To the Graduate Council:

I am submitting herewith a thesis written by Lisa Sophia Bienkowski entitled "The Paleoecology of Echinoderms of the Middle Ordovician Benbolt Formation of East Tennessee." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Geology.

Thomas W. Broadhead, Major Professor

We have read this thesis
and recommend its acceptance:

Accepted for the Council:

The Graduate School

THE PALEOECOLOGY OF ECHINODERMS OF THE MIDDLE ORDOVICIAN BENBOLT FORMATION OF EAST TENNESSEE

A Thesis

Presented For The

Master of Science

Degree

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Lisa Sophia Bienkowski

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Abstract

The Benbolt Formation is part of the Middle Ordovician Chickamauga Group of eastern Tennessee. It consists primarily of cobbly-weathering argillaceous biomicrite and contains a diverse fossil fauna. Benbolt outcrops at Evans Ferry and Stanley Farm in Granger and Union counties, Tennessee, can be divided into three units based on weathering characteristics and fossil content; in ascending order, they are: (1) thinly-bedded biomicrite containing abundant fossils which include a diverse assemblage of echinoderms, (2) a massive-weathering biosparite containing large amounts of echinoderm debris but few identifiable fossils, and (3) a biomicrite interbedded with shale which contains few fossils. These three units represent an environment which changed as the Benbolt was deposited. The first of these was a stable shallow shelf with low current energy which was followed by a shoaling region or a skeletal sand bar which had higher current energy and finally by a quiet mudbank which was often inundated by fine-grained terrigenous clastics and possibly subaerially exposed at rare intervals. The major differences in faunal composition and lithology between Evans Ferry and Stanley Farm seem mainly to be the result of the probability that the water at Evans Ferry was slightly shallower than at Stanley Farm for most of the period of deposition of the Benbolt.

Specimens of 26 different species of echinoderm were collected for this study, mostly from the first unit which supported a far more diverse echinoderm fauna than the other two. These echinoderms belonged to the classes of crinoids, paracrinoids, eocrinoids, rhombiferans, blastoids, edrioasteroids, stylophorans and homiosteleans. Echinoderms were collected from approximately 30 horizons at each of the Benbolt localities and the occurrence of each species was plotted against petrologic data.

The emphasis of this study was (1) to examine evidence for niche-differentiation in the community based upon feeding tiers above the substrate and food particle size selection, and (2) to study the species individually to determine mode of life and preferred environment. Distribution revealed that: (1) echinoderm diversity is highest where the environment was stable and relatively quiet and not greatly affected by influxes of terrigenous clastics, (2) low diversity areas were dominated in biovolume by species which fed in the highest feeding tier as adults, thereby keeping clear of influxes of terrigenous mud which appear to have been a major source of instability in the environment, and (3) in horizons of high diversity, low and middle tier suspension feeders dominated and were fairly evenly divided between small and medium sized food particle selectors, thereby reducing the possibility of competition.

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CHAPTER I

INTRODUCTION

1. THE MIDDLE ORDOVICIAN OF EAST TENNESSEE

The Benbolt Formation is one of the formations which make up the Middle Ordovician Chickamauga Group. This group of sedimentary rocks is composed of carbonate interbedded with fine-grained terrigenous clastic rocks which crop out in the Valley and Ridge Province of eastern Tennessee and southwestern Virginia.

The term Chickamauga was first used to describe the Middle to Upper Ordovician rocks of Hamilton County, Tennessee, and Catoosa and Walker counties, Georgia by Hayes (1891). However, the rocks which are currently included within the Chickamauga Group are different from those originally described by Hayes. Campbell (1894) and Keith (1896 and 1901) studied the rocks of what is now considered the Chickamauga Group and attempted to arrange them into stratigraphic units, but these rocks were not studied in detail until B. N. Cooper and C. E. Prouty (1943) recognized the formations which comprise the Chickamauga Group as used here from outcrops in Tazewell County, Virginia. From youngest to oldest, these were Cliffield, Benbolt, Gratton, Wardell, Bowen, Witten and Moccasin. In 1956, G. A. Cooper used brachiopods to biostratigraphically refine this classification in both Virginia and Tennessee. Cooper's names consisted of the Five Oaks, Lincolnshire, Rockdell, Benbolt, Wardell, Bowen, Witten and Moccasin Formations which are names in common use in eastern Tennessee (figure 1).

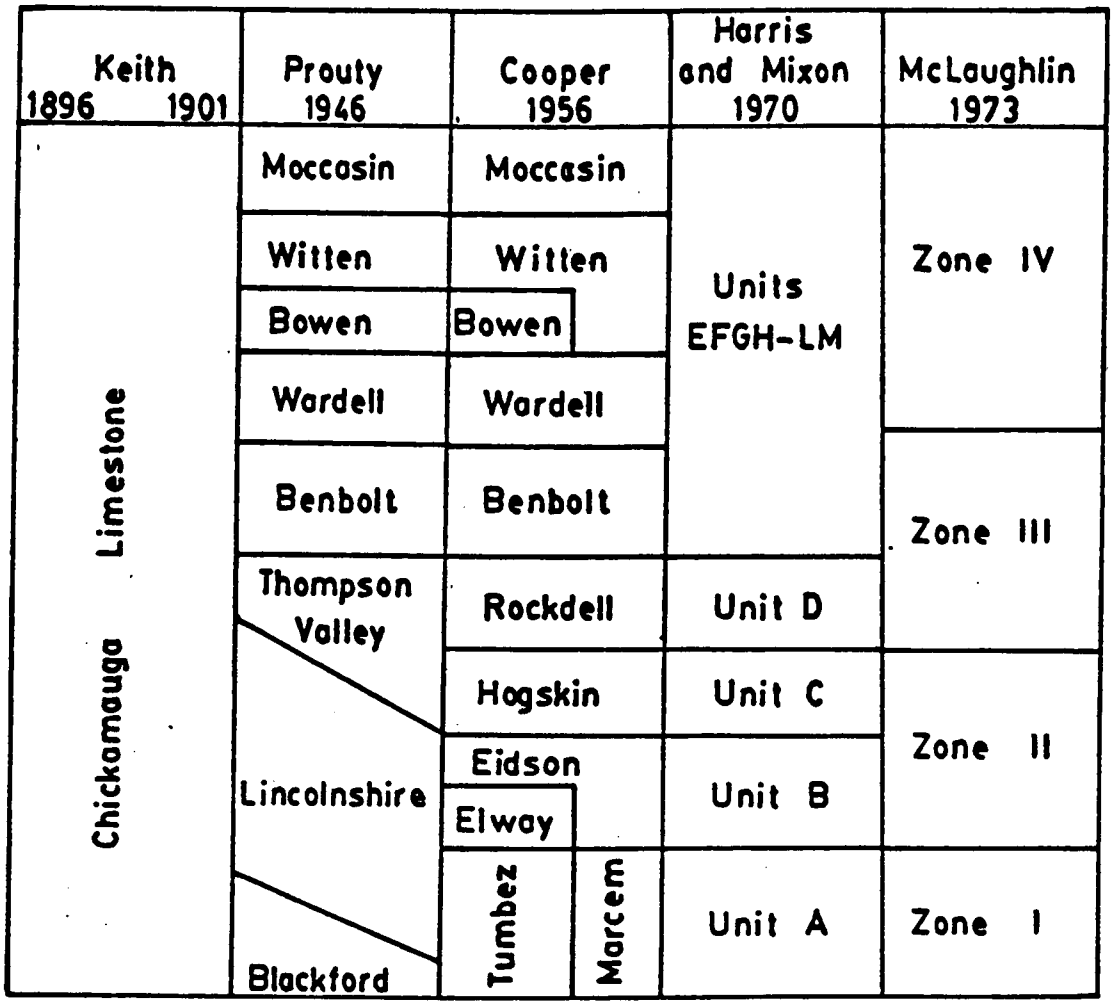


Figure 1. Major schemes of division of the Middle Ordovician rocks of the Hunter Valley Allocthon of northeastern Tennessee (modified from Sickafoose, 1979).

In 1970, Harris and Mixon made a geologic map of the Howard Quarter Quadrangle in northeastern Tennessee. Harris and Mixon divided the rocks in their study area into 13 units lettered A to M. Although these units are not in current use, the map is worthy of note here because Harris and Mixon defined a Member "a" of the Benbolt which is present at the localities studied in Virginia where the Benbolt was originally described.

McLaughlin (1973) devised a zonation of the Chickamauga Group based on recurrent lithofacies cycles and faunal assemblages. For this, he also primarily used brachiopods, recognising persistent association of taxa within generally definable lithologic sequences. However, the study of a single taxonomic group is perhaps not the best way to divide a sequence which can be over 500 meters thick (Walker, et. al., 1980). Thus McLaughlin's system of four units has not been widely used. Nevertheless, his zone III is important to this study because it was defined as containing a biota which is representative of the Benbolt.

Numerous papers have been published concerning the paleoenvironments of the Middle Ordovician in East Tennessee. Walker and Alberstadt (1973) concluded that, during this time period, the northeast portion of the rock-forming environments of eastern Tennessee, which includes the Chickamauga Group, was a shallow water carbonate bank while to the southeast a basin was filling with terrigenous clastics. In contract, they concluded that the source of the fine-grained terrigenous clastic material found in the lower

Chickamauga was probably derived by erosion from the Knox Group rocks exposed to the west.

In 1977, Walker described the sequence of events which led to the deposition of the Chickamauga Group and related rocks in greater detail. Sedimentation began with a transgression from the south which flooded a shelf area of low relief. This was accompanied by the formation of a basin to the east into which were deposited terrigenous clastics. This basin subsided at varying rates for a period of approximately 14 million years (Shanmaugam and Walker, 1980). During the early stages of development, the source of the clastics was the mainland to the west, but at the time of the deposition of the Benbolt, the basin had been largely filled and terrigenous muds were le to cross from the southeast (T_3, figure 2) and thus influence the environments of carbonate deposition. The Benbolt was part of a shallow shelf deposit in an environment of low-lying islands and shallow channels to the northwest of the basin. Moore (1977) used algae to determine the major environments of the Chickamauga Group. He stated that the Benbolt represented an environment of subtidal skeletal sands and mud flats. Walker et. al. (1980, p. 10) noted that the detailed facies pattern of the Chickamauga Group was extremely complex. This was due to the width of the shallow shelf area, the presence of the basin and the influence of terrigenous clastics from two different source areas.

Walker et. al. (1983, p. 705) mapped the paleobathymetric history of this region, showing a transgressional sequence which was followed by a regression. According to this paper, the dolomitic Five Oaks

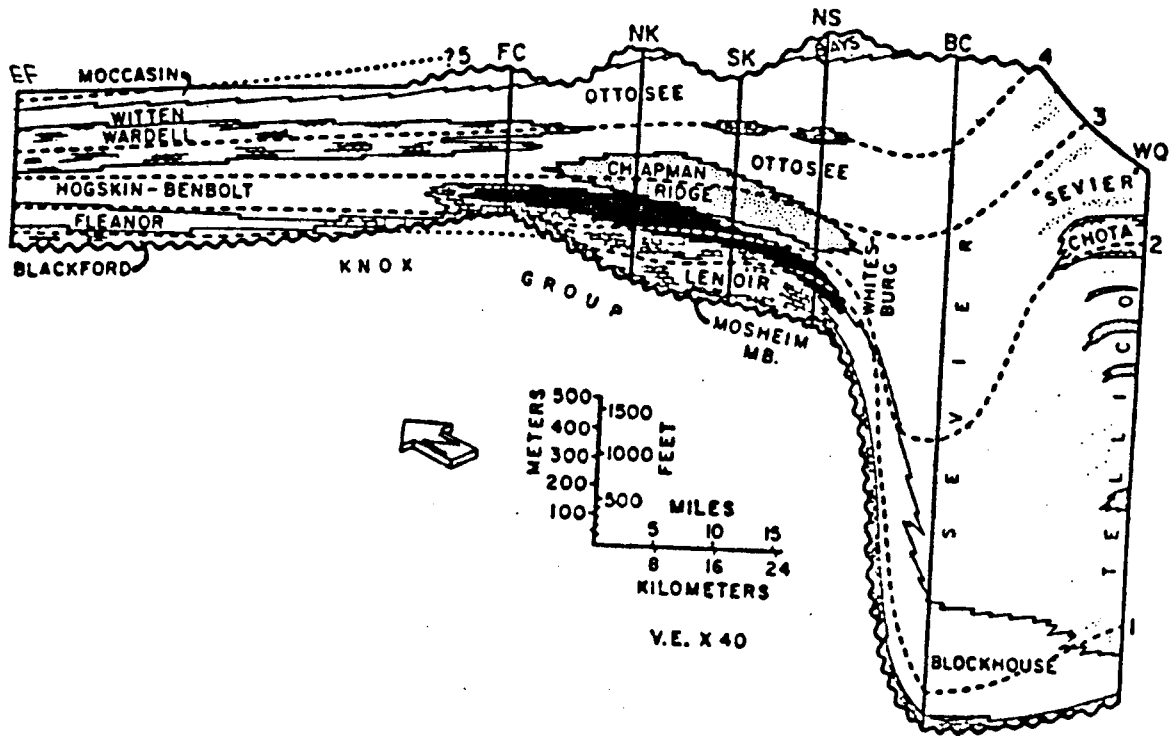


Figure 2. Stratigraphic cross-section from northwest (left) to southeast (right) of the Ordovician of East Tennessee showing palinspastic reconstructions of the Benbolt and neighboring formations (after Walker et. al., 1983); EF=Evans Ferry.

Formation represents a supratidal and intertidal environment. The Lincolnshire and Rockdell formed as a series of carbonate mudbanks intersperced with tidal islands and shallow tidal-basins. The Benbolt represents a deeper subtidal successor basin. The depositional environment of the Wardell and Witten was one of shallow tidal-basins and tidal islands, and the Moccasin represents a return of the shallow subtidal to supratidal environment.

The Chickamauga Group and its environments have been studied in greater detail by Sickafoose (1979), Breland (1980) and Ashworth (1982) among others. The three studies cited specifically are noteworthy on account of the completeness of Breland's study. The theses of Sickafoose and Ashworth were based upon data taken from Evans Ferry and Stanley Farm respectively, which are the two localities investigated for this study (figure 3).

2. THE BENBOLT FORMATION

The type locality for the Benbolt Formation is south of Benbolt in Tazewell County, Virginia (Cooper and Prouty, 1943). There it comprises two distinctive members--the Shannondale and the Burkes Garden, but these have not been identified to the south in Tennessee (Walker et. al., 1980, p. 28). One of the major features of the Benbolt Formation is its exceptional biotic diversity and abundance. The majority of the Benbolt is composed of cobbly-weathering, argillaceous limestone which is generally light-grey and weathers to buff. Fossils are commonly silicified and weather from the surrounding matrix, faci-

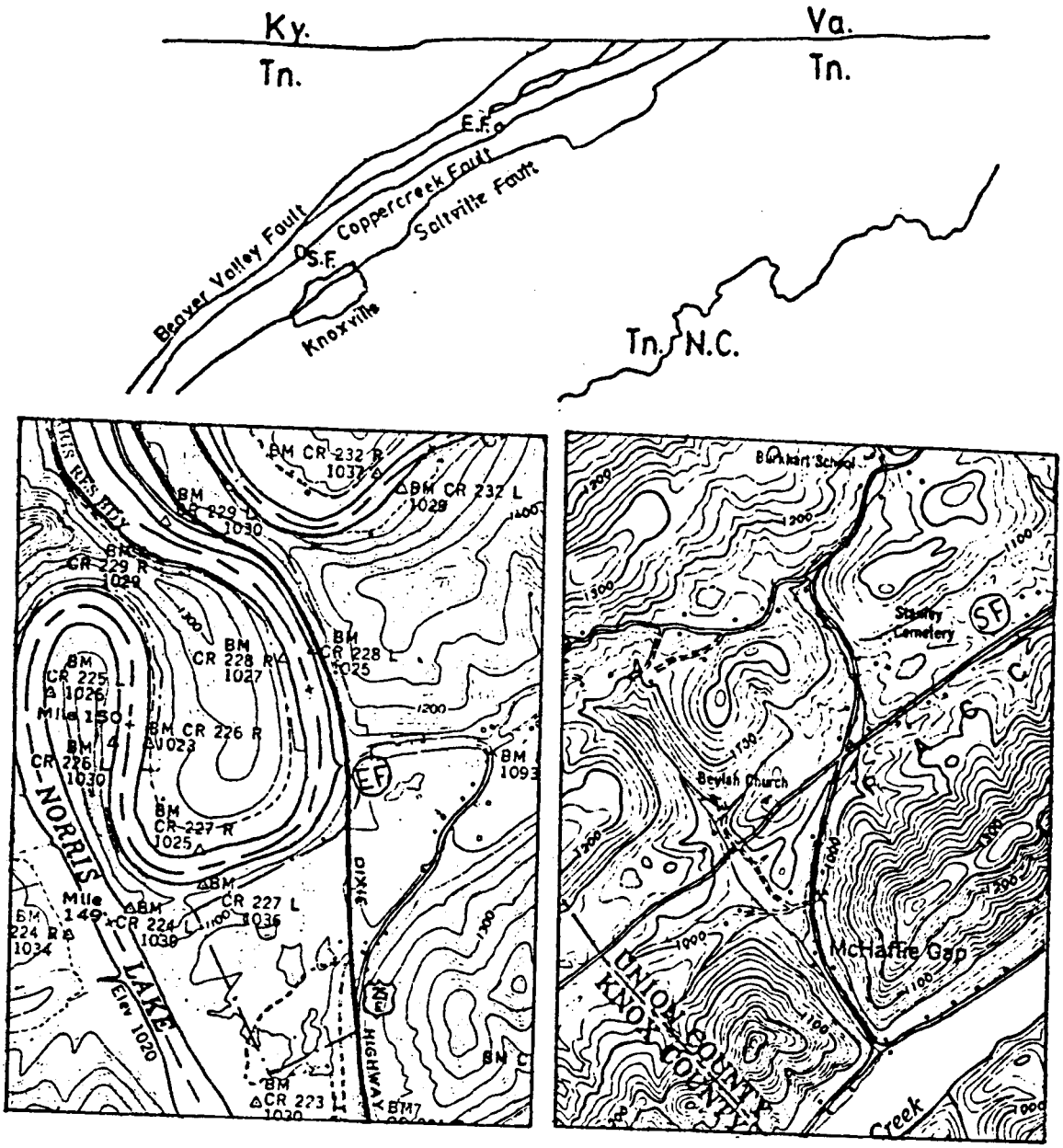


Figure 3. Map showing localities studied for this thesis and their relation to major faults.

litating collection. The dominant faunal elements are echinoderms, brachiopods, bryozoans and trilobites with gastropods, ostracodes, cephalopods and sponges in moderate abundance. Also present are problematical algae and algae assignable to the phyla Chlorophyta, Rhodophyta and Schizophyta.

The two localities studied for this paper, Stanley Farm in Raccoon Valley in Union County, and Evans Ferry in Granger County (figure 3), are within the same strike belt of the Hunter Valley Allocthon which is termed the St. Paul Strike Belt in earlier papers (Ashworth, 1982). Sickafoose (1979) studied most of the visible Chickamauga section at Evans Ferry which includes the Tumbez, Edison, Hogskin, Rockdell, Benbolt and Wardell Formations (figure 4). The Bowen and Witten Formations also occur at Evans Ferry, but were not studied by Sickafoose. That author paid particular attention to the fossils present in the lower 21 meters and the upper 6 meters of the Benbolt. He divided the formation into four units based on lithology and environmental interpretation. The first of these was a highly fossiliferous biomicrite which was overlain by the second, a massive biosparite which showed signs of having been formed under more agitated conditions than the underlying unit. Sickafoose interpreted the upper portion of the Benbolt at Evans Ferry as two alternating environments. One of these environments was muddy and subtidal with some biological abrasion of the fossil grains. The other environment which alternated with the one mentioned above consisted of a wave-baffled mudbank, commonly subaerially exposed. Mudcracks which occur

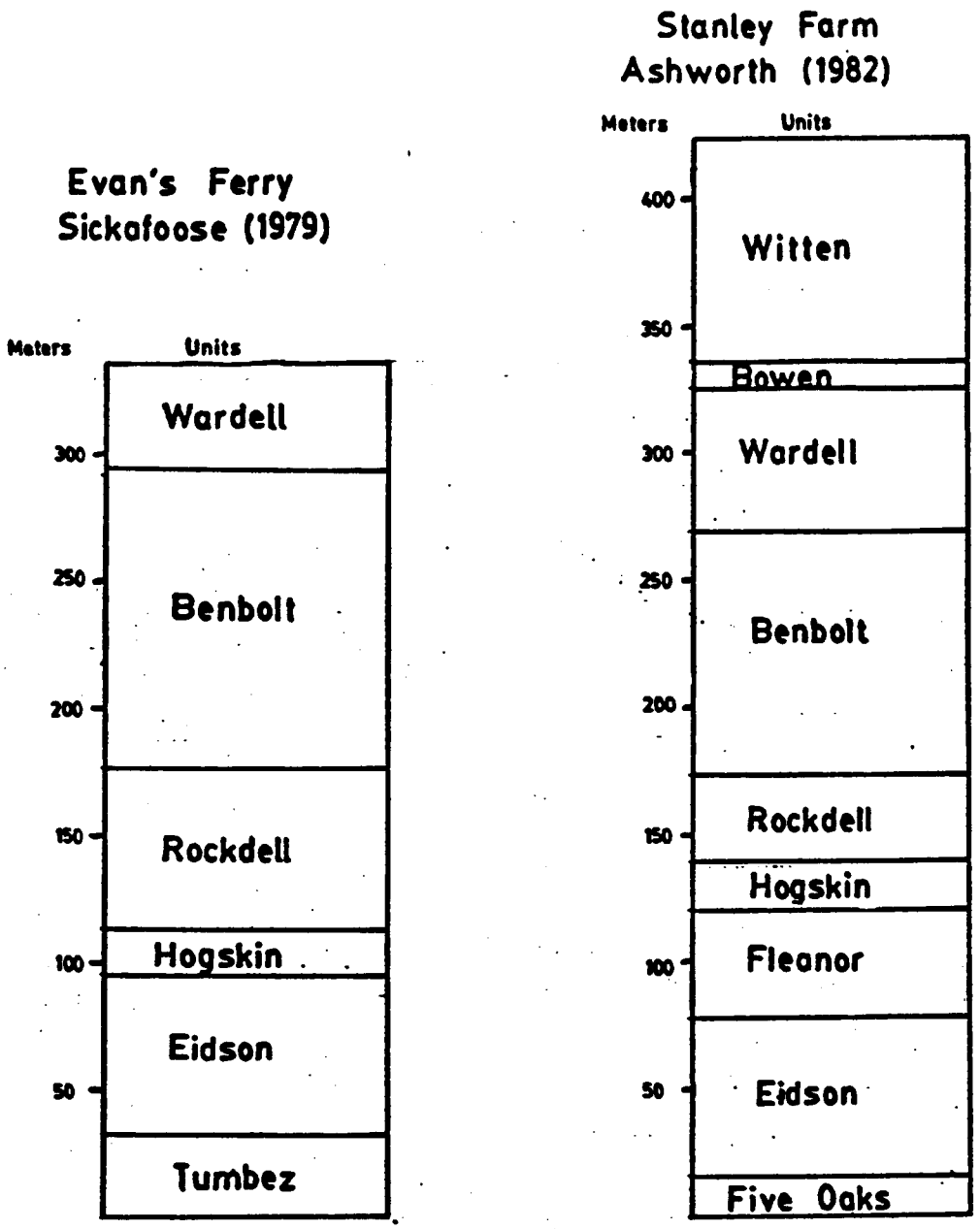


Figure 4. Comparative thickness of the Chickamauga sections studied by Sickafoose and Ashworth.

in the upper two meters of the Benbolt at Evans Ferry seem to indicate this exposure.

Ashworth (1982) studied the Chickamauga at Stanley Farm in Raccoon Valley. He divided the Benbolt into seven units according to lithology. These units were then grouped into three paleoecologic divisions based on fossil content. The first two units make up the first division which is highly fossiliferous. It represents a shelf lagoon environment which was occasionally disturbed by tidal scour and episodes of shoaling. The middle division is a thin but massive biosparite apparently deposited under agitated conditions such as those of a near reef area, a nearshore shoaling region or a tidal channel. Although the features of this division are not so clear as those of the similar unit at Evans Ferry, Ashworth prefers the tidal channel interpretation because the echinoderm grainstone lithology of the division implies a winnowing of the sediment. The remaining four units can be combined into a single division at the top interpreted as a return to a quiet shallow water deposition, interrupted by occasional influxes of fine-grained terrigenous clastics.

Ashworth also made a study of the paleoecology of all taxa present in the Benbolt. To do this, he chose 10 beds stratigraphically distributed through the formation from which he collected slabs. It was from these slabs that the majority of his fossils were identified. The diversity of echinoderms in his study ranged from zero to three species to a bed. In comparing the occurrence of echinoderms with that of other taxa, he stated that brachiopods rarely occur with echinoderms whereas bryozoans often occurred in the same beds.

3. THE ECHINODERMS OF THE BENBOLT

The largest single work on the echinoderms of the Benbolt Formation was published by Brower and Veinus in 1974. This work described most of the crinoid species that were known from the Benbolt at that time and includes a few interpretations of life mode and preferred environment of several of these species. Other crinoids which occur in the Benbolt but were not described by Brower and Veinus are Triboloporus, first mentioned by Kesling and Paul (1968) who also made some attempts to analyze its adaptive morphology, and Acolocrinus (Kesling and Paul, 1971).

