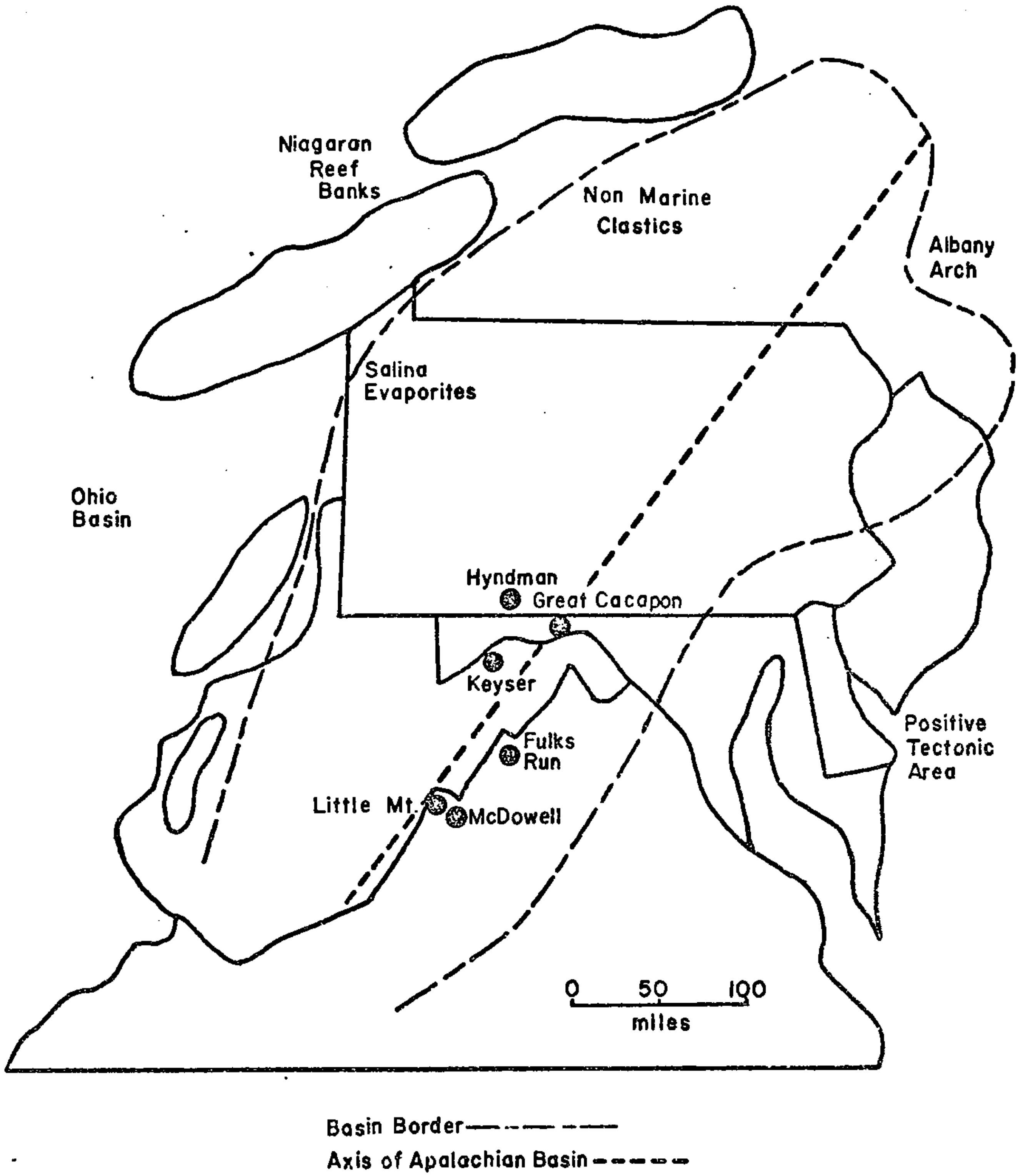


Figure 4. Configuration of Appalachian Basin and basin borders during late Silurian time.

the late Silurian Appalachian Basin. The stable reef platform effectively separated the dominantly marine Appalachian Basin from the highly restricted and evaporitic Ohio Basin to the northwest.

Northeastern borders are composed of a complex of positive structural areas. Naylor and Boucot (1965) have demonstrated the probable existence of a land area to the northeast extending through eastern New York into Quebec. The trend of this land area probably coincided with the Green Mountain-Sutton Mountain axis and is thought to have remained relatively stationary and to have been the source of some clastic material deposited along the extreme northeast margin of the basin during Cayugan time. Head (1969) included the Adirondack area and a lobe of folded Ordovician clastics, called the Albany Arch, as additional positive areas situated on the northeast border although he indicated the Adirondack area was not a major source of clastic sediment but served primarily to restrict this part of the basin. The southeast border is characterized by a tectonically active land area with higher relief. This land area appears to have been a major source of clastic material throughout the Silurian.

The basin borders outlined above persisted throughout Keyser deposition. Positions of the basin axis and margins remained relatively stationary with respect to the surrounding basin borders. However, along the western margin, very low slopes associated with the tectonic stability of this area permitted considerable lateral migration of facies belts. Asymmetry is therefore imposed on the epeiric model due to the disparity in the degree of slope and tectonic activity between the eastern and western basin margins.

Evolution of the Keyser Basin proceeded through a series of regular cyclic changes in sea level causing axial and lateral migration of facies belts (Head, 1969). The Byers Island and lower Jersey Shore Members record overall marine transgression from the southwest. Superimposed on this pattern are a number of brief regressive pulses. Terrigenous sand and shale of the Clifton Forge and Big Mountain Shale Members, introduced into the basin, were dispersed to the west and north. The restricted facies of the Jersey Shore Member when laterally equivalent to the LaVale Member document a major regressive phase during Upper Keyser time. The overlying New Creek Formation records renewed transgression.

IV. LOWER KEYSER LITHOFACIES

A. Techniques and Analysis

Geographic area of study

Within the established framework outlined in preceeding sections, analysis of lower Keyser lithofacies was initiated over a restricted geographic area to facilitate an understanding of the environmental significance of the variant lithofacies as well as the paleogeographic setting during this time interval. Although exposures were examined along the length of the outcrop belt, the central portion, including Maryland, southern Pennsylvania, northwest Virginia and northeast West Virginia was chosen for detailed study for the following reasons:

1. Preliminary investigation suggested cystoid diversity and abundance was greatest in the central portion. To the southwest into southern Virginia, or to the northeast into central Pennsylvania, terrigenous influx and more restricted conditions, respectively, seemed to have had adverse affects on cystoid populations.

2. This central portion of the outcrop belt includes described sections representing paleoenvironmental positions from the restricted eastern basin margin to the more open marine central basin axis.

3. The vast majority of the Keyser cystoids in the collection of the National Museum were collected from this part of the outcrop belt, particularly from the type locality at Keyser, West Virginia.

Stratigraphic interval

For the following reasons only the Upper Silurian (lower Keyser)interval was analyzed in detail:

1. It is possible to restrict stratigraphically paleoecologic study of cystoids to the lower Keyser interval because almost all Keyser cystoids occur in this interval in association with a series of transgressive pulses.

2. The lower Keyser represents a complete lateral sequence of nearshore environments within which the cystoids can be located.

3. At least three horizons are recognized in the lower Keyser which approximate time lines. These are used to produce paleogeographic reconstruction.

Analysis was confined to the first two basinwide events; a major transgressive phase terminated by a brief regressive pulse. The base of the second transgression was used as a sampling datum. The five exposures chosen for detailed sampling were those thought to represent the widest range of paleoenvironmental positions from the basin axis to both margins (fig. 4).

Sampling

Samples were systematically collected from each exposure. Approximately 150 two-inch by three-inch thin sections were prepared and a photomicrograph produced from each one (fig. 5). This material was examined petrographically for fossil content, texture, fabric, bioturbation and primary current structures. Nine lithofacies are recognized on the basis of this petrographic analysis and field relationships. The five more complex lithofacies including:

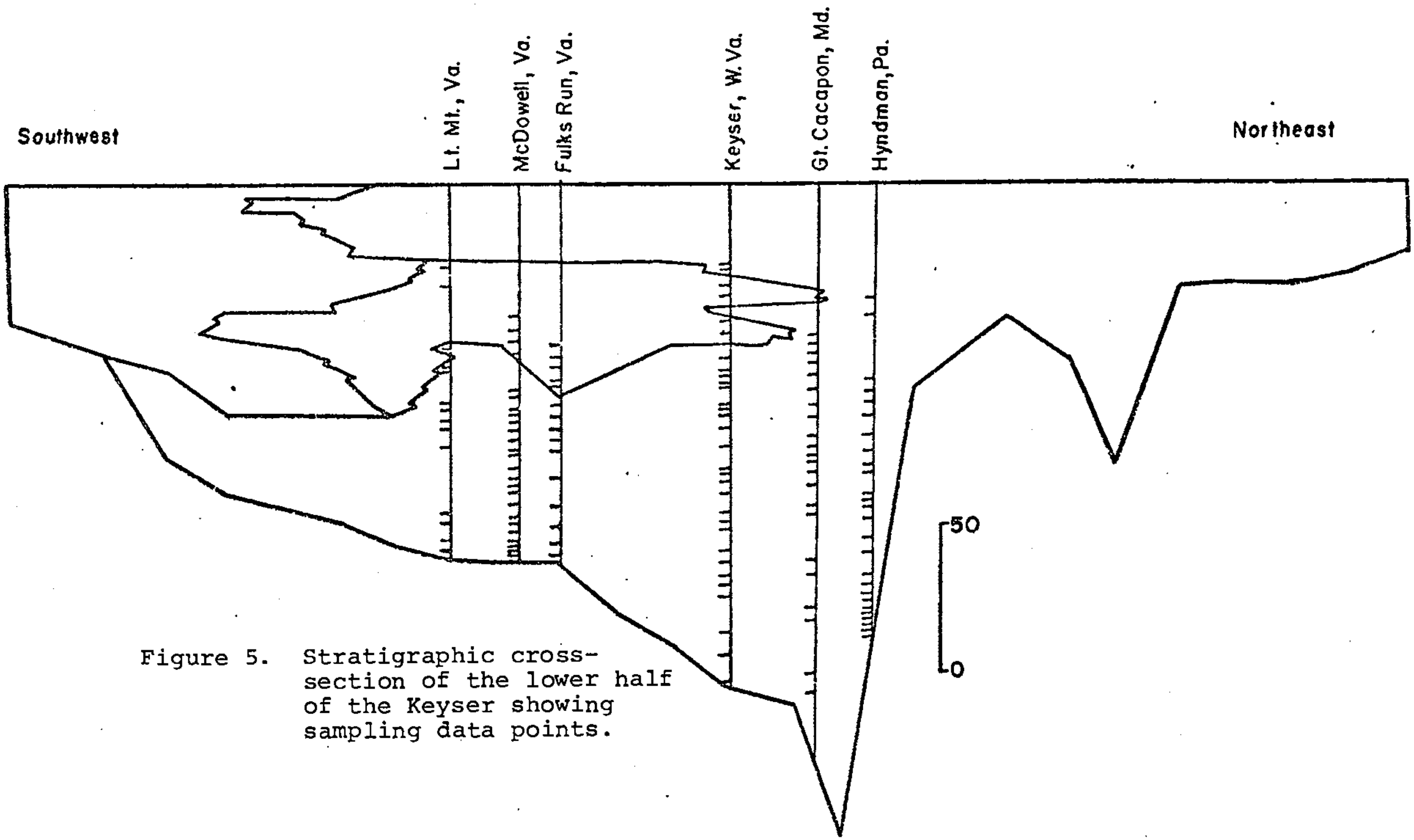


Figure 5. Stratigraphic cross-section of the lower half of the Keyser showing sampling data points.

Table 1. Point count data

	Lithofacies					
	Nodular (ost.-gas.) biomicrite)	Nodular (crin-ost. biomicrite)	Mixed Matrix biorudite	Well sorted calcarenite	Poorly sorted biosparite	Open shelf calcisiltite
Pelmatozoans	4%	24%	50%	46%	30%	24%
Bryozoans		2%	4%	12%	25%	23%
Brachiopods	4%	6%	5%	3%	8%	6%
Ostracods	10%	9%	2%	1%	2%	3%
Trilobites	2%	2%		1%	2%	4%
Gastropods	5%					
Corals			4%	1%	1%	1%
Unidentified	5%	3%		3%	6%	4%
Spar			19%	30%	20%	8%
Micrite	70%	54%	16%	2%	3%	5%
Calcisiltite					3%	22%

the nodular lithofacies (ostracod-gastropod biomicrite and crinoid-ostracod biomicrite), mixed matrix biorudite, well-sorted calcarenite, poorly sorted biosparite and open shelf calcisiltite were point counted by the standard technique to discriminate faunal differences as well as the ratio of skeletal components to matrix and/or cement. For each lithofacies three thin sections were chosen randomly and 400 point counts were taken from each section. Point count data are recorded in table 1. The other four, more simple lithofacies including: thinly laminated micrite, birdseye micrite, poorly fossiliferous calcisiltite and biomicrudite are verbally and photographically described.

B. Description and Interpretation

Thinly laminated micrite lithofacies

The laminated micrite lithofacies includes micrite grains (less than 4 microns) and silt sized pellets intercalated with thin micritic dolomite laminae (fig. 6a). Each couplet is generally less than one mm. in thickness. Common lithologic features are dessication cracks, scour surfaces, small irregularly shaped spar-filled vugs, occasional vertical burrows and micro-cross lamination. Fossil material is rare to absent. Ostracods, trilobites,gastropods and tentaculitids have all been observed but their distribution is very sporadic. Much of this material is fragmented and may well have been transported from adjacent environments.

The features outlined above are similar to those described from deposits accumulating in modern carbonate tidal flats in south Florida and Western Australia (Shinn et al, 1965; Davies, 1970). The genesis of deposits of this nature is documented by Hardie and Ginsburg (1971). They are the result of allocthonous material transported by severe onshore storms onto supratidal flats where it is trapped by filamentous blue-green algae.

All Keyser sections in which the lower contact with the underlying Tonoloway formation is exposed are characterized by an erosional contact between Tonoloway laminated micrite lithofacies and subtidal facies of the Keyser (figs. 12, 13). Within the Keyser the laminated micrite lithofacies is rare in the lower half of the formation due to the dominantly transgressive nature of the basin during this time interval. However, it marks a regressive maximum during early Keyser time along the western basin margin at Hyndman, Pennsylvania (fig. 13). It is well developed in the upper half (LaVale Member) where its presence is explained by the withdrawal of the sea during late Keyser time. Geographically, the laminated lithofacies is best developed along the western margins of the sedimentary basin (figs. 11, 13) due to the low bottom slopes. To the north, this facies is well developed due to the restricted nature of this portion of the basin.

