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Coral Growth and Adaptation in a Storm Influenced, Level-Bottom Setting, Lobelville Member of the Brownsport Formation (Upper Silurian), West-Central Tennessee

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Christopher D. Olson

August 1993

To Hazel Olson and the late Mabel Lee,

who made a young man,
a long way from home for the first time,
always feel loved.

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ABSTRACT

The Lobelville Member of the Brownsport Formation (Upper Silurian - Ludlow) is a part of a nearly continuous succession of Silurian and Devonian age limestones and shales exposed in a narrow outcrop belt in the western valley of the Tennessee River in Tennessee. The Lobelville is a 10.1-15.5 m thick sequence of interbedded echinoderm-bryozoan wackestone and gray shale, deposited in a level-bottom, tropical marine setting at depths below fairweather wave base, but still affected by episodic disturbances. Strong currents, associated with large storms, disturbed the slowly accumulating skeletal sediment and introduced terrigenous mud which blanketed areas of the seafloor. The frequency of disturbance and sediment influx increased over time, culminating in the deposition of 0.5-1 m thick sequences of gray shale, interbedded with thin limestone beds and lenses. Stratigraphically, the Lobelville is underlain by the Bob Member of the Brownsport Formation and overlain by the Decatur Formation. Both units are composed of massive-bedded echinoderm packstone, deposited in shallow water shoal environments at depths above normal wave base.

Within the Lobelville an abundant and diverse coral fauna is present. Two species of tabulate coral, *Favosites louisvillensis* and *Thecia minor* exhibit a distinctive large, platey growth habit which is interpreted to be an adaptation to the episodically disturbed, soft substrate environment. Genetic factors, governing corallite ontogeny and colony astogeny, appear to have had the greatest control on the growth form of these species. Individual corallites of *F. louisvillensis* and *T. minor,* had small mature diameters (1-2 mm wide), suggesting progenetic development, which allowed the corallites to reach maturity sooner. The resulting rapid generation of offsets, primarily at colony margins, promoted the development of large colony sizes, a trait which increased colony and species survival in the Lobelville environment. The large, platey colonies were less likely to be overturned during a disturbance, as well as less likely to be totally buried by

storm-derived sediment following a disturbance. When partially buried, the rapid generation of offsets promoted colony regeneration over sediment covered areas, resulting in colony reestablishment and further outward colony increase.

Four ecologic factors were identified as having some degree of effect on *F. louisvillensis* and *T. minor* colony growth: 1) rate and pattern of sediment accumulation; 2) normal and storm generated currents; 3) substrate conditions; 4) competitive interactions. Although colony development was often altered by one or more of these ecologic factors, genetic controls had a much greater affect on the overall development and growth form of *F. louisvillensis* and *T. minor* colonies.

Low velocity water currents often scoured small, ephemeral cryptic habitats beneath colony margins of large, platey tabulate corals living on the Lobelville mud-rich substrate. A low diversity, opportunistic assemblage, dominated by bryozoans and spirorbid worms, colonized these cryptic substrates. Cavity longevity was controlled by the rate of sedimentation, frequency of disturbance and host growth responses. These factors limited the duration of a cryptic habitat, which in turn limited the diversity and growth of colonizing epibionts.

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Chapter 1: Introduction

General Introduction

A nearly continuous succession of fossiliferous Silurian and Devonian age limestones and shales are exposed in a narrow outcrop belt in the Western Valley of the Tennessee river (Fig. 1). Many of these rocks have long been known to be richly fossiliferous. In this area, the Brownsport Formation (Upper Silurian, Ludlow), approximately 30 meters of interbedded limestone and gray shale (Fig. 2), has been divided into three members: (in ascending order) Beech River, Bob, and Lobelville (Pate and Bassler 1908). Fossils can be found in all three members, but fossils from the Beech River and Lobelville members have received the most study. The shale and argillaceous limestone of the Beech River and Lobelville members weather to form low "glades" which "are relatively free of vegetation, bearing only scattered clumps of grass and a few stunted cedar trees" (Amsden 1949, p. 9). "In the process of erosion the fossils are left behind, so that in the course of time most of the glades become ideal collecting grounds. Indeed, fossils are sometimes so abundant on the glades that specimens can be shoveled up literally by the bushel measure" (Pate and Bassler 1908, p. 407).

In addition to lithologic distinctions, each member of the Brownsport Formation is characterized by a particular dominant group of fossils. The interbedded limestone and shale of the Beech River Member is known for well preserved echinoderms, the massive limestones of the Bob Member are known for abundant brachiopods, and the interbedded limestone and shale of the Lobelville Member is known for a diverse tabulate and rugose coral fauna. The Lobelville strata and corals found within are the focus of this study. The coral fauna was first described by Roemer (1860) and also mentioned by Safford (1869), who noted that the number of "species of new corals, especially, are quite numerous." Pate and Bassler (1908) noted that the Lobelville was "characterized by a fauna of corals so abundant in species and specimens, that the identification of the beds is attended

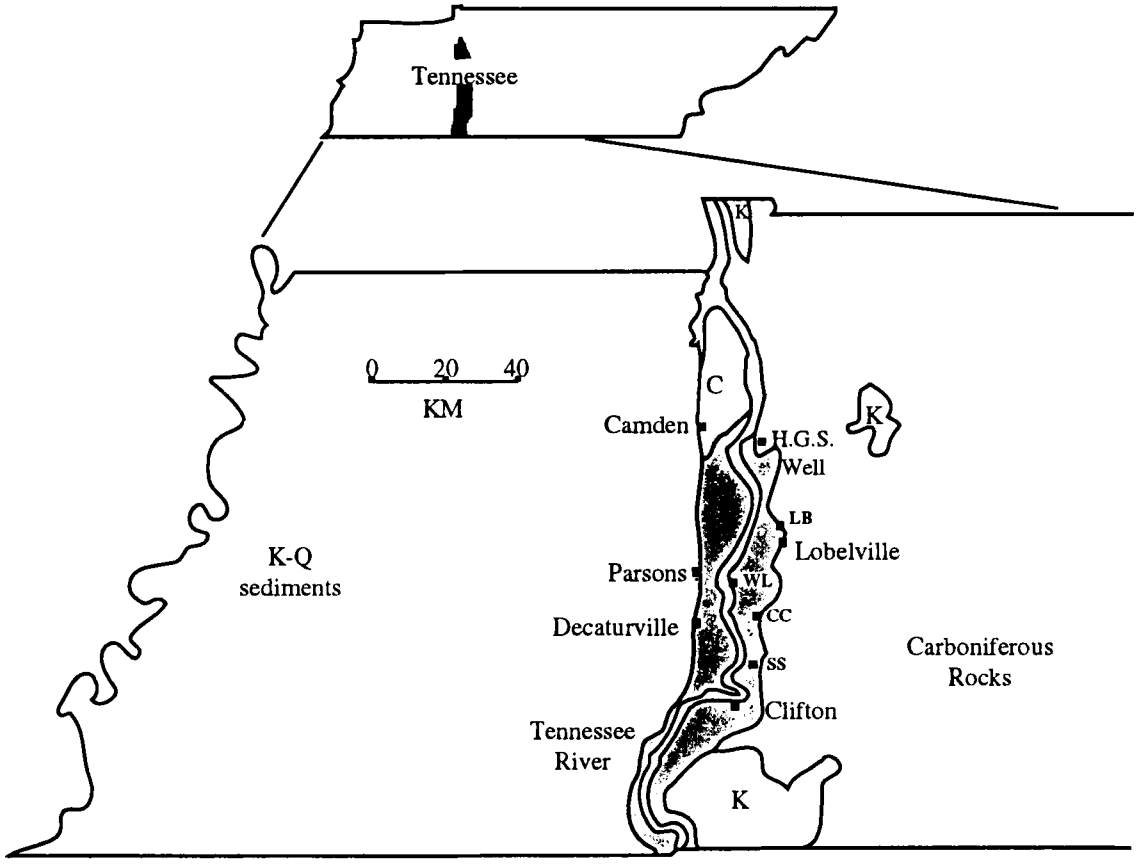


Figure 1. – Location of study area in a north-south trending outcrop belt of Silurian to Devonian age rocks (stippled region) along the Tennessee River in western Tennessee (modified from Broadhead and others, 1989). Location of measured sections labeled with abbreviations: LB - Lobelville, WL - Webb's landing section, CC - Cane Creek section, SS - Sewell Springs. Other abbreviations: H.G.S. Well - Dupont Hydrogeologic Survey Corehole; C - Carboniferous age deposits; K-Q - Cretaceous to Quaternary age deposits.

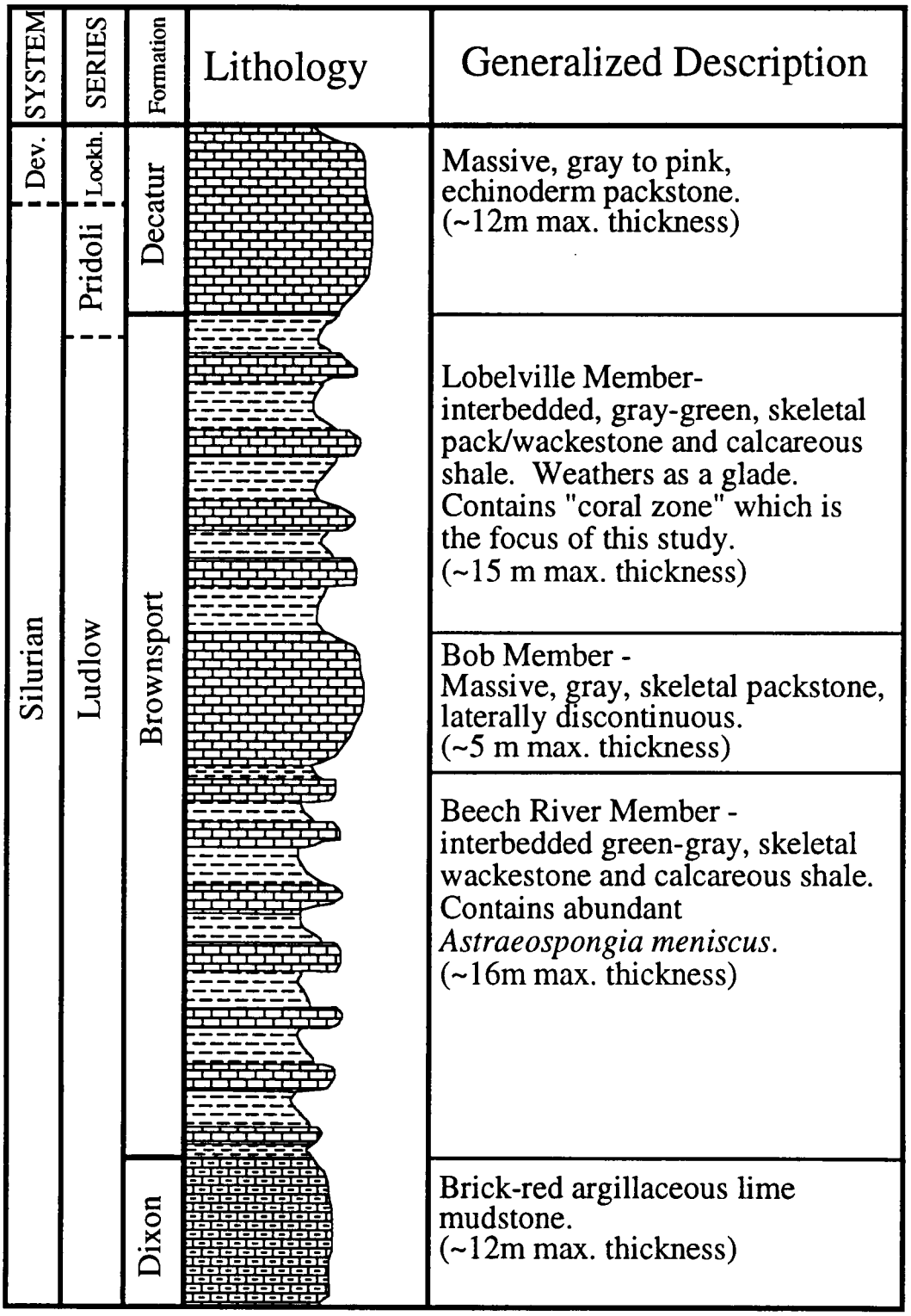


Figure 2. - Generalized stratigraphic section of the Brownsport Formation (Upper Silurian), west-central Tennessee (from Amsden, 1949; Wilson, 1949)

with little difficulty" (Pate and Bassler 1908, p. 422). The description and systematics of corals, brachiopods, and echinoderms from the Brownsport Formation done by Amsden (1949) are the most complete to date and are used here.

Geologic Setting

The Upper Silurian-Lower Devonian sedimentary rocks of the Western Valley were deposited on a gently sloping shelf at approximately 25-30° south latitude (Gibson 1988). This shelf was bounded by the Illinois Basin to the north, the Reelfoot Rift system to the west, the continental edge to the south and the Nashville Dome to the east (Fig. 3). Stearns and Reesman (1986) concluded that the Nashville Dome was a topographically positive feature during the Late Silurian-Early Devonian. It is unclear if the Nashville Dome was subareally exposed, providing a source of terrigenous sediment. Since the middle Paleozoic, the area has remained remarkably stable and was apparently little affected by the tectonic activity associated with Appalachian and Ouachita mountain building.

Historical Background

The "glades" of western Tennessee have attracted the attention of paleontologists and stratigraphers for over 150 years (Safford 1861; Pate and Bassler 1908; Amsden 1949). The first scientific study of west Tennessee fossils was made by German paleontologist, Ferdinand Roemer, who spent five weeks in West Tennessee near Decaturville during the summer of 1847. The publication of his collections made from the glades (Roemer 1860) was a "valuable and elegant monograph" (Safford 1861, p. 27) used as a reference of Late Silurian age fossils for many years.

Stratigraphic as well as further paleontologic description of the Brownsport Formation began when Safford (1861) published a description of the Silurian strata

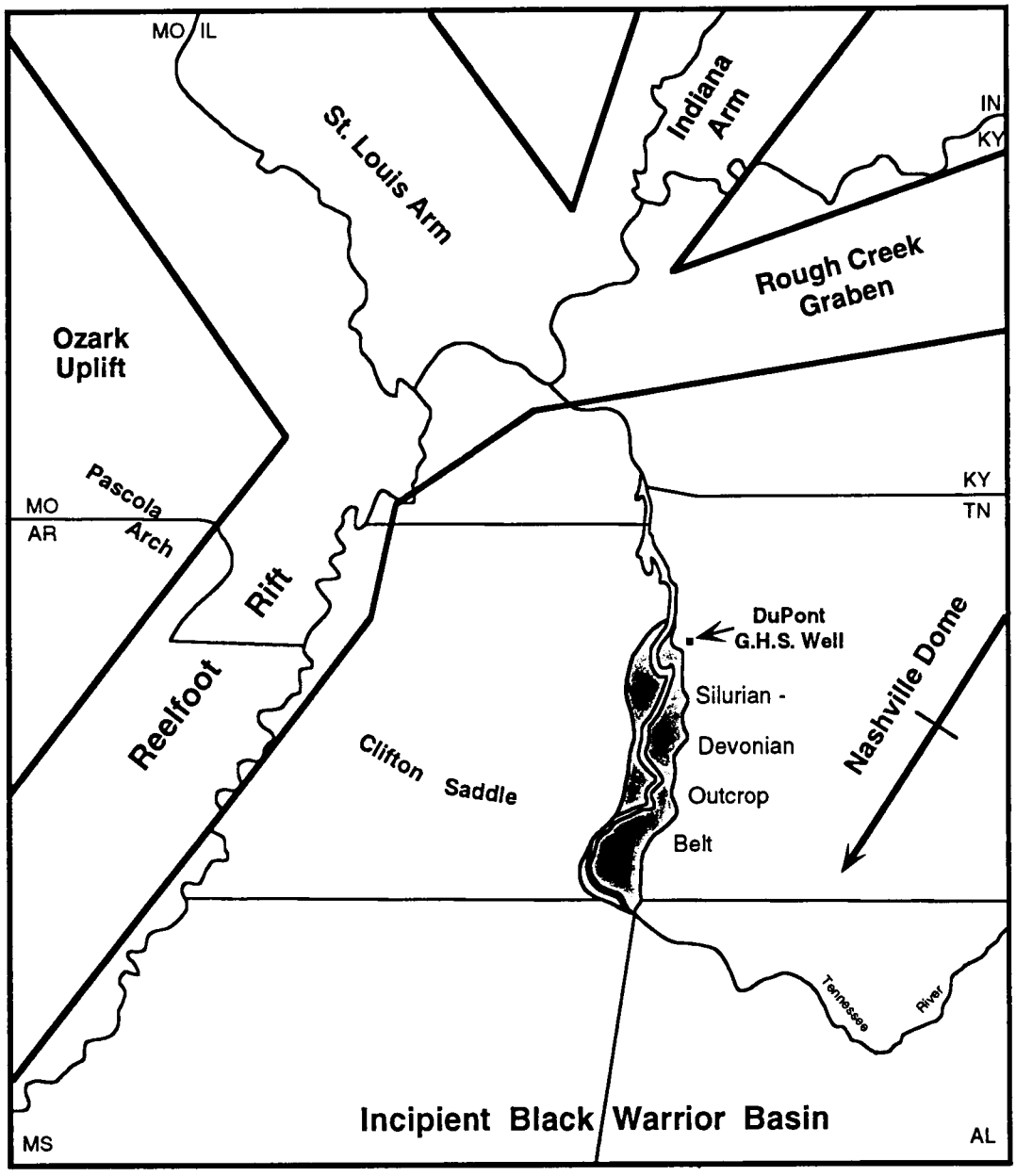


Figure 3. - Sketch map showing the regional tectonic features in vicinity of study area (Modified from Gibson 1988)

exposed near Clifton. He named the glade-forming limestones of the area the "Meniscus Beds" after the fossil sponge *Astraeospongia meniscus* Roemer. This unit rested on Safford's "variegated beds" now known as the Dixon Formation. The "Meniscus Beds" also included at the top, a "Grey Crinoidal Limestone", which is now referred to the Decatur Formation. Safford and Killebrew (1876) later changed the name of the "Meniscus Beds" to the Clifton Limestone, named for the exposures in the Clifton area.

Foerste (1903) was the first to propose the name Brownsport Formation for the Silurian beds overlying the red claystone of the Dixon Formation, in the area of the Brownsport Furnace. The Brownsport was described as 120 feet of massive limestone and limey shale beds. Foerste also included the massive limestone beds of the Decatur Formation as the upper part of his Brownsport Formation.

Pate and Bassler were contracted by Frank Springer to collect echinoderm specimens from the Silurian and Devonian strata of West Tennessee, and published one of the first lithologic descriptions of the Brownsport (Pate and Bassler 1908). They separated the "clayey shale and limestone" beds of the Brownsport and the upper massive limestone beds of the overlying Decatur Formation into separate units. The Brownsport was elevated to the status of group and subdivided into three formations: Beech River, Bob, and Lobelville. Pate and Bassler (1908) believed that these units were bounded by unconformities. The Beech River Formation, the stratigraphically lowest unit, was named for exposures along the Beech River near Perryville. The Bob Formation was named for exposures near Bob's Landing on the west side of the Tennessee River. The uppermost unit, the Lobelville Formation was named for exposures near Lobelville. This division of the Brownsport into three formations was based mainly on faunal content: the Beech River contains a diverse echinoderm fauna, the Bob contains brachiopod bearing beds and the Lobelville can be identified by the diverse coral fauna mentioned previously. A total composite thickness of 257 ft. was given for the entire Brownsport Group.

Since then only the Tennessee Geological Survey has used the Brownsport Group designation on a regular basis (Wilson 1949, 1967).

Later workers (Dunbar 1919; Miser 1921; Jewell 1931) concentrated on a lithologic subdivision of the Brownsport. Dunbar (1919) used the group designation but failed to directly correlate faunal composition and lithology. Miser (1921) and Jewell (1931) each revived the Brownsport Formation designation and named the Beech River, Bob and Lobelville as members. This classification scheme is used by the United States Geologic Survey (Wilmarth 1938), and will be used here. Ball (1941, 1942) briefly described the different lithologies of the Brownsport Formation and made tentative correlations to the Bainbridge Formation of southeastern Missouri. These correlations were based mainly on lithologic characteristics, therefore any time equivalence is suspect. Amsden (1949, p. 36) mentioned the possibility that the two units might be time equivalent, but stated "there does not appear to be sufficient evidence to justify any definite conclusion."

Wilson (1949) discussed and chose the group designation for the Brownsport in his study of the Pre-Chattanooga stratigraphy of Central Tennessee. He agreed with Pate and Bassler (1908) that the three members fit the requisites for formations, although he admitted that the Bob Formation is not everywhere present. Wilson based the division and identification of the individual formations on characteristic faunal assemblages, although he noted that the faunal zones may be present in more than one formation. For example he stated that the upper Beech River locally contains an "unusual concentration of corals" similar to the zone seen in the Lobelville. Based on this observation, Wilson's division of the Brownsport based on fossil assemblages is tenuous, and it is unclear exactly how he distinguished the individual formations.

Amsden's (1949) report is the most complete study of the Brownsport Formation to date. His stratigraphic work, based both on lithology and paleontology, indicated that

there is no evidence for a consistent three-fold subdivision of the Brownsport. Amsden objected to the formational subdivision because the crinoid, brachiopod and coral horizons, used by Pate and Bassler to divide the Brownsport, are not everywhere present, and those species numerous enough to be representative, are not confined to any particular horizon. Based on this evidence, he chose to use the Brownsport Formation designation. Amsden's detailed stratigraphic study also showed that the massive limestone beds of the Bob exist at approximately the same stratigraphic level, but are not everywhere present in the study area. Based on this information, coupled with his observation that the Beech River and Lobelville are very similar in lithology, Amsden chose not to divide the Brownsport into three members.

I argue that the Brownsport can be subdivided into members. The North American Commission on Stratigraphic Nomenclature (1983) states that a formation is divided into members to serve a useful purpose. The fossil zones that characterize each member allow determination of stratigraphic position within the formation. Due to the lithologic similarity of both the Beech River and the Lobelville, as well as the limited and widely spaced nature of outcrops in the study area, this is quite useful. Field observations made during this study lead me to conclude that the fossil "zones" noted by earlier workers, appear at approximately the same stratigraphic level within the Brownsport throughout the study area. Wilson's (1949) "concentration of corals" in the upper Beech River was not observed, seemingly confining this "zone" to the Lobelville. The fossils of these "zones" are used as distinctive lithic features to define the three members. These lithic constituents can be used to define separate formations, "but even if all the members are mappable, it does not follow that they should be raised to formational rank; proliferation of formation names may obscure rather than clarify relations in other areas" (North American Commission on Stratigraphic Nomenclature 1983)

Studies of the Brownsport Formation since 1949, have concentrated only on

individual fossil groups collected mainly from the prolific "glades" of the Beech River and Lobelville members. Amsden (1951) compared the brachiopod fauna of the Henryhouse Formation in Oklahoma to the fauna of the Brownsport. Of 27 genera present in the Henryhouse, 24 were present in the Brownsport, suggesting that the two formations "are closely related" (Amsden 1951). Stumm (1952) examined and reclassified previously collected rugose coral specimens, and Cooper (1955) identified a new genus of brachiopod. Perry and Hattin (1958) and Corneliussen and Perry (1973) described in detail the bryozoan fauna of the Brownsport. Edgecombe (1990, 1991) recently has revised the systematics of the trilobite fauna found in the Brownsport.

Purpose of Study

Previous work on the Brownsport has been limited to stratigraphic correlation and paleontologic studies. The purpose of this study has been to use macroscopic and petrographic examinations to develop a general paleoenvironmental interpretation for the Beech River and Bob members and a more detailed analysis of the paleodepositional environment of the Lobelville Member of the Brownsport Formation. Two species of tabulate coral exhibiting a large platey colony form, *Favosites louisvillensis* Davis and *Thecia minor* Rominger, found within the Lobelville were further examined to determine the relative affects of genetic and ecologic controls on colony growth. These interpretations were used to interpret the adaptive advantages of the growth forms exhibited by *F. louisvillensis* and *T. minor*. Furthermore, cryptic epibionts, found on the basal corallum surface of many Lobelville tabulate corals were examined to determine the conditions under which this particular form of colonization occurred.

Location of Study

Three stratigraphic sections (Fig. 1) located in Perry County, TN, were chosen for

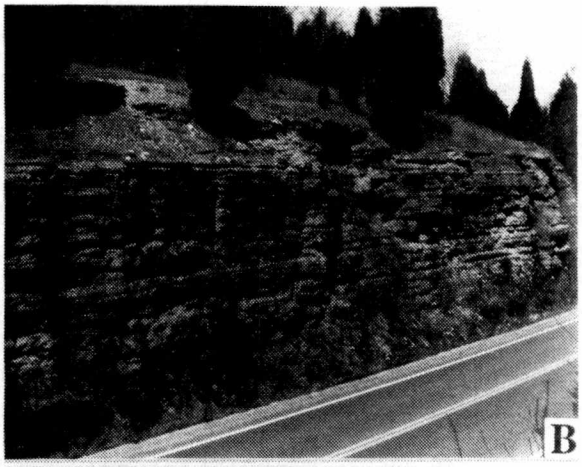
detailed examination: 1) Lobelville (LB): a road cut (Fig. 4B) along Tennessee State Highway 13, 1 mile north of Lobelville, TN; 2) Webb's Landing (WL): a road cut (Fig. 4C) along Marsh Creek Rd., approximately two miles southeast of the Tennessee River Bridge on State Highways 100/412; 3) Cane Creek (CC): an outcrop (Fig. 4D) along the west side of Cane Creek, 0.5 miles south the State Highway 50. Within these sections, all or nearly all of the Lobelville Member is present, along with a diverse and abundant coral "zone." Other tabulate corals were collected from different localities in the study area, but the typical "glade" exposures of the Brownsport Formation are not conducive to detailed stratigraphic sampling, eliminating the use of many exposures from this study. Appendix A gives a detailed description of the measured sections.

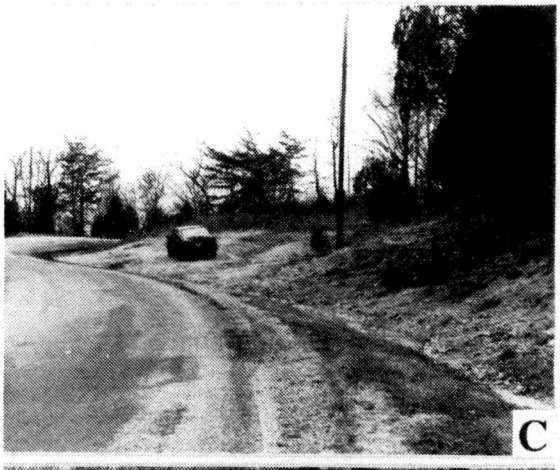
Methods

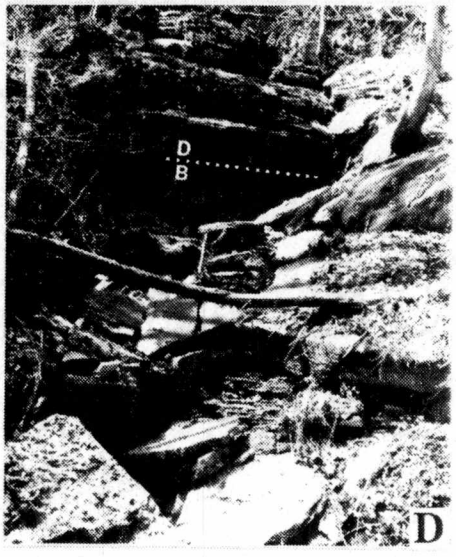
Each stratigraphic section was measured bed by bed, to the nearest centimeter, and beds were informally grouped as units based upon similarities observed in the field. The low "glade" type exposures (Fig. 4A) present at the top of the Lobelville and Webb's Landing sections were described as one unit in as much detail as possible. Each unit within the Lobelville Member interval was individually sampled, with an average sample interval of 60 cm (range 1 cm to 280 cm). From the 46 samples collected, 45 5 cm x 7 cm thin sections were made. Additionally, 16 thin sections were made from samples taken from the DuPont Geohydrological Survey Well Core (Fig. 1). Point counts of 17 thin sections were completed to determine abundance of allochems, cements and mud. This information was used in the formulation of a depositional model for the Lobelville Member. Numerous coral specimens from the study area were examined, including 97 *Favosities louisvillensis* colonies (21 of which had cryptic epibionts) and approximately 78 *Thecia minor* coralla (including large fragments). Approximately 25 coralla were found *in situ* and collected with attached matrix. Overlying shale layers were

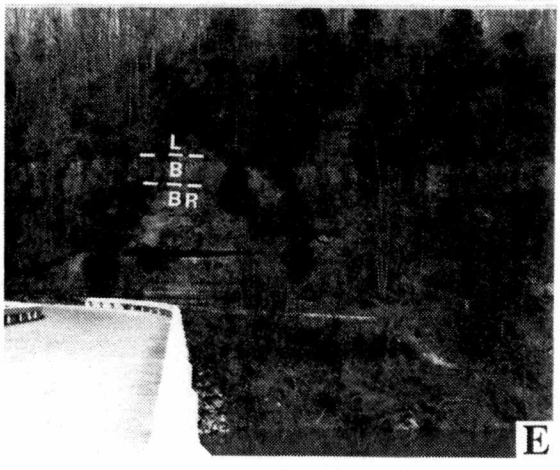
Figure 4.- Outcrops from study area. A) Low relief "glade" type exposure at top of section LB (Fig 4B). B) Section LB, along Tennessee State Highway 13. 9.8 m of the Lobelville Member of Brownsport Formation is exposed. "Glade" exposure present at top of outcrop. C) Low relief "glade" at section WL, exposing approximately 8 m of the Lobelville Member. D) Section CC, showing the upper 1.8 m of the Lobelville (B) and the contact with the overlying Decatur Formation (D). E) Photo of outcrop along Buffalo River, 1 mile east of Linden, TN, showing all three members of the Brownsport Formation (L - Lobelville, B - Bob, BR - Beech River).