Other echinoderm classes besides crinoids are also known from the Benbolt. Bassler (1950) published the first description of the genera Ulrichocystis and Batherocystis which he considered a rhombiferan cystoid and an eocrinoid, respectively. However, Broadhead (1982) reevaluated both genera and came to the conclusion that Batherocystis was a paracrinoid whereas Ulrichocystis was an eocrinoid. Parsley and Mintz (1975) and Frest, Strimple and Coney (1979) studied the paracrinoids as a group and reported the genus Canadocystis from the Benbolt. The rhombiferan cystoid Coronocystis was first described by Paul (1972) from the Benbolt. Parsley's (1970) paper on pleurocystitids provides information on the rhombiferan cystoid Coopericystis, which has been reassigned to Regulaecystis. The homalozoan Myeinocystites was also described from the Benbolt by Parsley (1972). In 1973, Sprinkle published the first report on the parablastoid genus Meristoschisma which occurs only in the Benbolt. Most recently,

Broadhead (1984) reported the oldest known genus of blastoid, Macurdablastus which is also known from the Benbolt. The present study has documented for the first time the occurrences of the crinoid Colpodecrinus and the homalozoan, Anatiferocystis in the Benbolt. However, there has not yet been published a complete study of the paleoecology of all the echinoderm species present in this formation.

Two areas with rock strata nearly time equivalent to the Benbolt and with echinoderm faunas which has been studied with published details available are the Middle Ordovician of the Twin Cities region of Minnesota (Brower and Veinus, 1978) and the Bromide Formation of Oklahoma (Sprinkle, 1982). Brower and Veinus investigated the crinoids of the Hidden Falls Member of the Plattville Limestone, and the Decorah Shale of Minnesota. Here they found representatives of the genera Carabocrinus, Archeocrinus and Paleocrinus which also occur in the Benbolt although as different species.

The fauna of the Bromide Formation, studied by Sprinkle (1982), shows a strong similarity in composition to the Benbolt except that it appears to be more diverse; more than 30 genera are represented within that formation compared with 24 genera from the Benbolt localities studied here. Genera which are common to both formations are the crinoids Acolocrinus, Carabocrinus, Diabolocrinus, Archeocrinus, Paradiabolocrinus, Hybocrinus, Paleocrinus, Colpodecrinus and Apodasmocrinus, the echinozoan, Cyathocystis, and the homalozoans Myeinocystites and Antiferocystis. However, at the species level, the Bromide and the Benbolt share only three species in common--

Acolocrinus hydraulicus, Colpodecrinus quadrifidus and Myeinocystites natus. Many other genera occur in the Bromide which belong to the same families as different genera found in the Benbolt. Data from the Bromide and the Twin Cities Area have been used as an aid in the paleoecological interpretation presented later in this paper.

4. PURPOSE

With the exception of Maitland (1979) and Breland (1980) recent papers on the Chickamauga Group have been concentrated on the lithology and paleoecology of the group as a whole at one locality rather than the study of a single formation at more than one outcrop. Neither have the authors of these papers concentrated on the echinoderms of the Benbolt, nor have they keyed this aspect of the fauna to the lithology. Therefore purpose of this study is to investigate the echinoderms of the Benbolt in greater paleoecologic detail than has been previously done and to observe how occurrance of particular species is related to petrology. Both laboratory and field data have been used to construct a sedimentary history of this formation over a distance of approximately 30 miles. This gives an impression of area as well as time for the formation of the Benbolt, thus providing a more precise picture of this part of the Middle Ordovician.

The high faunal diversity present in some portions of the Benbolt makes the formation ideal for the study of fossils, especially echinoderms, some of which are only known from the Benbolt. Unlike the Bromide, the Platteville Limestone and the Decorah Shale Formations,

identifiable echinoderm fossils occur through most of the Benbolt instead of just within a few thin beds. This allows for clearer observation of the effects of environment upon diversity within the community and the occurrences of individual species.

5. METHODS

The field portion of this study was conducted at Stanley Farm and Evans Ferry. At each locality, approximately 30 horizons were selected based on changes in visible lithology, weathering and slope. Each horizon was examined, echinoderm fossils were collected, and when possible, identified to the species level.

Approximately 60 thin sections made from rock specimens by previous investigators and taken at intervals with an average thickness of 5 meters and with a range of 1 to 12 meters throughout the entire thickness of the Benbolt were used in the previous studies representing the lithology of most of the formation; the author needed to add only four additional thin sections to fill in the gaps remaining. Each thin section was point counted (300 points) to determine the relative abundances of fossil allochems and matrix. Where the thin sections have been point counted before, it was recounted for the sake of consistency. This information is recorded in Appendix B. From these data, a number of graphs have been produced from which various aspects of the paleoecology of the Benbolt have been interpreted.

CHAPTER II

PETROLOGY

1. INTRODUCTION

The Benbolt localities studied for this paper have been investigated petrologically before, but in limited detail because the formation was studied in the context of the entire Chickamauga Group previously. Sickafoose's (1979) study of the Chickamauga section at Evans Ferry included examination of thirty-six thin sections of the Benbolt alone, of which he point counted nine. Ashworth (1982) investigated the Chickamauga outcrops at Stanley Farm in Raccoon Valley and also made a limited study of Benbolt paleoecology. Although he made twenty-seven thin sections from that formation, he point counted only six, thereby giving only a generalized view of the depositional history of Benbolt.

For this study, where the intent was to investigate the Benbolt specifically and in greater detail, all the available previously made thin sections were point counted, and a small number of additional ones were made in order to provide more uniform stratigraphic coverage and more detailed information on specific horizons. These data have provided for a more accurate and detailed picture of Benbolt deposition described here.

2. ENVIRONMENTS OF DEPOSITION

Sickafoose (1979) divided the Benbolt at Evans Ferry into four units which were easily recognised in the field, mostly by their gross lithologic characteristics. The lower 30 meters (Unit B1) was designated on the basis of lithology and fossil content. The 16 meters above this which corresponds with Member "a" mapped by Harris and Mixon (1970) was assigned to Unit 2. The final 71 meters of section consisted of two interbedded units, B3 and B4 which are distinguished from one another by lithology and weathering characteristics. Unit B3 lithology dominates in the 60 meters above Unit B2 whereas Unit B4 lithology becomes prominant only in the upper 11 meters of the formation. Both of these lithologies were considered indicative of different environments within a single sedimentary regime. Therefore, the present author has included the two of these into a single unit which includes all portions of the Benbolt which overlie Harris and Mixon's Members "a". This also facilitates comparison with the Stanley Farm section. Likewise, the lower 30 meters of the Benbolt at Evans Ferry have been designated Unit 1 for the purposes of this paper. The middle 16 meters have been included in Unit 2 and the Upper 71 meters comprise Unit 3 (figure 5).

Ashworth (1982), on the other hand, distinguished seven different units in the Benbolt, not all of which can be recognised at Evans Ferry and therefore cannot be used for correlation between the two localities. Ashworth's Unit 16 consisted of the lowermost 4 meters of the Benbolt at Stanley Farm. The 45 meters above this were designated

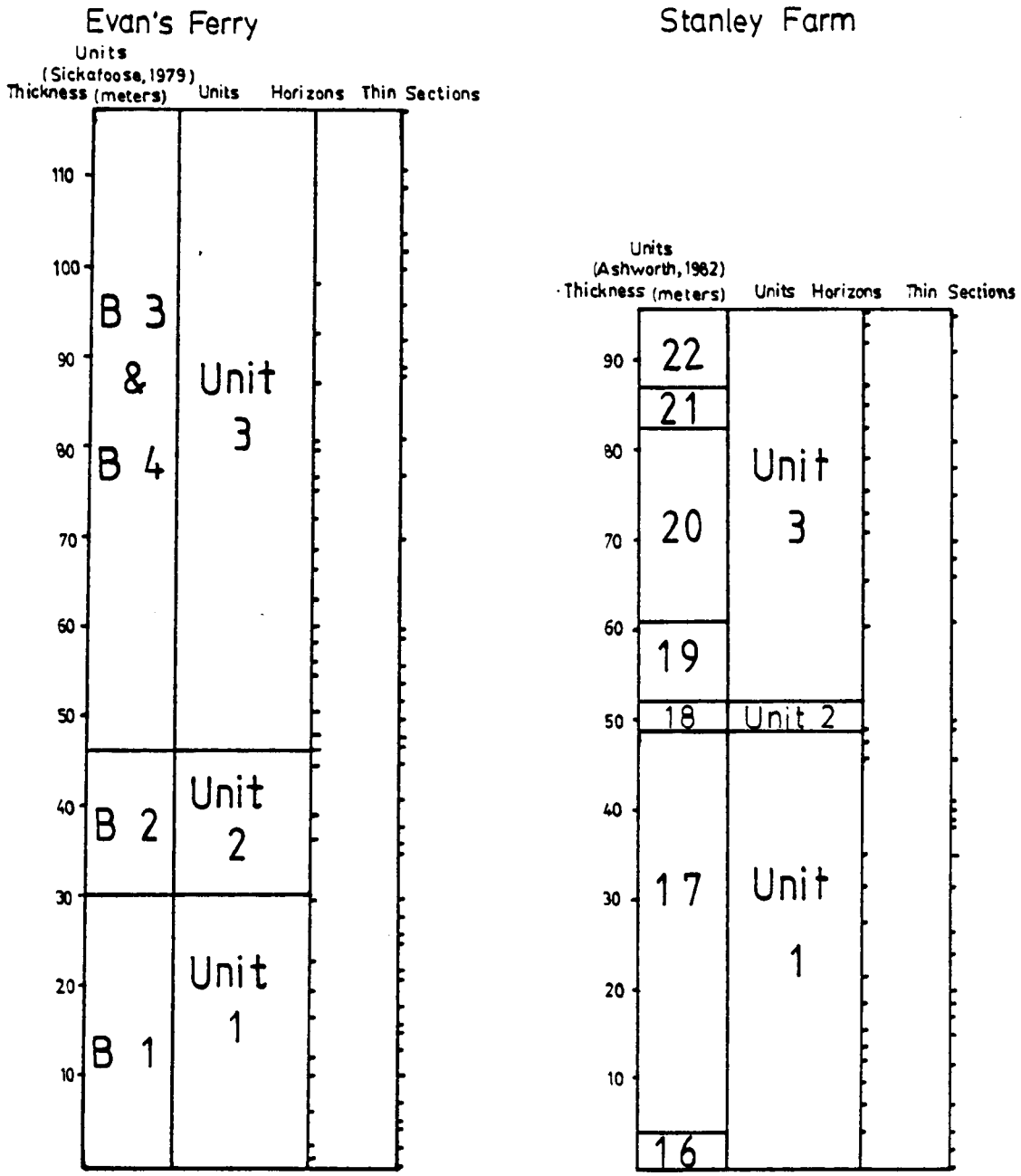


Figure 5. Comparative thickness of the Benbolt at Evans Ferry and Stanley Farm, showing the divisions used by Sickafoose (1979) and Ashworth (1982), those used for this thesis, sampling horizons, and positions of thin section samples.

Unit 17. Unit 18 was identified as the equivalent of Harris and Mixon's (1970) Member "a" and measured 3.3 meters in thickness. The overlying 8.9 meters was included in Unit 19 which was overlain by the 21.5 meters of Unit 20. Above this, Unit 21 measured 4.5 meters thick and the uppermost unit, Unit 22 was 8.4 meters thick. From his paleoenvironmental data, Ashworth combined Unit 16 and 17 into a single larger division. Unit 18 was treated independently while the upper four units were combined by Ashworth into a third division. This broader grouping provides units which can be used and compared at both localities studied for this paper. Therefore, in this thesis, all portions of the Benbolt which lie below Member "a" of Harris and Mixon will be referred to as Unit 1. All Benbolt rocks within Member "a" will be included in Unit 2, and all strata between Member "a" and the base of the Wardell will comprise Unit 3 (figure 5).

According to the criteria set forth by Benedict and Walker (1978), the Benbolt was deposited in water depths between 10 and 50 meters. This is a difficult bathymetric interval in which to determine environments because few sedimentary structures formed in this interval are of such a size as to be readily visible in the field. Therefore, point counting data and observation of the allochems were used in order to attempt to distinguish between the various subenvironments within this regime.

3. UNIT 1

At Evans Ferry, the total thickness of Unit 1 is 30 meters, Sickafoose (1979, p. 65) describes it as being highly fossiliferous. The majority of the rocks represent a shallow low energy environment. This was interrupted at cyclic intervals by influxes of fine-grained terrigenous clastics. Although the environment appears to have been generally quiet, there were good water circulation and occasional periods of higher energy as shown by the amount of abrasion on the fossil grains and the high percentage of spar present in some beds (see figure 6-D). Point count data show that, except in rare instances, micrite was the main matrix component throughout Unit 1 at Evans Ferry; it comprises from 31.3% to 60.6% of the total rock volume. Spar generally made up less than a third of the matrix with a range of 13.3% to 42.3% of all points counted. Approximately half of this appeared to be secondary--either infilling of fossils or replacing micrite matrix, but the other half appeared to be primary. The percentages of spar and micrite fluctuated through the section, but there were no trends apparent toward an increase of one or the other observed.

The most prominant allochem in Unit 1 was echinoderm debris the percentage of which also fluctuated throughout the section. At the base of the Benbolt, echinoderm debris makes up 22.3% of the total volume (figure 6-F), an amount that is rarely equaled anywhere else in the unit. The lowest percentage of echinoderm debris in this unit was 20.3% which occurred near the base of the unit. Brachiopods are

FIGURE 6

Photonegative prints of representative Unit 1 lithologies X3

A Stanley Farm, 39 meters. Micrite 59.0%, spar 18.0%, echinoderms 10.3%, brachiopods 7.3%. Print shows larger brachiopod (a) and Echinoderm (b) fragments. Discontinuous seam stylolites present (c). Sample Bn-39 of Ashworth (1982).

B Evans Ferry, 26 meters. Micrite 53.3%, spar 28.3%, echinoderms 12.3%, bryozoans 2.3%. Print shows oncolite (a), burrow (b), coated grains and abundant small fossil fragments. Sample EF-61 of Sickafoose (1979).

C Stanley Farm, 7 meters. Micrite 62.3%, spar 27.0%, trilobites 2.3%, bryozoans 2.0%, echinoderms 0.6%. Print shows large trilobite fragment (a), encrusting bryozoan (b), and coated grains. Discontinuous seam stylolites present. Sample Bn-7 of Ashowrth (1982).

D Evans Ferry, 21 meters. Micrite 49.0%, spar 32.0%, echinoderms 12.3%, bryozoans 2.3%. Print shows oncolites (a), abundant small fossil fragments and coated grains. Discontinuous seam stylolites present. Sample EF-58 of Sickafoose (1979).

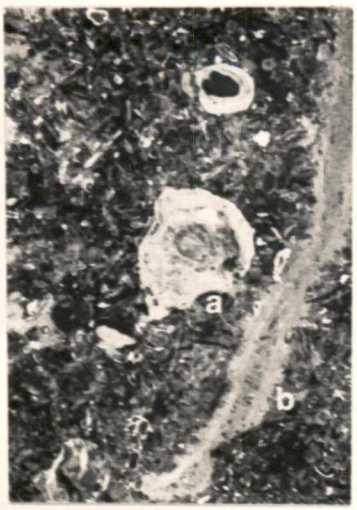
E Stanley Farm, 4 meters. Micrite 40.6%, spar 21.3%, Echinoderms 15.3%, bryozoans 12.3%. Print shows oncolite (a), large trilobite fragment (b), abundant debris and coated grains. Sample Bn-4 of Ashworth (1982).

F Evans Ferry, 0 meters. Micrite 50.6%, spar 16.0%, echinoderms 22.6%, bryozoans 1.6%. Print shows large echinoderm fragment (a), algal fragment (b) and abundant small fossil debris. Suture seam stylolites present. Sample EF-49 of Sickafoose (1979).

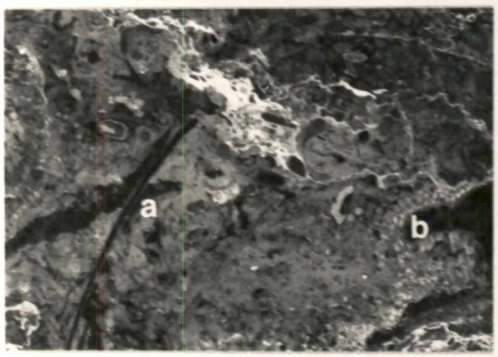
Figure 6



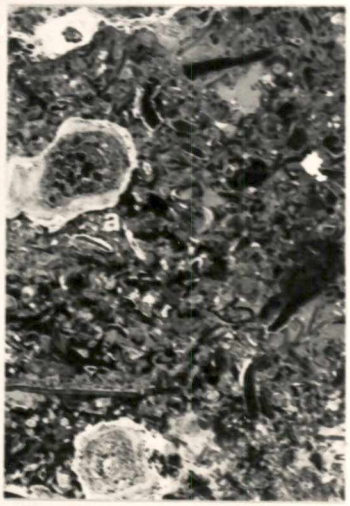
A



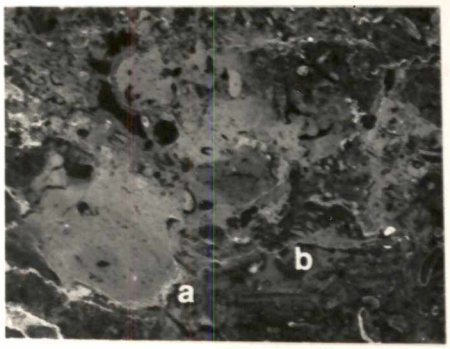
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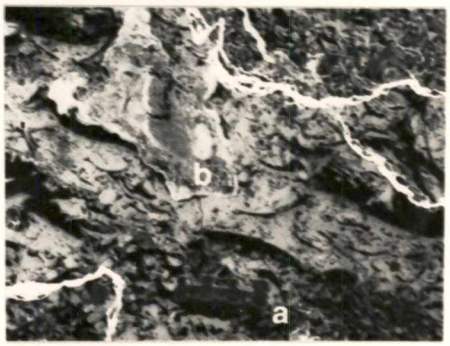
C



D



E



F

extremely rare in this unit, but bryozoans make up between 1.0% and 10.3% with an average of 3.2% of the total rock volume. Trilobites and ostracodes are scarse but regular constituents in these rocks while gastropods are rare. Like echinoderm debris, percentages of all allochems fluctuate throughout the unit. Except in areas where they dominate, the bryozoan percentage paralleled the percentage of echinoderm debris.

Algal diversity was also variable with Girvanella and Kazakhstanelia the most common taxa present but other genera were observed such as Nuia, Hedstromia and Contexta. Generally, algal diversity is higher in this unit than in other parts of the Benbolt. Toward the bottom of Unit 1, oncolites are scarce, but they become much more common towards the top (figure 6-B and D). They occur in every sample from 13 meters to the top of the unit. In the lower portions of the unit, fossil fragments tend to be larger than they are in Unit 2, but in the upper 10 meters of Unit 1, the size of fragments decreases.

Unit 1 measures 49 meters thick at Stanley Farm. The lower 4 meters is a thinly bedded biomicrite and cherty biomicrite interbedded with thin shales (Ashworth, 1982, p. 52). The remainder of the unit is a thin to medium bedded biomicrite and biosparite containing abundant fossils. Ashworth considers the lithology and biota to indicate an environment of quiet lagoonal muds which was occasionally interrupted by tidal channels and shoals, especially in the upper portions of the unit. As at Evans Ferry, point count data taken for this

study show that the matrix is composed mostly of micrite which ranges from 31.3% to 78.6% of rock volume. There are no apparent trends to this fluctuation, but generally the micrite content is higher here than it is at Evans Ferry. Spar usually makes up no more than a fifth of the total volume of the rock with a range of 40.0% to 43.3%. Echinoderm debris is the most common allochem, ranging from 0.6% to 35.3%. At the base, all fossil allochems are sparse, but both echinoderms and bryozoans increase in abundance upward within the lower four meters of the unit. Bryozoans range from 0% to 13.3% with an average of 4.7% which makes them generally more common here than in Unit 1 at Evans Ferry. Here also, they follow the same approximate fluctuations of percentage that the echinoderm debris does. Brachiopods are also more common at Stanley Farm although they are only abundant near the top of Unit 1 (figure 6-A) where echinoderm and bryozoan debris becomes less common. Of other allochems, trilobites, ostracodes and gastropods are never common, but they occur consistently through the unit. As at Evans Ferry, algal diversity is variable and again is largely dominated by Girvanella and Kazakhstanelia, but also includes representatives of other algal genera. The algal diversity here is higher then in most other portions of the Benbolt and it tends to increase with increases in percentage of echinoderm debris. Oncolites are much rarer at Stanley Farm then they are at Evans Ferry, and fossil fragments are generally larger (figure 6-A-F). Oncolites do not occur frequently at Stanley Farm until the upper 10 meters of Unit 1.

Unit 1 at both localities seems to represent a quiet stable environment below the wave base but within the photic zone.

Occasionally carbonate deposition was interrupted by cyclic influxes of fine-grained terrigenous clastic material. However, Stanley Farm rocks are higher in micrite and lower in spar than those at Evans Ferry. There are more brachiopods, fewer oncolites and more large fossil fragments which do not appear to have been broken or abraided by transport, all of which suggest a possibly lower energy environment than that represented by the rocks at Evans Ferry. The increase in oncolites toward the top of both units indicates a shallowing over time, but this happened more rapidly at Evans Ferry. Benbolt sedimentation at Evans Ferry began with a sketetal sand bank or period of shoaling as indicated by the high percentage of echinoderm debris and comparitively low micrite percentage of 50.6% at the base. At Stanley Farm, conditions wer less current active and continued so throughout the depositional history of Unit 1, probably because it took place in slightly deeper water. Another clue to differences between the two localities is the appearance of echinoderm holdfasts found at both localities. At Stanley Farm, all holdfasts were of the root-like soft sediment type described by Halleck (1973) whereas at Evans Ferry, some of the holdfasts were of the discoidal hardground type, thus giving the indication that the slightly lower rate of sedimentation at Evans Ferry produced a substrate of patchy hardground while, because of the high sedimentation rate at Stanley Farm, the substrate remained predominantly soft.

4. UNIT 2

Unit 2 of the Benbolt is easily recognised in the field by its massive bedding and resistence to weathering. Harris and Mixon (1970)

mapped this as Member "a" in the Howard Quarter Quadrangle in northeastern Tennessee, and while it is not visible in all outcrops of the Benbolt, it does occur at both Evans Ferry and Stanlyy Farm. At the former locality, Unit 2 has a thickness of 16 meters. In general, the micrite content is slightly lower than it is in Unit 1 and the fluctuations in percentage are greater, ranging from 27.6% to 65.6% with an average of 46.2%. Spar content is high in the upper and lower portions of the unit where it peaks at 46.6% (see figure 7-D), but lower in the middle with a minimum of 5.3%. Echinoderm debris is again the most prominant allochem (12.0%-21.0%) which like the spar decreases in abundance in the middle of the unit and increases toward the top. Bryozoans are moderately common (2.0% to 8.6%) but this abundance fluctuates and does not seem to be related to the fluctuations of percentage of any other allochems. Brachiopods only occur in the middle portion of the unit while trilobites and ostracodes are scattered sparsely throughout. Algae are less abundant in this unit than in Unit 1 and of lower diversity, entirely dominated by Girvanella and Kazakhstanelia. Oncolites are present only in the lower portions of Unit 2. Sickafoose (1979, p. 66-67) observed bidirectional cross beds approximately 5 cm in height in the lower part of the unit, suggesting the influence of tidal current ripples on deposition. He also noted abrasion of the fossils (figure 7-B) and a decrease in the size of fragments, implying transportation. Thus he interpreted the environment as a tidal channel or a skeletal sand bar. This author also noticed signs of abrasion on the fossil allochems,

Figure 7

Photonegative prints of representative Unit 2 lithologies X3

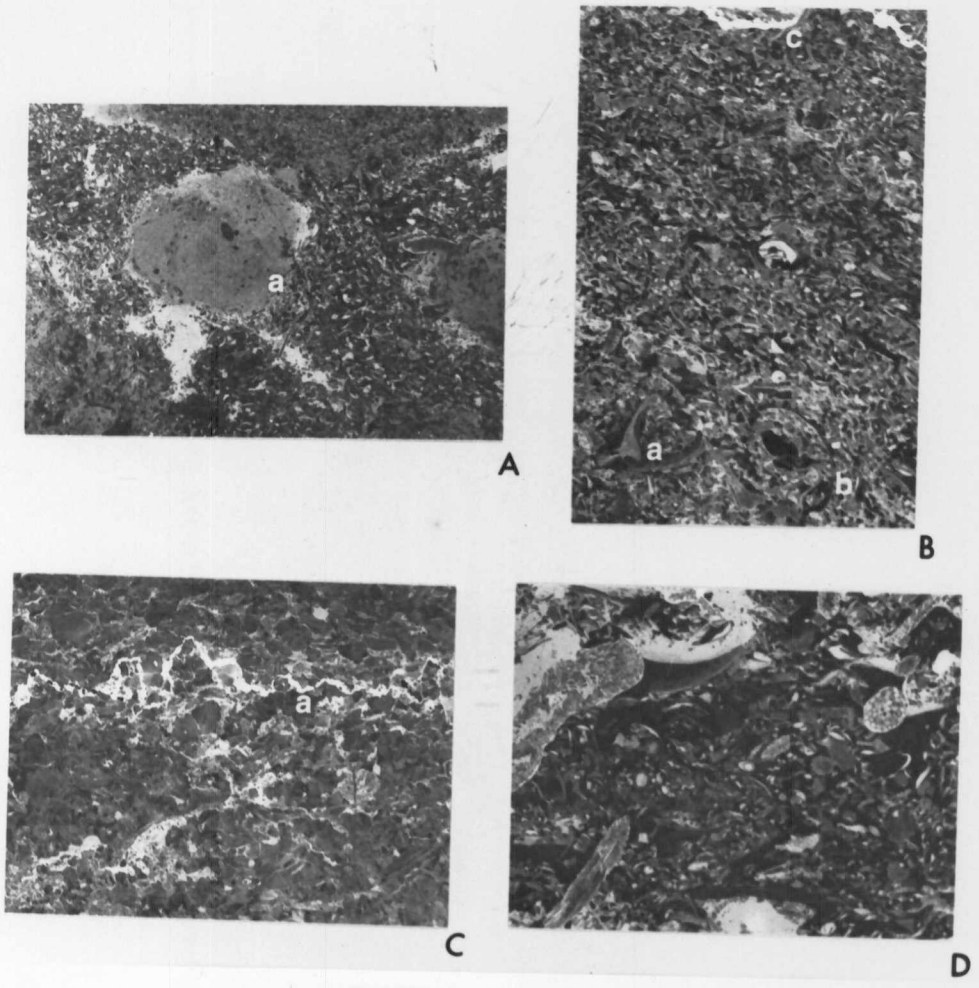
A Stanley Farm, 50 meters. Micrite 56.0%, spar 19.6%, echinoderms 28.3%, ostracodes 4.6%. Print shows oncolite (a), coated grains and abundant well-sorted small fossil fragments. Sample Bn-50 of Ashworth (1982).