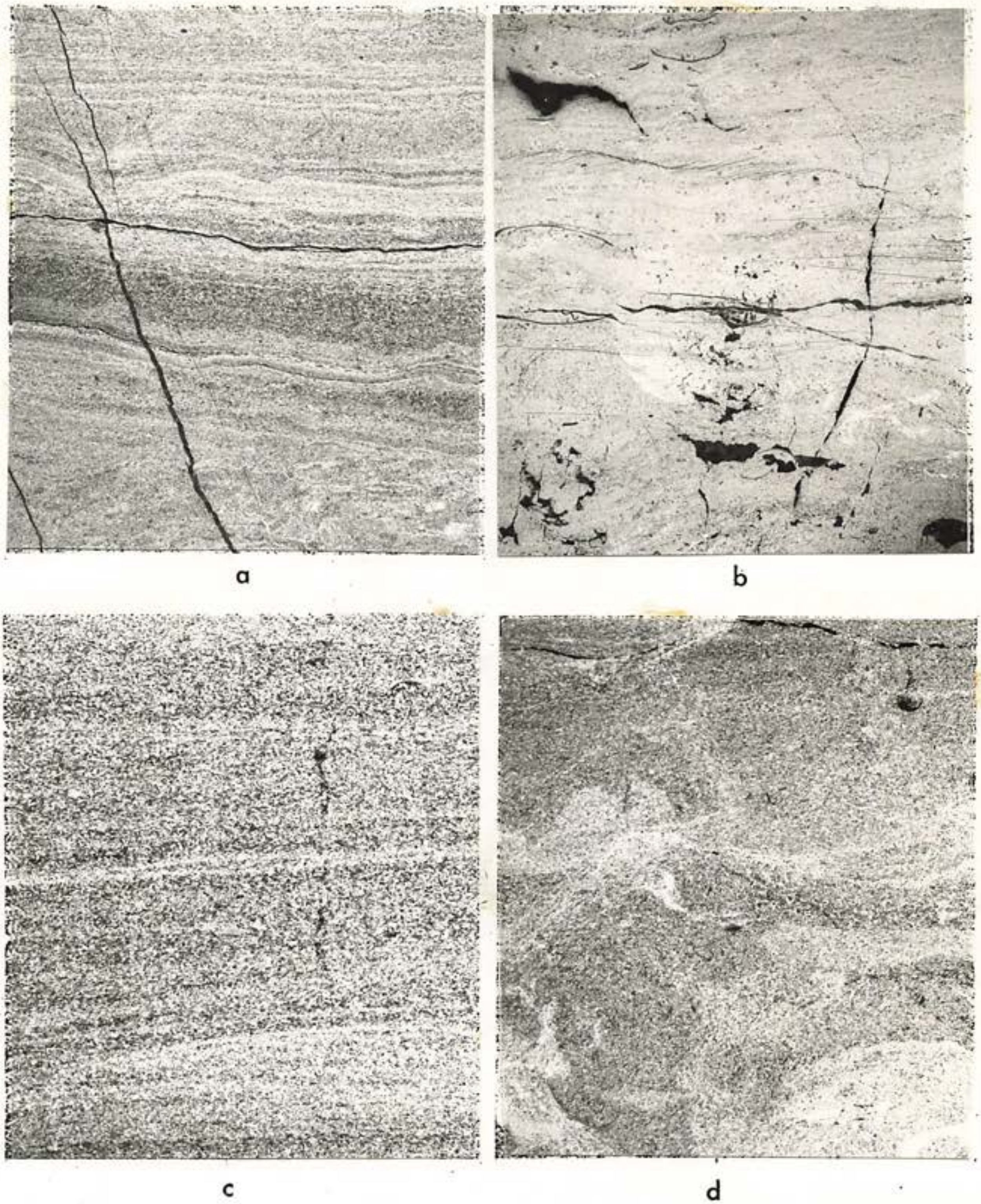


Figure 6a. Thinly laminated micrite lithofacies, Hyndman, Pennsylvania.
b. Birdseye micrite lithofacies, Hyndman, Pennsylvania.
c. Poorly fossiliferous calcisiltite lithofacies, Keyser, West Virginia.
d. Poorly fossiliferous calcisiltite lithofacies, Hyndman, Pennsylvania.

All photomicrographs X 4

Birdseye micrite lithofacies

In outcrop this lithofacies is a nearly unfossiliferous, dark, massive micrite with characteristic spar filled vugs. In thin section (fig. 6b) disarticulated ostracods are ubiquitous and in some sections thin laminations of calcisiltite are apparent. Within the Keyser, the birdseye micrite lithofacies is always closely associated with the thinly laminated micrite lithofacies (fig. 13), suggesting a tidal flat origin for these deposits. It is well developed at Hyndman, Pennsylvania, at the top of the first Keyser regressive interval. This lithofacies is deficient in many features described from present day carbonate tidal flats such as algal structures, mudcracks, scour surfaces and mud pebble conglomerate. Laboratory experiments and observations on recent core samples indicate that the vugs were initially formed by gas bubbles and shrinkage resulting from dessication of exposed mud sediments on supratidal flats (Illing, 1959; Shinn, 1968) and need not occur with other sedimentary structures to be used as supratidal indicators.

Poorly fossiliferous calcisiltite lithofacies

Constituent particle composition and sedimentary structures vary within this lithofacies. All variants have a restricted stratigraphic occurrence and are associated with facies representing restricted environments. For these reasons, all variants are grouped into a single lithofacies. Commonly, silt-sized skeletal debris are admixed with subordinate pellets in a micrite matrix. In thin section, current laminations and vertical burrows may be present although all gradations exist to a homogeneous calciltite (figs. 6c,d 7a). Usually this lithofacies is poorly fossiliferous but occasionally brachiopods, triolobites, ostracods and the coral *Favosites helderbergiae* are encountered. Locally, the brachiopods *Eccentricosta jerseynesis* and *Atrypa reticularis* are found in abundance where they constitute almost the entire fauna.

The laminations, vertical burrows, faunal composition and distribution indicate that all variants of this lithofacies were deposited under very restricted subtidal conditions. Poorly fossiliferous calcisiltite deposits are most commonly associated with regressive cycles (figs. 12, 13). This is most evident at localities on or near the basin axis. The initial transgressive pulse at these localities is punctuated by a rapid transition from extremely fossiliferous shelf sands and silts into the calcisiltite lithofacies. This transition is recognized throughout the area of study. When considering the shallow depths and low slopes proposed for the epeiric sea model, even a small relätive drop in sea level would have had a profound influence on basin geography by redistributing the environments. In this case, environments characterized by open marine shallow shelf deposition were brought into the realm of tidal flat and restricted subtidal deposition. This event appears to have been basin-wide and may be used as a time indicator.

Nodular biomicrite lithofacies

On weathered surfaces this lithofacies is easily distinguished from other Keyser lithofacies by its nodular or lumpy texture. The nodules are sub-angular, range in size from less than ½ inch to 3 inches and consist of biomicrite. The material surrounding the nodules is dominantly a highly argillaceous biomicrite but may be pelsparite and contains a more diverse and abundant fauna than the associated nodules. Both the nodules and the surrounding material (matrix) display evidence of considerable bioturbation.

The contact between the nodules and the matrix is sharp and often stylolitic. Frequently concentrations of shale, rich in organic matter, as thick as 5 mm wrap around the nodules or drape over them. Many of the nodules are cracked. Each crack is vertical with respect to bedding and may widen upward or downward. The cracks are infilled with material of the surrounding matrix.

The difference in lithology and faunal content between the nodules and matrix indicate these rocks were probably originally interbedded biomicrites and argillaceous biomicrite that were disrupted subsequent to deposition.

The sub-angular nature of the nodules, the presence, shape and infilling of the cracks and the lower relative content of insoluble residue in the nodules indicate that soft sediment boudinage may be the dominant agent. This does not preclude the possibility that syngenetic factors such as burrowing could have contributed.

Work by Daley (1970) on boudinage in limestones concludes that layers with carbonate in excess of the critical carbonate/clay ratio of 4:1 become limestones on penecontemporaneous lithification and remain relatively competent when affected by later diagenetic forces. Layers with lower carbonate content may become mobile and plastic when affected by diagenetic forces. Extensive pressure solution in the nodular lithofacies indicates that vertical pressure created by subsequent sedimentation caused the more competent beds to break up and the plastic layer to flow along planes of weakness. The sediment movement was strong enough to disrupt the competent layers and cause them to break into discrete nodules.

Although fairly homogeneous lithologically, the nodular biomicrite lithofacies is divisible into two sub-facies based on faunal content, and the ratio of matrix to constituent particles, (see table 1). The ostrocod-gastropod biomicrite sub-facies (fig. 7b) contains the more restricted

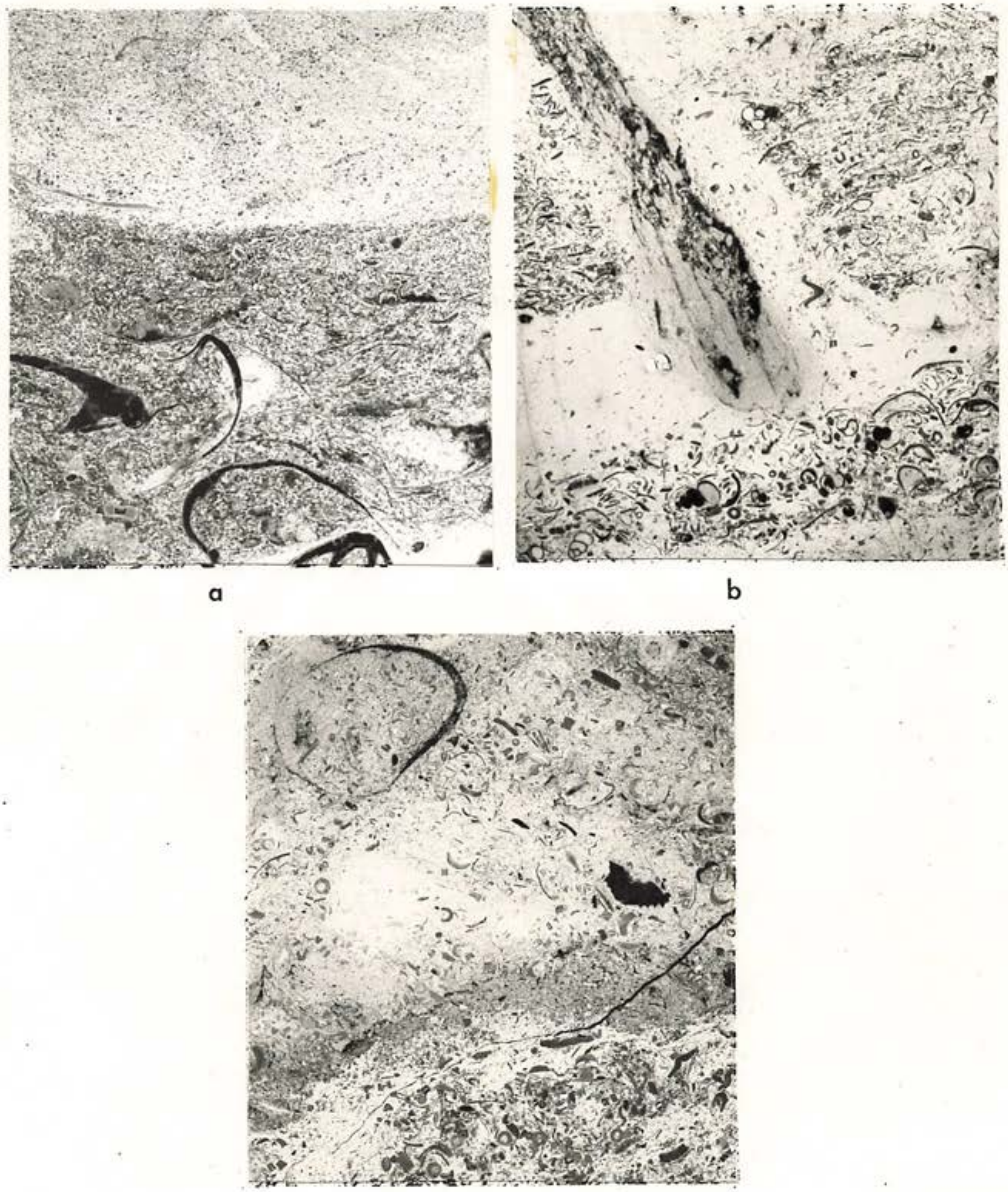


Figure 7a. Poorly fossiliferous calcisiltite lithofacies, Keyser, West Virginia
b. Nodular biomicrite lithofacies (ostracod-gastropod biomicrite, Great Cacapon, Maryland.
c. Nodular biomicrite lithofacies (crinoid-ostracod biomicrite), Hyndman, Pennsylvania.

All photomicrographs X 4

fauna of the two and occupies a lower stratigraphic position at the base of the formation in erosional contact with laminated supratidal deposits of the Tonoloway Formation (fig. 13). Based on point count analysis, this facies is dominated by micritic matrix (70%) and includes approximately 30% skeletal grains (ostracods 10%, gastropods 5%, brachiopods 4%, small echinoderm ossicles 4%, trilobites2%, unidentified 5%). The second sub-facies, the crinoid-ostracod biomicrite (fig 7c), at most exposures gradationally overlies the ostracod-gastropod biomicrites and is abruptly overlain by crinoidal biosparites (fig. 13). This facies consists of rock composed of 54% micrite matrix and 46% skeletal grains predominantly small echinoderm ossicles (echinoderms 24%, ostracods 9%, brachiopods 6%, trilobites 2%, bryozoan 2%, unidentified 3%).

The basal Keyser at most exposures is characterized by a thick interval of the nodular biomicrite lithofacies which is the first marine sequence deposited by the initial Keyser transgressive pulse. (Fig 13). In the central portion of the basin, the nodular biomicrite lithofacies is best developed at exposures near the proposed basin axis and thins to the east and west.

Faunal content, sedimentary textures, relative stratigraphic position and paleogeographic considerations testify that the environment of deposition was restricted subtidal. Thick deposits of restricted subtidal lithofacies may be explained in the context of the epeiric model of basin geometry where low slopes over broad shelves were sufficient in themselves to restrict circulation. The presence of associated barrier deposits or possible ravinements overlying this lithofacies stratigraphically, suggest that much of the nodular lithofacies was deposited behind a barrier system and thus is lagoonal in origin.

Well sorted calcarenite lithofacies

Well sorted calcarenites may be either biosparudite or biosparite. The biosparite is generally better sorted than the biosparudite and skeletal grains display a higher degree of fragmentation (figs. 8c,d). In outcrop these rocks are massive and frequently exhibit cross stratification. As shown in Table 1, skeletal grains are bound by spar cement 30% (micrite and calcisiltite 2%). Constituent particles are skeletal grains 68% (crinoids 46%, bryozoans 12%, brachiopods 3%, trilobites 1%,ostracods 1%, corals 1%, unidentified 3%). Cystoids, although encountered, are never diverse and are generally restricted to one species which is specially adapted to rough water conditions. Well sorted calcarenite beds are found in three stratigraphic positions in the lower Keyser (figs. 12, 13): 1. at the base of the formation in erosional contact with thinly laminated micrites of the Tonoloway Formation, 2. overlying and in erosional contact with the restricted subtidal biomicrites (nodular biomicrite lithofacies) and 3. interbedded with a complex of in-situ bryozoan crinoid root mounds (biomicrudite lithofacies). In the latter case, biosparudites dominate and are undoubtedly intermound channel deposits. Crinoid grains are abundant as single unbroken stem ossicles (fig. 8c). Brachiopods are also frequently preserved in an unfragmented state. In the first two cases, skeletal grains are present in approximately the same proportions as in the channel biosparudite deposits but are predominantly biosparites and are considerably more fragmented and better sorted (fig. 8a). These well sorted biosparites grade into the poorly sorted biosparite lithofacies. The sorting and general absence of lime mud in the matrix and faunal composition indicate deposition on the shallow shelf, above mean wave base. For reasons discussed in more detail later, these well sorted biosparites are interpreted to be the result of persistent reworking of nearshore environments.