A


B


C


D
B
D


L
B
BR
E

sampled to determine the nature, source, and composition of the gray shale. An additional 25 *Favosites louisvillensis* specimens, housed in the Yale Peabody Museum, were examined for additional taxonomic and paleobiologic information.

Individual colonies of *Favosites louisvillensis* and *Thecia minor* weathered free of the outcrop were collected for detailed study of growth patterns. Fourteen thin sections, five acetate peels and 17 longitudinal slab cuts were made of these samples to examine skeletal development patterns. The fossil specimens were cleaned by boiling in a solution of water and the industrial surfactant Miramine OC-ES. Growth patterns and epibiont-host relationships were interpreted based upon observations of external features, thin-sections and longitudinal slabs.

Chapter 2: Petrology and Paleodepositional Environment of the Lobelville Member and Stratigraphically Adjacent Units

Introduction

The stratigraphic record of Western Tennessee includes a nearly complete section of Early Silurian to Early Devonian carbonate rocks and interbedded shales (Fig. 5). Changes in carbonate lithologies, used to distinguish formations and members, represent relatively subtle megascopic changes in terrigenous mud content, in sediment texture, and in relative abundance of different types of fossil allochems (Broadhead and others 1992). Upon detailed examination, however, these subtle differences provide keys not only to differentiating each unit, but also to interpreting the depositional history of each unit. The Brownsport Formation (Upper Silurian), the focus of this study, has been subdivided (Fig. 2), based on similar criteria, into three members in ascending order: Beech River, Bob and Lobelville (Pate and Bassler 1908). The Lobelville Member of the Brownsport Formation consists of interbedded skeletal wackestone and terrigenous shale and contains an extremely diverse and abundant coral fauna, part of which is the focus of detailed study in chapters 3 and 4. The entire Brownsport is overlain by the Decatur Formation (Upper Silurian - Lower Devonian) and underlain by the Dixon Formation (Upper Silurian) of the Wayne Group. Deposition during the Dixon through Decatur interval appears to have been continuous.

Close examination of any sedimentary unit reveals that sediment did not simply accumulate on the seafloor in continuous succession. The entire stratigraphic record has a duality which can be defined by two temporally distinct processes: (1) physical disruptions superimposed upon the (2) background accumulation of sediments. Neither process is independent, both acting in concert to preserve the physical and biological conditions present during deposition (Speyer and Brett 1988, 1991). Distinct taphonomic signatures are produced by each of these processes, recording information invaluable for the correct interpretation of paleodepositional conditions.

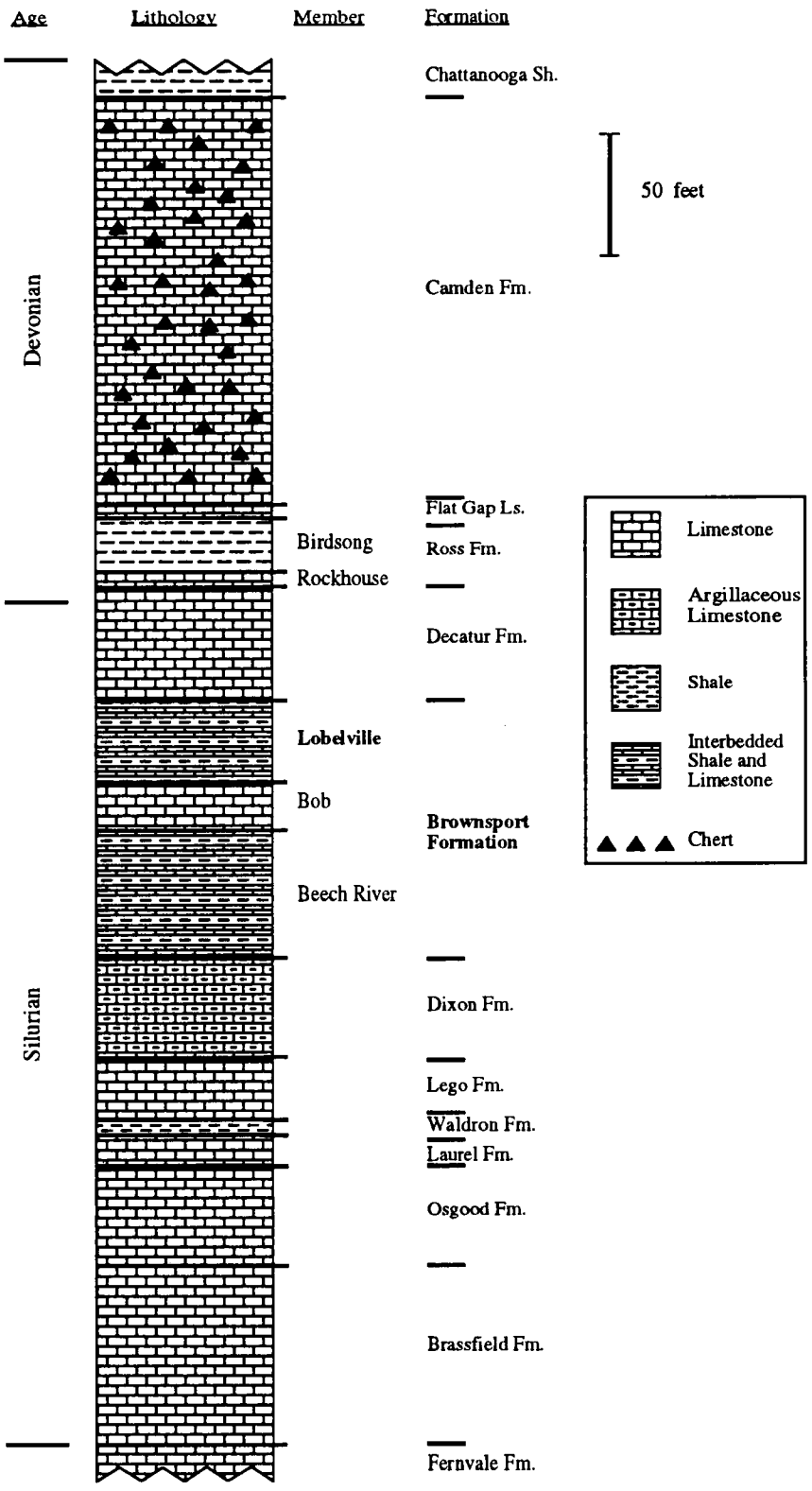


Figure 5. – Silurian - Devonian stratigraphic section described from the DuPont Geohydrological Survey Deep Well Core (Broadhead and others, 1992).

The accumulation and preservation of skeletal sediment is influenced by taphonomic processes which occur over long periods of time, on the order of hundreds to thousands of years. Background conditions are governed by three interrelated factors (Speyer and Brett 1991). First and most importantly is the rate of burial. In a sediment-deprived depositional setting, fossils and sediment are exposed to physical, chemical and biological degradation and overgrowth before burial. Secondly, environmental energy affects the original spatial relationships of allochems and other sedimentary particles. The third factor is bioturbation, which can have as much effect on preservation of sediment as both of the previously mentioned physical processes.

On the other end of the temporal scale, episodic sedimentary processes occur over relatively short periods of time, on the order of hours or days. Discrete events such as storms or debris flows mobilize and mix allochthonous and autochthonous fine-grained sediment, which is deposited elsewhere on the seafloor during the waning stages of the disturbance. Original community patterns and local substrate conditions will be preserved in areas negligibly disrupted and quickly buried by the fine-grained sediment blanket. These geologic "snapshots" can provide information which is normally erased by the daily taphonomic processes of the seafloor.

Strata of the Brownsport, with emphasis on the Lobelville Member are described and interpreted with this understanding of the dominant depositional processes. The results are presented below, along with brief description and interpretation of stratigraphically adjacent units.

Dixon Formation

The Brownsport Formation conformably overlies the Dixon Formation, which is the uppermost unit of the Wayne Group (Upper Silurian Wenlock) (Barrick 1983). In the study area the Dixon is a 11.3 m thick (12.5 m thick in the DuPont G.H.S. Core), uni-

formly bedded (Wilson 1949), red, earthy, calcareous mudstone, "locally mottled with green" (Amsden 1949). The red coloration is likely due to an increased amount of iron oxide in the terrigenous clastic sediment. Siliciclastic sediment, primarily clay and quartz silt, make up more than 20% by weight of insoluble residues (Barrick 1983). This proportion of fine-grained siliciclastic sediment is much higher than that of both the underlying Lego Limestone and overlying Brownsport Formation. Barrick (1983) attributed this to a relatively sudden influx of terrigenous clastic material from the east, into southern Kentucky and central Tennessee, which suppressed carbonate production. It does not appear that net rate of sediment accumulation slowed, but that siliciclastic sediment accumulated at the expense of carbonate sediment. Wilson (1949) noted that the "Dixon is practically unfossiliferous." The few fossils encountered during this study include disarticulated echinoderm columnals, ostracodes, small brachiopods, sponges, tabulate corals and molds of straight-shelled nautiloids. Corals and brachiopods are notably rare, and stromatoporoids are absent; all of these were common to shallow, subtidal marine conditions during the Silurian (Cocks and McKerrow 1978). Throughout the study area, the uppermost Dixon is a red, less commonly green, thin-bedded mudstone (Amsden 1949). The predominant red coloration suggests that shallow water, oxygen-rich conditions prevailed during deposition of the upper Dixon. The Dixon environment supported only a limited population of marine invertebrates: much of the skeletal component of the upper Dixon sediment apparently was washed in from offshore, open water environments. This evidence suggests that the Dixon was deposited in a variably oxygenated, shallow marine mudflat environment strongly influenced by terrigenous mud influx. The upper Dixon conformably grades into a green shale at the base of the Brownsport (Amsden 1949).

Brownsport Formation

Beech River Member

The Beech River Member is the lowest stratigraphic unit of the Brownsport Formation (Figure 2) and is composed of 16.1-20.4 m (Amsden 1949; Broadhead and others 1992) of interbedded, thin-bedded shale and thin- to medium-bedded echinoderm wackestone and packstone (Fig. 4E). Wilson (1949), placed the base of the Brownsport at the top of the green shale just below a "regionally persistent basal limestone bed." This "five-foot (1.5 m) average thickness" limestone unit, however, was not consistently present throughout the study area of this project. Amsden (1949) chose to place the formational boundary at the base of regionally persistent green shale, above the red mudstone of the Dixon Formation. Field observations made during this study agree that Amsden's boundary is an adequate, consistent marker for delineating the two units.

Above the basal green shale the Beech River is a sequence of interbedded thin-bedded terrigenous shale and thin- to medium-bedded of echinoderm wackestone and packstone. The glades formed during the weathering of the Beech River are fossiliferous, commonly producing many specimens of the sponge *Astraeospongia meniscus.* The Beech River glades also have provided one of the most diverse echinoderm faunas known from the southern United States (Pate and Bassler 1908; Springer 1926). Fossils of many other groups of organisms are also common, including species of sponges, corals, bryozoans and brachiopods.

Petrographic examination of Beech River samples reveals an allochem content dominated by echinoderm and bryozoan debris, with small percentages of brachiopods and ostracodes; minor amounts of sponge spicules and trilobite and algal fragments are present, but not volumetrically significant (Table 1). Quartz silt is rare in most of the Brownsport, but is a common component of the fine grained terrigenous sediment influxes which formed the many shale beds of the Beech River. The abundance of quartz

Table 1 : Volume Percentage of Allochems Determenied by Point Count (n=300)

Sample	Mud	Cement	All Allochems	Allochems								Total Allochems
				Echinoderm	Bryozoan	Coral	Brachiopod	Ostracode	Trilobite	Glauconite	Algae	
	% of sample	% of sample	% of sample	% of sample	% of sample	% of sample	% of sample	% of sample	% of sample	% of sample	% of sample	% of sample
Decatur Formation												
LB1-D	40.3	14.3	45.3	35.0	1.3	0.0	7.3	1.7	0.0	0.0	0.0	45.3
WL-D1	38.3	4.7	57.0	32.0	18.7	0.0	1.3	5.0	0.0	0.0	0.0	57.0
WL-D2	35.0	12.3	52.7	19.0	28.7	0.0	2.0	3.0	0.0	0.0	0.0	52.7
CC-4	29.7	8.7	61.7	33.3	22.3	2.0	3.0	1.0	0.0	0.0	0.0	61.7
Brownsport Formation												
Lobelville Member												
LB1-17	13.0	38.3	48.7	25.0	19.7	1.3	0.0	2.7	0.0	0.0	0.0	48.7
LB1-13-1	40.3	4.0	55.7	34.7	15.0	0.0	4.3	1.7	0.0	0.0	0.0	55.7
LB1-10-1	50.3	1.3	48.3	23.0	9.7	0.0	5.7	2.3	1.7	6.0	0.0	48.3
LB1-8	41.3	6.7	52.0	46.7	2.0	0.0	3.0	0.3	0.0	0.0	0.0	52.0
LB1-6-1	45.3	6.3	48.3	20.3	14.3	0.0	9.7	4.0	0.0	0.0	0.0	48.3
LB1-1	23.7	16.0	60.3	52.7	3.7	0.0	2.0	2.0	0.0	0.0	0.0	60.3
WL-20	25.0	5.0	70.0	53.3	13.7	0.0	1.0	2.0	0.0	0.0	0.0	70.0
WLS-6-4	39.0	7.3	53.7	26.3	15.7	0.0	7.3	2.7	1.7	0.0	0.0	53.7
CC-3-1	38.3	3.3	58.3	22.7	27.3	0.0	7.0	1.3	0.0	0.0	0.0	58.3
CC-2-1	33.3	4.0	62.7	23.3	36.0	0.7	2.0	0.7	0.0	0.0	0.0	62.7
Bob Member												
WL-3	7.0	25.7	67.3	39.0	9.7	0.0	10.7	5.0	1.7	0.0	1.3	67.3
WL-2	39.3	4.3	56.3	40.0	13.7	0.0	1.7	1.0	0.0	0.0	0.0	56.3
Beech River Member												
WL-1	42.0	3.3	54.7	27.7	22.7	0.7	2.3	1.3	0.0	0.0	0.0	54.7
Avg. of all samples	**33.4**	**8.2**	**58.4**	**35.2**	**15.9**	**0.1**	**4.7**	**2.0**	**0.3**	**0.0**	**0.1**	58.4

sediment and the absence of glauconite suggest a fairly rapid rate of net sediment accumulation. The continuous build up of Beech River sediment was occasionally punctuated by sedimentary events such as storms. These disruptions mobilized sediment on the seafloor forming 1 to 3 cm graded beds and accompanying shale blankets which rapidly buried benthic organisms.

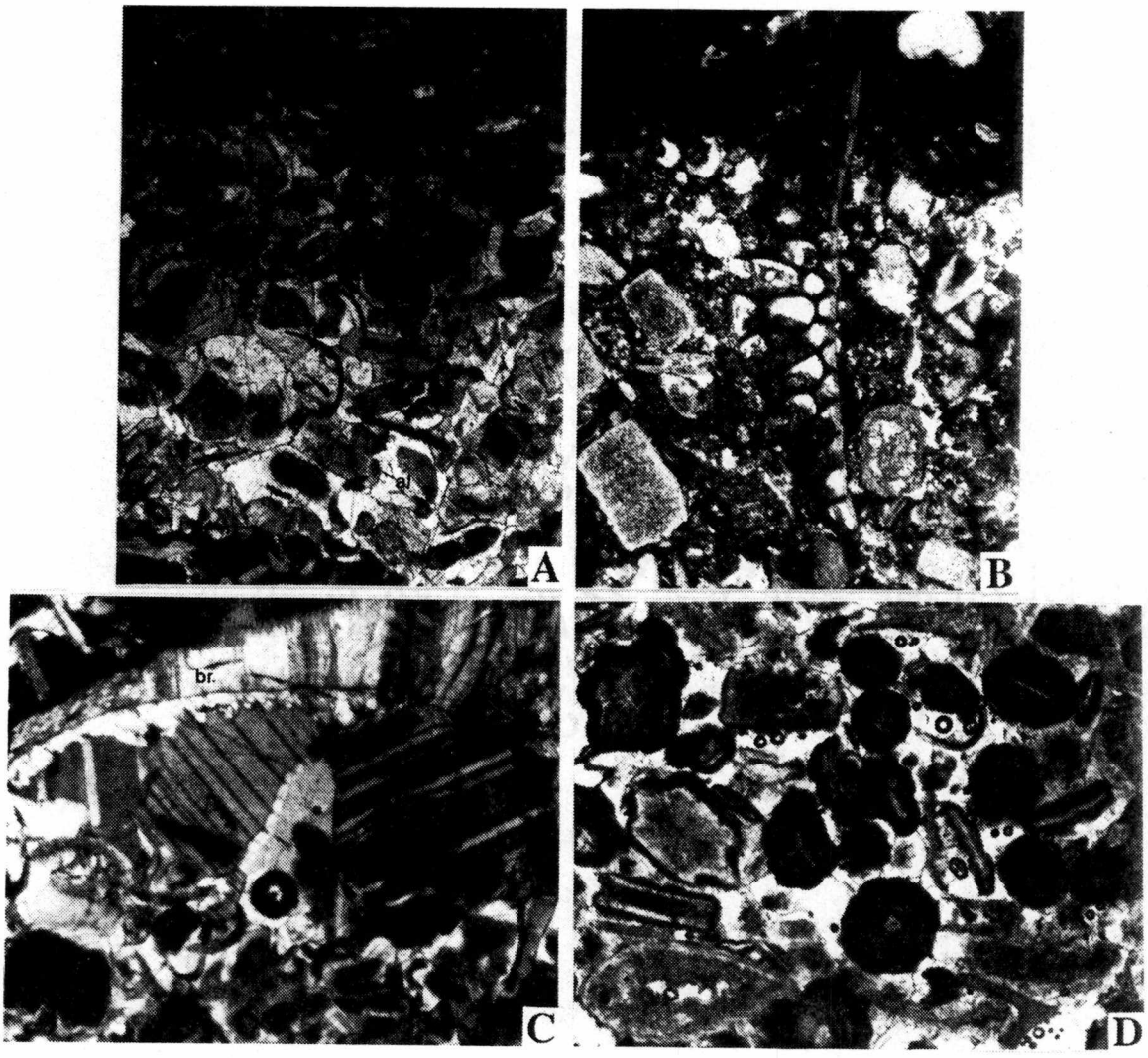
Fewer glades are developed near the top of the Beech River Member where the number and thickness of limestone beds increase and the number of shale interbeds decreases. The upper limestone beds of the Beech River grade conformably into the Bob Member (Amsden 1949).

Bob Member

Approximately 15-24 m above the base of the Brownsport (Amsden 1949), a 1.5-5 m thick (Amsden 1949; Broadhead and others 1992) unit (Fig. 4E) of medium- to thick-bedded, coarse grained, echinoderm packstone and grainstone (Fig. 6A and Table 1) is developed. These beds, known as the Bob Member, appear to have been deposited in shallower, more agitated water than the underlying Beech River. There are very few shale interbeds in this interval, indicating that either the source of terrigenous mud was cut off or mud introduced into the depositional environment was winnowed away by current or wave action. The limestone beds of the Bob are thicker and more evenly layered than those of the Beech River, suggesting a more constant, if not more rapid rate of net sediment accumulation.

Petrographic examination shows that skeletal grain composition of the Bob is dominated by echinoderm ossicles, similar to the rest of the Brownsport Formation, and locally greater in volume percent than in a sample from the Beech River Member (Table 1). Brachiopods and bryozoans are the next most abundant fossil grains, in contrast to the Beech River and Lobelville intervals where brachiopods commonly are only a minor

Figure 6.- Photomicrographs of significant petrographic features of the Bob Member. A) Graded bed showing upward gradation from grainstone texture to wackestone texture (sample WL-2). Note algal fragment (al) in bottom center of photo. B) Encrusting bryozoan, note the vertical orientation, indicating sediment disturbance prior to burial (sample WL-3). C) Shelter void beneath stably oriented, convex-up brachiopod valve. Note short bladed marine cements present along brachiopod grain (sample WL-3). D) Rhodolite grainstone (sample B-1). Note echinoderm and brachiopod grains as core fragments. Maximuim field dimension in all photomicrographs in this figure = 4.5 mm. Stratigraphic up-direction toward top in all photomicrographs.


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component. This led Pate and Bassler (1908) to designate the Bob interval the "Brachiopod Zone," although the volume percentage of brachiopods in one sample (WL-2) was lower than one Beech River sample and most Lobelville Member samples (Table 1). Also present are ostracodes, fragments of encrusting (Fig. 6B) and ramose bryozoan colonies, and rare corals. Fossil grains are comparatively large (avg. 1-3 mm; Fig. 6A) and often appear broken, but not significantly abraded. Most bivalved forms are found disarticulated. Large, unbroken articulate brachiopod valves are preserved convex up (Fig. 6C), which reflects a hydrodynamically stable orientation in higher energy conditions (Johnson 1957). These observations, as well as the more even and thicker bedding, suggest that the Bob was deposited in an environment that was more constantly agitated than those of the Beech River and Lobelville members.

Allochems interpreted to be calcareous red algae, not found in the Beech River Member and rare in the Lobelville, are common in the mud-poor limestones of the Bob (e.g., sample WL-3, Table 1). These algae appear as small fragments (Fig. 6C) and as concentric coatings of grains (Fig. 6D). The concentrically coated grains, superficially appear to be "ooids" (McComb 1987), but can more accurately be described as red algal encrustations, or rhodolites. The rhodolites are less than 5 mm in diameter, spherical or ellipsoidal in form and each contains a small core particle, most often a small echinoderm grain or an ostracode or brachiopod fragment. The concentric bands of the rhodolites indicate water energy in the Bob depositional environment strong enough to keep the grains constantly moving allowing the even coating (McComb 1987). The rocks consisting of rhodolites and associated large uncoated fossil grains are occasionally cross-bedded.

Amsden's (1949) correlations of measured sections showed the Bob not to be developed everywhere throughout his study area. Although not the focus of this study, sections that were examined in which all or nearly all of the Brownsport is exposed

contained a zone of relatively clean limestone near the stratigraphic middle of the formation. Some exposures attributed to the Bob have thin shale interbeds, but this interval of relatively clean limestone is distinctive and is considered to be the Bob Member. In every section, the limestones of the Bob conformably grade upward into the thinner-bedded shales and limestones of the Lobelville Member.

Lobelville Member

Superficial lithologic and bedding characteristics of the Lobelville are similar to those of the Beech River Member; important distinctions are related to bedding characteristics, although volume percentages of allochems, cement, and mud are similar (Table 1). The Lobelville was examined in detail at three exposures (sections LB, WL, CC - see Chapter 1). Each section contains all or nearly all of the Lobelville interval, which was measured bed by bed to the nearest centimeter. A single bed or a group of beds were recognized as a distinct unit based on lithologic, sedimentologic or paleontologic changes. Each unit was sampled at an average interval of 0.5 m, with a minimum to maximum sample interval of 0.02-2.5 m. Forty five thin sections were made from the samples collected at these three sections. Ten of these were point counted to determine volume percentages of principal skeletal allochems, mud, and cement (Table 1, Fig. 7). Overall, Lobelville Member samples contain 50% or more skeletal allochems (Fig. 7A), dominated by echinoderms and bryozoans (Fig. 7B), but individual samples show a considerable range of variation. Combined field, thin-section and acetate peel descriptions, and classification for all units is given in Appendix A.

Lobelville (LB): At least 9.8 m of Lobelville strata are exposed at LB (Fig. 8), which was the stratigraphic section examined in the most detail. The outcrop (Fig. 4B), along Tennessee State Hwy. 13, probably was not present when Amsden (1949) described his

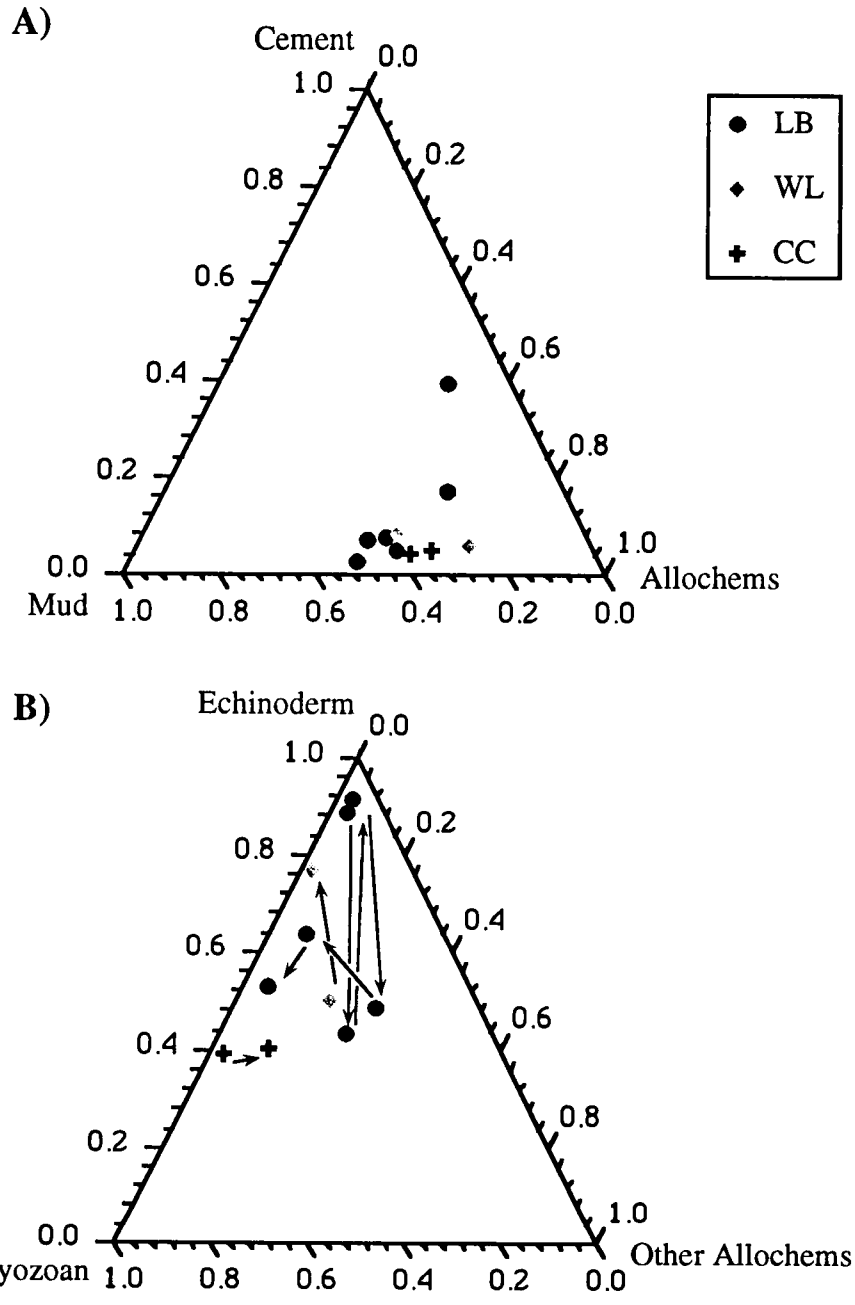


Figure 7. – Ternary plots of lithologic constituent volume percentages, determined by point count, of samples collected from the Lobelville Member of the Brownsport Formation (Silurian). A) Abundance of cement vs. mud vs. allochems. B) Major allochem volume percentages, illustrating trend of increasing bryozoan abundance up section. Arrows between samples point toward stratigraphically higher samples. Note that at section LB the percentage of bryozoan allochems increase up-section and at section CC, at which only the upper 2 m of the Lobelville is exposed, the bryozoan volume percentage is highest of all sections.