B Evans Ferry, 41 meters. Micrite 42.3%, spar 38.0%, echinoderms 13.6%, byrozoans 3.0%. Print shows large but abraided-looking echinoderm grains (a), large trilobite fragment (b) and abundant smaller fossil fragments. Sutured seam stylolite present (c). Sample EF-67 of Sickafoose (1979).

C Stanley Farm, 49 meters. Micrite 1.0%, spar 27.3%, echinoderms 52.6%, bryozoans 5.0%. Print shows high abundance of spar and echinoderm debris; echinoderm grains often abraided and coated. Sutured seam stylolite present (a). Sample Bn-49 of Ashworth (1982).

D Evans Ferry, 38 meters. Micrite 27.6%, spar 46.6%, echinoderms 12.0%, bryozoans 9.3%. Print shows high spar content, large bryozoan fragments, smaller fragments of echinoderms and trilobites, and coated grains. Sample EF-67 of Sickafoose (1979).

Figure 7



but noted that abrasion was less common in the central part of the unit.

At Stanley Farm, Unit 2 is only 3.1 meters thick and does not show the cross-bedding seen at Evans Ferry (Ashworth 1982, p. 61). Ashworth describes this unit as an echinoderm grainstone which he suspects may have formed as part of a tidal channel which washed away smaller particles. The base of Unit 2 at Stanley Farm is marked by a zone of exceptionally high content of echinoderm debris (52.6%). Next in abundance in this particular bed is spar (27.3%); micrite only makes up 1.0% (figure 7-C). The most common fossil allochems other than echinoderm debris are bryozoans and ostracodes. Trilobites and brachiopods are scarce; and gastropods and algae were present but not counted. Higher up in Unit 2, echinoderm debris drops to 28.3%, micrite increases to 46.0%, while spar drops to 19.6% (figure 7-A). Other than echinoderm debris, the only fossil allochems are ostracodes and trilobites, and all fossil fragments are abraided. The only alga present here is Kazakhstanelia which occurs rarely at the base of the unit.

At both Stanley Farm and Evans Ferry, deposition of Unit 2 began in an evironment of high energy, probably associated with a tidally-winnowed sand bank in which currents swept away all finer material. As the sand bank was moved away or tidal energy otherwise decreased, the micrite content of the sediments became greater. At Evans Ferry, the sand bank probably crossed the region more than once which explains the thickness of the unit there and the recurrence of the

pattern, while at Stanley Farm where Unit 2 is thick and without a notable cyclic pattern, the geographic limit of the environment was nearly reached. Again, Evans Ferry was generally shallower than Stanley Farm as shown by the presence of oncolites and by the smaller amount of echinoderm debris. This debris was unlikely to have been transported very far because abrasion of the ossicles is only moderate. Thus, the main factor which influenced the composition of the rock was the presence of larger grain-sized material which would not be swept away easily by currents.

5. UNIT 3

The greatest difference between the Evans Ferry and Stanley Farm sections lies within Unit 3. Sickafoose (1979) distinquished between two environments which alternated throughout the remaining 71 meters of the section. The one which is prevalent in the lower 60 meters of Unit 3 is a shaley micrite which he interprets to have been an inter-mound area which contained both non-detrital carbonate and clastic sediments derived from the southeast. Periodically mudmounds migrated across the Evans Ferry area and sediments locally were subaerially exposed. According to Sickafoose, mudcracks formed in some places, although most of the sediments retained a high water content. Sickafoose (p.72) described this environment as a wave-baffled mud-bank. The contact between the Benbolt and the Wardell at Evans Ferry is marked by oncolite beds.

At the base of Unit 3, the matrix is commonly dominated by spar

which varies from 62.0% to 9.3% (see figure 8-F) in samples from the lower 10 meters of the unit. Within this same part of the unit, micrite ranges between 65.6% and 19.6% with the highs generally corrsponding to the lows in spar percentage. Above the lower 10 meters of Unit 3, spar ranges between 32.2% and 1.3% and micrite composes between 88.6% and 46.3% of the rock. Within this area, the fluctuations of percentage for both constituents are much less than they are in lower portions of the Benbolt.

At the base of Unit 3, the percentage of echinoderm debris reaches a high at Evans Ferry of 37.3% but quickly decreases to a fairly constant level of about 10.0%. In the lower 6 meters of Unit 3, echinoderm debris is abundant while bryozoans are rare, but above that, bryozoans compose up to 15.0% of the rock (figure 8-F) before the levels of both fossil types decline toward the top of the unit.

Ostracodes, gastropods and brachiopods occur throughout the section, but never in great numbers. Algae are uncommon and oncolites do not occur below the top of the unit. At the base of Unit 3, the environment was similar to that of Unit 2, representing high current energy, but following the rapid reduction of this energy, the environment became continually quieter as shown by the increase of micrite. Although the environment was quiet, the presence of mudcracks show possibly very shallow conditions at times. These mudcracks appear to have the "v" shaped cross-section of true mudcracks, but they do not seem to form the proper polygonal pattern and therefore may in fact be cineresus cracks which are useless as environmental indicators. At

Figure 8

Photonegative prints of representative Unit 3 lithologies X3

A Stanley Farm, 95 meters. Micrite 35.3%, spar 7.3%, echinoderms 10.0%, bryozoans 26.3%, brachiopods 6.6%. Print shows large brachiopods fragment (a), large bryozoan fragment (b) and abundant micrite. Sample Bn-95 of Ashworth (1982).

B Evans Ferry, 100 meters. Micrite 88.6%, spar 1.3%, echinoderms 1.3%, bryozoans 1.6%. Print shows bryozoan fragment (a), echinoderm fragment (b), small trilobite fragments and abundant micrite. Discontinuous seam stylolite (c) present. Sample EF-84 of Sickafoose (1979).

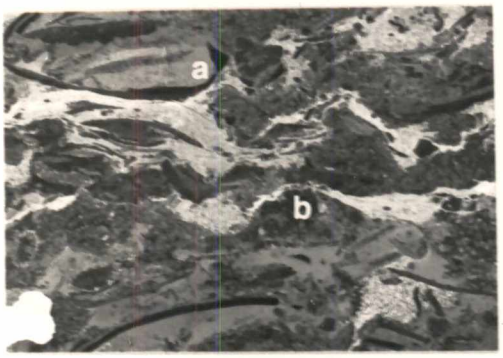
C Stanley Farm, 86 meters. Micrite 98.0%, spar 1.6%, echinoderms 0%. Print shows micrite mottled by horizontal burrows. Sample Bn-86 of Ashworth (1982).

D Evans Ferry, 89 meters. Micrite 50.3%, spar 21.3%, echinoderms 14.3%, bryozoans 1.6%. Print shows abundant echinoderm grains which have been abraided and coated. Sutured seam stylolite (a) present. Sample EF-81 of Sickafoose (1979).

E Stanley Farm, 68 meters. Micrite 50.3%, spar 2.3%, echinoderms 8.6%, bryozoans 33.6%. Print shows large trilobite fragment (a), abundant bryozoan debris and other fossil fragments. Discontinuous seams stylolites present. Sample Bn-68 of Ashworth (1982).

F Evans Ferry, 56 meters. Micrite 65.6%, spar 9.3%, echinoderms 3.3%, bryozoans 15.0%. Print shows large bryozoan fragment (a), unusual echinoderm fragment (b) and smaller fossil debris. Discontinuous seam stylolite present. Sample EF-75 of Sickafoose (1979).

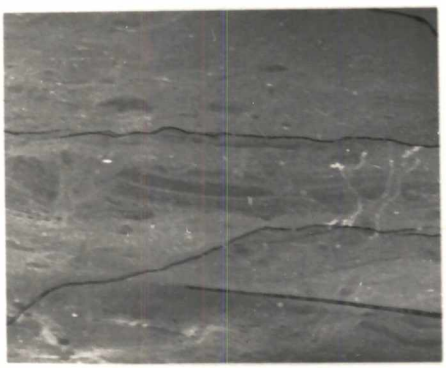
Figure 8



A



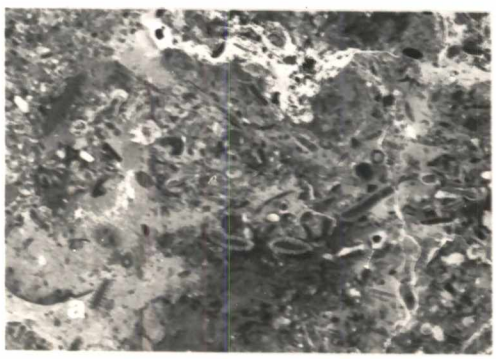
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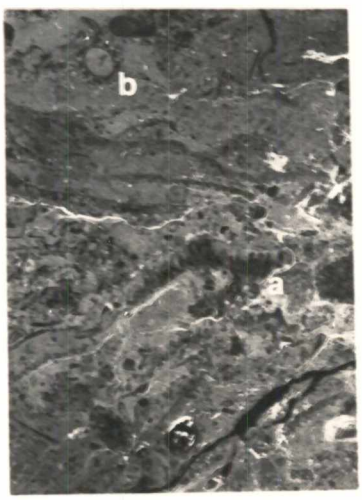
C



D



E



F

the top of the unit, the presence of oncolites show that the current activity in the environment returned although the water remained no more than 10 meters deep.

At Stanley Farm, Unit 3 is 43.3 meters thick. Ashworth describes the lowest portion of this unit as a shaley calcarious mudstone, highly weathered and usually covered by vegetation in outcrop, thus precluding the collection of samples for either his or the present study. A 21.5 meter thick sequence of biomicrite interbedded with shale above the mudstone is in turned topped by another bed of calcareous shale 4.5 meters thick. The uppermost part of Unit 3 at Stanley Farm is composed of a buff-colored calcareous shale interbedded with shaley biomicrite. As a whole, the petrology of Unit 3 shows strong influence by frequent influxes of fine-grained terrigenous clastic material which made the environment intolerable for most macrobiota in the greater part of the section (Ashworth, 1982, p. 62).

Micrite is almost always the major matrix component of Unit 3 of the Benbolt, but at Stanley Farm, the percentages fluctuate much more (33.0%-98.0%) than in the upper part of the Evans Ferry section. Generally the trend from the base to the top of Unit 3 is an increase in micrite and a decrease in spar (see figure 11).

Echinoderm debris is generally the most common fossil allochem with a range of 44.6% to 0% and an average of 16.0%, but at the top of the unit, bryozoans dominate, increasing to 33.0%. Otherwise, the trends of bryozoan percentages parallel those of echinoderm debris. Brachiopods maintain a low abundance level throughout the unit except

for the top of the section where they increase to 6.6% (see figure 8-A). Trilobites, ostracodes and gastropods occur regularly but never in high percentages. Algae are abundant and diverse, dominated by Kazakhstanelia and Girvanella in the middle portions of the unit, but becoming very scarce at the top. Oncolites are common in the lower 30 meters of Unit 3, but are absent in most of the overlying rocks except at the top of the unit. Even there, however, they are not as prevalent as at Evans Ferry. The environment represented by Unit 3 at Stanley Farm was one which became increasingly quiet over time, but showed periods of slight current activity. Carbonate sedimentation was frequently interrupted by the influx of terrigenous mud, but this did not prevent brachiopods, bryozoans and echinoderms from establishing living sites in the environment.

The shales which characterize Unit 3 at Stanley Farm are more abundant and more fissile than those at Evans Ferry. They are mostly a uniform buff color with faint burrow mottling which implies a high water content and swift deposition. Otherwise, these shales are nearly devoid of fossils which implies that they were probably deposited rapidly and thereby prohibited the colonization of their surface by suspension feeders until the rate of deposition decreased, because any sessile organism which attached itself to that substrate would have been buried before it reached maturity.

Unit 3 at Evans Ferry and Stanley Farm is similar in both areas in that conditions became quieter than they had been during Unit 2 deposition and sedimentation was repeatedly influenced by influxes of

terrigenous clastic debris. In both cases, agiated conditions marked deposition of the top of the unit, but the change was greater at Evans Ferry than it was at Stanley Farm. At Evans Ferry, the progression toward a quieter environment was more consistent than at Stanley Farm although the former area may have been subjected to occasional subaerial exposure while in the Stanley Farm area shallow water conditions remained uninterrupted for the duration of Benbolt deposition.

Despite differences between the sections at the two localities, they obviously developed under the same depositional regime during a period of slight fluctuations of sea level coincident with the migration of small low-lying mudmounds. Influxes of terrigenous mud which probably came from the southeast interrupted times of limestone production or other activity by organisms living in the region when it was relatively free of mud. As previously noted; the main difference between the Stanley Farm and Evans Ferry sections is that the latter apparently was deposited under usually slightly more shallow water conditions so that occasional subaerial exposure may have resulted.

A study of the stylolites which are present in many of the Benbolt thin sections also indicate the basic changes in the environment. According to the classification system of Wanless (1979), the stylolites of Units 1 and 3 (figures 6 and 8) are of the discontinuous seam variety whereas those of Unit 2 (figure 7) are sutured seam stylolites. The discontinuous seam type of stylolites appears to be an indication of a high clay content in the rock. Those which are present in Unit 3 tend to be a little thicker than those of Unit 1, thereby

showing a probably higher clay content in the former unit.

The point counting data collected for this thesis also show a correlation between the percentages of echinoderms, bryozoans and brachiopods. When plotted, these data reveal that peaks in echinoderm and bryozoan percentages occur within approximately the same beds at Stanley Farm (figure 9). The major exceptions to this rule are to be found at the base of Unit 2 where echinoderms dominate, and toward the middle of Unit 3 where bryozoans dominate. In the case of Unit 2, the cause of this is probably a preservational bias since echinoderm collumnals seem to survive abrasion better than bryozoans fragments. The dominance of bryozoans in the moddle of Unit 3 may have been due to conditions which favored bryozoans in competition between the two groups. The data for brachiopods are different from that for echinoderms and bryozoans. The brachiopod percentage peaks generally correlate to lows in percentages of echinoderms. This indicates that these two groups thrived in different types of environments. According to Ashworth (1982), the dominant brachiopod throughout the Benbolt above 30 meters is a representative of the genus Sowerbyella which is a strophomenid. The flattened shape of this type of brachiopod was best adapted to an exremely quiet environment with a substrate consisting of fine-grained terrigenous clastics with a high water content. Echinoderms on the other hand dominate in environments where the substrate consisted of micrite which has a generally lower water content than the terrigenous mud and therefore provided a firmer bottom for echinoderms to root in.

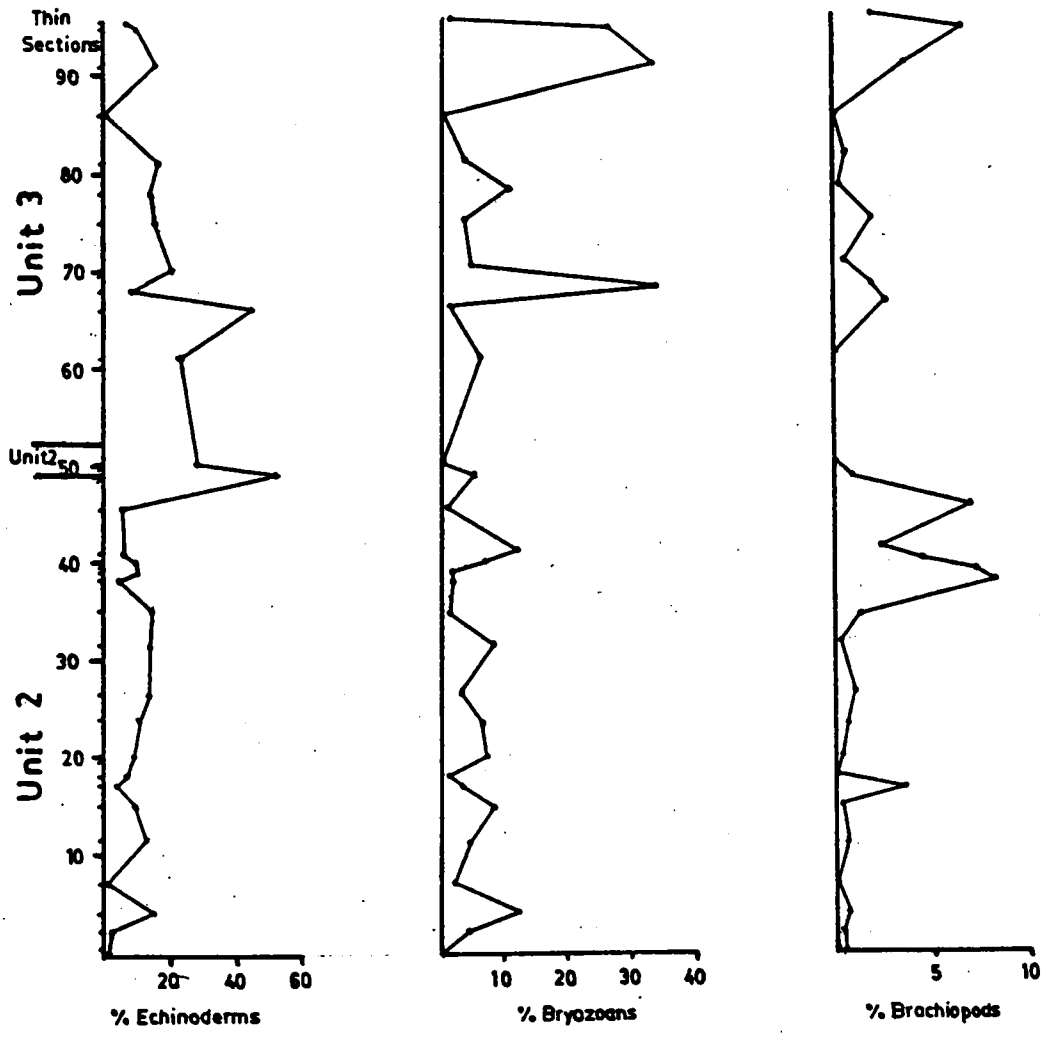


Figure 9. Plots of percentages of echinoderms, bryozoans and brachiopods for Stanley Farm.

6. SUMMARY

The Benbolt Formation in the study area can be divided readily into three units recognizable in the field. Unit 1 represents a quiet subtidal environment with sufficient water circulation to support a diverse biota. Because conditions at Evans Ferry were slightly shallower than at Stanley Farm, the accompanying higher energy conditions produced a patchy hard ground rather than an areally continuous soft substrate. Both areas were located within the shelf lagoon zone which formed to the west of the basin as shown in the reconstruction suggested by Walker, Shanmagam and Ruppel (1983). Unit 2 formed during a period of shallowing when current energy became higher and produced tidal sand bars in which the finer-grained material was swept away. The effects of further shallowing and the filling in of the basin can be seen in Unit 3 in which the lagoon was frequently flooded by terrigenous clastic material which came over the remains of the basin from the southeast. The Evans Ferry environment appears to have been similar to that of Stanley Farm throughout deposition except at the top where shallow, high current-energy conditions produced oncolites.

CHAPTER III

PALEOECOLGY

1. INTRODUCTION

The echinoderm fauna of the Benbolt Formation is exceptional in its diversity. Many of the species found in the formation are unknown elsewhere. Thus the Benbolt is an ideal formation for the study of the factors which influence the diversity and distribution of Middle Ordovician echinoderms.

Twenty-six species representing twenty-four genera from nine classes of echinoderms have been collected from the two areas studied for this paper (see table 1).

Most specimens are represented by collections of individual plates or partial calyces and thecae. Stems were rarely found connected to the original calyces and thecae, and the arms collected were entirely unattached. This places a limit on the amount of autecologic information to be gained by a study of a formation with as high a diversity as the Benbolt. However because other species of the same genera are known from other well studied localities, much can be postulated from a comparison with specimens from the Bromide Formation of Oklahoma (Sprinkle, 1982) and the Platteville and Decorah Formations of Minnesota (Brower and Veinus, 1978). The Platteville correlates to the Pooleville Member of the Upper Bromide and is overlain by the Decorah. The Benbolt was deposited slightly earlier than the Platteville but still within the time of the Pooleville Member of the

TABLE 1

ECHINODERM SPECIES OF THE BENBOLT FORMATION

Crinozoans	Blastozoans
Hybocrinus punctatus	*Ulrichocystis eximia*
Hybocrinus punctatocristatus	*Canadocystis tennesseensis*
Paleocrinus planobasalis	Rhombiferan A
Carabocrinus micropunctatus	*Coronocystis angulatus*
Acolocrinus hydraulicus	*Regulaecystis pyriformis*
Annulocrinus latus	*Macurdablastus uniplicatus*
Apodasmocrinus punctatus	*Meristoschisma hudsoni*
Triboloporus cyptoplicatus	Echinozoans
Archeocrinus peculiaris	*Cyathocystis sp.*
Diabolocrinus vesperalis	Homalozoans
Paradiabolocrinus irregularis	*Anatiferocystis barrandei*
Wilsonicrinus culmensinuousus	*Myeinocystites natus*
Colpodecrinus quadrifidus	
Rhaphanocrinus simplex	

Bromide Formation.

The horizons from which each species was collected are recorded in figures 10 and 11. Further data on characteristics of the specimens collected are presented in Appendix A.

2. SYNECOLOGY

Diversity

The subject of diversity is one that has been long debated by ecologists, and variety of theories have been proposed to explain why one area would have a large number of species living within it and another should have a small number of species. In the case of extinct animals, the reasons for differences in diversity are even more difficult to determine. Most of the original terrain has been obscured by lithification and there is little direct evidence of predation, competition and some physical environmental factors which might influence diversity. Nevertheless, many of these influences can be inferred from petrologic examination of the rocks and the fossils they contain.

Sanders (1968, p. 279) states that the two main causes of high diversity in the modern marine environment are stability of the environment, and, in low latitudes, biological competition which will cause animals to adapt to more specialized niches. Both of these factors are difficult to determine based solely upon fossil evidence. Many instabilities in the environment such as short-term climatic or salinity changes which would disrupt the animal population occur over such short periods of time that they are unlikely to be preserved in

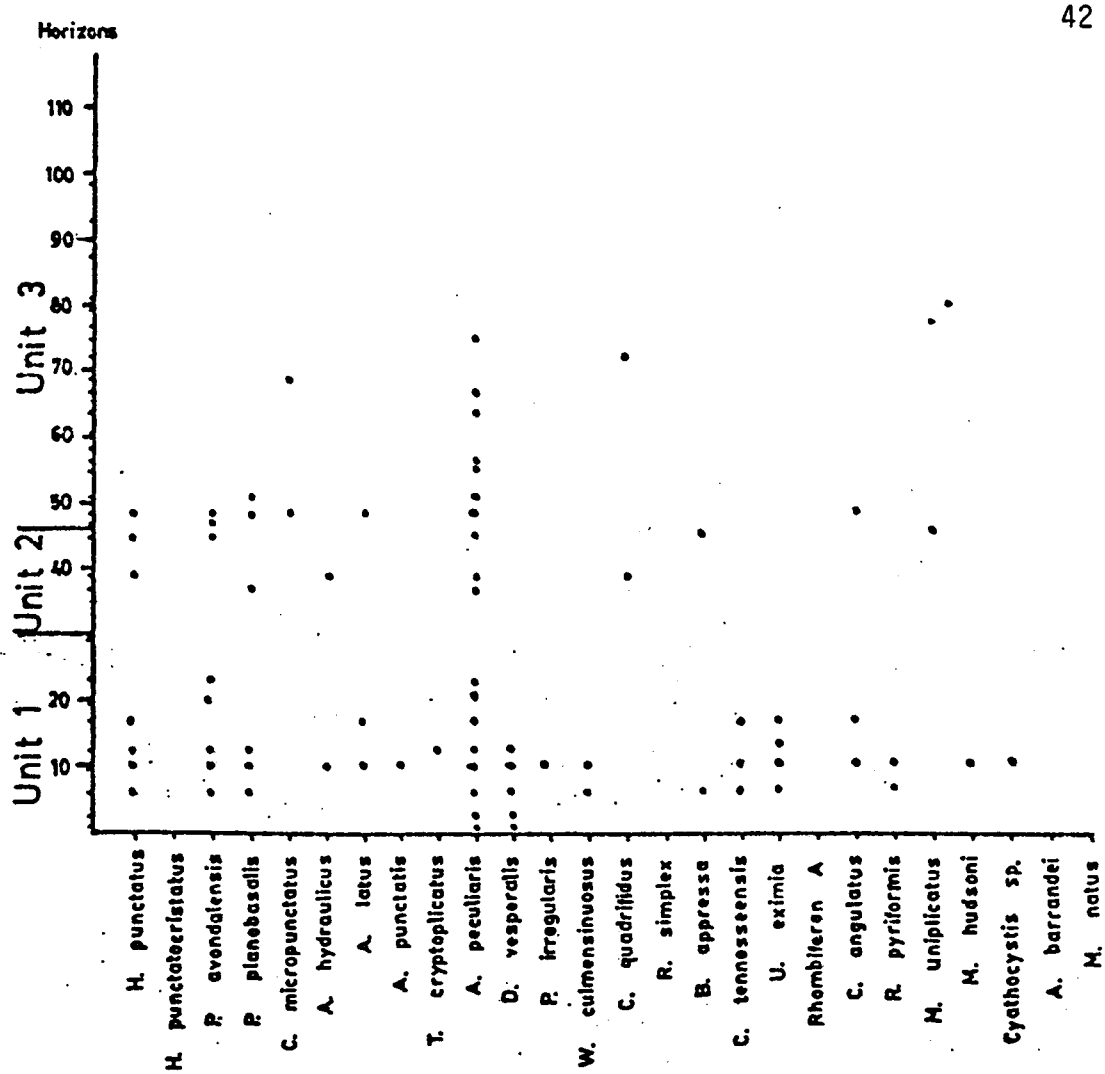


Figure 10. Distribution of echinoderm species at Evans Ferry.