Mixed-matrix biorudite lithofacies

In thin section (fig. 8b) this lithofacies is dominated by large unfragmented crinoid ossicles and articulated stem sections in a matrix composed of approximately equal amounts of micrite and sparry calcite cement. Matrix and cement constitute 35% of the rock and skeletal grains 65% (pelmatozoans, dominantly crinoids 50%, bryozoans and corals 8%,

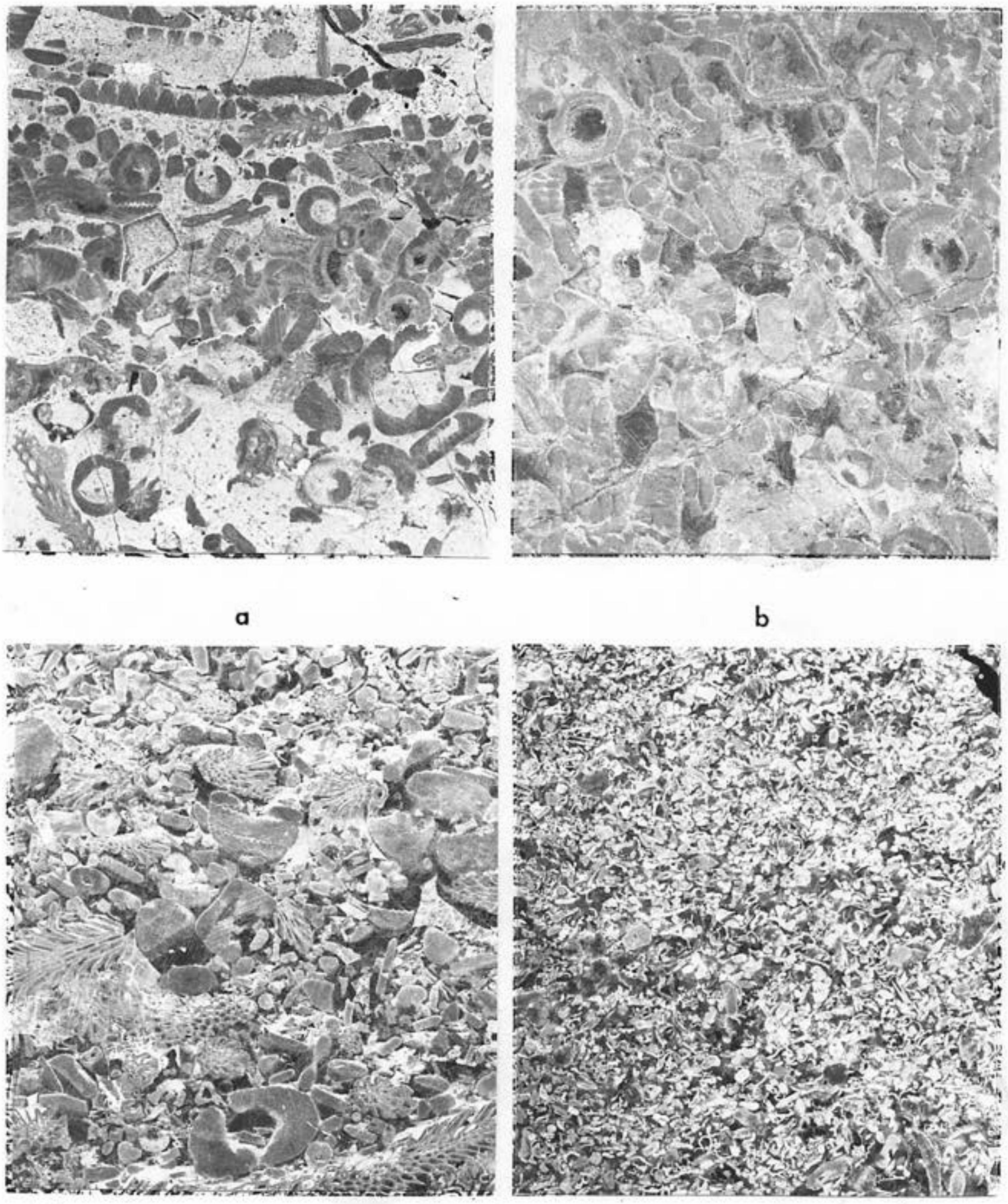


Figure 8a. Biomicrudite lithofacies, Mc Dowell, Virginia.
b. Mixed matrix biorudite, Mc Dowell, Virginia.
c. Well sorted calcarenite lithofacies (biosparudite), McDowell, Virginia.
d. Well sorted calcarenite lithofacies (biosparite), Keyser, West Virginia.

All Photomicrographs X4

brachiopods 5%, ostracods 2%). Within the lower Keyser this lithofacies is well developed at only one locality, near McDowell, Virginia, where for reasons discussed later, its association with the crinoid-bryozoan lithofacies indicates deposition on the flanks of inplace crinoid root mounds (See crinoid bryozoan biomicrudite lithofacies).

Crinoid-Bryozoan biomicrudite lithofacies

This lithofacies is characterized by an abundance of in-situ crinoid root systems and articulated stem sections, abundant ramose and fenestrate bryozoans, the branching coral *Cladopora rectilineata* as well as articulated brachiopods and ostracods in a micrite matrix (fig. 8a). These allochems make up only 40-60% of this rock. Rocks of this lithofacies form mounds with measurable positive relief of up to three feet and are associated with coral-stromatoporoid bioherms. Laterally adjacent lithofacies include mixed matrix biorudite and cross-bedded biosparudite previously described. These three lithofacies are easily differentiated by comparison of fabrics (as a product of degree of disarticulation and fragmentation of crinoid stems) and relative micrite content. From mound cores to intermound cross-bedded biosparudites, micrite content diminishes progressively while disarticulation and fragmentation of crinoid material increases substantially.

The lateral equivalence of these three lithofacies on single horizons and the frequent intercalation of cross-bedded biosparudites between biomicrudite units indicate probable above wave base deposition for all three lithofacies. The biomicrudite lithofacies is interpreted as core deposits of mounds or mud banks which originated from the baffle effect afforded by localized strands of crinoids, bryozoans and corals. Mixed matrix biorudites and cross-bedded biosparudites represent flank deposits and intermound channels respectively. Similar deposits have been described from the Lower Silurian in southwestern Ohio by Kissling (1969). Elevated mudbanks in South Florida and Western Australia are postulated by Kissling to be close modern analogs. In these situations, mud banks develop due to the modifying influence of sea grasses on the physical environment which results in the entrapment of lime mud in areas characterized by high wave and current activity (Davies, 1970).

Mound deposits of the nature described above have been observed at only one locality within the lower Keyser, near McDowell, Virginia (fig. 12). This exposure is situated on the southeast margin of the basin. Mound and associated flank and channel deposits are interbedded over a 50 foot interval at the base of the formation. Beds of the nodular lithofacies so characteristic of the lower Keyser are conspicuously absent. Anderson (1971a, 1972) has outlined two post depositional alternatives for high energy nearshore calcarenites, including beaches, barriers, submarine bars and banks, that develop during transgression over low slope carbonate shelves. In the first example, on stable shorelines where rate of deposition equals subsidence, environments do not migrate and as a result, nearshore deposits may be preserved by vertical accretion (fig. 9b). The second example is characterized by shoreward migration of nearshore environments. In this latter case, nearshore calcarenites are reworked at their seaward edge by the ravinement process and sands deposited offshore from this point overlie erosionally exposed,previously deposited lagoonal and tidal flat muds producing a disconformity in the record (fig. 9a). All nearshore coarse grained sediments are redeposited as shallow offshore shelf sands (Anderson, 1972). These are carbonate examples of the ravinement model proposed by Fisher (1961) for modern coastal erosion along the New Jersey coast and by Swift (1968) for New Jersey and the Cretaceous Coastal Plain of North Carolina.

The mound deposits at McDowell, Virginia are thought to represent part of an extensive shoal and barrier system that was preserved at this locality due to shoreline stability of the southeast margin of the basin (case 2). Elsewhere in the basin, shorelines were characterized by active shoreward migration (case 1) and as a result, shoal and barrier systems were reworked and redeposited as shallow shelf sands

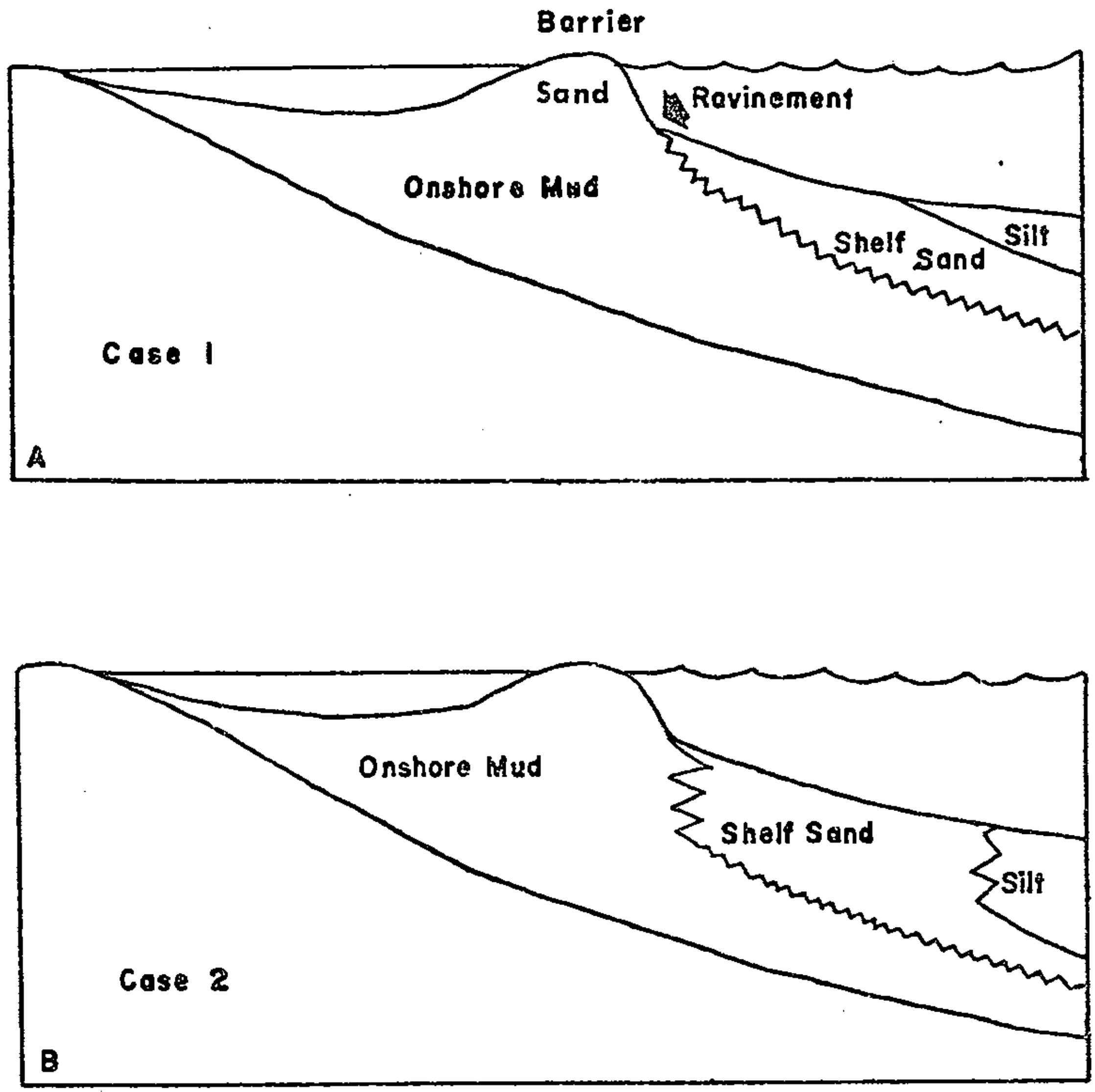


Figure 9a. Transgression with shoreward barrier migration, barrier sands are destroyed by ravinement.

b. Transgression with stable barrier position, barrier sands are preserved by vertical accretion (after Anderson, 1972).

(biosparites) with a high faunal diversity, unconformably on top of tidal flat (thinly laminated micrite lithofacies) and lagoonal biomicrite deposits with a restricted fauna (nodular biomicrite lithofacies).

Poorly sorted biosparite lithofacies

This lithofacies is a sequence of poorly sorted and diversely fossiliferous biosparites (fig. 10a) interbedded with calcareous shale. The biosparites are cemented by spar 20% (micrite and calcisiltite 6%). Skeletal grains constitute 74% of the rock (crinoids and cystoids 30%, bryozoans 25%, brachiopods 8%, trilobites 2%, ostracods 2%, corals 1%, unidentified 6%. Pelmatozoans, bryozoans and brachiopods all display a high degree of taxonomic diversity. The bryozoan fauna is dominated by encrusting and ramose colony forms. The biosparite beds are generally less than 3 inches thick and are in transitional contact with underlying well sorted calcarenites, and decrease in frequency and thickness until gradationally replaced by overlying and more diversely fossiliferous calcisiltite. These biosparites are distinguished from underlying well-sorted biosparites by their non-massive nature, relatively poorer sorting and higher taxonomic diversity. Rocks of this lithofacies are best developed at exposures on or near the basin axis and were deposited only during transgressive