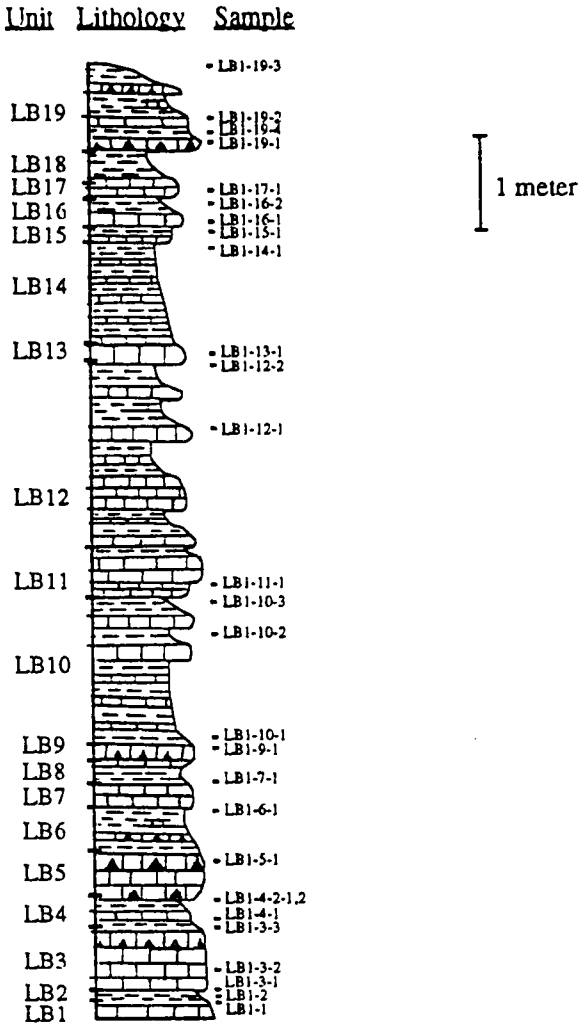


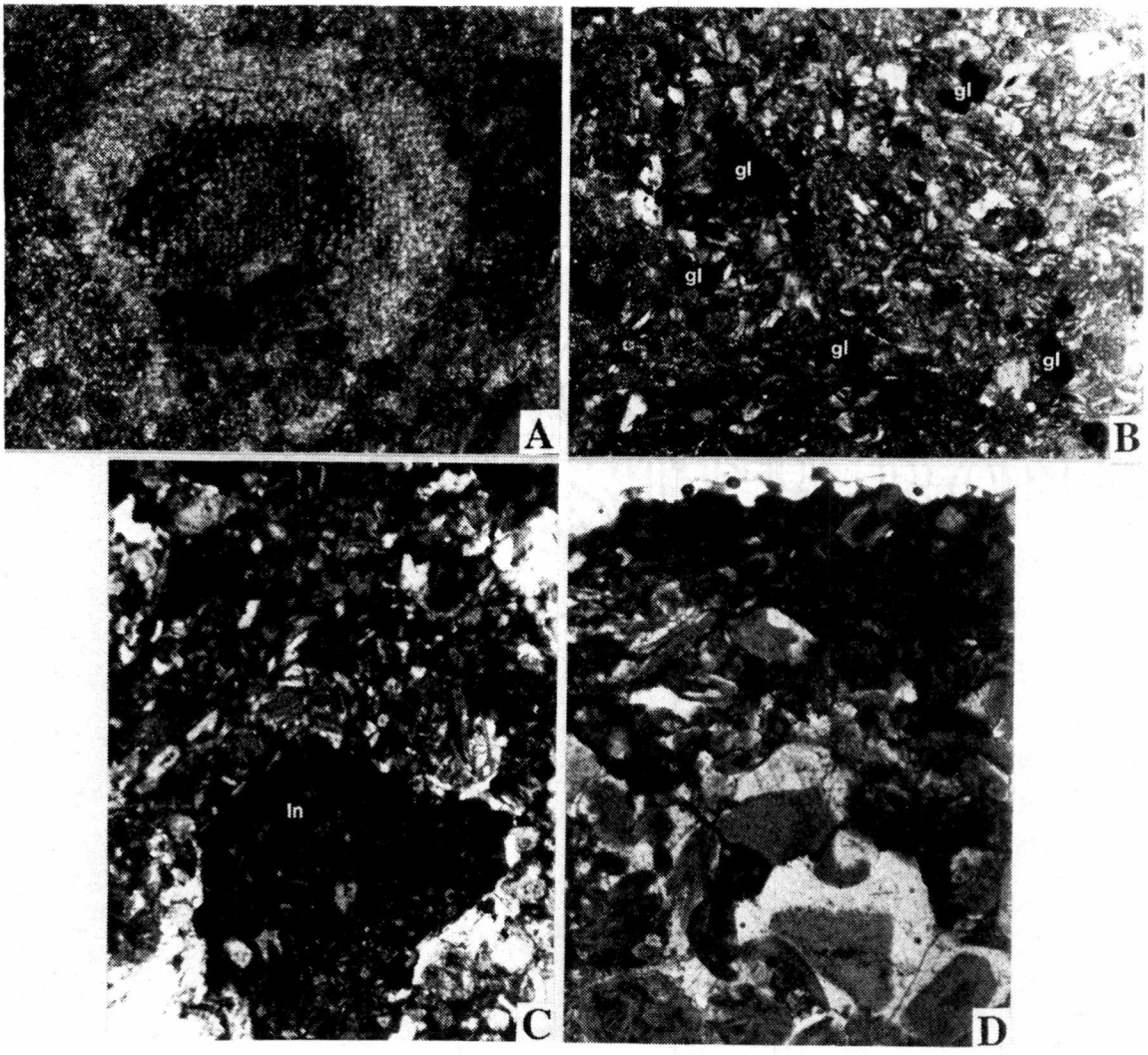
Figure 8.- Stratigraphic section of the Lobelville Member of the Brownsport Formation (Silurian) at Lobelville (LB). Unit numbers are listed along left side and sample numbers are listed along the right side of the stratigraphic column. Lithologic symbols same as in Figure 5.

section 38 in the Lobelville, Tennessee area. The outcrop Amsden measured is now poorly exposed along the west side of the Buffalo River less than 1/3 mile east of LB. Neither the top nor bottom contact of the Lobelville Member was exposed at LB, making the exact stratigraphic position of this key outcrop uncertain. Strata of the Decatur Formation are exposed along Hwy. 13, less than 0.25 km south, but the intervening distance is densely vegetated and lacks outcrop. The Lobelville Member interval exposed at this section was divided into 19 stratigraphic units. The lowermost unit exposed, LB1 (Fig. 8), has the characteristic lithology of the lowermost Lobelville at or near the gradual transition from the Bob Member. Abundant shale interbeds present throughout the entire length of section at this exposure define the interval as limited to the Lobelville Member.

In general appearance, an overall upward trend of decreasing limestone bed thickness and increasing proportion of shale beds is apparent. Near the top of the section, the dominant lithology is gray shale, interbedded with thin- to very-thin-bedded echinoderm wackestone and packstone. The limestone beds with minor interbedded shales, present at the base of the section, are dominated by thick- to medium-bedded wackestone and packstone. Blue chert nodules and thin beds, found throughout the section, are most common in limestone beds of units LB1 though LB9.

Coarse-grained glauconite is present in many of the thick limestone beds of units LB1 through LB14. Within limestone beds glauconite occurs in two forms: fillings of the stereom of echinoderm grains (Fig. 9A) and as discrete pellet-shaped grains (Fig. 9B). Most glauconite formed in the stromal galleries of echinoderm grains or within pores of organic-rich peloids exposed on the seafloor for extended periods of time. Small pore spaces, along with the associated decaying organic matter, provided the proper semi-confined, reducing microenvironments needed for glauconite development (Odin and Fullagar 1988). The presence of glauconite peloids indicates little sediment movement

Figure 9.- Photomicrographs of significant petrographic features of the Lobelville Member. A) Glauconite filling echinoderm grain stereom (sample LB1-2). Field width of photo = 1 mm. B) Individual glauconite grains (gl), note that many of the grains have cracks, indicative of an evolved stage of glauconizaton (sample LB1-10-1). C) Skeletal allochem and mud intraclast (In) (sample LB1-3-1). D) Graded bed in which textures grade upward from a skeletal grainstone at the base to wackestone at top. The clear area at top of photo was probably a thin shale layer which capped the sequence, washed away during thin section preparation (sample LB1-11). Field width of all photomicrographs in this figure = 4.5 mm, unless otherwise noted.


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from the site of formation, because even very short transport distances would easily have broken down the gelatinous mass. Many of these pellets are cracked (Fig 8B) due to differential crystal growth, indicative of an evolved stage of glauconitization (Odin and Fullagar 1988). Glauconite is also present at bedding surfaces, most commonly at the tops of limestone beds. It is unclear whether the glauconite formed at these boundaries or was concentrated there by pressure solution.

Intraclasts are rare, observed only in one thin section of a sample from unit LB3. These intraclasts are composed of grains less than 1 mm in diameter within a muddy matrix (Fig. 9C). The intraclasts were likely held together by weak cohesion of the fine-grained matrix, and would have been easily destroyed by moderate current energy. This weakness and thus the rarity of intraclasts is related to a lack of early marine cementation. Marine cement fabrics are rare in the Lobelville. Small bladed cements, formed in cavities beneath elongate grains, are positive evidence of early marine cement formation (Steinhauff 1989), and it is likely that the earliest stages of echinoderm overgrowth formation took place in the marine diagenetic environment (Walker and others 1990). Other cements, such as a majority of the pervasive, clear echinoderm overgrowths and silica replacement cements formed during later, post-burial diagenetic events (Foreman 1989; Roberson 1989).

Thin, graded beds (1-4 cm thick) are present within many of the Lobelville limestone beds (Fig. 9D). The grain size change is subtle, usually only seen in thin section. The base of a typical graded bed is a mixed medium- to fine-grained packstone or grainstone texture which grades upward to a fine-grained wackestone and sometimes mudstone texture. These graded beds are found in limestones at all three sections, and most often occur just below a shale interbed, suggesting a genetic relationship.

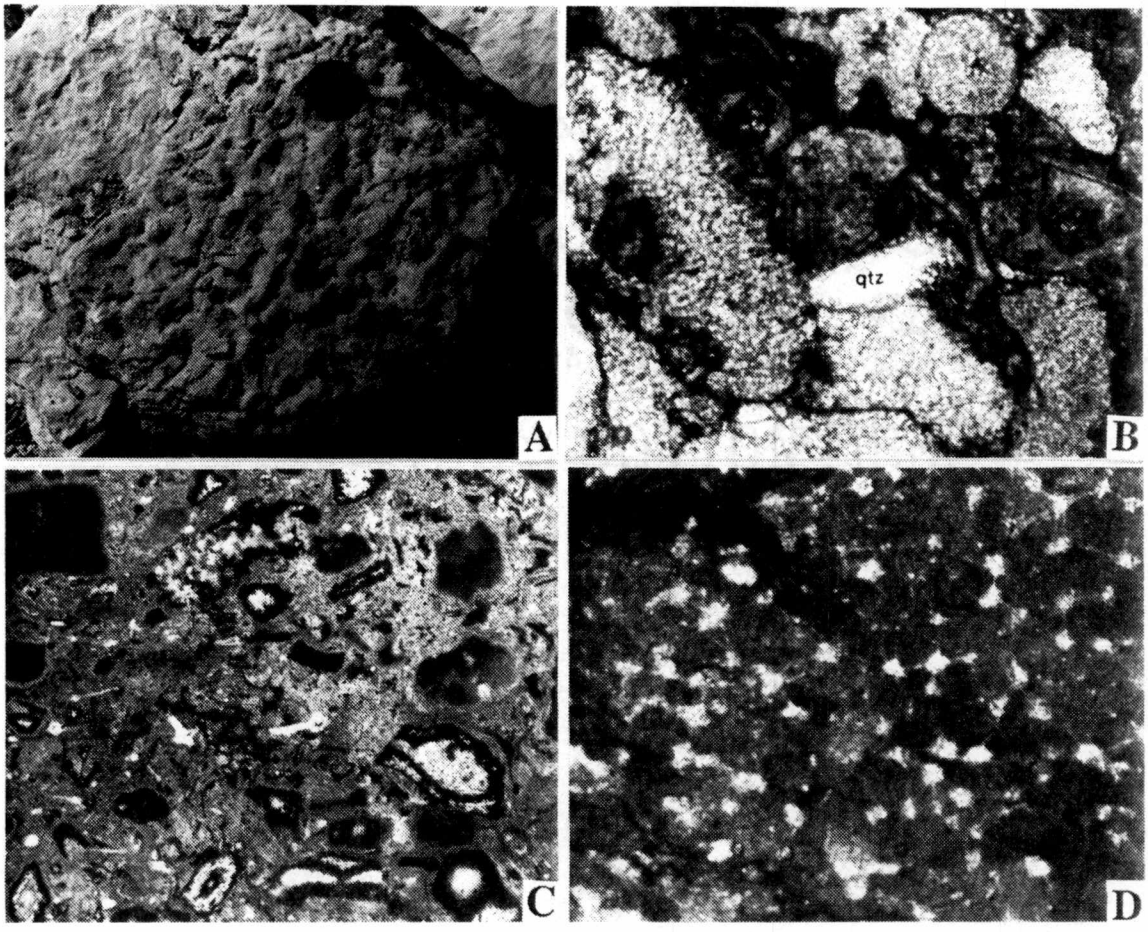
A notable interval of section LB is that of units LB4-LB9 (1.1-2.8 m above base of section). This is the most fossiliferous interval in units LB1-LB14. Pentamerid

brachiopods, rugose corals and large colonies of tabulate corals are more commonly observed within these units than in over- and underlying units. The proportion of shale to limestone is higher in this interval, with soft sediment deformation, especially loading features (Fig. 10A), common at the contact of shale beds and overlying limestone beds.

An increasing proportion of shale to limestone is noticeable above unit LB9. Short (~0.5 m), upward-thinning bedding sequences were observed on the outcrop. Each sequence begins sharply with thin- to medium-bedded wackestone, grading upward to thin-bedded shale. The shales which compose the upper part of each sequence contain some fossils, but are not extremely fossiliferous, as are the shales of the LB4-LB9 interval or the shales at the top of the outcrop.

Above unit LB14, the discrete fining upward packages are not as obvious, and there is an overall trend of increasing proportion of shale to limestone to the top of the outcrop. Limestone beds range from medium-bedded echinoderm grainstone to medium- to thin-bedded echinoderm-bryozoan wackestone. Rare quartz silt (Fig. 10B) is observed in thin sections of samples from units LB14, LB15, and LB16 (Fig. 9). Silt is found in samples of the these three units and in only one sample (WLS 6-2) from section WL. The appearance of quartz grains coincides with an increased proportion of shale interbeds (>50%). Much of the non-terrigenous, fine-grained material filling grain interstices, is finely comminuted fenestrate bryozoan debris. The increased abundance of bryozoan fragments, especially fenestrate bryozoans, correlates with an increased proportion of shale beds and an abundance of especially large fragments and whole skeletons of all types of fossils (see discussion below of biogneic composition and characteristics). The most notable fossil components of this interval are the corals. Many species of both rugose and tabulate corals, including *Favosites louisvillensis* and *Thecia minor,* have been collected from both the thin limestones and shales of this interval. Also present is a great diversity of cryptostome, cystoporate, trepostome and fenestrate bryozoans, stalked

Figure 10.- Significant sedimentologic and petrographic features of the Lobelville Member. A) Soft sediment deformation features on base of limestone slab overlying shale layer. From unit LB7, section LB. Lens cap width = 6.5 cm. B) Photomicrograph of echinoderm wackestone containing a detrital silica grain from sample LB1-14-1. Field width = 1 mm. C) Photomicrograph of chert sample WL-20. All original calcite has been replaced with silica. Note sponge spicules in ground mass. D) Photomicrograph of well preserved sponge body and spicule network (form DuPont Core, sample 197). Field width of all photomicrographs in this figure = 4.5 mm, unless otherwise noted.


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echinoderms, and a small number of lithistid demosponges and stromatoporoids.

The uppermost unit, LB19, is a glade at the top of the outcrop. The base of the glade is marked by a persistent echinoderm-bryozoan grainstone bed overlain by a >1 m sequence of 0.1 - 0.5 m packages of gray shale containing thin lenses of bryozoan-echinoderm wackestone. A greater concentration of fossils is found along bedding planes containing limestone lenses, suggesting periodic recolonization of the muddy substrate between events of terrigenous mud influx. Apart from these fossiliferous layers, much of the interval is devoid of skeletal grains larger than 1-2 mm.

Webb's Landing (WL): The Webb's Landing section is a long, low road cut along Marsh Creek Rd.(Fig. 4E), approximately two miles southeast of the Tennessee River Bridge on Tennessee State Highways 100/20. This exposure is the most stratigraphically complete of the sections examined. Over 13 meters of the Brownsport Formation is exposed at this locality (Fig. 11), including a 7.1 meter thick section of the Lobelville Member. Because of poor vertical exposure, the Lobelville was only divisible into 7 units, leading to greater generalization in lithologic description. The most striking feature of this outcrop is the diversity of the invertebrate fauna, similar to that seen at certain levels of section LB. The fauna is dominated by echinoderms but includes many species of bryozoans, corals, sponges, brachiopods and trilobites.

At WL, the base of the Lobelville is recognized at the level where shale interbeds appear above the relatively shale-free packstone and grainstone beds of the Bob Member. As at section LB, the amount of shale increases upward, and limestone bed thickness decreases upward. Glauconite is absent in units WL7 to WL11, but scattered glauconite grains are present in the thicker limestone beds throughout the upper Lobelville (WL12-13). Near the top of the exposure, wackestone beds nearly completely replaced by silica are present (Fig. 10C). The matrix of these beds has a green tint, suggesting an original

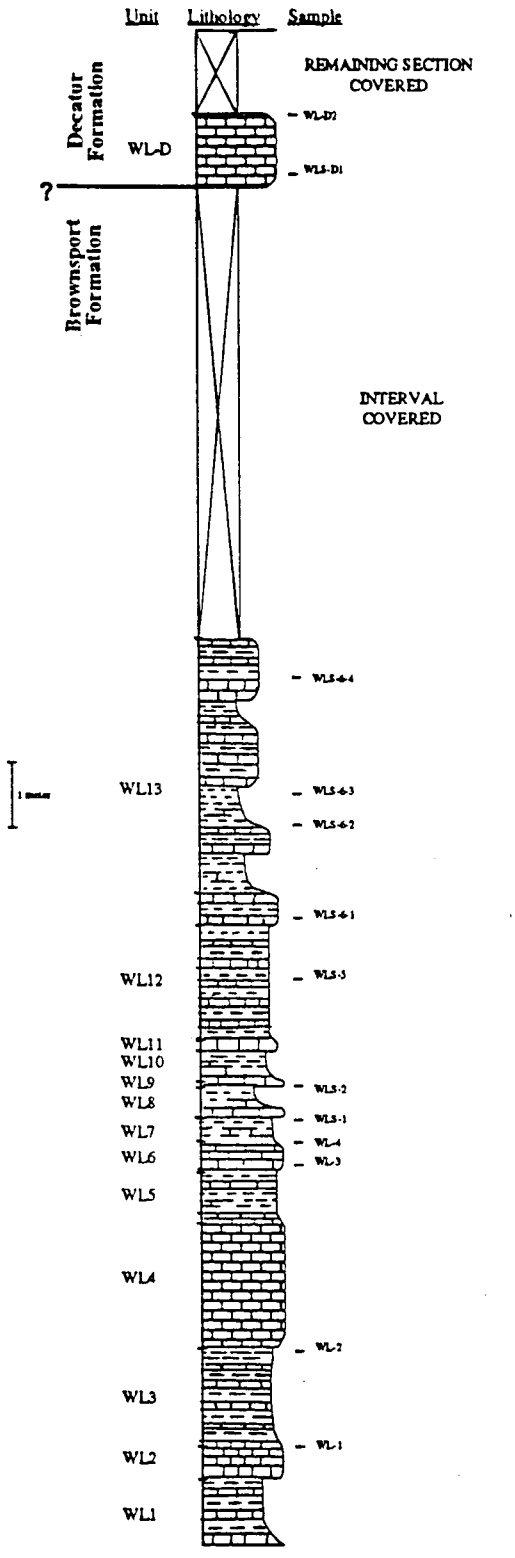


Figure 11.- Stratigraphic section of the Brownsport Formation (Silurian) at Webb's Landing (WL). Unit numbers are listed along left side and sample numbers are listed along the right side of the stratigraphic column. Lithologic symbols same as in Figure 5.

high concentration of glauconite. Quartz silt is observed in a sample from unit WL13 near the 10 m level of section WL. The silt is coincident with the increasing proportion of terrigenous shale at this level and above.

An interval of increased bryozoan, especially fenestrate, and coral abundance, similar to the interval at the top of section LB, is present in unit WL13. Large tabulate coral colonies (up to 0.5 m diameter) were collected from this interval. The lower diversity of the coral fauna at section WL is the main difference between the "coral zones" of sections WL and LB. Rugose corals are present at WL, but are not nearly as diverse and abundant as at LB. Stromatoporoids are rare at WL, whereas lithistid demosponges are more common and diverse than at LB.

The uppermost Lobelville is extremely shaley and is covered for a thickness of approximately 7.8 m at WL. Isolated outcrops of the overlying Decatur Formation can be found on the hill above the outcrop, and the contact probably is at the base of the Decatur exposure.

Cane Creek (CC): At the Cane Creek section, an outcrop (Fig. 4D) along the west side of Cane Creek, 0.5 miles south of the Tennessee State Highway 50, a short (< 2 m) interval (Fig. 12) of upper Lobelville strata is exposed. Most notable at this location is the contact between the Brownsport Formation and the overlying Decatur Formation (Fig. 4D). The boundary is marked by a sharp contact between the thin-bedded wackestone and shale of the upper Lobelville and the medium-bedded echinoderm wackestone of the Decatur which forms an erosionally resistant overhang. The contact is sharp, but no significant break in sediment accumulation is indicated lithologically (i.e., no evidence of bed truncation by erosion).

The lowest unit exposed at CC is similar to one of the fining upward sequences present at section LB. The remaining section is mainly composed of interbedded shale

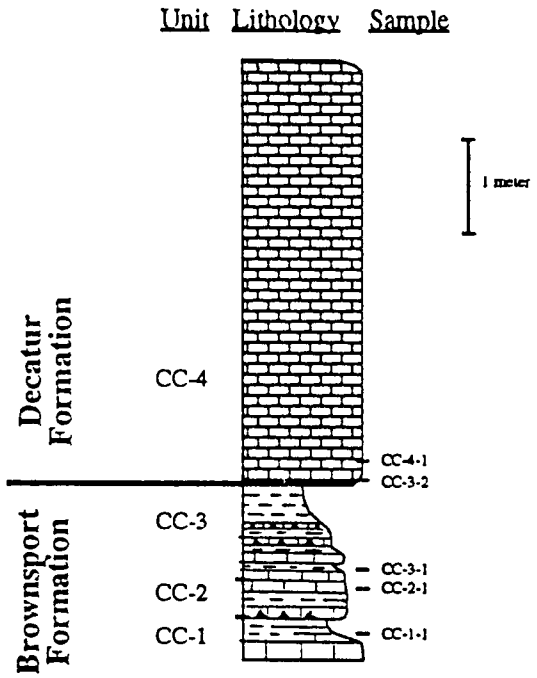


Figure 12.- Stratigraphic section of the Lobelville Member of the Brownsport Formation and the lower Decatur Formation along Cane Creek (CC). Unit numbers are listed along left side and sample numbers are listed along the right side of the stratigraphic column. Lithologic symbols same as in Figure 5.

and thinly-bedded wackestone. Glauconite is present in the thicker limestone beds and along bed surfaces. Quartz silt is present only in the shale-dominated unit CC3.

As at sections LB and WL, the dominant fossil allochems at CC are disarticulated echinoderm debris. Bryozoan fragments, especially fenestrates, and corals are also significant components, similar to the fossil assemblages of the upper Lobelville interval at LB and WL. Thin tabulate corals, especially *Thecia minor*, are present on many of the bedding surfaces (Fig. 17A). Ostracodes and brachiopods are minor components of the fossil assemblage.

Biologic Characteristics of the Lobelville

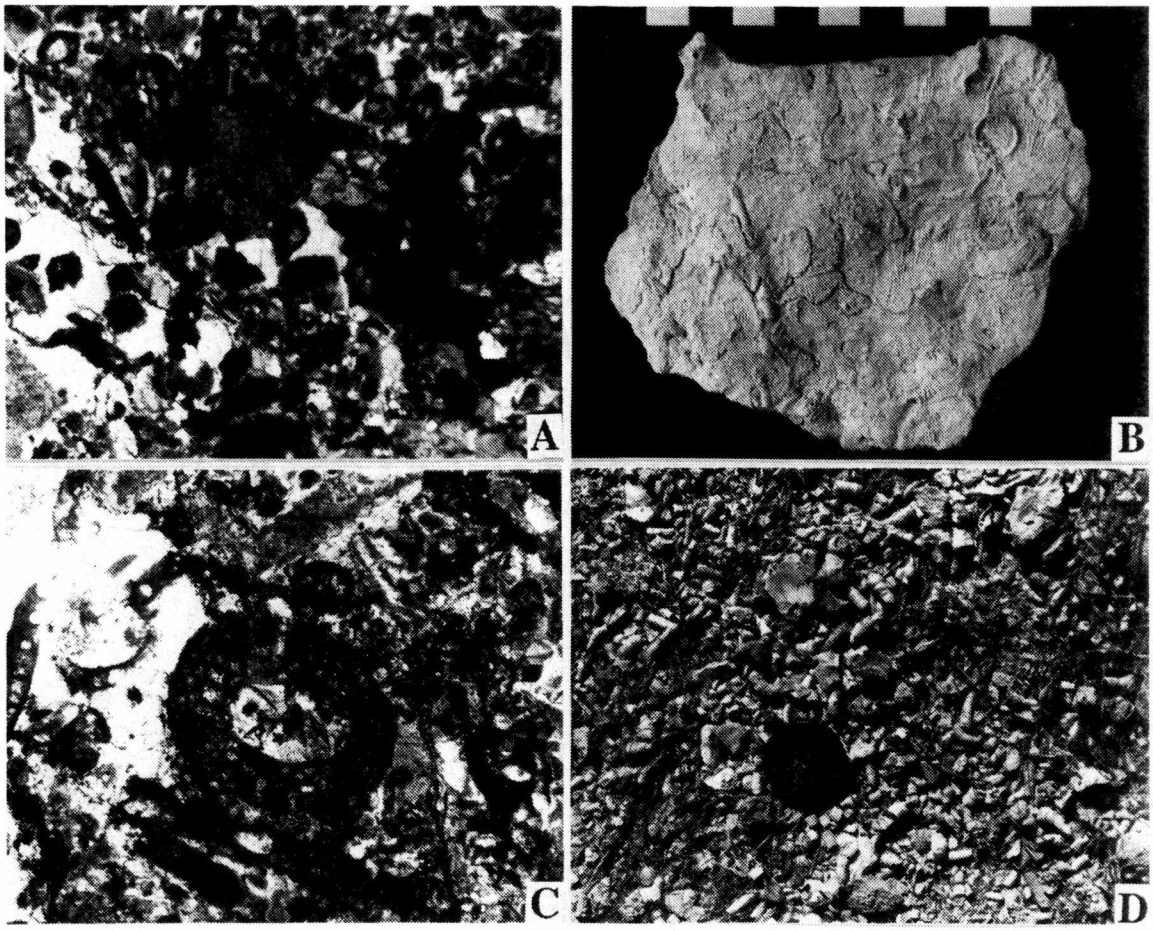
The preserved composition of Lobelville invertebrate assemblages, observed at all three sections, provides additional information about the depositional conditions. The Lobelville environment was dominated by stalked echinoderms, which produced most (37-90 volume percent; Table 1) of the skeletal allochems. This is not unusual, as pelmatozoans are thought to be the primary coarse carbonate sediment producer during the Silurian (Brett 1991). Most grains are disarticulated, and slightly disturbed calyxes and articulated stem pieces are common mainly at the tops of limestone beds or within shale beds. Calyxes of both crinoids and blastoids are present in various stages of disarticulation; intact specimens are rare. Most are disturbed to some degree, so that thecal plates are in proximity, but not in contact. This is probably the result of the activity of near surface, substrate grazing deposit feeders, such as trilobites or gastropods. Many of the undisturbed stem pieces have cirri projecting downward into the underlying sediment similar to those observed by Clement and others (1987). Large echinoderm root attachments are uncommon, suggesting that many of the stalked echinoderms outgrew initial attachment sites on skeletal fragments and developed secondary attachment to the substrate using stem cirri, an attachment mechanism detailed by Brett (1991).

Within limestone beds, articulated echinoderm stems or calyxes are uncommon. Echinoderm grains occur in high proportion (usually >50 volume percent) to other skeletal grain types. The chemical and physical stability of echinoderm grains probably allowed some concentration of this type of grain by a limited degree of reworking. The presence of relatively fragile thecal and arm/brachial plates suggests that grains were not transported any significant distance as suggested elsewhere by Brett (1991). Long residence time (i.e., slow burial) on the seafloor is confirmed by glauconite fill of the stereom in many grains (Fig. 9A). Stromal galleries, within which the chemically unique reducing conditions required for glauconite formation were present, became primary nucleation sites for glauconite formation (Odin and Fullagar 1988).

Lobelville bryozoans are very diverse. Identification and study of some species of trepostome and cystoporate bryozoans has been completed (Corneliussen and Perry 1973; Perry and Hattin 1958), but many of the bryozoans, including the very abundant fenestrates, have not been investigated in detail.

A trend of increasing abundance and diversity of bryozoans upward in the Lobelville Member is considered significant. At the all three sections, LB, WL and CC, the increased amount of bryozoans (from $< 20\%$ to $> 40\%$; Fig. 7) in the upper few meters of the out crop is easily noted. Samples of units LB17-LB19, WL13, CC2-CC3, contain bryozoan skeletal debris in nearly equal and sometimes greater proportion to echinoderm skeletal grains. Both large colony fragments of trepostomes and cystoporates and finely comminuted skeletal fragments of fenestrates are common. This fine skeletal debris fills interstices between larger allochems, constituting a large part of the matrix of the wackestone/packstone beds of these upper intervals. Large fragments of fenestrate bryozoans (Fig. 13A) are most common in units LB18 and LB19. Thin limestone lenses enveloped by thicker (>2 cm) shale beds of these units, are almost wholly composed of fenestrate zoaria lying one on top of the other.