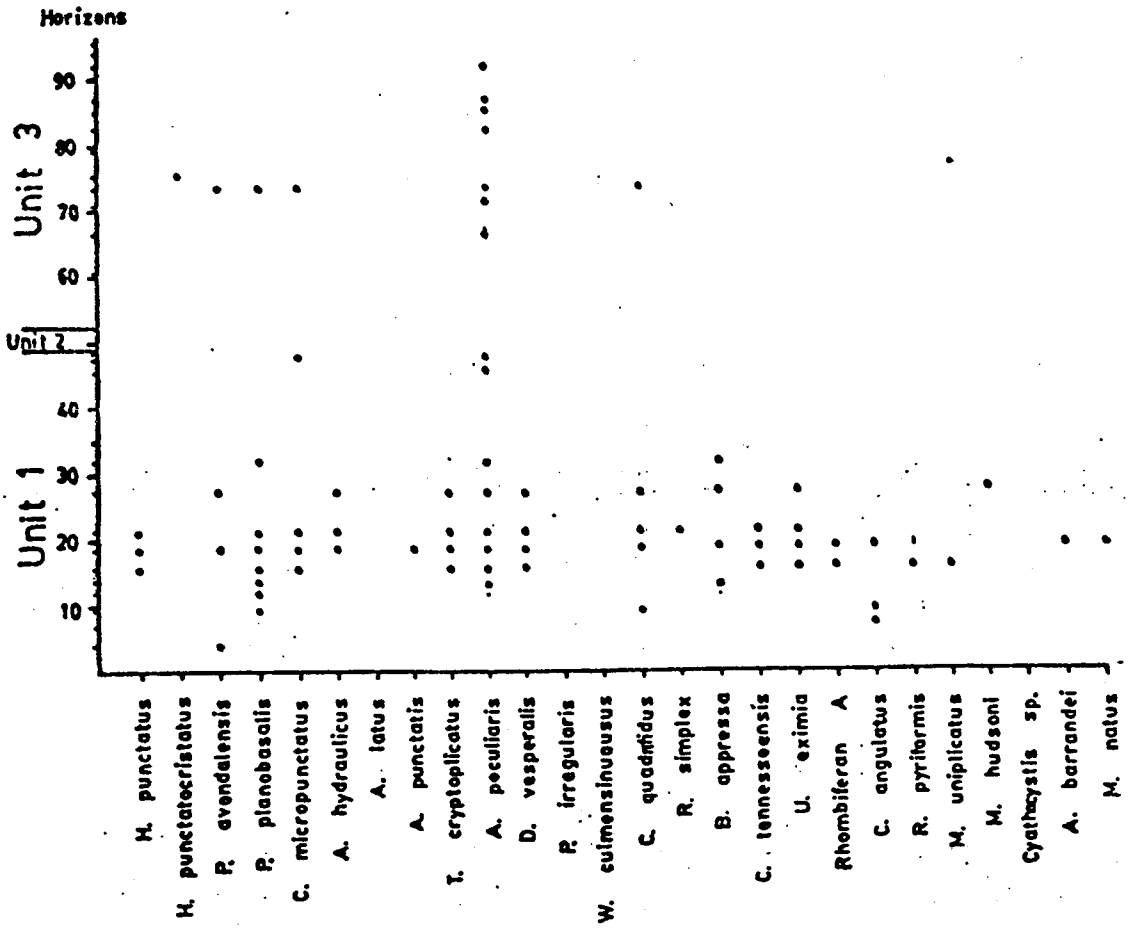


Figure 11. Distribution of echinoderm species at Stanley Farm.

the sediments. However, another type of instability may be preserved and that is the influx of terrigenous mud which can smother communities which would otherwise thrive in the conditions of temperature and salinity.

Competition, if it occurred, among species which are known only from fossils is even more difficult to determine because active competition cannot be directly observed. Furthermore, the hard parts of some species can be transported into environments that they did not inhabit. Meyer and Ausich (1983) state that competition among echinoderms probably only occurred during the early stages of community diversification and ceased once the community had stabilized. Whatever was the case in the Middle Ordovician, the feeding habits and mode of life of the echinoderms of the Benbolt must be inferred from the observation of adaptive morphology and extrapolation from the modern marine community.

Apparently the most stable environment in the Benbolt was that of Unit 1 which remained for the most part quiet and micritic with only slight current disruption and introduction of terrigenous mud throughout its development as shown by the high micrite content of the limestone within it, lack of abrasion of the fossil grains, and the absence of oncolites in the lower portions of the unit. The currents which would produce a rock of this type would not have been strong enough to uproot stalked crinoids, nor was the environment disturbed by frequent massive influxes of terrigenous clastic or by subaerial exposure. The limestone of Unit 1 is rarely interbedded with large

amounts of shale and lacks mudcracks. Unit 1 at Stanley Farm appears to have been slightly quieter than at Evans Ferry as shown by the higher percentages of micrite in the Stanley Farm thin sections, but both environments had enough water movement to support a large and diverse sessile population.

Stanley Farm appears to have had a slightly more stable environment than Evans Ferry over a period of time as the diversity shows. In the Evans Ferry section a diversity of 10 species or more was maintained for only 6 meters within the same general interval as the high diversity portion of Stanley Farm with a maximum of 17 species in a single horizon (figure 12). Unit 1 at Stanley Farm on the other hand includes horizons containing 10 or more echinoderm species for a thickness of 15 meters with a maximum of 19 species in a single horizon (figure 13). Fluctuations of matrix percentages at Stanley Farm are less frequent than they are at Evans Ferry which could imply a more stable environment. However, the differences between Unit 1 and the units which succeed it at both localities are more pronounced than the differences between Unit 1 at Stanley Farm and Evans Ferry. Above Unit 1, the diversity never rises above 7 species in a horizon. In Unit 2 at both localities, the diversity is difficult to determine because the massive nature of the biosparite hampers collection and identification of echinoderms. Also the higher current energy of the environment as shown by the large grain size of the rock and the cross-bedding found in one part of Evans Ferry, appears to have caused echinoderm debris to collect in dispreportionate amounts compared with

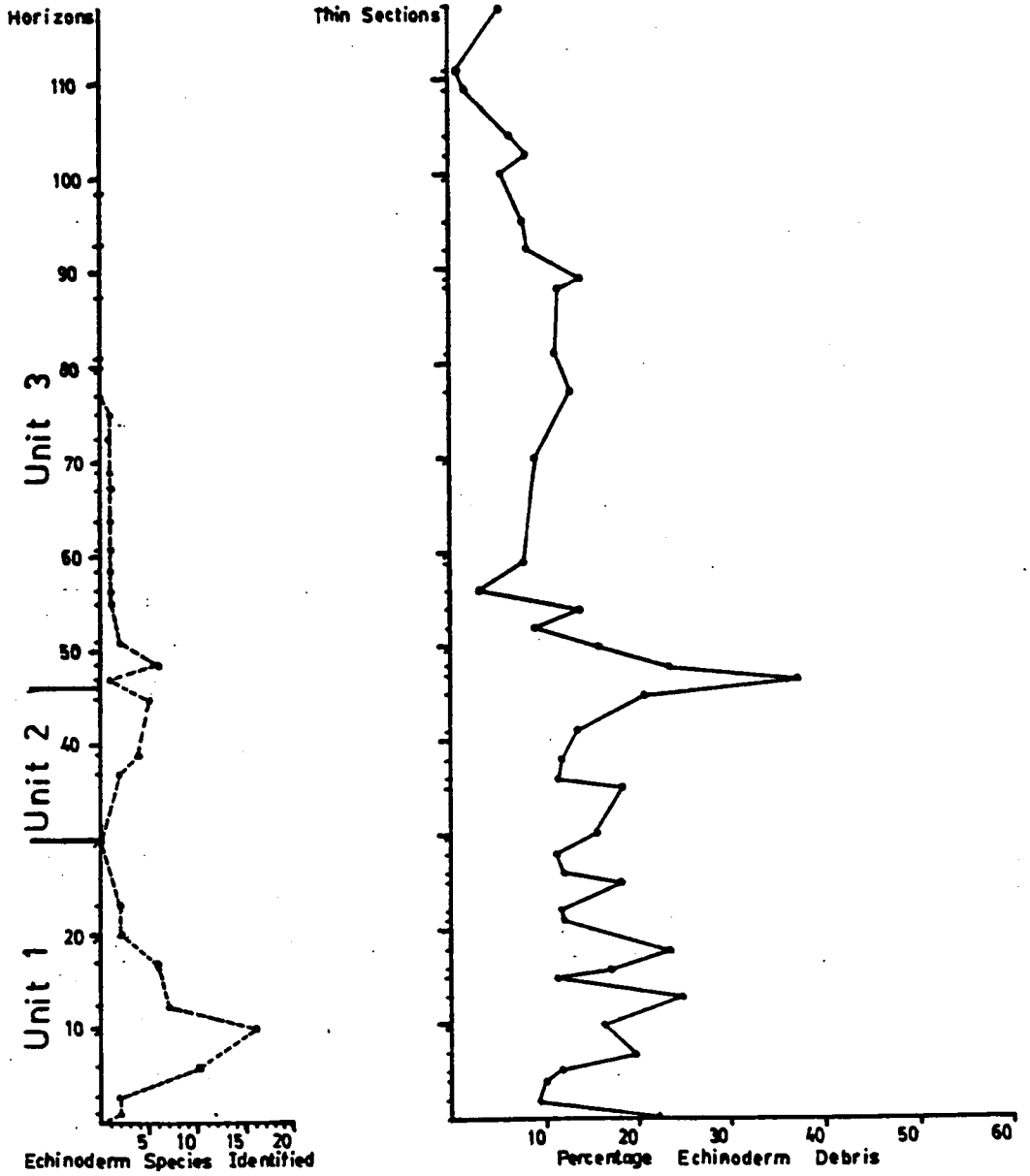


Figure 12. Plots of echinoderm diversity of taxinomically identified forms and percentage of echinoderm debris for Evans Ferry.

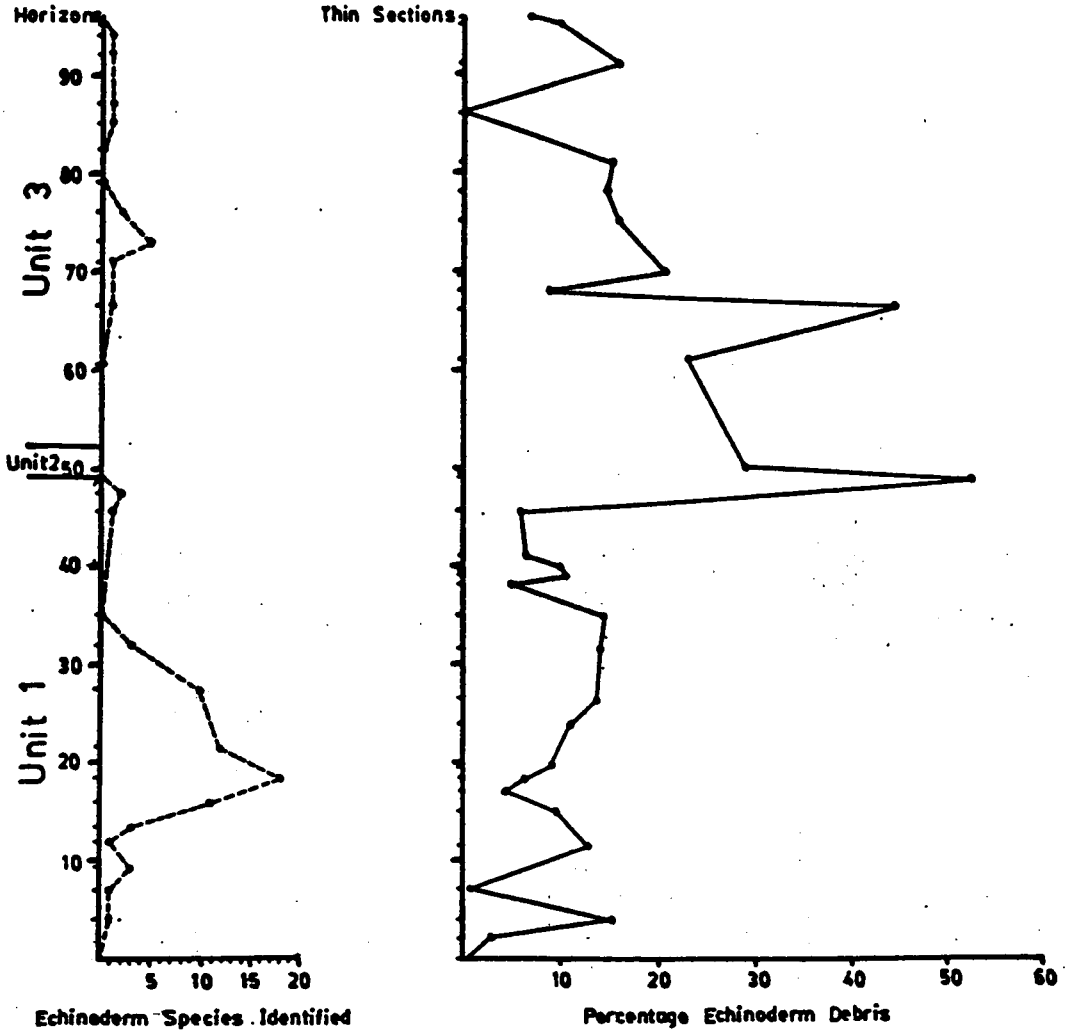


Figure 13. Plots of echinoderm diversity of taxinomically identified forms and percentage of echinoderm debris for Stanley Farm.

smaller grains that were carried away by the currents. However, where collecting was possible, Unit 2 showed moderate diversity. Most notable are horizons 11 and 12 at Evans Ferry where diversity rose to 4 and 5 species, respectively (figure 12). In contrast, Unit 2 at Stanley farm showed no identifiable species at all, but there the unit is extremely thin and entirely massive. At Evans Ferry, some of Unit 2 had weathered enough to allow for the collection of identifiable samples, but even there, as noted above, the diversity was lower than in the middle of Unit 1.

The deposition of Unit 3 was primarily in an unstable environment. At Stanley Farm, large periodic influxes of fine-grained terrigenous clastic material apparently made colonization impossible for most species. This part of the Benbolt was dominated by Archeocrinus peculiaris, Paleocrinus avondalensis and Carabocrinus micropunctatus which seem to have been more able to tolerate conditions influenced by influxes of terrigenous mud than most other Benbolt echinoderm species. Odum (1971) states that high diversity can occur in unstable environments if the adverse conditions occur at regular intervals, thus allowing the animals to adapt. This is known as pulse stability. Although this could have been the case for Unit 1, Unit 3 was either influenced by mud influx at irregular intervals or so often that most echinoderms could not survive and larvae could not settle.

In previous studies of echinoderm paleoecology, Titus (1973;1975) found that the greatest diversity was in areas of low energy and high stability. Low diversity was typical of areas which had extremely

high energy mud content. Bretsky and Lorenz (1969, p. 531) state that stability was the direct cause of higher diversity.

Sprinkle (1982) reached similar conclusions to those of Titus when he studied the echinoderms of the Middle Ordovician Bromide Formation. His more diverse zone was the "Lower Ecinoderm Zone" which contained 35 species representing 32 genera. This zone is composed of a shaley limestone containing lenses of calcarenitic limestone made up primarily of echinoderm and bryozoan fragments. The zone itself is only 1 meter thick and is contained within a thicker unit of shaley biomicrite indicative of a shallow quiet water environment for most of its depositional history. In contrast, the "Upper Echinoderm Zone" was more current active and less stable. It consists of several beds of alternating biosparite and shale. This zone contains the fossils of 25 species representing 21 echinoderm genera. The "Carabocrinus Beds" of the Bromide resemble Unit 3 of the Benbolt as they are thinly bedded bimicrite interbedded with grey shale. Only 9 species of 9 genera were found in that unit, making it comparable to Unit 3 of the Benbolt in diversity as well.

In apparent contradiction, Brower and Veinus (1978) dispute the conclusions of Titus (1973;1975), Sprinkle (1982) and Bretsky and Lorenz (1969) by stating that they found high diversity in unstable, high energy conditions, while areas of quiet water displayed the lowest diversity. In the Twin Cities area, the most active environment with high diversity, according to Brower and Veinus is represented by the Decorah Shale, a unit of interbedded biosparite and

biomicrite, while a quiet water environment is represented by the Lower Hidden Falls of the Platteville Limestone which they describe as a soft, yellow to buff, fine-grained, dolomitic limestone. While the Decorah Shale is similar to units found in the Benbolt and Bromide, the Lower Hidden Falls Member is distinctly different and thus could imply different conditions of formation and perhaps, therefore, should not be used in such comparisons. Also, the higher diversity Decorah Shale portion of the Twin Cities section, with 9 species in 6 genera has considerably lower diversity than the high diversity portions of the Benbolt and the Bromide. The low diversity Hidden Falls Member contained only 2 species of as many genera.

There is a definite similarity between the highest diversity zones at Stanley Farm and Evans Ferry. Both occur in areas of high micrite and low spar content (figures 14 and 15). Fossil debris is low in percentage which implies that conditions might have been too quiet to support large numbers of individuals, but were stable enough to allow for fine partitioning of the available resources among the members of the fauna. The fact that Stanley Farm section shows very similar diversity trends to those at Evans Ferry demonstrates that stability was a greater factor than environmental complexity, which is sometimes the cause of high diversity in the modern environment (Pianka, 1965).

The diversity and how it is related to lithology from the Benbolt largely coincides with the patterns seen in the Bromide. The conditions most conducive to high diversity of echinoderm genera are a quiet environment with enough current activity to circulate the water

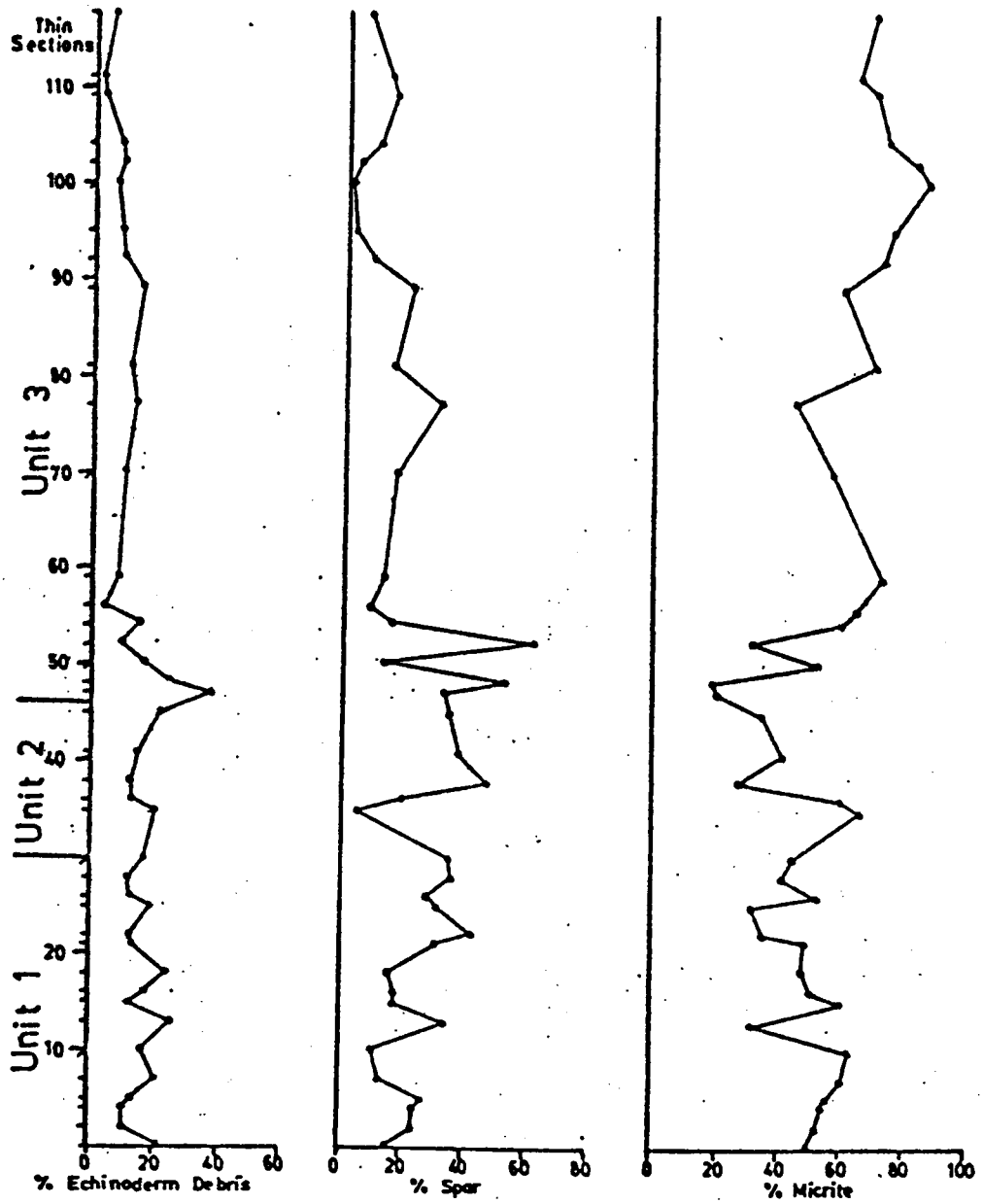


Figure 14. Plots of percentages of echinoderm debris, spar and micrite for Evans Ferry.

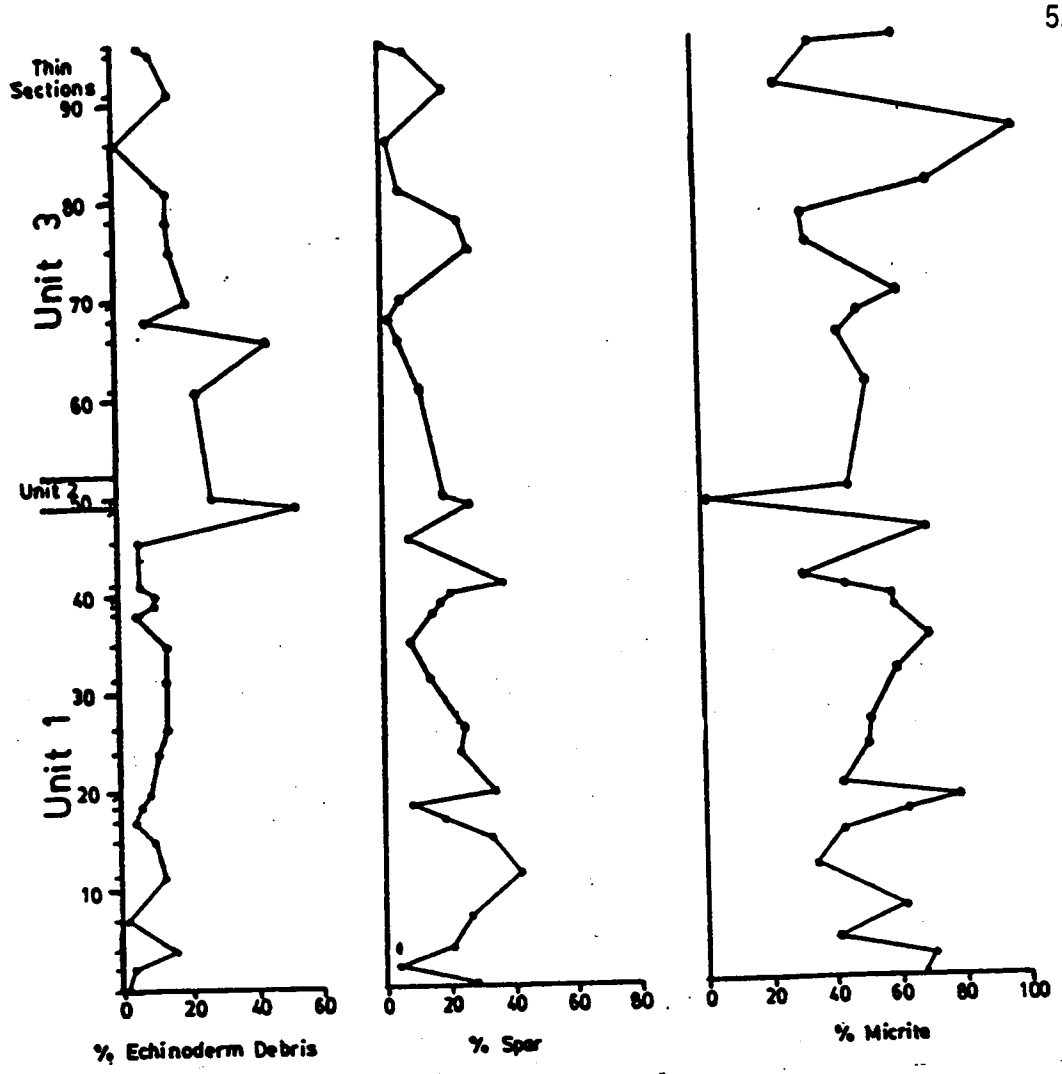


Figure 15. Plots of percentages of echinoderm debris, spar and micrite for Stanley Farm.

and thereby supply food and oxygen, and only minor influx of terrigenous clastics. The type of environment which produces a moderate species diversity among echinoderms is one with slightly stronger currents which provide good water circulation, abundant substrate and a low rate of sedimentation. Lowest in diversity are those environments which were commonly extremely quiet and muddy, conditions in which a high rate of terrigenous sedimentation would smother most species as adults or prevent larval survival, or in which shallow nearshore conditions with fluctuating salinity extremes were unfavorable to organisms requiring normal salinity.