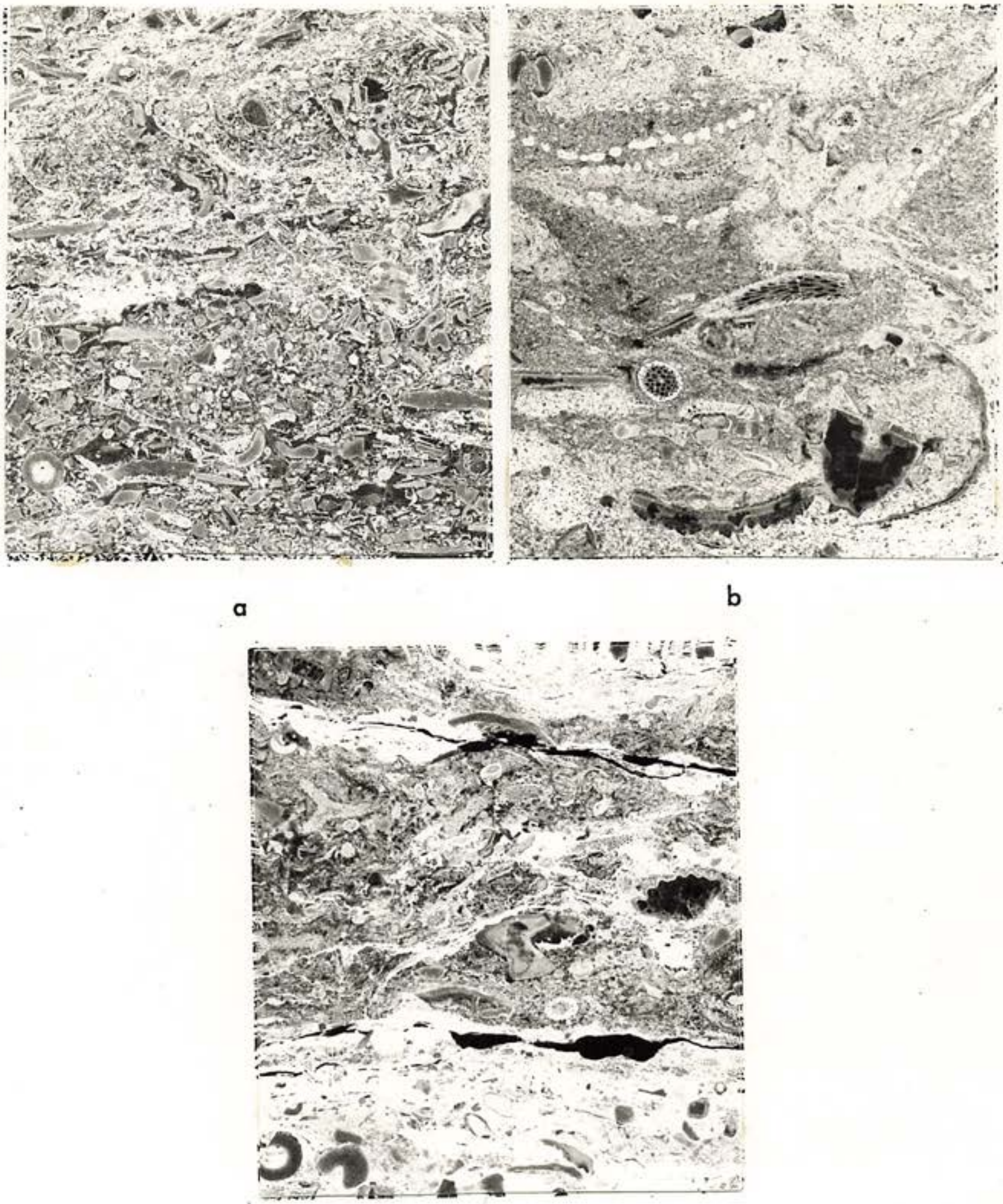


Figure 10a. Poorly sorted biosparite lithofacies, Hyndman, Pennsylvania.
b. Open shelf calcisiltite lithofacies, Hyndman, Pennsylvania.
c. Open shelf calcisiltite lithofacies, Great Cacapon, Maryland.

All photomicrographs X4

phases (figs. 12, 13). They are interpreted as open shelf sediments deposited above to near wave base, just seaward of persistently reworked skeletal sands.

Open shelf calcisiltite lithofacies

Thin beds of diversely fossiliferous calcisiltites (figs. 10b,c) are characteristically interbedded with poorly fossiliferous to unfossiliferous shale. Skeletal grains making up about 87% of the rock are bound by spar 8% and micrite 5%. Primary faunal contituents include 24% echinoderms (Cystoids, crinoids and rare edrioasteroids), 23% bryozoans (fenestrate, ramose and encrusting colony forms), 6% brachiopods, 4% trilobites, 3% ostracods, 1% corals, 28% unidentified silt grains. The taxonomic diversity of this fauna is highest of any lithofacies within the lower Keyser (Table 6). Faunally it is distinguished from the poorly sorted biosparite lithofacies by having a more diverse echinoderm fauna (mostly cystoids) and a greater diversity and abundance of bryozoans (most evident in the variety of colonial forms). Current stratification is largely disrupted by burrow mottles. This lithofacies is usually in gradational contact with underlying poorly sorted biosparite and abruptly overlain by poorly fossiliferous calcisiltite or nodular beds (figs. 12,13).

Associated fauna, texture, sorting and relative stratigraphic position all testify that the open shelf calcisiltite lithofacies was deposited just offshore from skeletal sands under near to below wave base conditions. The bottom was sufficiently undisturbed to allow silt sized skeletal material to accumulate. Circulation was however sufficient to provide well oxygenated water, continual replenishment of suspended nutrients and to support a diverse fauna of suspension and filter feeding animals on a firm skeletal silt substrate. All of the major faunal elements of this lithofacies are markedly intolerant of high turbidity or sedimentation rate in modern marine environments. The environment of deposition is envisioned as having been characterized by clear water but subject to rapid influxes of terrigenous mud which periodically exterminated most of the local fauna.

The frequency and thickness of the shale interbeds increase in the direction of the proposed source area, to the south and east. These shale beds seem to have been deposited very rapidly as evidenced by their sharp contact with the fossiliferous calcisiltite beds and the well preserved fossils underneath. The upper bedding surfaces of the calcisiltites not uncommonly reveal cystoid thecae, occasionally with the stem and delicate brachioles intact.

Within the stratigraphic interval studied, the open shelf calcisiltite lithofacies records maximum transgression at all exposures. This transgressive phase is terminated at most sections by a return to restricted subtidal conditions (figs. 12,13).

V. PALEOGEOGRAPHY AND EVOLUTION OF THE BASIN

Paleogeographic reconstruction of marine basins is concerned with a specific epoch of the past for which one can depict, on a map, the distribution of land including source areas and the disposition of major marine environments (Potter and Pettijohn, 1963). Reconstruction of the past distribution of sediments and their contained fauna can proceed only from data obtained from the present distribution of rock units. These data must include environmental interpretation of each rock unit under consideration, knowledge of their relative environmental positions, and demonstration of their time equivalency. Epeiric marine basins are particularly well suited for paleogeographic analysis for the following reasons:

1. Time lines representing synchronous horizons drawn through a stratigraphic cross-section should be nearly parallel since depositional rates are theorized to have been nearly constant throughout epeiric basins (see Rickard, 196s, for a treatment of the Helderberg Group of New York State, pp. 104-105). This is attributed to relatively little and uniform subsidence as evidenced by the low slopes, lack of major terrigenous influx and the nearly uniform production of lime sediments in the major environments.

2. Fine terrigenous clastic sediment introduced into an epeiric basin is evenly dispersed and therefore does not disrupt time lines (Shaw, 1964, pp. 38-47).

3. Due to the exceedingly low bottom slopes even slight fluctuations in relative sea level may be manifested over the entire basin. These changes if sudden and and of short duration result in a lithologic time plane approximation (Rickard, 1962; Laporte, 1967), and if long term produce recurrent cycles which also aid in correlation.

4. Carbonate rocks lend themselves to environmental interpretation due to their distinctive textures, structures, well preserved biota and by comparison to recent analogs.

The first reconstructions of Keyser basin paleogeography were by Head (1969). In this study, he presented a series of five maps which span all of Keyser time. Two of these maps fall within the time interval of this study. These two maps are of a more generalized nature than the five presented in this study for approximately the same interval and were used in this study primarily to establish basin borders. In addition to Head's work, Anderson (1971b) and Makurath (1972) recognized onshore to offshore relationships of environments and Makurath recognized similar cycles of deposition.

A. Vertical Sequence of Environments

Figures 12 and 13 are stratigraphic cross-sections constructed along the traverses plotted on the map of the study area (fig. 11). They show that vertical repetition of rock units is a characteristic feature of the lower Keyser.

Head (1969) characterized the lower Keyser as being dominantly transgressive but interrupted by cyclic regressive phases. A diagrammatic section of the lower Keyser at Hyndman, Pennsylvania identifying the two complete cycles of deposition studied is shown in figure 14. The initial transgressive pulse is evident at the base of the formation where

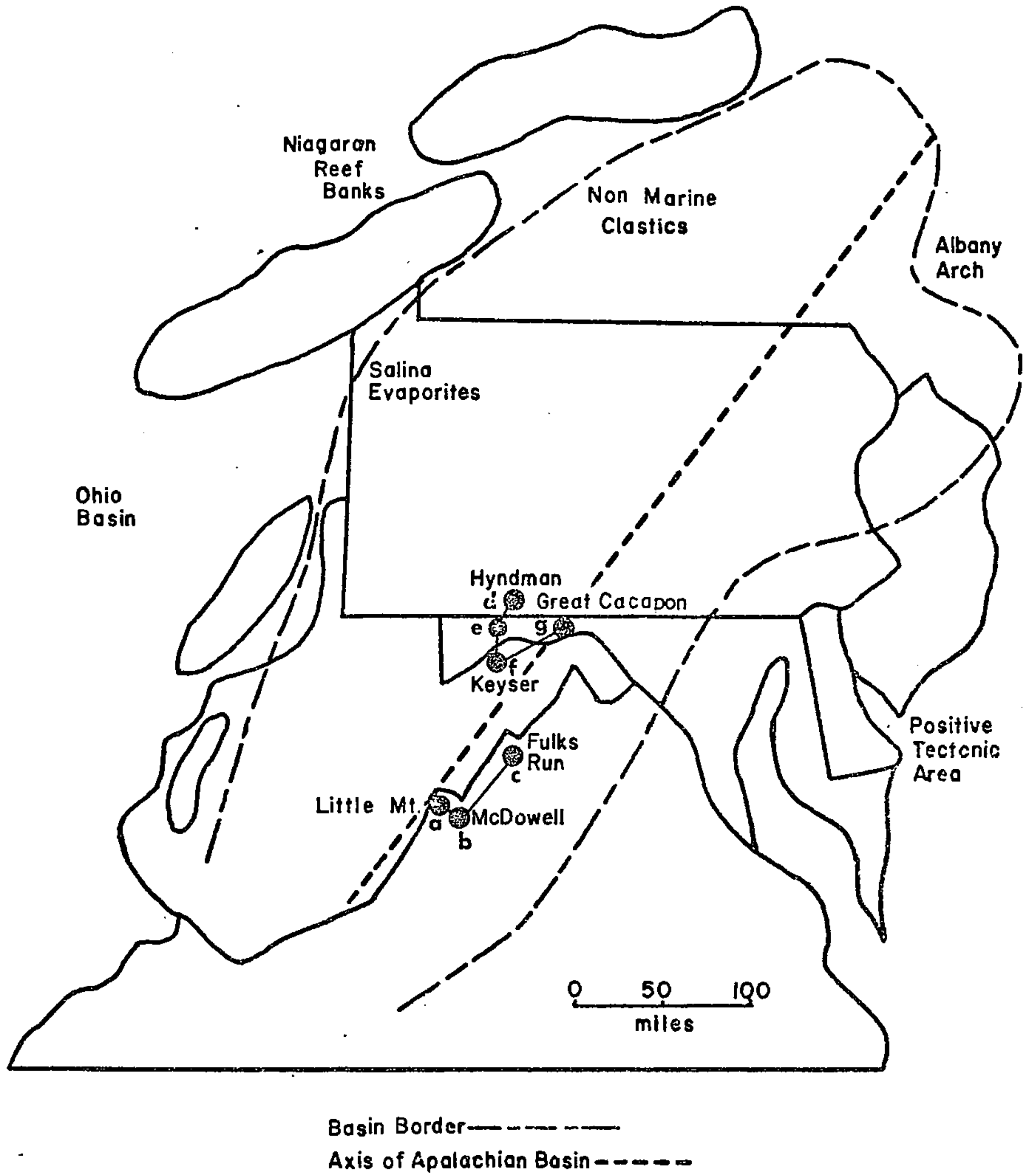


Figure 11. Configuration of Appalachian Basin showing sampling localities and traverses used in constructing cross-sections.

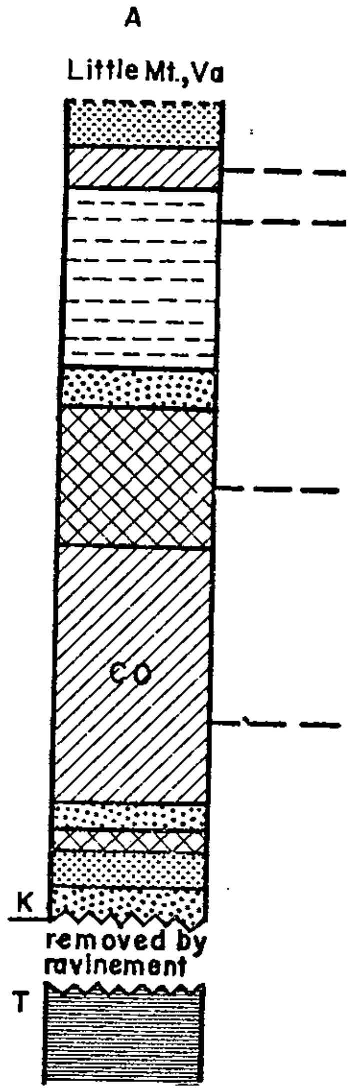


Figure 12. Stratigraphic cross-section of the lower Keyser illustrating the sequence of lithofacies and time correlation lines.

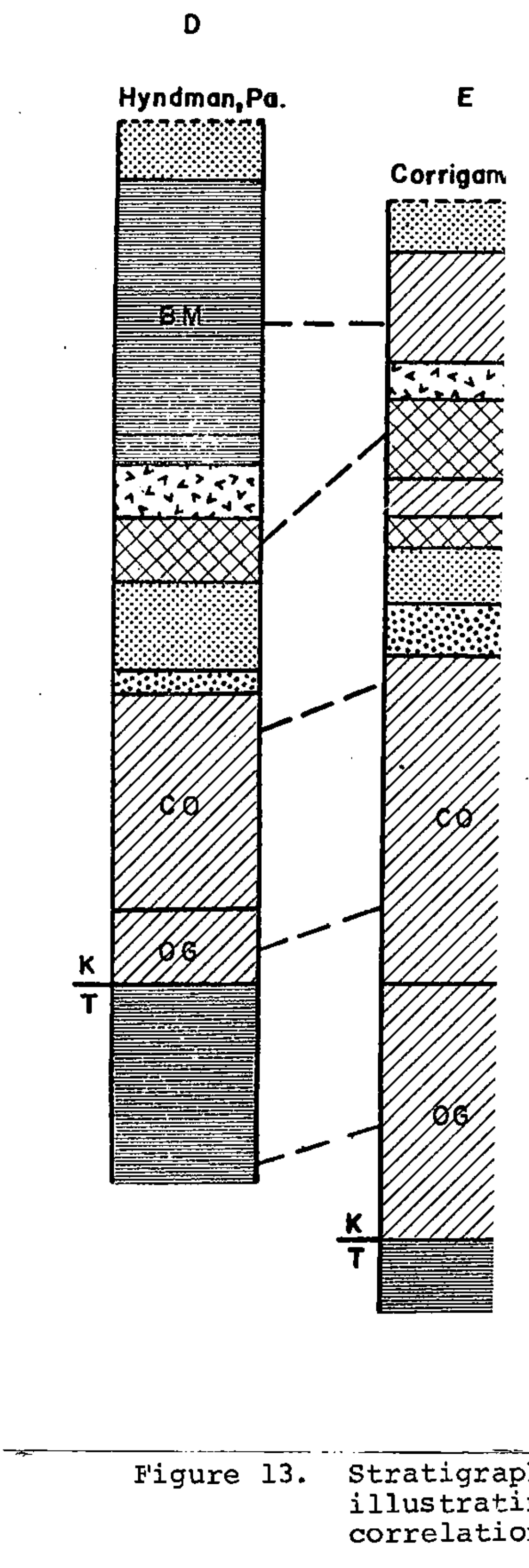


Figure 13. Stratigraphic cross section of the lower Keyser illustrating the sequence of lithofacies and time correlation lines.