Figure 13.- Bryozoans and rugose corals from the Lobelville Member. A) Photomicrograph of bryozoan-rich layer with abundant fenestrate bryozoans (sample LB1-17). B) Typical bryozoan lens, from within a thick shale bed in unit LB19. Divisions on ruler = 1 cm. C) Cystoporate bryozoan with hollow ramose zooarium suggesting growth around a non-skeletonized alga, which was not preserved (sample LB1-19-3). Field width of both photomicrographs = 4.5 mm. D) Outcrop of abundant *Cyathophylum* sp. (Rugosa) coralla weathering from one layer in unit LB19. Lens cap width = 6.5 cm.


A
B
C
D

Mound-shaped trepostome colonies are more common in muddy intervals, and initial attachment to small skeletal grains or the exposed surfaces of coral and bryozoan colonies is common. These substrates appear to have been quickly overgrown, and the colonies appear to have become free lying later in life. This is settlement and growth pattern has been termed an "ambitopic" life strategy and is known elsewhere in many bryozoans from the Silurian shales of Gotland (Brood 1984).

Smaller colonies (< 3 cm max. dimension) of encrusting bryozoans inhabited nearly every type of hard substrate available. In both grainy and muddy intervals, bryozoans covered the skeletons of other organisms, including other bryozoans, echinoderms (mainly recumbent stem sections), corals and rarely brachiopods (Fig. 15A,C and 20). Sheet-like colonies inhabited cryptic niches (Kershaw 1980) on coral epithecas (Fig. 27B) exposed at colony margins (see Chapter 4 for further discussion. Bryozoan colonies encrusting recumbent echinoderm stems may have done so while the host was still alive, but a majority of colonies are parts of multiple generation overgrowths which began on the top of coral or bryozoan colonies or other large skeletal fragments suggesting post-mortem encrustation. Carnivorous suspension feeders, such as tabulate corals, would have eaten any larvae attempting to settle on the calical surface of a live coral.

A cystoporate species with a hollow ramose zoarium (Fig. 13C) is one form which is present only in the uppermost beds of the Lobelville. Capaccioli (1987) noted the occurrence of this fistuliporid bryozoan (superficially similar to *Diamesopora*, Utgaard 1983:385-389) from the Ross Formation (Lower Devonian). She speculated that the bryozoan may originally have encrusted an organism, possibly an alga, that was not preserved.

Ostracodes, common at nearly all levels in the Brownsport, were important components of Lobelville benthic communities. Lundin and Newton (1970) studied the ostracode populations of the Brownsport, but made few interpretations of their paleoecol-

ogy. Most specimens are small, less than 5 mm maximum dimension. Articulated ostracode valves are most common in grainy intervals, where they may have inhabited grain interstices on or in the substrate (Siveter 1984). This life habit would exclude ostracodes from very muddy conditions where the oxygen content at the sediment-water interface may have been low. This idea is supported by observations of the Lobelville in which ostracodes are much less common in shale beds of the upper Lobelville, where little oxygen would have been available. The few found are usually disarticulated, probably washed in from surrounding grainy substrates.

Brachiopods, a significant skeletal component (up to 15 volume percent) of the Bob Member, are not nearly as abundant (< 8 volume percent of skeletal allochems) in the Lobelville. This is surprising considering the importance of brachiopods in other Silurian benthic communities (Boucot 1975, p 241; Cocks and McKerrow 1978, p. 93). Brachiopods are most common within the wackestones and packstones of the lower Lobelville. Valves are commonly disarticulated and preserved in a hydrodynamically stable concave down orientation (Johnson 1957) indicative of post-mortem disturbance. Most specimens are small (< 2 cm) impunctate or pseudopunctate. An exception to this size range are occurrences of the large pentamerid, *Rhipidium* sp. Where present, these pentamerids are commonly confined to discrete horizons, almost always within limestone beds, where they can be quite abundant.. At one outcrop of the Brownsport near Sewell Spring, *Rhipidium sp.* valves form layers of coquina at the base of thick graded beds. The precise stratigraphic position of these graded beds is unknown, but they appear to be a localized high-energy facies developed in the upper Lobelville Member.

Valve articulation of both ostracodes and brachiopods, is a good indicator of the rate of sediment accumulation. An interval with many articulated valves indicates a rapid, event-type burial. Disarticulated valves are the product of long residence time prior to burial which would have exposed ostracodes, already partially buried in the

substrate, and brachiopods to more chance of disruption, either by grazing scavengers or physical environmental events.

Trilobites are rare, both in thin section and outcrop. Broken and unbroken fragments of molted exoskeletons are seen in thin section. Whole skeletons are preserved only when a trilobite was quickly buried by an influx of sediment. Many species of Silurian trilobites grazed at or below the sediment-water interface (Brett 1991) probably including those of the Brownsport. This activity probably contributed to dissociation of echinoderm calyx and stem ossicles common in Lobelville strata. Indications of other infaunal organisms are notably absent. Physical sedimentary features, such as shale laminations, graded beds and articulated skeletal pieces within shales are often preserved, suggesting little homogenization of sediment due to infaunal activity.

Lithistid demosponges are an important component of the Lobelville fauna with a variable distribution. Along with calcisponges, demosponges are abundant throughout Beech River Member strata, but in the Lobelville, sponge abundance varies between localities. At section WL, a range of growth forms, from laminar to bulbous, were collected. A poorly preserved bulb shaped body was the most common growth form observed. Demosponge spicules are often seen in thin section and are a significant skeletal component of chert layers (Fig. 10C,D). The sponges, growing in patches of individuals, concentrated the small amount of dissolved silica present in seawater, forming opaline spicules (C.W Stock pers. comm. 1992). During later diagenesis the metastable opaline spicules transformed to stable microcrystalline silica, obscuring and coalescing individual body shapes, forming thin chert lenses and layers.

Stromatoporoids are not common in the Lobelville, present only in units LB18 and LB19. An encrusting lamellar form is most common, often seen as one generation in a multiple generation overgrowth of tabulate coral colonies. There is one example from LB, of a stromatoporoid encrusting directly on a grainy substrate, taking on a lamellar

form. Large, domical, free-lying colonies have been collected, but are more rare than encrusting lamellar forms.

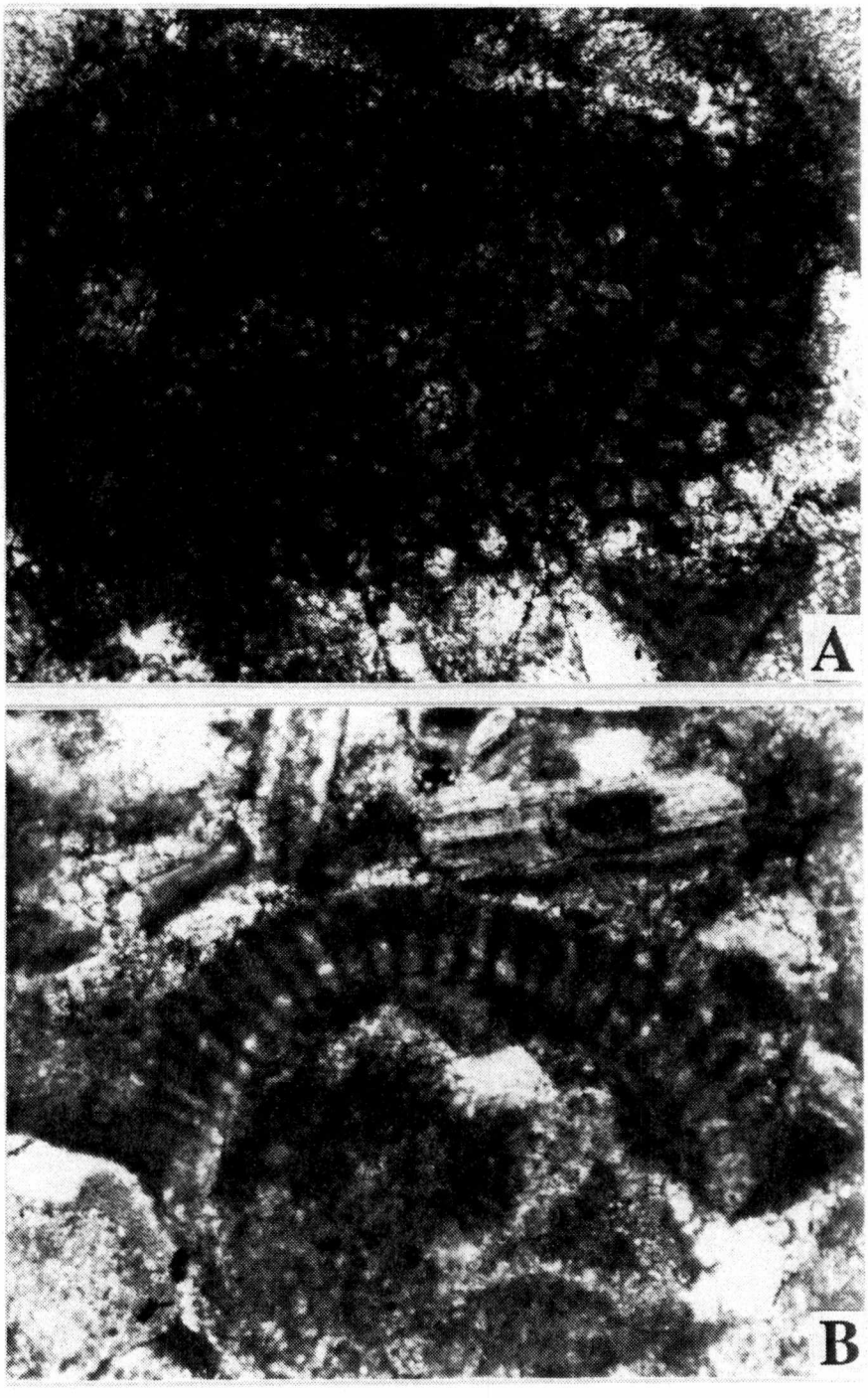
Evidence of algae in the Lobelville is rare and equivocal. Small fragments of an unidentified organism (Fig. 14A,B), similar to skeletal fragments seen in the Bob, are present in thin sections from units LB3, LB12 and LB13. These are similar to a type of dasyclad alga (Capaccioli 1987), but no positive identification has been made. Other indirect evidence of algae is the cavity within a cystoporate bryozoan with a hollow ramose zooarium (Fig. 13C), which may represent an encrustation of a non-calcified alga (Capaccioli 1987).

The principal group of organisms that has been used as the key indicator of Lobelville strata, is the corals. Pate and Bassler (1908), who first separated the Brownsport into three units, used a "coral zone" as a key to identifying Lobelville strata. At each section measured and sampled for this study, there was an interval within the upper Lobelville that contained a coral fauna that is diverse in growth forms of both rugose and tabulate corals.

Rugose corals are rare in the lower Brownsport but have provided much insight into depositional conditions during upper Lobelville time. Specimens are most common to intervals of interbedded, thinly-bedded wackestone and shale. Where rugose corals are present, they commonly occur in great abundance, dominating the assemblage. For example, at section LB, thousands of coralla of the rugosan *Cyathophylum* sp. weather out of a single layer in the LB19 glade (Fig. 13D). This is one specific example, yet it may represent a larger pattern of monospecific or nearly monospecific patches scattered about the Lobelville seafloor. Proliferation of one species took advantage of favorable substrate and other environmental conditions, but would not have been persistent through time.

At an individual scale, rugose coral growth forms are of many different shapes

Figure 14.- Photomicrographs of probable dasycladacean green alga from the Brownsport (sample WL-4). A) View of a section transverse to thallus surface. B) View of a section tangential to thallus surface. Field width = 1 mm.


A
B

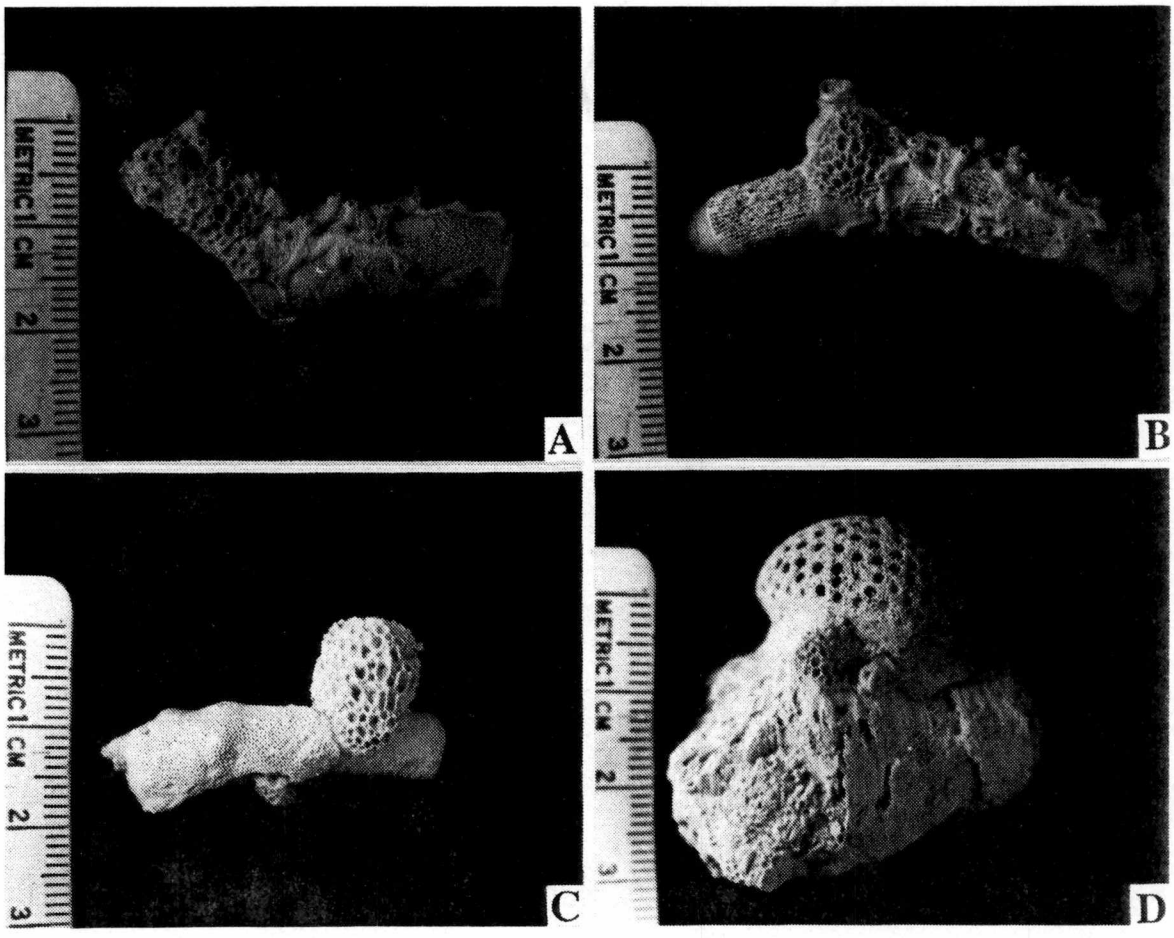
and sizes, but most show evidence of some degree of reorientation during life. Many coralla are extremely contorted or scolecoid. A physical disturbance, such as storm currents, toppled upright coralla, which later regenerated back to a preferred vertical growth direction. Repeated disruption sometimes resulted in three or more skeletal geniculations. Lobelville rugose corals employed an liberosessile life strategy (Neuman 1988). That is, larval settlement and initial development occurred on a small piece of skeletal debris, followed by a free-lying, recumbent or partially buried vertical mode of life upon reaching an individually stable size. This strategy is an important and successful adaptation to conditions of unconsolidated and sometimes very soft substrate (Neuman 1988).

Along with rugosans, there are many species of tabulates present within these coral assemblages. Amsden (1949) collected 12 different species of tabulate coral from outcrops in the vicinity of sections LB, WL and CC. I have collected at least 12 different species of non-rugosan colonial coral, including specimens of auloporid, halysitid, favositid, heliolitid, alveolitid and theciid tabulates. Colony shape varies among and within the different species, and reflects variations of genetic and ecophenotypic controls on colony growth.

Auloporid colonies are most often observed as single layer, individual or anastomosing chains encrusting on a hard skeletal substrate, such as another tabulate or a crinoid stalk (Fig. 15A,B). Auloporid colonies are rarely observed to continue growth off the original substrate onto the surrounding loose skeletal substrate. Only one example of a multigeneration colony growing directly on a mixed skeletal substrate was collected (WL13).

Halysitid corals formed anastomosing chains encrusting large skeletal fragments or growing across the mud-rich, skeletal substrate, rarely forming tabular colonies. Commonly, halysitid colonies began as long irregular rows of corallites, with no charac-

Figure 15.- Examples of epitaphic encrustation. A) Bryozoan, favositid coral and auloporid coral colonies encrusting echinoderm stem fragment. B) Favositid and auloporid coral colonies encrusting fallen rugose coral. C) Bryozoan and favositid (2) colonies encrusting echinoderm stem fragment. Favositid colony facing downward, on bottom of stem fragment suggests an earlier generation of encrustation when substrate was inverted from present orientation. D) Bulbous *Heliolites tennesseensis* and favositid colonies encrusting large fallen rugose coral. All samples collected from the Lobelville Member.


METRIC 1 CM 2 3
A
METRIC 1 CM 2 3
B
METRIC 1 CM 2 3
C
METRIC 1 CM 2 3
D

teristic form (Buehler 1955), growing directly on the substrate.

The other Lobelville tabulate corals, including species of *Favosites*, *Heliolites*, *Alveolites* and *Thecia*, fall into two growth-form groups: small, domical or bulbous colonies typically encrusting on other skeletal fragments or large, platey, tabular or domical colonies lying on the substrate. Small encrusting colonies are dominantly species of heliolitids (Fig. 15D) and less commonly favositids (Fig. 15C). Common substrates of encrusting corals include recumbent and fallen echinoderm stems, rugose corals, stromatoporoids, and bryozoan and other tabulate coral colonies. These encrusting corals are found most often within intervals of interbedded, thin-bedded wackestones and shales.

Free-lying favositid (Fig. 16A) and theciid (Fig. 17A) coralla are found in both interbedded limestone and shale intervals, and in relatively pure limestone intervals. These platey tabulates are commonly quite large (up to 1 m across), and thin (typically less than 3 cm high) (Olson and Broadhead 1989). Favositid coralla found in intervals of interbedded shale and limestone usually have an extremely thin, platey shape. Cross-sectional views of coralla show ragged colony margins formed by multiple, lateral regeneration over shale surfaces which partially covered colony margins (Fig. 16, 17B and 18A). The locus of colony reestablishment is usually a point of positive colony relief left exposed after partial burial. Cross-sectional views also show evidence of internal growth reorientation (Fig. 16A), indicating the tipping of a colony from original horizontal attitude.

Colonies found within limestone beds most often have a thicker, tabular or domical colony form. Internal colony regeneration is less common and colony margins are more uniform and unbroken (Fig. 19A), although internal growth reorientation is sometimes observed. Presumably these slight differences in colony form are due to a lesser amount of fine-grained sediment influx affecting growth at colony margins. Fur-

Figure 16.- Regeneration in tabulate coralla. A) Longitudinal cut through a platey *Favosites louisvillensis* corallum. Partial burial by terrigenous mud can be seen within left margin of colony. This burial surface (white dashed line) is concordant with inflection in corallite growth paths (black dashed line), indicating that the colony was tipped from original orientation, most likely into a scour cavity, and subsequently reestablished vertical growth. Divisions on photoscale = 1 cm. B) Longitudinal cut through a typically thin *Thecia minor* corallum, showing regeneration (r) over sediment burial surface. Note that the regeneration originates from the interior of the colony, not at the colony margin.

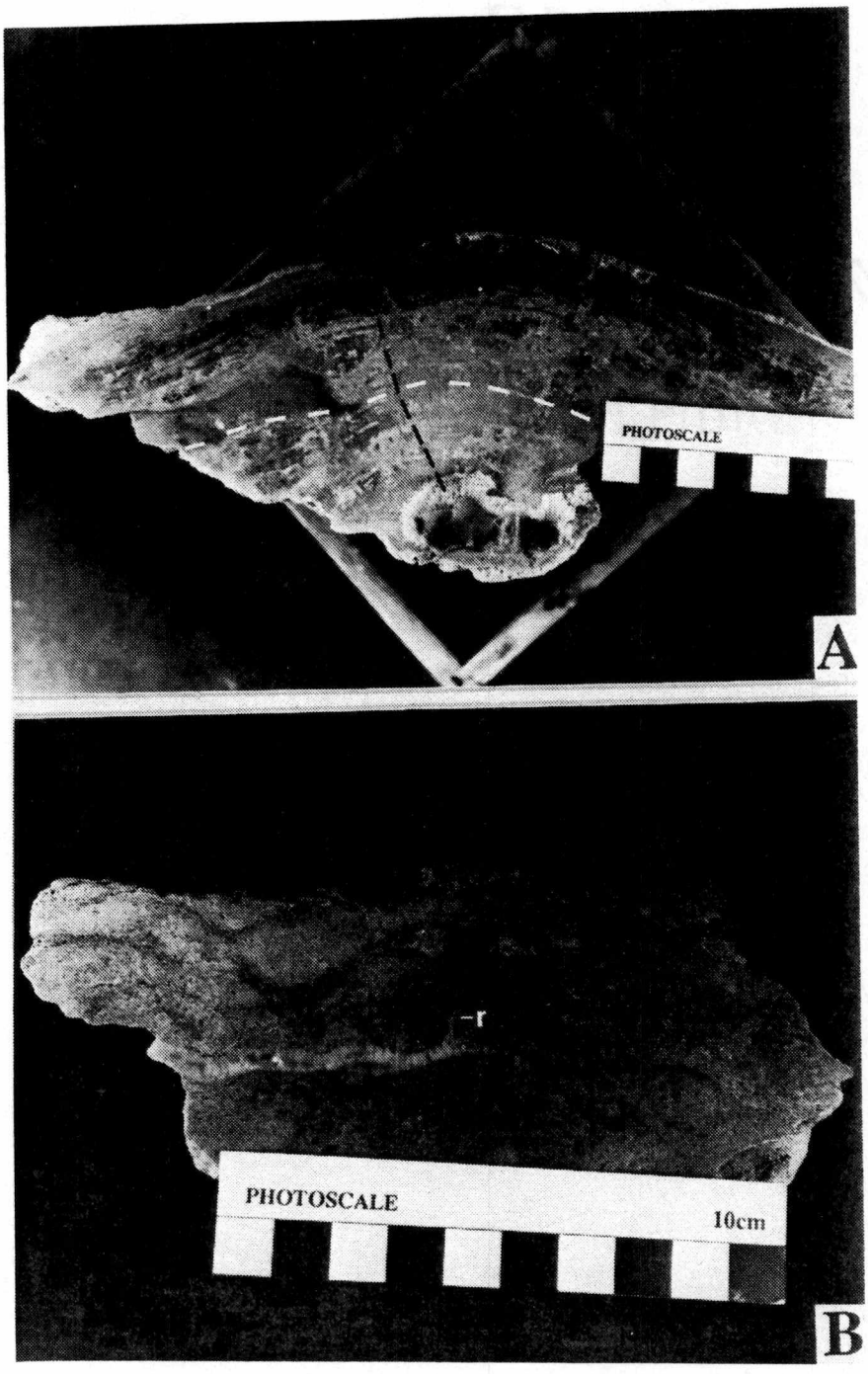

PHOTOSCALE
A
-r
PHOTOSCALE
10cm
B

Figure 17.- *Thecia minor* coralla morphology. A) *T. minor* corallum growing on a preserved mud-rich skeletal substrate. Surface undulations due to growth over the uneven substrate. Divisions on scale = 1 cm. B) Longitudinal cut through a compound *T. minor* colony mass, composed of multiple growth laminae produced by several episodes of burial and colony regeneration.

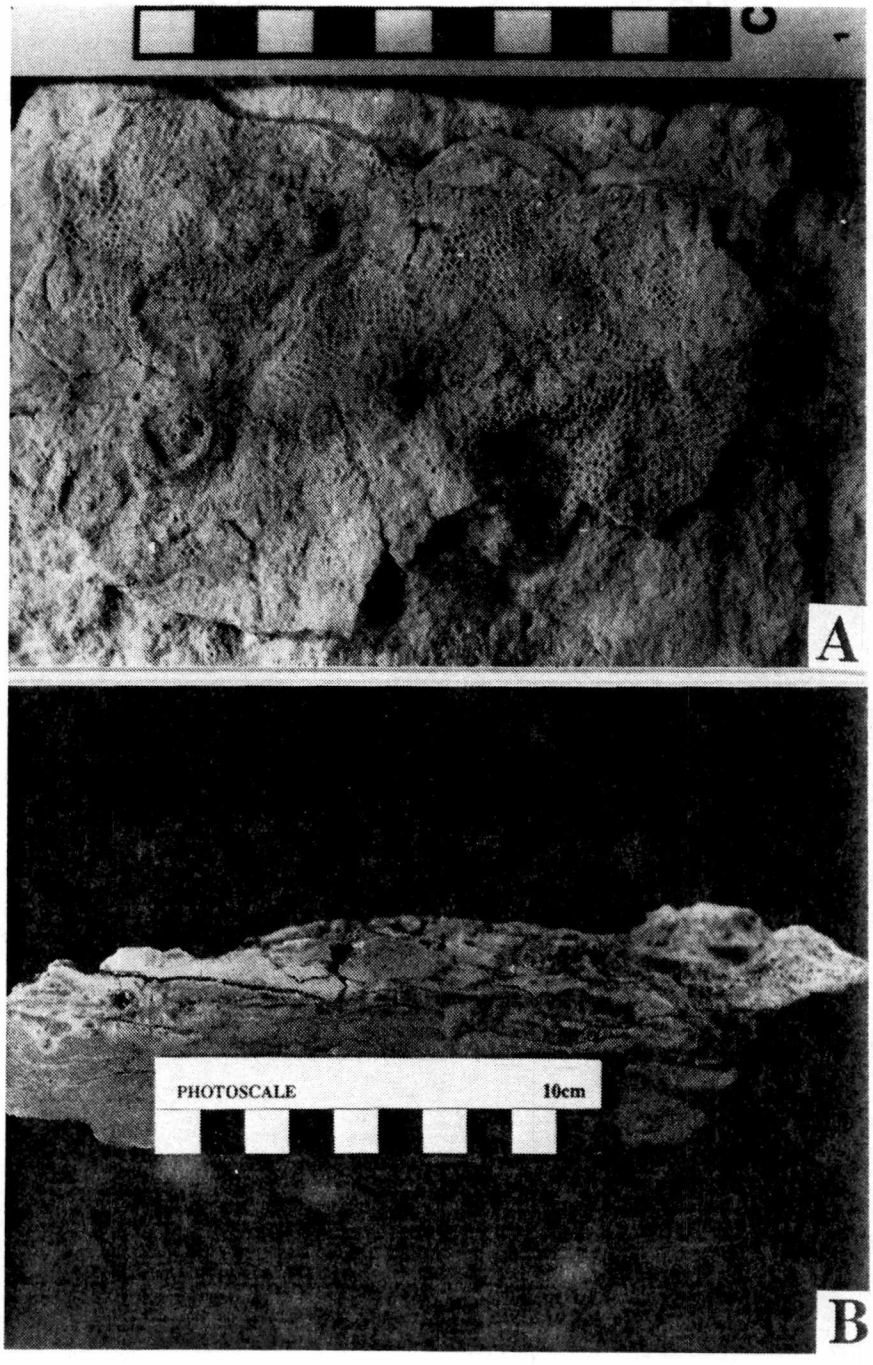

A
PHOTOSCALE
10cm
B

Figure 18.- Photonegative prints from thin sections of the marginal areas of two *Favosites louisvillensis* coralla. A) Note the sediment intercalation (sed), area of regeneration and bryozoan (br), which lived in a cryptic habitat beneath the corallum periphery. B) Note the sub-horizontal-to-vertical horn shape of newly developed corallites (h) along base of corallum. Divsions on scale = 1mm.