Niche Differentiation

Ausich (1980) has concluded that niche differentiation among sessile echinoderms can occur along three basic lines. The first of these is the height above the substrate, and the second is selection for food particle size. Other factors include time of feeding, the presence of non-particulate nutrients and the type of substrate. Ausich and Bottjer (1982, p. 173) believe that there were three main feeding levels or tiers of feeding among sessile echinoderms during the Middle Ordovician. These were (1) below 5 cm above the substrate, (2) between 5 and 10 cm, and (3) from 10 to 50 cm above the sea floor. In this study, these will be referred to, respectively, as the lower, middle and upper feeding tiers. As few stems were found still attached to calyces at the two localities studied for this paper, the echinoderm fauna of the Benbolt has been assigned to these feeding

tiers based on evidence from other papers on the same or related species as those collected for this study, e.g., Sprinkle (1982), Brower and Veinus (1974), Parsley and Mintz (1975) and others.

Secondary niche differentiation was by selection of food particles by size. There is evidence that certain sessile echinoderm species may feed on non-particulate organic nutrients in the modern environment. However, Meyer, 1979 used modern crinoids to estimate the maximum food-particle size selected by a study of the width of the ambulacral grooves and his data did show examples of niche partitioning. This method is not entirely suitable in the case of Benbolt echinoderms because feeding appendages are rarely observed attached to calyces. The average calyx size cannot be used, either, because this is often unrelated to the width of the ambulacral grooves in the case of unrelated species. Ausich (1980) noted that the food grooves of diplobathrid camerates were the narrowest of the crinoids that he studied while those of the disparid inadunates were the widest. This information was used in conjunction with measurements of the ambulacral grooves of congeneric species from other areas to further divide the echinoderms of the Benbolt into three generalized feeding catagories based on selection of particle sizes. These are referred to as (1) small--crinoids with pinnulate arms and other small-armed crinoids, (2) medium--echinoderms with branching arms with a food groove width between 1.0 and 2.0 mm wide proximally or those with unbranching arms with the food groove more than 0.8 mm wide, and (3) large--echinoderms with branching arms with food grooves more than

2.0 mm in width. Such general groupings were chosen because of the inavailability of more precise data and to allow for differences among individuals of the same species. Perhaps these data are not true examples of niche differentiation as some of the species from the Benbolt may have fed on non-particulate nutrients, but this is difficult to determine from fossil specimens. Determining further partitioning by feeding times is plainly impossible for Middle Ordovician species, but the methods available to allow for recognition of approximate feeding niches and the suggestion of possibilities for competition appear in figure 16.

3. AUTECOLOGY

Introduction

Of the twenty-six species of echinoderms collected for this study, five are known only from single specimens while five others were represented by fewer than five specimens. These were probably not important members of the community and had little effect upon other echinoderm species. Therefore, these have only been discussed in the following section if they are unusual enough to merit special attention or if they have been compared with other species. In the following section, the common and some of the unusual members of the echinoderm community have been discussed individually. Information collected for this study and provided by previous papers was used to postulate the life position, feeding tier, particle size selection category, preferred environment and other aspects of the interaction

	Small (W < 1.0mm)	Medium (W < 1.0-2.0mm)	Large (W < 2.0mm)
Upper (10-50cm)	Archeocrinus peculiaris Diabolocrinus vesperalis (Paradiabolocrinus irregularis) (Wilsonicrinus culmensinuousus) (Rhaphanocrinus simplex)	Colpodecrinus quadrifidus	Carabocrinus micropunctatus
Middle (5-10cm)	Acolocrinus hydraulicus Rhombiferan A (Macurdablastus uniplicatus) (Apodasmocrinus punctatus)	Ulrichocystis eximia Paleocrinus planobasalis Meristoschisma hudsoni	Paleocrinus avondalensis (Hybocrinus punctatocristatus)
Lower (0-5cm)	Triboloporus cryptoplicatus (Cyathocystis sp.) (Anatiferocystis barrandei) (Myeinocystites natus)	Canadocystis tennesseensis Hybocrinus punctatus Batherocystis appressa Coronocystis angulatus	Regulaecystis pyriformis (Annulocrinus latus)

Figure 16. Division of Benbolt echinoderms into niches based upon height above the substrate and width of the food grooves measured proximally (W); species represented by fewer than 5 specimens in parentheses.

between individuals of a single species and the environment. When a single species has been said to dominate in a particular horizon, it appears to represent a larger percentage of the echinoderm biovolume in that horizon than most other species.

Crinoids

There has been some dispute over the life position of Hybocrinus punctatus. Strimple (1975) believes that Hybocrinus inhabited the sea bottom, half buried in the sediment, using its short tapering stem as an anchor. However, Brett and Liddell (1978) disagree, suggesting that hybocrinids attached themselves to bryozoans and brachiopods and raised themselves to a higher feeding level. Later, Sprinkle (1982, p. 119) agreed with Brett and Liddell for specimens which he studied from the Bromide Formation. But neither Brett and Liddell nor Sprinkle studied Hybocrinus punctatus, the principal Benbolt hybocrinid and thus their data may not apply to that particular species. This author is more inclined to agree with Strimple's initial theory in the case of H. punctatus because of the extreme asymmetry of the calyx of this particular species. The hybocrinids studied by Brett and Liddell, and Sprinkle (in the Bromide) are generally less asymmetrical and thus probably had a different lift position than did H. punctatus. In H. punctatus the shape of the calyx is such that it would appear to be more efficient for the animal to have rested on sediment, allowing for the ambulacral area to be oriented "up" rather than having that area directed to one side of the calyx and therefore subject to more force from water currents than would a crinoid with a

more symmetrical calyx. Another difference between H. punctatus and the hybocrinid studied by Brett and Liddell is that the adult H. punctatus generally appears in horizons which had a soft substrate whereas Brett and Liddell's hybocrinids colonized the hard ground surfaces of more current-active environments in which it would have been difficult for hybocrinids to become partially buried.

Another possible indication of the life position of H. punctatus is that whole calices are commonly preserved unlike most other echinoderms in the Benbolt. Sprinkle (1982, p. 119) suggests that hybocrinids generally remained articulated after death because they had few plates which were well attached to each other, yet the same could be said of Acolocrinus which is only rarely found articulated in the Benbolt. Perhaps this attribute could have been aided by a life position which allowed H. punctatus to be buried quickly after death. Johnson (1977) and Rudwick (1970, p. 91-94) state that brachiopods which had a semi-infaunal mode of life in fine-grained sediments are often warped or distorted during the process of fossilization. Similarly, many specimens of H. punctatus collected from the Benbolt show signs of having been distorted after death which also suggests a semi-infaunal life position.

Sprinkle (1982) studied two hybocrinid species from the Bromide--H. nitidus which was very common in the quieter portions of the Bromide and was somewhat asymmetrical, and H. crinerensis, which was less asymmetrical and is more common in the current-active "Upper Echinoderm Zone". Larvae of H. punctatus in the Benbolt appear to

have favored a soft substrate in which they could have anchored themselves, but one that did not contain too much terrigenous mud so that they would not sink or be covered over. It generally occurs in horizons of moderate to high diversity where it is one of the more common species, especially at Stanley Farm. It could probably tolerate some variation in the energy of the environment so long as the water currents carried sufficient oxygen and nutriments and the environment was not frequently indundated by terrigenous mud.

The same evidence noted above suggests that H. punctatus fed in the lower feeding tier. The arms were unbranched, and in the slightly larger H. nitidus, these arms ranged from 2.7 mm deep and 2.2 mm wide at the base to 0.8 mm deep and wide at the apex. The feeding grooves in those arms were wide and deep (Sprinkle, 1982 , p. 125). If the arms of H. punctatus were similar, it probably fed in the medium size-selection category.

Hybocrinus punctatocristatus was more likely than H. punctatus to have been raised above the substrate during life. It is more symmetrically conical than H. punctatus such that it probably fed effectively at the end of an upright stem. This allowed it to live in the extremely muddy conditions which characterize the uppermost portions of the Benbolt, the area in which the only specimen of this species was found for this study. H. punctatus, which lived partly buried in the sediment, would have been quickly buried by any influx of fine-grained terrigenous clastics, H. punctatocristatus, raised above the level of burial by its stem, would therefore have been able to survive

in some areas where H. punctatus could not. However, it does not seem to have been an important member of the Benbolt community because only one speciment was collected for this study and individual plates are distinctive enough to be recognisable. Similarly, Brower and Veinus (1974) also only found one example. Because of the upright orientation of the stem, H. punctatocristatus probably occupied the middle to high feeding tier and its proportionally wider food grooves placed it in the large particle selection category.

Paleocrinus avondalensis was not a common member of the Benbolt community in any one horizon, but it was wide spread, occurring in areas of both high and low diversity. This implies that the animal could tolerate conditions which would have been inhospitable to most other echinoderms, but did not have qualities which would have allowed it to be the most common species in any one horizon, such as a rapid growth rate or a low rate of larval mortality. These are the characteristics of a species that was not highly specialized and tended to move into newly habitable regions more quickly than more specialized species. Sprinkle (1982) reports that Paleocrinus hudsoni from the Bromide bore a short tapering stem only slightly longer than the calyx as did Paleocrinus angulatus from the Twin Cities area (Brower and Veinus, 1978). Therefore, it seems likely that other members of the genus Paleocrinus would have similar stems. This places Paleocrinus avondalensis in the middle feeding tier. Although the arms are unknown for this species of Paleocrinus, the arms of Paleocrinus hudsoni which had a calyx no more than 20.5 mm long were

branched and had a food groove 1.6 mm wide. As some plates of Paleocrinus avondalensis measured 18 mm in diameter, this implies that P. avondalensis was somewhat larger than P. hudsoni and thus could have placed it in the medium to large size category.

Paleocrinus planobasalis as a generally smaller crinoid than P. avondalensis, but it was much more common, especially in areas of high diversity. Like other representatives of the same genus, it most likely had a short tapering stem which supported the calyx a short distance from the substrate.

Crinoids of the genus Paleocrinus had a low ratio of cup surface to volume, and Sprinkle, (1982,p. 145) suggests that they might have had respiratory difficulties in regions of low oxygen content. This could have been compensated by the crenulations on calyx plates which Brower and Veinus (1974) consider probable respiratory structures. P. planobasalis seems to have been more specialized than P. avondalensis as indicated by the greater number of P. planobasalis specimens recovered from horizons of high diversity. But P. planobasalis does not seem to have been as tolerant of conditions of high terrigenous mud influx as P. avondalensis. Like P. avondalensis, P. planobasalis probably occupied the middle feeding tier. The arms of the two species were probably similar in structure, but P. planobasalis was generally smaller, so it likely fed in the medium particle-size category.

In many ways, Carabocrinus micropunctatus was similar to Paleocrinus avondalensis. It was also a large, flat-plated inadunate

which seems to have been tolerant of a wide variety of environments and which was never represented by a large number of specimens from a horizon of high diversity. C. micropunctatus seems to have been particularly adapted to existence in an environment where the influx of fine-grained terrigenous clastics was a major limiting factor. One specimen of C. tredwelli which occurs in the Bromide (Sprinkle, 1982, p. 153) had a stem 74mm long which could have kept the calyx well clear of the thickest mud. This species dominated the "Carabocrinus Beds" of the Bromide which are characterized by biomicrite interbedded with grey shale, indicating an environment somewhat like parts of the Benbolt in which the influx of terrigenous clastics made survival difficult for most species. Brower and Veinus (1978, p. 383) state that carabocrinids solved the problem of an incohesive substrate by cementing the root to an area that was large in comparison to the size of the calyx. This characteristic would have been an advantage in some of the unstable muddy portions of the Benbolt. However, Brower and Veinus described C. dicyclicus from the Twin Cities section as having a very short stem which they state (p. 373) places it in the lower level feeding niche.

In the Benbolt, a crinoid with a short stem would have been engulfed by sediment in some of the horizons of Unit 3 where C. micropunctatus has been collected. Thus, it may have had a longer stem, being more comperable to C. tredwelli than to C. dicyclicus. In this study, specimens of C. micropunctatus were collected from areas that are believed to have had a muddy bottom and variable diversity. A

number of C. micropunctatus plates were found on the shaley undersides of thin slabs of limestone collected from horizons in Unit 3 of the Stanley Farm section. These suggest the recolonization of the substrate by pioneer species after the original community had been destroyed by a rapid influx of terrigenous mud. When the C. micropunctatus died, their broad flat plates formed a patchy pavement and may have made it suitable for colonization by other species, much in the same way that strophomenid brachipods did at other localities in the Middle Ordovician (see Walker and Alberstadt, 1975). The long stem postulated for C. micropunctatus placed it within the middle to upper feeding tier. The arms of Carabocrinus tredwelli, a species from the Bromide, were branching and measured approximately 4.2 mm wide and 6.1 mm deep proximally with a food groove 4.0 deep and about the same wide. This places it in the large food selection category and implies the same for C. micropunctatus.

Acolocrinus hydraulicus, like several other crinoids from the Benbolt, has specialized respiratory structures (Sprinkle, 1982, p. 111). In the Bromide, representatives of this species were found in beds of biomicrite interlayered with shale, an environment dominated by Carabocrinus and most likely very unstable. However, in the Benbolt, A. hydraulicus is only found in areas of moderate to high diversity with conditions stable enough for a large variety of other species. Carabocrinus seems to have been much better adapted to conditions of high terrigenous-clastic influx than Acolocrinus whose special respiratory structures alone don't seem to have given it much added

advantage over other species in the Benbolt. The stem of A. hydraulicus was probably short, but long enough to have elevated the calyx into the middle feeding tier. Sprinkle reports that a similar species from the Bromide had a large number of small armlets about 2.5 mm long. In these, the food grooves were small and slightly raised, thus placing A. hydraulicus in the small particle selection category.

Apodasmocrinus punctatus was an inadunate crinoid with a small calyx compared to the length of the arms and stem. Specimens were found in the high diversity horizons at Evans Ferry and Stanley Farm but they were not common. From its occurrance, A. punctatus appears to have been a specialized species. A. daubei, a closely related species which occurs in the Bromide (Sprinkle, 1982), only occurs in the highest diversity part of that formation and makes up only a small portion of the echinoderm fauna. This crinoid had a stem many times the length of the cup, placing it in the middle feeding tier. The calyx then supported ten pinnulate arms which were thin enough for it to feed on small food particles.

Triboloporus cryptoplicatus was a small crinoid with a short tapering stem which placed it in the lower feeding tier. It was one of the more common species in the high diversity horizons at Stanley Farm, but it was much less common at Evans Ferry, perhaps because of the slightly higher current energy. An environment with strong currents would probably have carried T. crytoplicatus away or made it difficult for the animal to feed, while one which was frequently buried in terrigenous mud would engulf an animal which fed so close to

the substrate. This would explain the absence of this crinoid in all but the most quiet and stable of the environments present in the Benbolt. Kesling and Paul (1968) believe that pores in the lower portions of the Triboloporus calyx represent a specialized respiratory structure which would give it an advantage in areas of low oxygen content; however, there is little indication of any shortage of oxygen in the horizons where T. cryptoplicatus occurs, making it unlikely that its distribution was limited by competition with other echinoderms which did not have specialized respiratory structures. Porocrinus bromidensis, from the Bromide, a species related to T. cryptoplicatus (Sprinkle, 1982), had a slightly larger calyx and food grooves which were 0.5 mm wide proximally. If Triboloporus had similar arms, it would have selected some of the smaller food particles.

Archeocrinus peculiaris was a large camerate crinoid with a long stem. Along with Diabolocrinus and Carabocrinus, it probably occupied the highest feeding tier in the Benbolt community. As this was the tier least affected by influxes of terrigenous clastics, which appear to have been the major cause of instability in the Benbolt environment, the adult A. peculiaris was apparently well able to tolerate a wide range of conditions. Thus, it is the most widespread species at both localities. It was never a common species at any one horizon, but it was one of the first to appear and the last to disappear stratigraphically through the Benbolt. Representatives of the genus Archeocrinus show similar characteristics in the Bromide (Sprinkle, 1982) where they occur in all but the "Carabocrinus Beds" where they

might have been outcompeted for living space although not for food because of a difference in the organization of feeding apparatus. Throughout the Bromide, as in the Benbolt, Archeocrinus was never dominant in any single community. Brower (1974) states that camerate crinoids grew very quickly in the early stages of development and slowed as they became larger. This would have been an advantage in an unstable environment as it would raise the calyx well above the substrate fast enough to avoid periodic disturbances such as influxes of terrigenous clastic material. Like most camerates, A. peculiaris had pinnulate arms with narrow food grooves which placed it in the small category of food size selection. Thus, while it occupied the same tier as Carabocrinus, it may not have been in direct competition for food.

Diabolocrinus vesperalis was another camerate crinoid which shared the highest feeding tier with Archeocrinus. It was not as common as A. peculiaris at the two localities discussed here, although Brower and Veinus (1974) state that it is the most common crinoids in the Benbolt over-all. At both Stanley Farm and Evans Ferry, D. vesperalis plates were usually found in horizons of high diversity or other environments where conditions appear to have been relatively stable. In the Bromide (Sprinkle, 1982) representatives of the genus Diabolocrinus were collected from all fossil beds, indicating that this crinoid was extremely adaptable. Like A. peculiaris, it was probably aided by a long stem which raised it above the level of most influxes of terrigenous clastics. The fact that the calyx of

Diabolocrinus was approximately the same size as that of Archeocrinus and that the two genera had very similar arm types suggests that both occupied the same food-size selection category, and also the same tier. This leads to the further suggestion that A. peculiaris and D. vesperalis may have competed with each other. However, because Diabolocrinus was more common in areas of higher stability than Archeocrinus, it is possible that D. vesperalis was a more specialized species that A. peculiaris and thus it tended to be more successful in areas of high diversity. This helps explain its dominance over Archeocrinus reported in most studies based on data taken primarily from zones of high diversity.

Colpodecrinus quadrifidus is an unusual camerate crinoid which occurs in both localities of the Benbolt and in the "Upper Echinoderm Zone" of the Bromide as well. Like other camerates, it possessed a long stem which placed it in the higher feeding tier, but unlike other camerates, its arms were branched rather than pinnulate (Sprinkle, 1982, p. 206). The secundibrachs of this species were wide enough to place the species in the middle food selection category, thus keeping it out of competition with either Archeocrinus or Carabocrinus. C. quadrifidus occurs at two horizons at Evans Ferry and five horizons at Stanely Farm, and it is never one of the more common species. The horizons where it does occur are either ones of high diversity or those with a high spar content. The "Upper Echinoderm Zone" where C. quadrifidus was found in the Bromide is also spar-rich which indicates that Colpodecrinus was best adapted to an environment of active sedi-

ment winnowing. Sprinkle (1982) considers the rhombs located on the edges of the plates to have been respiratory structures. Probably these worked best when water currents were strong, which explains the presence of C. quadrifidus in current-active environments.

Other camerates which occur at Stanley Farm and Evans Ferry are Paradiabolocrinus irregularis, Wilsonicrinus culmensinuousus and Rhaphanocrinus simplex. However, these are only represented by two or three specimens apiece and therefore do not appear to have been important members of the Benbolt community. Like Archeocrinus and Diabolocrinus, the three listed above probably also fed in the upper tier on small-sized food particles, but dwelled exclusively in high diversity communities (figure 16, page 56).

An inadunate crinoid which occurs at Evans Ferry alone is Annulocrinus latus, another species only represented by a small number of plates. It fed in the lower tier and in the large particle selection category. This species also does not seem to have been important in the Benbolt community.

Blastozoans

The life modes of blastozoan echinoderms seem to have been considerably more varied than those of crinoids. Many blastozoans were suspension feeders which could have entered into competition with some species of crinoids, but others appear to have been mobile and could have been either suspension or detritus feeders and thus responded differently to environmental changes than did crinoids. Bassler (1950) identified Batherocystis appressa as an eocrinoid, but

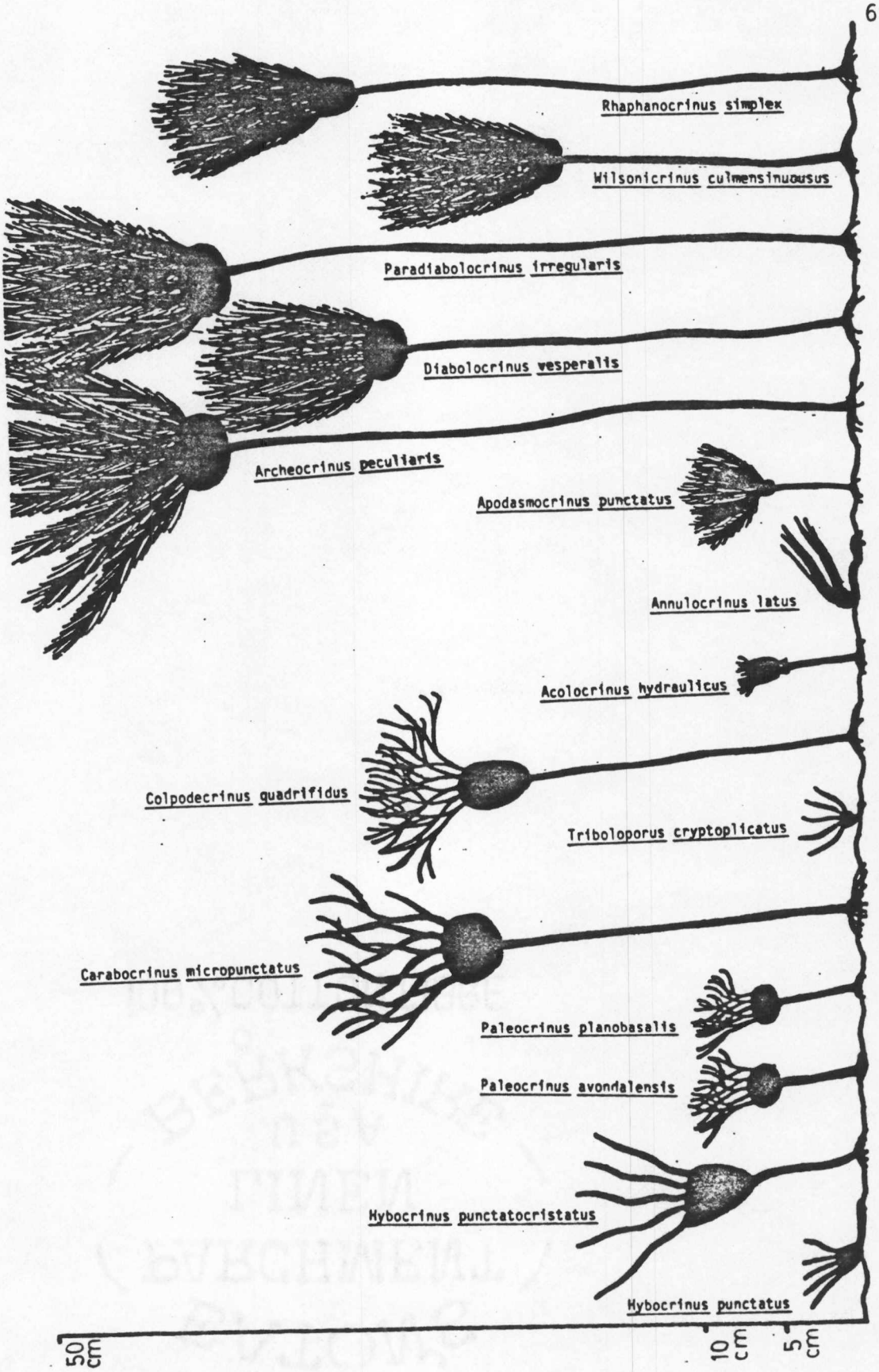


Figure 17. Crinoids of the Benbolt Formation.

Broadhead (1981) included it in the paracrinoids. The stem of this animal consisted of two small bead-like ossicles which confined it to the lowest feeding level; the paddle-shaped theca may have lain on the substrate. Specimens of B. appressa were mainly collected from horizons of moderate to high diversity which demonstrates a preference for stable environments and an inability to survive in unstable ones. This animal could easily have been buried by an influx of terrigenous mud or uprooted by strong currents because it apparently was not very firmly attached to the sediment. Therefore, it would have been compelled to live in a quiet, stable environment in which it could lie prone or sink its short stem into a soft substrate. The arms of Batherocystis, like those of the related genus Rhipidocystis (see Moore, 1967), were long and unbranched with massive ossicles. The food grooves were narrow to medium width.

Like Hybocrinus punctatus, the life position of Canadocystis tennesseensis, another paracrinoid, has been disputed in the literature. Frest, Strimple and Coney (1979) believe that Canadocystis lived semi-infaunally, using its short tapering stem as an anchor in the substrate. However, Parsley and Mintz (1975) believe that Canadocystis raised itself above the sediment on a short stem with the calyx tilted to make the arms vertical. Sprinkle (1982, p. 219) suggests that the paracrinoid genera Oklahomacystis and Platycystities from the Bromide lived with the theca off the bottom with the left side facing currents. However, Oklahomacystis had a more symmetrical theca than Canadocystis, and Platycystities is more lenticular and

symmetrical, which would make it more likely to have stood above the substrate supported by a stem than the highly asymmetrical Canadocystis. Such a lopsided animal would have had to expend prohibitive amounts of energy to maintain its feeding posture, especially where water currents were moderately strong. As a juvenile, this animal had a more symmetrically rounded theca which became markedly asymmetrical when the paracrinoid was between 8 and 12 mm in height (Parsley and Mintz, 1975, p. 77). It probably began life after metamorphosis perched above the substrate and later became semi-infaunal as an adult when the thecal size and convexity rapidly increased with respect to stem size. This would be a good adaptation to a micritic environment such as that which characterizes the major echinoderm beds of the Benbolt. Young animals would have been prevented by the stem from burial, but older individuals would have been large enough to avoid a similar fate so long as sediment accumulation was not rapid, and also could have used the stem as an anchor to keep from being carried away by strong currents. Also, like H. punctatus, C. tennesseensis is commonly preserved as whole thecae, again supporting an interpretation of a semi-infaunal life mode. However, unlike H. punctatus, C. tennesseensis thecae recovered from the Benbolt are rarely distorted; this could have been due to the fact that C. tennesseensis was more coherently constructed without the open ambulacral area which was commonly the site of deporation and disarticulation in H. punctatus, C. tennesseensis occurs in horizons of high diversity at both localities in which it made up a high percen-

tage of the echinoderm biovolume. The food grooves of the adult Canadocystis had a width of slightly greater than 1.0 mm which places it in the middle size selection category. As this animal fed in the lower tier, it might have competed with H. punctatus.