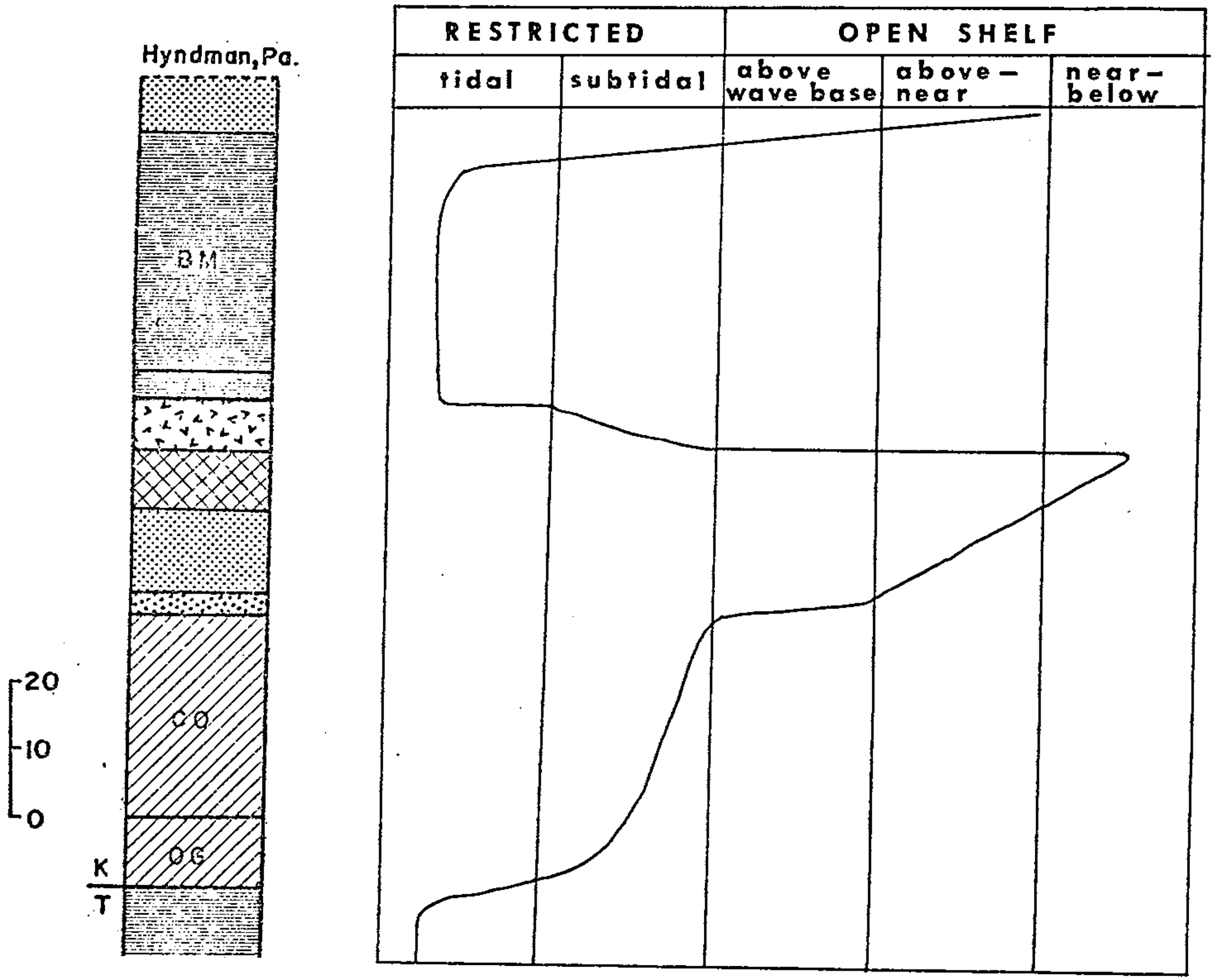


Figure 14. Diagrammatic cross-section of the Lower Keyser at Hyndman, Pennsylvania, illustrating the cycles of transgression and regression.

thinly laminated supratidal micrites of the Tonoloway Formation are abruptly overlain by faunally restricted subtidal biomicrites of the Keyser (ostracod-gastropod biomicrite). These grade into more faunally diverse muds (crinoid-ostracod biomicrite) which are erosionally overlain by a thin but massive bed of open shelf sand (well sorted biosparite). Faunal diversity continues to increase as these biosparites grade into shaley and poorly sorted biosparite and the the open shelf calcisiltite lithofacies indicating progressively more open marine conditions (see tables 4,5,6). Similar sequences are evident at Corriganville and Great Cacapon, Maryland and at Keyser, West Virginia (fig. 13). Further south, at McDowell and Fulks Run, Virginia, restricted subtidal biomicrites are missing at the base due to the ravinement process (fig. 12).

The next basinwide event, a regressive pulse, is recorded at Hyndman and other localities by a rapid transition from open shelf calcisiltite into restricted subtidal and tidal flat lithofacies which are usually poorly fossiliferous calcisiltite but may include nodular biomicrites and at Hyndman, laminated and birdseye micrites (figs. 12,13). These restricted deposits are sharply overlain by open shelf biosparite usually characterized by a profusion of the brachiopod Gypidula prognostica. The reappearance of biosparite signifies the start of the second transgressive cycle. The broken line at the top of all columnar sections marks the approximate position of Gypidula prognostica peak zone of other writers (see Bowen, 1967; Makurath, 1972; Anderson and Makurath, 1973) and the upper limit of sampling in this study.

B. Correlation and Reconstruction

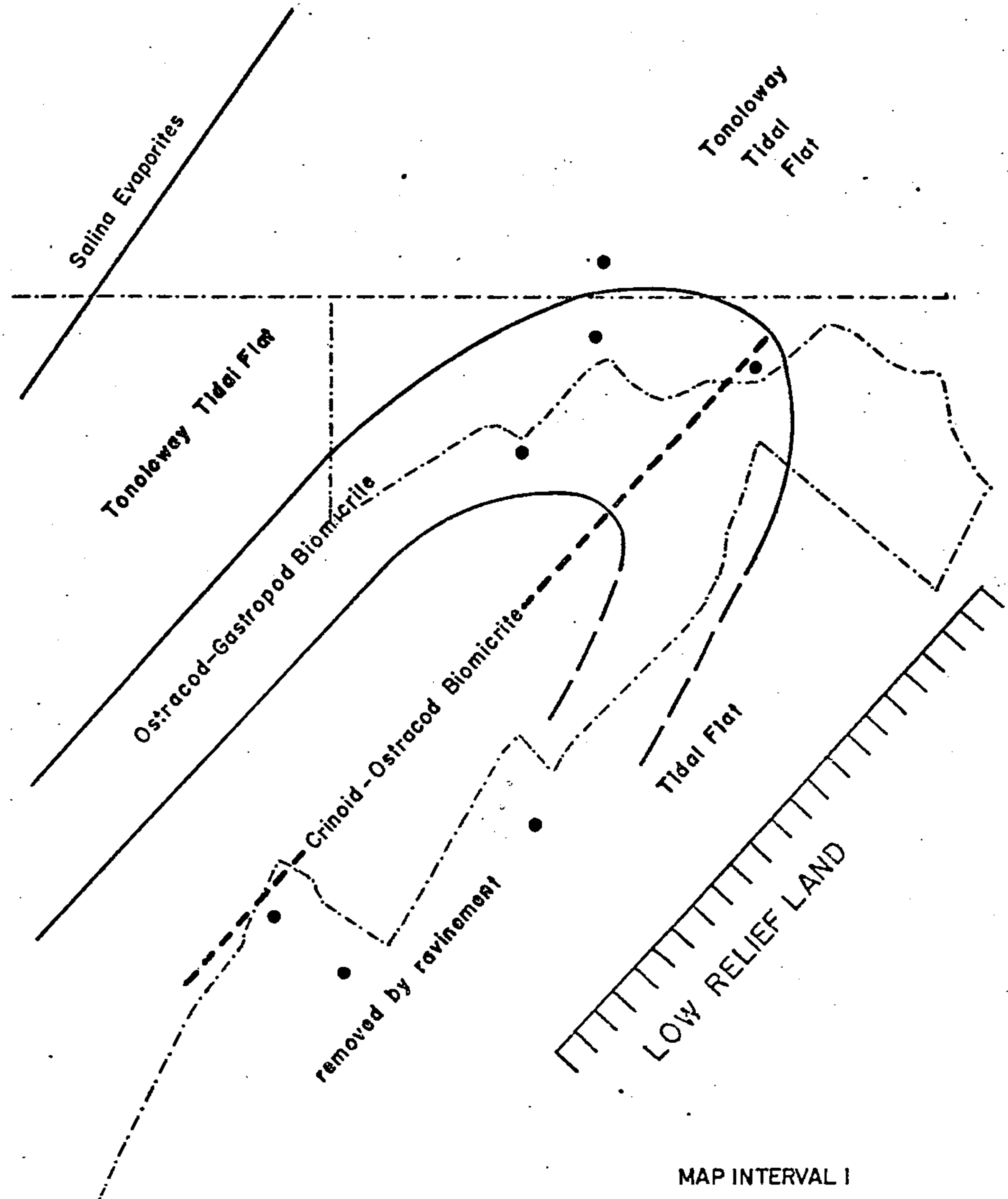
Correlation between sections by matching events provides the best approximation of synchronous time horizons. At this scale, traditional biostratigraphic techniques are of less value due to the time transgressive nature of the Keyser and the strong facies control on most faunal elements.

Time correlation line 5 (figs. 12-13) is drawn through the center of the regressive interval which separates the two major transgressive cycles. Thickness of this interval varies from 40 feet of supratidal micrites at Hyndman, Pennsylvania, located on the restricted northwest margin of the basin, to less than 10 feet of restricted subtidal biomicrites and calcisiltites at localities nearer the basin axis. This unit abruptly overlies open shelf lithofacies and may be traced over the entire basin. It records a drop in sea level or basinwide progradation.

Time line 4 connects beds that are the most open or deepest water deposits of the initial transgressive cycle (open shelf calcisiltite lithofacies). This horizon can be easily determined at each section and its stratigraphic position must be considered nearly time equivalent at each locality studied. In addition, it closely parallels time line 5 and maintains a constant position with respect to the top of the Big Mountain Shale Member.

Time correlation line 3 is mapped on the basis of the upper range limit of the brachiopod Protathyris minuta (upper boundary of Protathyris minuta Assemblage Subzone of Head, 1969). This correlation is supported by its marked parallelism with the two previous time lines. Time lines 1 and 2 are traced at 30 foot intervals beneath 3 and should approximate synchronous horizons. Rocks beneath time line 3 are largely free of terrigenous clastics. Assuming uniform production and dispersal of lime sediments, these lower three time lines should be closely parallel.

Map interval 1 (fig. 15) is constructed on the basis of time correlation 1. It depicts a time which immediately followed the deposition of tidal flat facies of the Tonoloway Formation over most of this portion of the basin. Basin borders are adapted from figure 11. During this early stage of the initial transgressive phase, low energy restricted subtidal facies extended to the southern border of Pennsylvania. Crinoid-ostracod biomicrite occupied the basin axis while more restricted ostracod-gastropod biomicrite dominated the basin margins. Further south, into southeastern West Virginia and southwestern Virginia, the basin



MAP INTERVAL I

Figure 15

Upper Silurian paleogeography showing distribution of lithofacies.

axis was characterized by more open marine facies. Subtidal facies of the Keyser gave way laterally to tidal flat facies of the Tonoloway.

Map interval 2 (fig 16) illustrates the migration of restricted subtidal biomicrites into Pennsylvania with continued transgression. Crinoid-ostracod biomicrite still dominated the basin axis. The southeast margin was characterized by an extensive calcarenite shoal. Most shoal deposits were eventually reworked by the ravinement process and redeposited offshore as shallow shelf sands. This accounts for both the strong disconformable contact between high energy open shelf biosparites of the basal Keyser and laminated supratidal micrites of the underlying Tonoloway Formation (compare figures 12 and 13) as well as the conspicuous lack of restricted biomicrites along the southeast margin, so characteristic of the basal Keyser elsewhere.

With continued transgression (fig. 17) open shelf calcisiltites were deposited near the basin axis through northeast West Virginia while restricted subtidal facies extended from these into central Pennsylvania. Barrier and shoal facies were well developed and continuously paralleled the basin margins. This barrier system deposited poorly sorted biosparites. Most of the shoreline was characterized by active landward migration. Nearshore deposits were reworked by ravinement and and redeposited unconformably on top of lagoonal biomicrites (fig. 13). However, parts