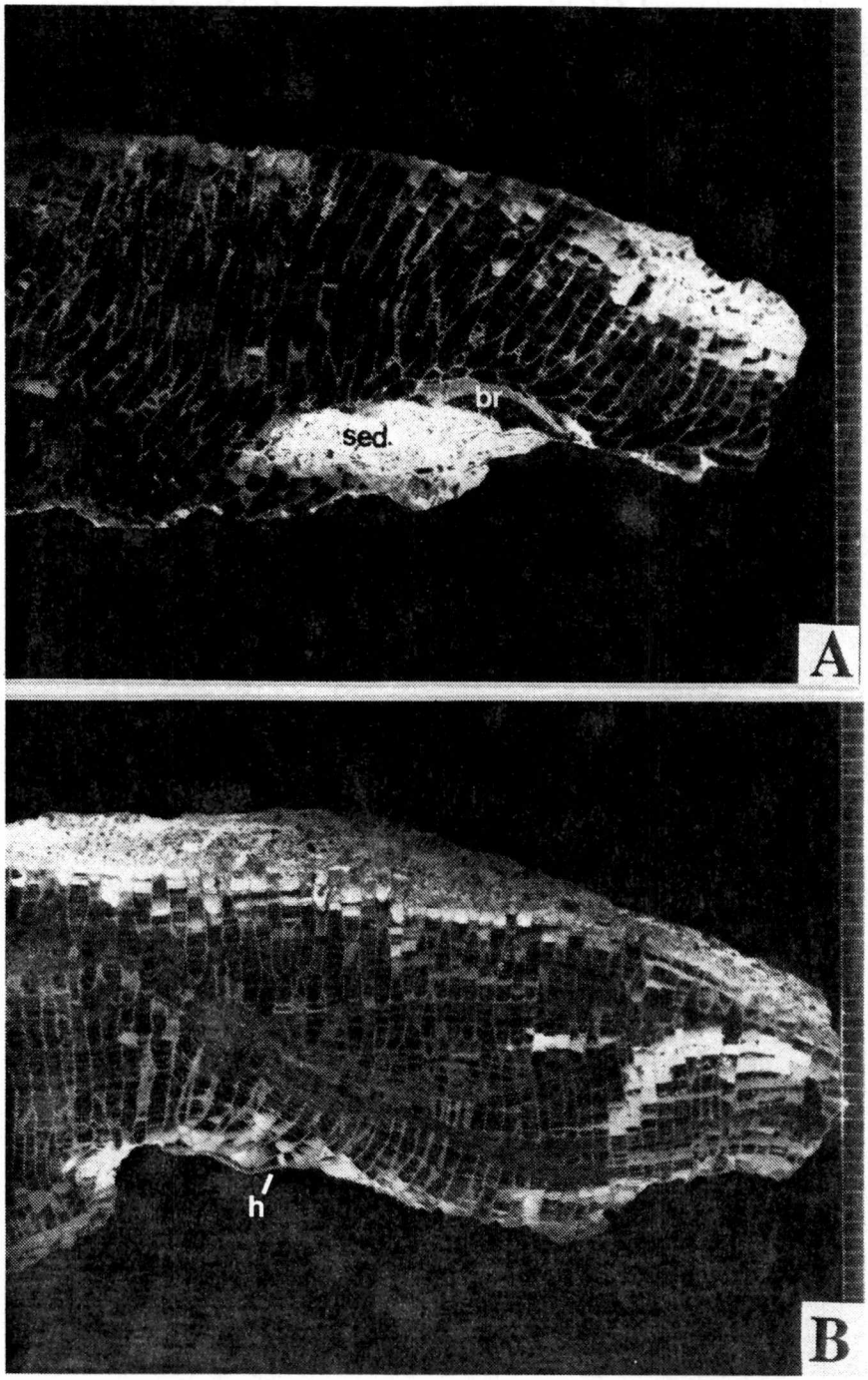
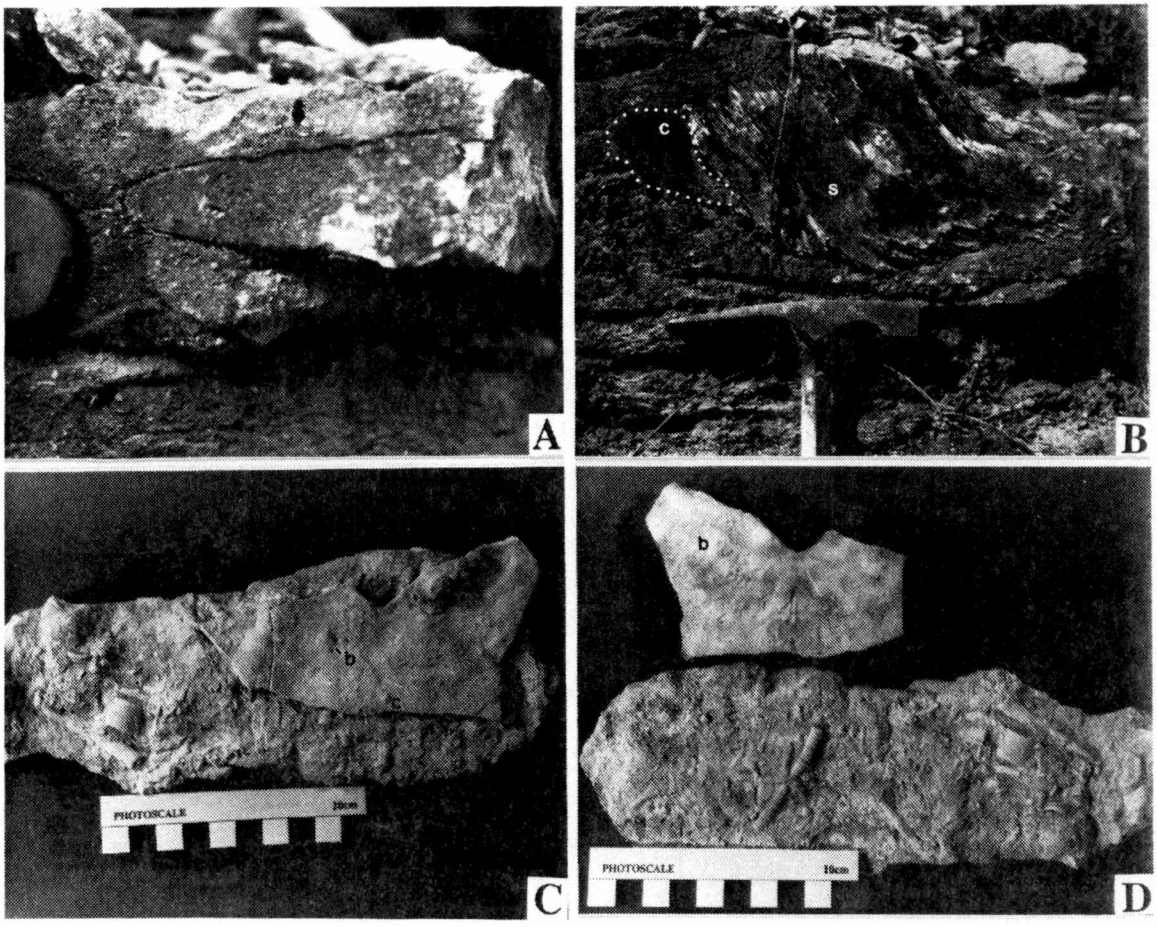

br
sed.
A
h
B

Figure 19.- Effects of sedimentation and currents on colonial organisms from the Lobelville Member. A) Outcrop exposure of a *Favosites louisvillensis* colony within a predominantly grainy bed. Note the continuous colony margin with no sediment intercalation, suggesting a period of negligible fine-grained sediment influx. Lens cap width = 6.5 cm. B) Large stromatoporoid (s) lying on side, suggesting large scale disturbance. Note encrustation by *F. louisvillensis* colony (c) at upper left side of stromatoporoid. C) Photograph of flipped *Thecia minor* corallum fragment, showing epitaphic encrustation of basal epitheca by bryozoans (B) and small tabulate coral colony (c). D) Same sample as 19c, with *T. minor* corallum turned over to show earlier epitaphic encrustation by many gregarious bryozoans (b) on colony upper surface.


A
B
C
S
b
PHOTOSCALE
D
b
PHOTOSCALE

ther analysis and interpretation of tabulate coral growth forms is the subject of Chapter 3.

Small bryozoan zooecia and spirorbid worm tubes are common in cavities on the undersides of large tabulate coral colonies (Fig. 18A), especially those colonies which lived on mud-rich skeletal substrates (see Chapter 4 for further discussion). Current scour of unconsolidated sediment from beneath the peripheries of living corals, produced short lived refugia inhabited by these organisms. Severe disturbances buried or flipped and fragmented large flat colonies (Fig. 19C,D). Fragments and whole colonies later reexposed, became substrates for colonization by other corals, bryozoans, spirorbid annelids and stalked echinoderms.

Paleodepositional Environment of the Lobelville Member

To best understand the paleodepositional conditions under which the Lobelville was deposited the examination and subsequent paleodepositional interpretation of the over- and underlying units is important. The Bob Member, which conformably underlies the Lobelville, is composed of medium- to thick-bedded, coarse grained, echinoderm packstone and grainstone, with rare interbedded, thin shales. The skeletal allochem component of the Bob is dominated by disarticulated echinoderm grains, bryozoan fragments and disarticulated brachiopod valves; the latter are often preserved in hydrodynamically stable orientations (Fig. 6C). Also present are abundant small fragments of a dasyclad alga (Fig. 6C) and beds of concentrically laminated rhodolites (Fig. 6D). There is no indication of sub-areal exposure. This evidence supports an interpretation that Bob sediments were deposited in highly agitated, shallow conditions (<< 30 m; Benedict and Walker 1978) on a constantly sub-aqueous shoal at or near normal fair-weather wave base. It is uncertain if the Bob was a significantly contemporaneous facies of the Lobelville, because it exhibits a strongly consistent stratigraphic position within the Brownsport. Stratigraphic work by Amsden (1949) and during this study (including

stratigraphic information from the DuPont Geohydrological Deep Well Core; Broadhead and others 1992) suggest that shoaling may have been a shelf-wide feature. Poor exposure limits any confident interpretation on the original facies relationships, lateral extent or possible migration of this shoal environment during Brownsport time.

The contact of the Bob Member with the Lobelville Member, as defined previously, is the transition from medium- to thick-bedded limestone to interbedded, medium- to thin-bedded limestone and shale. In the field, this contact can easily be picked as a discrete horizon, but no break in sedimentation is interpreted at the boundary. The lower Lobelville is dominated by echinoderm wackestone and packstone, which is genetically comparable to Bob lithology. Shale interbeds are present, but a minor component (< 10%). Lithologic differences between units, based mainly on qualitative comparison, are an increasing proportion of fine grained matrix, decreased grain size, decreased proportion of brachiopod valves, presence of glauconite peloids, and chert nodules and layers.

Two significant changes in depositional conditions mark the beginning of Lobelville deposition. First, a decrease in current and wave energy, most likely due to increasing water depth. Second, increased influx of fine-grained terrigenous sediment. During deposition, most Lobelville sediment accumulated slowly on the seafloor, under processes of background sedimentation at shallow depths, remaining unburied for long periods of time, allowing for glauconite formation..

However, as in most shallow marine environments, this sediment was episodically interrupted by physical disturbance. A disruption, such as a storm with associated deeply reaching storm waves, may have been accompanied by an influx of fine-grained sediment. Many limestone beds record such high energy disruption in the form of 1-3 cm graded beds (Fig. 9D). The base of a typical graded bed is scoured with a mixed medium- to fine-grained packstone or grainstone texture above the uneven surface, grading upward to a fine-grained wackestone or mudstone texture. When a disturbance was

accompanied by a large sediment influx, a graded bed is overlain by a shale. Much of the benthic fauna present at the time of such an event was preserved with little destruction at the base of and within these shales.

Upward in the Lobelville, thin (0.5-1.0 m), bed-thinning upward intervals appear at LB (units LB3-4, LB12 and LB19; Fig. 8), at CC (units CC1 and CC3; Fig. 12), and at WL (unit WL13; Fig. 11). These bed-thinning upward sequences appear to be the result of a combination of an increase in frequency of physical disturbance, but a decrease in magnitude of disturbance. An increase in the frequency of physical disturbance can be explained most simply in one of two ways: either a decrease in the water depth, or a period of increased storm disturbance. Decreased water depth, by either eustatic sealevel drop or rapid build up of sediment is unlikely for three reasons. First, it is unlikely that eustatic sealevel changes occurred rapidly enough to create such small scale sequences. Second, each sequence is not composed of a regular pattern of successively shallower water facies. Third, a decrease in water level would increase the water energy, inhibiting the deposition of the fine-grained sediment, a significant sediment component of the wackestones and mudstones which form the top of a bed thinning-up sequence. Thus, the origin of a thinning-upward sequence is best explained by an increase in the frequency, but a progressive decrease in the magnitude of storms and associated input of fine-grained mud. Thicker skeletal packstone beds at the base of a sequence represent deposition during a cessation of disturbance. As time progressed, the background accumulation of skeletal sediment and fine-grained mud was more often disturbed by storm events and augmented by the influx of storm-derived mud. These short sequences, at a small scale, reflect an overall trend of increasing frequency of disturbance and terrigenous sediment influx upward in the Lobelville. The sequence of the lower Lobelville section, dominated by limestone lithologies, gradually changes to a sequence of interbedded limestone and shale, with the frequency and thickness of shale interbeds increasing upward, culminating

in the deposition of 0.1-0.5 m thick shale beds and associated thin limestone lenses.

Physical and biological evidence indicates a slow change of environmental conditions during the time of Lobelville deposition. The thickness and quantity of wackestone and packstone beds decrease upward, whereas the thickness and number of shale interbeds increase upward in the Lobelville. Lithologic changes can be attributed to a long term decrease in environmental energy, punctuated by an increased frequency of episodic physical disturbance. Such events may or may not have included the additional influx of fine-grained terrigenous sediment to form shale interbeds. It is important to note the increased thickness of shale units at the top of the Lobelville. Each of these beds is probably not the result of a single large sediment influx, but of many smaller successive events preserved together. Thin lenses of bryozoan-echinoderm wackestone can be found interbedded in some shale sequences, indicating a limited period of seafloor recolonization between sediment influx events. The lack or near lack of interbedded limestone in some of these shale units suggests that background carbonate buildup did not have time to resume between events.

The benthic community of the lower Lobelville was composed of many types of organisms, but was dominated by stalked echinoderms. Echinoderm remains contributed up to 89% (Table 1) of the accumulating skeletal sediment. Other significant members of the benthic community were small ostracodes, possibly living in interstices within the grainy substrate, ramose and some fenestrate bryozoans, tabulate corals, trilobites and occasionally lithistid sponges and brachiopods (mainly pentamerids). In most limestone beds, especially those making up the lower Lobelville interval, skeletal grains at the base and in the middle of the beds are comminuted and broken, indicating that under background conditions, skeletal sediment accumulated slowly on the seafloor.

As the physical environmental conditions slowly changed, the associated biologic component also changed to take advantage of the available substrates. Firm or hard

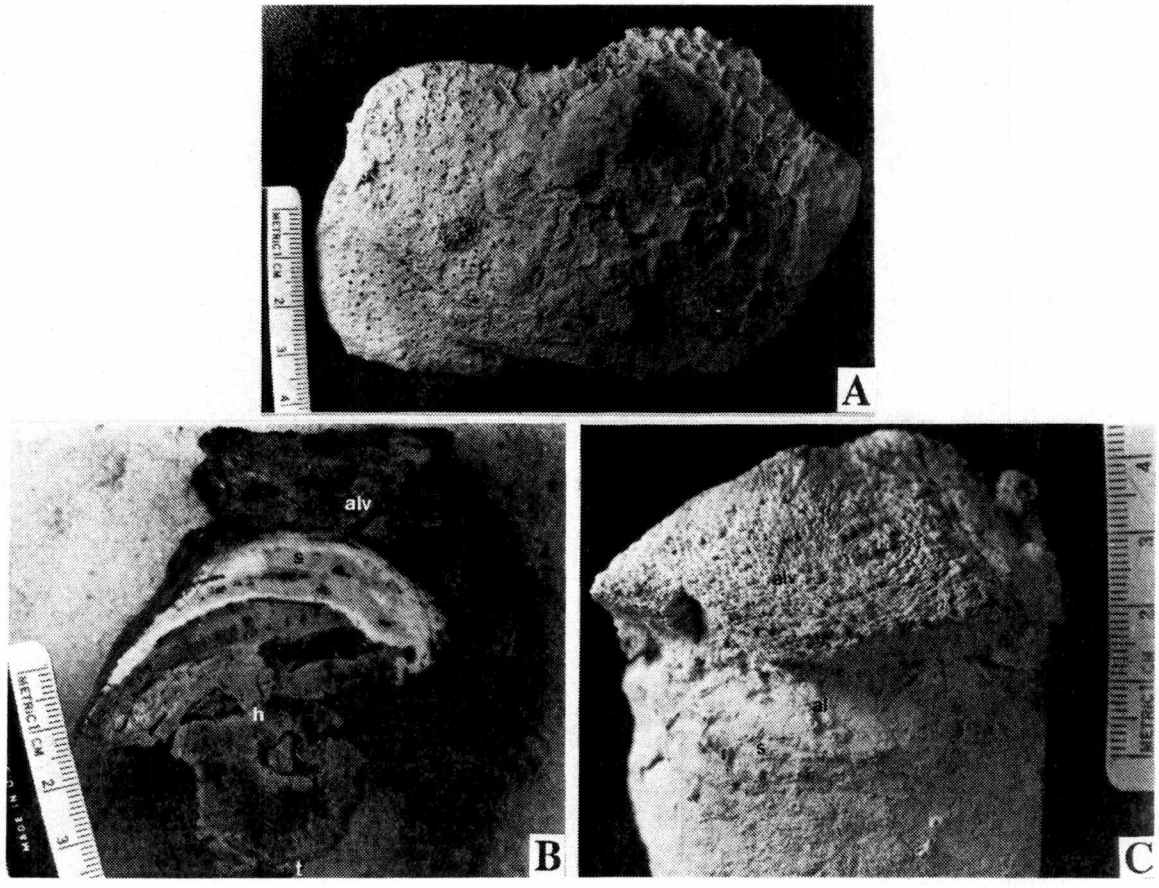
skeletal substrates needed by many organisms for attachment were scarce. Storm currents often mobilized mud from the substrate producing suitable substrates for colonization, but the mud was redeposited elsewhere on the Lobelville seafloor, covering areas under a blanket of fine-grained sediment. This redistribution of sediment created patches of grainy substrates and mud-rich skeletal substrates scattered across the seafloor. Different patches were sometimes colonized by a single or just a few species best adapted to the conditions of that particular substrate. Local concentrations of brachiopods, sponges, bryozoans, or corals were common on the Lobelville seafloor. These concentrations were preserved as layers within limestone beds containing many large shells or chert nodules (sponge-derived), or single beds dominated by a single taxon, such as fenestrate bryozoans or the rugose corals. The patchy distribution of substrates and organisms, and frequent disturbances promoted an increased overall diversity of the community (Osman 1977; Dollar 1982) upward in the Lobelville interval. The heightened diversity of the benthic fauna of the upper Lobelville increased the chances of recolonization of the seafloor following a disturbance.

Along with the presence of soft-sediment deformation loading features (Fig. 10A), many distinctive biotic adaptations suggest that the mud-rich skeletal substrates were unconsolidated and sometimes very soft. Large pelmatozoan root attachments are rare, but many echinoderms developed secondary attachment to the substrate using stem cirri. This adaptation provided stability on the loose substrate. Lobelville corals and bryozoans also employed life strategies well-suited to a soft substrate. Liberosessile and ambitopic strategies allowed the organisms to use available small skeletal grains for initial attachment, followed by rapid development into larger, more stable, free-lying forms (see Chapter 3 for further discussion). Rugose corals commonly took on a recumbent life position, lying on a flattened side of the corallite, after outgrowing initial attachment sites. A low, tabular or platey growth form was common to most free-lying colo-

nial corals and bryozoans. This form was advantageous both for expansion over sediment surfaces which were soft and mobile as well as for perpetuating colony growth following partial burial during sedimentary "crises" (Olson and Broadhead 1992). The colony margins of tabulate corals and larger bryozoans reflect the pattern of sediment accumulation during the life span of individual colonies. A colony with a ragged margin (Fig. 16A), formed by many regenerations, reflects growth during a period of frequent sedimentary disturbance. Thick, tabular colonies with uninterrupted margins (Fig. 19A), are common to grainy intervals which contain a smaller proportion of allochthonous mud. The large platey growth forms of many tabulate corals, especially those of *Favosites louisvillensis* and *Thecia minor*, further suggest that the low net rates of sediment accumulation on the Lobelville mud-rich substrate, allowed stable, undisturbed living assemblages to exist for several years (Olson and Broadhead 1989).

Physical disturbances toppled, reoriented and buried organisms, many of which regenerated. Bryozoans, and rugose and tabulate corals often recorded these events within their skeletons. Geniculated rugosan coralla and deflected growth trajectories within bryozoan and tabulate colonies (Fig. 16A) reflect reorientation from original positions. Epibiotic colonization, both pre- and post-mortem, was a successful and often employed adaptation to Lobelville soft-substrate conditions. Recumbent echinoderm stems and the scoured margins of tabulate coralla became sites of attachment while that host was still living. Multiple post-mortem overgrowths (Fig. 20A,B,C) of both upper and lower colony surfaces, indicate that large platey forms were not immune to mortality following a physical disruption. Coral and bryozoan colonies were sometimes completely buried and killed under a blanket of fine-grained sediment and later reexposed, or broken and overturned by strong storm currents (Fig. 19C,D).

Figure 20.- Examples of multigeneration epitaphic encrustation. A) Multigeneration epitaphic encrustation of *Heliolites* sp. colony. Encrusters include large auloporid colony, and multiple favositid coral and bryozoan colonies. B) Longitudinal slab cut through a multigeneration skeletal mass. The original organism at base is a heliolitid coral colony (h) which grew on a fragment of a theciid corallum. The heliolitid is overgrown by a stromatoporoid (s), which is in turn overgrown by an alveolitid coral colony (alv). C) Reverse view of same multigeneration skeletal mass, revealing additional overgrowth of stromatoporoid by an auloporid coral (al).


A
alv
h
t
B
C

Decatur Formation

The Brownsport Formation is conformably overlain by the medium- to coarse-grained, echinoderm packstones of the Decatur Formation. It is distinctive from the Brownsport in that it is thicker bedded, contains much less shale (Amsden 1949), and commonly forms ledges above the less resistant outcrops of the upper Brownsport (Fig. 4D). Shale interbeds occur near the base of the Decatur (McComb 1987), but become fewer and thinner upward, indicating a gradual cessation of terrigenous mud influx (Clement 1989).

Fossils from the Decatur include articulated echinoderm stem fragments, disarticulated brachiopods and ostracodes, comminuted bryozoan fragments and tabulate corals. Cryptostome and fenestrate bryozoans present in McComb's samples of the Decatur are finely comminuted and fill spaces between grains. McComb (1987) interpreted the overall depositional environment of the lower Decatur in water depths below normal wave base, similar to that of the Brownsport. He also noted cross-beds and laterally restricted zones of "ooids" similar to the rhodolites found in the Bob Member of the Brownsport Formation. The Decatur rhodolites are less than 5 mm in diameter, circular or rounded-elongate in form and have a small skeletal grain center, often small echinoderm grains, but occasionally ostracode and brachiopod fragments. The coatings formed by the successive encrustation of red algae on a skeletal grain The concentric bands indicate a water energy in this environment strong enough to keep the grains moving allowing an even coating (McComb 1987). Larger grain size, less shale, broken skeletal grains, cross-beds and presence of rhodolites indicate a shallower water depositional environment, at least periodically, than the Lobelville.

Depositional Summary and Conclusions

The upper Dixon through lower Decatur stratigraphic interval represents a period

of nearly continuous carbonate deposition in various shallow marine environments. Water depths and frequency of physical disturbance varied during deposition of this interval, resulting in the sedimentologic and biologic differences between units. The predominant red coloration of the fine-grained terrigenous and carbonate sediments and sparseness of fossils, most of which are disarticulated skeletal grains, suggest that the Dixon was deposited in a shallow mud flat environment.

Dixon sediments conformably grade upward into the interbedded echinoderm wackestone and packstone and allochthonous shale of the Beech River Member of the Brownsport Formation. Limestone beds of the Beech River contain little glauconite and many articulated multielement skeletons. Small scale (1-4 cm thick) graded intervals are present at the top of most limestone beds which are directly overlain by gray shales. This evidence suggests that Beech River skeletal sediment accumulated rapidly on a level-bottom seafloor below normal wavebase. The accumulating sediment was periodically disturbed by turbulent storm events accompanied by the influx of varying amounts of fine-grained allochthonous sediment.

A cessation of allochthonous sediment influx and decrease in water level marked the conformable shift to deposition of the Bob Member of the Brownsport Formation. Bob skeletal sediment is medium- to coarse-grained, predominantly disarticulated echinoderm and brachiopod grains. Fragments of green algae are present along with faintly cross-bedded layers of concentrically coated rhodolites. Bob sediments were deposited in a shallow water shoal environment. The concentrically coated rhodolite grains indicate constant agitation, suggesting deposition at a depth above normal wave base.

The Bob-Lobelville contact preserves a gradual, conformable transition to deeper-water depositional conditions. There is an upward trend of decreasing limestone bed thickness and increasing proportion and thickness of shale interbeds. The dominant lithologies are echinoderm and echinoderm-bryozoan wackestone interbedded with

allochthonous gray shale. These two dominant lithologies represent temporally different scales of sediment accumulation.

The skeletal component of Lobelville limestone beds, such as multielement echinoderm skeletons, and brachiopod and ostracode valves are typically disarticulated. Larger skeletal pieces are commonly encrusted by several generations of epibionts. Along with the presence of glauconite and the distinctive large, platey coralla of tabulate corals, such as *Favosities louisvillensis*, suggest that autochthonous skeletal sediment accumulated slowly on the Lobelville seafloor. Soft sediment deformation features, an increased number of fragile organisms such as fenestrate bryozoans, and the dominantly ambitopic and encrusting life habits of most benthic organisms, suggest a soft substrate at depths well below normal wave base.

Thin, storm-generated graded sequences are common sometimes within, but mainly at the top of limestone beds and frequently are overlain by rapidly deposited gray shales. The frequency of such disturbances increased over time, culminating in the deposition of thick sequences of shales interbedded with thin limestone beds and lenses. Less severe, but more frequent physical disturbances, not accompanied by large sediment influx, are recorded within the contorted and regenerated skeletons of the Lobelville corals. This evidence suggests water depths within the reach of storm generated waves and currents.

The Lobelville is conformably overlain by the Decatur Formation. Differences in Decatur lithology are larger grain size, less allochthonous mud, more graded beds and the reappearance of rhodolites (McComb 1987). The Decatur sediments represent a gradual return to a shallower, somewhat higher energy environment, which may have experienced less allochthonous mud influx.

Chapter 3: Coral Colony Form and Adaptation: Implications for Depositional Environment

Introduction

Many factors have been attributed to exert an influence on the growth of colonial organism, affecting the growth rate of a colony, the growth form of a colony, or both. Interpretations of the absolute growth rate of some Paleozoic fossil corals have been presented by Wells (1963, 1970), Scrutton (1965, 1970), Sorauf (1974), Rosenberg and Runcorn (1975), and Gibson and Broadhead (1989). Additionally, certain skeletal features exhibited by many tabulate corals such as tabulae spacing and epithecal banding, are thought to reflect regular periodic growth (Ma 1933, 1943; Philcox 1971; Scrutton and Powell 1980; Hill 1981; Olson and Broadhead 1989; Baarli and others 1992). Determination of the absolute growth rate of tabulate colonies is difficult, because the lack of living tabulate corals precludes determination of the presence of algal symbionts and of absolute growth rate.

The effects of relative growth rate variations within a single colony should not be overlooked when evaluating the development of colony shape. For example, any reduction in normal growth rate of a colony, or even part of a colony, will affect the final shape of that corallum. Repeated changes in growth rate may represent regularly recurring events within the depositional environment, thus providing information important to an accurate paleoenvironmental reconstruction. Because absolute growth rate and age determination are still equivocal, the emphasis of this study has been placed on interpreting factors affecting colony growth form. Many of these factors are reflected in growth rate variations, but do not require the absolute age of a colony to be known.

Specimens examined for this study were collected from the Lobelville Member of the Brownsport Formation (Upper Silurian, Ludlow) of West Tennessee, which is noted for an abundant and diverse coral fauna (Roemer 1861; Pate and Bassler 1908; Amsden 1949). These corals lived in a level bottom, mixed terrigenous/carbonate environment,

characterized by periods of low net sediment accumulation, punctuated by frequent physical disruption, such as storm events. These storms were often accompanied by biologically devastating influxes of terrigenous mud. Tabulate corals, which lived in this disturbed environment, exhibit a wide range of colony forms. The purpose of this study is to evaluate the relative importance of genetic and ecologic controls on the colony form of two species of tabulate coral. Ultimately an attempt has been been made to analyze colony form in terms of adaptation which allowed these species to proliferate in a periodically disrupted soft substrate environment.

Methods

Tabulate corals were observed and collected both *in situ* and in associated talus at three stratigraphic sections: LB, WL, CC (See Chapter 1 for location information). *In situ* specimens were collected, where possible, with surrounding matrix, and overlying shale layers were sampled to determine the nature, source and composition of mud influxes. Fossil samples and attached matrix were examined in detail and cleaned by boiling in a solution of water and Miramine OC-EC, an industrial surfactant. Corals were examined for growth form and epibiont encrustation.

Paleontology

Material

The Lobelville Member of the Brownsport Formation is well know for a diverse assemblage of well preserved tabulate corals, consisting of at least 25 different species (Amsden 1949). Two species of tabulate coral, *Favosites louisvillensis* Davis and *Thecia minor* Rominger, were chosen for this study because of the distinctive low, platey growth form. Certain specimens were cut longitudinally to reveal internal growth features and thin sections or acetate peels were made for further detailed observation. All specimens

illustrated are housed in the Department of Geological Sciences at the University of Tennessee, Knoxville.