Although it was originally thought to be a rhombiferan cystoid (Bassler, 1950), Ulrichocystis eximia has now been placed among the eocrinoids (Broadhead, 1982). Its plate are commonly found in the high diversity horizons of both Benbolt localities, thus indicating that it was possibly a good compeditor. It was not able to tolerate unstable conditions, perhaps due to respiratory or feeding constraints; unlike some of the smaller species from the Benbolt, it was unlikely to have been buried by an influx of sediments. Bromidocystis is a genus related to Ulrichocystis occurring in the Bromide. Like Ulrichocystis it had a club-shaped theca, but it is common in the low diversity portions of the Bromide. Thus Sprinkle (1982, p. 289) suggests that it may have been an r-selection opportunist. However, the occurrence of Ulrichocystis in the Benbolt shows that U. eximia was more likely a specialist and therefore probably k-selective, a disadvantage in less stable environments. Although the stem of U. eximia is unknown, if it was comparable to that of related species it was long enough to place the animal at least into the middle feeding tier. The food grooves of Bromidocystis were shallow and wide in narrow brachioles which placed the animal in the middle food-size category.

Rhombiferan A was collected only from two horizons at Stanley

Farm, but in these horizons it is common. Sprinkle (1974) suggests that there were several types of mobile rhombiferan cystoids which used their stem for swimming. Those with a flattened theca (Pleurocystitids) were detritus feeders while those with rounded thecae (Cheirocrinids and Glyptocystitids) were filter feeders and moved only when necessary. It was to this latter group that Rhobiferan A belonged. It seems likely that Rhombiferan A may have attached itself to bryozoans or crinoid stems by a short tapering stem and fed at higher levels than it could have reached by this stem alone. Therefore, the absence of Rhombifern A from less stable environments cannot be entirely explained by the danger of burial in sediments, nor by a shortage of places for attachment since both bryozoans and crinoids are common in horizons other than 6 and 7 at Stanley Farm. In more current active environments, Rhombiferan A would have had difficulty remaining in position, but in more stagnant environments the problem would have been the clogging of respiratory porerhombs. Although Rhombiferan A is placed in the lower tier by the probable length of its stem, it may commonly have fed in the middle level by attaching itself to bryozoans and crinoid stems. The food grooves of most rhombiferan are wide, but the brachioles of Rhombiferan A must have been very small and probably placed it in the small food-particle selection category.

Coronocystis angulatus was a larger rhombiferan cystoid than Rhombiferan A and thus was not likely to enter into competition with it. It was generally found in horizons of high diversity except near

the base in the Stanley Farm section where it occurs in a horizon of low diversity, high current energy and low fossil content. As a cylindrical rhombiferan similar to the glyptocystitids collected from the Bromide by Sprinkle (1982), C. angulatus was probably an unattached mobile suspension feeder which could have swum short distances when necessary (p. 231). Thus it could have survived more successfully in some areas where other echinoderms would have had difficulty. However, it might have had respiratory problems in the extremely quiet regions which is why it is not found in low diversity muddy areas and is more common in the Evans Ferry section than at the Stanley Farm. It probably fed in the lower feeding tier, perched on the end of its short stem. The brachioles of related species were narrow with wide food grooves which placed C. angulatus in the medium food-size selection category.

Regulaecystis pyriformis was a pleurocystitid rhombiferan and thus had a flattened, nearly bilaterally symmetrical theca. Sprinkle (1974;1982) and Parsley (1970) assert that most pleurocystitids were mobile detritus feeders which used two brachioles to sweep food particles from on or near the substrate. Thus, it would not appear that R. pyriformis entered into competition with the sessile suspension feeders which make up most of the Benbolt echinoderm fauna. This species is moderately common in horizons of high diversity at both localities. It does not occur in strata representing areas of high current activity either because it could not remain close enough to the bottom to feed effectively, or because the food particles on which

it fed were small enough to be carried away by the currently. A bottom which had too much terrigenous mud would have impeded respiratory and feeding structures which explains the presence of R. pyriformis only in the stable, high diversity horizons of the Benbolt.

Macurdablastus uniplicatus, the oldest known blastoid (Broadhead, 1984) was not a common species in the Benbolt. It has only been found in one horizon of merate diversity at Stanley Farm. As most blastoids were middle tier suspension feeders (Ausich and Bottjer, 1982), it is likely that M. uniplicatus occupied a similar feeding position, therefore keeping the calyx free of minor influxes of terrigenous mud. However, M. uniplicatus must not have been tolerant of changing conditions, nor a good compeditor, or it would have occurred over a wider range than observed here. Paul (1977) states that blastoids needed less oxygen than most other stalked echinoderms and that this gave them an edge during the Paleozoic where there was possibly less free oxygen in the atmosphere. But as has been previously stated, oxygen does not seem to have been in such short supply in any portion of the Benbolt that competition for it would have been a factor in comparative survival. Further, the scarsity of M. uniplicatus due to the absence of competitive advantage in well-oxygenated environments. Like other blastoids, it probably fed with narrow brachioles which placed it in the small size selection category.

The only parablastoid collected from the Benbolt is Meristoschisma hudsoni occurring mostly at Evans Ferry, though it is known from rare specimens at Stanley Farm. M. hudsoni mainly occurs

in areas of moderate to high diversity, but it is not represented by a large number of specimens. It seems to have preferred a quiet stable enviornment with stronger currents than were prevalent in the highest diversity portions of the Stanley Farm section. This is most likely to have been because respiration might have been difficult for this animal in areas of low current energy. Although the stem of M. hudsoni is unknown, the size and shape of the theca imply that it fed in the middle tier as did the true blastoids. The theca bore numerous thin brachioles (Sprinkle, 1972) which would have collected particles of small to medium size.

Echinozoans

The edrioasteroid, Cyathocystis sp, is known only from one specimen from Evans Ferry collected from the horizon of highest diversity. It appears to have been fastened to a patch of hard ground in this stable environment of moderate energy. In the highest diversity horizon at Stanley Farm, conditions were probably too micritic with too few large brachiopods for edrioasteroids to attach to, in the lower tier where they fed. Sprinkle (1982) collected specimens of Cyathocystis from the Bromide. These had ambulacral tunnels which were less than 1 mm wide, implying that the animal fed in the small food-size group.

Homalozoans

Anatiferocystis barrandei was a stylophoran with a small streamlined theca. The thecal shape with a short curved appendage at

the posterior imply that the animal was probably a quick-moving mobile detritus feeder. The single representative of this species collected in this study was found in the highest diversity horizon at Stanley Farm. In contrast, Anatiferocystis papillata was a common species in the Pooleville Member of the Bromide Formation (Sprinkle, 1982), representing a moderate energy environment with high echinoderm diversity much like the high diversity portions of the Benbolt. The scarsity of A. barrandei in the Benbolt may be due to perhaps to a shortage of the food particles it fed on. The Pooleville Member supported a diverse population of detritus-feeding echinoderms and trilobites--19 species of trilobites as opposed to 9 species in the Benbolt (Maitland, 1979)--whereas these groups show less diversity in the Benbolt, possible reflecting that detritus abundance was lower in the Benbolt environments (figure 17).

Myeinocystites natus was a small homiostelean with an ovoid theca and a tapering stem. It was probably a mobile detritus feeder (Parsley, 1972). It also occurs in the Bromide (Sprinkle, 1982) but only as a rare species in a high diversity zone duplicating the mode of occurrence in the Benbolt. Therefore, it appears that this was another possibly highly specialized species which as not a good competitor, but had larval dispersal over a wide geographic range.

Summary

The highest diversity horizon at Evans Ferry represents an environment of stable carbonate deposition in a region where the sedimentation rate was slow enough to leave patches of hard ground

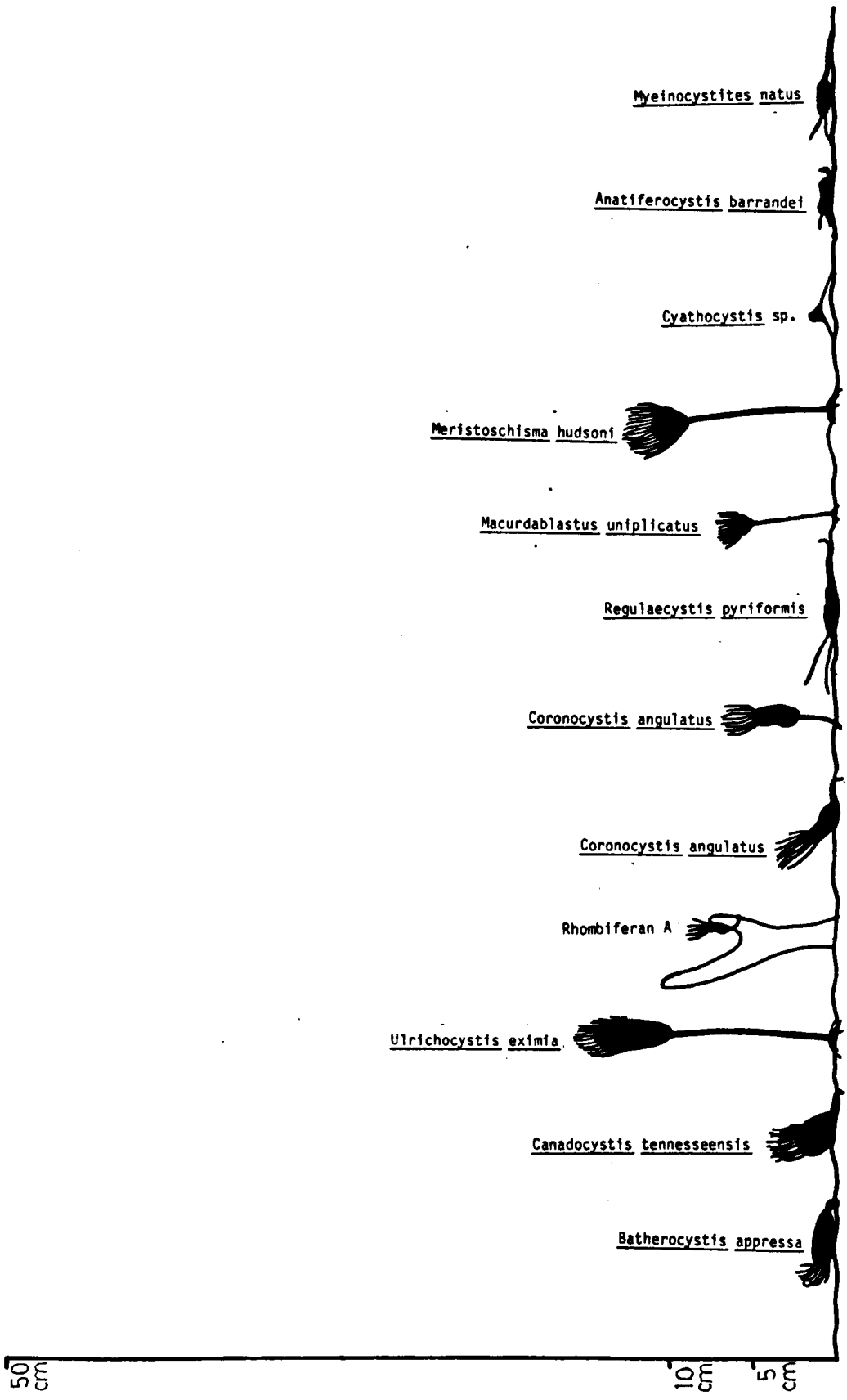


Figure 18. Blastozoans, Echinozoans and Homalozoans of the Benbolt.

exposed or allow them to develop. This environment supported a total of 16 different species of echinoderm. The dominant species in biovolume was Canadocystis tennesseensis where occupied the lower height, medium food-size feeding niche (figure 16). The only occupant of the small food-size lower height feeding niche here was Cyathocystis sp. Along with C. tennesseensis, Coronocystis angulatus and Hybocrinus punctatus were part of the lower height medium food-size niche whereas Regulaecystis pyriformis and Annulocrinus latus occupied the lower height large food-size niche. In the middle feeding tier were the small particle ingesters Acolocrinus hydraulicus and Apodasmocrinus punctatus, medium size selectors Paleocrinus planobasalis and Meristoschisma hudsoni, and the largest selector, Paleocrinus avondalensis. In the upper height small food-size feeding category were Diabolocrinus vesperalis, Archeocrinus peculiaris, Paradiabolocrinus irregularis and Wilsonicrinus culmensinuousus. In each of these niches, there were no more than two common species, so that competition was apparently avoided.

The highest diversity horizon at Stanley Farm appears to have been slightly less current-active than that of Evans Ferry. There the substrate was entirely soft and the percentage of echinoderm debris in the matrix low. However, this horizon contained 18 different species of echinoderms. The most commonly occurring of these were Paleocrinus planobasalis, Hybocrinus punctatus and Canadocystis tennesseensis. The niche differentiation placed Triboloporus cryptoplicatus, Anatiferocystis barrandei and Myeinocystites natus in the lower height

small food-size category. Hybocrinus punctatus, Canadocystis tennesseensis, Batherocystis appressa and Coronocystis angulatus in the medium food-size lower height niche, and Regulaecystis pyriformis in the large food-size lower height cateory. The small food-size middle height niche contained Rhombiferan A, Acolocrinus hydraulicus and Apodasmocrinus punctatus while two species shared the middle height medium food-size niche--Ulrichocystis eximia and Paleocrinus planobasalis. In the large food-size middle height niche was Paleocrinus avondalensis. Diabolocrinus vesperalis and Archeocrinus peculiaris shared the small food-size upper height niche while Colpodecrinus quadrifidus had the medium food-size upper height niche alone and Carabocrinus micropunctatus had the large food-size upper height niche. From these data, it would appear that the highest potential for competition was in the small particle size selection groups in all feeding tiers and in the medium size categories in the lower two tiers. Probably the most abundant food here was in the medium particle size in the middle and lower tiers because this supported the largest number of individuals.

The fact that the majority of the echinoderm specimens collected from the Benbolt had weathered out of the rock does indicate that preservational bias may have had an influence on the data. Species such as Ulrichocystis eximia, Acolocrinus hydraulicus and Paleocrinus planobasalis which had thick plates might have been less well-represented in the original community than the number of their plates collected implies. Likewise, thin-plated species may have been more

common in comparison. However, this fact is unlikely to severely alter the data taken from the Benbolt because most of those species which appeared common in horizons of high diversity were not especially thick-plated, nor was the percentage of thin-plated echinoderms found on slabs sufficiently greater to warrant a revision of the paleoecology.

CHAPTER IV

SUMMARY AND CONCLUSIONS

The Middle Ordovician Benbolt Formation was deposited as part of a sequence of shallow marine carbonates. The Benbolt of northeast Tennessee can be divided into three basin units which are distinguishable in the field at the two localities, Evans Ferry and Stanley Farm. Petrologic study of 71 thin sections indicates that these are in ascending order: (1) a sequence of highly fossilferous echinoderm-rich biomicrites which represent a quiet, stable environment with minor influx of terrigenous mud, (2) a unit of massive-weathering biosparite containing abundant echinoderm debris which was probably deposited in a skeletal sandbar where current energy was high, and (3) a shaley biomicrite which contains fewer echinoderm fossils than the lower two units and probably represents an extremely quiet, shallow environment in which influxes of terrigenous mud often buried communities. Throughout the period of deposition, there are indications that water depth at the Evans Ferry locality was usually slightly shallower than at Stanley Farm.

Twenty-six different species of echinoderm representing the crinozoans, blastozoans, echinozoans and homalozoans were collected from the rocks of the Benbolt for this study. Fifteen of these represent genera known from two other areas which have been studied extensively--the Bromide Formation of Oklahoma and the Platteville and Decorah Formations of Minnesota. Also two species--Anatiferocystis

barrandei and Colpodecrinus quadrifidus are described for the first time from the Southern Appalachians. The majority of these echinoderm species occurred toward the middle of Unit 1 at both localities with a maximum of 18 species to a single horizon. Unit 2 often contained large amounts of echinoderm debris, but few identifiable fossils. The highest recorded diversity for this unit is five species. Although some portions of Unit 3 display a diversity of up to seven echinoderm species, generally the diversity of this unit is very low, and in the upper portions at both localities, the number of identifiable species drops to zero. Here it appears that the conditions of high terrigenous clastic influx created an environment which was too inhospitable for echinoderms to inhabit.

The data of this study agree with the finding of Titus (1973;1975), Bretsky and Lorenz (1969) and Sprinkle (1982) who all observed high echinoderm diversity in areas of high stability and low current energy. Moderate diversity was typical of regions having slightly higher current energy, and low diversity was characteristic of extremely quiet environments which were frequently influenced by the deposition of terrigenous mud such as most of Unit 3 of the Benbolt. In the areas of high diversity, the echinoderms occupied niches, the most readily observable of which were according to elevation from the substrate and possibly also maximum size of food particles selected. The less hospitable environments were largely inhabited by individuals belonging to genera such as Carabocrinus, Archeocrinus and Diabolocrinus which as adults fed well above the

substrate and thereby avoided burial by terrigenous mud.

This study is unique in that it attempts to compare changes in the echinoderm abundance and diversity with changes in petrologically decernable environmental factors. In addition to general environmental interpretations, relative abundances as point counted in thin sections of echinoderms and other fossil allochems suggest that bryozoans and echinoderms required similar environmental factors based on their relative abundances. Brachiopods however differed from echinoderms and bryozoans in that they appeared to make up a greater percentage of the biovolume in environments which were not hospitable to the other two groups, such as those with a substrate of fine-grained terrigenous clastics rather than a more micritic substrate.

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APPENDIXES

APPENDIX A

DESCRIPTION OF BENBOLT ECHINODERM SPECIES

Subphylum Crinozoa Matsumoto, 1929

Class Crinoidea Miller, 1821

Subclass Inadunata Wachsmuth and Springer, 1885

Order Hybocrinida Jaekel, 1918

Family Hybocrinidae Zittel, 1879

Genus Hybocrinus Billings, 1857

Hybocrinus punctatus Miller and Gurly, 1985

(Plate 1, fig. 1-5)

Description--H- punctatus was a small inadunate crinoid with a cup-shaped calyx. This cup was extremely asymmetrical with a posterior edge 9.7 mm high on average, and the anterior edge 7.0 mm high. The plates bear a pitted ornament which does not penetrate. The calyx consists of five BB plates which are nearly equal in size, five RR plates, one large RA and five small OO plates.

Occurance--27 whole calyces, 4 partial calyces, 2 RR and 1 BB plate from Stanley Farm; 7 whole calyces, 2 partial calyces and 1 B plate from Evan's Ferry. Stanley Farm--horizons 6, 7 and 8, and Evan's Ferry--horizons 3, 4, 5, 6, 11, 12 and 13.

Hybocrinus punctatocristatus Bower and Veinus, 1974

(Plate 1, fig. 8)

Description--H. punctatocristatus was similar in structure to H. punctatus, but much larger in size, having a posterior height of 38

mm. It had a broadly conical calyx with a crest-like proturbance on the RA plate. This animal was asymmetrical, but not so much as H. punctatus. It also bore a pitted ornament on all plate surfaces. Brower and Veinus (1974) described this species from a single incomplete specimen.

Occurrence--A single nearly complete calyx from horizon 19 at Stanley Farm.

Order Cladida Moore and Laudon, 1943

Family Sphaerocrinidae Jaekel, 1985

Genus Paleocrinus Billings, 1859

Paleocrinus avondalensis Brower and Veinus, 1974

(plate 1, fig. 9-10)

Description--P. avondalensis was a crinoid with a bowl-shaped calyx with a flattened base. This calyx consisted of 5 iBB, 5 BB, 5 RR, 1 RA, and a variable number of OO plates. The entire calyx was covered with an ornamentation of fine ridges located in rhomb-shaped areas which are not raised into bundles as are those of P. planobasalis. Complete specimens of P. avondalensis ranged from 5 to 20 mm in width across the calyx, but some individual plates have been measured at up to 18 mm in diameter.

Occurrence--Six isolated plates from Stanley Farm; 10 plates from Evans Ferry. Horizons 1, 7, 9, and 18 at Stanley Farm, horizons 3, 4, 5, 7, 8, 13 and 14 at Evans Ferry.

Paleocrinus planobasalis Brower and Veinus, 1974

(Plate 1, fig. 12-16)

Description--P. planobasalis was another crinoid with a small subglobular cup and flattened base. The plate ornamentation consisted of a variable number of fine ridges raised into bundale which formed rhomboids on the calyx. The largest dimension was width, which ranged from 14 to 35 mm. A statistical study of the growth of P. planobasalis is included in Brower and Veinus (1974).

Occurrence--Two complete calyces, four partial calyces and 37 isolated plates from Stanley Farm and 13 individual plates from Evans Ferry. Horizons 3, 4, 5, 6, 7, 8, 10 and 18 at Stanley Farm; horizons 3, 4, 5, 10, 12, 14 and 15 at Evans Ferry.

Family Carabocinidae Bather, 1899

Genus Carabocrinus Billings, 1857

Carabocrinus micropunctatus Brower and Veinus, 1974

(Plate 2, fig. 1, 4)

Description--C. micropunctatus was a crinoid with a wide-rounded conical calyx ornamented by numerous fine V-shaped ridges arranged in a stellate pattern and a finely pitted plate surface. The iBB are elongate, topped by 5 BB plates, IRA and sRA plates, 5 RR plataes with a medium-sized anal X and a variable number of OO plates. The average dimensions of C. micropunctatus are 27 mm wide and 20 mm high, but the width can vary between 5 and 32 mm (Brower and Veinus, 1974).

Occurrence--Twenty-four individual plates from Stanley Farm, 2 plates from Evans Ferry. Horizons 6, 7, 8, 13 and 18 at Stanley Farm; horizons 14 and 22 from Evans Ferry.

Family Porocrinidae Miller and Gurly, 1984

Genus Triboloporus Kesling and Paul, 1968

Triboloporus cryptoplicatus Kesling and Paul, 1968

(Plate 2, fig. 2-3, 5)

Description--T. cryptoplicatus was a small crinoid with a rounded conical to nearly spherical calyx consisting of 5 BB, 5 RR, 1 RA and 5 OO plates with little ornamentation. The lower margins of the RR plates were indented by a slit which ran from the corner toward the center of the plates. RR plates bore two of these and BB plates bore one slit on the apex. The stem was no more than 4 mm long and tapered abruptly. The calyx itself ranged from 4 to 8 mm in height.

Occurrence--Eighteen whole calyces from Stanley Farm; one from Evans Ferry. Horizons 6, 7, 8 and 9 at Stanley Farm; horizon 5 at Evans Ferry.

Order Disparida Moore and Laudon, 1943

Family Acolocrinidae Brett, 1980

Genus Acolocrinus Kesling and Paul, 1971

Acolocrinus hydraulicus Kesling and Paul, 1971

(Plate 2, fig. 6-12, 16)

Description--A. hydraulicus was a crinoid with a goblet-shaped calyx composed of 3 unequal BB, 5 iRR directly overlain by 5 sRR and a rounded triangular anal X on the posterior side surrounded by 2 iRR and 2 sRR plates each of which bears a prominant crest on the upper right edge and a flat shelf bearing ambulacral grooves extending toward the central mouth. BB plates are deltoid in shape. All plates are very thick and covered with a finely-pitted ornament. A hydrauli-

cus was approximately 20 mm high (Kesling and Paul, 1971) which was the largest dimension of the calyx.

Occurrence--Stanley Farm--7 BB and 15 RR plates; Evans Ferry--4 RR and 2 BB plates were found. Stanley Farm horizons 7, 8 and 9; Evans Ferry horizons 4 and 11.

Family Calceocrinidae Meek and Worthen, 1869

Genus Annulocrinus Ramsbottom, 1961

Annulocrinus latus Brower and Veinus, 1974

(Plate 1, fig. 6-7)

Description--A. latus was a crinoid with massive plates which were usually wider than they were tall and were covered with coarse pits. The calyx of this species was conical in shape composed of iR, sR, R and BB plates and averaged about 27 mm high. This animal lived reclined upon the substrate with the arms extended back over the stem.

Occurrence--Horizons 4, and 6 at Evans Ferry; 2 BB and 1 RR plate.

Family Homocrinidae Kirk, 1914

Genus Apodasmacrinus Warn and Strimple, 1977

Apodasmocrinus punctatus (Brower and Veinus, 1974)

(Plate 1, fig. 11)

Description--A. punctatus was a small inadunate crinoid with a barrel-shaped dorsal calyx. This was composed of 5 BB, 5 RR, 2 Irr and 2 IBr plates which were all wider than they were high and covered with a pitted ornament. This calyx ranged from 2.5 to 6.5 mm in height.

Occurrence--One whole calyx from horizon 7 at Stanley Farm; one partial calyx from horizon 4 at Evans Ferry.

Subclass Camerata Wachsmuth and Springer, 1885

Order Diplobathrida Moore and Laudon, 1943

Family Rhodocrinitidae Bassler, 1938

Genus Archeocrinus Wachsmuth and Springer, 1881

Archeocrinus peculiaris Miller and Gurly, 1894

(Plate 3, fig. 12-13, 16-19)

Description--A. peculiaris was a large crinoid with a globose calyx which was wider than it was high. The plates consisted of 5 iBB, 5 BB, 5 RR, iRR, IBr, IIBr and IIIBr plates. There were no visible median ray ridges on the cup. The plates bore a finely-pitted ornament and between them were strongly depressed sutures. The calyx of A. peculiaris averaged 23 mm in height and 40 mm in width (Brower and Veinus, 1974). The stem was apparently longer than the calyx was high.