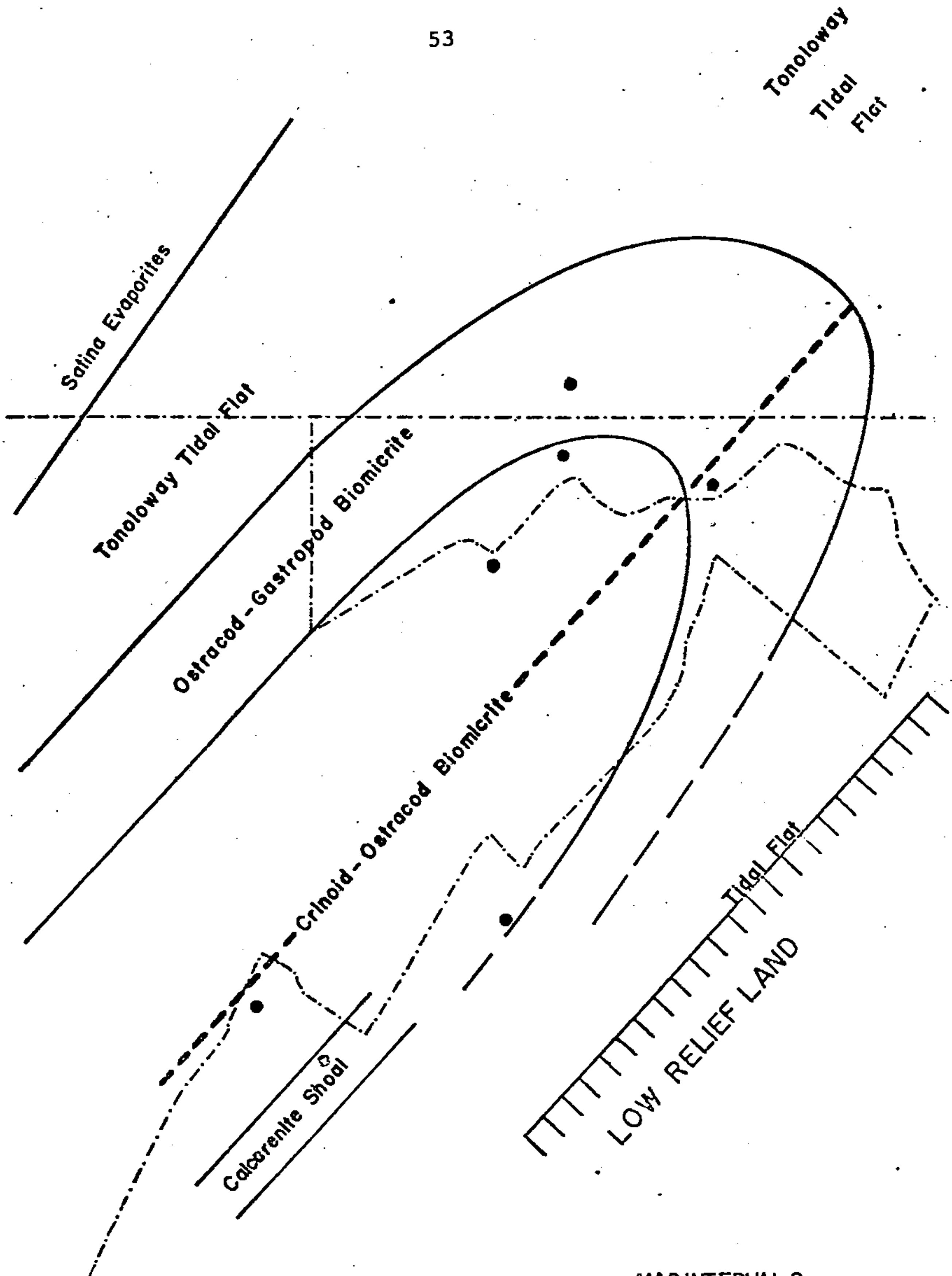
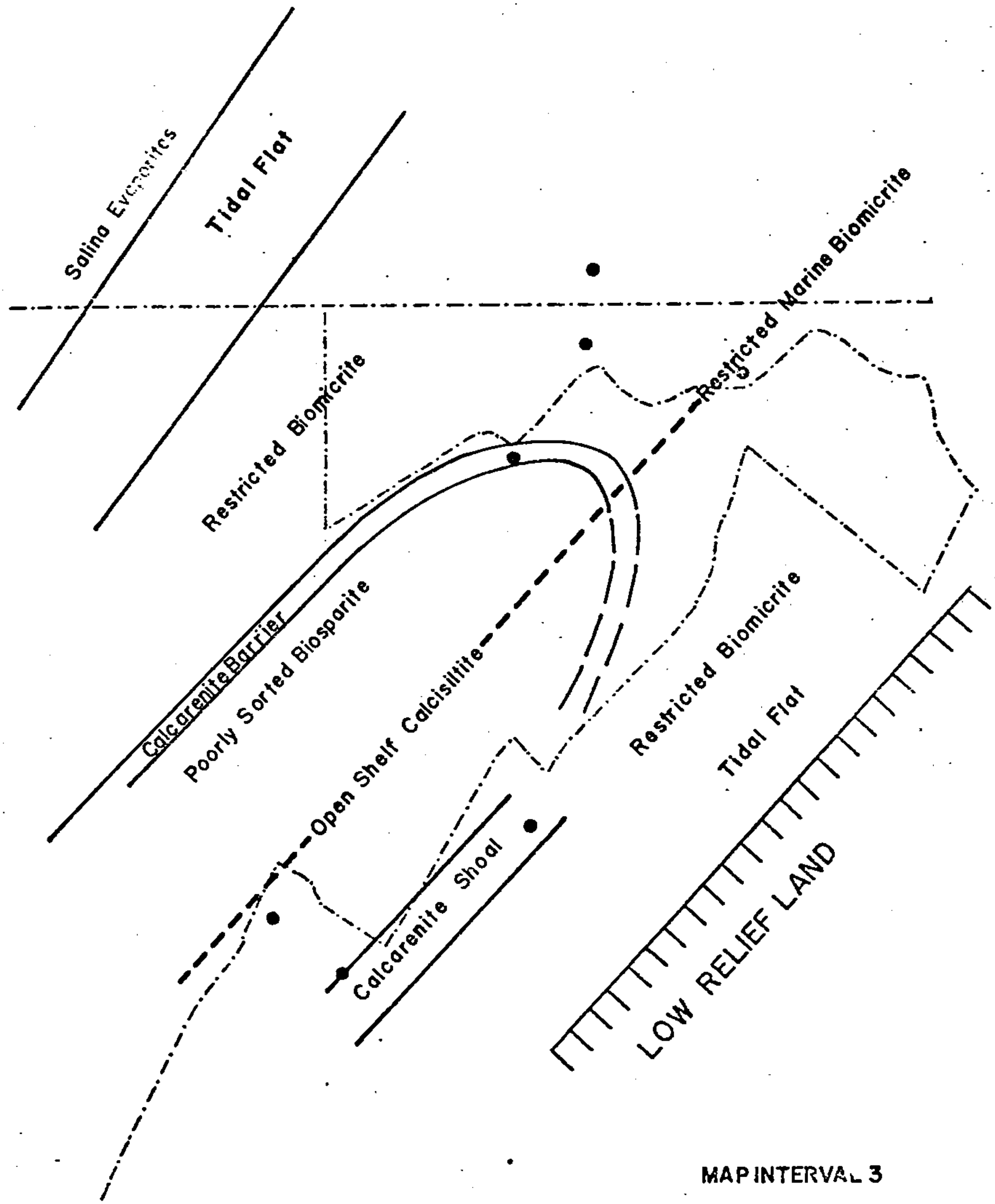


Figure 16

Upper Silurian paleogeography showing distribution of lithofacies.



MAP INTERVAL 3

Figure 17

Upper Silurian paleogeography showing distribution of lithofacies.

of the southeast margin were characterized by considerable shoreline stability. Near McDowell, Virginia,a stable shoreline position was maintained throughout a large portion of lower Keyser time. As discussed in a previous section, shoreline stability at this locality is evidenced by the preservation of a complex of crinoid root mounds (biomicrudite lithofacies) and coral stromatoporoid bioherms. This affords an insight into the probable constitution of nearshore deposits that in other parts of the basin were lost to ravinement. Periods of shoreline stability during transgression appear to have been more common in later Keyser time. Coral-stromatoporoid bioherms and crinoid root-mounds are frequently preserved in the Jersey Shore Limestone Member.

Map interval 4 (fig. 18) illustrates the maximum extent of the initial transgressive phase. Open shelf calcisiltite and poorly sorted biosparite occupied most of the central basin. Restricted subtidal facies extended into northeastern Pennsylvania. Deposition in Maryland and Pennsylvania at this time interval coincided with an influx of terrigenous clastic sediment from a proposed source area to the southeast, near Roanoke, Virginia (Dennison, 1973, written commun.). Shale was deposited near the basin axis and distributed, at this time, north into the basin as far as Pennsylvania.

Overall transgression was punctuated by a brief regressive phase as more restricted conditions returned to

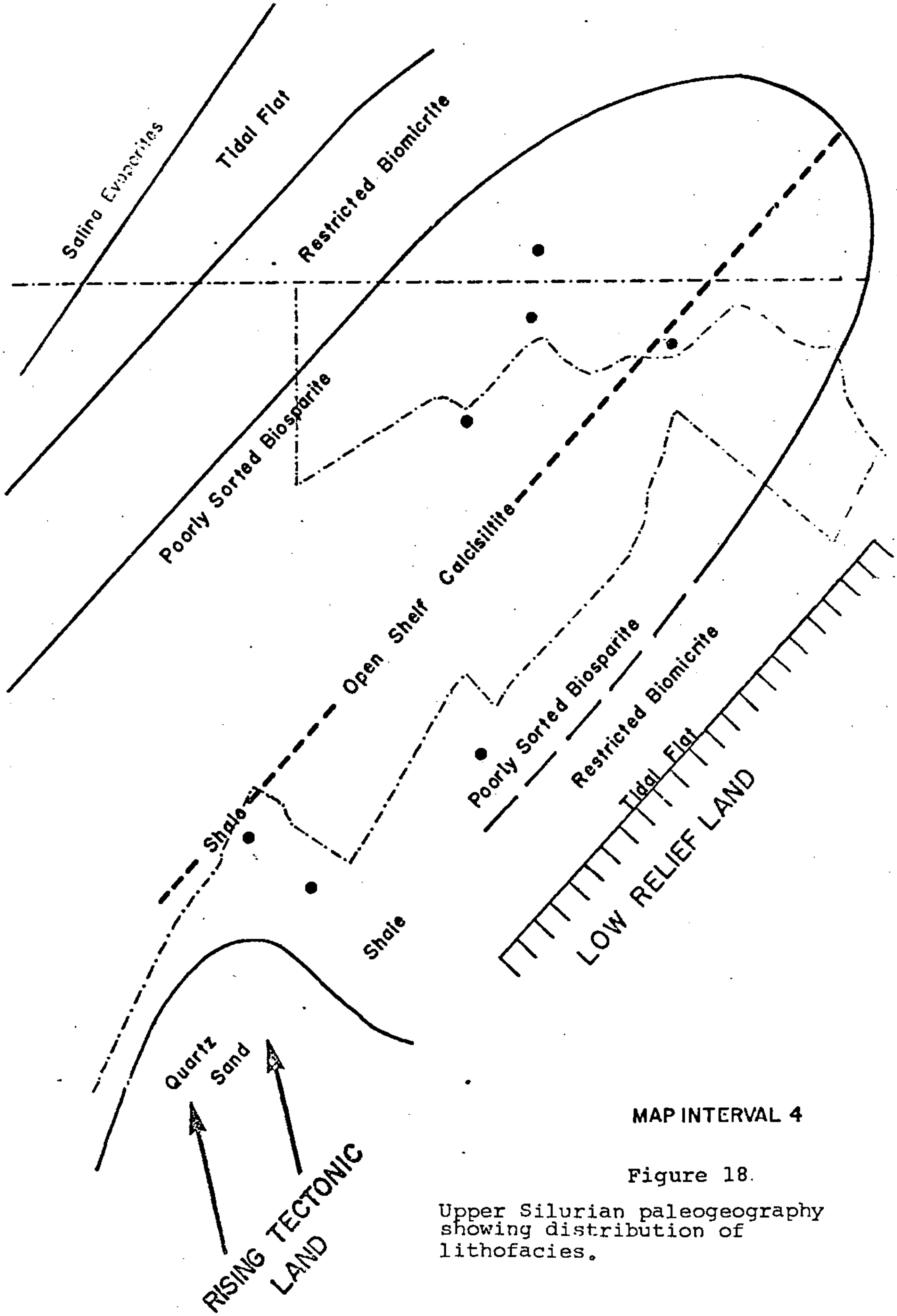


Figure 18.

Upper Silurian paleogeography showing distribution of lithofacies.

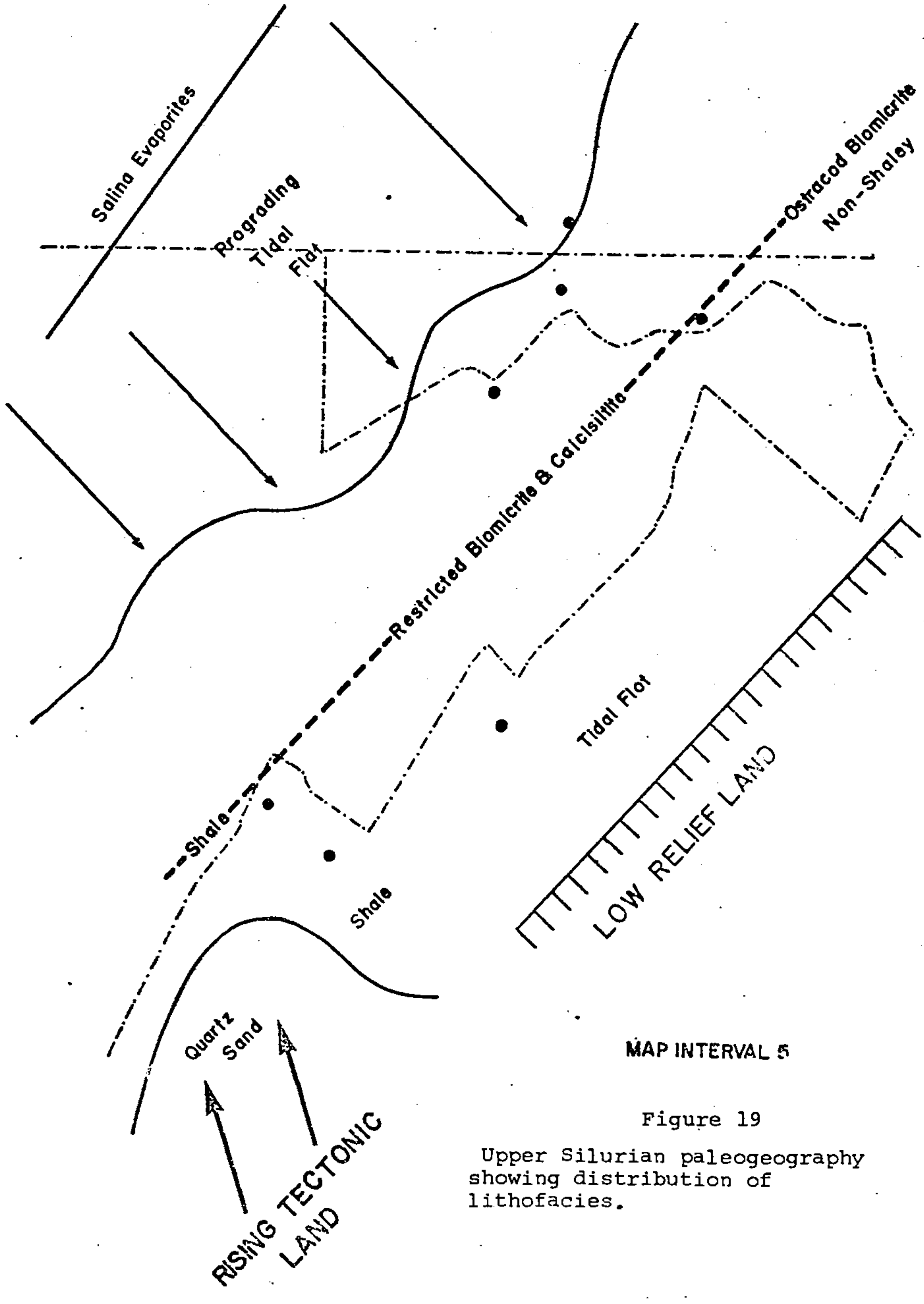


Figure 19

Upper Silurian paleogeography showing distribution of lithofacies.

the basin (fig. 19). Restricted subtidal biomicrites and poorly fossiliferous calcisiltite generally were deposited along the basin axis to the north, while tidal flat conditions were characteristic of the margins, particularly along the low slope northwest margin. Terrigenous clastics continued to be introduced into the basin from the southeast. The second cycle of transgression then began, depositing open shelf sediments over most of the central basin. This transgression is marked at the top of figures 12-13 by the reappearance of skeletal sand beds on top of restricted muds and silts deposited during the regression.

VI. THE KEYSER CYSTOID FAUNA

A. Distribution and Techniques

Near the turn of the century, the Upper Silurian beds of the Keyser Formation yielded the most diverse fauna of rhombiferan cystoids previously described from any single formation in North America. This fauna represents, to date, over one half of the total generic diversity of Upper Silurian rhombiferans described from all continents and approximately thirty percent of all Silurian rhombiferan cystoids (table 2). All forms are members of the Callocystitidae (table 3), the most diverse family within the superfamily Glyptocystitidae. The Callocystitidae originated in North America and range from Lower Ordovician to late Devonian time (Kesling, 1967). Three of the six Keyser genera are restricted to North America and three have been described from Middle Silurian and Lower Devonian strata of England.