FAVOSITES LOUSIVILLENSIS Davis. - *F. louisvillensis* coralla are platey or tabular (Fig. 16A) with a flat or slightly convex base. Of the free-lying specimens collected, colony diameters range from approximately 3 cm across up to 1 m across. Colonies are distinctive for large diameters, but thin profiles (most < 3 cm thick). Generally, the upper surfaces of *F. louisvillensis* colonies are flat, but may be slightly convex. The colony base is covered with a thin skeletal epitheca with approximately 1 cm wide, concentric undulations, which on some specimens are partly or wholly eroded. Specimens retaining an epitheca commonly display colonization by epibionts, such as bryozoan colonies and spirorbid worms. Small to medium sized colonies are commonly found complete, whereas larger coralla usually become fractured as they weather from surrounding shales. Ninety-seven specimens from the study area and approximately 25 specimens housed at the Yale Peabody Museum were examined for this study.

Individual corallites are of uniform size, with an average diameter of 1.5 mm (Amsden 1949). Initially, offsets bud horizontally at the colony margin and turn sharply upward forming a horn-shaped corallite (Fig. 18B). The asexual budding of corallites is by lateral increase, almost exclusively at the colony margin. The outward directed budding pattern promoted horizontal expansion (non-radial of Philcox 1971) creating a platey colony form. A lesser amount of growth is by intracalicular increase, present in the convex central area of some colonies.

THECIA MINOR Rominger - *T. minor* coralla are characteristically very thin and laminar (Fig. 17A,B). Most colonies are approximately 2-5 mm thick, up to 2 cm thick. Colony diameters are commonly up to tens of centimeters wide, but most specimens

found are colony fragments. These thin, fragile colonies appear to have been broken (Fig. 19C,D) either syndepositionally during turbulent disruption, later becoming attachment sites for other sessile benthic organisms, or postdepositionally by compaction of shales and by subsequent exposure and weathering. Undulations in the colony upper surface (Fig. 17A) reflect the effects of growth over the irregular substrate. The lower colony surface is covered with a thin, irregularly wrinkled epitheca. Whole colonies regularly display multiple regenerations, branching upward and then growing outward at peripheries covered by sediment (Fig. 17B). Colony growth pattern and growth form observations are based upon the examination of approximately 78 *T. Minor* coralla and large corallum fragments.

Average corallite diameter is less than 1 mm wide. A pattern of lateral increase is exclusive, with offsets originating at colony margins promoting rapid lateral expansion of the colony, similar to *F. louisvillensis*. This pattern of offset created a single growth lamina, consisting of a discrete series of peripherally budded corallites. The component of upward growth of *T. minor* corallites was minimal; the maximum thickness of a single growth lamina is approximately 1 cm. Commonly, thicker colony masses, composed of multiple growth laminae, formed in conditions of episodic partial colony burial

Controls on Coral Growth

Genetic Controls

Clonal organisms develop at two distinct levels (Pandolfi 1988): the level of the individual module (ontogeny), which in this case is the corallite, and at the level of the colony of modules (astogeny). Development at each level is controlled in great part by the genetic make-up of the organism, which exerts control on colony development in three ways. First, at the ontogenetic level, budding and development of the individual corallite is genetically determined. Secondly, at the astogenetic level, the rate and pattern

of skeletal increase affects the development of the entire colony (Oliver 1968; Hill 1981; Pandolfi 1988). Finally, a factor affecting development at both levels is the degree of colony integration or the interconnectedness of individual corallites (Coates and Jackson 1985; Pandolfi 1988; Noble and Lee 1990).

At the ontogenetic level, the origin of new corallites in coralla of *Favosites louisvillensis* and *Thecia minor* was by lateral increase. Offsets formed on one side of a mature-size corallite located at the colony margin: a joint epitheca developed beneath both corallite and offset. At the point of origin, the offset was commonly much less than half the diameter of the mature-size corallite and was oriented sub-horizontally (Fig. 18B). During subsequent growth the offset expanded over a length of less than 1 mm to a mature diameter and curved upward to a near-vertical mature orientation. This array of upward facing corallites created a nearly flat colony upper surface.

The corallites of both *F. louisvillensis* and *T. minor* had small mature diameters (1-2 mm) and extremely short lengths to reach full diameter, suggesting that the development period to mature size was quite short. There is no direct evidence that these corallites necessarily grew faster than larger diameter corallites of other tabulate coral species (e.g., the 4-5 mm diameter corallites of *F. brownsportensis*), but because of the smaller mature diameter, mature size was reached sooner (Fig. 21). Once full diameter was reached, corallites formed offsets, the small size allowing for approximately 8 times the number of corallites per unit area of colony surface. The small size of *F. louisvillensis* corallites, in comparison with the corallites of other species, is consistent with an interpretation of progenetic development as described by McKinney (1988) and McKinney and McNamara (1991). Progenesis does not involve changes in shape or developmental rate during ontogeny, but defines an early offset of morphological change and size increase (McKinney and McNamara 1991). Termination of growth is often associated with reaching sexual maturity, but in tabulate corals, there is no evidence for

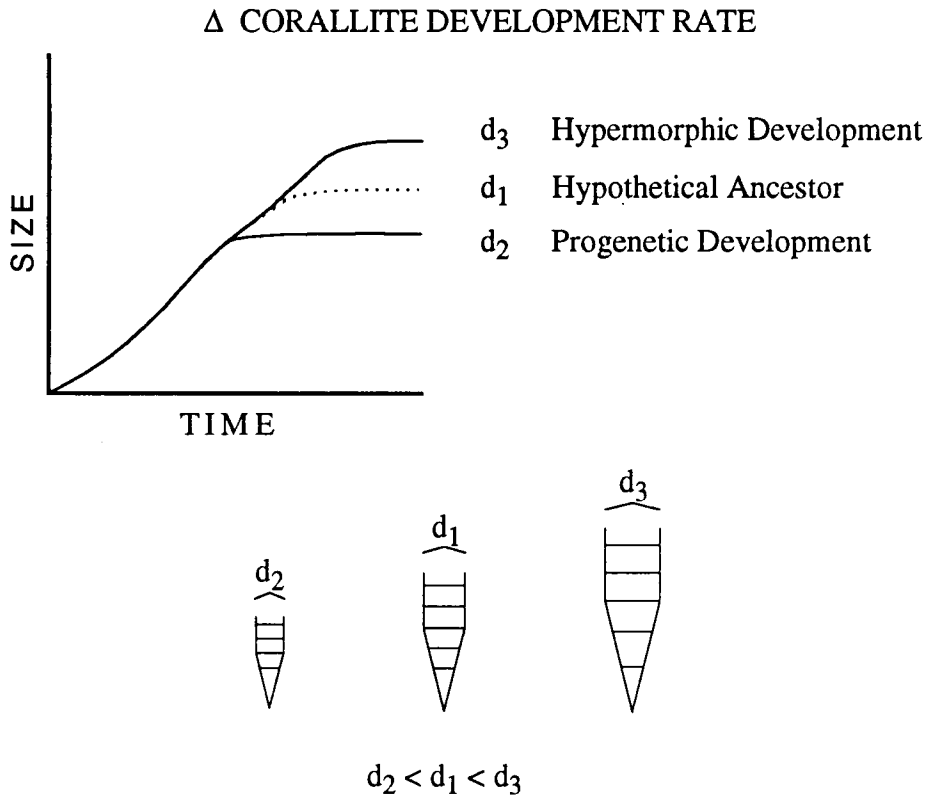


Figure 21.- Diagrammatic representation of relative changes in the timing of offset of growth. A shorter development time (d2), due to ontogenetic truncation, led to smaller mature corallite diameter. This size decrease is representative of the apparent progenetic character of *Favosites louisvillensis* and *Thecia minor* corallites.

the timing of sexual maturity or its relationship to the attainment of mature size. However, ontogenetic truncation may be the result of reaching a size at which asexual budding occurred. Whatever the cause for ontogenetic truncation, the apparent progenetic development of corallites in these species affected the development of the colony as a whole. These observations agree well with the conclusions of Pandolfi (1988), who implied a relationship between altered development of individuals and colony growth (astogeny) in colonial organisms.

This study is not the first to attempt to evaluate the significance of coral colony form or to suggest heterochrony as a process in coral evolution. Lee and others (1990) provide the best documented case of heterochrony in the *Heliolites interstinctus-decipiens* lineage. The reduction of septa and the replacement of crenulate corallites with smooth corallites in the descendant appear to have been by paedomorphosis from the ancestor (see also Noble and Lee (1990) for a preliminary reinterpretation of comparative work by Stumm (1962) on *Propora tubulata*). The lack of distinctive morphological characters in favositid corals, makes such detailed analysis of development difficult, but not impossible. Young and Elias (1992) examined the relationship between growth form and internal morphology of *Paleofavosites subelongus*. Two different "modes" of initial colony growth, defined by astogenetic (rate of axial offsetting) and ontogenetic (rate of corallite expansion) developmental changes, created either a bulbous or domical colony shape. From this information, it would seem possible to to identify the heterochronic process(es) which created different developmental patterns in specimens of the same species. Although these studies attempt to analyze evolutionary and developmental features of tabulate corals, they do not attempt to interpret their adaptive significance.

The astogeny of a colony is greatly affected by both the rate of expansion (increase) and direction of growth of offsets composing the colony (Oliver 1968; Hill 1981). In general, rapid outward development creates a sheet or platey shape, whereas equal

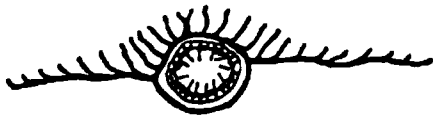
outward and upward expansion produces a mound shape (Pandolfi 1984). In *F. louisvillensis* and *T. minor* the dominant form of expansion was by lateral increase (Olson and Broadhead 1992), with apparent rapid formation and development of corallites at the colony margin creating a platey growth form. Only within higher areas of the corallum, near the centers of large *F. louisvillensis* colonies, are a small number of offsets formed by intracalicular lateral increase, which produced slightly higher, "domed" areas of the colony.

Initial astogenetic development (the period following settlement and metamorphosis of the coral larvae on a hard substrate) in these species was primarily directed outward. A broad colony base was established, which contributed to colony stability on the substrate (Fig. 22). This developmental pattern, in which only a small hard or firm substrate was necessary only for larval attachment, was superseded by the substrate produced by later skeletal increase (Neuman 1988), and is known as ambitopism. Ambitopic growth is well suited to conditions of soft or limited hard substrate and appears to have been a successful and commonly employed adaptation of colonial corals and some bryozoans and stromatoporoids to the Lobelville environment.

Many species of tabulate coral had characteristic colonial growth patterns and were able to repair damage in order to restore the original shape of the colony (Hill 1981; Pandolfi 1988). Following a physical or biological disturbance the surviving corallites, commonly in higher areas of the colony surface, became a locus of colony regeneration. Regenerative growth followed the pattern of initial astogenetic development of the colony; outward directed asexual budding caused horizontal expansion over the sediment drape reestablishing a broad colony base for subsequent outward growth (Fig. 22). Both *F. louisvillensis* and *T. minor* appear to have been quite capable of regeneration. Many colonies of both species preserve multiple regenerations, the net effect of which created an exaggerated vertical dimension in larger (older) colonies.



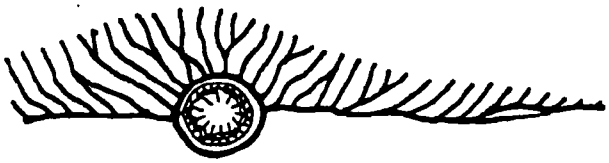
1. Colonization of isolated hard substrate



2. Development of stable substrate by skeletal increase



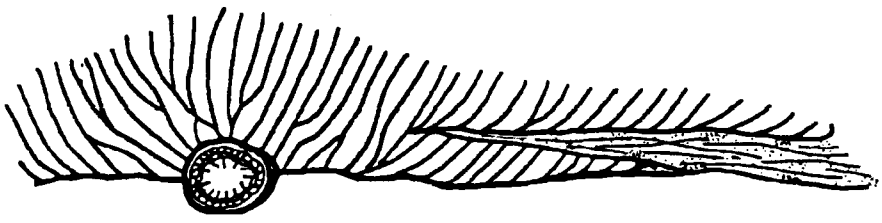
3. Scouring at colony periphery produces cryptic habitat for colonization



4. Further outward expansion of corallum margin isolates cryptic biota
(Repetition of stages 3 and 4)



5. Storm deposited terrigenous sediment partly buries corallum and smothers cryptic biota



6. Corallum "regenerates" and continues to extend over unconsolidated substrate
(Repetition of stages 3 and 4, 5 and 6)

Figure 22. - Diagrammatic representation of ambitopic development, including stages of sediment scour, partial burial and subsequent colony regeneration.

The astogenetic development of *F. louisvillensis* and *T. minor*, both initially and during regeneration allowed a more rapid outward colony growth than was possible in colonies with different budding patterns or possibly also those with similar budding, but larger corallites. The asexual multiplication of corallites during colony growth would have been preferred at the expense of module growth (Pandolfi 1988). This may have been due to a shorter development period of modules, not because of faster growth. Mature corallite diameter was small, therefore mature size and the ability to bud new polyps may have been reached quickly. The net result allowed the colony to grow rapidly, which would have been particularly important in times of crisis (e.g., partial burial, physical damage, competitive interaction). Following a crisis, such as partial burial under storm derived sediments, colonies of *F. louisvillensis* and *T. minor* were able to expand rapidly, recreating a stable colony base. Rapid growth not only increased skeletal area, but also increased the population of living individuals, enhancing the population's survival under stressed conditions.

Colony interconnectedness is difficult to evaluate for these two species. Mural pores between corallites are present in coralla of both species, but are irregular in number and often poorly developed. The pattern of regeneration, which *F. louisvillensis* and *T. minor* exhibit, suggests a significant degree of colony communication and colony plasticity. The redirection of growth to reestablish the colony shape could have been communicated through the interconnection of living tissue along the colony surface and the limited number of mural pores. It is apparent that individual polyps retained the ability to bud offsets even after becoming surrounded by neighboring corallites. Thus, a disturbance, such as partial colony burial, ultimately had little effect on the pattern of colony growth.

There is an "ideal" growth form for all colonial organisms determined by the inherited "genetic program." Barring external influence, a colony will develop into this

ideal form. Examination of many specimens of both *F. louisvillensis and T. minor* suggests that, unaffected by external controls, both species would have formed flat circular colonies which would have expanded indeterminately across the seafloor while developing only a minor component of upward growth. Examination of fossil specimens of these species indicates that this ideal form is largely prevented by the extrinsic influence of small-scale sediment effects, and not by genetically influenced variability.

Ecologic Controls

There are many ecologic factors which modify an ideal colony shape. A review of published literature has revealed many environmental factors which affect the growth of colonial organisms, of which 8 ecologic factors (Table 2) are considered here to be important. Their predicted effects on coral colony growth are summarized below, and are applied to the analysis of which factors most affected growth of *Favosites louisvillensis* and *Thecia minor* coralla.

Sediment accumulation. - The effect of sediment accumulation on the growth form of colonial organisms is dependant on both the net rate and episodic rate of sediment accumulation. Abrupt influx of sediment will disrupt normal growth and, depending on the magnitude of the sediment influx, may damage part or kill an entire colony. Where a colony is only partially buried, most colonies have the ability to regenerate, that is redirection of growth upward and outward over covering sediments (Philcox 1971; Stel 1978; Kershaw 1981, 1984, 1990; Baarli and others 1992). Regenerative growth is common in colonial organisms (Philcox 1971; Stel 1978; Kershaw 1984, 1990 [stromatoporoids]; Parsons and others 1988 [bryozoans and corals]; Noble and Lee 1990; Baarli and others 1992). Such alteration of growth usually does not radically alter normal colony development, but impedes the outward expansion of the colony (Fig. 23A) and leads to an exag-

Table 2 : Ecologic Factors Altering Normal Growth Pattern

Ecologic Factor	Reference
Sediment accumulation	Philcox 1971 Stel 1978 Kershaw 1981, 1984, 1990 (stromatoporoids) Stearn 1982 (stromatoporoids and modern corals) Hughes and Jackson 1985 (modern corals) Harrington 1987 (stromatoporoids) Pandolfi and Burke 1989 Baarli and others 1992
Currents	Philcox 1971 Dustan 1975 (modern corals) Kershaw 1981, 1984, 1990 (stromatoporoids) Dollar 1982 (modern corals) Stearn 1982 (stromatoporoids and modern corals) Pandolfi and Burke 1989 Baarli and others 1992 Stel 1978 Harrington 1987 (stromatoporoids)
Substrate conditions	Kershaw 1984, 1990 (stromatoporoids) Baarli and others 1992
Competition	Philcox 1971 Lang 1973 (modern corals) Dustan 1975 (modern corals) Jackson 1977 Stel 1978 Kershaw 1981, 1990 (stromatoporoids) Meyer 1981 (stromatoporoids) Stearn 1982 (stromatoporoids and modern corals) Hughes and Jackson 1985 (modern corals)
Light intensity	Goreau 1963 (modern corals) Baker and Weber 1975 (modern corals) Dustan 1975 (modern corals) Stearn 1982 (stromatoporoids and modern corals) Hughes and Jackson 1985 (modern corals) Huston 1985 (modern corals) Pandolfi and Burke 1989 Baarli and others 1992
Food supply	Stel 1978 Kershaw 1981, 1984 (stromatoporoids) Stearn 1982 (stromatoporoids and modern corals) Pandolfi 1984 Baarli and others 1992
Bioerosion	Dustan 1975 (modern corals) Stel 1978 Stearn 1982 (stromatoporoids and modern corals) Hughes and Jackson 1985 (modern corals)
Water chemistry	
Oxygen	Stearn 1982 (stromatoporoids and modern corals) Kershaw 1984 (stromatoporoids) Pandolfi and Burke 1989
Salinity	Stearn 1982 (stromatoporoids and modern corals)

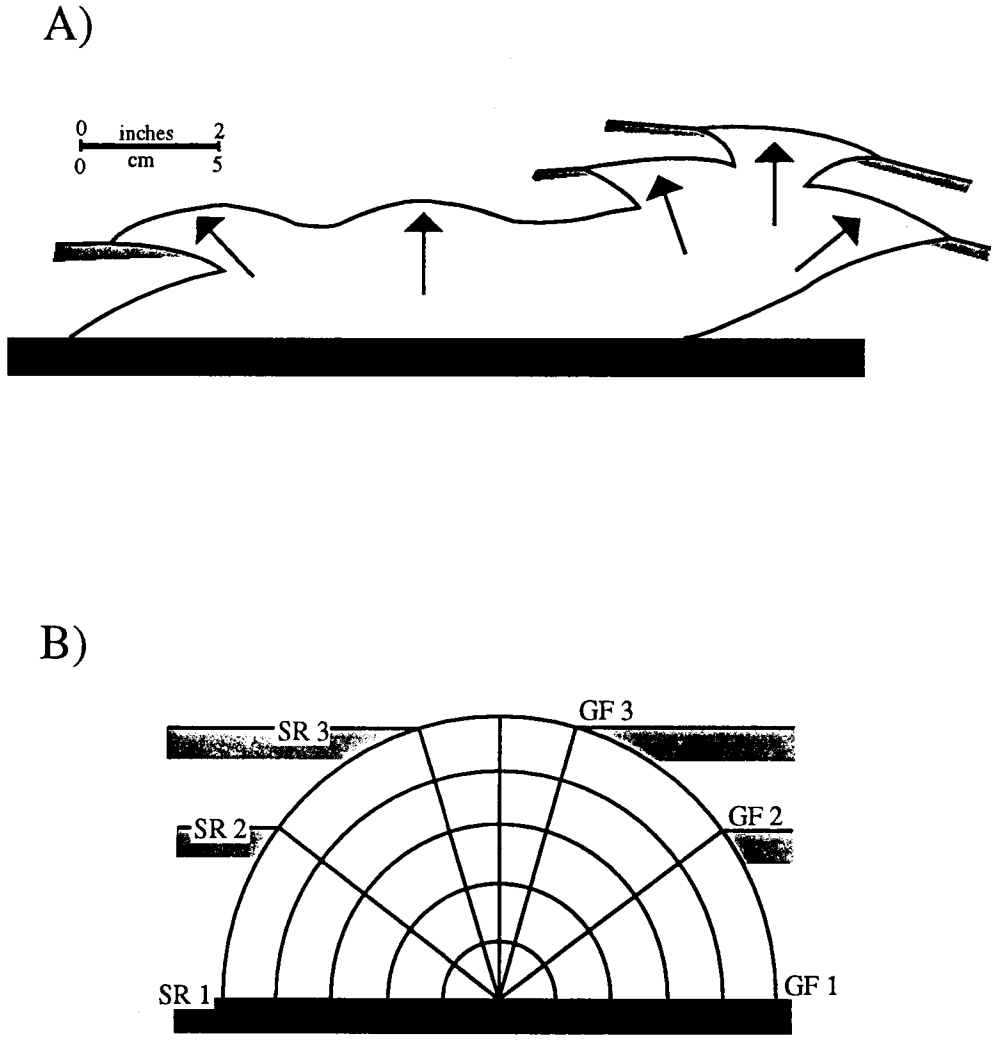


Figure 23. - Sedimentation and coral colony growth form. A) Effects of sediment accumulation and regeneration on favositid coral colony shape and thickness. B) Influence of sedimentation rate on shape of colony base in colonial corals. Corals will form a more convex colony base in conditions of greater sedimentation rate (SR 1 < SR 2 < SR 3). SR - sedimentation rate; GF - colony base growth form (Modified from Philcox, 1971)

gerated vertical dimension (Kershaw 1984).

Slow, steady accumulation of sediment similarly will promote upward colony growth, but at a more constant rate. The accumulating sediment prevents outward growth, forcing a colony to expand upward in order to stay above the sediment-water interface (Fig. 23B). Under these conditions colonies tend to be convex-based (Philcox 1971; Gibson and Broadhead 1989), growing vertically to keep up with the accumulating sediment.

Currents. - Colony shape is influenced by both strong and weak currents. The effects of strong currents are more easily identified and probably of more consequence. Tipping, flipping and breaking of colonies by strong currents has great impact on colony growth. Several episodes of regeneration following displacement of a colony will considerably alter the growth form, and a non-domical or non-tabular growth form will develop even though colony growth may be controlled by a domical or platey style of growth (Kershaw 1984). At a population scale the frequent occurrence of strong currents will remove taller colony forms from the population, leading to apparent dominance of more stable platey or low domical colony forms (Dollar 1982; Kershaw 1990; Baarli and others 1992).

Moderate currents also affect colony growth. A moderate prevailing current can influence colony growth in three ways: 1) Removal of unconsolidated sediment from beneath colony peripheries. This will destabilize the colony base increasing the chance that the colony will be tipped during a period of stronger currents (Fig. 19B). 2) Mobilization of sediment increasing water turbidity. The subsequent reduction in sunlight level reaching the seafloor may affect the colony growth rate or cause the development of flattened forms. 3) Preferential colony growth parallel to prevailing currents (Stel 1978; Harrington 1987). The rate of growth increased at the upstream side of the colony because of increased food supply. It is also possible that the concurrent removal and subse-

quent redeposition of loose sediment from beneath colony margins had an effect on growth. If currents deposited the sediment next to or on low-lying colony margins, lateral growth would have been restricted temporarily in those areas creating a similar elongate form.

Slow currents can interact with colony form creating turbulence over higher areas of a colony (Kershaw 1984, 1990). The turbulent currents created may concentrate nutrients at these higher areas, enhancing growth to that part of the colony.

Substrate conditions. - The effect of substrate conditions on colony growth is related to the cohesiveness of the sediment, grain size of sediment, the pattern of sediment accumulation and the current energy of the environment. Fine-grained, loose sediment can be scoured from beneath colony peripheries and often relocated to other parts of the colony margin. Areas covered with sediment would be overgrown by "regenerative" growth, again causing peripheral increase in the thickness of the colony. Irregularities present on the basal epitheca and concave basal surface suggest positive geotropic growth occurred at points of scour.

Colonies with a wide base, particularly flatter forms, are well adapted to soft substrate conditions. Even though a platey shape is more likely to be partially or totally buried, the uniform weight distribution not only provides stability to free-lying colonies but prevents the colony from sinking into the sediment ("snowshoe" adaptation of Thayer 1975; see also Philcox 1971; Kershaw 1984, 1990; Baarli and others 1992). Taller, narrow-based colonies tend to subside into soft substrates forming cone shaped colonies (Philcox 1971; Gibson and Broadhead 1989; "iceberg" adaptation - Thayer 1975). The upper surfaces of tabulate corals commonly reflect the topography of the encrusted substrate. Unusual shapes and profiles are formed by the overgrowth of an uneven seafloor and the skeletons of other organisms (Stel 1978). Colonies growing over sub-

strate topography increase contact with the substrate, thus increasing the colony stability (Harrington 1987).

Light intensity. - It is difficult to determine the affects of light intensity on Paleozoic organisms such as tabulate corals. It has not yet been unequivocally proven that tabulate corals possessed photosynthetic symbionts, such as zooxanthellae (Dodge and Vaisnys 1980; Cowen 1983, 1988; Coates and Oliver 1986; Coates and Jackson 1987); for the sake of completeness the potential affects need to be considered. Low light levels are typically due to great water depth or increased turbidity. The most obvious effect, specifically on modern symbiont-bearing corals, is reduced growth rate, which can cause non-uniform growth. In reef environments a coral at one level on the reef may grow outward shading corals lower on the reef. Shaded areas of a coral will not grow as rapidly, affecting the colony shape (Hughes and Jackson 1985).

Different specimens of the same species of modern coral have been observed to have different growth form in low-light conditions (Goreau 1963; Baker and Weber 1975; Dustan 1975; Hughes and Jackson 1985; Baarli and others 1992). Scleractinians forming domal colonies in shallower waters develop a shelf-like platey form in deeper darker waters. This form increases the area of upward-directed colony surface and therefore the number of symbionts receiving attenuated vertically incident light (Goreau 1963).

Competition. - Growth modifications caused by competitive interaction between organisms most greatly affect the loser (Fig. 24). The growth of the less competitive organism is interrupted or reversed (Philcox 1971; Hughes and Jackson 1985) as the organism tries to escape the conflict. In situations involving competition for living space, rapidly growing colonies usually have the advantage, commonly overgrowing the loser (Lang

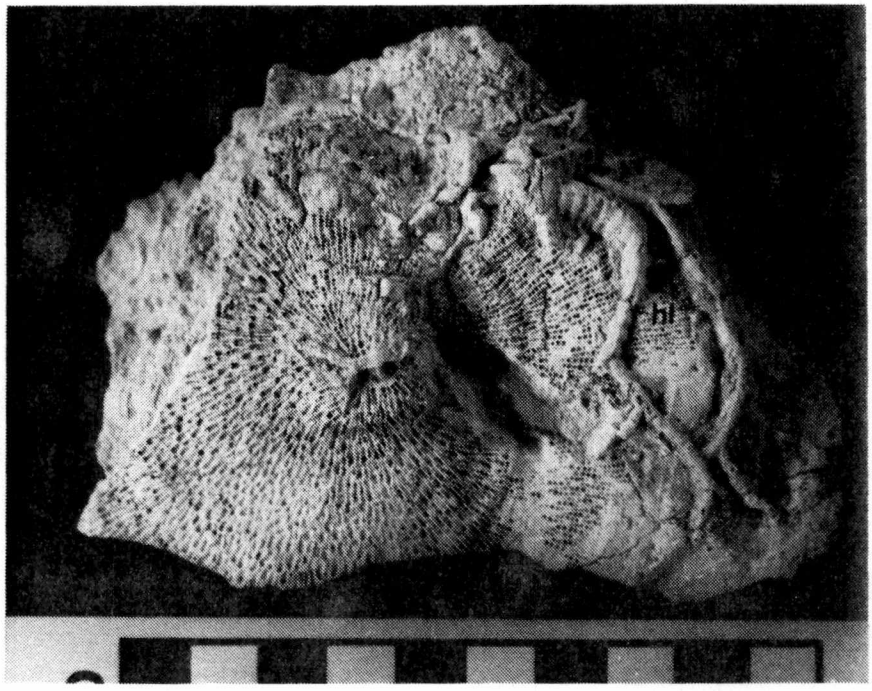


Figure 24.- Competitive interaction between a *Favosites louisvillensis* colony and a *Halysites* sp. (hl) colony. The irregular growth pattern of the halysitid suggests a response to avoid being overgrown by faster spreading favositid. Divisions on scale = 1 cm.

1973; Stel 1978; Kershaw 1981, 1990; Meyer 1981), such interactions may affect the growth form of both.

The fusion of two or more same-species colonies and mutual intergrowth of different organisms must also be considered. Colony fusion (Hughes and Jackson 1985) reduces the number of individual colonies in a population, creating a smaller number of larger colonies. Algal (Stel 1978), stromatoporoidal (Kershaw 1981) and bryozoan (McKinney and others 1990) intergrowths with corals ultimately lead to the formation of different colony shapes than if each organism grew separately.

Bioerosion. - Boring organisms physically remove previously formed skeletal material altering already formed colony shapes. Predators and scavengers feed on polyps interrupting colony growth (Stearn 1982). Hard and soft tissue destruction will force either regenerative growth to reestablish colony form or will halt growth in those areas altogether. Areas cleared of soft tissue are susceptible to epibiont colonization creating competitive situations.