Occurrence--At Stanley Farm, one complete calyx and 66 individual plates; Evans Ferry, one partial calyx and 33 plates. Stanley Farm horizons 5, 6, 7, 8, 9, 10, 12, 13, 16, 17, 18, 19, 22, 23, 24 and 25; Evans Ferry horizons 1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 12, 14, 15, 16, 17, 18, 20, 21 and 24.

Genus Diabolocrinus Wachsmuth and Springer, 1897

Diabolocrinus vesperalis White, 1880

(Plate 3, fig. 9-11, 22)

Description--D. vesperalis was another large crinoid with a depressed globular cup without any median ray ridges. The plate distribution on the calyx is similar to that of Archeocrinus, but more

variable. Ornamentation is also extremely variable and can consist of sinuous ridges, stellate ridges, or nodes. These forms of ornamentation can be absent or in any combination. The usual dimensions of D. vesperalis are 18 mm high and 25 mm wide (Brower and Veinus, 1974).

Occurrence--One partial calyx and 11 isolated plates from Stanley Farm; one partial calyx and 11 plates from Evans Ferry. Stanley Farm horizons 6, 7, 8 and 9, and Evans Ferry horizons 1, 2, 3, 4 and 5.

Genus Paradiabolocrinus Brower and Veinus, 1974

Paradiabolocrinus irregularis Brower and Veinus, 1974

(Plate 3, fig. 20-21)

Description--P. irregularis was another crinoid with a depressed globular cup of similar structure to Diabolocrinus and Archeocrinus, but the BB and RR plates bear heavy stellate ridges which grade upward into median-ray ridges. The individual plates had a nodal ornament and tend to be small in comparison to the size of the calyx. The complete calyx measures 40 mm wide and 23 mm high (Brower and Veinus, 1974).

Occurrence--A single nearly complete calyx from horizon 4 at Evans Ferry.

Genus Wilsonicrinus Springer, 1926

Wilsonicrinus culmensinuousus Brower and Veinus, 1974

(Plate 3, fig. 15)

Description--W. culmensinuousus was a small camerate crinoid with a broad flat calyx. The plates are marked by an ornament of raised sinuous ridges. Common dimensions for W. culmensinuousus as reported

by Brower and Veinus (1974) are 10 mm high and 20 mm wide.

Occurrence--Two isolated plates from Evans Ferry horizons 3 and 4.

Genus Rhaphanocrinus Wachsmuth and Springer, 1885

Rhaphanocrinus simplex Brower and Veinus, 1974

(Plate 2, fig. 17-18)

Description--R. simplex was a crinoid with a conical dorsal calyx with slightly rounded sides. The upper portions of the cup bear well-defined median-ray ridges, but the lower plates are smooth. The specimen described in this paper measured 20 mm high and 18 mm wide.

Occurrence-- Two whole calyces from horizon 8 at Stanley Farm.

Order? Monobathrida Moore and Laudon, 1943

Family Colpodecinidae Sprinkle and Kolate, 1982

Genus Colpodecrinus Sprinkle and Kolata, 1982

Colpodecrinus quadrifidus Sprinkle and Kolate, 1982

(Plate 2, fig. 13-15)

Description--C. quadrifidus was a "rhomb-bearing" camerate with a steeply conical aboral calyx about 35 mm high (Sprinkle, 1982). This calyx consists of 4iBB, 4 BB, 5 RR and 10 iBr without prominant ray ridges. The plates bear a depressed sutural fold which contains 6 to 17 foldlike rhombs separated by radiating ridges. The rhombs occupy one fourth to one half of the plate surface. The plate center is flat to slightly depressed with a light nodular ornament. Unlike most other camerates, C. quadrifidus had branching rather than pinnulate arms.

Occurrence--Thirteen individual plates from Stanley Farm; two plates from Evans Ferry. At Stanley Farm, horizons 3, 7, 8 and 9; at

Evans Ferry, horizons 11 and 23.

Subphylum Blastozoa Sprinkle, 1973

Class Paracrinoidea Regnell, 1945

Order uncertain

Family uncertain

Genus Bathercystis Bassler, 1950

Batherocystis appressa Bassler, 1950

(Plate 4, fig. 10-12)

Description--B. appressa had a paddle-shaped theca about 25 mm high which was connected to a short stem composed of two or three bead-like elements. The plates are smooth and generally thin except for the BB plates which are thick at the base and therefore more commonly preserved.

Occurrence--Twelve isolated BB plates and one columnal from Stanley Farm, and four BB plates and one columnal from Evans Ferry. Stanley Farm horizons 5, 7, 9 and 10, and Evans Ferry horizons 3 and 12.

Order Comarocystitida Parsley and Mintz, 1975

Family Amygdalocystitiae Jaekel, 1900

Genus Canadocystis Jaekel, 1900

Canadocystis tennesseensis Parsley and Mintz, 1975

(Plate 4, fig. 18-21, 14)

Description--C. tennesseensis was a paracrinoid with a globular to subfusiform theca composed of between 21 and 40 individual plates. This theca measures between 10 and 23 mm in height and is smooth

except for the "S"-shaped peristome which is situated on the right side of the theca near the distal apex.

Occurrence--Fifteen complete and seven partial thecae from Stanley Farm; nine whole and nine partial thecae from Evans Ferry. At Stanley Farm horizons 6, 7 and 8 and at Evans Ferry horizons 3, 4 and 6.

Class Eocrinoidea Jaekel, 1918

Family Paleocystitidae Ubaghs, 1968

Genus Ulrichocystis Bassler, 1950

Ulrichocystis eximia Bassler, 1950

(Plate 4, fig. 13-14, 16, 22-23)

Description--U. eximia had an elongate theca approximately 35 mm in height (Bassler, 1950), sub-pyriform or clavate which tapered from the ovate oral region to a small base. The theca was composed of approximately 75 hexagonal plates which were steeply convex and covered by a light radial ornament.

Occurrence--Thirty-four plates from Stanley Farm and 14 from Evans Ferry. Stanley Farm horizons 7, 8 and 9; Evans Ferry horizons 3, 4, 5 and 6.

Class Rhombifera Zittel, 1879

Order Dichoporita Jaekel, 1899

Rhombiferan A

(Plate 4, fig. 1-3)

Description--Rhombiferan A was a small blastozoan which has not yet been assigned a genus and species designation. The theca was roughly eliptical and strongly asymmetrical and measures approximately

9 mm in height. The oral region is flatter than the more rounded basal area. Located in the radial, lateral and basal plates are a varied number of conjunct rhombs.

Occurrence--Seven complete and eight partial thecae from horizons 6 and 7 at Stanley Farm.

Family Cheirocrinidae Jaekel, 1899

Genus Coronocystis Paul, 1972

Coronocystis angulatus Paul, 1972

(Plate 4, fig. 7)

Description--C. angulatus was a medium-sized rhombiferan with a theca approximately 20 mm tall by 20 mm wide (Paul, 1972). The slightly asymmetrical theca was composed of 4 unequal basals, 5 iLL, 5 LL and 6 RR plates. The radials have deep rhomb-bearing sinuses. The 5 ambulacra were unusually long, each bearing 9 to 13 brachioles.

Occurrence--Three isolated plates from Stanley Farm; nine from Evans Ferry. Horizons 2, 3 and 7 at Stanley Farm and horizons 4, 6 and 14 at Evans Ferry.

Family Pleurocystitidae Neumayr, 1889

Genus Regulaecystis Dehm, 1932

Regulaecystis pyriformis (Parsley, 1970)

(Plate 4, fig. 4-6)

Description--R. pyriformis had a pyriform theca nearly equal in length and width. This bore one small pectinirhomb on the left anterior of the dorsal side. The theca was composed of 4 BB, 4 iL, 4 LL, 4 TT, 2 D and 1 "O_3" plates. The larger thecal plates have

radiating ridges which can be single or double extending from the center of the plates to the corners and midpoints of the edges.

Occurrence--Three isolated plates and partial stem with two plates attached from Stanley Farm; four single plates from Evans Ferry. Stanley Farm horizons 6 and 7; Evans Ferry horizons 3 and 4.

Class Blastoidea Say, 1825

Genus Macurdablastus Broadhead, 1984

Macurdablastus uniplicatus Broadhead, 1984

(Plate 4, fig. 8-9, 15, 17)

Description--M. uniplicatus had a broadly subconical theca with a pentagonal form in trasverse section. The ambulacral sinuses were narrow and shallow and the deltoids were small. All plates bore no ornament and averaged 4 mm in length.

Occurrence--One whole crushed theca and three isolated plates from horizon 6 at Stanley Farm.

Class Parablastoidea Hudson, 1907

Family Blastocystidae Jaekel, 1918

Genus Meristoschisma Sprinkle, 1972

Meristoschisma hudsoni Sprinkle, 1973

(Plate 3, fig. 1-3, 6, 14)

Description--M. hudsoni had a theca which was biconical and had well-developed pentagonal symmetry. The calyx vault was composed of 5 deltoids, 5 orals and 5 basals and supported about 70 long brachioles. The complete calyx studied by Sprinkle (1973) was 25 mm tall and bore a light radial ornament.

Occurrence--One deltoid plate from Stanley Farm; four oral and 3 deltoid plates from Evans Ferry. Horizon 9 at Stanley Farm and horizons 4 and 12 at Evans Ferry.

Subphylum Echinozoa Zittel, 1895

Class Edrioasteroidea Billings, 1858

Order Isorophida Bell, 1976

Family Cyathocystidae Bather, 1899

Genus Cyathocystis Schmidt, 1879

Cyathocystis sp.

(Plate 3, fig. 5)

Description--Cyathocystis sp. was a small edrioasteroid which in the specimen collected for this study, had had the apex removed. The diameter of the specimen was approximately 4 mm and it was attached to a hardground surface.

Occurrence--A single specimen from Evans Ferry horizon 4.

Subphylum Homalozoa Whitehead, 1941

Class Stylophora Gill and Caster, 1960

Family Kirkocystidae Caster, 1952

Genus Anatiferocystis Chauvel, 1941

Anatiferocystis barrandei Bassler, 1943

(Plate 3, fig. 3, 7)

Description--A. barrandei had a planoconvex, asymmetrical theca composed of two adorals, two marginal and one subanal. The plates bear a very light nodal ornament.

Occurrence--A single nearly complete theca from horizon 7 at

Stanley Farm.

Class Homiostelea Gill and Caster, 1960

Family Belemnocystitidae Parsley, 1963

Genus Myeinocystities Strimple, 1953

Myeinocystites natus Strimple, 1953

(Plate 3, fig. 4, 8)

Description--M. natus was a homalozoan which had a flattened ovoid theca with unornamented plates. These consisted of 13 marginals, 4 ventrals, 10 dorsals 1 H and 1 Y plates.

Occurrence--A single complete theca from horizon 7 at Stanley Farm.

Plate 1. Inadunate Crinoids

Fig. 1-5. Hybocrinus punctatus; 1. B-ray view with summit distorted, X3, Stanley Farm, horizon 6. 2. B-ray view of undistored calyx, X3, Evans Ferry, horizon 4. 3. E-ray view with base distorted, X3, Stanley Farm, horizon 7. 4. RR plate, exterior, X3, Stanley Farm, horizon 7. 5. B-ray view of latterally compressed calyx, X3, Stanley Farm, horizon 7.

Fig. 6-7. Annulocrinus latus; 6. BB plate, exterior. 7. RR plate, exterior, X3, Evans Ferry, horizon 4.

Fig. 8. Hybocrinus punctatocristatus; calyx, basal view, X3, Stanley Farm, horizon 19.

Fig. 9-10. Paleocrinus avondalensis: 9. RR plate, exterior. 10. RR plate, interior, X3, Stanley Farm, horizon 7.

Fig. 11. Apodasmocrinus punctatus; laterally flattened calyx, X3, Stanley Farm, horizon 7.

Fig. 12-16. Paleocrinus planobasalis; 12. RR plate, exterior, X3, Stanley Farm, horizon 7. 13. calyx, A-ray view, X3, Stanley Farm, horizon 7. 14. RR plate, interior, X3, Evans Ferry, horizon 4. 15. calyx, basal view, X3, Stanley Farm, horizon 7. 16. calyx, summit view, X3, Stanley Farm, horizon 7.

PLATE NO. 1

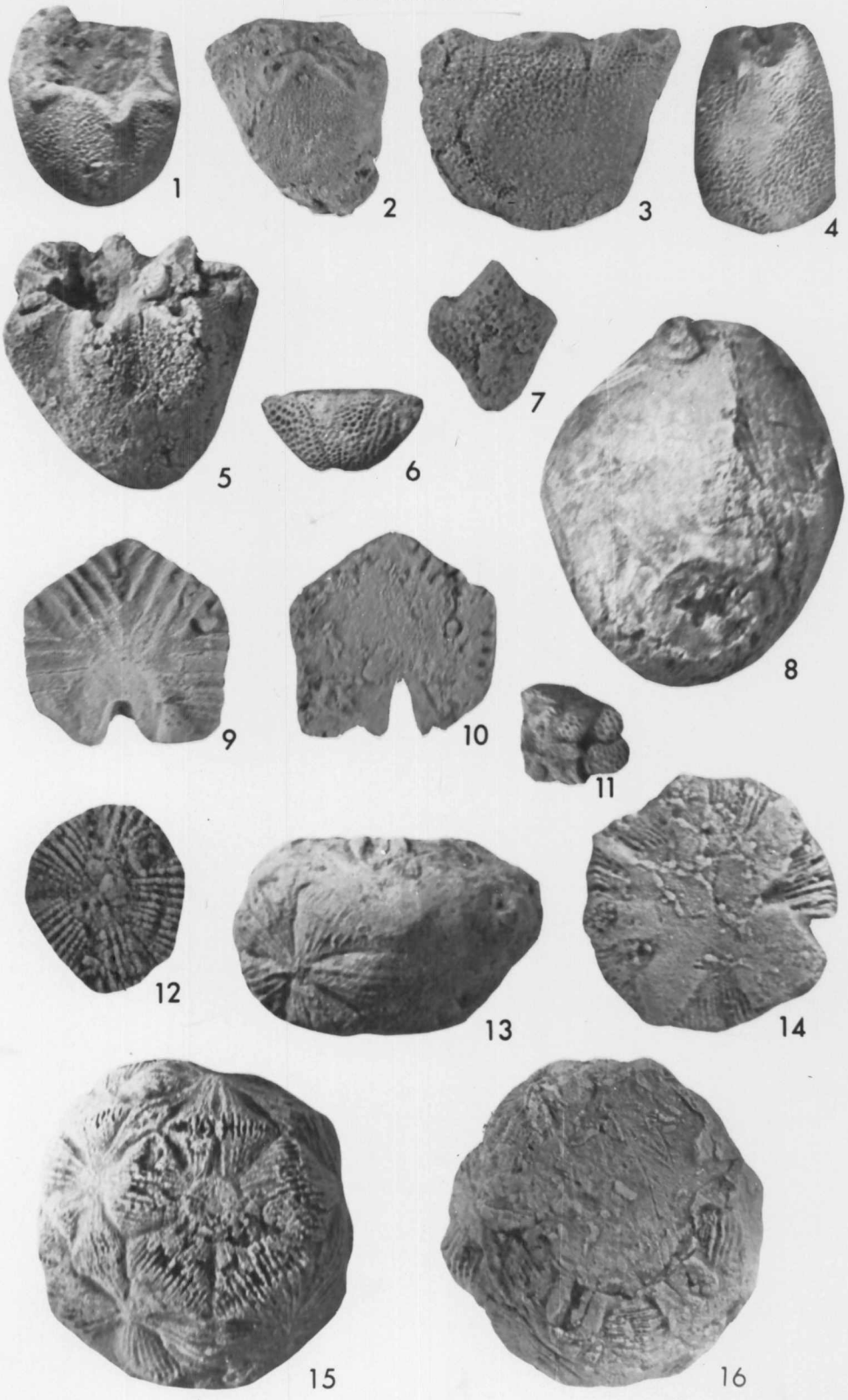


Plate 2. Inadunate and Camerate Crinoids

Fig. 1, 4. Carabocrinus micropunctatus; 1. RR plate on underside of slab, X3, Stanley Farm, horizon 18. 4. BB plate on underside of slab, X3, Stanley Farm, horizon 18.

Fig. 2, 3, 5. Triboloporus cryptoplicatus; 2. Calyx, posterior view, X3, Stanley Farm, horizon 7. 3. calyx, anterior view, X3, Stanley Farm, horizon 7. 5. calyx, summit view, X3, Stanley Farm, horizon 8.

Fig. 6-12, 16. Acolocrinus hydraulicus; 6. sRR plate, exterior, H3, Evans Ferry, horizon 4. 7. iRR plate, interior, X3, Stanley Farm, horizon 7. 8. iRR plate, exterior, X3, Stanley Farm, horizon 7. 9. BB plate, exterior, X3, Stanley Farm, horizon 7. 10. BB plate, interior, X3, Stanley Farm, horizon 7. 11. BB plate, exterior, X3, Stanley Farm, horizon 6. 12. BB plate, interior, X3, Stanley Farm, horizon 6. 16. calyx, CD side view, X3, Stanley Farm.

Fig. 13-15. Colpodecrinus quadrifidus; 13. iBr plate, exterior, H3, Stanley Farm, horizon 7. 14. iBr plate, interior, X3, Stanley Farm, horizon 7. 15. RR(?) plate, interior, X3, Stanley Farm, horizon 8.

Fig. 17-18. Rhaphanocrinus simplex; 17. calyx, basal view, 19. calyx, side view, X2, Stanley Farm, horizon 8.

PLATE NO. 2

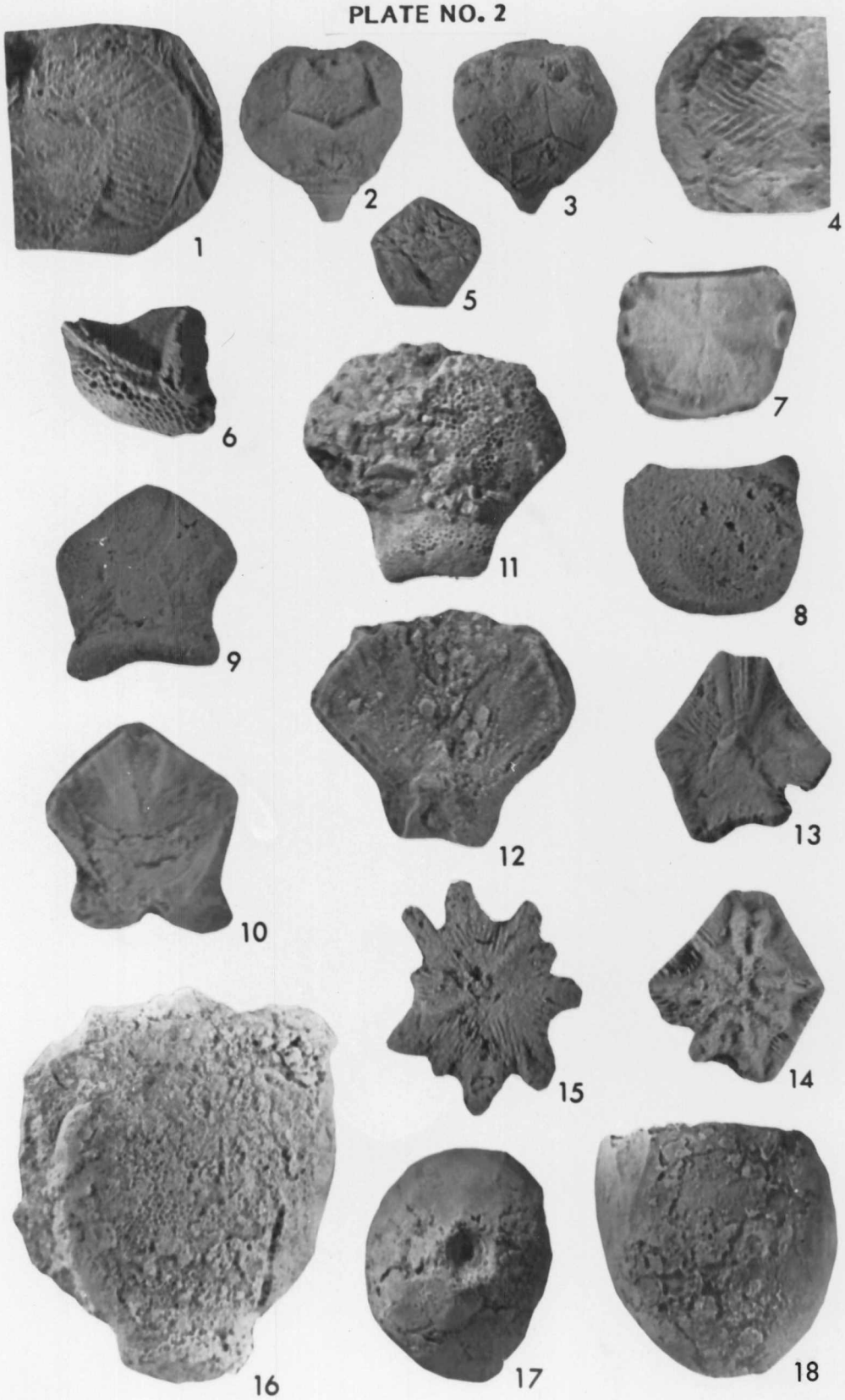


Plate 3. Camerate Crinoids, Blastozoans, Echinozoans and Homalozoans

Fig. 1-2, 6, 14. *Meristoschisma hudsoni*; 1. DD plate, exterior. 2. DD plate, interior, X3, Evans Ferry, horizon 4. 6. RR plate, exterior. 14. RR plate, interior, X3, Evans Ferry, horizon 4.

Fig. 3, 7. *Anatiferocystis barrandei*; 3. theca, ventral view. 7. theca, dorssal view, X3, Stanley Farm, horizon 7.

Fig. 4, 8. *Myeinocystitities natus*; 4. theca, ventral view. 8. theca, dorsal view, X3, Stanley Farm, horizon 7.

Fig. 5. *Cyathocystis sp.*; summit view, X3, Evans Ferry, horizon 4.

Fig. 9-11, 22. *Diabolocrinus vesperalis*; 9. RR(?) plate, X3, Stanley Farm, horizon 6. 10. BB plate, X3, Evans Ferry, horizon 4. 11. RR(?) plate, exterior, X3, Evans Ferry, horizon 4. 22. calyx, side view, X3, Stanley Farm, horizon 7.

Fig. 12-13, 16-19. *Archeocrinus peculiaris*; 12. iBr plate, exterior. 13. iBr plate, interior, X3, Stanley Farm, horizon 7. 16. calyx, basal view, 17. calyx, side view, X1, Stanley Farm, horizon 8. 18. RR plate, interior. 19. RR plate, exterior, X3, Stanley Farm, horizon 7.

Fig. 15. *Wilsonicrinus culmensinuousus*; BB plate, exterior, X3, Evans Ferry, horizon 4.

Fig. 20-21. *Paradiabolocrinus irregularis*; 20. calyx, summit view. 21. calyx, basal view, X2, Evans Ferry, horizon 4.

PLATE NO. 3

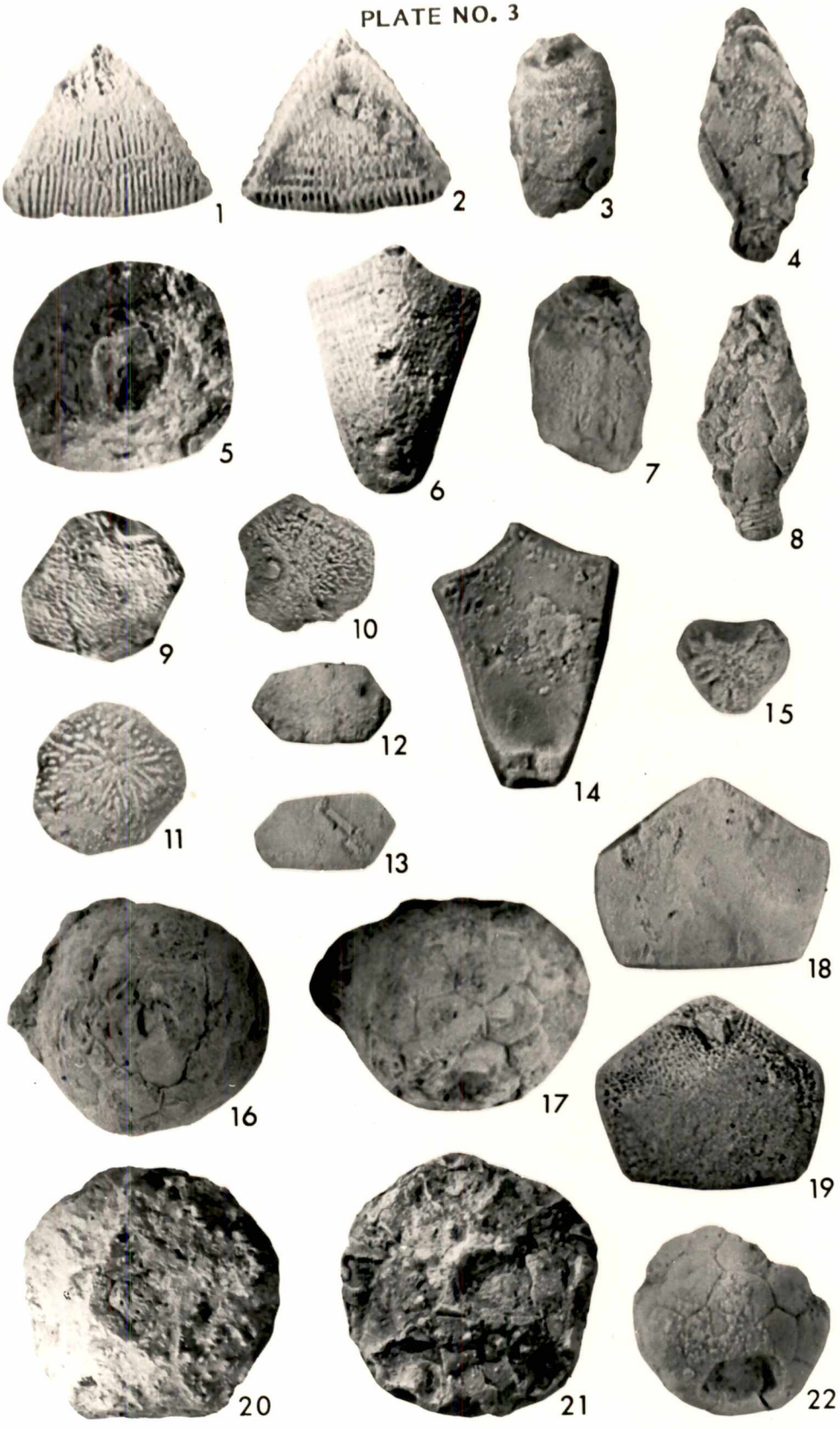


Plate 4. Blastozoans

Fig. 1-3. Rhombiferan A; 1. theca, anterior view, X3, Stanley Farm, horizon 6. 2. theca, side view, X3, Stanley Farm, horizon 7. 3. theca, summit view, X3, Stanley Farm, horizon 6.