All of the species dealt with in this study are confined to the Upper Silurian portion of the Keyser Formation. In North America only two genera have been reported outside of the Keyser. _Tetracystis_ _fenestratus_ has been described from the Middle Silurian Beech River Formation (Niagaran Group) of Tennessee where it is found in abundantly fossiliferous, thin bedded limestones intercalated with calcareous shale. This lithology is very similar to that described

	Silurian Lower	Middle	Upper
Echinoencrinidae	1	2	
Callocystitidae	1	8	5
Carocrinitidae		2	
Heterocystitidae		1	

Table 2. Number of genera belonging to families of Silurian Rhombifera by order of appearance

Class CYSTOIDEA von Buch, 1846

Order RHOMBIFERA Zittel, 1879

Superfamily GLYPTOCYSTITIDA Bather, 1899

Family CALLOCYSTITIDAE Bernard, 1895

Subfamily CALLOCYSTITINAE Bernard, 1895

Sphaerocystites multifasciatus Hall, 1859

Sphaerocystites globularis Schuchert, 1903

Subfamily APIOCYSTITINAE Jaekel, 1899

Lepocrinites manlius Schuchert, 1904

Jaekelocystis hartleyi Schuchert, 1903

Jaekelocystis papillatus Schuchert, 1904

Jaekelocystis avellana Schuchert, 1904

Subfamily STAUROCYSTINAE Jaekel, 1899

Tetracystis chrysalis Schuchert, 1904

Pseudocrinites gordoni Schuchert, 1903

Pseudocrinites claypolei Schuchert, 1904

Pseudocrinites stellatus, Schuchert, 1903

Pseudocrinites clarki, Schuchert, 1903

Pseudocrinites perdewi Schuchert, 1903

Pseudocrinites subquadratus Schuchert, 1904

Laosacystis monterey n. gen., n. sp.

Table 3. The Keyser cystoid fauna.

in this study for the later Silurian species <u>Tetracystis chrysalis</u> from the Keyser Formation. The writer has observed distal stem sections of <u>Lepocrinites gebhardii</u> in Lower Devonian strata of New York State. They are frequently abundant in coarse cross-stratified crinoidal sands in the Dayville and Ravena Members of the Coeymans Formation and in the Olney Member of the Manlius Formation. Anderson (1971a) has demonstrated that rocks of this lithology are above wave base, intershoal channel deposits (Dayville and Olney) and open shelf sands deposited near and above wave base (Ravena).

Cystoid thecae representing all five genera previously described from the Keyser and including eleven species were obtained on loan from the National Museum. These specimens, in addition to numerous thecae discovered in the course of the study,were cleaned by air abrasive technique. This material was studied morphologically, functionally and to a lesser extent statistically. Detail of exterior plate ornamentation, pore rhomb shape and structure and position of ambulacra enables all genera and many isolated plates to be assigned readily to their respective genera and species.

B. Functional Morphology

<u>Stem</u>

With one exception, all Keyser cystoids possessed a well developed stem with a terminal attachment process.

Cystoids apparently evolved an attached stem in the Uppermost Ordovician with the appearance of the Callocystitidae. All other stemmed Ordovician cystoids were unattached and free living (Paul, personnel commun.).

The structure and function of the stem is a characteristic feature of the Callocystitidae. The proximal section tapers downward and is composed of thin columnals with a wide lumen. These columnals are of two alternating sizes: large diameter and small diameter. The larger columnals have internal flanges or rims into which the smaller diameter columnals fit (fig 20a). Presumably this arrangement enabled the larger columnals to move over the outer surface of the smaller when the stem bent (Kirk, 1911; Kesling 1967). This would impart considerable flexibility to the proximal stem section.

The distal stem section is also composed of alternating large and small diameter columnals, which are the morphological homologues of the corresponding elements in the proximal section (Paul, 1967b). They differ in being taller and in having a narrower diameter, a narrower lumen, and the larger diameter columnals have a sharp medial encircling ridge. In contrast to the proximal section, the distal stem tapers only slightly.

Stem sections in which the terminal process is preserved display an irregular swelling of the distalmost columnals by which attachment was affected by cementation to hard substrates. A highly aberrant distal stem form is found in

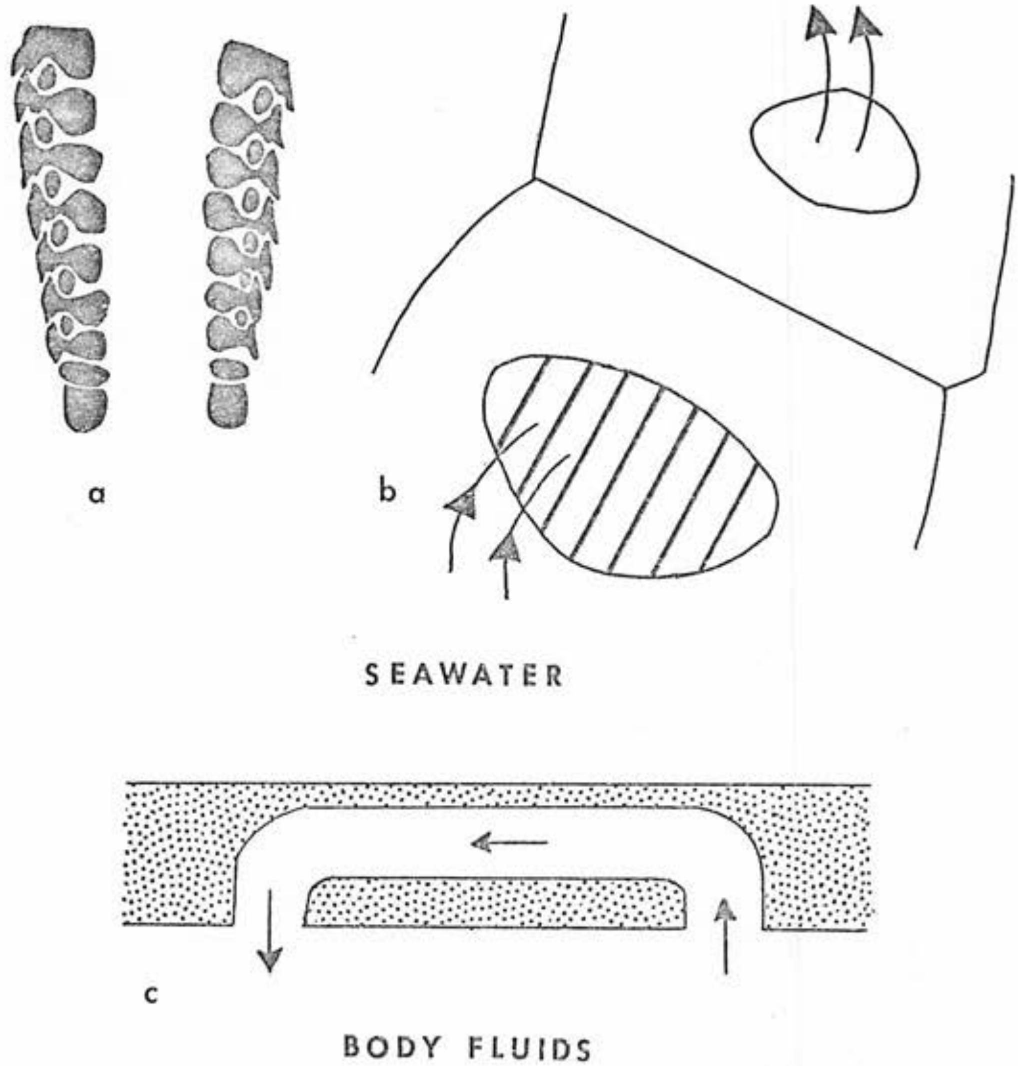


Figure 20 a. Longitudinal section through proximal stem illustrating the two alternating columnal sizes.

b. Circulation of seawater through endothecal pore rhombs of Jaekelocystis.

c. Section through plate displaying a type of exothecal circulation

Lepocrinites. The entire distal stem was modified by secondary deposition of calcite to form a long and enlarged club shaped body that tapered distally. This secondary secretion fused the distal columnals. Unbroken specimens show the terminal end to be sealed off by secondary deposition.

All described species, with the exception of Lepocrinites, probably had the typical callocystitid stem with a terminal attachment process. Permanent fixation required a firm substrate for attachment and a constant supply of food in suspension. Paul (1967b) summarized the advantages of permanent fixation by means of a flexible stem for the Glyptocystitida:

1. Allow the mouth to be directed upwards at all times.

2. Raise the theca up off the substrate providing a feeding advantage over lower level feeders and keep the rhombs and food collecting apparatus clear of the turbulent zone just above bottom, reducing the chances of fouling by mud particles.

3. Provide a leverage point that would allow the flexible stem to sweep a considerable area around the base of attachment.

4. Allow the stem flexure in currents and thus reduce the chances of the stem snapping.

Schuchert (1904), with reference to the distal stem of Lepocrinites, stated that the lower end of the fused piece seemed to have articulated directly with a basal expansion. There is no evidence to support either the existence of a basal expansion or articulation surfaces on the lower end of the stem. Lepocrinites is interpreted in this study as having led a free living life habit. The secondary deposition of calcite on the distal stem simply provided a weighting mechanism which enabled this portion of the stem to serve as a ballast. Burial attitude on bedding surfaces indicates the distal stem probably rested flat on the substrate, the flexible proximal stem section would have raised the theca off the substrate and oriented the filtration net in the most favorable feeding position. It would have been advantageous for Lepocrinites to have possessed a ballast thereby increasing variety of substrates it could have successfully inhabited relative to attached forms. For example, this form would have allowed inhabitation of rough water nearshore zones where sands were occasionally shifting and as a consequence sessile faunal elements were likely to be uprooted or buried. The general exclusion of an attached invertebrate fauna from environments of this nature is well documented in modern seas (see Yonge, 1949; Allee et al, 1950; Purdy, 1964; Graig and Jones, 1966). The adaptive advantage of weighting mechanisms to normally sessile invertebrates to achieve a free living mode of life and resultant stability on mobile sand substrates is evident in many fossil groups (see McIntosh and Schreiber, 1971, for crinoids; Anderson and Makurath, 1973, for brachiopods). In areas of gentle current or wave agitation where a firm substrate was present, Lepocrinites would not have had to compete with bottom cementing invertebrates for solid attachment sites. The environmental distribution of Lepocrinites supports this functional interpretation. Of all Keyser cystoid elements, it is the most facies tolerant and the only form found in abundance in nearshore higher energy sands.

Pore rhombs

All Keyser cystoids possess three disjunct pectinirhombs on the theca, two adoral and one aboral. These structures are composed of folds which extend as canals into the interior surface of the theca and terminate in perforations in the form of slits that open to the exterior of the theca. Each pectinirhomb lies across an interplate suture that divides the unit into half-rhombs. On the surface of the theca, the slits do not extend across the interplate suture but are separated by a flooring sheath of calcite which divides each slit into a pair of pores called dichopores (fig. 20b). Sinclair (1948) theorized that the dichopores housed ciliary cells through which seawater was pumped thus implying a respiratory function for the rhombs. One pore of each dichopore unit would function as the incurrent aperture and its counterpart across the interplate suture as the excurrent aperature. Functional analysis by Paul (1968) has substantiated this hypothesis. Paul (1972) further recognizes an additional type of canal structure which also served a respiratory function but in a radically different manner. In this type, pores are connected by canals that open to the interior of the theca (exothecal) and had coelomic fluids flowing through them in life (fig. 20c).

Existing crinoids are intolerant of persistently turbid waters. The hydropores and ambulacral system are particularly sensitive to sediment fouling (Fell, 1966). However, the food grooves within the ambulacral system of all existing crinoids may be sealed off by cover plates and therefore temporarily protected from external influences. Although hydropores in crinoids open into the coelom by ciliated funnels, water does not pass through them and their function is not respiratory but probably to aid in maintaining pressure differences within the water vascular system for locomotion and feeding (Nichols, 1972). Crinozoa in which respiration was maintained by body fluids flowing through canals which did not open to the exterior, as in crinoids and exothecal cystoids, could probably tolerate short periods of turbid waters by cessation of feeding. The respiratory canals were covered and thus protected from sediment clogging. On the other hand, Crinozoa in which respiratory exchange was maintained by seawater pumped through canals that opened to the exterior, including all cystoids with pectinirhombs, were probably intolerant of even short periods of high turbidity or sedimentation rate, as the canals would at all times be exposed to possible sediment fouling. It is postulated that this is one factor that restricted the Glyptocystitida, all of which possessed pectinirhombs, to areas characterized by clear water.

Ambulacral system

The ambulacral system includes the ambulacra and the brachioles. The ambulacra are channels or conduits on the surface of the theca. The brachioles are appendages which collect and transport food to the ambulacra. Based on the structure of the ambulacral system, Keyser cystoids may be grouped in 4 categories: genera with four long and unbranched ambulacra, those with four long branched ambulacra, those with four short unbranched ambulacra confined largely to the adoral portion of the theca and those with two long and unbranched ambulacra.

In the past, attempts have been made to correlate the number of brachioles or disposition of ambulacra with food supply or environmental position. Brachiole number per individual depends on the number and length of ambulacra as well as the spacing of brachioles. Clark (1915-50) observed that the number of feeding arms in existing crinoids seems to be correlated with temperature and water depth, increasing with higher water temperatures and shallower depths. Paul (1967b) compared the number and arrangement of brachioles on Pseudocrinites with other members of the British Silurian cystoid fauna. He concluded that

Pseudocrinites having only two ambulacra on which the brachioles were widely spaced "would seem to have been at a considerable disadvantage compared with other species". He further hypothesized that the lenticular shape of the theca in combination with the disposition of the two ambulacra would have made Pseudocrinites ideally suited for feeding in a reversing tidal current.

When the relative environmental distribution of Keyser cystoids is considered with respect to ambulacral structure or position of the ambulacra on the theca, no clear trend emerges. In addition, Pseudocrinites appears to have tolerated only shallow shelf sands and silts, suggesting that thecal shape and position of ambulacra were not adaptive for efficient feeding in tidal currents.

C. Taxonomy

Taxonomy of the Keyser cystoid fauna originally published by Charles Schuchert (1903, 1904) has undergone little revision to date. The generic status of the Keyser cystoids and their assignment to the Callocystitidae is well established. However, in some cases the assignment of specific genera to the various subfamilies within the Callocystitidae is an area of active revision. Paul 1967b) transferred the genus Tetracystis from the subfamily Apiocystitinae to the Staurocystinae. This transference is accepted and further substantiated by the discovery of a new genus in the course of this study. Paul (1967c) further suggested that Sphaerocystites, in having four ambulacra, probably does not belong in the Callocystitinae, all of which have five ambulacra. In addition, some species within the genus Pseudocrinites are not clarly separated. Kesling (1961) considered Schucherts' P. abnormalis and Trimerocystis pecularis to be abnormal individuals of P. gordoni. Schuchert (1904) erected a new species, P. elongatus, on a single incomplete specimen. He noted a close similarity to P. subquadratus and separated the two solely on size and slight shape differences. In this study, P. elongatus is considered a large individual of P. subquadratus representing normal variation within a species population. Similar reasoning raises questions on the validity of Schuchert's separation of P. subquadratus and P. claypolei from P. clark and P. gordoni, respectively, although a comprehensive examination is beyond the scope of this study.