Food supply. - As with light intensity, the supply of nutrients mainly affects the rate of colony growth. An area of a colony receiving more nutrients will grow more rapidly than the rest of the colony creating non-uniform colony growth, particularly at the up-current side and higher areas of a colony (Stel 1978; Kershaw 1981, 1984).

Water Chemistry. - Growth of organisms is greatly affected by extremes in water chemistry. High salinity produces coral growth forms that are globular and small, in species that normally do not create such forms. Low oxygen conditions produce thin, bizarre colony shapes (Stearn 1982). Coral growth under these extreme conditions is rare and here considered insignificant when examining the growth forms in a normal marine,

level-bottom environment, such as that of the Brownsport Formation.

Interpretation

Four ecologic controls are suggested to have had the greatest affect on the growth form of *F. louisvillensis* and *T. minor* coralla: 1) the rate and pattern of sediment accumulation; 2) currents, both normal and storm derived; 3) condition of the substrate; and 4) competitive interactions. Of these four factors the accumulation of sediment and the effects of currents seemed to have the greatest influence on growth.

During Lobelville deposition, the net accumulation of sediment was probably quite low but was occasionally punctuated by reworking and introduction of storm derived sediment. Evidence of this periodic influx of fine-grained sediment is preserved within many *F. louisvillensis* (Fig. 16A) and *T. minor* (Fig. 16B) coralla. Due to the low, platey corallum profiles, these colonies were not capable of efficiently shedding sediment (Pandolfi 1984). Sediment intercalations seen at the margins of many coralla indicate that sediment-covered areas of a colony were usually later overgrown. Multiple regenerations exaggerated the normal vertical dimension of most larger coralla, creating a thickened profile (Fig. 17B and 23A).

Currents scoured sediment from beneath colony peripheries creating small cavities (See discussion in Chapter 4). In many cases subsequent colony growth was directed downward toward the substrate to increase colony stability by direct contact with the substrate. This downward growth created a thickened marginal profile. Progressive scouring of sediment may have undermined a colony to a critical destabilization point. Beyond this point, a strong current would have tipped a colony into the scour (Harrington 1987). After the colony restabilized, growth would have been redirected upward (Fig. 16A), resulting in colony regeneration and associated offset skeletal growth trajectories.

In competitive situations, it appears that both *F. louisvillensis* and *T. minor* pos-

sessed a competitive advantage compared to other sessile benthic organisms living on the Lobelville substrate. Growth up and over other organisms, including other corals (Fig. 24), is often observed, preserved within and on the undersides of larger coralla. The advantage is attributed to the rapid rate of lateral increase possessed by these species. The magnitude of growth modification resulting from a competitive interaction in most cases is not great, but redirection of growth upward over the losing competitor, increased the vertical dimension and also formed undulations on the colony surface.

Two factors which may have affected coralla growth form, yet are difficult to qualify, are light intensity and food supply. It would seem easy to conclude that a platey growth form was preferred to maximize the area of the living colony surface receiving vertically incident sunlight. The modern coral, *Montastrea annularis*, is known to form a self-like, platey colony shape at water depths reaching the base of the photic zone (Goreau 1963; Baker and Weber 1975; Dustan 1975; Hughes and Jackson 1985; Huston 1985). Yet, there is no obvious evidence that *F. louisvillensis* and *T. minor* possessed zooanthellae, nor that the Lobelville environment was exceptionally turbid or at extreme water depth, requiring the necessity of such a growth form.

Directional colony growth attributable to increased food supply at the upstream side of a colony (Stel 1978) is not apparent. Pandolfi (1984) concluded that the "tabular" growth form of tabulate corals of the Centerfield Limestone (Middle Devonian) allowed for efficient acquisition of nutrients. The variety of tabulate coral growth forms (bulbous-platey) coeval with *F. louisvillensis* and *T. minor* does not indicate that a platey growth form provided any superior nutrient gathering advantage in the Lobelville environment.

Factors of bioerosion, changes in water chemistry and subareal exposure appear to have had negligible effect on the growth form of *F. louisvillensis* and *T. minor*. There is no pre- or post-mortem evidence of bioerosion of coralla . Sedimentologic and other

paleontologic evidence suggest that the Lobelville was entirely subtidal, below the zone of fair-weather wave agitation and would not have been subjected to wide variations in water chemistry or depth.

Discussion

The platey coralla of *Favosites louisvillensis* and *Thecia minor* are typically less than 3 cm thick, but commonly range up to 20 cm or more in diameter. Coralla of such dimensions could only have formed during periods of little or no net-sediment accumulation (Philcox 1971; Kershaw 1984; Olson and Broadhead 1989). Domical colony forms would not necessarily be excluded from environments of low net accumulation of sediment and low turbidity (Harrington 1987), accounting for the wide range of growth forms of other tabulate coral found in the Lobelville (Olson and Broadhead 1991). Then what was the advantage of the platey colony shape of *F. louisvillensis* and *T. minor*? The platey form appears to be an adaptation to maintaining a stable position on a soft substrate during periods of turbulent water flow (Kershaw 1984, 1990; Baarli and others 1992) and a regime of constant current flow which undercut the colony (Kershaw 1984; Harrington 1987).

Stearn (1982) concluded that generalizations about the relationship between growth form and environment are unreliable and have not been clearly demonstrated in modern scleractinians or stromatoporoids. Since Stearn published his review, many studies concerning both ecologic and genetic influences on growth form have been published (Kershaw 1984, 1990; Pandolfi 1984; Harrington 1987; Gibson and Broadhead 1989; Olson and Broadhead 1989, 1992; Pandolfi and Burke 1989; Noble and Lee 1990; Baarli and others 1992; Young and Elias 1992; Dixon 1993). These studies have shown that the analysis of growth form is important to correctly determining depositional conditions. One point that has been made clear is that the degree of phenotypic plasticity (i.e.

intraspecific variation in colony form) is directly related to a species' genetic inheritance. In addition, the degree of intraspecific variability differs among species (Harrington 1987; Gibson and Broadhead 1989; Pandolfi and Burke 1989; Young and Elias 1992; Dixon 1993).

Pandolfi and Burke (1989) used harmonic shape analysis to compare the range of coralla shapes of populations of the tabulate coral *Pleuordictyum americanum.* They examined 51 samples, each representing numerous populations of colonies. They found a large scale (basin wide) trend of subtle differences in corallum profile; more-hemispherical coralla forms dominant onshore to more-flattened coralla forms dominant offshore. This trend, allowed by the limited phenotypic plasticity of *Pleuordictyum americanum,* was influenced by various depositional conditions in different parts of the basin. However, Pandolfi and Burke (1989) also found a large degree of variation between specimens from the same inferred depositional environment as well as from different inferred depositional environments. They concluded that there may be only a subtle relationship between corallum growth form and environment of deposition. They cautioned, however, that the identification of particular environments using specific growth forms is not reliable, because within-species genetic variability causes too much shape variation within a population.

It is apparent that understanding the degree of genetic variation within a species is important when using shape analysis to interpret environmental conditions, but Pandolfi and Burke seem to overstate this point. Many ecologic factors have similar effects on organisms with different genetic (i.e. budding patterns) make-ups. Therefore examining the shape of a single colony or a single time restricted population will provide information about environmental conditions during the lifetime and sometimes the death of that colony or population of colonies (Philcox 1971; Parsons and others 1988; Olson and Broadhead 1991; Ketcher and Allmon 1993)

If genetic factors, namely budding pattern, exert the greatest control on the growth form of *Favosites louisvillensis* and *Thecia minor*, then it is important to examine the adaptive advantages provided by growth form to the survival of a population through time. In the study of clonal organisms, the term population can be defined at two scales: the population of colonies living in an environment and the population of individual polyps (modules) living on a single colony. Adaptation at one or both levels can provide an advantage, ensuring the propagation of a species over time, in settings of unfavorable or unstable conditions.

Gibson and Broadhead (1989) studied the species specific growth responses of 3 species of favositid coral from the Upper Silurian and Lower Devonian of Tennessee, each living on a terrigenous mud-rich substrate. *Favosites conicus* created a small, flat-based colony, which sat on the mud-rich substrate. *F. conicus* colonies reproduced and died after reaching the first reproductive cycle, living between major episodes of sediment influx and remaining small enough to prevent subsidence into the soft substrate. The larger colonies of *Favosites foerstei* suggest longer lived growth, surviving by continuous growth upward and outward to keep pace with sediment accumulation. A third species, *Favosites forbesei* adapted to the conditions of an episodically disturbed soft substrate in two ways: 1) by symbiotic growth, attaching and growing to echinoderm stalks, remaining well above the substrate. 2) by ambitopic growth on skeletal grains on the substrate, creating a steeply convex base while growing upward at a rate that likely just exceeded the rate of sediment accumulation.

Each of these species exhibits a different adaptation which increased, or at least maintained, the population of colonies, therefore increasing the success of that species in a terrigenous mud-rich environment. The number of individual polyps on a single colony was not a critical factor to the adaptations of these three species. To best interpret and understand the adaptations of *F. louisvillensis* and *T. minor*, examination of both scales of

population is important.

Earlier it was suggested that individual corallites of *F. louisvillensis* and *T. minor* exhibit progenetic characteristics. Corallites, which may have undergone a short period of ontogenetic development to a relatively small mature size, provided the means for rapid development of a large population of individual polyps living on the colony. Although not clearly demonstrated, the onset of "asexual maturity," or time of budding of new polyps, may have truncated the ontogenetic growth of polyps, resulting in small size. Gould (1977) has suggested that progenesis is ecologically advantageous in stressful environments where rapid increase in population size increases the chances of a population's success. The ability of these coral species to grow quickly, forming large coralla, thus producing a large colony population or large number of larvae during sexual reproduction, ultimately increased the chances of colony survival.

Hughes and Jackson (1985) studied the population dynamics of five species of modern scleractinian coral living on Jamaican reefs. Over the four year period of their study, they found two forms of mortality dominant: 1) partial mortality, in which some but not all polyps on a colony are killed and 2) whole-colony mortality, in which the colony is killed outright. Following a disturbance, such as an influx of sediment, larger colonies were found to have an increased chance of injury (partial mortality) because of the larger surface area which can be affected. Smaller colonies, with a limited surface area, have a greater chance of suffering either no injury or fatal injury (whole-colony mortality).

The fossil coral populations of the Brownsport show similar patterns. Small colonies of heliolitids, such as those formed by *Heliolities tennesseensis* and colonies of *Favosites brownsportensis*, which have large diameter corallites, show little evidence of regeneration from injury. This suggests that colonies of these species either survived a disturbance entirely or not at all. Colonies of *F. louisvillensis* and *T. minor*, both with

small diameter corallites, grew to large sizes, often regenerating many times over damaged areas of the colony. The increased surface area and associated large population of polyps produced a greater chance that part of a colony would survive to regenerate. Connell (1973) suggested that larger colonies of modern colonial coral may also have larger energy reserves and materials to be transferred from living tissues on undamaged parts of colony, which can be utilized in regenerative growth.

The larger colonies of *F. louisvillensis* and *T. minor* may have been highly susceptible to colony damage, as evidenced by slightly ragged corallum margins and included sediment observed in cut specimens. By retaining their primary generative abilities, i.e. the rapid asexual budding of corallites to establish a stable colony size, *F. louisvillensis* and *T. minor* were able to quickly reestablish colony growth following partial mortality. The progenetic characteristics of individual modules (polyps) facilitated efficient regeneration and enhanced colony reestablishment and survival.

A contrasting population pattern is observed for small heliolitid colonies, such as those formed by *Heliolites tennesseensis* (Fig. 15D) and for solitary rugose corals (Fig. 13D), which can be found in great abundance within the Lobelville. The survival strategy of these corals seems to have been to create a large population of small colonies or individuals, attached to any available substrate, similar to *Favosites conicus* of the Birdsong (Gibson and Broadhead 1989). Following a disturbance, the large number of colonies in the population, improved the chance of part of that population surviving to reproduce.

F. louisvillensis, which produced larger colonies, did not rely on a large population of colonies, but on the increased chance that part of a colony would survive and then regenerate and reform a stable colony. *T. minor* similarly relied on the advantages that a large colony size provides, but the great abundance of *T. minor* fragments in outcrop suggests that it may have reproduced prolifically, ensuring survival by creating a large

number of colonies. With a high rate of larval recruitment, rapid growth rate and extraordinary regenerative ability, it is likely that *T. minor* was able to invade and colonize newly disturbed substrates, possibly acting as a "pioneer" species following substrate disruption and sediment influx.

Conclusions

The Lobelville Member of the Brownsport Formation consists of interbedded terrigenous shale and limestone which preserve a rich coral fauna. The growth form of two species of tabulate coral, *Favosites louisvillensis* Davis and *Thecia minor* Rominger were examined to assess the affects of genetic and ecologic factors on coralla development. *F. louisvillensis* coralla are commonly quite large (up to 1 m across), but have a thin profile (2-5 cm). *T. minor* coralla are composed of thin (1-2 cm thick) growth laminae which grow directly on the substrate. Repeated regeneration following partial burial created thicker colony masses composed of multiple lamina.

Genetic controls on colony growth had the greatest effect on the growth forms of *F. louisvillensis* and *T. minor*. At the ontogenetic level, individual corallites of both species have small mature diameters (1-2 mm wide). Possible progenetic development (reduced mature size) truncated corallite ontogeny at a small size, which allowed for a high rate of colony growth. In both *F. louisvillensis* and *T. minor* the dominant form of increase is lateral, offsets forming mainly at colony margins. Rapid generation of offsets, allowed at the expense of corallite development, promoted colony growth on the mud-rich Lobelville substrate and facilitated rapid regeneration following times of crisis.

Ecologic controls had less effect on colony development and form, and four were deemed to have the greatest affect. The overall low net rate of sediment accumulation allowed *F. louisvillensis* and *T. minor* to form large platey coralla. Episodic sediment influx partially buried large colonies, which then regenerated, allowing subsequent

development. Growth on the mud-rich substrate required an ambitopic development pattern, exhibited by both species. Competitive interaction periodically disrupted outward development of coralla, but rapid colony growth was a competitive advantage.

Gould (1977) remarked that the success of heterochrony is most commonly measured in a retrospective manner, viewing the proliferation of descendants as success, rather than interpreting what adaptive value the heterochronic change gave to the species affected. For *Favosities louisvillensis* and *Thecia minor*, two species for which descendants have not yet been interpreted, and for which even ancestors are uncertain, an apparent developmental shift at the ontogenetic level promoted increased colony and species survival in the frequently disrupted, mud-rich Lobelville environment.

Chapter 4: Cryptic Habitats and Epibionts

Introduction

Many studies of cryptic epibiotas have concentrated on cryptic habitats found within reef frameworks (see Kobluk 1988, for review); fewer studies have been published on cavities and associated cryptic epibionts beneath individual (non-reef) colonial skeletons (Spjeldnaes 1974; Kershaw 1980; Segars and Liddell 1984, 1988). The conditions needed for the creation and colonization of such cavities appear to have limited the number and diversity of cryptic communities, and thus, the number of paleoecological studies.

Skeletal debris was a common substrate for attachment and growth of sessile benthic organisms found in the interbedded limestones and shales of the Lobelville Member of the Brownsport Formation (Upper Silurian) of West Tennessee. Most colonization was epitaphic (Olson and Broadhead 1991), occurring after the host had died (Fig. 20A). Yet, colonization on live hosts did occur, especially on very common, recumbent echinoderm stems. Close examination of the basal epitheca of many tabulate coralla from the Lobelville also reveals the common presence of epibionts. These organisms inhabited cryptic cavities beneath the margins of live coral colonies (Fig. 18A).

In this chapter, the creation, colonization and maintenance of cavities beneath corals in the Lobelville level-bottom environment is examined. Substrate conditions, prevailing current regime and host growth response affected the composition and longevity of cryptic habitats formed beneath individual coralla.

Formation of Cryptic Habitats

Tabulate corals found in the Lobelville, lived on a level-bottom, mud-rich skeletal substrate. These corals employed an ambitopic development pattern (Fig. 22), using a small grain of hard or firm substrate for initial colonization, followed by development of

a stable substrate produced by skeletal increase. Growth of the coral colony was primarily at the colony margin, producing lateral expansion across the seafloor along the substrate. Undulations in colony profile suggest that the corals grew in direct contact with the substrate and reflect substrate topography.

Kershaw (1980), suggested that stromatoporoids on level-bottom substrates from the Silurian of Gotland, were not actively forming cavities by growing above the substrate. These stromatoporoids were not growing on reefs, where outward growth alone could create overhangs. Similarly, tabulate corals of the Lobelville, inhabited a mud-rich level bottom environment, yet the presence of cryptic epibionts on basal surfaces of coralla raises a question about the generation of cavities, which exposed areas of the coral epitheca to colonization. Kershaw (1980) suggested two mechanisms for cavity formation involving the hydrodynamic interaction between a skeletal mass and water flow around it (Kershaw 1980, used stromatoporoid coenostea). First, the scouring activity by bottom currents removed sediment from around and beneath the edges of a corallum. Secondly, movement of a corallum by stronger currents, may have lifted and imperfectly placed a corallum on an uneven substrate or partially overlying skeletal debris creating overhangs.

Kershaw (1980) modelled current flow interaction and cavity creation beneath laminar and domical stromatoporoid coenostea (following earlier work of Brenchley and Newall 1970 and Abbott 1974). For the present study, similar experiments were carried out, specifically to examine the effects of short duration, slow currents around platey tabulate coralla. A 6.1 m long by 30.5 cm deep x 20.2 cm wide recirculating flume, located in the Department of Geological Sciences at the University of Tennessee, was used. Beginning water depth in the flume was at 12 cm and the bed of the flume was horizontal during all experiments. Fossil coralla were placed on 2-3 cm thick, level bed of modern mixed carbonate sand (1ϕ) and mud, collected from the Florida Keys. The

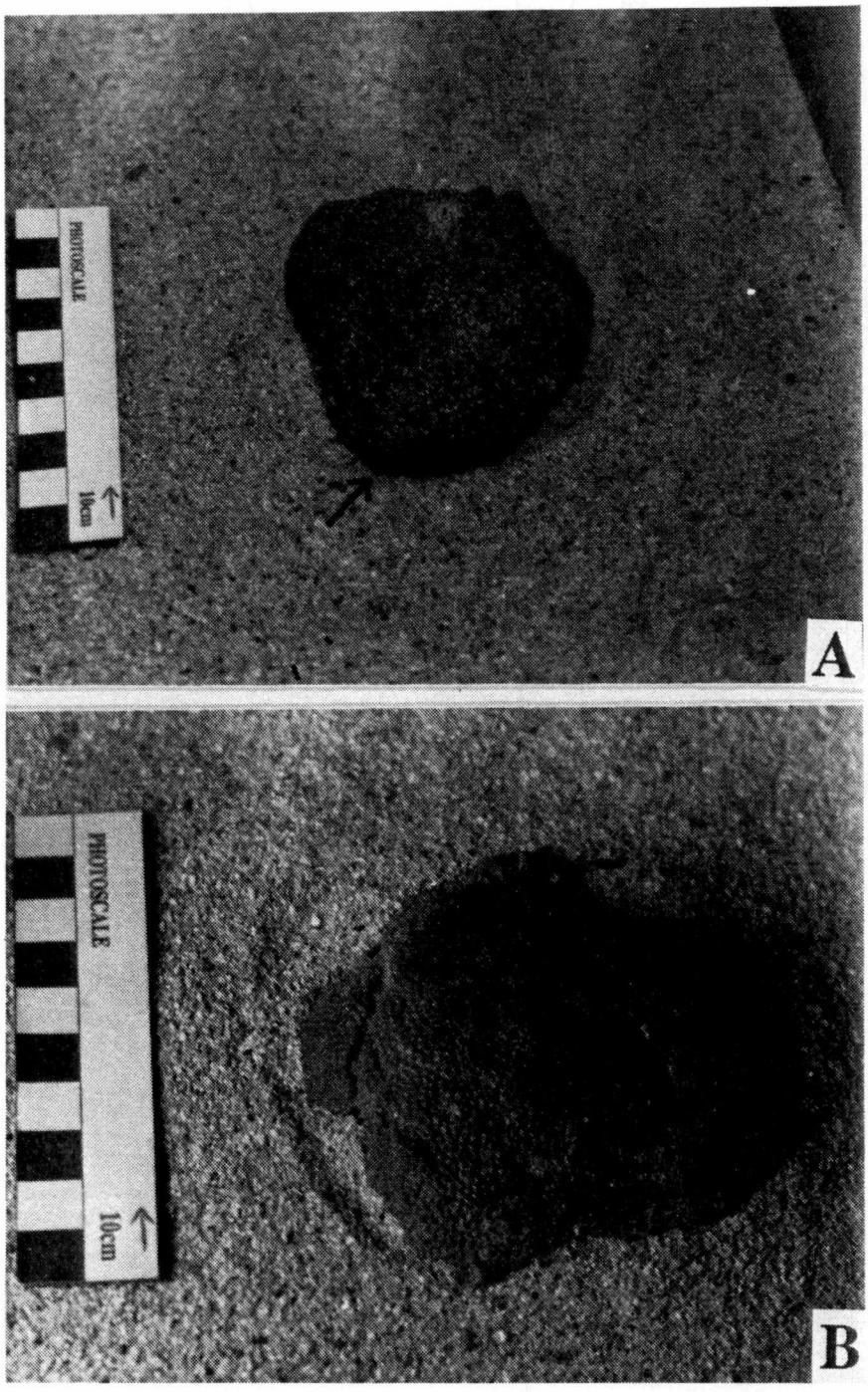
sediment composition was texturally similar to the unlithified, mud-rich skeletal (mainly crinoidal) substrates of the Lobelville.

A range of current velocities (17 cm/sec to 20 cm/sec) was initially used to determine the lowest current velocity at which scouring would occur. A velocity of 19 cm/sec, just above the threshold of grain movement, caused scouring (Fig 25A) after only a few minutes. A crescentic scour formed at the front edge of the corallum, wrapping around the sides of the coralla (Fig. 25B). The scouring is a direct result of the disruption of laminar flow over the object (Kershaw 1980) creating vortices which lift and move sediment grains (Abbott 1974). At the lowest water velocities (19 cm/sec) a small (<1 cm deep), stable scour formed. At higher water velocities (> 20 cm/sec), the scour cavities continued to enlarge beneath a coralla. Continued sediment scouring destabilized coralla on the substrate and ultimately led to coralla falling forward into the scour cavity. A simple change in current direction could also have tipped only partially destabilized colonies into scours. It is interesting to note that at low current velocities, scour formation was almost instantaneous and scours remained stable in size and shape. This suggests that small inhabitable cavities, can be formed by short periods of water movement, without the need for currents to reach a flow equilibrium.

These results, for low current velocities, agree with those of Abbott (1974) and Kershaw (1980). Both did further experimentation with higher current velocities (30-60 cm/sec; Kershaw 1980) leading to simple translation and often rotation of models down current. Placement of models in conditions of higher current velocities (> 60 cm/sec; Kershaw 1980) caused colonies to flip and rotate.

The effects of sediment movement from around Lobelville tabulates is preserved in fossil coralla. The formation of scour cavities, exposed hard substrates on coral epitheca to colonization by epibionts, such as bryozoans and spirorbid worms. Continued scouring to the point of colony tipping is preserved as deflected growth trajectories

Figure 25.- Experimentally produced scour around tabulate coralla. A) Front view of scour (arrow) formed beneath front edge of colony margin. The cavity formed after just few minutes of scour at a flow velocity of 19 cm/sec. B) Top view of crescentic scour formed around and under colony margins. Flow conditions same as those in 25A.


PHOTOSCALE
10cm
A
PHOTOSCALE
10cm
B

within colony skeletons. The individual corallites of a number of species including *Favosites louisvillensis* and *Thecia minor* appear to have preferred a vertical growth orientation. Following reorientation of a colony, corallites diverted growth back to vertical, forming an inflection in the corallite growth path (Fig. 16A).

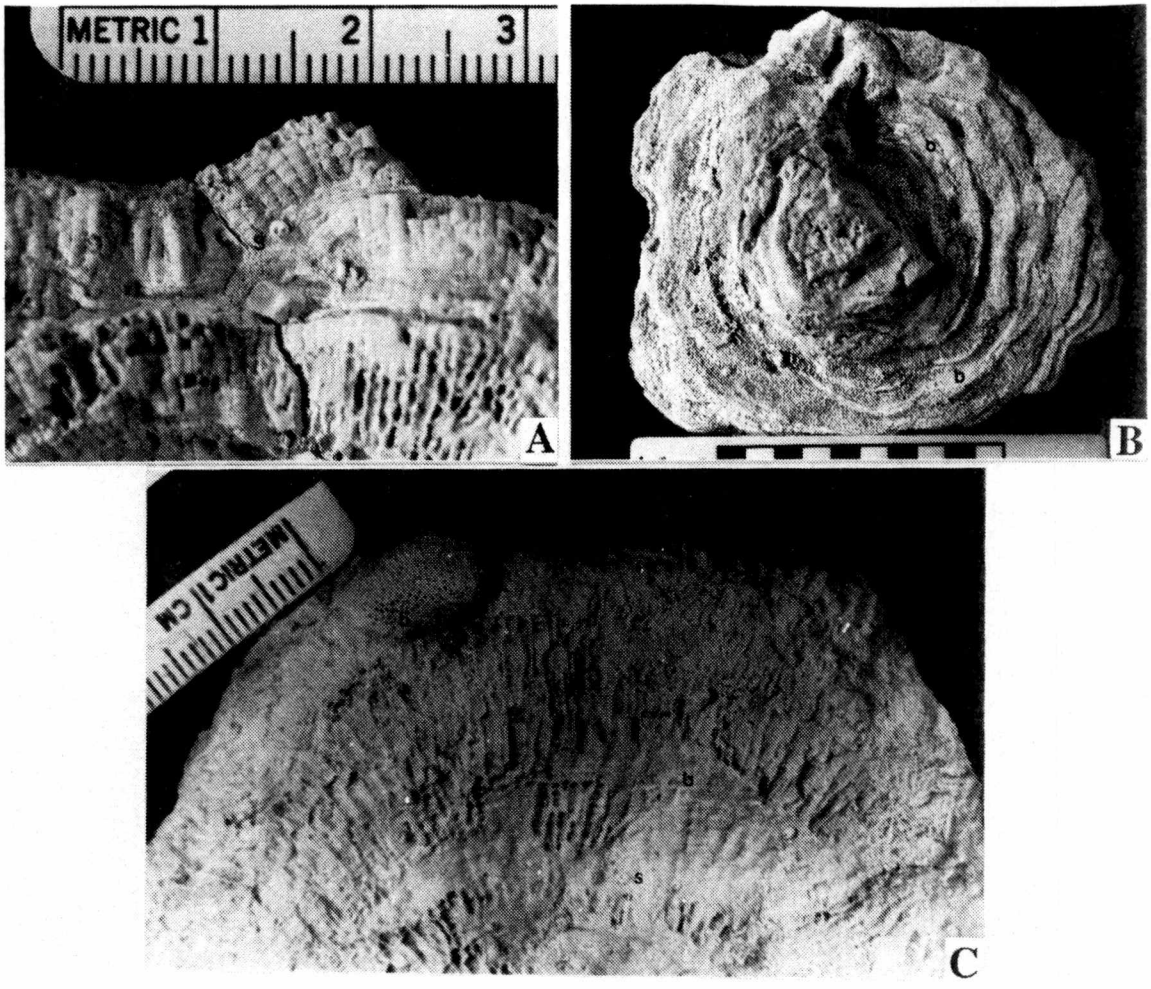
Collection of *in situ* inverted coralla and extensive colonization of coralla bottom surfaces provide evidence of the total overturning of a colony (Fig. 19C,D). Epibionts encrusting large areas of the basal epitheca, especially those organisms that appear to have been uncommon inhabitants of small cryptic cavities, must have done so only after a colony was inverted. It is likely that this process was important to the creation of new substrates for colonization on the soft, mud-rich substrate.

Cryptic Epibiota

The cryptic epibionts found attached to coralla under surfaces are typically small and of limited diversity. The biota is dominated by cystoporate and trepostome bryozoans, which formed small (2-5 mm across; < 3 mm thick) mound shaped colonies (Fig. 26B) and larger lamellar colonies (Fig. 26B), with maximum dimensions up to 20 mm across. Spirorbid worms (Fig. 26A), which formed small (1-2 mm across) spiral tubes, are another common component of the Lobelville cryptic biota. Spirorbids did not make up a large proportion of the areal coverage, but produced a large number of individuals. Spirorbids have a gregarious settlement behavior (Bordeaux and Brett 1990), explaining the close grouping of individuals present on Lobelville coralla epithecas. Small mound shaped bryozoan colonies are often similarly grouped. Auloporid corals are relatively rare in comparison with bryozoans and spirorbids.

The size and composition of the cryptic epibiota appears to have been limited by a number of ecologic factors, including: water movement, resource availability, sedimentation rate (Spjeldnaes 1974; Kobluk 1988), frequency of disturbance (Gibson 1992), and

Figure 26.- Lobelville cryptic epibiota. A) Spirorbid worm tube (s) on basal epitheca of a *Favosites louisvillensis* corallum. B) Basal epitheca of a *Favosites louisvillensis* corallum exhibiting centimeter-wide undulations. Note gregarious grouping of small bryozoan mound shaped colonies near top of photo (b) and larger sheet-like bryozoan colony (b) near bottom of photo. C) Cryptic epibionts (b- bryozoan colonies; s - spirorbid worm tubes) encrusting basal epitheca of a *Favosites louisvillensis* corallum.