Fig. 4-6. Regulaecystis pyriformis; 4. plate, X3, Evans Ferry, horizon 3. 5. stem with plates, dorsal view, X3, Stanley Farm, horizon 7. 6. plates, X3, Stanley Farm, horizon 7.

Fig. 7. Coronocystis angulatus; RR plate, interior, X3, Evans Ferry, horizon 4.

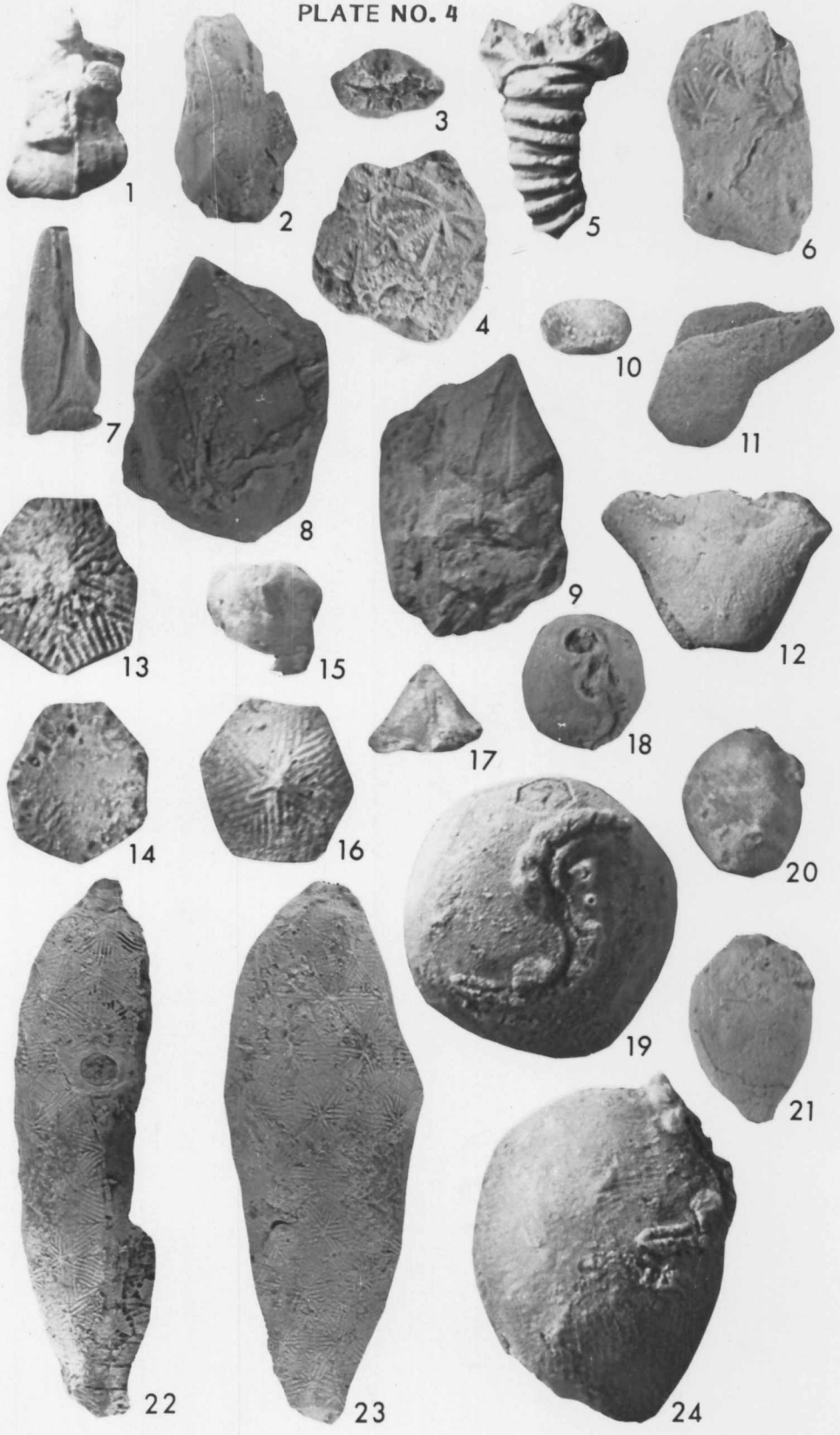
Fig. 8-9, 15, 17. Macurdablastus uniplicatus; 8. latterally flattened theca, basal view. 9. latterally flattened theca, summit view, X3, Stanley Farm, horizon 6. 15. Br plate, side view. 17. Br plate, summit view, X3, Stanley Farm, horizon 6.

Fig. 10-12. Batherocystis appressa; 10. stem ossicle, X3, Evans Ferry, horizon 3. 11. BB plate, ventral view. 12. BB plate dorsal view, X3, Evans Ferry, horizon 12.

Fig. 13-14, 16, 22-23. Ulrichocystis eximia; 13. plate, exterior, X3, Evans Ferry, horizon 4. 14. plate interior. 16. plate, exterior, X3, Stanley Farm, horizon 7. 22. theca, posterior view. 23. theca, side view, X1.5, Stanley Farm.

Fig. 18-21, 24. Canadocystis tennesseensis; 18. theca, juvenile, summit view. 19. theca, adult, summit view. 20. theca, juvenile, anterior view. 21. theca, juvenile, anterior view. 24. theca, adult, anterior view, X3, Stanley Farm, horizon 7.

PLATE NO. 4



APPENDIX B
POINT-COUNTING DATA

Evans Ferry

Thin Section	Thickness (m)	Micrite	Spar	Dolomite	Echinoderms	Brachiopods	Trilobites	Bryozoans	Ostracodes	Gastropods	Algae	Stylolites	Fossil Debris
49	0	50.6	16.0	0	22.6	1.0	0.6	1.6	0.6	0	1.0	5.6	0.3
50	2	53.0	24.3	0	19.6	0	0.3	10.3	0	0	0.3	2.0	0.3
51	4	54.6	24.6	1.0	10.3	0	2.6	5.0	1.0	0.6	0	1.0	0
52	5	56.3	27.3	0	13.0	0	0.3	0.3	1.3	0	0	0.3	0.3
53	7	60.6	13.3	0	20.0	0	0	2.3	1.0	0	0.3	1.6	0.6
LB4	10	62.3	10.3	0	16.6	0	0	0.6	1.3	0.3	0	7.6	0.6
54	13	32.0	33.6	0	25.0	0	0.6	6.0	2.6	0	0.3	0	0.6
55	15	60.6	18.3	0	11.6	0	2.0	2.6	1.3	0	1.6	0.3	1.3
56	16	51.6	18.0	0.3	17.3	0	0.6	5.3	1.0	0	1.0	4.6	0
57	18	48.6	16.3	0	23.6	0	0	4.3	1.3	0.6	0.3	4.3	0.3

Thin Section	Thickness (m)	Micrite	Spar	Dolomite	Echinoderms	Brachiopods	Trilobites	Bryozoans	Ostracodes	Gastropods	Algae	Stylolites	Fossil Debris
58	21	49.0	31.0	0	12.3	0	0.6	1.3	2.0	0.3	1.3	0	2.0
59	22	36.3	42.6	0	12.0	0	1.0	2.3	0.3	0	0.3	4.3	0.6
60	25	31.6	31.0	0.3	18.3	0	0	1.6	0.6	0	0	14.6	1.6
61	26	53.3	28.3	0.6	12.3	0	1.0	2.3	0.3	0	0	0.6	1.0
62	28	42.0	35.6	0	11.3	0	0	2.6	0	0	0	5.6	2.6
63	40	45.0	35.0	0	15.6	0	0	2.0	1.0	0	0.6	0	0.6
64	35	65.6	5.3	0	18.6	3.0	0.6	4.6	0.6	0	0.6	0.3	0.3
65	36	60.3	19.6	0	11.6	1.3	0.6	4.0	1.3	0	0	0	1.0
66	38	27.6	46.6	0	12.0	0.3	2.0	9.3	1.6	0	0	0	0.3
67	41	42.3	38.0	0	13.6	0	0.3	3.0	0.6	0	0.3	1.0	0.6
68	45	35.0	34.6	0	21.0	0	0.6	8.0	0.6	0	0	0	0.3
69	47	20.6	34.0	0	37.3	0	0	7.0	0	0	0	0.3	0.6
70	48	19.3	52.6	0	23.6	0	0	4.0	0.3	0	0	0	0

Thin Section	Thickness (m)	Micrite	Spar	Dolomite	Echinoderms	Brachiopods	Trilobites	Bryozoans	Ostracodes	Gastropods	Algae	Stylolites	Fossil Debris
72	50	53.3	14.0	0	16.0	0	0.3	0.6	1.0	0	0	12.6	2.0
73	52	22.3	62.0	0	9.3	0.6	0.6	1.0	1.6	0.3	0	0	2.0
74	54	61.0	16.0	0	14.0	1.0	0	0.3	0.6	0	0	7.0	0
75	56	65.6	9.3	0	3.3	0	1.3	15.0	1.0	0	0	4.3	0
76	59	74.0	14.0	0	8.0	0	0.3	1.3	0.3	0	0	1.3	0.3
77	70	57.6	17.0	0	9.0	0	0.3	8.6	6.0	0	0	0	1.0
78	77	46.3	32.3	0	23.0	1.0	0.3	3.6	0.6	0	0	1.0	1.6
79	81	71.3	16.6	0	11.3	0.3	0	0.6	0	0	0	0	0
81	89	61.3	21.3	0.3	14.3	0	0	1.6	0	0.3	0	0	0
82	92	73.6	9.0	0.3	8.3	1.3	0	2.0	2.0	1.0	1.3	0	2.3
83	95	77.3	3.0	0	8.0	0	0.3	2.6	0	0	0	6.6	0.6
84	100	88.6	1.3	0	5.6	0	1.0	0.6	1.6	0.6	0	0	0.3
85	102	84.0	4.0	0	8.3	0	0	1.3	1.0	0.3	0	0	1.0

Thin Section	Thickness (m)	Micrite	Spar	Dolomite	Echinoderms	Brachiopods	Trilobites	Bryozoans	Ostracodes	Gastropods	Algae	Stylolites	Fossil Debris
86	104	75.0	11.3	0	6.6	0	0.3	1.3	2.0	0	0	0	3.3
88	100	71.6	17.0	0.3	1.6	0	0	0	0	0	1.0	6.6	1.6
89	111	66.3	15.0	0	1.0	5.0	0	1.0	0	0	7.3	1.6	2.6
90	118	71.3	7.0	1.3	5.3	1.3	1.6	2.3	0.3	0	6.3	1.3	1.6
					Stanley Farm								
LC	0	68.3	29.0	0	0.6	0.3	0.3	0	0	0	1.3	0	0
2	2	70.3	4.0	0	3.0	0.3	0.3	4.3	6.3	0	8.0	0	0
4	4	40.6	21.3	0	15.3	0.6	2.3	12.3	2.3	0.6	4.3	0	0
7	7	62.3	27.0	0	0.6	0	2.3	2.0	2.0	0	1.6	0	0
11.5	11.5	34.3	43.3	0	13.0	0.6	0.3	4.6	2.3	0	1.0	0	0.3
15	15	43.0	34.0	0	9.6	0.3	0.6	8.3	2.0	1.0	0	0.3	0.6
17	17	62.6	19.0	0	4.3	3.6	1.6	3.6	3.0	0.6	0	0.6	0.6

Thin Section	Thickness (m)	Micrite	Spar	Dolomite	Echinoderms	Brachiopods	Trilobites	Bryozoans	Ustracodes	Gastropods	Algae	Stylolites	Fossil Debris
LB7	18	78.6	9.3	0	6.3	0	0.6	1.3	1.6	0	0.3	0.6	1.0
20	20	43.3	34.6	0	9.0	0.3	0	7.3	3.6	0	0	0	1.6
23.8	23.8	50.6	23.6	0	11.0	0.6	0	6.3	3.0	0.3	2.3	2.0	0
26.5	26.5	51.3	25.0	0	13.6	1.0	0.3	3.3	1.0	0	2.0	1.3	0.3
31.6	31.6	59.3	14.3	0	14.0	0.3	0.3	8.3	6.3	1.0	0	1.3	0.6
LB11	35	69.3	8.3	0	14.3	1.3	0.6	1.3	4.0	0.6	0	0	0.3
38.2	38.2	59.6	15.6	0	5.0	8.6	0.3	1.6	5.3	0	0	1.3	2.3
39	39	69.0	18.0	0	10.3	7.3	0.3	1.6	2.3	0	0	0.3	0.6
40	40	44.3	20.6	0	10.0	4.6	2.0	7.0	0.6	1.3	9.0	1.3	0
41	41	31.3	38.0	0	6.3	2.3	1.6	12.0	3.0	0	4.0	0.3	1.0
LB12	45.6	69.6	8.3	0	5.6	7.0	0	1.0	1.0	0	0	6.3	1.0
49	49	1.0	27.3	0	52.6	1.0	0.3	5.0	3.6	0	0	1.6	7.3
50	50	46.0	19.0	0	28.3	0	1.0	0	4.6	0	0	0	0.3

Thin Section	Thickness (m)	Micrite	Spar	Dolomite	Echinoderms	Brachiopods	Trilobites	Bryozoans	Ostracodes	Gastropods	Algae	Stylolites	Fossil Debris
61	61	51.0	13.0	1.0	23.0	0	1.3	6.3	1.6	0.3	1.3	3.6	0.3
66	66	43.0	5.3	0	44.6	2.6	0.3	1.3	1.0	0	0.6	1.0	0
68	68	50.3	2.3	0	8.6	2.0	3.3	33.6	1.0	2.3	5.0	2.3	9.0
70	70	62.3	6.6	0	20.6	0.6	0	4.6	1.6	0.6	1.0	0.6	0.6
75	75	44.3	28.0	0	16.0	2.0	2.0	3.6	1.3	0	2.3	0.3	0
78	78	33.0	25.0	0	14.6	0.3	0.6	10.6	1.0	0.3	1.0	13.3	0
81	81	71.3	6.0	0	15.3	0.6	0	3.6	1.3	0.3	0	0	1.3
86	86	98.0	1.6	0	0	0	0	0	0	0	0	0.3	0
91	91	24.6	21.3	0.6	16.0	3.6	0	33.0	0.3	0	0.3	0	0
95	95	35.3	7.3	6.3	10.0	6.6	4.3	26.3	0	0	0	0	0
95.4	95.4	61.3	0	0	6.6	2.0	1.0	1.3	14.6	1.0	0	0	1.0

APPENDIX C

COLUMNAR SECTION OF BENBOLT HORIZONS

Evans Ferry

Unit	Sample	Cumulative Thickness (m)	Description
1	1	1	Thinly bedded and cobbly weathered micrite interbedded with thin shales A. peculiaris D. vesperalis
	2	2.6	Cobbly weathering, medium bedded biomicrite which forms small ledges A. peculiaris D. vesperalis
	3	6.1	Straight-bedded grey biomicrite with beds thin to medium in thickness H. punctatus P. avondalensis P. planobasalis A. peculiaris D. vesperalis W. culmensinuousus B. appressa C. tennesseensis V. eximia R. pyriformis
	4	10.3	Thinly bedded buff-colored shaley biomicrite interbedded with shales H. punctatus P. avondalensis A. hydraulicus A. latus A. punctatus A. peculiaris D. vesperalis P. irregularis W. culmensinuousus

Unit	Sample	Cumulative Thickness(m)	Description
			C. tennesseensis U. eximia C. angulatus R. pyriforms M. hudsoni Cyathocystis sp.
1	5	12.2	Medium bedded dark grey biomicrite H. punctatus P. avondalensis P. planobasalis T. cryptoplicatus A. peculiaris D. vesperalis U. eximia
	6	16.8	Thickly bedded cobbly weathering dark grey biomicrite sparsely interbedded with thin shale H. punctatus A. latus A. peculiaris C. tennesseensis U. eximia C. angulatus
	7	20.0	Massively bedded dark grey biomicrite with hackly brownish weathering, forming small ledges P. avondalensis A. peculiaris
1	8	23.1	Medium bedded, uneven dark grey biomicrite with hackly weathering P. avondalensis A. peculiaris
Total thickness Unit 1 = 30.0 meters			
2	9	30.1	Very massively bedded biosparite
	10	36.8	Thinly bedded, cobbly weathering biomicrite with buff weathering P. planobasalis A. peculiaris

Unit	Sample	Cumulative Thickness (m)	Description
	11	39.3	Thinly bedded shaley biomicrite with shaley weathering H. punctatus A. hydraulicus A. peculiaris C. quadrifidus
	12	44.9	Thinly bedded biomicrite interbedded with shale H. punctatus P. avondalensis A. peculiaris B. appressa M. hudsoni
Total thickness Unit 2 = 16.0 meters			
3	13	46.7	Thickly bedded grey biosparite P. avondalensis
	14	48.3	Thin to medium bedded buff weathering biomicrite with shaley weathering H. punctatus P. avondalensis P. planobasalis C. micropunctatus A. latus A. peculiaris C. angulatus
3	15	50.9	Thinly bedded, cobbly weathering buff and light grey biomicrite P. planobasalis A. peculiaris
	16	54.8	Medium bedded, shaley weathering buff and light buff biomicrite A. peculiaris
	17	56.4	Thickly bedded tan mixed biomicrite and biosparite A. peculiaris

Unit	Sample	Cumulative Thickness (m)	Description
	18	58.4	Thin to medium bedded cobbly weathering light grey to buff biomicrite A. peculiaris
	19	60.4	Thickly bedded light grey micrite with hackly to cobbly weathering
	20	63.3	Medium bedded light grey biomicrite with thin interbedded shale A. peculiaris
	21	67.2	Medium bedded light grey biomicrite with slabby weathering A. peculiaris
3	22	68.9	Medium to thinly bedded cobbly weathering buff to grey biomicrite C. micropunctatus
	23	72.3	Medium to massively bedded slabby weathering biomicrite C. quadrifidus
	24	75.2	Unevenly bedded light grey biomicrite with pebbly weathering A. peculiaris
	25	77.0	Cobbly weathering buff and grey micrite with medium bedding
	26	80.0	Medium bedded dark grey micrite with interbedded shales
	27	81.1	Cobbly to slabby weathering buff to light grey micrite with thin to medium bedding and mudcracks (Plate 5, fig. A)
	28	87.3	Thin to medium bedded grey micrite with slabby to shaley weathering

Stanley Farm

Unit	Sample	Cumulative Thickness (m)	Description
1	1	4.1	Unevenly bedded micrite containing chert and interbedded with shale P. avondalensis
	2	6.9	Thinly bedded biosparite C. angulatus
	3	9.7	Thinly bedded biomicrite with slabby weathering P. planobasalis C. quadrifidus C. angulatus
	4	12.0	Thickly bedded, cobbly weathering biomicrite (Plate 5, fig. E) P. planobasalis
	5	13.5	Cobbly weathering, unevenly bedded buff to grey biomicrite interbedded with shale P. planobasalis A. peculiaris B. appressa
	6	15.6	Thinly bedded, pebbly weathering bimicrite H. punctatus P. planobasalis C. micropunctatus T. cryptoplicatus A. peculiaris D. vesperalis C. tennesseensis U. eximia Rhombiferan A R. pyriformis M. uniplicatus

Unit	Sample	Cumulative Thickness(m)	Description
1	7	18.4	Cobbly weathering biomicrite with thin uneven beds interbedded with shale (Plate 5, fig. F) H. punctatus P. avondalensis P. planobasalis C. micropunctatus A. hydraulicus A. punctatus T. cryptoplicatus A. peculiaris D. vesperalis C. quadrifidus R. appressa C. tennesseensis U. eximia Rhombiferan A C. angulatus R. pyriformis A. barrandei M. natus
	8	21.3	Dark grey thickly bedded biomicrite which weathers to large slabs (Plate 5, fig. C) H. punctatus P. planobasalis C. micropunctatus A. hydraulicus T. cryptoplicatus A. peculiaris D. vesperalis C. quadrifidus R. simplex C. tennesseensis U. eximia
1	9	27.4	Thinly bedded light grey biomicrite which weathers to small cobbles P. avondalensis A. hydraulicus T. cryptoplicatus A. peculiaris D. vesperalis

Unit	Sample	Cumulative Thickness (m)	Description
			C. quardifidus B. appressa U. eximia M. hudsoni
	10	31.8	Thinly bedded slabby weathering dark grey biomicrite P. planobasalis A. peculiaris B. appressa
	11	35.1	Thickly bedded dark and light grey biomicrite with slabby weathering
	12	45.6	Unevenly bedded light grey biomicrite with interbedded shale A. peculiaris
	13	47.5	Cobbly weathering biomicrite interbedded with thick shale C. micropunctatus A. peculiaris
Total thickness Unit 1 = 49.0 meters			
2	14	49.1	Thickly bedded dark grey biosparite (Plate 5, fig. D)
Total thickness Unit 2 = 3.3 meters			
3	15	60.5	Massively bedded dark grey micrite which forms a shallow slope
	16	66.7	Thinly bedded, slabby weathering biomicrite interbedded with thick shale units A. peculiaris
	17	70.9	Medium bedded biomicrite interbedded with shale units up to 3 cm thick A. peculiaris

Unit	Sample	Cumulative Thickness (m)	Description
	18	73.1	Thickly bedded light grey biomicrite with slabby weathering (plate 5, fig. B) P. avondalensis P. planobasalis C. micropunctatus A. peculiaris C. quadrifidus
	19	75.3	Thinly bedded light grey biomicrite with cobbly weathering H. punctatocristatus A. peculiaris
3	20	79.4	Slabby to cobbly weathering light grey to buff micrite interbedded with thin shale
	21	82.3	Unevenly bedded dark grey biomicrite with slabby weathering A. peculiaris
	22	84.7	Slabby to cobbly weathering biomicrite interbedded with thick shale units A. peculiaris
	23	86.5	Cobbly weathering biomicrite with few distinct beds, interbedded with thick shale units A. peculiaris
	24	92.0	Slabby weathering micrite interbedded with shale
	25	94.7	Thickly bedded slabby micrite interbedded with buff-colored shale A. peculiaris
	26	95.3	Thinly bedded slabby micrite interbedded with thick shale units

Unit	Sample	Cumulative Thickness(m)	Description
	29	93.1	Massive dark grey sparite with slabby weathering and interbedded with buff-colored shale
	30	98.5	Massive to thinly bedded mixed sparite and micrite with clay partings and stromatolitic structures

Total thickness of Unit 3 = 44 meters

Plate 5. Outcrop Photographs

Fig A. Slab surface showing possible mudcracks. Slab is composed of buff-colored shale and was dampened to show the cracks more clearly. Sample is from Evans Ferry, horizon 27, 81.1 meters, XO.5.

Fig B. Stanley Farm, horizon 18, 73.1 meters. Outcrop surface showing distinctive bedding.

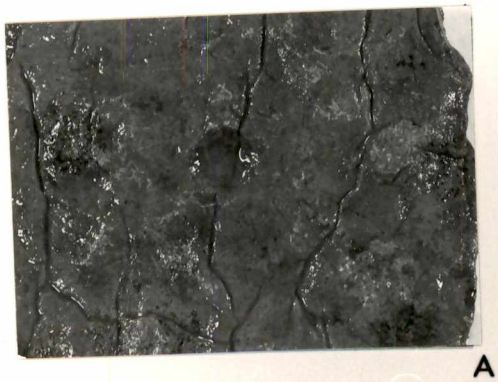
Fig. C. Stanley Farm, horizon 8, 21.3 meters. Photograph shows characteristic weathering to large slabs.

Fig D. Stanley Farm, horizon 14, 49.1 meters. Outcrop surface showing standard massive Unit 2 weathering.

Fig. E. Stanley Farm, horizon 4, 12.0 meters. Photograph shows weathered but thickly bedded outcrop.

Fig. F. Stanley Farm, horizon 7, 18.4 meters. Typical collecting surface from the horizon of highest faunal diversity. Most specimens had been weathered out of the underlying rock.

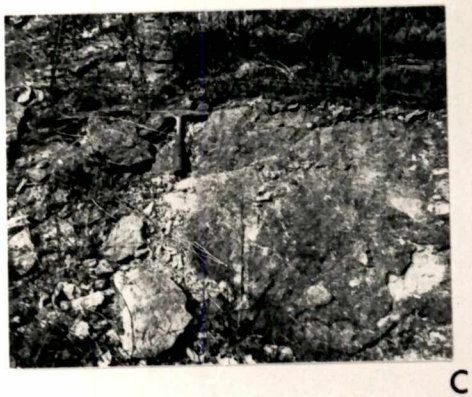
Plate 5



A



B



C



D



E



F

VITA

Lisa Sophia Bienkowski was born in Boston, Massachusetts on October 17, 1960. She received her elementary education in Pasadena, California; Taplow, Buckinghamshire, England, and Princeton, New Jersey. She graduated from Princeton High School in 1978 and afterwards attended Bryn Mawr College in Pennsylvania. In 1982, she graduated with a B.A. in Geology and accepted a teaching assistantship at the University of Tennessee, Knoxville where she began her study for the Master of Science degree. This degree was awarded in March, 1985.