It is not the intent of this study to include complete systematic descriptions of the Keyser cystoid fauna as this information may be readily obtained from other sources (see Schuchert, 1903, 1904; Kesling, 1961, 1967; Paul, 1967b). General descriptive information is provided to the extent that individual species within the fauna may be differentiated on the basis of fairly complete thecae. However, variation in plate ornamentation and pore rhomb shape and structure is discussed since this enables all genera and many species to be distinguished from one another by identification of single plates.

Superfamily GLYPTOCYSTITIDA Bather

Family CALLOCYSTITIDAE Bernard

A diverse family of the Glyptocystitida characterized by 26 basic thecal plates arranged in 5 concentric rings or circlets around the theca in the following fashion: 4 BB (basals), 5 ILL (infralaterals), 5 LL (laterals), 5RR (radials), and 7 OO (orals). Plate arrangement sometimes modified by intercalation with adjacent circlet. The theca may have two to five endothecal pore rhombs. Slits of adjacent half-rhombs do not extend across plate suture (disjunct pectinirhombs). Ambulacra typically recumbent and long, branched or unbranched ambulacral grooves number two, four or five and usually extend down over the theca.

Subfamily CALLOCYSTITINAE Bernard

A subfamily of exclusively North American cystoids. Thecal shape may be ovate, ellipsoidal or spherical. Basic plate arrangement outlined for the Callocystitidae is modified by intercalation of ILL or LL circlets. Four or five ambulacra are long and branched. Three pectinirhombs always present. Brachioles small and widely spaced.

Genus SPHAEROCYSTITES Hall

Theca spherical to subspherical. The four ambulacra are long, extend almost to the base and contain numerous bifurcations which increase in number with specimen size. Pectinirhombs are three in number, two upper and one lower. Pore rhombs long and slender, extending across the entire suture and contain numerous slits. One half-rhomb of each pectinirhomb unit enclosed by narrow elevated rim. Adjacent half rhomb has similar rim only along edge opposite suture. The L1 and L3 plates are deeply intercalated into the IL circlet. The bifurcation of ambulacra in *Sphaerocystites* allows many isolated plates of this genus to be distinguished easily from other Keyser genera, all of which have unbranched ambulacra.

Sphaerocystites multifasciatus Hall

Theca is generally subspherical. The ratio of width to height increases with increasing size of specimen, smaller specimens being almost spherical. Base of theca depressed. Plate ornamentation near oral region comprised of discrete and confluent shallow pits or dents. Lower half of theca also has numerous pits but in addition, short and narrow ridges, many of which approximately parallel the ambulacra.

Figure 21

Sphaerocystites multifasciatus Hall

a. Adoral view showing detail of ambulacrum, L1/R5 pore rhomb, periproct and plate ornamentation. Note branching of ambulacra. USNM No. 35052, Keyser, West Virginia. X 2.5

b. View of L4/R3 pore rhomb of same specimen. X 5.5

c. Lateral view of slightly smaller specimen showing L4/R3 pore rhomb. Open shelf calcisiltite lithofacies, Keyser, West Virginia. X 3

d. Lateral view of same specimen including large portion of proximal stem. X 3

e. Detail of L1/R5 pore rhomb of smaller specimen showing hydropore. Same occurrence as 21c. X7.5

Sphaerocystites globularis Schuchert

f. Lateral view.USNM No. 35053, Keyser, West Virginia. X 4.


a


b


c


d


e


f

Sphaerocystites globularis Schuchert

Theca is generally spherical regardless of size. Base of the theca is not depressed as in multifasciatus and bifurcations of ambulacra are less numerous causing a smoother surface. In other features, such as plate arrangement and pore rhomb structure it is very similar to S. multifasciatus.

Subfamily APIOCYSTITINAE Jaekel

A subfamily of Callocystitidae with ovate or elipsoidal theca. The ambulacra are four or five in number, are simple, unbranched, not strongly protuberant and contained in shallow grooves in thecal plates. Brachioles are widely shaped.

Genus JAEKELOCYSTIS Schuchert

Theca ovate to subspherical and small, maximum height about 15 mm. Ambulacra four in number, narrow, deeply embedded into but slightly elevated above the theca plates and extend to base of theca except in immature specimens. Relative positions of ambulacra are variable. Brachiole facets small and numerous. Anal pyramid small and composed of a small circlet of six plates. The ILL plate circlet is complete. IL4 and IL5 are conspicuously large, RR circlet interrupted by large L5 plate. Pore rhombs three in number, each half-rhomb discrete, set far back from the suture. Half-rhombs are semicircular to oval and surrounded by an elevated rim. Dichopore slits are few, usually about 8, although as many as 15 are known to occur. Plate ornamentation is variable.

Jaekelocystis hartleyi Schuchert

A common member of the Keyser fauna. Ambulacra prominent and extend to base, except in immature specimens. Half-rhombs of each pore rhomb pair asymmetric and of different sizes, usually containing about eight slits. Plate ornamentation well developed as numerous and discrete pits. Plate edges outlined by deep furrows. These features allow isolated plates of this species to be easily identified.

Jaekelocystis papillatus Schuchert

A rare species of Jaekelocystis having many features in common with J. hartleyi but differing in having a more spherical theca, absence of furrows along the plate edges. In addition, adjacent half-rhombs of each pore rhomb pair are approximately symmetrical with respect to size and shape and contain more dichopore slits than J. hartleyi. Plate ornament not comprised of discrete pits but of numerous fine nipples projecting from the thecal surface. Only two specimens known.

Figure 22

Jaekelocystis hartleyi Schuchert

a. Lateral view showing detail of B2/IL2 pore rhomb, ambulacra and plate ornament. Note furrows along plate sutures. Open shelf calcisiltite lithofacies, Fulks Run, Virginia. X 5.4

b. Lateral view of same specimen showing periproct region. X 5.4

c. Isolated thecal plate. Poorly sorted biosparite lithofacies, Hyndman, Pennsylvania. X 13

d. Detail of L4/R3 plates showing distinctive structure of pore rhomb. X 8

e. Isolated plate of Jaekelocystis, species uncertain. Open shelf calcisiltite lithofacies, Little Mountain, Virginia. X 8

Jaekelocystis avellana Schuchert

f. Anterior lateral view showing ambulacra detail and faint evidence of papillose plate ornamentation. USNM NO. 35056-A, Keyser, West Virginia. X 6.

a

b

c

d

c

f

Figure 23

Jaekelocystis avellana

a. Right lateral view of L4/R3 pore rhomb. USNM No. 35056-A, Keyser, West Virginia. X6.

b. Lateral view of same specimen. X6

Lepocrinites manlius Schuchert

c. Rare specimen with nearly complete stem including most of modified distal portion. Only known example of this species with attached stem. Poorly sorted biosparite lithofacies, Hyndman, Pennsylvania. X 2.3

d. Isolated IL5 plate. Poorly sorted biosparite lithofacies, Hyndman, Pennsylvania. X 5

e. Isolated R5 plate. X4


a


b


c


d


e

Jaekelocystis avellana Schuchert

Another rare form of Jaekelocystis originally described as having a thecal shape resembling a hazel nut. Thecal plates are nearly smooth and dichopore slits slightly more numerous than in J. hartleyi, but otherwise quite similar to J. hartleyi. Plate ornamentation as in J. papillatus. Only four specimens known in addition to two poorly preserved examples discovered during this study.

Leopocrinites manlius Schuchert

Theca pyriform, sides somewhat compressed. The four ambulacra are unbranched and extend down the theca to a level slightly below mid-height. Each ambulacrum bears about 24 brachiole facets. Anal pyramid comprised of 6 triangular plates surrounded by a circlet of 18 smaller plates. The BB, ILL, and LL circlets are complete but L5 is intercalated between R4 and R5. Three large pectinirhombs containing numerous dichopore slits extend across the entire suture. One half-rhomb of each unit is surrounded by a narrow elevated rim as in Sphaerocystites and Pseudocrinites. Structure of the proximal portion of the column similar to other Glyptocystitida. Entire distal stem, including terminal end, modified by secondary deposition of calcite to form an ankylosed club shaped process which tapers distally. Discovery during the course of this study of a *L. manlius* theca complete with attached stem enables, for the first time, members of this species to be identified solely on the basis of the modified distal stem (fig. 23c).

Subfamily STAUROCYSTINAE Jaekel

Theca ovate to subquadrate or biconvex. Two to four undivided and strongly protuberant ambulacra developed on smooth bands not in shallow grooves. Brachioles numerous and closely spaced. Shape of theca modifies plate arrangement and shape.

Tetracystis chrysalis Schuchert

Theca elongate and subquadrate with four narrow and strongly protuberant ambulacra which extend to the base of the theca. Brachioles relatively few and widely spaced. Periproct elevated and composed of an anal pyramid of 7 plates surrounded by an outer circle of 17 plates. The 3 pectinirhombs are long, containing numerous dichopore slits. Shape and structure of pore rhombs resembles that described for *Sphaerocystites* and *Pseudocrinites* although dichopore slits are not as numerous for a given pore rhomb length and ratio of width to length is greater. Ornamentation weakly developed and appears nearly smooth without aid of magnification. Close inspection reveals many small

Figure 24

Tetracystis chrysalis Schuchert

a. Left lateral view L1/R5 pore rhomb and faint evidence of papillose plate ornamentation. Open shelf calcisiltite lithofacies, Fulks Run, Virginia. X 3.8

b. Right lateral view of same specimen. X3.8

c. Anterior lateral view of same specimen. X 4.4

Pseudocrinites stellatus Schuchert

d. Gonal face showing prominently sculptured plate ornamentation. USNM No. 35069, Keyser, West Virginia. X 3.5

E. Periproctal face of same specimen. X 3.5

f. Detail of L1/R5 pore rhomb of same specimen. X 6.5

a

b

c

d

e

f

bumps rather evenly spaced over each thecal plate. Some are confluent and arranged to form a weakly stellate pattern.

Genus PSEUDOCRINITES Pearce

A genus of Staurocystinae with circular to ovate bi-convex theca, the sides being strongly compressed. The two ambulacra are protuberant by thick flooring plates which raise the ambulacral groove above the level of the thecal plates. Ambulacra extend to base of theca in most species. Pectinirhombs large and structured as in Sphaerocystites with many dichopore slits. Four different points on the theca serve as the juncture for four thecal plates decreasing the number of sutures for the same number of plates relative to other members of the Callocystitidae. Thecal plates usually highly ornamented by ridges radiating from the center of each plate and on this basis readily distinguished from other Keyser genera.

Pseudocrinites gordoni Schuchert

Thecal outline circular with two convex faces. Ambulacra extend to column. Anal pyramid depressed and consisting of seven plates surrounded by a circlet of eight larger plates (auxiliary plates). Plate ornamentation is very distinctive over most of the theca. Narrow and sharply defined ridges radiate from the center to the corners of thecal plates, and between these are a series of parallel ridges approximately normal to the plate edges. Plate

Figure 25

Pseudocrinites gordoni Schuchert

a. Gonal face showing pore rhombs L1/R5, B2/IL2 and plate ornamentation. Open shelf calcisiltite lithofacies, Keyser, West Virginia. X3

b. Lateral periproctal face of larger specimen showing L4/R3 pore rhomb and detail of periproct. USNM No. 35071 X 2.5

c. Detail of L1/R5 pore rhomb and plate ornamentation of same specimen. X6

d. Isolated thecal plate of *P. gordoni*. Poorly sorted biosparite lithofacies, Hyndman, Pennsylvania. X 5.5

e. Lateral periproctal view of well preserved example of *P. gordoni* including most of stem and some brachioles. Open shelf calcisiltite lithofacies, Hyndman, Pennsylvania. X 2.5

a

b

c

d

e

Figure 26

a. Isolated L4 plate of *Pseudocrinites*, probably *P. stellatus*. X4

Pseudocrinites perdewi Schuchert

b. Lateral view of weathered periproctal face. Note that the ambulacra extend less than half of the length to the base. USNM No. 35072, Keyser, West Virginia. X 2.5

Pseudocrinites clarki Schuchert

c. Lateral view of gonal face showing detail of plate ornamentation. USNM No. 35070, Keyser, West Virginia. X 3.5

d. Periproctal face of same specimen. X 3.5

e. View of L1/R5 pore rhomb of same specimen. X 7

f. Isolated R5 plate of *Pseudocrinites*, species indeterminable. Poorly sorted biosparite lithofacies, Hyndman, Pennsylvania. X6

a

b

c

d

e

f

ridges near the top of the theca have a more irregular veriform pattern.

Pseudocrinites claypolei Schuchert

Similar to P. gordoni in most respects and obviously closely related. Plates characterized by veriform ornamentation over the entire theca.

Pseudocrinites stellatus Schuchert

Closely related to P. gordoni but readily distinguished by subspherical theca, large gonopore, fewer brachiole facets, and by having considerably more prominent radiating ridges on the thecal plates. For plates of similar size P. stellatus has fewer parallel ridges between those that radiate to plate corners than either P. gordoni or P. clarki.

Pseudocrinites clarki Schuchert

Theca ovate with ambulacra extending to base, and having narrow groves. Circlet of plates surrounding anal pyramid is incomplete. Thecal plate ornamentation similar to P. Gordoni.

Pseudocrinites subquadratus Schuchert

Differentiated from P. clarki by veriform plate ornamentation.

Pseudocrinites perdewi Schuchert

Theca pyriform and ambulacra extend less than two-thirds of way down the theca,tapering rapidly. Ambulacra broad and strongly protuberant as in other Pseudocrinites, but have very narrow grooves. Anal pyramid small and depressed, surrounded by a complete circlet of auxiliary plates as in P. gordoni.

Laosacystis monterey (n. gen. n. sp.)

Diagnosis: A genus of Staurocystinae with four short unbranched and protuberant ambulacra.

Material: One partially complete theca.

Horizon and locality: Keyser Limestone Formation (Byers Island Member) Upper Silurian, eight feet above basal contact with Tonoloway Formation, in open shelf calcisiltite lithofacies of this paper. From a roadcut exposed on the western slope of Little Mountain, along route 250 to Bartow, West Virginia, about five miles west of Monterey, Virginia.

Description: Theca elongate pyriform, tapering aborally, about 11 mm. high and 5 mm. wide. Four ambulacra are short (largely confined to apex) unbranched and strongly protuberant on the thecal surface by thick flooring plates. Two of the four ambulacra extend slightly onto two plates of the radial circlet (R1 and R4)

Figure 27

a. Isolated L4 plate of P. gordoni. X 7

Laosacystis monterey n. gen., n. sp.

b. Anterior lateral view showing protuberant nature of ambulacra. Open shelf calcisiltite lithofacies, Little Mountain, Virginia. X 6

c. Lateral view of same specimen showing periproct region and plate ornamentation. X 6

d. Left lateral view of same specimen showing L1/R5 pore rhomb. Note very prominent R5 half-rhomb.

e. Apical view showing disposition of the four short ambulacra and prominent radial plates. X 13

f. Right lateral view of same specimen. X 6