METRIC 1 2 3
A
b
b
B
METRIC CM
b
s
C

host growth response (Chatterton 1975; Olson and Broadhead 1989).

The availability of resources, or lack thereof, had a major control on the distribution of epibionts. The intensity of water flow and light can diminish significantly over a distance of only a few centimeters in cryptic habitats (Segars and Liddell 1988). The affects of diminished light intensity were probably insignificant to these organisms, but water exchange was critical. During periods of quiet water, food and oxygen supplies would have been depleted. Due to their dominance in these cryptic settings, bryozoans and spirorbids must have been able to survive short term drops in food and oxygen levels (Spjeldnaes 1974). Even with that tolerance, the varying conditions must have restricted the maximum growth size of the cryptic organisms.

The most important limiting factor appears to have been the longevity of the cavity, or in other words the availability and duration of substrates. The cavities formed beneath coralla margins were probably short lived, with an effective lifetime restricted mainly by the rate of sediment accumulation (Spjeldnaes 1974). In the Lobelville, episodic sedimentation events, related to the occurrence of strong storms, destroyed cryptic cavities by fine-grained sediment influx and burial. In addition, changes in current direction may have caused scouring and sediment movement along different areas of the colony margin, eliminating previously formed cavities by infilling with newly excavated sediment (Kershaw 1980).

The lifetime of cavity had a great effect on the composition of the epibiota. In cryptic reef habitats, substrates are larger and more stable, partly due to elevation above the seafloor. Less fine-grained sediment is present in reef environments, reducing the effect of sediment accumulation, therefore prolonging the life of a cryptic habitat. With sufficient time, ecologic succession is permitted in these settings (Jackson and others 1971), which can greatly affect the preserved composition of the epibiota. Later colonizers, which in modern examples are commonly non-skeletonized clionid sponges, may

erase the record of previous forms, such as skeletonized bryozoans and serpulid worms, through bioerosion (Rasmussen and Brett 1985). This is probably of little concern to Lobelville assemblage preservation. The smaller, less stable substrates formed beneath coralla margins would have been more readily buried, and epibiont assemblages would have experienced negligible information loss due to succession. Rasmussen and Brett (1985) suggest that assemblages of this type are dominated by pioneer species. Spjeldnaes' (1974) conclusions agree, stating that these short lived settings were especially suited to opportunistic species with rapid growth and short generation times.

The short lived conditions restricted not only the diversity of the epibiota, but effectively limited the size of individual cryptic organisms. Gibson (1992) studied non-cryptic epibiont relationships from the Birdsong Shale Member of the Ross Formation (Lower Devonian) and suggested that epibionts colonizing skeletal debris on the muddy Birdsong seafloor remained small because of the frequency of disturbance. Obviously, organisms such as spirorbids, could not attain large sizes, but bryozoan colonies, most of which can grow indeterminately, commonly did not have time to form colonies larger than 2-5 mm across.

Growth response of the host also affected the longevity of a cryptic habitat and colonizing epibiota. Often life associations between epibiont and host are indicated by the growth response of the host in relation to presence of epibionts (Chatterton 1975). Lobelville corals do not appear to have directly responded to presence of cryptic epibionts, but did respond to the presence of cavities beneath the colony margin (Fig. 22). To improve stability, the large platey tabulate corals of the Lobelville, including *Favosites louisvillensis* and *Thecia minor*, grew down toward the substrate maximizing contact with the substrate. This downward growth, apparently related to the centimeter thick growth undulations on the basal epitheca (Fig. 26B), effectively cut off the cryptic habitat from the open environment, killing the inhabitants (Olson and Broadhead 1989).

Conclusions

Tabulate corals of the Lobelville lived on a mud-rich, level-bottom substrate and did not actively create cavities beneath colony peripheries. Short duration water currents scoured small, ephemeral cryptic habitats beneath coral colony margins. The exposed coral epitheca provided a hard substrate for colonization by epibionts. The cryptic epifauna was a low diversity, opportunistic assemblage, dominated by bryozoans and spirorbid worms. The short term nature of the cavities and poor resource supplies within cavities effectively limited the composition and size of the cryptic epibiota. Cavity longevity was controlled by the rate of sedimentation, frequency of disturbance and host growth responses. These factors, independently and in concert, limited the duration of the cryptic habitats, which in turn limited the diversity and growth of the colonizing epibionts.

Chapter 5: Conclusions

1. The stratigraphic succession of the Dixon, Brownsport, and Decatur formations represents a period of nearly continuous carbonate deposition on a shallow marine shelf during the Late Silurian. Water depth and frequency of physical disturbance varied during this interval, resulting in sedimentologic and biologic differences upon which formations and members can be separated.

2. The predominant red coloration of the fine-grained terrigenous and carbonate sediment, and sparseness of fossils, suggest that the Dixon Formation was deposited in a shallow mud-flat environment.

3.The formal subdivision of the Brownsport Formation into three members (in ascending order: Beech River, Bob, Lobelville), is justified based upon consistent stratigraphic relationships and lithologic characteristics that are apparent in outcrop.

4. The Beech River Member of the Brownsport Formation is composed of interbedded allochthonous shale and echinoderm wackestone and packstone. The rarity of glauconite, but abundant articulated multielement skeletons, suggests that Beech River skeletal sediment accumulated rapidly on a level-bottom seafloor below normal wave base. Accumulating sediment was periodically disturbed by turbulent storm events accompanied by the influx of varying amounts of fine-grained allochthonous siliciclastic sediment.

5. The Bob Member of the Brownsport Formation is composed of thick-bedded, medium- to coarse-grained, echinoderm and brachiopod packstone and grainstone. The mud-poor texture, in addition to the presence of faintly cross-bedded layers of concentrically coated

rhodolites suggests that the Bob was deposited at shallow depths above normal wave base.

6. The Lobelville Member of the Brownsport Formation is composed of echinoderm to echinoderm-bryozoan wackestone, interbedded with allochthonous gray shale. Distinctive features include disarticulated multielement echinoderm skeletons, disarticulated brachiopod and ostracode valves, multigeneration overgrowths on larger skeletal pieces, glauconite, and the distinctive large, platey coralla of tabulate corals, such as *Favosites louisvillensis* and *Thecia minor*. Autochthonous skeletal sediment accumulated slowly at depths well below normal, fair-weather wave base. Thin (1-3 cm) graded sequences, commonly overlain by allochthonous gray shale, suggest water depth within a range affected only by occasional storm currents and sediment influx. The frequency of such disturbances increased over time, culminating in the deposition of thick sequences of shale interbedded with thin limestone beds and lenses.

7. The lower Decatur Formation, composed of echinoderm wackestone and rare shale interbeds, represents a gradual return to a shallower, somewhat higher energy environment, which experienced less allochthonous mud influx than the Lobelville.

8. Genetic controls on colony growth had the greatest affect on the growth forms of *F. louisvillensis* and *T. minor*: At the ontogenetic level (individual corallite development), the truncation of ontogeny of individual corallites, possibly the result of the onset of asexual reproduction, produced corallites with small mature diameters (1-2 mm). This apparent progenetic developmental shift (reduced mature size) allowed corallites to reach maturity in a short time. At the astogenetic level (corallum development) the progenetic development of corallites, accelerated colony astogeny. The rapid generation of offsets

(allowed at the expense of corallite development) coupled with a pattern of lateral increase promoted rapid outward growth over the mud-rich substrate and facilitated rapid regeneration during times of physical environmental crisis and increased colony and species survival of *F. louisvillensis* and *T. minor*.

9. Ecologic controls had much less effect on colony development and form. Four ecologic controls were deemed to have had the greatest influence on colony growth: (1) Rate and pattern of sediment accumulation: The overall low net rate of sediment accumulation allowed *F. louisvillensis* and *T. minor* to form large platey coralla. Episodic sedimentation events partially buried corals which then regenerated. (2) Normal and storm generated currents: Normal currents scoured small cavities beneath colony margins. Episodic storm events and associated currents flipped or tipped colonies. (3) Substrate conditions: Growth on the mud-rich substrate required an ambitopic development pattern, exhibited by both species. (4) Competitive interactions: Competitive interaction periodically disrupted outward growth of coralla, but rapid colony growth provided an advantage.

10. Short duration water currents scoured small, ephemeral cryptic habitats beneath colony margins of large platey tabulate corals living on the mud-rich substrate. A low diversity, opportunistic assemblage, dominated by bryozoans and spirorbid worms, colonized these cryptic substrates. Cavity longevity was controlled by the rate of sedimentation, frequency of disturbance and host growth responses. These factors limited the duration of the cryptic habitats, which in turn limited the diversity and growth of the colonizing epibionts.

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Appendix: Measured Section Descriptions

Introduction

The study area is located in the western valley of the Tennessee River in West-central Tennessee. Three stratigraphic sections were measured: LB, WL, CC. Each section is described below in detail from the bottom (oldest unit) to the top (youngest unit) of the section. Sample numbers and cumulative stratigraphic positions of sample bases are given following unit descriptions. Unit thicknesses are tallied with the start of description at the base of the section, and thicknesses are rounded to the nearest centimeter. Units are informal and were determined from field relations, plus slab and thin-section study. Bedding thickness and grain size conventions are listed below; the colors referred to in descriptions are not standardized. The rock classification used is that of Dunham (1962). Fossil allochems are listed in order of decreasing abundance. Unless otherwise stated all brachiopods impunctate.

Bedding thickness (after Mckee and Weir, 1953, as modified by Ingram, 1954):

Very-thick-bedded	> 1.0 m
Thick-bedded	0.3-1.0 m
Medium-bedded	0.1-0.3 m
Thin-bedded	0.03-0.1 m
Very-thin-bedded	0.01-0.03 m
Laminated	0.003-0.01 m
Thinly-Laminated	< 0.003 m

Grain size descriptions (modified after terminology established by Wentworth, 1922):

Coarse-grained	> 1.0 mm
Medium-grained	0.25-1.0 mm
Fine-grained	0.1-0.25 mm
Very-fine-grained	< 0.1 mm

Lobelville Section Description

Unit	Meters	Cum. m.	Description
LB1	0.33	0.33	BROWNSPORT FORMATION - LOBELVILLE MEMBER. Gray, slightly wavy, medium-bedded echinoderm packstone grading upward to wackestone. Dominantly echinoderm grains with bryozoans, brachiopods, disarticulated ostracodes. Coarse, sparsely disseminated glauconite. Thin shale partings separate beds. Contact with LB2 gradational. SAMPLE: LB1-1 (0.33m)
LB2	0.02	0.35	Dark gray-green, thin-bedded shale interbedded with discontinuous nodular echinoderm wackestone. Dominantly echinoderm grains, with ostracodes common, and rare bryozoans and brachiopods. Widely disseminated glauconite grains and rare quartz silt trapped in finely laminated mud. Sharp contact with LB3. SAMPLE: LB1-2 (0.35m)
LB3	0.76	1.11	Gray, thin- to thick-bedded, ostracode-echinoderm wackestone/packstone. Allochems dominantly echinoderm fragments and ostracodes, with brachiopod grains common and rare bryozoan and coral fragments. Proportion of echinoderm grains increases upward. Bedding is nodular grading to wavy beds, separated by thin shale partings. Glauconite present in middle layers. Nodular blue chert, containing remnant shadows of sponge spicules, present at base of upper beds. Contact with LB4 irregular but sharp. SAMPLES: LB1-3-1 (0.35m); LB1-3-2 (0.50m); LB1-3-3 (1.11m)
LB4	0.31	1.42	Interbedded, gray, irregularly-bedded, fossiliferous shale, with discontinuous, blue chert nodules and gray, irregular, thin-bedded echinoderm wackestone. Echinoderm fragments dominate, with rare broken brachiopod and bryozoan fragments. Whole sponge bodies and disseminated spicules identified in thin section. Proportion of shale deceases upward in unit. Whole echinoderm stem pieces, rugose and tabulte corals, and brachiopods present in shale. Soft sediment deformation features present at shale-limestone bed contacts. Contact with LB5 uneven but sharp. SAMPLES: LB1-4-1 (1.20m); LB1-4-2-1 (1.42m) (coral in shale); LB1-4-2-2 (1.42m)

LB5	0.46	1.88	Gray, wavy, medium-bedded, ostracode-echinoderm packstone/grainstone with fine grained glauconite. Echinoderm grains and disarticulated ostracode valves most common with rare trilobite, bryozoan (including encrusting forms) and brachiopod grains. Tabulate coral colonies present within limestone bed at unit base. The unit is composed of limestone beds separated by gray, thin-bedded, unfossiliferous shales. Mud distribution in limestones quite variable, forming areas of mudstone and grainstone. Blue nodular chert present in center of middle bed and at top of upper bed. SAMPLE: LB1-5-1 (1.60m)
LB6	0.42	2.3	Gray, glauconitic, nodular to wavy, interbedded, fossiliferous, shale and bryozoan-echinoderm wackestone. Echinoderm grains, bryozoan fragments, ostracode valves, sponge spicules and rare brachiopod fragments and tabulate coral colonies. Wavy chert layers present at the top of each limestone bed. Contact between limestone and chert sharp, cross cutting grains. Amount of shale proportional to limestone increases upward in unit. Areas of laminated mud similar to LB2. Whole brachiopod valves and echinoderm stem pieces present in shales. Contact with LB7 sharp. SAMPLE: LB1-6-1 (2.30m)
LB7	0.24	2.54	Gray, wavy, thin-bedded echinoderm wackestone. Echinoderm fragments and articulated stem pieces most common with rare brachiopod and ostracode valves and bryozoan fragments. Thin chert bed present in center of unit. Fine-grained glauconite disseminated throughout unit. Thin shale partings separate limestone beds near top of unit. Gradational contact with LB8. SAMPLE: LB1-7-1 (2.54m) Sample includes both units LB7 and LB8
LB8	0.21	2.75	Interbedded gray, laminated, fossiliferous shale. and thin to medium bedded echinoderm wackestone/packstone. Thin, echinoderm grainstone nodules present in center of unit. Echinoderm grains and stem pieces most common brachiopod valves including large pentamerid specimens, ostracode valves and bryozoan fragments. Proportion of shale decreases upward in unit. Contact with LB9 sharp. SAMPLE: See unit LB7

LB9	0.13	2.88	Gray, medium-bedded echinoderm packstone. Echinoderm grains dominant, ostracodes and bryozoans, and rare brachiopod and trilobite fragments. Thin chert layer at top of unit with irregular base seemingly penetrating down into limestone bed. Irregular clumps of pentamerid brachiopods within limestone bed observed on outcrop face. Contact with LB10 gradational, glauconite very abundant at contact. SAMPLE: LB1-9-1 (2.80 m)
LB10	1.48	4.36	Interbedded gray, thin-bedded shale and gray, nodular, thin- to medium- bedded echinoderm wackestone. Echinoderm grains predominate, bryozoan fragments, ostracode valves and rare brachiopod, tabulate coral and trilobite fragments. The upper 1/3 of unit is composed of two packages of gray, medium-bedded wackestone grading upward into gray, fossiliferous, thin-bedded shale. The upper contact of each package, between the underlying shale and overlying wackestone is sharp. Echinoderm stem fragments, brachiopods, rugose corals, tabulate corals common within shale Contact with LB11 sharp. SAMPLES: LB1-10-1 (2.88m); LB1-10-2 (4.00m); LB1-10-4 (4.36m)
LB11	0.27	4.63	Gray, medium-bedded bryozoan-echinoderm wackestone/packstone. Echinoderm grains and articulated stem pieces and bryozoan debris codominant with rare brachiopod valves and trilobite fragments. Long axis of many grains parallel with bedding. Thin shale partings separate limestone beds. Proportion of shale decreases upward in unit. Glauconite peloids scattered through limestone beds. Contact with LB12 gradational. SAMPLE: LB1-11-1 (4.55m)
LB12	2.16	6.79	Interbedded gray, thin-bedded fossiliferous shale and wavy, thin-bedded, coarse-grained echinoderm wackestone. Echinoderm grains dominant, brachiopod and bryozoan fragments and rare ostracode valves and trilobite fragments. Glauconite peloids present, but rare. This unit is comprised of three of shaling upward sequences as in unit LB10. Limestone beds near top of unit contain less mud. Contact with LB13 sharp. SAMPLES: LB1-12-1 (6.05m); LB1-12-2 (6.75m)

LB13	0.15	6.94	Gray, medium-bedded, coarse-grained, echinoderm wackestone. Echinoderm grains dominant, bryozoan debris (many fenestrate forms), broken trilobite fragments, rare ostracode and brachiopod valves. Scattered, coarse-grained glauconite. Limestone beds are separated by thinly-laminated shale partings. Contact with LB14 gradational. SAMPLE: LB1-13-1 (6.90m)
LB14	1.02	7.96	Interbedded gray, thin-bedded, fossiliferous shale and very-thin-bedded wackestone lenses. Echinoderm grains dominant, with rare ostracodes, bryozoan and brachiopod fragments. Most grains broken and some appear to be rounded. Fine grain glauconite common. Trace of quartz silt present in shale. Thin tabulate corals observed *in situ*. Contact with LB15 sharp. SAMPLE: LB1-14-1 (7.95m)
LB15	0.18	8.14	Gray, medium-bedded, coarse-grained skeletal wackestone/mudstone. Echinoderm grains dominant with rare bryozoan, brachiopod, ostracode fragments and trace of quartz silt. Limestone layers (3) separated by thin, gray, shale partings. Contact with LB16 gradational. SAMPLE: LB1-15-1 (8.10m)
LB16	0.34	8.48	Prominent, gray, medium-bedded, echinoderm packstone bed, grading to interbedded gray shale and and gray, thin-bedded echinoderm wackestone. Echinoderm fragments most common, bryozoan and ostracode fragments, and rare brachiopod, trilobite fragments. The amount of shale increases and amount of limestone decreases (nearly absent) upward within the unit. A corallum of *Favosities brownsportensis* collected *in situ*. Contact with LB17 sharp. SAMPLE: LB1-16-1 (8.20m); LB1-16-2 (8.30m)
LB17	0.05	8.53	Gray, very-thin-bedded, coarse-grained, fenestrate bryozoan-echinoderm packstone/grainstone. Echinoderm grains dominant, fenestrate bryozoan debris and rare ostracode, brachiopod and coral fragments. Coarse grained glauconite present. Gradational contact with LB18. SAMPLE: LB1-17-1 (8.48m)

LB18	0.34	8.87	Interbedded, gray, thin-bedded, very fossiliferous shale and gray, thin-bedded, skeletal wackestone. Echinoderm grains and stem pieces dominant with, rugose corals, fenestrate bryozoans, tabulate corals and brachiopods. Contact with LB19 sharp. NO SAMPLE COLLECTED
LB19	0.91+	9.78+	Interbedded, thin-bedded fossiliferous shale and gray to pink, very-thin- to medium-bedded, echinoderm wackestone/grainstone. Shale interbeds up to 0.3m thick. Limestone beds become thicker and cleaner upward in unit. Red to gray chert nodules present in limestone beds. Large body fossils collected include echinoderm fragments, rugose corals, fenestrate and cryptostome bryozoans (inc. unidetified hollow form), tabulate corals, brachiopods and sponges. Top of this unit and remaining Lobelville section covered. SAMPLES: LB1-19-1 (8.90m); LB1-19-2 (9.30m); LB1-19-3 (9.78m); LB1-19-4 (9.00m)

Webb's Landing Section Description

Unit	Meters	Cum. m.	Description
WL1	0.94	0.94	BROWNSPORT FORMATION - BEECH RIVER MEMBER. Poorly exposed, interbedded gray shale and tan to gray, medium-grained, thin- to medium-bedded echinoderm wackestone.
WL2	0.51	1.45	Tan, medium-grained, thin- to medium-bedded echinoderm wackestone. Echinoderm grains and bryozoan fragments codominant, brachiopod valves, ostracode valves (most articulated), tabulate coral fragments and a trace of quartz silt. Nearly all fossil fragments exhibit some degree of silicification. SAMPLE: WL-1 (1.45 m)
WL3	1.42	2.87	Mostly covered interval of interbedded tan shale and tan, thin-bedded echinoderm wackestone. Amount of limestone compared to shale increases upward. Echinoderm grains dominant, bryozoan fragments, brachiopod valves and *Astraeospongia meniscus*.
WL4	1.93	4.80	BOB MEMBER. Pink to tan, fine- to coarse-grained, medium- to thick-bedded echinoderm packstone/grainstone. Echinoderm grains dominant, with bryozoans, whole and fragmented brachiopod valves and ostracodes. SAMPLE: WL-2 (2.87 m)
WL5	0.79	5.59	Mostly covered interval of interbedded tan shale and tan, thin-bedded echinoderm wackestone grading to medium-bedded brachiopod-echinoderm packstone. Fossils in unit include echinoderm grains, with brachiopods, bryozoan fragments and ostracode valves.
WL6	0.43	6.02	Tan, thick-bedded, medium- to coarse-grained echinoderm packstone, containing scattered dark-gray chert nodules. Fossils in unit include echinoderm grains, impunctate and pseudo-punctate brachiopods, bryozoan fragments, ostracode valves, trilobite fragments and small fragments of algae(?). SAMPLE: WL-3 (5.68 m)

WL7	0.36	6.38	LOBELVILLE MEMBER. Mostly covered interval, forming small glade of tan, very-thin-bedded shale interbedded with thin-bedded, echinoderm wackestone lenses. Echinoderm fragments dominant with brachiopods, bryozoans, sponges, trilobites and tabulate corals present. Fossils diverse, but not extremely abundant. No glauconite present. SAMPLE: WL-4 (6.02 m)
WL8	0.48	6.86	Interbedded tan shale and tan, fine- to medium-grained, wavy, thin- to very-thin-bedded echinoderm wackestone. Limestone beds become thinner and amount of shale increases upward within unit. Echinoderm grains dominant, with finely comminuted bryozoan fragments, brachiopod and ostracode valves. SAMPLE: WLS-1 (6.38 m)
WL9	0.09	6.95	Gray, medium- to coarse-grained, medium-bedded wackestone/packstone. Oblong, dark-gray chert nodules at base of unit. Echinoderm grains dominant, with bryozoan fragments, ostracode and brachiopod valves and trilobite fragments. Many fossil grains silicified. SAMPLE: WLS-2 (6.86 m)
WL10	0.46	7.41	Low glade exposure of interbedded tan shale and tan fine- to medium-grained, very-thin- to thin-bedded echinoderm wackestone. Echinoderm fragments, large tabulate coral colonies and fragments of colonies common, also bryozoans including fenestrate forms and brachiopods.
WL11	0.12	7.53	Gray, fine- to medium-grained, thin-bedded wackestone/mudstone. Gray chert nodules at base of unit. Wackestone beds become thinner and grade into mudstone beds upward in unit. Few fossils larger than 3 cm length. Gradational contact with WLS unit 5.

WL12	1.73	9.26	Poorly exposed gray to tan fine- to medium-grained, thin-bedded echinoderm wackestone. Limestone beds separated by thin shale partings. Dark gray chert nodules common in limestone beds. Corals nearly absent from unit. Fossil fragment include echinoderm grains, bryozoan fragments, ostracode and brachiopod valves. Very few tabulate corals found in this unit. Scattered glauconite grains present. Many fossil grains silicified. Gradational contact with WLS unit 6. SAMPLE: WLS-5 (8.45 m)
WL13	4.27	13.53	Low glade exposure of interbedded gray to tan shale and green to tan-gray fine- to medium-grained, very-thin to thin-bedded wackestone. Chert and glauconite present Limestone beds become thicker and amount of glauconite increases upward. Large body fossils (>3 cm) including tabulate corals abundant and diverse at base of unit, decreasing abundance upward in unit. Echinoderm grains and articulated stem pieces common, bryozoans including fenestrate forms, tabulate corals, brachiopods, and trilobites. Silt size quartz grain identified in thin section. Very fine-grained glauconite common enough in upper part of unit to give some beds a dark-green color. Amount of silicified grains increases upward in unit. SAMPLE: WLS-6-1 (9.26 m), WLS-6-2 (10.73 m), WLS-6-3 (11.26 m), WLS-6-4 (12.99 m)
	7.83	21.36	Mostly covered interval of gray shale and interbedded echinoderm wackestone. One sample collected from one of the few in place beds observed. SAMPLE: WL-20 (20.0 m)
WL-D	1.09	22.45	DECATUR FORMATION. Pink to tan, medium- to coarse-grained, thick- to very-thick bedded echinoderm wacke/packstone. Echinoderm stem fragments and brachiopods visible on outcrop. Echinoderm grains and finely comminuted bryozoan fragments codominant with ostracode and brachiopod valves. Many grains silicified. Remainder of section covered. SAMPLE: WL-D-1 (21.59 m), WL-D-2 (22.35 m)

Cane Creek Section Description

Unit	Meters	Cum. m.	Description
CC-1	0.44	0.44	BROWNSPORT FORMATION - LOBELVILLE MEMBER. Interbedded, gray, thin-bedded fossilferous shale and gray, thin-bedded echinoderm wackestone/packstone. Echinoderm fragments dominant, bryozoan fragments, brachiopod valves, and tabulate coral fragments. Chert nodules present in minor quantity. Amount and thickness of lens-like limestone beds decrease upward. Shale beds increase thickness upward in unit. Similar bed-thinning upward sequences observed at Lobelville measured section. Samples contain rare quartz silt. Contact with unit CC-2 sharp. SAMPLE: CC-1-1 (0.25 m)
CC-2	0.39	0.83	Interbedded gray, thin-bedded shale and gray, thin- to medium-bedded, fine- to medium-grained bryozoan-echinoderm wackestone. Shale beds are a minor component of unit. No glauconite present in sample. Echinoderm grains and bryozoans (including cryptostome and fenestrate forms) codominant, brachiopod valve and tabulate coral fragments. Contact with unit CC-2 gradational. SAMPLE: CC-2-1 (0.75 m)
CC-3	1.01	1.84	Interbedded, gray to green, thin bedded fossiliferous shale and gray medium to thin-bedded, bryozoan-echinoderm wackestone. Echinoderm grains and bryozoan fragments (including cryptostome and fenestrate forms) codominant, brachiopod and ostracode valves, and tabulate coral fragments. Fistuliporid bryozoans with hollow ramose zooarium present in sample. Unit grades from roughly equal amounts of shale and limestone to nearly all shale upward, similar to unit CC-1, but stratigraphically thicker. Shales near top of unit are less indurated and green, due to the presence of fine-grained glauconite. Many species of tabulate corals present in a zone 0.08-0.60 m below contact with overlying unit. Samples contain rare quartz silt. Contact with overlying unit CC-4 is sharp. SAMPLE: CC-3-1 (0.95 m), CC-3-2 (1.84 m)

CC-4	5+	6.84+	DECATUR FORMATION. Forms an overhang above less resistant Brownsport strata. Gray grading upward to pink, thin- to medium-bedded, medium- to coarse-grained echinoderm packstone. Large glauconite grains, echinoderm fragments, and tabulate coral visible on outcrop. Echinoderm grains dominant, finely comminuted cryptostome and fenstrate bryozoans, brachiopod and ostracode valves, small, broken trilobite fragments and single tabulate coral colony (observed on outcrop). Fistuliporid bryozoans with hollow ramose zooarium present in sample. Bedding becomes thicker upward in unit. Entire section inaccessible due to fence: top covered. SAMPLE: CC-4-1 (1.98 m)

VITA

Christopher David Olson was born in Milwaukee, Wisconsin on August 3, 1966. He grew up in Muskego, Wisconsin, a small town (at that time) 15 miles southwest of Milwaukee. During childhood, he collected many things, including "rocks", many with interesting shapes and impressions (which he later found out were external molds of fossils). He attended Muskego High School, graduating in June of 1984, but not before his interest in geology was rekindled by a very influential science teacher, Mr. Jerome Steuber.

In the fall of 1984, Chris enrolled in the University of Wisconsin at Milwaukee. After a short period as a chemistry major, he followed his true scientific interests and entered the geology program at UW-Milwaukee. During his undergraduate years, Chris developed an interest in Silurian carbonates, which lead to a volunteer position as a field and research assistant at the Milwaukee Public Museum. In May of 1989, he received his Bachelor of Science Degree with a Major in Geology from UW-Milwaukee.

Following graduation, Chris accepted a Science Alliance Internship at the University of Tennessee during the summer of 1989. In the fall of that year, he enrolled in the graduate program at UT, continuing research began during the summer, on the Silurian of west-central Tennessee. During his extended tenure at UT, Chris had many memorable experiences, including his first view of an ocean, his first Tennessee football game (and his blood will always "run orange"), many camping trips in the Southern Appalachians, two summer internships with Exxon, in New Orleans, LA and Houston, TX, teaching field camp in West Virginia, a year-long research assistantship with the Tennessee Valley Authority Engineering Lab and one significant non-credit scuba diving course, which involved a long drive to Florida with one, Miss Kelly Gardner. Chris completed his thesis research in May of 1993 and graduated with a Masters of Science degree in August of 1993. He is currently seeking employment as an environmental geologist in the Southeastern U.S.

GO VOLS!